Vertebrate Burrows from Triassic and Jurassic Continental Deposits of North America and Antarctica: Their Paleoenvironmental and Paleoecological Significance

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Comparisons of recently identified Triassic and Jurassic continental trace fossils in North America and Antarctica to modern mammal and reptilian burrows facilitate the identification and interpretation of the ancient burrows as vertebrate in origin, indicating advanced behaviors. Hollow, bowl-shaped depressions in the Petrified Forest Member of the Upper Triassic Chinle Formation in Petrified Forest National Park, Arizona, are interpreted as nest-holes constructed possibly by phytosaurs, aeotosaurs, turtles, or rauisuchians. Large-diameter, multiple-branching, and interconnected burrows in the Owl Rock Member of the Chinle Formation in southeastern Utah are tentatively interpreted as vertebrate burrows indicating communal behavior. Complex, large-diameter burrows in the Salt Wash Member of the Upper Jurassic Morrison Formation near the Henry Mountains in southern Utah are interpreted as burrow systems of fossorial mammals. Large-diameter, gently dipping, simple, subhorizontal burrows in the Salt Wash Member are interpreted as possible dwelling burrows of sphenodontids. Other vertebrate trace fossils, such as the large-diameter burrows from the Lower Triassic Fremouw Formation in the Queen Maud Mountains of Antarctica, are reinterpreted as vertebrate burrows and were likely constructed by small mammal-like reptiles. These burrows were thought to have been enigmatic in origin and different from very large-diameter burrows interpreted as therapsid dwelling burrows. Descriptions and interpretations of all these trace fossils are important because most vertebrate ichnology research to date has focused on trackways or locomotion experiments with modern reptiles and birds.

These Triassic and Jurassic ichnofossils represent fossorial and nesting behavior of several different groups of vertebrates. The Fremouw Formation burrows indicate fossorial behavior in several sizes of vertebrates, including small and large therapsids. The burrows were likely used for shelter, giving birth, raising young, and hibernation. During the early Mesozoic, the Fremouw landscapes were thought to have had cold winters due to their high-paleolatitude position. The bowl-shaped depressions from the Petrified Forest Member of the Chinle Formation likely represent the earliest known structures excavated by reptilians for the sole purpose of reproduction. Basic nest-hole architecture in extant reptiles with early Mesozoic ancestry has changed minimally in nearly 220 million years. Large-diameter, multiple branching, and interconnected burrows in the Owl Rock Member of the Chinle Formation were likely constructed by fossorial vertebrates that had communal family groups. Simple, gently dipping, subhorizontal burrows

in the Morrison Formation were used by crocodiles or sphenodon-tids as dwelling structures constructed in firm, subaerially exposed substrata close to open bodies of water. Complex, large-diameter burrows in the Salt Wash Member suggest subsocial behavior of fossorial mammals, where the burrow was used for raising young, storage and disposal of food and wastes, and coping with episodic water inundation.

Research demonstrates that fossorial behavior of reptiles, therapsids, and mammals was established by the beginning of the Mesozoic and prior to the break-up of Pangea. The basic architecture of vertebrate nest construction has changed little in nearly 280 million years. Fossorial burrowing behavior likely evolved several times in different vertebrate groups during this time. These basic burrow architectures are also used by invertebrate groups. This overlap in burrow architectures between vertebrates and invertebrates suggests strongly that paleoenvironmental and paleo-climatic organism-substrate relationships dictate the architecture used by the organism. These burrow morphologies indicate particular physicochemical conditions in terrestrial and freshwater settings that are unique to the continental realm.

INTRODUCTION

This paper describes enigmatic, small- to large-diameter burrows occurring in Triassic and Jurassic continental deposits of North America and Antarctica. A comparison of modern mammalian and reptilian burrows to these Mesozoic burrows leads to their interpretation as vertebrate burrows. Their morphology is indicative of behaviors that ranged from cooperation between communal groups and parental care during incubation to sub-social behavior of family groups within one burrow system. These advanced behaviors are associated more typically with insects than with Mesozoic tetrapods (Wilson, 1971; Hasiotis and Bown, 1992; Hasiotis, 2003). Descriptions and interpretations of these types of vertebrate ichnofossils are important because most research to date has focused on trackways or locomotion experiments with modern reptiles and birds (Hitchcock, 1858; Sarjeant, 1983; Gillette and Lockley, 1989; Lockley, 1991; Lockley and Hunt, 1995).

Small to large amphibians, reptiles, and mammals construct burrows of varying architectural complexity and size (e.g., Chamberlain, 1975; Voorhies, 1975; Martin and Bennett, 1977; Bown and Kraus, 1983; Smith, 1987; Hasiotis and Wellner, 1999; Groenewald et al., 2001; Miller et al., 2001; Hasiotis, in press; Hembree et al., in press). Modern vertebrate burrows represent solitary, communal, colonial, and in rare cases, eusocial behavior as occurs among the naked mole rats (Walker, 1996). Mammal burrows tend to be the most complex (Voorhies, 1975) and are characterized as subterranean systems that contain one or more openings with shallow vertical shafts that lead to low-angle, diagonal, or spiraling shafts and tunnels. The vertically disposed spiraling tubes in vertebrate burrows replace the deep vertical shafts typical of such decapod crustaceans as crayfish and crabs (Hasiotis et al., 1999), though these and other decapods

are known to use spiral ramps as part of their vertical shaft systems (M. Gingras personal communication, 2003; Hasiotis, unpublished data). In the most complex burrow systems multiple entrances, spiral ramps, and adjoining tunnels form underground mazes that can extend over 10,000 m^2 and contain as many as 20 nest members (Voorhies, 1975).

The ichnofossil record of vertebrate burrows extends as far back as the Early Devonian. The earliest vertebrate ichnofossils are interpreted as lungfish burrows (Allen and Williams, 1981). The oldest evidence of tetrapod burrowing is from the Lower Permian of the southwestern and midwestern United States (Olson and Bolles, 1975; Hasiotis et al., 1993a; Hembree et al., in press). Vertebrate burrows representing complex behavior in the geologic record have been considered rare (Voorhies, 1975). The earliest evidence of advanced social behavior is from the Upper Permian of South Africa (Smith, 1987). Only two occurrences of pre-Cenozoic complex vertebrate burrows, both of which were reported from South African Gondwana (Smith, 1987; Groenewald et al., 2001), have been studied previously in detail. More recently a third occurrence of vertebrate burrows from the Transantarctic Mountains in Antarctica was added to this list (Miller et al., 2001). All three occurrences, however, are from continental strata deposited while Africa and Antarctica were part of Gondwana and represent the only pre-Cenozoic occurrences of advanced tetrapod behavior. The best-known ichnofossil vertebrate nests are those designated as *Daimonelix circumaxilis* (see Fig. 6D, F, G), which were interpreted convincingly to have been constructed by the Miocene beaver *Paleocaster* (Voorhies, 1975; Martin and Bennett, 1977). These burrows reach nearly 3 m in depth and terminate in an inclined large chamber. These burrows are also interpreted to have been constructed and maintained by mammals that behaved communally or subsocially (Martin and Bennett, 1977).

Vertebrate burrows in the geologic record recently have received much attention. Studies during the past decade show that vertebrate burrows are well preserved in the geologic record (e.g., Groenewald, 1991; Schult and Farlow, 1992; Hasiotis et al., 1993a, 1999; Hasiotis and Martin, 1999; Hasiotis and Wellner, 1999; Meyer, 1999; Groenewald et al., 2001; Miller et al., 2001; Hembree et al., 2004; Hasiotis, in press). This body of research demonstrates 1) vertebrate burrows can be used as proxies in units where body fossils of fossorial tetrapods are scarce or absent, and 2) they are linked closely to the paleoenvironmental, paleohydrologic, and paleoclimatic settings.

GEOLOGIC SETTINGS

Enigmatic, large- to very large-diameter burrows recently have been documented in Mesozoic continental strata that were deposited in low- and high-paleolatitude settings. Some of these units also contain small- to large-diameter burrows interpreted to have been constructed by crayfish (Hasiotis and Mitchell, 1993; Hasiotis et al., 1993b; Hasiotis and Demko, 1996; Hasiotis et al., 1998). The larger enigmatic burrows, however, do not share the

same type of architectural and surficial burrow morphologies as those interpreted as crayfish. These Mesozoic burrow-bearing units and their burrow occurrences are described in the following sections.

Triassic Rocks

Lower Triassic Fremouw Formation

This unit contains large- to very large-diameter burrows in the Shackleton Glacier area of the central Transantarctic Mountains (Fig. 1A). At the time of deposition this area of the Gondwanan subcontinents was located at about 65° S paleolatitude (Powell and Li, 1994). The Fremouw Formation comprises intercalated sandstone, siltstone, and mudstone deposited in alluvial-channel, crevasse-splay, and overbank settings (Collinson and Elliot, 1984a, b). The burrows are found in floodplain deposits of the upper part of the Fremouw Formation at Kitching Ridge and at Shenk Peak. The burrows occur in drab green to olive overbank mudrock occasionally interbedded with thin crevasse-splay sandstones (Miller et al., 2001). They were filled with sand and mud laid down during crevasse-splay deposition. The mudrocks are composed of stacked, immature to moderately mature paleosols that contain siliceous nodules and downward-bifurcating siliceous rhizoliths in the upper two-thirds of the each stacked profile. The siliceous nodules and rhizoliths are thought to have been originally carbonate, but these were later replaced by silica in concert with of the intrusion of Late Jurassic-age sills.

The climate during the Early Triassic is interpreted as having been warm based on the diversity of therapsid, diapsid, and synapsid reptiles and temnospondyl amphibians (Hammer, 1990; Hammer et al., 1996). The red and green, noncarbonaceous paleosols are consistent with a climate with seasonal rainfall substantial enough to support plants and to produce nodules.

Miller et al. (2001) identified Type G (giant) and Type L (large) burrows from the Fremouw Formation and interpreted the Type G burrows to have been constructed by therapsids. Type L burrows, reexamined here, were not ascribed definitively to a specific burrower. Both burrow types were originally described as having been constructed by crayfish (Babcock et al., 1998).

Upper Triassic Chinle Formation

This unit contains abundant and diverse trace fossils (Hasiotis and Dubiel, 1993, 1994, 1995). The Chinle Formation was deposited in a broad, continental cratonic basin on the western margin of the supercontinent Pangea between 5 to 15° N paleolatitude (Dubiel, 1994). In the Four Corners area (Arizona, Colorado, New Mexico, and Utah) the Chinle Formation is underlain by the Lower to Middle(?) Triassic Moenkopi Formation and is overlain by the Lower Jurassic Wingate Formation. The Chinle Formation (Fig. 1B) comprises, in ascending order from oldest to youngest, the Shinarump, Monitor Butte, Moss Back, Petrified Forest, Owl Rock, and Church Rock Members (Stewart et al., 1972; Dubiel, 1994). The lower part of the Chinle Formation (Shinarump, Monitor Butte, and Moss Back Members) was
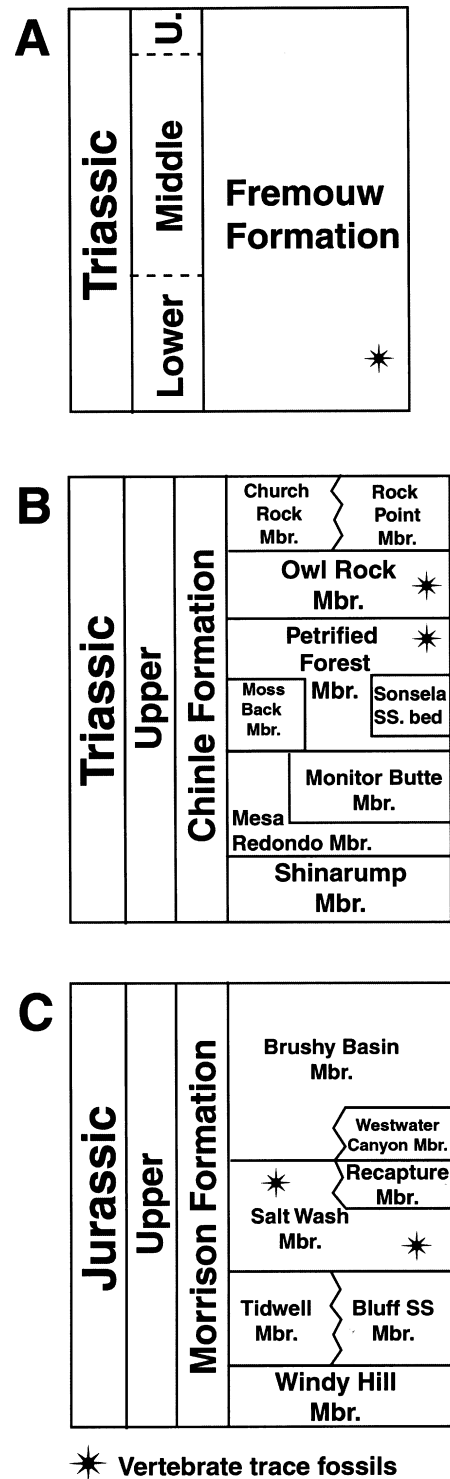
FIG. 1. Stratigraphic nomenclature of vertebrate ichnofossil sections discussed in this study. Asterisks in the stratigraphic columns denote the units and relative position in which occur the vertebrate ichnofossils. **A.** Lower to Middle Triassic Fremouw Formation, Kitching Ridge, Shackleton Glacier area, Antarctica (modified from Miller et al., 2001). **B.** Upper Triassic Chinle Formation, near Kayenta, Arizona (from Dubiel, 1989b; Dubiel et al., 1999). **C.** Upper Jurassic Morrison Formation, southern Henry Mountains, Utah (modified from Peterson, 1994).
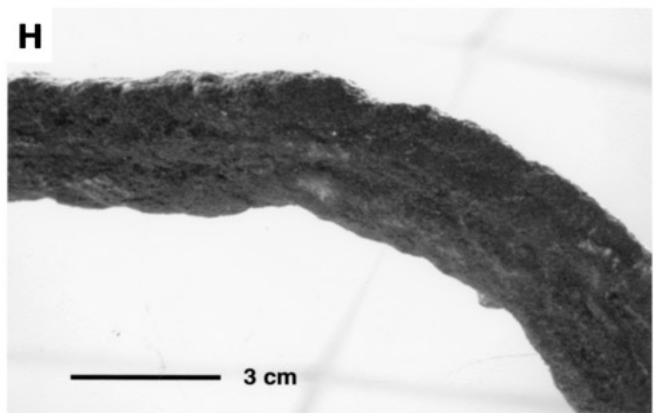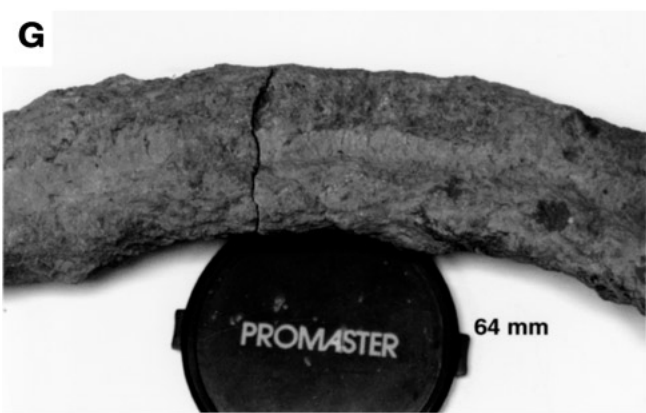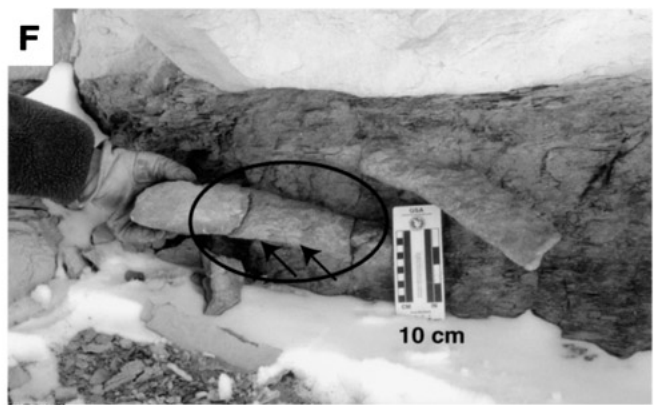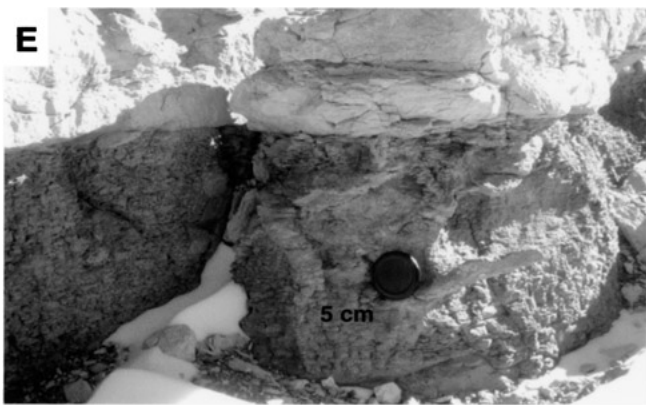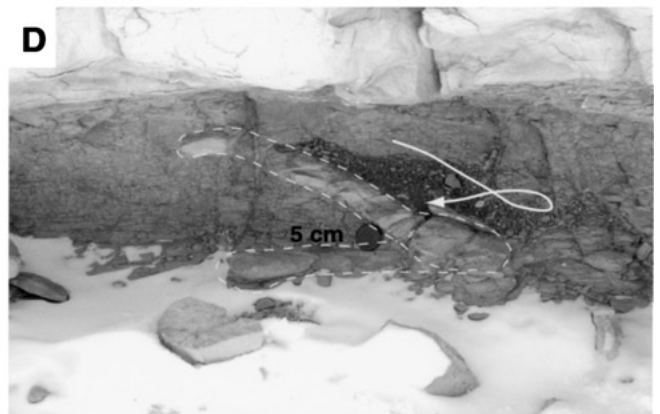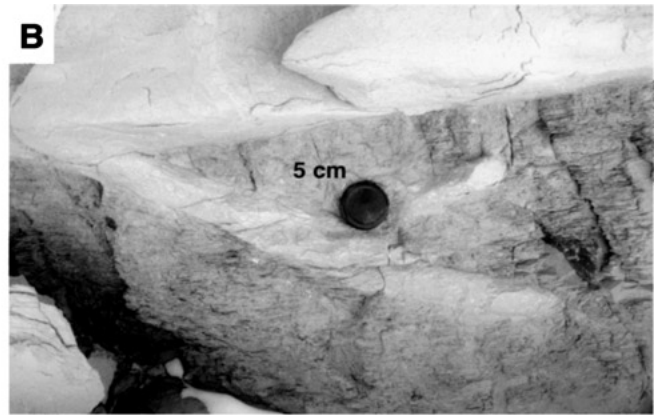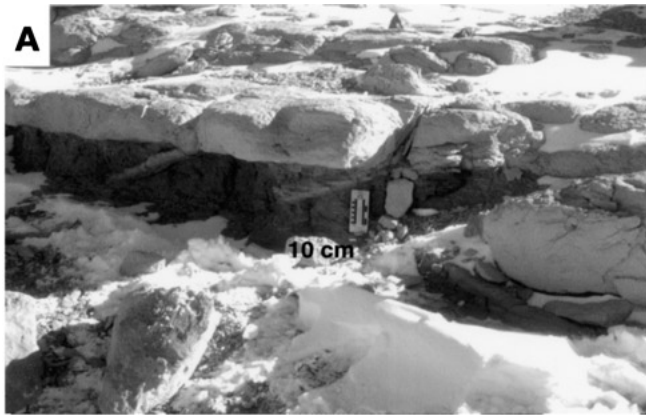
deposited in a succession of valley-fill sequences under monsoonal climates (Cooley, 1958, 1959; Repenning et al., 1969; Stewart et al., 1972; Blakey and Gubitosa, 1983, 1984; Blakey, 1989; Dubiel, 1994; Demko, 1995; Demko et al., 1998). The upper part of the Chinle Formation (Petrified Forest, Owl Rock, and Church Rock Members) was deposited in a regionally dynamic basin complex of alluvial-lacustrine systems with an increasingly arid climate (Stewart et al., 1972; Dubiel, 1989a, 1994).

