

Tetrapod trace fossils from lowermost Jurassic strata of the Moenave Formation, northern Arizona, USA

Lawrence H. TANNER¹ and Spencer G. LUCAS²

¹Department of Biological Sciences, Le Moyne College, Syracuse, NY 13214 USA; e-mail: tannerlh@lemoyne.edu

²New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, NM 87104 USA;

e-mail: Spencer.Lucas@state.mn.us

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ABSTRACT: At Moenkopi Wash along the Ward Terrace escarpment of northern Arizona strata of the upper Dinosaur Canyon Member of the Moenave Formation contain sedimentary structures we interpret as casts of tetrapod burrows. Sandstone casts and in situ burrows occur concentrated in two horizons that extend several hundred meters along the Ward Terrace escarpment. The structures, hosted in beds of eolian sandstone, form interconnecting networks of burrows that branch at right angles. Individual burrow casts have sub-circular cross sections and consist of near-vertical tunnels and horizontal to low-angle galleries that connect to larger chambers. Most burrow casts measure 5 to 15 cm in diameter, are filled by sandstone of similar grain size as the host rock, and have walls that are unlined and lack external ornamentation. Bedding plane exposure of the lower horizon reveals that the density of burrows exceeds 30 vertical tunnels per square meter. One exposure in the upper horizon reveals burrows concentrated in a mound-like structure with 1 m of relief. Rhizoliths, distinguished from burrows by their typical smaller diameters, calcareous infilling, and downward branching, co-occur with these burrows in the upper horizon. The fossil burrows in the Moenave Formation appear to have been constructed by a fossorial tetrapod with social behavior similar to the modern Mediterranean blind mole-rat. Although no skeletal remains are associated with the burrows, the fossil record suggests that the most likely producers of the Moenave burrows were tritylodontid cynodonts.

INTRODUCTION

There exist relatively few definitive examples of trace fossils attributable to the burrowing activity of Mesozoic tetrapods. For example, in their review of vertebrate trace fossils, Shult and Farlow (1992) described no occurrences of tetrapod burrows from the Mesozoic. Although some authors (*e.g.*, Hasiotis 2004; Hasiotis *et al.* 2004) have claimed identification of tetrapod burrows in Triassic and Jurassic strata of North America, the structures described by these authors cannot be unambiguously distinguished from rhizoliths and calcrete nodules.

The best previously described examples of Mesozoic tetrapod burrows occur in Lower Triassic strata of the Karoo basin of South Africa and in Antarctica (Groenewald 1991; Groenewald *et al.* 2001; Miller *et al.* 2001). The structures described by these authors have distinctive sizes, morphologies and architectures that are consistent with their construction by therapsids and generally are inconsistent with other origins (*e.g.*, rhizoliths and decapod or lungfish aestivation burrows). The occurrence in the Lower Triassic of the Karoo basin of skeletal remains of multiple individuals of the cynodont *Trirachodon* in a single burrow

