

Dry-Season Tracks in Dinosaur-Triggered Grainflows

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Thousands of animal tracks are preserved in wind-blown cross-strata of the Lower Jurassic Navajo Sandstone at Coyote Buttes on the Arizona-Utah border, USA. Tracks deform thin grainflows that were deposited on the slip faces of large dunes. In cross-section, laminae (pin stripes) are smoothly folded, and are only very rarely broken. There is no sign of a central shaft left open when the trackmaker's foot was withdrawn from the substrate. At the top of each track, folded laminae are truncated by the pin stripe that marks the base of the next (younger) grainflow. Within some trackways, progressively younger tracks move up-section to younger grainflows. The folded, unbroken pin stripes and absence of a distinct shaft fill are inconsistent with a moist-sand (cohesive) substrate. Stratigraphic relationships between tracks and grainflows indicate that, as the animals moved across the slip face, they triggered dry avalanches, and then stepped on the newly deposited grainflows. Although scour by grainflows can remove shallow tracks, the loose packing (high porosity) of grainflows ensures that the feet of larger animals will penetrate well below the level of the next erosive surface. Although dry dune sand previously has been denigrated as a medium for track preservation, this example shows that dry eolian grainflows, due to their loose packing and their position in the zone of flow separation on the dune lee slope, can preserve abundant, clear tracks. A dry-sand origin of the tracks corroborates an earlier interpretation of the grainflows as December–February (dry season) deposits of cross-equatorial winds.

INTRODUCTION

The geological literature contains dozens of reports of animal tracks preserved within the deposits of ancient dunes (see references in McKeever, 1991, and Fornos et al., 2002). Most authors have concluded that tracks in ancient eolian cross-strata either were made in moist sand, or were preserved only because they were moistened immediately before burial. According to McKeever (1991), crudely formed, shapeless depressions made in dry sand are more vulnerable to wind erosion than the well-formed tracks of moistened substrates. Two observations, however, cast some doubt on the moist-sand interpretation of these ancient tracks: (1) well-sorted, highly permeable, surficial sands on the slip faces of modern desert dunes are nearly always dry; and (2) well-formed tracks sometimes are preserved on a high percentage of the bedding surfaces that separate adjacent dry-avalanche deposits (grainflows). This paper presents structural, sedimentologic, stratigraphic, and paleoclimatic evidence that supports a dry-sand origin for most, if not all, the abundant,

well-formed tracks preserved in grainflows of the Lower Jurassic Navajo Sandstone of the southwestern USA.

The tracks at the study site (Figs. 1, 2) most likely were made by small theropod dinosaurs and tritylodont therapsids that moved up, down, and across angle-of-repose slopes on the lee sides of large dunes. The Navajo Sandstone accumulated in a vast inland sand sea that lay near the western edge of the supercontinent Pangea, and about 10° north of the equator (Loope et al., 2004b). Evidence that the abundant tracks were emplaced and preserved in dry, cohesionless sand is provided by: (1) smoothly folded (unbroken) laminations seen in vertical cross-section; (2) absence of a central shaft where the track maker's limb was withdrawn from the substrate; and (3) records of dynamic interactions between the track maker and the avalanching substrate.

Sand transported over the crest of a dune rests on the upper lee face until the slope on the growing deposit reaches the critical angle of yield and the stored sand flows down the lee face as a dry grainflow (Allen, 1970). Because much of the Navajo Sandstone of southwestern Utah is composed of very thick (up to 17 cm) grainflow cross-strata, it follows that very large volumes of sand typically were stored on the upper lee slope before avalanching took place, thus, avalanching was relatively infrequent. The tracks described here, however, lie within very thin grainflows. Animal activity on lee slopes can trigger avalanching on surfaces sloping at less than the critical angle of yield. Because animals can increase the frequency of avalanching, the thinness of the track-bearing grainflows of the Navajo also is a direct product of their activity.

STRATIGRAPHIC, SEDIMENTOLOGIC, AND PALEOCLIMATIC SETTING

The Lower Jurassic Navajo Sandstone accumulated in a vast inland sand sea that covered more than 350,000 km²; the formation reaches thicknesses of over 700 m in southwestern Utah and southern Nevada (Kocurek and Dott, 1983). More than 60 track sites are known from the Navajo Sandstone and its correlative strata (Lockley, 1998). The greatest density of Navajo Sandstone tracks yet reported lies near the middle of the Navajo at Coyote Buttes, astride the Arizona-Utah border (Loope and Rowe, 2003; Fig. 1). Well-formed tracks of theropod dinosaurs (*Grallator*) and tritylodont therapsids (*Brasilichnium*) are visible on many hundreds of closely spaced, steeply dipping depositional surfaces (Fig. 2).