Several enigmatic, large-diameter ichnofossils occur within the Petrified Forest Member in Petrified Forest National Park (PEFO), Arizona, and within the Owl Rock Member at Owl Rock, in the Navajo reservation. Bowl-shaped pits occur at the south end of PEFO in flattop sandstone #1 (Billingsley, 1985) above the Sonsela-Rainbow Forest Sandstone complex in the upper part of the Petrified Forest Member. These ichnofossils occur in the uppermost part of a 1.5-m-thick, upper fine- to medium-grained, trough cross-stratified sandstone. The unit has a relatively planar base and a slightly undulatory top representative of an exposure surface with pedogenic features. Farther north, this unit contains inclined, heterolithic, accreted strata composed of trough cross-bedded and ripple-bedded sandstones interbedded with mudstone and siltstone. The ichnofossil-bearing rocks are interpreted as deposits of a high-sinuosity meandering river. The floodplain contained immature, cumulative paleosols capped by a simple, mature paleosol. The bowl-shaped pits are interpreted as having formed in areas close to the active channel where paleosols were weakly developed.

Multiple branching and interconnected large-diameter burrows occur in one of the relatively thick (~0.7 to 1.0 m) limestone units of the Owl Rock Member. The limestone is composed of fine-grained calcite in the form of laminated to massive and crystalline carbonate. These limestone units also contain pedogenically modified carbonate represented by nodules, fracture fills, rhizoliths, backfilled burrows, and adhesive meniscate burrows. The degree of pedogenesis varies in thickness and lateral extent through the Four Corners area. The deposits of the Owl Rock Member have been interpreted to represent a large semipermanent lacustrine system that expanded and contracted with seasonal rainfall delivered by the Pangean monsoon (e.g., Dubiel et al., 1991; Dubiel, 1994; Hasiotis, 1997). This resulted in the pedogenically modified lacustrine carbonates and lacustrine-margin calcareous siltstones. These large-diameter burrow networks have not been described from the Chinle Formation.

Jurassic Rocks

Upper Jurassic Morrison Formation

This unit, containing abundant fossils and ichnofossils, was deposited throughout the Rocky Mountain region from New Mexico to Montana between 30 and 45° N paleolatitude (Peterson, 1994). These deposits are from latest Oxfordian or early Kimmeridgian (~155 Ma) to early Tithonian (~148 Ma) (Kowallis et al., 1998). The Morrison includes the Tidwell, Salt Wash, and Brushy Basin Members in the Colorado Plateau area (Fig. 1C). The Tidwell Member interfingers with the Bluff Sandstone and Junction Creek Sandstone Members in the Four Corners region, whereas the lower Brushy Basin and Salt Wash Members grade into and interfinger with the Recapture and Westwater Canyon Members in the same area (Peterson and Turner-Peterson, 1989; Peterson, 1994).

The Morrison Formation comprises successions of conglomerate, sandstone, siltstone, mudstone, limestone, and evaporites that were deposited in alluvial, lacustrine, palustrine, eolian, and continental-marine transitional environments (Brady, 1969; Peterson and Turner-Peterson, 1989; O'Sullivan, 1992; Peterson, 1994; Dunagan, 1998; Turner and Peterson, 1999). Many of the alluvial, lacustrine, palustrine, and eolian deposits throughout the Morrison Formation were modified by some degree of pedogenesis after deposition, producing a variety of immature to mature paleosols.

Two types of enigmatic, large-diameter burrows occur in the Salt Wash Member in the Henry Mountains area. Gently dipping, subhorizontal burrows composed of a single tunnel occur in thin, interbedded sandstone and siltstone-mudstone succession that is overlain commonly by a thick sequence of amalgamated channel sandstones. The burrows are filled with sandstone derived from the overlying deposits. Burrow networks of interconnected horizontal, vertical, and spiral tunnels occur in relatively thick sequences of red mudstone overlain by relatively continuous amalgamated channel sandstones. The red mudstone is characterized by weakly to well-developed paleopedogenesis represented by massive or disrupted mudrock to subangular blocky peds with minor amounts of clay cutans and slickensides. The large-diameter burrows are filled with calcareous siltstone

FIG. 2. **A.** Outcrop of simple, inclined, large-diameter burrows in overbank deposits of the Lower Triassic Fremouw Formation at Kitching Ridge, Queen Maud Mountains, Antarctica. **B.** Gently inclined, curvilinear burrow with another burrow to the right of the lens cap coming out of the outcrop and curving to the left. Note the strongly elliptical shape of the burrow cross-section. **C.** Gently inclined large-diameter burrow with longitudinal scratches (arrows) visible on the outside edge of the burrow wall. Note the widened entrance diameter at the top of the burrow, which is similar to Miocene beaver burrows illustrated by Meyer (1999), and longitudinal scratches circled. **D.** Inclined, large-diameter burrow with ladle-shaped path leading to a compressed, downward helical ramp; the burrow continues from out of the ramp and beneath the lens cap to the left of the photograph (dotted line with solid line showing coiling direction). **E–F.** Several examples of gently inclined large-diameter burrows that may or may not be associated with the same burrow complex. Note the strongly elliptical shape of the burrow cross-section. Also note and longitudinal scratches (arrows) circled in (F). **G.** Example of the longitudinal median groove along the base of roughly many burrows collected from this outcrop. The groove is not continuous within a single burrow. **H.** Example of a longitudinal median groove along the base of several portions of skink burrows cast from soils within the Simpson Desert, Australia. Note that the groove is found in a part of the burrow that curves, similar to the example of the Triassic Fremouw burrow in G.
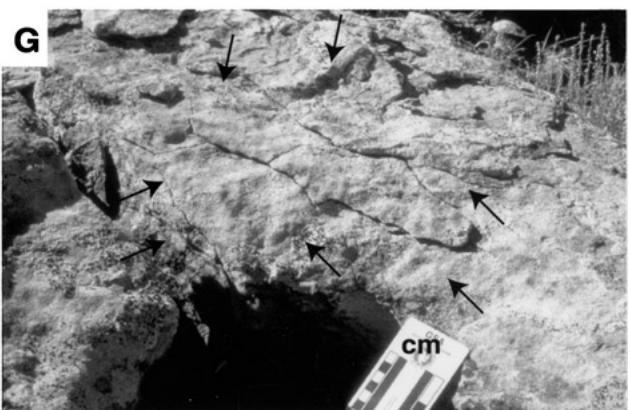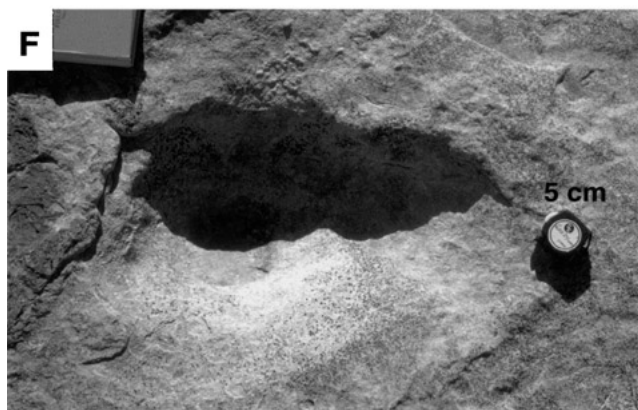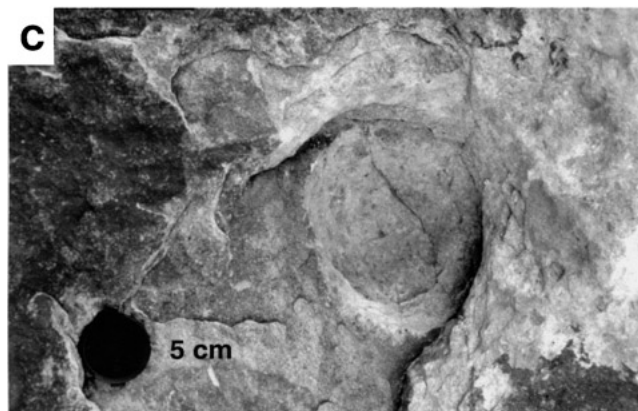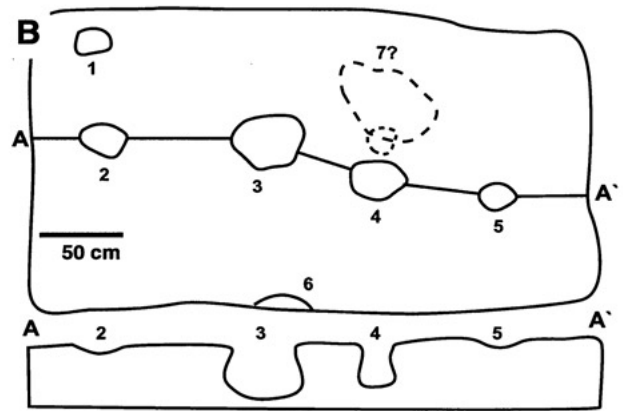
or very fine-grained sandstone from crevasse-splay deposition. The fill of the burrows was cemented preferentially later by pedogenic carbonate and were simultaneously penetrated by roots and smaller burrows.

DESCRIPTION OF THE ENIGMATIC LARGE-DIAMETER ICHNOFOSSILS

Triassic and Jurassic enigmatic, large-diameter burrows have been described by their architectural and surficial morphologies (e.g., Hasiotis and Mitchell, 1993; Hasiotis et al., 1993a; Hasiotis, 2003). The architectural morphology pertains to the gross burrow structure including the general dimensions, cross-sectional shape of the burrow, orientation in outcrop, type of branching, and degree of interconnectedness of burrow elements. Herein, vertical parts of a burrow are termed shafts and horizontal parts of a burrow are termed tunnels. Spiral shafts are portions of a burrow that coil upwards or downwards in a loose or tight pattern. Chambers refer to sections of a burrow that are slightly to greatly enlarged in size and found either within a shaft or tunnel of a burrow or at its terminus. The surficial morphology pertains to the large to diminutive structures on the burrow walls that indicate the methods of excavation used in burrow construction and maintenance of the structure or the patterns of locomotion used by the organism while the burrow was inhabited. The interpretation of the tracemakers for these enigmatic burrows is given in the succeeding section to facilitate comparisons between features of each burrow used in the interpretation of the tracemaker.