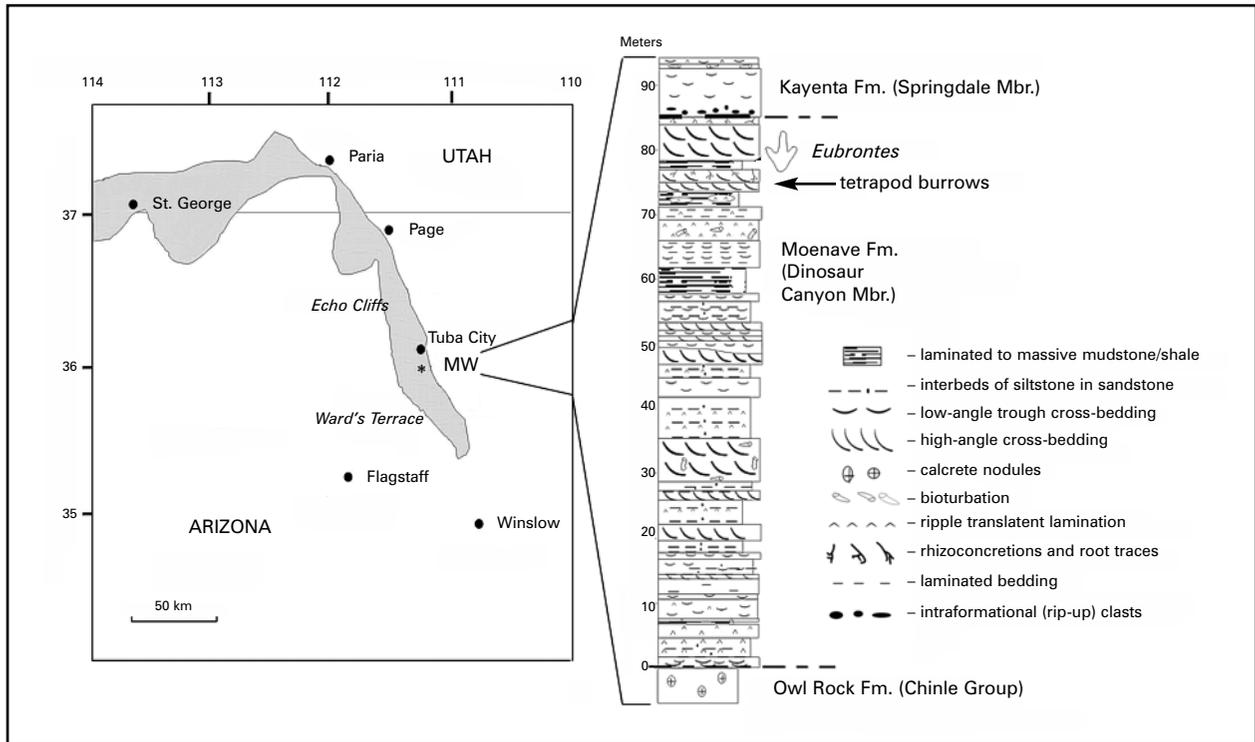


Fig. 1. Index map of the area of outcrop of the Moenave Formation with location of the burrow locality at Moenkopi Wash (MW) and measured section at this location of the Dinosaur Canyon Member of the Moenave Formation.

complex is particularly noteworthy in that it both allows positive identification of the burrower and also demonstrates social burrowing behavior (Groenewald *et al.* 2001). Recently, Lucas *et al.* (2006) described a similar burrow complex from the Lower Jurassic Navajo Sandstone of the southwestern USA, but lacking skeletal remains. Based on burrow size and morphology, and the fossil record of potential burrowing tetrapods, these authors attributed the burrows to the activity of tritylodontid cynodonts. We report here the presence of burrows with similar morphology and architecture as those described by Lucas *et al.* (2006) in even older strata of the Lower Jurassic Moenave Formation.

STRATIGRAPHY AND AGE

The Moenave Formation, of Late Triassic to Early Jurassic age, is exposed in Arizona and Utah as cliffs, buttes, and hoodoos in the Echo Cliffs, on Ward Terrace, and along the Vermillion Cliffs from Lee's Ferry to Zion National Park (Fig. 1; Harshbarger *et al.* 1957; Irby 1996; Lucas and Heckert 2001; Lucas *et al.* 2005). The formation comprises a succession of terrestrial redbeds,

including sandstone, siltstone, and mudstone deposited by fluvial, lacustrine, and eolian processes. The lowermost unit in the Glen Canyon Group, the Moenave Formation is subdivided into the Dinosaur Canyon and Whitmore Point members, in ascending order (Fig. 2). The Moenave Formation unconformably overlies the Owl Rock Formation of the Chinle Group (Lucas 1993; Lucas *et al.* 1997) along most of the outcrop belt. This unconformity has been termed the J-0 unconformity and was once considered by some to coincide with the Triassic/Jurassic boundary (*e.g.*, Pippingos and O'Sullivan 1978). The Moenave Formation is overlain disconformably by the Kayenta Formation (Glen Canyon Group).

