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LIFE BENEATH THE SURFACES OF ACTIVE JURASSIC DUNES: BURROWS FROM THE ENTRADA SANDSTONE OF SOUTH-CENTRAL UTAH

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ABSTRACT

Within the Middle Jurassic Entrada Sandstone of south-central Utah, cylindrical burrows, 15–95 mm diameter, are abundant in large-scale, eolian cross-strata. Burrows are oriented at a high angle to stratification and commonly extend more than 30 cm below their surface termini. They are rarely inclined more steeply than 22°. Many are sinuous, and they sometimes branch (~120°) at bends. Burrows terminate upward against flat-topped cones of structureless sandstone that are up to 15 cm deep and present at numerous, closely spaced stratigraphic horizons. Entrada eolian dune deposits also host abundant burrows likely produced by small insects. Both large and small burrows are most numerous in the uppermost parts of very thick (up to 35 m) compound sets of cross-strata generated by superimposed dunes migrating along the lee slopes of giant dune ridges. The size and morphology of the large burrows and the nature of their fills suggest that they were excavated by vertebrates, possibly insectivores, but the possibility that scorpions or spiders dug the burrows cannot be ruled out. In modern dunes, the top 20 cm of rain-moistened sand dries quickly, but underlying sediment can remain moist for long periods. Conical pits formed on the dry surface of Jurassic dunes at the tops of burrows that were primarily excavated in underlying moist sand. Cones composed of structureless sandstone are active fills produced when burrowers pushed moist sand to the surface, forming spoil piles. Most cylindrical portions of the burrows were also actively backfilled; remaining parts were passively filled when burrow walls collapsed. Cones at burrow tops now delineate thin (~5–10-cm-thick) packages of cross-strata that record slow (seasonal?) dune migration. Rainfall on dune surfaces allowed scattered plants, insects, and insectivorous vertebrates to inhabit the Entrada sand sea. Burrows provided animals with refuge from the hot, desiccating surface conditions.

INTRODUCTION

Although active, subtropical sand dunes support the lowest biomass of any continental ecosystem (Robinson and Seely, 1980), diverse animals have evolved convergent behavioral patterns to cope with the hot, dry substrate and low availability of prey. In modern deserts, most vertebrates, spiders, and scorpions pursue insect prey by night and escape high diurnal surface temperatures by burrowing (Louw and Seely, 1982; Reichman and Smith, 1990). The purpose of this paper is to show that trace fossils within cross-strata of ancient eolian sandstones can be a rich source of information on the physical and biological processes that operated in ancient dune fields.

On the Colorado Plateau, burrows are abundant in several of the extensive wind-blown sandstones of late Paleozoic and early Mesozoic age (Loope, 1984; Ekdale and Picard, 1985; Loope and Rowe, 2003; Hasiotis, 2004). Large-scale cross-strata in the Middle Jurassic Entrada Sandstone of south-central Utah contain abundant large, sinuous, branching trace fossils. These cylindrical trace fossils are 15–95 mm in diameter and penetrate wind-ripple deposits that are also replete with 3–12-mm burrows. This paper presents evidence that the larger traces were excavated by insectivorous animals into moist, cohesive sand that lay just below the surfaces of large, active dunes.

Loope (2006) described 14 examples of vertebrate burrows in the Entrada Sandstone that reach diameters of >0.5 m and lengths of >3.0 m. Those large, rare burrows descended from a small number of bounding surfaces that divide sets of cross-strata; they were excavated in moist sand and were partially filled by wind-blown, cross-stratified sand. The burrows described here are an order of magnitude smaller, are much more abundant, and descend from a large number of different stratigraphic horizons. They demonstrate that moist sand was quite often present just below the surfaces of slow-moving dunes.

GEOLOGIC AND PALEOCLIMATIC SETTING

This study is based on strata exposed within the Escalante Member of the Middle Jurassic Entrada Sandstone along 30 km of the northeastern edge of the Kaiparowits Plateau (Fig. 1). In south-central Utah, the Escalante Member is a prominent, white-to-grey eolian sandstone forming the uppermost part of the Entrada Sandstone (San Rafael Group; Thompson and Stokes, 1970). The Escalante Member lies below a flooding surface that Thompson and Stokes called the sub-Curtis Formation unconformity (the J-3 unconformity of Peterson, 1988a) and is directly overlain by marine mudstone of the Summerville Formation. No outcrops with interbedded marine and eolian facies were observed or previously

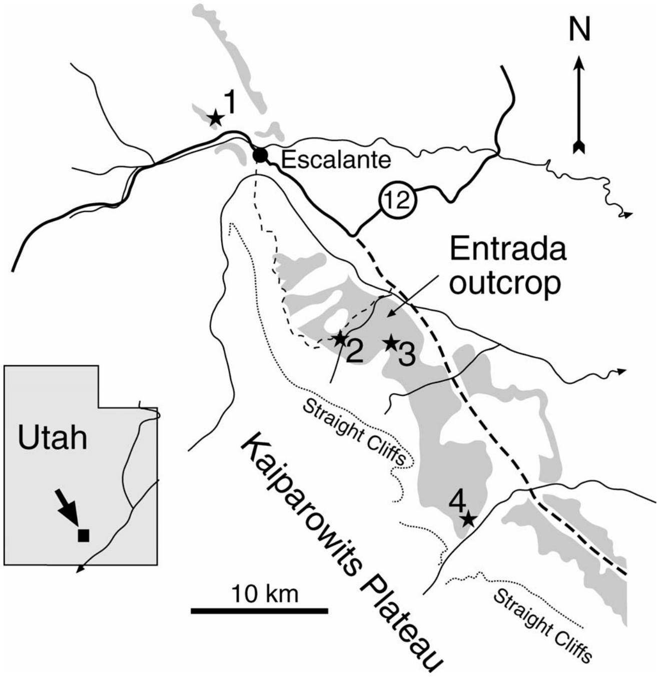

FIGURE 1—Location of study sites 1–4.