Lower Triassic Fremouw Formation
Simple to Complex Subhorizontal Burrows

The architectural morphology of the Type L burrows (Figs. 2A–F) is dominated by shallowly dipping tunnels with or without a spiral shaft (Fig. 2D) or laterally downward-oriented tunnels (Miller et al., 2001). The sand-filled burrows are predominantly subhorizontal, formed at a low-angle of 10 to 40°, with one or more openings to the paleosurface (Figs. 2A–C). The burrows are also curvilinear, with the steeper part of the tunnel near the paleosurface and the more gently inclined part of the tunnel downward along the path of the burrow. The cross section of the burrows is slightly to strongly elliptical. The maximum burrow diameter ranges from two to more than 8 cm, with a length: width ratio of 1.0 to 2.6. Roughly half of these burrows also have a longitudinal medial groove along their base that forms a shallow, upside-down U shape (Fig. 2G). Intertwining, irregular tubules interpreted as rhizoliths run commonly along the surfaces of the burrows as well as along the longitudinal medial groove.

The surficial burrow morphology exhibits longitudinal ridges along the axis of the burrow that are predominantly two sizes. Larger burrows have larger longitudinal ridges, while smaller burrows have smaller sets (Figs. 2C, F). In some, the longitudinal median groove bears short and thin longitudinal ridges (Fig. 2G). In general, the longitudinal ridges also produce somewhat overlapping ridges from 0.2 to 1.0 cm in height and width that form a bumpy texture along the burrow surface. A similar burrow surface texture is produced by the hackly fracture of the surrounding mudstone around the outside of the burrow that is not related to the excavation or use of the burrow.

Upper Triassic Chinle Formation
Bowl-Shaped Depressions: Petrified Forest Member

Two localities with a total of more than 100 pits occur in flattop sandstone #1 (*sensu* Billingsley, 1985). Many of the pits at the first locality occur in large float blocks weathered from the outcrop (Figs. 3A, B). The pits at the second locality occur *in situ*. The density of pits is about one per square meter based on measurements for blocks with more than one pit. Proximity of pits averaged $64 +/- 38$ cm (n = 19), although at least one pair of pits overlap each other (Fig. 3F) and another pair has a distance between them of 150 cm.

The architectural morphology of the traces is characterized as discrete, hollow, bowl-shaped pits (Fig. 3). The circular to elliptical pit openings range in diameter from 10 to 20 cm and average 15 to 16 cm (Figs. 3C–F). They have occasionally a constriction at or just below the paleosurface (Fig. 3B). Below the opening the internal part of the structure ranges in diameter from 11 to 44 cm with an average of 30 to 35 cm. In some, a shallow, broad depression from 53 to 65 cm long and 35 to 40 cm wide is present above the deeper, larger pits. The surfaces of these depressions are highly irregular with bumpy protrusions and multidirectional elongate furrows found clustered with one another. Poorly preserved, individual vertebrate tracks occur with the irregular surfaces (Fig. 3G).

The surficial morphology of the pits has few distinctive features. The walls and floors of the pits appear to have been compacted with several layers of sediment. Rare, narrow and elongate furrows 7 to 15 cm long and less than 1 cm deep are preserved along the walls (Fig. 3D). The bottoms of a few of the pits contain crescentic to oval indentations about 4 to 5 cm long and 2 to 4 cm wide (Fig. 3F).

FIG. 3. Examples of bowl-shaped pits and depressions in alluvial deposits of the Petrified Forest Member, Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. **A–B.** Block with several bowl-shaped pits (A) and interpretive drawing of the weathered out pits (B) in the middle of the block. Note that the pits are slightly wider than the diameter of the opening. **C–D.** Examples of bowl-shaped pits in plan view (C) and in cross section (D) that still contain their original fill. Note the sandstone-sandstone contact within (D) that also accents the cross-section of longitudinal scratches along the burrow wall next to the tape measure (arrows). **E.** Partially weathered bowl-shaped pit with a rounded opening. **F.** Partially weathered bowl-shaped pit with an adjoining pit that shallows upwards and to the lower right-hand corner of the photograph. **G.** Example of an apparent trampled ground with interpenetrating shallow footprints around the entrance of the bowl-shaped pit in the lower center of the photograph (between arrows).
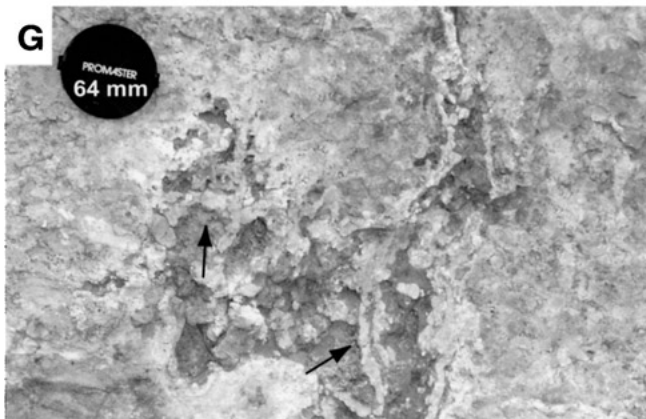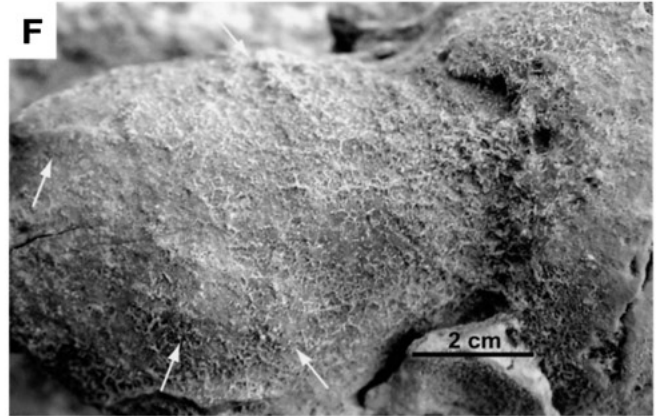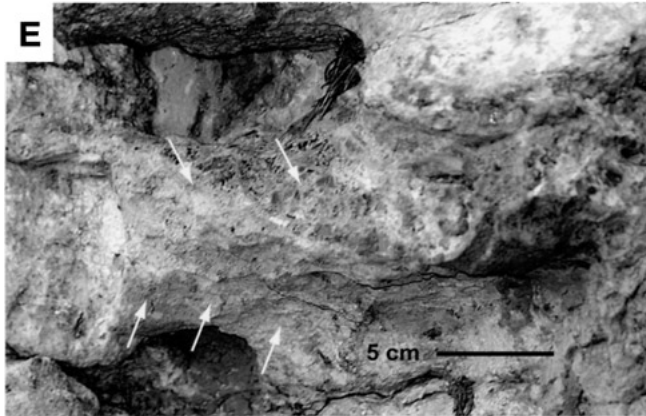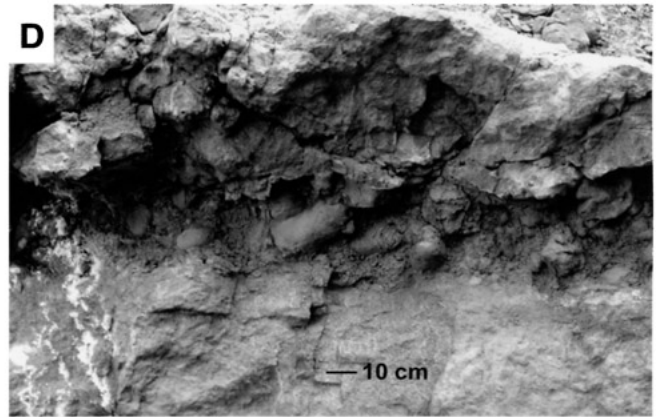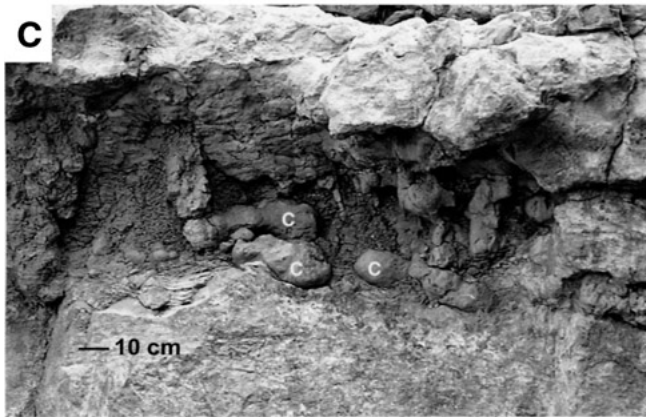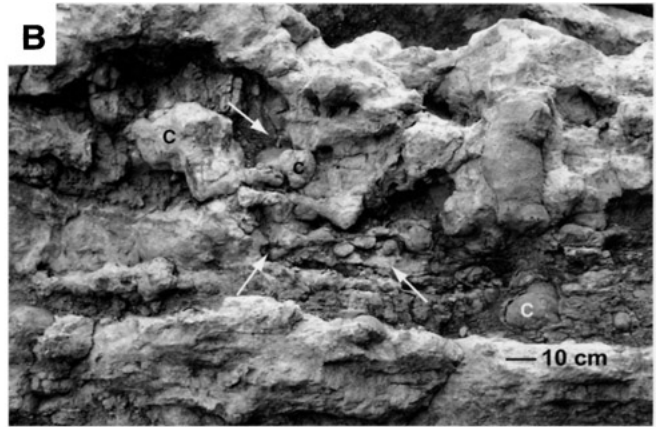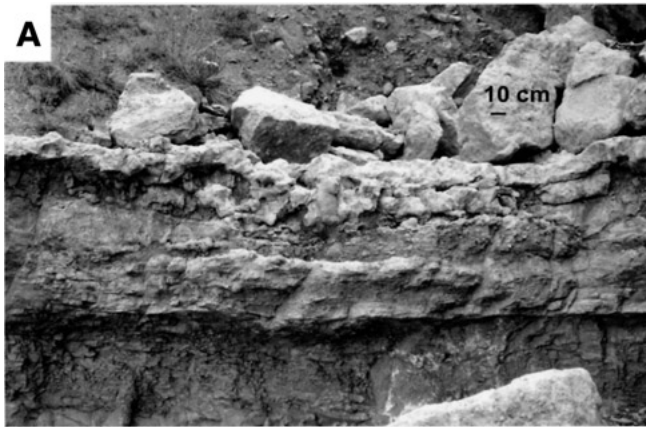
Complex Burrow Networks: Owl Rock Member

The architectural morphology of these burrows is characterized by short, interconnected horizontal tunnels, vertical shafts, spiral shafts, and chambers that form a relatively complex network (Figs. 4A–D). Burrow diameter ranges from 4 to 15 cm within one network. The cross section of the burrows tends to be circular to subcircular, with height : width ratios of about 1.0 to 1.6. In some cases semi-helical shafts are formed by more steeply dipping and curving shafts that intersect with gently inclined tunnels; these intersections are slightly wider than either the tunnel or the shaft (Fig. 4B). Smaller diameter tunnels connect typically into horizontal or vertical parts of the network with larger diameter tunnels or shafts over short distances of 10 to 35 cm. Chamber dimensions are highly variable and are commonly two to three times the diameter of the burrow (Figs. 4B, C).

The surficial morphology of the burrows is mainly bumpy and irregular (Figs. 4E–F). In some, faint remnants of thin, longitudinal ridges are preserved (Fig. 4E). In many, the burrow surfaces are covered by fine rhizoliths that can be traced into the surrounding matrix but are seen best on the burrow walls (Fig. 4F). Along some parts of the burrow walls, the texture becomes pustulose with nodes 0.2 to 0.5 cm in height. Most of the burrow surfaces, however, have been obscured to a large degree by carbonate precipitation, evidenced by the preservational state of pedogenic and other biogenic structures (Figs. 4G–H).

Upper Jurassic Morrison Formation

Simple Subhorizontal Burrows: Middle Part of the Salt Wash Member

The architectural burrow morphology is characterized by a subhorizontal tunnel gently inclined from 5 to 25° with respect to the paleosurface (Figs. 5A–F). The burrows commonly are filled with fine- to coarse-grained sandstone and conglomerate. In cross section the burrows are elliptical and have a maximum diameter that ranges from 15 to 50 cm (Fig. 5A, D). The width: height ratio ranges from 1.5 to 3.5, with larger burrows having a larger ratio. The burrows are commonly 75 to greater than 200 cm long; however, the full length of most burrows is obscured by the outcrop. Burrow terminations, where observable, tend to be slightly wider than the burrow diameter; however, very little is known about the occurrence of chambers. These features are seldom seen because of the expression of the burrows in outcrop.

Surficial morphology of the burrows includes low to high densities of short to long, longitudinal grooves that vary in length from 0.3 to 2.0 cm and 15 to 25 cm, and depth from 0.2 to 1.0 cm (Figs. 5C, E). The lateral walls and floors of the narrower burrows have grooves in very high densities (Fig. 5E). Larger and more elliptical burrows (Fig. 5F) have fewer, less dense grooves.

Simple to Complex Burrow Networks: Upper Part of the Salt Wash Member

The architectural burrow morphology is characterized by a simple to complex arrangement of interconnected shafts, tunnels, and chambers (Figs. 6A–F). The burrows are filled predominantly by siltstone and very fine-grained sandstone and are preferentially cemented with calcite. The length of individual parts of the burrow ranges from 10 to more than 400 cm. The overall vertical depth of a burrow network ranges from 50 to more than 150 cm. The burrow networks consist of several short and inclined shafts that form a U- or Y-shaped pattern of openings. The entrance is connected to one or more shallow to steeply dipping tunnels that lead to a low-angle, diagonal, or spiral shaft. Most burrows are circular to slightly elliptical in cross section, with width : height ratios of about 1. Burrow diameters range from 5 to 20 cm. Similar burrow diameters are associated commonly with one another, but several burrow complexes contain nested small- and large-diameter tunnels and shafts (Figs. 6C–D). The distribution and dimensions of the chambers within the burrow network are also variable. The largest chamber has a length of 60 cm, a width of 40 cm, and a height of 30 cm.

The surficial burrow morphology is dominated by nodular and pustular textures (Figs. 6F–H). The nodes and pustules have a maximum height above the burrow wall of 1 cm. In some places the burrow walls have short to elongate, longitudinal ridges 2 to 10 cm in length that protrude 1 cm or less from the wall. Most of the surficial burrow morphology, however, is obscured by carbonate precipitated during pedogenesis and from groundwater after burial.