At its type area east of Cameron, Arizona, the Dinosaur Canyon Member comprises mainly reddish-orange to light brown siltstones and sandstones of fluvial and eolian origin (Harshbarger *et al.* 1957; Tanner and Lucas 2007). In the northern and western reaches of the outcrop belt, the upper Moenave strata comprise laminated mudstones and claystones containing abundant fish remains. These lacustrine strata are the Whitmore Point Member of Wilson (1967). The eolian sandstone-dominated Wingate Formation, which is exposed to the east of the

Moenave Formation outcrop belt, intertongues with the Dinosaur Canyon Member to some degree, and thus is regarded as a partial lateral correlative (Harshbarger *et al.* 1957; Clemmensen *et al.* 1989; Marzolf 1993; Tanner and Lucas 2007).

Although the lower Dinosaur Canyon Member strata lack age-diagnostic fauna or ichnotaxa, paleomagnetic data (Molina-Garza *et al.* 2003) and the lateral relationship with the Wingate Formation, which contains a demonstrably Upper Triassic fauna and ichnotaxa (Lockley *et al.* 1992, 2004; Lucas *et al.* 1997, 2005), indicate that the lower Dinosaur Canyon Member is of Late Triassic age. Fossils of *Protosuchus* and tracks of the theropod dinosaur ichnogenus *Eubrontes* from the middle to upper Dinosaur Canyon Member indicate that this part of the formation is of likely Hettangian age (Lucas and Heckert 2001; Lucas and Tanner 2007). Thus, the Triassic/Jurassic boundary lies within the Dinosaur Canyon Member.

LITHOSTRATIGRAPHY

At Moenkopi Wash, ~6 km south of Tuba City, Arizona, the Dinosaur Canyon Member comprises 84 m of ripple-laminated to cross-bedded sandstone and blocky, planar laminated and ripple-laminated siltstone (Fig. 1). Lenticular to tabular beds of sandstone display small-scale trough cross-beds, locally pebbly, climbing ripples, and ripples with mud drapes. They are interpreted as the deposits of single and multi-storeyed ephemeral streams on an open floodplain (Tanner and Lucas 2007). Siltstone was deposited mainly by sheetflow across broad interchannel flats. Sandstone beds displaying trough to planar-tabular sets, and large-scale, steeply dipping (over 20°) and sigmoidal cross-beds are interpreted as the deposits of migrating eolian dunes. Fluvial and eolian strata are interbedded throughout the section, with eolian dune sandstones accounting for about 25% of the section thickness. The proportion of eolian facies increases to the south and east, recording the proximity to the Wingate erg (Tanner and Lucas 2007).

Various indistinct invertebrate burrows occur in both water-laid and eolian sandstones and siltstones at several levels in the section. Rhizoliths and burrows assigned to *Pustulichnus gregarious* occur in the eolian dune sandstones (Tanner *et al.* 2006). The burrows that are the subject of this study occur in two vertically superposed beds of

sandstone located 73 m to 77 m above the formation base (Fig. 1). A track surface with abundant *Eubrontes* tracks and numerous invertebrate traces occurs about one meter above the upper bed. Both beds consist of very well-sorted, fine-grained sandstone with a pink-orange hue. The lower bed is bleached at its upper contact and also displays rhizoliths. Bioturbation has eliminated all sedimentary structures in the lower bed, whereas the upper bed preserves relict high-angle cross-bedding. We interpret both beds as deposits of eolian sand stabilized by moisture and vegetation. The bleached zone at the top of the lower bed probably indicates a break in sedimentation and pedogenic alteration of the stabilized surface prior to the resumption of eolian deposition. The zone of burrowing can be traced laterally along an escarpment for a distance of several hundred meters.

DESCRIPTION OF MOENAVE BURROW CASTS

The Moenave burrows (Pl. 1) commonly weather out of the host rock to form casts with cylindrical to flask-shaped, prolate spheroidal and irregular structures. The casts have a bleached color relative to the host rock and, in some instances, display preferential cementation. In situ burrows are filled with sandstone with the same grain size and