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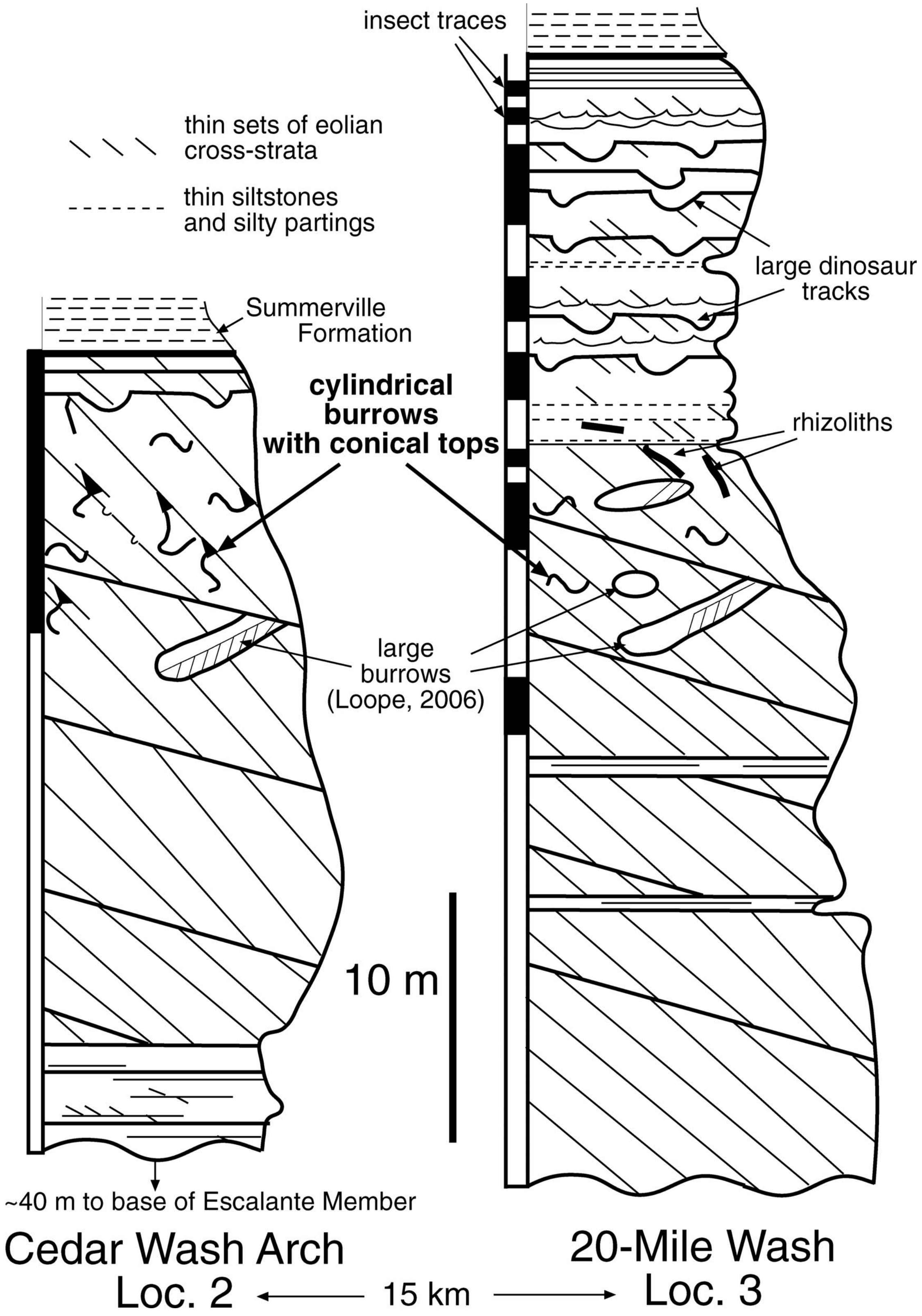

FIGURE 2—Stratigraphic sections at localities 2 and 3 (Fig. 1).

reported. The proximity of the dune field to a shoreline is therefore unknown.

The Escalante Member is 65–85 m thick in the study area (Thompson and Stokes, 1970). The lower part of the unit is dominated by relatively thin sets of eolian cross-strata separated by numerous, closely spaced horizontal erosion surfaces and is nearly devoid of trace fossils. Trace fossils are abundant in the upper part of the unit, however, where compound sets of eolian cross-strata attain thicknesses >30 m (Figs. 2–3). Second-order bounding surfaces dip 10–15° to the east and south and separate sets of cross-strata deposited by relatively small dunes that were

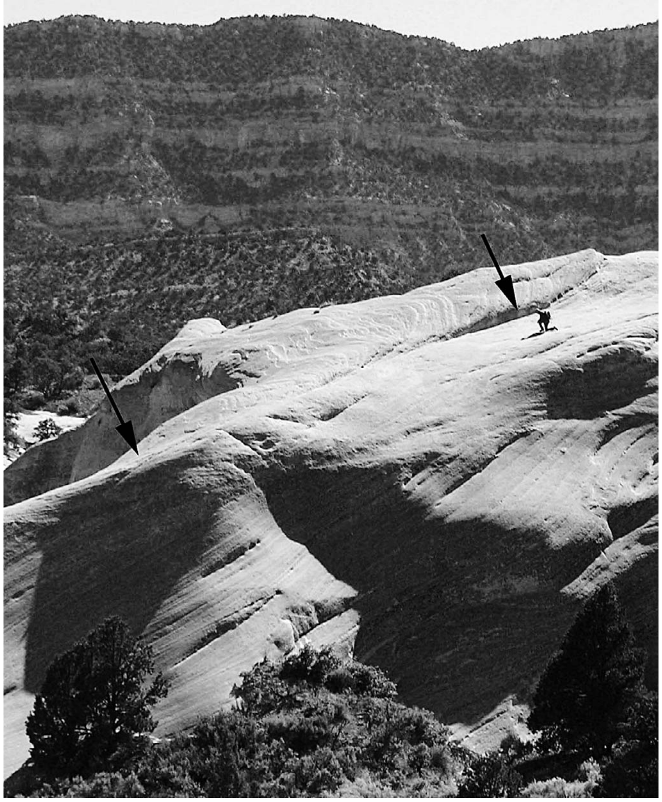

FIGURE 3—Cross-stratification near the top of the Escalante Member of the Entrada Sandstone, south-central Utah (locality 2). Arrows point to sloping erosion surfaces generated by small dunes migrating down the lee face of large dune. Both dunes moved right to left. Burrows are abundant near and above kneeling person (upper arrow), but are absent below the lower arrow.