INTERPRETATION OF TRACEMAKERS AND BEHAVIOR

The interpretation of the tracemakers that constructed the enigmatic, large- to very large-diameter burrows is based on the architectural and surficial burrow morphologies as well as

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FIG. 4.   **A.** Outcrop of burrow networks in lacustrine margin deposits of the Owl Rock Member, Upper Triassic Chinle Formation, Owl Rock, Navajo Nation. **B.** Interconnected horizontal tunnels and short, vertical shafts around a much larger central chamber (c). Partial helical ramps as a short of switch-back connect tunnels to inclined shafts in the middle of the photograph (arrows). **C.** Large-diameter shafts and tunnels with locally enlarged swellings at the terminus that likely represent chambers (c). **D.** Large-diameter shafts and tunnels that appear to have been dissected by large pedogenic pseudoanticlinal fractures reminiscent of mukkara structures produced by swelling and shrinking clays. **E.** Elliptical cross-section of burrow to the left edge of the photograph with the texture of the burrow wall to the center and right. Note the faint longitudinal striations beneath the thick cover of pedogenic carbonate and rhizoliths (arrows). **F.** Texture of the burrow wall dominated by finely matted and interconnected rhizoliths. Also note the faint nodes and ridges on the burrow wall (arrows). **G.** Example of well-developed pedogenic carbonate nodules (left of photograph) and rhizotubules (middle of photograph, arrow). Note that the mudstone in the middle of the photograph was the original substrate now dominated by translocated pedogenic carbonate (arrows). **H.** Example of adhesive meniscate burrows within the carbonate-dominated paleosols that also contain the burrow networks.
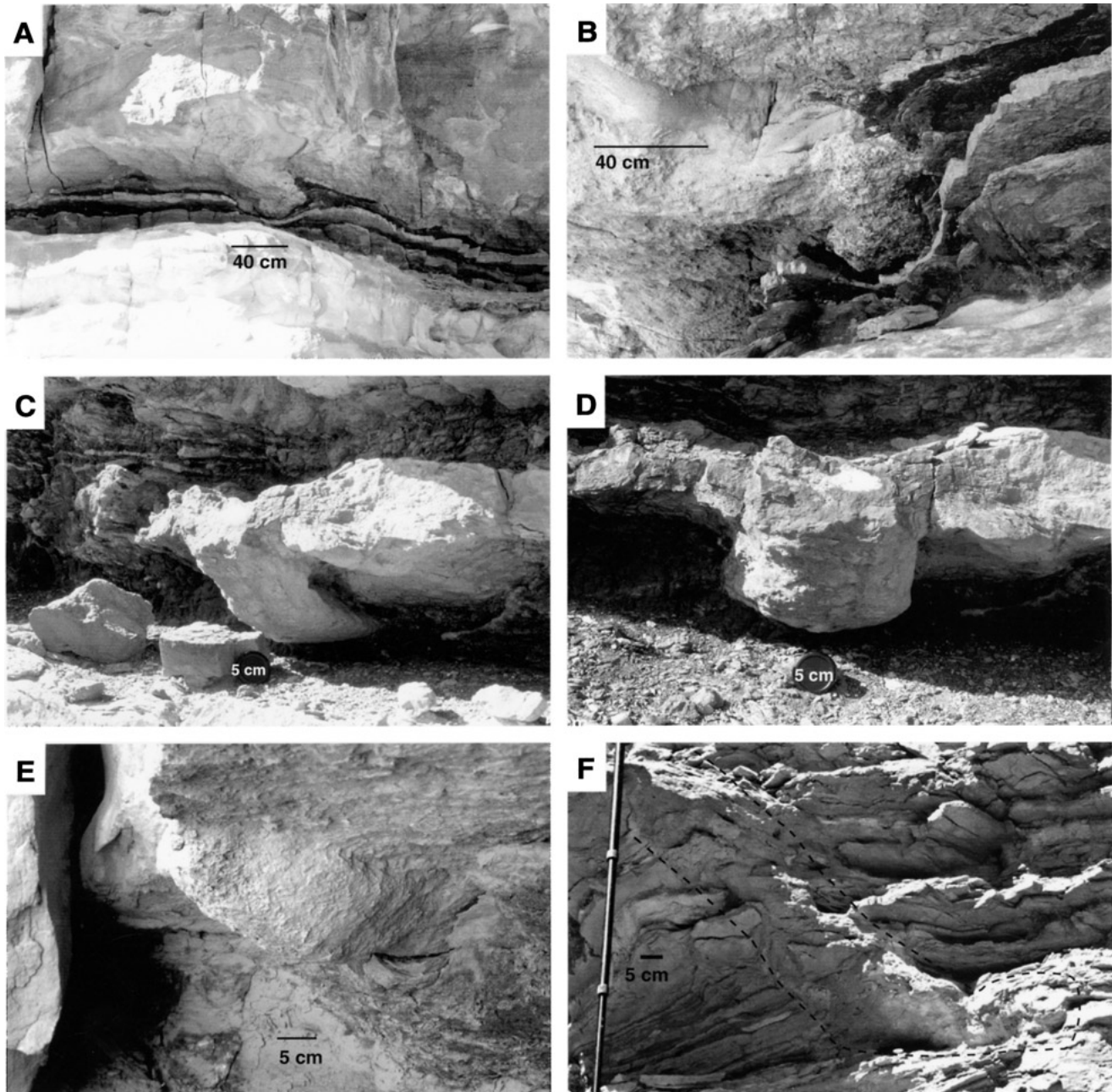
FIG. 5. Simple, large-diameter inclined burrows of the Salt Wash Member, Upper Jurassic Morrison Formation in the Henry Mountains of southeastern Utah. **A–B.** Lateral (A) and close-up (B) view of a very large-diameter, gently inclined burrow filled with conglomerate. Note the sinuous path that leads from the base of the channel sandstone downward into the thin, interbedded mudstone, siltstone, and sandstone. **C–D.** Lateral (C) and front (D) view of a large diameter burrow with a highly elliptical opening. The burrow continues downward and parallels the overlying bed for an unknown distance into the outcrop. Note the longitudinal scratches along the burrow wall (C) and the widened opening at the burrow surface (D). **E.** Example of small and densely packed longitudinal and transverse scratches along the burrow wall and widened portion near the burrow entrance. **F.** Very large-diameter, more steeply inclined burrow that curves to the lower right of the photograph at its base. Note the chaotic texture that fills the burrow.

on their comparisons to structures built by modern terrestrial and freshwater burrowing organisms. Extant and late Cenozoic tetrapod burrows (Figs. 7A–G) are the best analogs for the Triassic and Jurassic burrows, facilitating their identification and interpretation. A similar approach has been successful for interpreting the tracemakers of marine and continental ichnofossils described from Mesozoic and Cenozoic deposits (e.g., Bown, 1982; Bown and Kraus, 1983; Retallack, 1984; Hasiotis and Mitchell, 1993; Hasiotis et al., 1993a, b; Hasiotis and Dubiel, 1995; Genise and Bown, 1994, 1996; Hasiotis, 2003).

Lower Triassic Fremouw Formation

Simple to Complex Inclined Burrows: Therapsid Burrows?

The burrow morphologies preserved in Type L burrows suggest that they were also constructed by tetrapods, albeit smaller than those therapsids that constructed the type G burrows (*sensu* Miller et al., 2001). This interpretation is based on several key burrow morphologies of the Triassic burrows and those found in modern reptile burrows (Figs. 2G, H). The overall architectural morphology is not much different from the Type G burrows, including the inverted U-shape of the burrow cross-section (see figures in Miller et al., 2001). The Type G burrows are also similar to therapsid burrows described from Permian and Triassic continental rocks of the southwestern part of the Karoo basin in South Africa (Smith, 1987; Groenewald et al., 2001). The surficial morphology of the Type L burrows also bear short to long longitudinal grooves on the outside of the burrow wall as well as along the longitudinal median groove (Fig. 2G). These short to long longitudinal grooves are interpreted as scratch marks produced during burrow construction and habitation. Most importantly, these latter two features are found also on skink burrows (Fig. 2H) cast in the Simpson Desert of Australia (Hasiotis and Burke, in preparation). The longitudinal median groove in the Australian burrows was produced by the sprawling stance of the lizard and the locomotion of the front and rear limbs on either of the body that formed the groove. The longitudinal scratches on the outside of the burrow and along the median groove are produced by the predominantly lateral digging motion used by these lizards. Other such burrowing organisms with fossorial behavior as moles, mole rats, and voles construct elliptical burrows with a longitudinal median groove, producing an upside-down U-shaped burrow in cross section (Walker, 1996).

The large-diameter burrows in the Lower Triassic Driekoppen Formation of South Africa ascribed to therapsids by Groenewald et al. (2001) also have an elevated central ridge in the floor of burrows. They attributed this feature to the passage of several individuals in opposite directions through the burrow. Their interpretation was also based on the size of individuals preserved in the terminal chambers of the burrows, whose skulls could be placed side-by-side within the diameter of the burrow (Groenewald et al., 2001). Based on the patterns seen in small to large-diameter skink burrows, the central ridge in the burrow floor is interpreted as having been made by the burrower and represents its full size. The offspring of the Australian skinks, however, would be much smaller than the burrow diameter and more similar in size to the grooves on either side of the median ridge. Perhaps the Triassic burrows described by Groenewald et al. (2001) were constructed by larger adults that survived the conditions that terminated the lives of their smaller offspring, or perhaps smaller therapsids took over the burrow after it was abandoned. Nevertheless, these alternative suggestions do not change the interpretation of Groenewald et al. (2001) that the South African Triassic burrows represent colonial dwelling structures. The architectural burrow morphology and the number of fossil individuals found within the burrows attests to its use by several individuals that are likely to have been related to one another.

Discussion

The Type L burrows share burrow morphologies that are extremely similar to other burrows constructed by large to small dicynodonts and demonstrate that they were also constructed by tetrapods similar to smaller mammal-like reptiles. The Type L burrows were unlikely to have been constructed by crayfish or small reptiles. The architectural and surficial morphologies of the Type L burrows do not have an adequate number of key burrow characteristics that occur in ancient and extant crayfish burrows (Hasiotis and Mitchell, 1993; Hasiotis et al., 1993; Hasiotis and Honey, 2000). Like extant terrestrial reptiles, Triassic reptiles were ectotherms that would not have been able to tolerate extended periods of cold weather and freezing temperatures because ice crystals physiologically damage cells and tissues, as well as destroying cytoplasmic structures and cell membranes (Zug et al., 2001).

This new interpretation of the Antarctic burrows is still quite important because they suggest mammal-like reptiles may have been present in the southernmost, high-paleolatitude portions of Pangea. These burrows suggest that small mammal-like reptiles may have been capable of short-term hibernation during cooler seasons prior to the warmer climatic periods that occurred in the Middle and Late Triassic (Groenewald et al., 2001; Miller et al., 2001). The subterranean environment within the burrow likely provided more stable temperatures and humidity, which would have facilitated hibernation (e.g., Vaughn, 1961; Bourliere, 1964). These subterranean conditions, perhaps combined with some form of hibernation, probably allowed small vertebrates to inhabit the Fremouw landscape despite the cooler temperatures, frozen precipitation, and extended periods of darkness during the Austral winters.

Upper Triassic Chinle Formation

Bowl-Shaped Depressions: Reptile Nest Holes

The architectural and surficial morphologies preserved in the pits and associated depressions are interpreted as nest holes constructed by reptiles. This interpretation is supported further by comparisons of the Triassic pits to modern nests constructed by most sea and terrestrial turtles (Reptilia: Cheloniidae) and few crocodiles and alligators (Repitilia: Crocodylidae). These ichnofossils are quite similar to the nest holes excavated by extant crocodiles, alligators, and sea and terrestrial turtles (Webb et al., 1983; Woodward et al., 1984; Hailman and Elowson, 1992; Brannen and Bishop, 1993; Bishop et al., 1997; Zug et al., 2001). The extant female turtles and alligators construct a circular to elliptical pit with their hind limbs, from which sediment is scooped out as the pit is widened below the surface (Carr, 1967; Webb et al., 1983; Woodward et al., 1984). Several test pits may be excavated in search of the appropriate substrate conditions of texture, consistency, and moisture to construct the nest (Hailman and Elowson, 1992; Brannen and Bishop, 1993). A trampled,
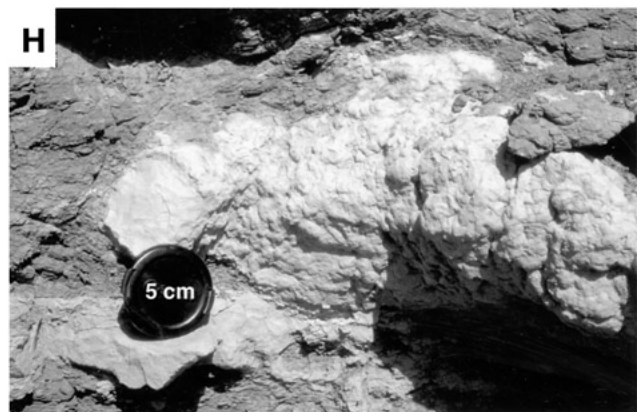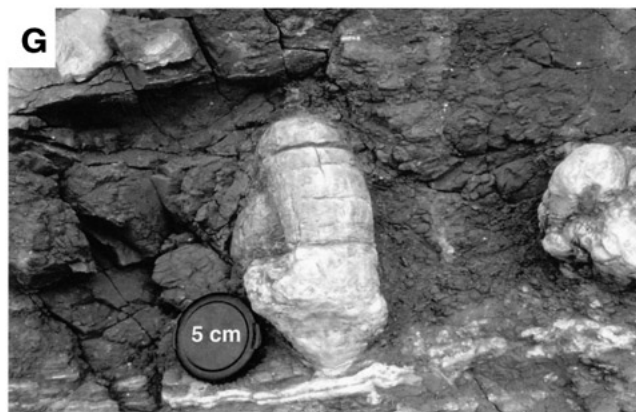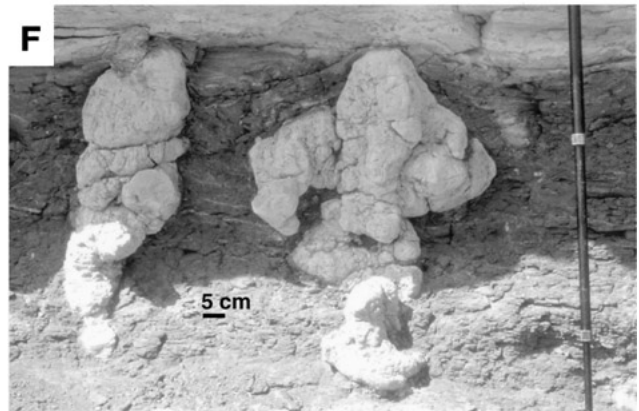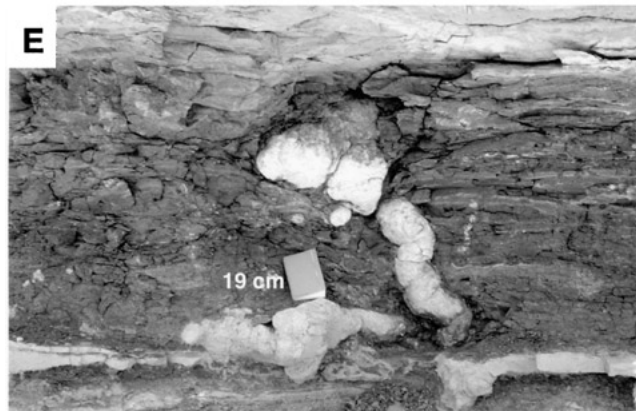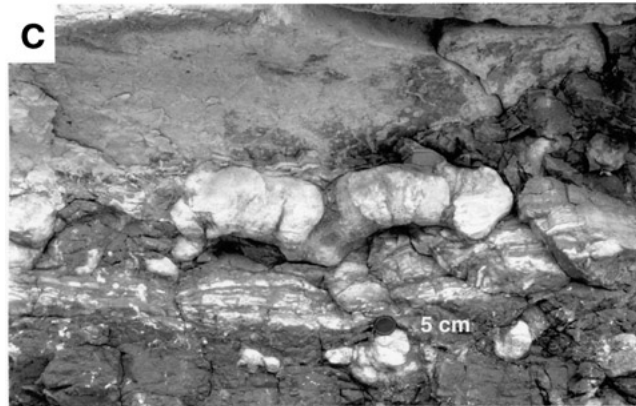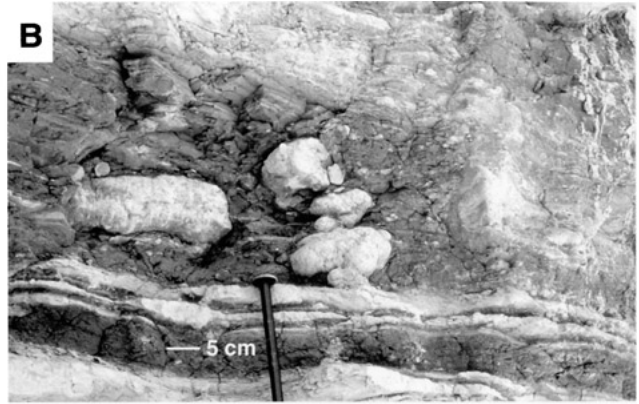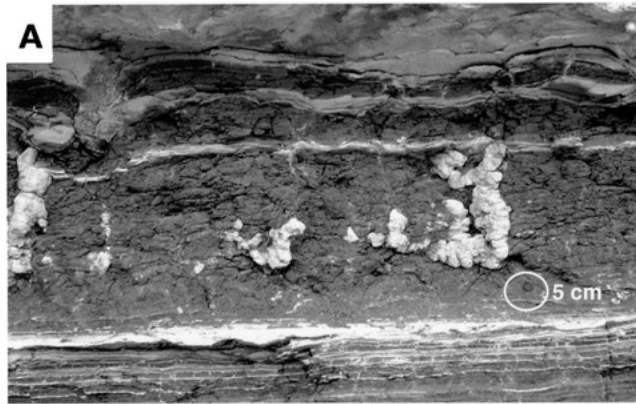
shallow depression is also produced above the pit during the excavation and egg laying. Once the eggs are laid, the female buries the eggs and leaves the area (e.g., Cott, 1961; Carr, 1967; Webb et al., 1983; Woodward et al., 1984; Hailman and Elowson, 1992; Thorbjarnarson, 1996). Some species of crocodile and alligator stay in the area of the nest to protect the eggs before they hatch.