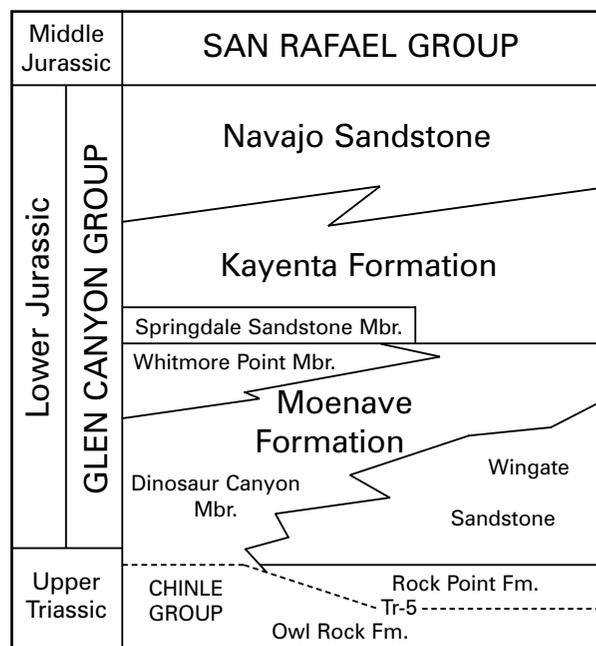


Fig. 2. Stratigraphy of the Upper Triassic and Lower Jurassic in the study area.

sorting as the host rock, and some burrows display a bleached halo that extends several centimeters into the host rock. The burrows are unlined and display no type of ornamentation, grooving or regular scratching. Cylindrical casts are mostly tubular structures that are circular to elliptical in cross section, measure 5 cm to 15 cm in diameter, and attain a maximum exposed length of 50 cm (Pl. 1: A). The exhumed and in situ cylinders are commonly connect to flask or satchel-shaped chambers with a maximum width of 30 cm (Pl. 1: B).

Bedding-plane and cross-sectional exposures reveal that the burrows form a complex network with an elaborate architecture (Pl. 1: C-F). Burrows are oriented vertically where they intersect the top surface of the lower bed (Pl. 1: A, B, G); we refer to these burrows as primary tunnels. Optimal bedding plane exposure of the lower bed reveals the concentration of primary tunnels attains a maximum density of 32 tunnels/m² (Pl. 1: G). Cross-sectional exposures demonstrate that primary tunnels connect at right angles to sub-horizontal shafts, or galleries, at a depth of 15 cm to 50 cm below the surface (Pl. 1: B, C). The intersections between tunnels and galleries are typically enlarged to form bulbous to larger satchel-shaped chambers (Pl. 1: C, E). Most commonly, vertical secondary tunnels extend downward and connect to galleries at a lower stratigraphic level (Pl. 1: C, F). Thus, these burrows formed a labyrinthine complex of tunnels, galleries and chambers at multiple stratigraphic levels. Unfortunately, no bedding exposures allow examination of the lateral extent or branching geometry of the horizontal galleries.

The upper sandstone bed hosts a unique exposure of cylindrical burrows concentrated in an exhumed mound-like structure within the eolian sandstone host (Pl. 1: H). Within this structure, the tunnels, which are up to 12 cm in diameter and up to 40 cm long, curve and slope at low angles to bedding, in contrast to the architecture described above. Rhizoliths co-occur with the burrows at the top of the bed.