superimposed on the lee slopes of very large, slowly migrating dune ridges (Kocurek, 1981). First-order bounding surfaces in the Escalante Member are nearly horizontal (bounding tabular co-sets of cross-strata) and are associated with thin (15–30 cm) sets of cross-strata with irregular upper surfaces that indicate deposition and erosion near the ancient water table (Loope and Simpson, 1992). Both grainflow and wind-ripple deposits are abundant within the cross-strata between second-order bounding surfaces. In many cases the cross-strata between two successive second-order bounding surfaces (Fig. 3) are continuously exposed and accessible for many tens of meters. At localities 2 and 3, the lower (downslope) parts of these sets of cross-strata are fine grained and devoid of trace fossils, but the higher, coarser-grained parts have abundant burrows (Figs. 2–3).

During the Middle Jurassic, Pangea was moving northward, and southern Utah lay within the subtropics, at a paleolatitude of about 22° N (Peterson, 1988b). In the study area, the Escalante Member of the Entrada Sandstone represents the last of many widespread sand seas that developed during the late Paleozoic and early Mesozoic (Blakey et al., 1988). The compound cross-strata in the Entrada and their highly variable dip directions (Peterson, 1988b) indicate a wind regime that was more complex than the one that had prevailed in the region during the Permian, Triassic, and Early Jurassic, when abundant sets of southeast-dipping cross-strata were deposited (Peterson, 1988b; Loope et al., 2004).

SMALL BURROWS

Description

Simple cylindrical burrows, 3–12 mm in diameter, are abundant in wind-ripple deposits at all the study localities. These burrows are smooth walled, and faint menisci are sometimes visible (Fig. 4A). At locality 4, small burrows rimmed by calcite-cemented sandstone are aggregated into cylindrical masses of widely varying forms and sizes (Figs. 4B–C). Few traces appear in grainflow strata, but because bedding planes separating these structureless deposits are spaced only a few centimeters apart, traces may be present but imperceptible. At localities 2 and 3, small-diameter traces, like the large-diameter traces described later, are abundant only in the uppermost parts of very thick sets of cross-strata.

Interpretation

The small traces are interpreted as burrows made by insects. Most traces are similar to those described from eolian strata of the Lower Jurassic Navajo Sandstone (Loope and Rowe, 2003; Ekdale et al., 2007) and the Lower Jurassic Clarens Formation (Bordy et al., 2004, 2005). The calcite-rimmed burrows resemble structures that have been interpreted as termite galleries (Hasiotis, 2004; Bordy et al., 2004, 2005). Seely and Mitchell (1986) described calcite-cemented tubular structures from eolian strata of the Tertiary Tsondab Sandstone of Namibia and noted the similarity of these structures to the casts of the modern harvester termite *Hodotermes mosbambicus*. The rare, cylindrical masses of intertwining burrows at locality 4 (Figs. 4B–C) strongly resemble the rhizolith-engulfing termite traces of Hasiotis (2004). The abundance of calcite cement associated with some small burrows and rhizoliths suggests at least a brief cessation of sand movement (Loope et al., 1998).

Vegetation is typically more abundant on the lower slopes of modern dunes than on the upper (where wind velocity is greater and sand movement more frequent). The abundance of the insect burrows within the upper parts of the lee deposits (and their absence within the lower slope deposits) is thus an enigma. The rarity of rhizoliths points to another enigma: what was the source of fixed carbon for the dune ecosystem? One possibility is that growth on the dunes was seasonal and that, because plants were ephemeral, they did not generate rhizoliths. Another possibility is that animal life on the dunes depended on wind-transported organic detritus. In the Namib desert, such detritus is trapped in eddies that form just downwind of dune slip faces (Robinson and Seely, 1980). A possible explanation for the abundance of life on the upper parts of the preserved Jurassic dune strata is that the bulk of the organic detritus was trapped on the slip faces of the small dunes that were highest on lee slopes of the larger dunes—the first ones leeward of the dune crest.

LARGE CYLINDRICAL BURROWS WITH CONICAL TOPS

Description

These burrows are 15–95 mm in diameter (Fig. 5) and penetrate thin, distinct, inverse-graded wind-ripple strata that are also replete with the smaller diameter burrows described above (Fig. 6). The large burrows typically are inclined 15–22° to the horizontal, oriented perpendicular to the strike of the depositional surface (which typically sloped at 10°–15°), and intersect wind-ripple stratification at an angle of ~35°. Planar sandstone outcrops that cut cross-strata and slope at ~20° reveal that some of the exposed traces are >1.0 m long and are broadly sinuous. The greatest measured vertical extent of an individual burrow is 50 cm. At localities 2 and 3, burrows are abundant only in the uppermost parts of very thick sets of cross-strata (see Fig. 2).

Flat-topped, sand-filled cones form the upper termini of many of the burrows (Figs. 7–8). Most of these cones are internally structureless, but others have laminated, concave-up fills (Fig. 8). Burrows are not strongly clustered at a few stratigraphic levels but instead terminate at many different, closely spaced bedding surfaces. On one 6 m^2 outcrop, burrows with flat-topped cones terminate at 14 different bedding planes within a single meter of stratigraphic section (Fig. 9).