The Triassic pits have similar features to some extant nest holes. In the Triassic ichnofossils, the elongate furrows and compacted thin layers of sediment along the walls and floors likely indicate the excavation and completion of the nest prior to egg laying. The large shallow depressions associated with some of the pits are interpreted as body pits made by the female excavating her nest and laying her eggs. The highly irregular bumpy protrusions, multidirectional elongate furrows, and partial footprints associated with the shallow depressions probably represent trampled ground (Fig. 3F, G). Longitudinal striae are interpreted as scratch marks made by the claws of the female during excavation of the nest hole and preparation of its internal walls (Fig. 3C, D). The crescentic to oval patterns seen in the bottom of one of the pits grossly resemble impressions of eggshells or eggs. Smaller, incomplete pits associated with the nests are perhaps test pits made by females that were assessing the substrate conditions (Hailman and Elowson, 1992; Brannon and Bishop, 1993).

The distribution of the Chinle nest holes is also similar to the nest distribution of some extant turtles, hole-nesting crocodiles, and hole-nesting alligators (Cott, 1961; Webb et al., 1983; Thorbjarnson and Hernandez, 1993). Today, the females of these reptiles assemble along rivers, swamps, and beaches to construct their nests and lay their eggs. The females, as well as their offspring when reproductively fit, return to the same areas to nest for many consecutive years, a behavior referred to as nesting-site fidelity (Cott, 1961; Carr, 1967; Mazzotti, 1989; Leslie, 1997). In some cases, nesting sites can be occupied by more than one species of such reptiles as iguanids and crocodilians (Dugan et al., 1981; Bock and Rand, 1989). Similar patterns of nest-site fidelity have also been interpreted from nests constructed by Late Cretaceous dinosaurs (Horner, 1982). These nests, believed to indicate a single reproductive season, have a spacing of approximately one adult hadrosaur.

The spacing between the ichnofossil nest holes in the Chinle Formation is similar to the length of the depressions interpreted as body pits. A few nest holes overlap (Fig. 3F) and likely signify reoccupation of the nesting site. The overall morphology of the Chinle nests suggests, however, that only one type of nest maker was present. The various sizes of the nest holes suggest different sizes of egg-bearing females and different stages of preservation and exhumation of the ichnofossils by weathering. There is no way, however, to rule out multiple species as the constructors of these Chinle nest holes.

The constructors of the nest holes in the Petrified Forest Member were likely phytosaurs, aeotosaurs, chelonians, or rauisuchians. Within 1,500 m of the nesting sites is fossil evidence of reptiles that lived within the same stratigraphic interval, which include a partial skull, teeth, and armor plates of phytosaurs; armor plates of aeotosaurs; and tracks and trackways of swimming reptiles (Martin and Hasiotis, 1998). Phytosaurs, aetosaurs, and rauisuchians have body plans similar to crocodilians (see papers in Lucas and Morales, 1993), and any one of these organisms could have excavated the nests. Phytosaurs and rauisuchians are semiaquatic organisms that would have been more likely to have constructed the nests. Aeotosaurs occupied terrestrial habitats and were less likely to have constructed nests in such close proximity to the river bank where they would have been prey for the larger phytosaurs.

Discussion

The Chinle nest-holes preserve one of the earliest records of parental care such that eggs were place in specialized structures. The Triassic nest ichnofossils are nearly 120 million years older than nests previously described from the Late Cretaceous of the Western Interior of the United States (Bishop et al., 1997). The Chinle nests suggest that the constructors were gregarious, lived and bred along perennial watercourses, and exhibited basic parental instincts. There is no way to tell if these reptiles tended to their nests, eggs, or young after hatching. The pattern of nests, however, is analogous to that observed for dinosaurs in the Late Cretaceous which are purported to have cared for their eggs and offspring (Horner and Makela, 1979; Horner 1982; Novell et al., 1995; Varricchio et al., 1997), and to hole-nesting crocodilians and alligatorids (e.g., Kushlan and Simon, 1981; Mazzotti, 1989;

FIG. 6. Large-diameter burrow complexes of the Salt Wash Member, Upper Jurassic Morrison Formation in the Henry Mountains of southeastern Utah. **A.** Outcrop example of two burrow networks with one network occupying the right to center of the photograph and the other just visible on the left side of the photograph. Note the multiple branching pattern formed by short, interconnected shafts and tunnels, and the helical ramp of the upper part of burrow network on the right coming out of the outcrop. Also note how the base of the burrow forms an upward inclined tunnel. **B.** A compressed column of helical ramps or spiral tunnels; to the left is a large chamber likely connected to a burrow system within the outcrop. **C.** Shallow, large-diameter lateral tunnel system with a downward spiraled tunnel that leads to a central chamber from which originate several other tunnels. **D.** Burrow networks side by side with downward spiraled tunnels and small tunnels that radiate from it. Note that burrow network on the right has a network of smaller tunnels and shafts at its base. **E.** Burrow network with a shallow central chamber with an inclined ramp leading to a downward spiraled tunnel that terminates in a deeper chamber, from which originate several other tunnels. Note the small invertebrate network of stacked chambers and galleries at the base of the lowest chamber; this network is interpreted as a termite nest. **F.** Two large burrow networks of compressed downward spiral tunnels with several lateral tunnels branching outwards. Note the extent of pedogenic and groundwater carbonate plating of the burrow networks. **G.** Example of longitudinal striations along the burrow wall as well as the swollen diameter at the base that likely acted as a turnaround point. **H.** Pustulose texture of chamber wall with remnant pattern of longitudinal ridges to the right of the lens cap.
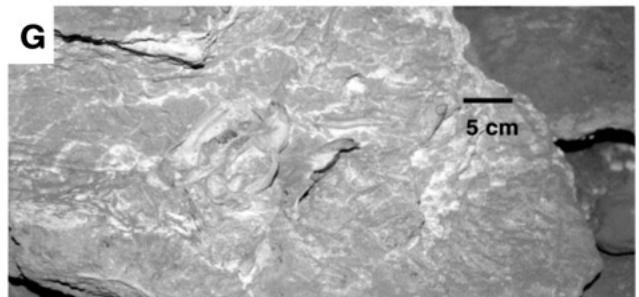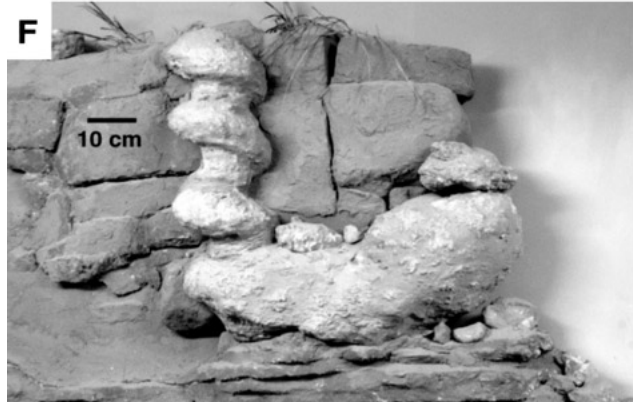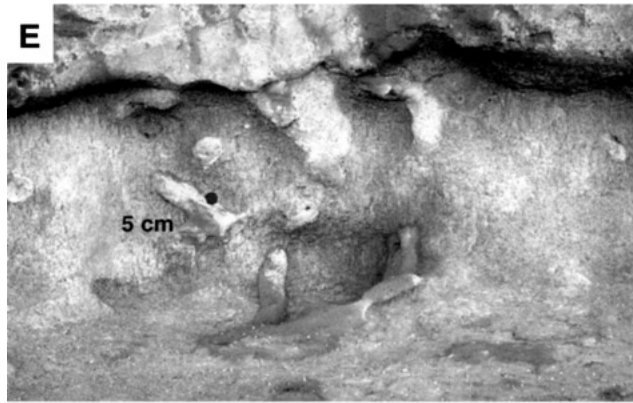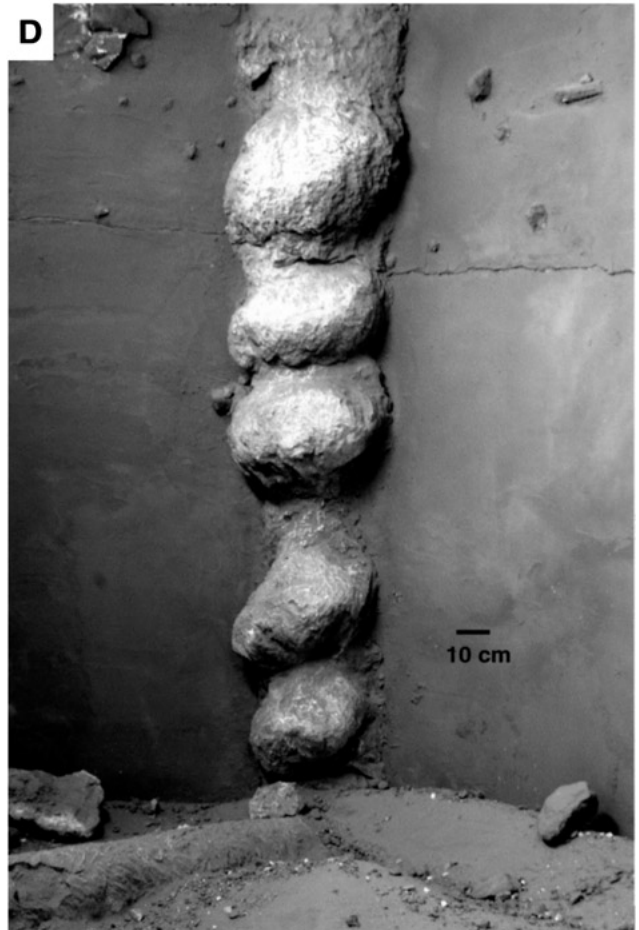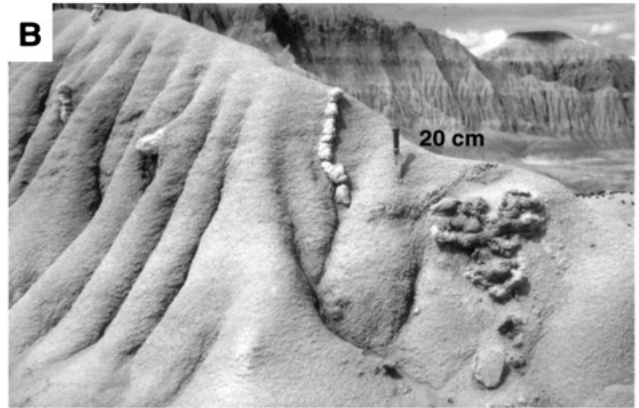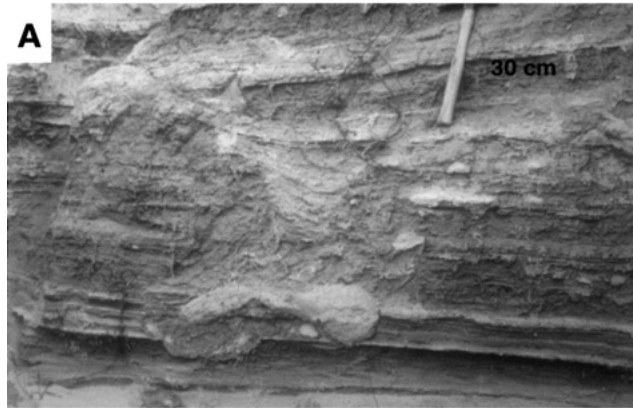
Thorbjarnson, 1996). The Chinle ichnofossils of nest-holes imply that eggs were cared for insofar as they were deposited in excavated nests, rather then simply laid on the ground or in vegetation. This observation indicates that rudimentary parental care in reptiles may have begun at least by the Triassic and may be even older. Thus, the Chinle nest-holes represent a major step toward the rearing of offspring and advanced parental care.

Complex Burrow Networks: Mammal-Like Reptile Burrows?

The architectural and surficial morphologies indicate that these burrows were constructed by vertebrates with burrowing behaviors most similar to mammals and mammal-like reptiles. The network of short, interconnected, horizontal tunnels; vertical shafts; and spiral tunnels is quite similar to burrows of such extant rodents as gophers, golden moles, and kangaroo rats (Voorhies, 1975). Fossorial mammals, however, were not likely the constructers of the burrow networks in the Owl Rock Member since mammals were very small and not diverse in the Late Triassic (Benton, 1997). The size and range of burrow diameters implies that the tracemakers were relatively small, no larger than a modern Norwegian rat or small house cat. The circular to subcircular burrow cross-section is also similar to some of the cross-sections of Type G burrows from Antarctica (Miller et al., 2001) and to the South African burrows (Smith, 1987; Groenewald et al., 2001); however, the Owl Rock burrows tend to be rounder and do not have a longitudinal median groove in the base of the burrow. The Owl Rock burrow network would also be similar to the helical burrows constructed by Permian mammal-like reptiles (Smith, 1987) if the helical tunnels were connected vertically by shafts. The Owl Rock burrow network is most similar to some of the burrow networks preserved in the Upper Jurassic Morrison Formation (see Fig. 6). The bumpy and irregular textures of the burrow surfaces are similar to some of the surficial burrow morphologies of the Morrison burrows (see Fig. 6G, H) and the Miocene burrow *Daimonelix* (Fig. 7D, F, G). The longitudinal grooves indicate scratch marks emplaced during construction, habitation, and maintenance of the burrow. These comparisons suggest that the tracemaker may have been a dicynodont that survived well into the Late Triassic.