ORIGIN OF THE MOENAVE BURROWS

Criteria for identification

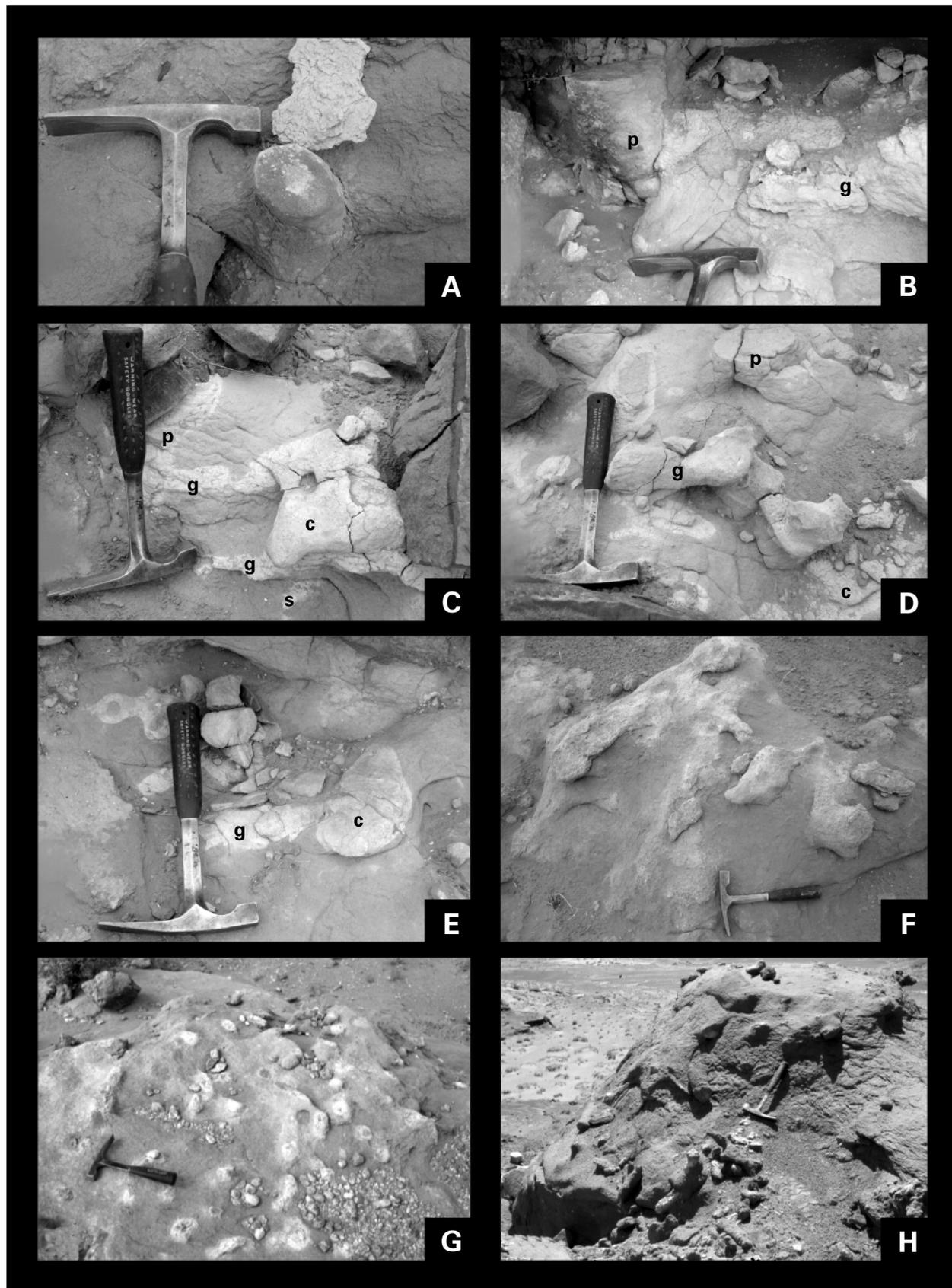
Attribution of sedimentary structures to the burrowing activity of tetrapods requires the elimination of alternative organic and inorganic origins (see review in Lucas *et al.* 2006). Invertebrate trace fossils, for example, are generally constructed by organisms much smaller than most tetrapods, so the burrows are of small diameter. A notable exception to this may be the structures produced by decapod crustaceans (discussed below). Most invertebrate traces are oriented either perpendicular or parallel to bedding, rather than inclined, as are most tetrapod burrows. Additionally, the walls of invertebrate burrows are commonly lined or ornamented (Hasiotis and Mitchell 1993; Hasiotis 2002), in contrast to tetrapod burrows, which may display scratch marks or grooves made by teeth or claws (Smith 1987; Martin and Bennett 1977; Groenewald *et al.* 2001; Gobetz 2006).

Burrows produced by some invertebrates, such as decapod crustaceans and by non-tetrapod vertebrates, such as lungfish, are of similar size as those constructed by tetrapods, but both of these tend to be oriented vertically. Additionally, the former are vertically elongate, commonly branch upwards, display scratch marks and/or pleopod striae and chimney construction (Hasiotis and Mitchell 1993). In contrast, the latter are shorter (typically less than 50 cm), smooth-walled and commonly exhibit bulbous terminations (Hasiotis and Mitchell 1993). Furthermore, these structures are formed by organisms that dwell in ephemeral aquatic environments. Therefore, identification of the environmental context of the host sediment may help discriminate among possible origins for burrows.