Nearly all of the burrows have very sharp contacts with surrounding, thin-bedded, unfolded strata. The nature of the burrow fill often varies along the length of an individual burrow. Fills typically are massive (structureless), but lamination parallel to cylinder walls is present in some

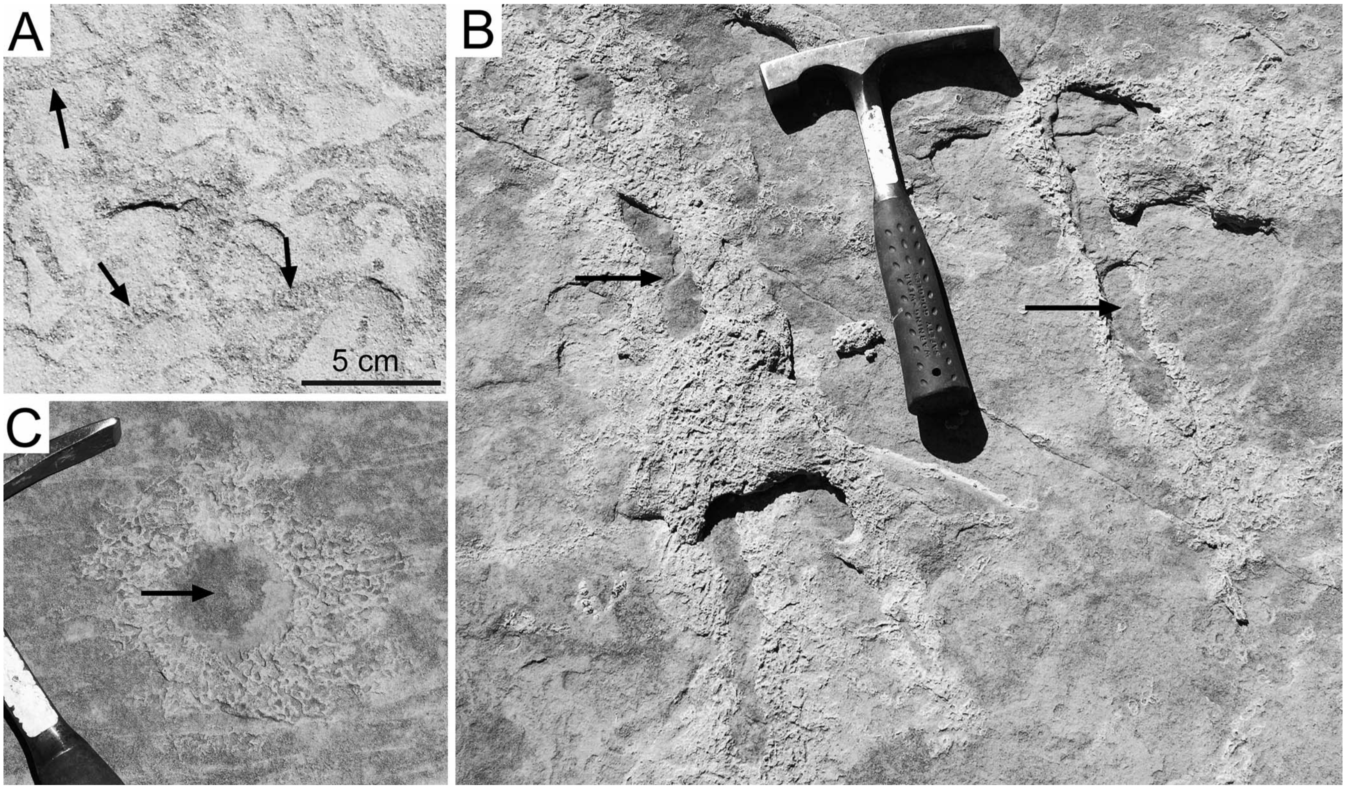

FIGURE 4—Small-diameter trace fossils and associated rhizoliths. A) Burrows with faint meniscate structure (arrows). B) Longitudinal sections through two bedding-parallel rhizoliths that are surrounded by calcite-rimmed, small-diameter burrows (arrows). C) Close-up of calcite-rimmed burrows that surround a central rhizolith (arrow) seen in transverse section.

traces (Fig. 6), and faint menisci are present in one (Fig. 10A). In other cases, tilted blocks of laminated sand are present within the burrow fills (Fig. 7).

About 5–10% of the exposed burrows are branched (~120° junctions; Fig. 10B). No chambers or expanded zones were observed. Branches are always of the same diameter as the primary cylinder. At some of the branching points, a faint boundary separates sand fill in one branch from the fill of the other (Fig. 10B).

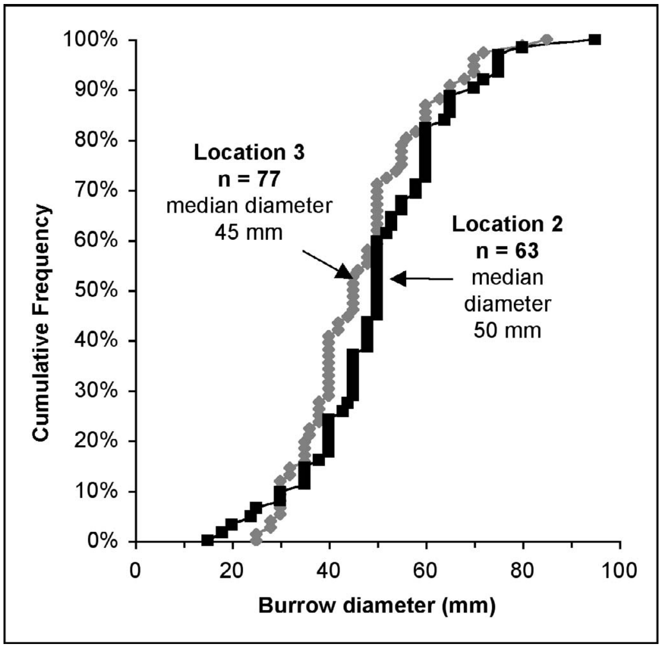

FIGURE 5—Cumulative frequency diagram of the diameters of large, cylindrical burrows measured at localities 2 and 3.