Discussion

The Late Triassic architectural and surficial burrow morphologies demonstrate that the tracemaker was a vertebrate rather than an invertebrate, based on comparisons to modern and ancient organisms. Burrows interpreted to have been con-structed by crayfish also occur in the Owl Rock Member, as well as in nearly all the members of the Chinle Formation in the Four Corners area of the southwestern United States (Hasiotis and Mitchell, 1993; Hasiotis et al., 1993a; Hasiotis and Dubiel, 1994; Hasiotis, 1999). The combination of architectural and surficial morphologies interpreted as crayfish burrows are distinct from the architectural and surficial morphologies of the Owl Rock burrow networks. Crayfish burrows are predominantly vertical with a combination of short transverse scratches, short and thin longitudinal striae, knobby and hummocky textures, and mud- and conglomeratic lag-liners along the length of the burrows. Crayfish burrows that have multiple branches and chambers bear the same types of surficial morphologies, which allow them to be distinguished from other similar burrow types (see Hasiotis and Mitchell, 1993; Hasiotis et al., 1993a).

The burrow morphologies also indicate that a vertebrate similar in anatomy and behavior to mammal-like reptiles and mammals constructed the burrow network in the Owl Rock Member paleosols. Although no body fossils of fossorial reptiles, mammal-like reptiles, or mammals that could have possibly constructed these burrows are known currently from the Chinle Formation, body fossil evidence may be found eventually within the burrows themselves. Further work on these Owl Rock Member ichnofossils is necessary to provide more conclusive evidence as to their origin, as well as to find other localities in the Chinle Formation with similar burrow networks.

The presence of these burrow networks in this part of the Owl Rock Member also attests to pedogenesis that was active at the time of deposition (e.g., Hasiotis and Mitchell, 1993). The burrows, rhizoliths, and pedogenic features (Fig. 4) demonstrate that this area of the Owl Rock Member was periodically part of the lake plain. The large pseudoanticlines that dissect and relocate large segments of the burrow networks (Fig. 4C, D) are interpreted here as mukkara structures. These pedogenic features indicate the wetting and drying of substrates with shrink-swell clays, suggesting that the landscape was subaerial with seasonal flooding. The accumulation of pedogenic carbonate in and around ichnofossils of soil biota indicates that the incorporation and downward translocation of carbonate likely brought in by wind and water (Fig. 4E–H). Similar linked patterns of bioturbation, soil formation, and groundwater fluctuations have also been observed elsewhere in other Mesozoic and Cenozoic continental deposits (e.g., Hasiotis et al., 1993b; Hasiotis and Dubiel, 1994; Hasiotis and Honey, 2000).

FIG. 7. Examples of Cenozoic-age mammal burrows from North and South America. **A.** Late Pleistocene vertebrate burrows from the Vanhem Formation in southwestern Kansas. The two types of burrows represent a coyote digging downward toward a rodent burrow (photo courtesy of T. M. Bown). **B.** Rodent burrow system in the Pinturas Formation in Patagonia in eolian deposited ash (photo courtesy of T. M. Bown). **C and E.** Large rodent burrow networks with several different expressions in the outcrop of shafts, tunnels, spiral ramps, and chambers in a cumulative late Pleistocene soil horizon, Mar Del Plata, Argentina. Note the similarities of burrow network expression to those in the Upper Triassic Chinle Formation and the Upper Jurassic Morrison Formation. **D and F.** Examples of *Daimonelix circumaxilis* in the collections at the University of Kansas Natural History Museum and Biodiversity Research Center. Note the somewhat obscured downward spiraling tunnel and its massive nature in preservation. Also note the similarities of the architectural and surficial morphology to that of the burrow networks in the Upper Jurassic Morrison Formation. **G.** Part of a large terminal chamber with the skull of *Palaeocaster* preserved inside. The outside and inside of the chamber is riddled with rhizoliths, which facilitated the preservation of the burrow.

Upper Jurassic Morrison Formation

Large-Diameter Simple Subhorizontal Burrows: Reptile Burrows

The architectural and surficial morphologies preserved in simple subhorizontal burrows suggest that they were likely constructed by vertebrates similar to crocodiles, sphenodontids, or turtles. This interpretation also is based on burrow morphologies that comprise other Mesozoic ichnofossils and the burrows of extant crocodilians and turtles (Cott, 1961; Voorhies, 1975; Zug et al., 2001). Many species of modern crocodilians and turtles construct burrows ordinarily with gently dipping tunnels that eventually open into a slightly wider to large spherical den or form a T-intersection with another tunnel (Cott, 1961; Chamberlain, 1975; Leslie, 1997). This type of burrow is used mainly by these reptiles during the dry season to escape desiccation when water levels are low and water flow is sluggish (Cott, 1961; Webb et al., 1983; Leslie, 1997).

The gently dipping, subhorizontal burrows in the Morrison Formation have a combination of burrow morphologies that distinguish them from other subhorizontal burrows constructed by vertebrates. The Morrison burrows share few overall features with burrows in the Lower Triassic Fremouw Formation of Antarctica and even fewer characters with the burrows of the Lower Triassic Driekoppen Formation of South Africa. The Morrison burrows are the most simple of the Mesozoic subhorizontal vertebrate burrows. The cross-sectional shape of the Morrison burrows is much larger, and they have a greater height: width ratio than the subhorizontal burrows in Triassic deposits. The Morrison burrows also lack the longitudinal median groove of the Antarctica and South African burrows.

Discussion

The substrate in which the subhorizontal burrows are found in the Morrison allows a more accurate interpretation of vertebrate behavior that is unique from that of organisms that produced similar burrow morphologies in Triassic continental deposits. The interbedded sandstone and mudstone deposits that the Morrison burrows are found were part of the channel margin, levee, and proximal floodplain environments that existed during the deposition of the Salt Wash Member. These deposits had little or no pedogenic alteration that would have been evident otherwise from subaerial bioturbation, rhizoturbation, and illuviated-eluviated pedostructures (Birkeland, 1999; Retallack, 2001). The nearly pristine nature of the primary sedimentary structures associated with Morrison burrows suggests relatively high-water tables and high-sedimentation rates, which would have precluded soil formation and the mixing of the substrate by other soil biota. The proximity of the burrows to bodies of water and evidence of high-water tables or standing water suggests that these burrows were used by organisms that needed to be in or near damp environments. The morphology and filling of the Morrison burrows also indicates that they were open and constructed in firm, subaerially exposed substrata. Last, all the Morrison burrows are overlain directly by amalgamated channel deposits, which also suggest close proximity to flowing water and areas of active sedimentation.

The paleoenvironmental settings of subhorizontal burrows in Antarctic and South African Triassic deposits are markedly different than those of the Morrison. The Antarctic burrows occur in floodplain sequences with well-drained immature to mature paleosols whose development was punctuated by crevasse-splay deposition (Collinson and Elliot, 1984a, b; Miller et al., 2001). Immature paleosols were relatively massive with a mixture of platy structure and original parent material bedding, which also contained rhizoliths and smaller burrows. Mature paleosols had incipient enriched horizons of clay and mobile cations evidenced by blocky ped structures and few nodules. These pedogenic features indicate that the floodplain was predominantly subaerial with water table levels greater than 1 m beneath the paleosurface. Groenewald et al. (2001) described similar paleoenvironmental settings of the burrow-bearing horizons in South Africa, with the exception that one of the localities was constructed in a levee-proximal floodplain setting with intermittent soil development punctuated by temporary standing water. The subhorizontal burrow complexes at both localities are recorded from mottled maroon mudstone and siltstone, sometimes co-occurring with carbonate nodules and rhizoliths. They interpreted the sedimentologic and pedogenic features in these South African deposits to indicate subaerial conditions and soil development (Groenewald et al., 2001).

Large-Diameter Burrow Complexes: Mammal Burrows

The Jurassic burrow networks in the Upper Jurassic Morrison Formation are interpreted as burrow systems most similar to those constructed by fossorial mammals (Hasiotis and Wellner, 1999). This interpretation is supported by comparisons to other fossil vertebrate burrow structures (Fig. 6) and to modern burrows and is based on combination of burrow morphologies that indicate a unique method of burrow construction mostly found in mammals. The Late Jurassic complex ichnofossils display architectural elements also found in the burrow systems of (1) Permian and Triassic mammal-like reptiles, (2) Neogene canines and rodents, and (3) modern fossorial marsupial and placental mammals (Chamberlain, 1975; Voorhies, 1975; Martin and Bennet, 1977; Bown, 1982; Bown and Kraus, 1983; Smith, 1987; Boucot, 1990; Walker, 1996; Hasiotis et al., 1999; Meyer, 1999; Groenewald et al., 2001; Miller et al., 2001; and references therein). These elements include: one or more openings to the surface; a circular to slightly elliptical burrow cross-section; downward spiraled shafts; short vertical to subvertical shafts; gently dipping subhorizontal tunnels; short to long lateral tunnels; and one or more chambers of various size and position within the substrate. The thin and elongate longitudinal ridges on the burrow and chamber walls indicate scratches made by the organism during construction, habitation, and maintenance of the structure.

The only organisms likely to have constructed such burrow networks were mammals (Hasiotis and Wellner, 1999). The

mammals diversified and radiated during the Jurassic; there were as many as eight mammalian lineages by the end of the Late Jurassic (Lillegraven et al., 1979; Benton, 1997). At least one of these lineages may have made these burrows. Jurassic mammals were insectivores thought to be mainly arboreal, though many of them had the sharp claws and teeth crucial to construct burrows. By analogy, prairie dogs at first glance do not appear to be the best fit for burrowing, but the burrow networks they construct attest to their abilities (Voorhies, 1975; Butler, 1995). Comparison of the Morrison burrow networks to Cenozoic mammal burrow networks in Figure 7 demonstrates the high degree of similarity between the architectural and surficial morphologies, further supporting the interpretation that fossorial mammals probably constructed the Late Jurassic burrows.

Reptiles and therapsids were unlikely to have dug these burrows. Therapsids were extinct before the end of the Triassic, while the mammals began their diversification in the Late Triassic (Benton, 1997). Although reptiles were in great abundance and diversity during the Jurassic, no body fossils with the appropriate anatomy necessary to construct such burrow networks are known (e.g., Benton, 1997). Also, extant reptiles have not been observed to construct such complex burrow networks as mammals or similar to those found in the Morrison (Butler, 1995; Zug et al., 2001).

Discussion

The interpretation of the large-diameter, complex ichnofossils in the Upper Jurassic Morrison Formation as mammal burrow networks has several major implications. There is no pre-Cenozoic evidence of burrowing behavior in mammals even though their fossil record dates back to the Late Triassic (Benton, 1997). The previously oldest known mammal burrows with body fossils within them were described in detail from the Miocene by Martin and Bennett (1977). Burrows from the Eocene (Bown and Kraus, 1983) and Oligocene (Bown, 1980) were interpreted as mammal burrows, but no body fossils were found within them. The interconnectedness of the architectural elements found in the Jurassic burrow networks suggest communal or subsocial behavior where several individuals in one or more family units lived together and were responsible for the burrow network. The expenditure of energy necessary for one organism to maintain such a complex structure is impractical and nearly impossible (Butler, 1995; Walker, 1996). The complexity of the burrows also suggests strongly that they were designed for long-term use that included: 1) a permanent dwelling; 2) raising young; 3) storage and disposal of food and wastes; 4) coping with episodic inundation by water; and 5) protection from diurnal and seasonal extremes in climate (Voorhies, 1975; Butler, 1995; Walker, 1996). Evidence for the number of organisms and extended use of the Morrison burrow networks is found in the several different diameters of tunnels and shafts in a single network (Figs. 6C, D, and F). The different-sized tunnels and shafts do not cross cut the larger diameter burrows but instead originate from them and are intimately associated with the overall burrow system. In

at least two instances, small-diameter burrow networks extend from the lowest chambers, suggesting that these are burrows of juveniles. In another example, a large and deep chamber of one of the burrow networks is intimately associated with a complex of very small diameter (about 0.5 cm) network of interconnected shafts, tunnels, and chambers (Fig. 6E) interpreted as a termite nest (Hasiotis, in press). This close association is analogous to modern insectivores that burrow or nest in and around the insect nests from which they feed (e.g., Wilson, 1971; Butler, 1995; Walker, 1996). Together these examples suggest strongly that the Morrison burrow networks present the earliest evidence of fossorial mammals that displayed advanced subsocial behavior and maintained long-term subterranean residences.

PALEOENVIRONMENTAL AND PALEOECOLOGICAL SIGNIFICANCE OF VERTEBRATE BURROWS

Burrows and nests are used by vertebrates as an external mechanism for thermoregulation in environments with climate extremes produced by major seasonal fluctuations in temperature or precipitation (e.g., Vaughn, 1961; Bourliere, 1964; Butler, 1995; Zug et al., 2001). The microclimate within a burrow structure is milder and more equable than that of the aboveground habitat, which changes in temperature, humidity, and windiness according to changes in the weather pattern (Vaughn, 1961; Wallwork, 1970; Martin and Bennett, 1977; Meyer, 1999; Groenewald et al., 2001). Subterranean burrow systems with high surface-area that limit air flow and exchange with the atmosphere aboveground provide a habitat with consistent subsurface temperature and humidity regardless of surface conditions (Vaughn, 1961; Meyer, 1999).

Late Paleozoic and Mesozoic tetrapods likely adapted different levels of burrowing and fossorial behavior as a means to mitigate seasonal extremes in environmental and climatic conditions. Besides the obvious protection from predators that nests and burrows provided tetrapods and their offspring (Voorhies, 1975; Butler, 1995; Walker, 1996; Zug et al., 2001), the structures also protected the burrowers from other unforeseen dangers. Late Triassic ichnofossils interpreted as nest holes were used by females to protect egg clutches from low-paleolatitude climate extremes produced by the dry season of the Pangean megamonsoon (e.g., Dubiel et al., 1991; Dubiel, 1994). The simple subhorizontal burrows and complex burrow networks in low-paleolatitude Triassic and Jurassic environments provided protection from evaporative losses and extreme heat during the dry season and safety from drowning during the wet season (Dubiel et al., 1991; Dubiel, 1994; Peterson, 1994; Hasiotis, in press). Inclines and chambers with the burrow network provide pockets of air where burrow occupants can find refuge while the floodplain and burrow are flooded. The high-paleolatitude, Permian subhorizontal helical burrows of South Africa provided protection from evaporative losses and heat during the dry season and drowning or cooler temperatures during the wet season (Smith, 1987). The simple to complex subhorizontal burrow networks

of South Africa and Antarctica provided a subterranean environment of more consistent temperature and humidity in semiarid and cool temperate to polar, high-paleolatitude climatic settings (Collinson and Elliot, 1984 a, b; Groenewald et al., 2001; Miller et al., 2001).