Vertebrate burrows may be distinguished from rhizoliths on the basis of size, morphology and architecture (Klappa 1980; Ekdale *et al.* 1984). The latter are generally (but not always) smaller (1 mm – 20 cm diameter) than most vertebrate

Plate 1

Examples of burrows at Moenkopi Wash: A – vertically oriented burrow cast weathered out in relief from upper bed; B – vertical cast of primary tunnel (p) in lower burrow horizon at junction with near-horizontal gallery (g) that extends to the right; C – large rectangular chamber (c) joined to upper and lower horizontal galleries (g). A vertical primary tunnel (p) can be seen behind the hammer, additional vertical secondary tunnels (s) extend downward from the chamber; D – horizontal gallery (g) connects to chamber (c), a large primary tunnel (p) is visible above; E – horizontal gallery (g) connects to the right with a bulbous chamber (c); F – weathered complex of tunnels and galleries in the upper burrow horizon; G – weathered surface of the upper horizon exposes high concentration of primary tunnels; H – burrow-mound complex in the upper horizon exposes numerous curving tunnels and galleries.



burrows, have consistent cylindrical to conical shapes, and typically bifurcate and taper downward, whereas burrow shapes are more variable. Further, burrows may display scratch marks or striations on the outer surface of the casts, which rhizoliths lack.

Post-depositional processes, such as pedogenesis, groundwater cementation and burial diagenesis, when combined with differential weathering, can form structures that may be misinterpreted as burrows. However, pedogenic calcretes have nodular to laminar morphologies, and groundwater calcretes and diagenetic concretions form simple sheetlike to tabular bodies resulting from preferential cementation along permeable pathways (Alonso-Zarza 2003).

The burrows at Moenkopi Wash display an architectural complexity that is inconsistent with an inorganic origin; *i.e.*, the three-dimensional system of tunnels, galleries and chambers we observe cross-cuts bedding (Pl. 1) and therefore is inconsistent with its formation as sedimentary concretions, diagenetic cementation, pedogenic calcrete or groundwater calcrete. Similarly, the morphology of these burrows rules out their origin as rhizoliths; although rhizoliths can form an interconnected, box-like network (Glennie and Evamy 1968), the occurrence of chambers at the junctions of tunnels and galleries is inconsistent with this origin. Furthermore, rhizoliths that co-occur with the Moenave Formation burrows are readily distinguished by their smaller diameter, rough surface texture and downward branching pattern. As discussed above, the burrows of decapod crustaceans and lungfish have dimensions that overlap with those of the Moenave burrows. However, the former are generally (although not always) oriented vertically, do not display the observed system of enlarged chambers at the intersections of burrows and are not found in eolian (paleo-) environments (Miller *et al.* 2001).

Tetrapod construction of the Moenave burrows

Although no fossil remains have been found in or associated with the Moenave burrow casts, we note that the Moenave burrows are similar in dimension to structures in the Lower Triassic of Antarctica (the Type G burrows of Miller *et al.* 2001), interpreted as the burrows of therapsids. Groenewald *et al.* (2001) described burrows in Lower Triassic strata of the Karoo basin with dimensions and architecture, including right-angle

intersections and chambers, strikingly similar to the Moenave burrows. The former, associated with skeletal remains of the cynodont *Trirachodon*, display axial-converging scratch marks on the surface of the casts. Scratch marks and ridges of this nature, produced by scratch-digging behavior (*i.e.*, excavation by the mani) are characteristic of modern and ancient fossorial rodent burrows (Gobet 2006; Gobetz and Martin 2006). These types of markings are absent from the Moenave burrows, but we note that they are not universally present on ancient burrows, as in those described by Groenewald *et al.* (2001). We speculate that preservation of these features is, in part, dependent on the grain size and/or the moisture content of the host sediment.