Interpretation

Morphological, sedimentologic, and stratigraphic evidence shows that these larger structures are animal burrows rather than rhizoliths; this evidence includes the following. 1) A parallel-sided cylindrical shape with equal-diameter branching is required for branched burrows but is highly uncharacteristic of rhizoliths, which have downward bifurcations with diminishing diameters of second-, third-, and fourth-order branches (Klappa, 1980). 2) Rhizoliths in cross-stratified dune deposits are best developed parallel to those planes (Fig. 4B; Glennie and Evamy, 1968; Loope, 1988), because vadose water preferentially moves down the dip of cross-strata (Stephens, 1996, p. 86). The larger Entrada traces are instead preferentially oriented at a high angle to bedding. 3) The structures are never mineralized, nor are they associated with gray mottling (rhizohaloes of Kraus and Hasiotis, 2006). 4) Sedimentologists have long used the distribution of marine trace fossils to decipher relative rates of deposition (Dott, 1983). If the traces in Figure 9 were rhizoliths, not burrows, they would record the growth of large, woody roots downward from a series of very closely spaced surfaces. Each stratigraphic horizon bearing a flat-topped cone (Fig. 9) would be a paleosol—a distinct episode of plant colonization and new growth on a fresh dune surface. Thin sand accumulations are unlikely to have killed plants with large roots; a better interpretation is that each increment required a new generation of burrows.

In modern sand seas, many reptiles use lateral undulation to swim through cohesionless sand (e.g., Pough, 1980; Hembree and Hasiotis, 2007), but the sharp contacts of these trace fossils with surrounding undeformed, thin-bedded strata suggest they are excavated burrows rather

FIGURE 6—Longitudinal section through the cylindrical portion of a burrow. Note sharp truncations of thin laminae in surrounding sediment. Wind-ripple laminae dip 15° toward top of photo; burrow is inclined ~22° to the horizontal.

than products of compaction around a sand-swimming animal (or a growing plant root) (e.g., Hembree and Hasiotis, 2006). Further, the vertical extent of individual burrows (up to at least 50 cm) appears to preclude such an origin, as sand swimmers must bear the full weight of overlying, cohesionless sediment and are typically shallow (Fielden et al., 1990). These observations are inconsistent with an earlier, sand-swimming interpretation (Loope, 2005).

Faint, rare meniscate structures indicate active backfilling by the burrower, as do the faint boundaries between structureless burrow fills at branching points (Fig. 10). Brecciated fills (Fig. 6B) demonstrate that at least some portions of some burrows remained open after passage of the burrower and filled via roof collapse. The main (cylindrical) portions of these burrows were not likely filled by dry sand flowing down their axes, because they are inclined at angles well below the angle of repose.

The burrowers excavated open tunnels in medium-to-coarse sand that was free of silt and clay—material that is cohesionless when dry. As the dune surface was several tens of meters above the water table, the cohesion required for construction of the lower portions of the burrows beneath the sandstone cones (Fig. 8) could only have been supplied by intergranular water derived from rainfall events. In modern dunes, diurnal temperature changes drive circulation of dry air, causing surficial sand to dry quickly after rains. Unless penetrated by the roots of vascular plants, however, the sand below 20 cm can remain moist for years (Bagnold, 1954, p. 245). Some of the Jurassic burrows may have been completed while the sand was still moist all the way to the dune surface. Some shallow, angle-of-repose, conical pits could thus have formed when sand collapsed into the entrances of these burrows as the surficial layer of sand dried. Most of these burrows, however, were probably excavated after the surficial 5–10 cm of sand had already dried and lost cohesion. From the time of construction, these burrows would have had conical, angle-of-repose entrances. The vertical extent of the largest sandstone cones (~20 cm) corresponds well with Bagnold's (1954) observations of the depth of rapid drying in rain-moistened, modern dune sand.

Some modern fossorial mammals are known to backfill their burrows and to generate surficial spoil piles (e.g., Bromley, 1990, p. 10–11; Vleck, 1981). The fills of many rodent burrows in late Holocene deposits of the Nebraska Sand Hills display a crude, meniscate structure. The relatively shallow angle (~22°) of the Jurassic burrows is consistent with observations of modern burrowers that backfill their tunnels. Vleck (1981) noted that the slope of tunnels constructed by pocket gophers varies with soil texture; although the animals can backfill vertical burrows constructed in fine-textured soils, burrows in sandy soils ascend to the surface at shallow angles.

The structureless sandstone within each terminating cone is probably the remainder of a surficial spoil pile (Fig. 7D). In southern Utah, small rodents that burrow in moist dune sand commonly bring spoil to the surface. When the surface sand is dry, the piles of cohesive spoil commonly fill or partially fill angle-of-repose pits (Fig. 7D). Drying and subsequent deflation of ancient spoil piles would leave flat-topped cones filled by structureless sand (Fig. 7C). No distinction is recognized here between cones representing points of burrow entry and those representing exits, nor is it clear how much (if any) time the animals spent above ground on the dune surface, i.e., whether the Jurassic animals were facultative or obligate burrowers.

The cones with bedded fills probably represent burrow openings that were passively filled. During windstorms, rolling and creeping coarse sand grains (driven by fine, saltating grains) became trapped in the steep-walled pits while many of the saltating grains bypassed them. The very large burrows (>50 cm diameter) reported from the Entrada Sandstone by Loope (2006) are partially filled by drifts of cross-stratified sand, but those burrows are, like the burrows described here (Fig. 8), capped by concave-up layers of coarse sand.

DISCUSSION

The large number of different burrowed intervals within a given thickness of accumulated sediment (14 distinct intervals in a one-meter-thick interval, Fig. 9) indicates that each depositional episode added a thin sediment package to the dune lee slope and was followed by a hiatus. Partially vegetated dunes composed of coarse sand move much more slowly than unvegetated, finer-grained bedforms. The thin increments of coarse sediment, therefore, are tentatively interpreted as seasonal or storm accumulations that record slow, episodic dune migration. For comparison, in the Early Jurassic Navajo Sandstone, large-scale, cyclic cross-strata indicate that large, unvegetated dunes composed of medium sand migrated more than a meter per year (Hunter and Rubin, 1983; Loope et