The Permian, Triassic, and Jurassic subhorizontal and complex vertebrate burrows interpreted to represent subsocial to advanced colonial behavior by Smith (1987), Hasiotis et al. (1999), Groenewald et al. (2001), Miller et al. (2001), and in this paper belong to the behavioral category **polychresichnia** (Hasiotis, 2003). Polychresichnia was proposed for trace fossils that represent many simultaneous, multiple behaviors and uses that include obtaining and assimilating nutrients; producing and raising offspring; and maintaining, regulating, and defending the burrow structure (Hasiotis, 2003). Polychresichnia includes ichnofossil nests of subsocial, parasocial, presocial, primitively social, social, and eusocial behavior displayed by such invertebrates as termites, bees, wasps, ants, burying beetles, and many types of dung beetles. The Late Cretaceous ichnofossil nests of hadrosaur dinosaurs are also polychresichnia because the adults cared for their eggs and offspring as evidence from the traces of regurgitated material and the post-hatching condition of the offspring (Horner and Makela, 1979; Horner 1982; Varricchio et al., 1997). The ichnofossils from the Upper Triassic Chinle Formation interpreted as nest holes belong to the behavioral category **calichnia** (Genise and Bown, 1994) because the structures were constructed exclusively for reproduction.

CONCLUSION

In general, ancient subsocial to social vertebrate burrow systems excavated by reptiles, therapsids, and mammals form a pattern of short vertical to subvertical shafts, helically spiraled shafts, short to long subhorizontal straight and curvilinear tunnels, with intertunnel and terminal chambers (Voorhies, 1975; Hasiotis et al., 1999). The shape of the burrow cross-section ranges from circular to elliptical, and indicates the shape of the organism that excavated and lived in the burrow. The surficial morphology of these burrows is dominated by a series of linear, longitudinal, and circumferential scratch marks created by the claws on the manus and pes, and the anterior dentition (e.g., beak or incisor teeth) of the animal during burrow construction and maintenance. The burrow morphologies suggest that they were constructed for long-term use where the organisms maintained a residence, raised young, stored food, disposed of wastes, and coped with episodic inundation by flooding and precipitation (e.g., Voorhies, 1975; Groenewald et al., 2001).

Fossorial behavior in reptiles, therapsids, and mammals was established by the beginning of the Mesozoic and prior to the break-up of Pangea based on the ichnofossil data summarized in this paper (see also Voorhies, 1975; Smith, 1987; Groenewald et al., 2001). The basic architecture in vertebrate nest-hole and burrow-network construction has changed minimally in nearly 280 million years. Fossorial burrowing behavior evolved likely several times in different vertebrate groups through this expanse of time. Ichnofossils attributed to therapsids and early mammals, however, provide physical evidence linking potentially the role of burrowing behavior in the evolution of mammals from mammal-like reptiles (Voorhies, 1975; Smith, 1987). Burrowing would have allowed mammals to develop adaptations for different types of fossorial habitats (Groenewald et al., 2001) in different climatic settings. The basic burrow architectures present in vertebrate burrows are also present in invertebrate burrows and nests (differing primarily in size), changing minimally since the Permo-Triassic (Hasiotis, 2003). The overlap in burrow architectures between vertebrates and invertebrates strongly suggests that organism-substrate relationships are dictated by extrinsic factors found in paleoenvironmental and paleoclimatic settings. The result of this is a predictable pattern of burrow architectures used by the organism for particular physicochemical conditions and degree of social lifestyle.

Vertebrate burrows and other traces (Voorhies, 1975; Martin and Bennet, 1977) can be useful for interpreting environmental conditions, especially when used in conjunction with invertebrates and their traces, and the paleosols in which they were excavated. Vertebrate trackways, however, are limited in extent and utility as specific environmental and ecological indicators. Vertebrates are not as sensitive as invertebrates and plants to environmental conditions because vertebrates can move to more favorable environments (Wallwork, 1970; Hole, 1981; Hasiotis and Bown, 1992; Hasiotis, 2000). Trackways represent a very short period of time that record the substrate consistency with respect to the degree of saturation.

Temporary to permanent vertebrate burrows, on the other hand, record behavioral traits that indicate to some degree the physicochemical characteristics of the local environmental and equability of climatic conditions. Respiration in the soil environment is different than in aboveground habitats. Levels of O_2 in soil are reduced and CO_2 levels are elevated (Villani et al., 1999). The concentration of soil gases is dependent on such abiotic factors as soil structure, texture, and moisture, and such biotic factors as root density, soil animal density, and the amount of decaying organic matter. The movement of O_2 and CO_2 is controlled nearly exclusively by diffusion through the soil substratum, and is influenced by the size of the soil channel or burrow opening. The rate of gas exchange varies slightly with changes in temperature, wind speed across the ground surface, and atmospheric pressure. Normal O_2 concentrations decrease with depth in the soil profile and water infiltration inhibits diffusion, drastically reducing O_2 levels (Glinski and Lipiec, 1990). Thus, the dwelling and reproductive behavior of soil organisms must be adapted to localized and widespread hypercarbic (elevated CO_2) and hypoxic (oxygen deprived) conditions because of water inundation and competition for O_2 from nearby microbial decomposers. Vertebrate burrows and nests must also be constructed in such a way that the subterranean environment maintains equable temperature, moisture level, and gas exchange to avoid hypercarbic and hypoxic conditions (e.g., Vaughn, 1961).

Bowl-shaped depressions interpreted as reptile nests from the Upper Triassic Chinle Formation represent temporary structures that were used to protect eggs prior to hatching. The structures were most likely constructed above the water table and in close proximity to the shoreline of the ancient river system. The female likely excavated the nest during the middle part of the wet season, particularly after the period of high or flashy discharge and overbank flooding brought on by the Late Triassic megamonsoon (Dubiel et al., 1991) that would have inundated or destroyed the nest. The sediments would have been moist but relatively well-drained so that the eggshells' gas exchange was maintained with the ambient atmosphere. The eggs buried within the nests would have been at an appropriate temperature that remained relatively constant and protected the eggs from overheating.

The simple, subhorizontal burrows interpreted as reptile burrows from the Upper Jurassic Morrison Formation most likely represent temporary to semipermanent dwelling structures closely associated with river channels. Possibly these burrows were most likely used when the water levels of rivers were low during the dry season portion of the Tropical wet-dry climate of the Late Jurassic (Hasiotis, in press). The subhorizontal burrows may have kept the reptile moist and protected it from predators. The temperature in the burrows would have been likely lower than that of the atmosphere. During the wet season, these structures may have been partially or mostly submerged, so that the occupant would have spent its time hunting or hiding in the open water and in the vegetation along the shoreline.

Moderately complex burrow systems in the Lower Triassic Fremouw Formation are interpreted as semipermanent to permanent burrows of subsocial mammal-like reptiles. The shallow burrows were constructed in the vadose zone of relatively well-drained, immature floodplain paleosols. The burrow fill and overlying sheet sandstones indicate that the burrows were in the proximal portion of the floodplain and thus prone to flooding and filling by crevasse-splay deposition. The architecture of the burrows was such that ample exchange of atmospheric and burrow gases was enough to allow one or more individuals to live comfortably in a subterranean habitat. The temperature of the burrows was probably warmer than the ambient temperature at ground level, based on the paleoclimate reconstruction for the Early Triassic and burrow temperature that would have been necessary to support an organism (e.g., Vaughn, 1961; Powell and Li, 1994; Walker, 1996; Zug et al., 2001). The burrows were likely heated and the temperatures mediated by the body position of the organism with respect to the diameter of the burrow and its place in the tunnel.

Complex burrow systems that occur in the Chinle and Morrison Formations are interpreted as permanent dwelling structures in megamonsoonal and tropical wet-dry climates, respectively, that served multiple functions of related individuals or family units. These burrow systems were constructed in the vadose zone well above the water table in the proximal and distal portions of the floodplain. The burrow atmosphere was likely moister and cooler than the aboveground ambient atmosphere and temperature. Gas exchange between the burrow complex and atmosphere was sufficient to support multiple individuals in various parts of the burrow complex without producing hypoxic or hypercarbic conditions.

These and other burrow morphologies produced by vertebrates and invertebrates indicate particular physicochemical conditions in terrestrial and freshwater settings that are unique to the continental realm. Burrowing marine invertebrates also produce burrow structures and complexes that are similar to those in the continental realm (see examples in Ekdale et al., 1984; Bromley, 1996; Pemberton et al., 2001; Hasiotis, 2003). The burrow morphologies of marine organisms, however, do not signify the same behavior behind the construction and utilization of the burrow, nor do they indicate the same physicochemical conditions of the environment that regulate the burrow morphologies. For instance, a burrow system composed of interconnected shafts, tunnels, and chambers produced by a family of rodents in the distal floodplain indicates a relatively deep water table, appropriate construction for appropriate air circulation and modification to diminish effects of hypoxia and hypercarbia, a burrow network used to exploit above-ground setting by moving below-ground to avoid predators, above- and below-ground feeding, and some degree of social behavior. A burrow network constructed by a thalassinid shrimp indicates subaqueous and saturated conditions of the substratum, appropriate circulation of seawater, a deposit-feeding mode of life, in a solitary or commensil lifestyle.

REFERENCES

Allen, J. R. L. and Williams, B. T. 1981. *Beaconites antarcticus*: A giant channel-associated trace fossil from the Lower Old Red Sandstone of South Wales. *The Welsh Geological Journal,* 16:255–269.

Benton, M. J. 1997. Vertebrate Paleontology (second edition). Chapman and Hall, London: 452 p.

Babcock, L. E., Miller, M. F., Isbell, J. L., Collinson, J. W., and Hasiotis S. T. 1998. Paleozoic-Mesozoic crayfish from Antarctica: Earliest evidence of freshwater decapod crustaceans. *Geology*, 26:539–542.

Billingsley, G. H. 1985. General stratigraphy of the Petrified Forest National Park, Arizona. *Bulletin of the Museum of Northern Arizona*, 54:3–8.

Birkeland, P. W. 1999. Soils and Geomorphology, 3rd edition. Oxford University Press, New York: 430 p.

Bishop, G. A., Marsh, N. B., Barron, J., Pirkle, F. L., and Smith, R. S. U. 1997. A Cretaceous sea turtle nest, Fox Hills Formation, Elbert Co., CO. *Geological Society of America, Abstracts with Programs*, 29:104.

Blakey, R. C. 1989. Triassic and Jurassic Geology of the southern Colorado Plateau. *In* Jenny, J.P. and Reynolds, S. J. (eds.), Geologic evolution of Arizona. Arizona Geological Society Digest, 17:369–396.

Blakey, R. C. and Gubitosa, R. 1983. Late Triassic paleogeography and depositional history of the Chinle Formation, southern Utah and northern Arizona. *In* Reynolds, M. W. and Dolly, E. D. (eds.), Mesozoic Paleogeography of the West-Central United States. Rocky Mountain Section SEPM, pp. 57–76.

Blakey, R. C. and Gubitosa, R. 1984. Controls of sandstone body geometry and architecture in the Chinle Formation (Late Triassic), Colorado Plateau. *Sedimentary Geology*, 38:51–86.

Bock, B. C. and Rand, A. S. 1989. Factors influencing nesting synchrony and hatching success at a green iguana nesting aggregation in Panama. *Copeia*, 1989:978–986.

Boucot, A. J. 1990. Evolutionary Paleobiology of Behavior and Coevolution. Elsevier Publishers, Amsterdam: 725 p.

Bourliere, F. 1964. The Natural History of Mammals. Knopf, New York: 387 p.

Bown, T. M. 1982. Ichnofossils and rhizoliths of the nearshore fluvial Jebel Qatrani Formation (Oligocene), Fayum Province, Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 40:255–309.

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*, 43:95–128.

Brady, L. L. 1969. Stratigraphy and petrology of the Morrison Formation (Jurassic) of the Cañon City area, Colorado. *Journal of Sedimentary Petrology*, 39:632–648.

Brannen, N. A. and Bishop, G. A. 1993. Nesting traces of the loggerhead sea turtle (*Caretta caretta* Linne), St. Catherine Island, Georgia: Implications for the fossil record. *In* Farrell, K. M., Hoffman, C. W., and Henry, V. J., Jr. (eds.), Geomorphology and Facies Relationships of Quaternary Barrier Island Complexes near St. Mary's, Georgia. Georgia Geological Society Guidebook, 13:30–96.

Bromley, R. G. 1996. Trace Fossils: Biology and taphonomy, 2nd edition. Special Topics in Paleontology, no. 3. Unwin Hyman, London: 361.

Butler, D. R. 1995. Zoogeomorphology: Animals as Geomorphic Agents. Cambridge University Press, New York: 231 p.

Carr, A. 1967. So excellent a fishe: a natural history of turtles. The Natural History Press, American Museum of Natural History, New York: 248 p.

Chamberlain, C. K. 1975. Recent lebensspuren in nonmarine aquatic environments. *In* Frey, R. W. (ed.), The Study of Trace Fossils. Springer Verlag, New York: 431–458.

Collinson, J. W. and Elliot, D. H. 1984a. Geology of Coalsack Bluff, Antarctica. *In* Turner, M. C. and Splettstoesser, J. F. (eds.), Geology of the central Transantarctic Mountains. American Geophysical Union, Washington, D.C., Antarctic Series, 36:97–102.

Collinson, J. W. and Elliot, D. H. 1984b. Triassic stratigraphy of the Shackleton Glacier area. *In* Turner, M. C. and Splettstoesser, J. F. (eds.), Geology of the central Transantarctic Mountains. American Geophysical Union, Washington, D.C., Antarctic Series, 36:103–117.

Cooley, M. E. 1958. The Mesa Redondo Member of the Chinle Formation, Apache and Navajo counties, Arizona. *Plateau*, 31:7–15.

Cooley, M. E. 1959. Triassic stratigraphy in the state line region of west-central New Mexico and east-central Arizona. New Mexico Geological Society Guidebook of West-Central New Mexico, Tenth Field Conference, pp. 66–73.

Cott, H. B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and northern Rhodesia. *Transactions of the Zoological Society of London*, 29:211–356.

Demko, T. M. 1995. Taphonomy of fossil plants in the Upper Triassic Chinle Formation. Unpublished Ph.D. Dissertation, University of Arizona, 274 p.

Demko, T. M., Dubiel, R. F., and Parrish, J. T. 1998. Plant taphonomy in incised valleys: Implications for interpreting paleoclimate from fossil plants. *Geology*, 26:1119–1122.

Dubiel, R. F. 1989a. Depositional and climatic setting of the Upper Triassic Chinle Formation, Colorado Plateau. *In* Lucas, S. G. and Hunt, A. P. (eds.), Dawn of the Age of the Dinosaurs in the American Southwest. New Mexico Museum of Natural History, 1989 Spring Field Conference Guidebook, pp. 171–187.

Dubiel, R. F. 1989b. Sedimentology and revised nomenclature for the upper part of the Upper Triassic Chinle Formation and the Lower Jurassic Wingate Sandstone, northwestern New Mexico and northeastern Arizona. *In* Anderson, O. J., Lucas, S. G., Love, D. W., and Cather, S. M. (eds.), New Mexico Geological Society Guidebook, 40th Field Conference, Southeastern Colorado Plateau, pp. 213–223.