Lucas *et al.* (2006) described complex burrows in the Lower Jurassic Navajo Sandstone (Glen Canyon Group) and noted, in particular, the architectural similarities to the burrow systems and mounds of the modern Mediterranean blind mole rat, *Nannospalax* [= *Spalax*] (Nevo 1961; Nowak 1999). However, for most modern mammals, burrow diameter generally matches body size (Hickman 1990), and most Early Jurassic mammals, such as morganucodontids and haramiyids would have been too small (Kielan-Jaworowska *et al.* 2004) to have constructed most of the burrows in either the Navajo Sandstone or the Moenave Formation. Furthermore, Lucas *et al.* (2006) noted that Jurassic mammals known to be fossorial, such as *Fruitafossor* from the Upper Jurassic Morrison Formation (Luo and Wible 2005) were much too small to have excavated burrows more than a few cm in diameter.

As described above, fossorial behavior is well known from Permian and Early Triassic therapsids (Smith 1987; Groenewald *et al.* 2001). Lucas *et al.* (2006) discuss the arguments that the Navajo Sandstone burrows were excavated by tritylodontid cynodonts, which are known from the Early Jurassic of the Colorado Plateau (Sues 1986), including the Navajo Sandstone (Winkler *et al.* 1991). This evidence includes appropriate body size for construction of the Jurassic burrows, and morphological and anatomical characteristics suggestive of fossorial behavior, such as a large and blunt head attached by a short neck, a cylindrical and streamlined body with short limbs, a robust humerus, very long olecranon on the ulna and narrow claw pattern, all features consistent with scratch-digging behavior (*cf.* Gambaryan 1960; Hildebrand 1974, 1985). Alternatively, the possi-

bility of chisel-tooth digging by tritylodontids is suggested by the large, chisel-like anterior teeth, relatively large skull with large sagittal and nuchal crests and stout zygomatic arches (Hildebrand 1974, 1985).

In addition to tritylodontid skeletal remains (Winkler *et al.* 1991), the Moenave Formation (and laterally equivalent Wingate Sandstone) and the Navajo Sandstone host small therapsid tracks (possibly *Brasilichnium*: Rainforth, Lockley 1996; Schultz-Pittman *et al.* 1996; Lockley *et al.* 2004) that may be attributable to tritylodontids. Thus, the fossil record suggests that tritylodontids were Early Jurassic desert dwellers and likely filled an ecological niche somewhat akin to modern fossorial rodents in desert regions (*e.g.*, gophers). Therefore, we concur with the interpretation of Lucas *et al.* (2006) in regard to the Navajo Sandstone burrows and extend this interpretation to the very similar Moenave burrows.

PALEOECOLOGICAL INTERPRETATION

As described above, the strata of the Dinosaur Canyon Member of the Moenave Formation in which the burrows described here occur, represent a mosaic of interfingering fluvial and wet eolian facies deposited at the margin of the Wingate erg (Tanner and Lucas 2007). The dune facies in which these burrows occur also host rhizoliths and various probable arthropod burrows (Tanner *et al.* 2006). Therefore, the dunes that were colonized by the tetrapod burrowers were stabilized by high water table and vegetation. As noted by Lucas *et al.* (2006), the social behavior evidenced by the complex and abundant burrowing necessitates sufficient vegetation to sustain a colony of small Early Jurassic herbivores. The wet, interdunal areas of modern deserts commonly host abundant rodents (Ahlbrandt *et al.* 1978; Gee *et al.* 2003), thus it is not surprising that tritylodontids, apparently fossorial herbivores, occupied a similar ecological niche during the Early Jurassic.

Modern fossorial mammals burrow for a combination of reasons, the most important of which are protection from predation, nesting and mitigation of harsh environmental conditions (Reichman and Smith 1987; Smith 1987; Groenewald 1991). The last of these is particularly relevant to modern desert dwellers and so was likely of importance to the inhabitants of the Early Jurassic ergs of North America; *i.e.*, fossorial

behavior allowed tritylodontids to ameliorate the strongly seasonal climatic conditions of Early Jurassic Pangea. Lucas *et al.* (2006) noted mound-like structures associated with the Navajo Sandstone burrows. We note only one occurrence of such a mound structure in the Moenave Formation, but it matches the Navajo examples in size and morphology. Lucas *et al.* (2006) interpreted these structures as analogous to the breeding mounds constructed by the Mediterranean mole rat (*Nannospalax*) during the wet season to locate nests and storage chambers above the water table. We interpret the Moenave burrow-mound similarly; thus we suggest a significant climatic control on the burrowing behavior of Early Jurassic tetrapods.

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