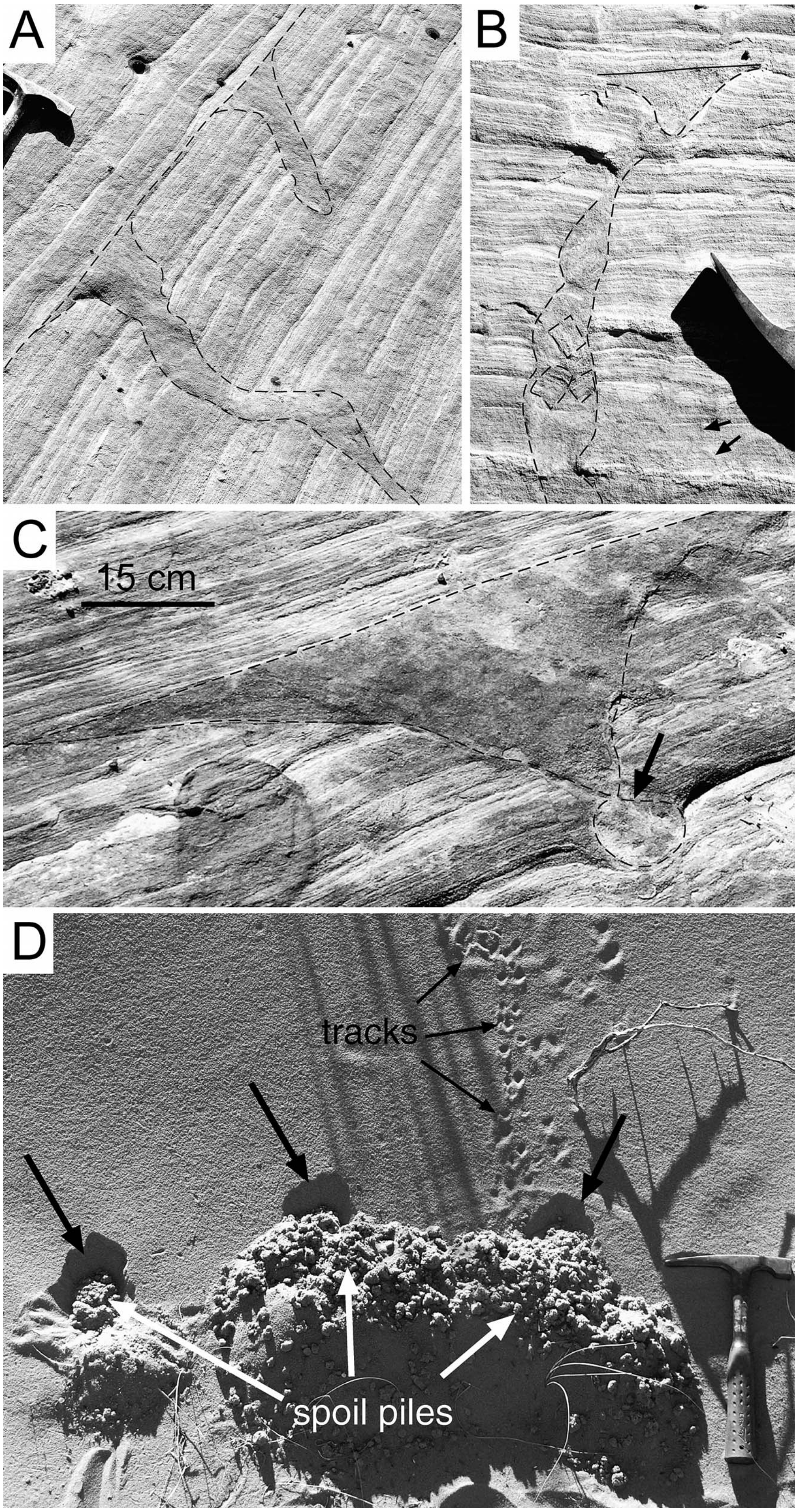

FIGURE 7—Burrows with conical, angle-of-repose terminations. A) Two adjacent burrows with structureless fill that both terminate upward as structureless, flat-topped cones. Lower part of burrow was excavated in moist sand, but uppermost sand was dry. Both parts of burrow were actively backfilled (see D for possible modern analog). Rock surface slopes to lower right; strata dip 15° into the slope. B) Burrow terminating in flat-topped cone (top, center) and partially filled by blocks of laminated sandstone. Blocks record collapse of a portion of the burrow that was not actively backfilled. Arrows = burrows of small insects. C) Flat-topped cone filled by structureless sand adjacent to cylindrical burrow (arrow). Cone fill is interpreted as a product of active backfilling (see view D). D) Rodent diggings and tracks (kangaroo rat?) at the base of a modern dune in southern Utah. Three dry-sand, angle-of-repose pits (black arrows) are partially filled by piles of moist sand (white arrows) excavated from underground tunnels and pushed to the surface. After drying and deflation, these pit fills would resemble the structures shown in views A, B, and C.

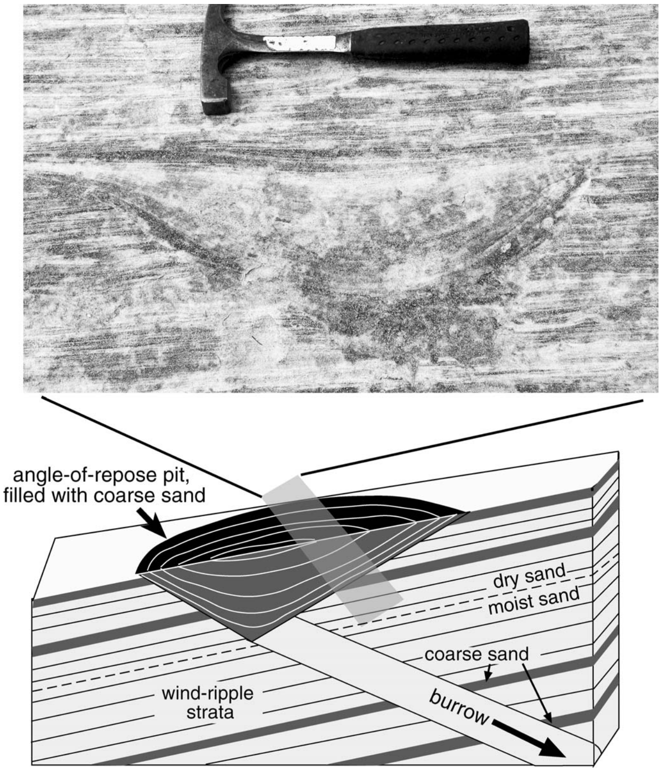

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FIGURE 8—Stratified cones and their interpretation. Photograph shows cross section of a passively filled cone in the Entrada Sandstone. Dashed line in interpretive drawing marks boundary between dry surficial sand and underlying sand that still retains moisture from a previous rainfall event. Conical pits formed at the tops of cylindrical burrows that were excavated when the surface sand was dry and subsurface sand was moist. Some of these pits were later filled by coarse, wind-driven sand (this figure), others were actively backfilled or plugged (Fig. 7).

al., 2001), which is probably many times the migration rate of the dunes that deposited the uppermost portion of the Entrada Sandstone.