Dubiel, R. F. 1994. Triassic deposystems, paleogeography, and paleoclimate of the Western Interior. *In* Caputo, M. V., Peterson, J. A., and Fronczyk, K. J. (eds.), Mesozoic Systems of the Rocky Mountain Region, USA. Rocky Mountain Section Society for Sedimentary Geology (SEPM), Denver, CO, pp. 133–168.

Dubiel, R. F., Hasiotis, S. T., and Demko, T. M. 1999. Incised valley fills in the lower part of the Chinle Formation, Petrified Forest National Park, Arizona: Regional stratigraphic implications. *In* Santucci, V. and McClelland, L. (eds.), National Park Service Paleontological Research, 4:78–84.

Dubiel, R. F., Parrish, J. T., Parrish, J. M., and Good, S. C. 1991. The Pangaean megamonsoon-Evidence from the Upper Triassic Chinle Formation, Colorado Plateau. *Palaois*, 6:347–370.

Dugan, B. A., Rand, A. S., Burghardt, G. M., and Bock, B. C. 1981. Interactions between crocodiles and iguanas. *Journal of Herpetology*, 15:409-414.

Dunagan, S. P. 1998. Lacustrine and palustrine carbonates from the Morrison Formation (Upper Jurassic), east-central Colorado, USA: Implications for depositional patterns, paleoecology, paleohydrology, and paleoclimatology. Ph.D. Thesis, University of Tennessee, Knoxville.

Ekdale, A. A., Bromley, R. G., and Pemberton, S. G. 1984. Ichnology: the use of trace fossils in sedimentology and stratigraphy. SEPM Short Course 15: 1-317.

Genise, J. F. and Bown, T. M. 1994. New Miocene scarabeid and hymenopterous nests and early Miocene (Santacrucian) paleoenvironments, Patagonian Argentina. *Ichnos*, 3:107–117.

Genise, J. F. and Bown, T. M. 1996. *Uruguay* Roselli 1938 and *Rosellichnus*, n. ichnogenus: two ichnogenera for clusters of fossil bee cells. *Ichnos*, 4:199–217.

Gillette, D. D. and Lockley, M. G. (eds.) 1989. Dinosaur Tracks and Traces. Cambridge University Press, Cambridge: 454.

Glinski, J. and Lipiec, J. 1990. Soil Physical Conditions and Plant Roots. CRC Press, Boca Raton: 250 p.

Groenewald, G. H. 1991. Burrow casts from the *Lystrosaurus-Procolophon* Assemblage Zone, Karoo sequence, South Africa. *Koedoe*, 34:13–22.

Groenewald, 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. *Palaois*, 16:148–160.

Hailman, J. P. and Elowson, A. M. 1992. Ethogram of the nesting female loggerhead turtle (*Caretta caretta*). *Herpetologia*, 48:1–30.

Hammer, W. R. 1990. Triassic terrestrial vertebrate faunas of Antarctica. *In* Taylor, T. N. and Taylor, E. L. (eds.), Antarctic Paleobiology: Its Role in the Reconstruction of Gondwana. Springer-Verlag, New York:42–50.

Hammer, W. C., Hickerson, W. J., and Collinson, J. W. 1996. Preliminary analysis of Triassic vertebrates from the Shackleton Glacier region. *Antarctic Journal of the United States*, 31:8-12.

Hasiotis, S. T. 1997. Redefining continental ichnology and the *Scoyenia* Ichnofacies. Ph.D. dissertation, University of Colorado, Boulder: 182 p.

Hasiotis, S. T. 1999. The origin and evolution of freshwater and terrestrial crayfishes based on new body and trace fossil evidence. *Freshwater Crayfish*, 12:49–70.

Hasiotis, S. T. 2000. The Invertebrate Invasion and Evolution of Mesozoic Soil Ecosystems: The Ichnofossil Record of Ecological Innovations. *In* Gastaldo, R. and Dimichele, W. (eds.), Phanerozoic Terrestrial Ecosystems. Paleontological Society Short Course, 6:141–169.

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

Hasiotis, S. T. in press. Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain region, USA: environmental, stratigraphic, and climatic significance of terrestrial and freshwater ichnocoenoses. *Sedimentary Geology*, 181 manuscript pages.

Hasiotis, S. T. and Bown, T. M. 1992. Invertebrate trace fossils: The backbone of Continental Ichnology. *In* Maples, C. and West, R., (eds.), Trace Fossils: Their paleobiological aspects, Paleontological Society Short Course, 5:64–104.

Hasiotis, S. T. and Burke, M., in preparation. Traces of modern organisms in dryland river systems, Todd and Hale Rivers, Simpson Desert, Australia.

Hasiotis, S. T. and Demko, T. M. 1996. Terrestrial and freshwater trace fossils, Upper Jurassic Morrison Formation, Colorado Plateau. Continental

Jurassic Symposium, *Museum of Northern Arizona Bulletin*, 60:355–370.

Hasiotis, S. T. and Dubiel, R. F. 1993. Trace fossil assemblages in Chinle Formation alluvial deposits at the Tepees, Petrified Forest National Park, Arizona. *In* Lucas, S. G. and Morales, M. (eds.), The Nonmarine Triassic—Field Guidebook, *New Mexico Museum of Natural History and Science, Bulletin*, 3, pp. G42–G43.

Hasiotis, S. T. and Dubiel, R. F. 1994. Ichnofossil tiering in Triassic alluvial paleosols: Implications for Pangean continental rocks and paleoclimate. *In* Beauchamp, B., Embry, A. F., and Glass, D. (eds.), Pangea: Global Environments and Resources. Canadian Society of Petroleum Geologists Memoir 17:311–317.

Hasiotis, S. T. and Dubiel, R. F., 1995. Termite (Insecta: Isoptera) nest ichnofossils from the Triassic Chinle Formation, Petrified Forest National Park, Arizona. *Ichnos*, 4:119–130.

Hasiotis, S. T. and Honey, J. 2000. Paleocene continental deposits and crayfish burrows of the Laramide basins in the Rocky Mountains: Paleohydrologic and Stratigraphic significance. *Journal of Sedimentary Research*, 70:127–139.

Hasiotis, S. T. and Martin, A. 1999. Probable reptile nests from the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. *In* Santucci, V. and McClelland, L. (eds.), National Park Service Paleontological Research (U.S. government report), 4:85–90.

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*, 2:291–314.

Hasiotis, S. T. and Wellner, R. W. 1999. Complex large-diameter burrow systems, Upper Jurassic Morrison Formation, southeastern Utah: Are these evidence of fossorial mammals? *Geological Society of America Abstracts with Programs*, 31:385.

Hasiotis, S. T., Kirkland, J. I., and Callison, G. 1998. Crayfish fossils and burrows, Upper Jurassic Morrison Formation, western Colorado: Evolutionary and paleohydrologic implications. *Modern Geology Special Paper*, 22:481–491.

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

Hasiotis, S. T., Aslan, A., and Bown, T. M. 1993b. Origin, architecture, and paleoecology of the early Eocene continental ichnofossil *Scaphichnium hamatum*. *Ichnos*, 3:1–9.

Hasiotis, S. T., Miller, M. F., Isbell, J. L., Babcock, L. E., and Collinson, J. W. 1999. Is Triassic Crayfish Fossil Evidence from Antarctica Really Burrow Evidence of Mammal-like Reptiles? Resolving vertebrate from invertebrate burrows. *Freshwater Crayfish*, 12:71–81.

Hembree, D. I., Martin, L., and Hasiotis, S. T. 2004. Amphibian burrows and ephemeral ponds of the lower Permian Speiser Shale, Kansas: Evidence for seasonality in the Midcontinent. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 53 manuscript pages.

Hitchcock, E. 1858. Ichnology of New England. A report of the sandstone of the Connecticut Valley especially its footprints. W. White, Boston: 220 p.

Hole, F. D. 1981. Effects of animals on soil. *Geoderma*, 25:75–112.

Horner, J. F. 1982. Evidence of colonial nesting and "site fidelity" among ornithiscian dinosaurs. *Nature*, 297:676–678.

Horner, J. F. and Makela, R. 1979. Nest of juveniles provides evidence of family structure among dinosaurs. *Nature*, 282:296–298.

Kowallis, B. J., Christiansen, E. H., Deino, A. L., Peterson, F., Turner, C. E., Kunk, M. J., and Obradovich, J. D. 1998. The age of the Morrison Formation. *Modern Geology Special Paper*, 22:235–260.

Kushlan, J. A. and Simon, J. C. 1981. Egg manipulation by the American alligator. *Journal of Herpetology*, 15:477–488.

Leslie, A. J. 1997. The ecology and physiology of the Nile crocodile, *Crocodylus niloticus*, in Lake St. Lucia. Kwazulu/Natal, South Africa (osmoregulation, estuary, sex determination). Unpublished dissertation, Drexel University, Philadelphia, Pennsylvania, 316 p.

Lillegraven, J. A., Kielan-Jaworoska, Z., and Clemens, W. A. (eds.), 1979. Mesozoic mammals: The first two-thirds of mammalian history. University of California Press, Berkeley: 311 p.

Lockley, M. G. 1991. Tracking Dinosaurs: A New Look at an Ancient World. Cambridge University Press, New York: 238 p.

Lockley, M. G. and Hunt, A. P. 1995. Dinosaur Tracks and other fossil footprints of the western United States. Columbia University Press, New York: 338 p.

Lucas, S. G. and Morales, M. (eds.), 1993. The Nonmarine Triassic—Field Guidebook. New Mexico Museum of Natural History and Science, Bulletin 3.

Martin, A. and Hasiotis, S. T. 1998. Vertebrate tracks and their significance in the Chinle Formation (Late Triassic), Petrified Forest National Park, Arizona. *In* Santucci, V. L. and McClelland (eds.), National Park Service Paleontological Research, Technical Report NPS/NRGRD/GRDTR-98/01 (U.S. government report), p. 138–143.

Martin, L. D. and Bennet, D. K. 1977. The burrows of the Miocene beaver *Paleocaster*, western Nebraska, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 22:173–193.

Mazzotti, F. J. 1989. Factors affecting the nesting success of the American crocodile, *Crocodylus acutus*, in Florida Bay. *Bulletin of Marine Science*, 44:220–228.

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

Miller, M. F., Hasiotis, S. T., Babcock, L. E., and Isbell, J. L. 2001. Tetrapod and large burrows of uncertain origin in Triassic high latitude floodplain deposits, Antarctica. *Palaios* 48, 218–232.

Novell, M. A., Clark, J. M., Chiappe, L. M., and Dashzeveg, D. M. 1995. A nesting dinosaur. *Nature*, 378:774–776.

Olson, E. C. and Bolles, K. 1975. Permo-Carboniferous fresh water burrows. *Fieldiana Geology*, 33:271–290.

O'Sullivan, R. B. 1992. The Jurassic Wanakah and Morrison Formations in the Telluride-Ouray-western Black Canyon area of southwestern Colorado. *United States Geological Survey Bulletin*, 1927: 24 pp.

Pemberton, S. G., Spila, M., Pulham, A. J., Saunders, T., MacEachern, J. A., Robbins, D., and Sinclair, I. 2001. Ichnology and Sedimentology of Shallow to Marginal Marine Systems. Geological Association of Canada, Short Course Notes volume 15:343 p.

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

Peterson, F. and Turner-Peterson, C. E. 1989. Geology of the Colorado Plateau. International Geological Congress Field Trip Guidebook T130, 65 pp.

Powell, C. McA. and Li, Z. X. 1994. Reconstruction of the Panthalassan margin of Gondwanaland. *In* Veevers, J.J. and Powell, C. McA. (eds.), Permian-Triassic Basins and Foldbelts along the Panthalassan Margin of Gondwanaland. *Geological Society of America, Memoir*, 184:5–9.

Repenning, C. A., Cooley, M. E., and Akers, J. P. 1969. Stratigraphy of the Chinle and Moenkopi Formations, Navajo and Hopi Indian Reservations, Arizona, New Mexico, and Utah. *United States Geological Survey Professional Paper*, 521–B:B1–B31.

Retallack, G. J. 1984. Trace fossils of burrowing beetles and bees in an Oligocene paleosol, Badlands National Park, South Dakota. *Journal of Paleontology*, 58:571–592.

Retallack, G. J. 2001. Soils of the Past: An Introduction to Paleopedology, 2nd edition. Blackwell Science, Oxford, 404 p.

Sarjeant, W. A. S. (ed.), 1983. Terrestrial Trace Fossils. Hutchinson Ross Publishing Company, Benchmark Papers in Geology, 76:415 p.

Schult, M.F. and Farlow, J.O. 1992. Vertebrate Trace Fossils. In Maples, C.G., West, R.R. (eds.), Trace Fossils. Paleontological Society Short Course, no. 5:34–63.

Smith, R. M. H. 1987. Helical burrow casts of therapsid origin from the Beufort Group (Permian) of South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 57:285–331.

Stewart, J. H., Poole, F. G., and Wilson, R. F. 1972. Stratigraphy and origin of the Chinle Formation and related Triassic strata in the Colorado Plateau region with a section on sedimentary petrology by R. A. Cadigan and on conglomerate studies by W. Thordarson, H. F. Albee, and J. H. Stewart. *United States Geological Survey Professional Paper*, 690:336 p.

Thorbjarnson, J. B. 1996. Reproductive characteristics of the order Crocodylia. *Herpetologia*, 52:8–24.

Thorbjarnson, J. B. and Hernandez, G. 1983. Reproductive ecology of the Orinoco crocodile (*Crocodylus intermedius*) in Venezuela. I. Nesting ecology and clutch relationships. *Journal of Herpetology*, 27:363–370.

Turner, C. E. and Peterson, F. 1999. Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the Western Interior. *In* Gillette, D. D. (ed.), Vertebrate Paleontology in Utah. Utah Geological Survey, Miscellaneous Publications 99-1:77–114.

Varricchio, D. J., Jackson, F., Borkowski, J. J., and Horner, J. R. 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature*, 385:247–250.

Vaughn, T. A. 1961. Vertebrates inhabiting pocket gopher burrows in Colorado. *Journal of Mammalogy*, 42:171–174.

Villani, M. G., Allee, L. L., Diaz, A., and Robbins, P. S. 1999. Adaptive strategies of edaphic arthropods. *Annual Review in Entomology*, 44:233–256.

Voorhies, M. R. 1975. Vertebrate burrows. *In* Frey, R. W. (ed.), The Study of Trace Fossils, Springer Verlag, New York: 325–350.

Walker, E. P. 1996. Mammals of the World. Johns Hopkins University Press, Baltimore.

Wallwork, J. A. 1970. Ecology of Soil Animals. McGraw-Hill, London: 283 p.

Webb, G. J. W., Buckworth, W. R., and Manolis, S. C. 1983. *Crocodylus johnstoni* in the McKinley River area, N. T. VI. Nesting biology. *Australian Wildlife Research,* 10:607–637.

Wilson, E. O. 1971. The Insect Societies. Belknap Press, Harvard University, Cambridge: 548 p.

Woodward, A., Hines, T., Abercrombie, C., and Hope, C. 1984. Spacing patterns in alligator nests. *Journal of Herpetology*, 18:8–12.

Zug, G.R., Vitt, L. J., and Caldwell, J. P. 2001. Herpetology. Academic Press, San Diego: 630 p.