The surfaces of subtropical sand dunes can often exceed 50° C during midday (Robinson and Seely, 1980). The Jurassic animals entered wind-rippled sand on dune lee slopes at a shallow vertical angle and moved downward into the substrate in the up-dip direction—a behavior that would have efficiently taken them to surroundings appropriate for thermoregulation. Few animals reached as far as 50 cm below the dune surface, but because of the low thermal conductance of dry sand, a depth of only 20 cm would have provided them refuge from lethal temperatures. The high moisture content of the sand (and high humidity) below 20 cm would have diminished their evaporative water loss.

The animals that produced the larger burrows may have preyed on the invertebrates that made the smaller (3–12-mm-diameter) burrows (Fig. 6B). The large diameter of the burrows and their backfilled structure suggest the possibility that small vertebrates dug the burrows. Both scorpions and spiders, however, commonly construct burrows in dune sand, and their burrow diameters and lengths overlap with those described here (Hasiotis and Bourke, 2006). Scorpions construct deep, sinuous burrows,

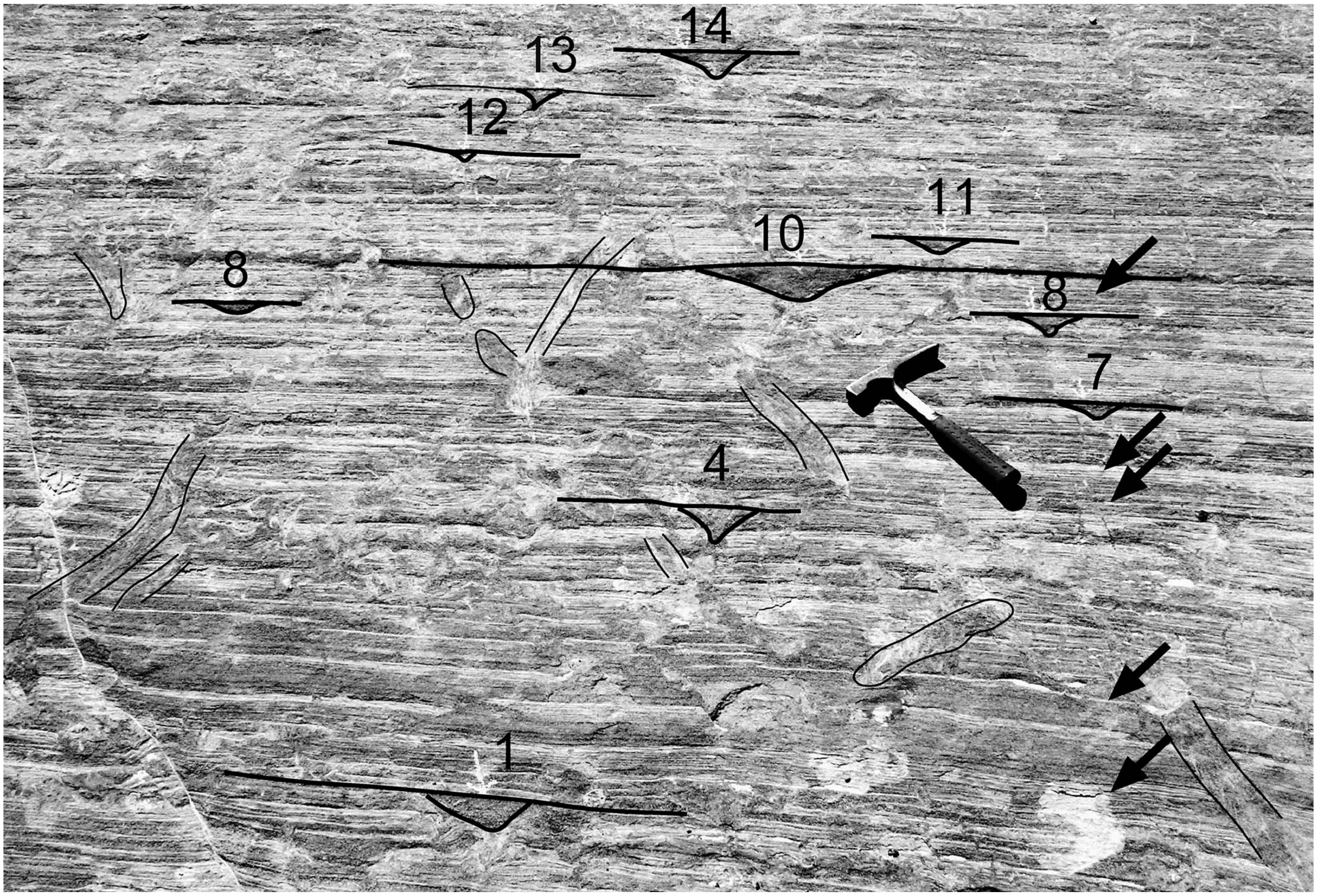

FIGURE 9—Stratigraphic spacing of cone-shaped burrow tops at locality 3. Distribution of terminations shows that each burrowing episode took place after a thin (5–10 cm thick) sand layer was deposited. View shows a portion of a 6 m^2 outcrop in which burrow tops are present at 14 different stratigraphic horizons. Stratigraphic levels with visible terminations are numbered; black arrows show stratigraphic positions of out-of-view burrow tops. Dune cross-strata dip away from viewer at 15°; rock surface slopes ~20° toward viewer; white arrows mark burrow tops and were chalked in the field.

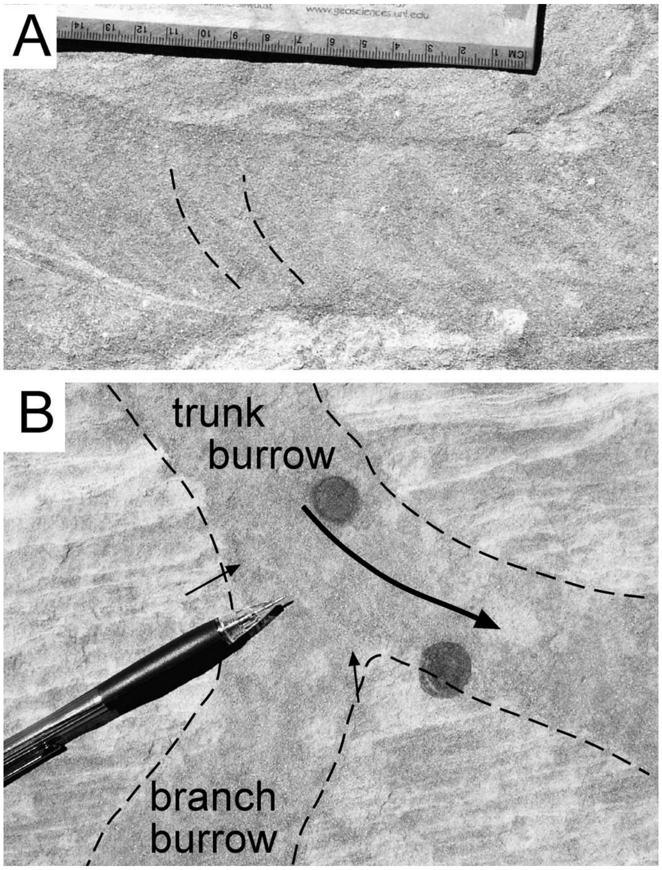

FIGURE 10—Backfilled portions of cylindrical burrows. A) Backfilled burrow with faint menisci (parallel to dashed lines). Scale = 15 cm. B) Junction of two burrows. Small arrows and tip of pencil point to boundary between the structureless fills of the two burrow segments. Burrower backfilled the branch burrow (lower left) while keeping the trunk burrow open, then backfilled the trunk. Long arrow shows interpreted direction of burrower's movement.

but their tunnels are strongly flattened in cross section (Hasiotis and Bourke, 2006). Spider burrows are typically vertical, with the terminus and upper portion lined with silk to prevent collapse (Ahlbrandt et al., 1978). Although modern scorpions and spiders may plug the mouths of their burrows, they apparently do not backfill long portions of their tunnels.

The taxonomic affinities of the Middle Jurassic burrowers are unknown. Although the Lower and Upper Jurassic strata of the western United States are rich in vertebrate skeletal material, very little Middle Jurassic material has been reported from North America (Hunt and Lockley, 1995; Irmis, 2005). A single vertebrate specimen, collected in eastern Utah, is known from the Entrada Formation. *Entradasuchus* is a small crocodylomorph that was preserved within the Moab Member of the Entrada Sandstone (Hunt and Lockley, 1995), a cliff-forming unit that, like the Escalante Member in south-central Utah, is dominated by large-scale, eolian cross-strata (Peterson, 1988b). The bone material of this remarkable specimen was replaced by calcite. The skull is ~25 mm wide, and the total length of the specimen about 20 cm. Small, Early Cretaceous crocodylomorphs are known from specimens fossilized within burrows (Gomani, 1997). Other possible vertebrate trace makers include sphenodontians similar to those found in the Early–Middle Jurassic La Boca Formation in Mexico (Reynoso, 1996; Reynoso and Clark, 1998) and fossorial mammals like *Fruitafossor*, which was collected from the Late Jurassic Morrison Formation (Luo and Wible, 2005) but is not known from Middle Jurassic rocks. Lucas et al. (2006) described cylindrical structures from eolian strata within the Lower Jurassic Navajo Sandstone that they interpret as the burrows of small mammals. Unlike the burrows described here, the Navajo features weather out of structureless sandstone interpreted as interdune deposits and appear as networks of primarily vertical and horizontal elements.

Sand dunes are widespread in the subtropics today but were probably much more extensive in the late Paleozoic and early Mesozoic when strong winds were generated by intense summer heating of the Supercontinent Pangea (Kocurek, 1988; Loope et al., 2004). Starting at least in the early Permian and continuing into the Late Jurassic, great numbers of small, burrowing invertebrates lived within these deposits (Loope, 1984; Ekdale and Picard, 1985; Loope and Rowe, 2003; Hasiotis, 2004; Ekdale et al., 2007). These animals would have been available as prey to larger dune-dwelling animals that were capable of maintaining a viable body temperature and water balance.

CONCLUSIONS

1. The uppermost portion of the Escalante Member of the Entrada Sandstone contains evidence of a Middle Jurassic subtropical dune ecosystem that included rooted plants, abundant small insects, and larger, possibly insectivorous animals that backfilled their extensive burrows and avoided lethal daytime temperatures by staying a few tens of cm below the dune surface. These animals may have been small vertebrates, but the possibility that the larger burrows were made by scorpions or spiders cannot be ruled out.
2. Burrows were constructed in wind-ripple strata high above the water table, on the flanks of actively migrating, compound dunes.
3. Burrows were excavated in cohesive sand that had been moistened by rainfall. Cone-shaped burrow termini show that the dune surface had dried before the next increment of dune sand accumulated. Cones of structureless sand found at the tops of many burrows are the eroded remains of spoil piles brought up to the dune surface by the burrowers. Conical pits at the tops of other burrows were passively filled by wind-transported sand.
4. Packages of coarse-grained, wind-ripple strata punctuated by burrow horizons suggest seasonal or wind-storm deposition. The close spacing of these burrow horizons imply that the large bedforms migrated slowly.
5. The large burrows show that seasonal rainfall allowed moist, cohesive sand to persist long enough through the year to sustain a population of relatively large, probably insectivorous animals in this Middle Jurassic sand sea.

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