At Coyote Buttes and throughout southern Utah and northern Arizona, the Navajo Sandstone is composed of large-scale, southeast-dipping eolian cross-strata (Loope and Rowe, 2003). Tracks deform angle-of-repose cross-strata that comprise sets up to 8 m thick. Although the full

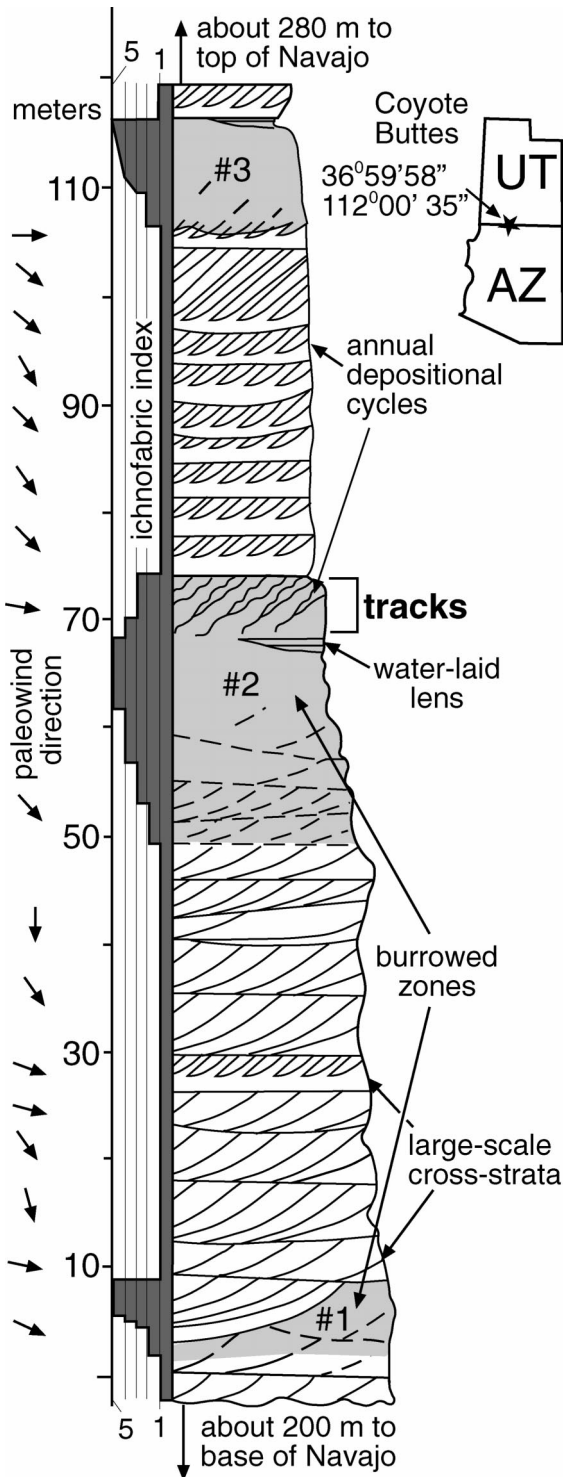


FIGURE 1—Stratigraphic section from Coyote Buttes showing position of tracks and burrowed zones, large-scale cross-stratification, and annual depositional cycles. Numbered, shaded intervals record long-lived pluvial episodes (modified from Loope and Rowe, 2003).

height of the bedforms that generated these cross-strata is uncertain, Hunter and Rubin (1983) estimated a dune height of about 30 m for nearby Navajo cross-strata of similar scale. Nearly all of the cross-strata in the Navajo Sandstone at Coyote Buttes can be attributed to two of the

basic types of eolian stratification identified by Hunter (1977)—grainflow (avalanche) strata and wind-ripple deposits (Fig. 3A, D). Although grainfall laminae can be preserved in the deposits of large dunes (especially as a record of higher wind speeds; Kocurek, 1996), most are reworked by grainflows. Grainflows are composed of well-sorted medium sand, have steep dips, and taper rapidly at their distal edges where they intertongue abruptly with wind-ripple strata that are more poorly sorted, have lower depositional dips, and are inversely graded. Grainflows are delineated by thin laminae composed of very fine sand and coarse silt (pin stripes of Fryberger and Schenk, 1988). One proposed origin for these laminae is distal fallout of fine grains, but they also can form when fine grains percolate downward through coarser particles during avalanching to accumulate along the basal shear plane (Fryberger and Schenk, 1988; Makse et al., 1997; Fig. 3B). In southern Utah, grainflow strata in the Navajo Sandstone reach thicknesses of 17 cm (Loope et al., 2004a; Fig. 3A), but in the track-bearing strata at Coyote Buttes, thicknesses of about 1 cm are typical (Fig. 2B; Table 1).

At Coyote Buttes, abundant burrows and tracks are restricted to three distinct stratigraphic intervals that are up to 25 m thick; the tracks described here are from the middle interval (Fig. 1). Loope and Rowe (2003) interpreted these intervals as evidence for enhanced summer-monsoon rainfall during pluvial episodes that lasted for thousands to tens of thousands of years. During these times, plant and animal life flourished, but, during the dry (winter) season, the dunes continued to migrate in the same direction, and at about the same rate as during the dry (non-pluvial) intervals.

Many of the sets of cross-strata (including those with abundant tracks) contain compound cyclic cross-stratification (Fig. 3C, D), a structure that Hunter and Rubin (1983) interpreted as annual cycles of dune migration brought about by seasonal changes in wind speed and direction. The cycles are defined by alternations of grainflow-dominated and wind-ripple-dominated strata. The distribution of rain-induced slumps within the depositional cycles led Loope et al. (2001) to interpret the wind-ripple strata as deposits of the summer (wet) season, and the grainflow-dominated strata as the record of the dominant winter winds (dry season; Fig. 3E). Studies of the paleomagnetic properties of adjacent formations (Steiner, 1983; Bazard and Butler, 1991) indicate that the Navajo Sandstone accumulated about 10° north of the equator. At this latitude, cross-equatorial winds swept the dunes southeastward in December–January–February, and the northward migration of the intertropical convergence zone brought rain in June–July–August (Loope et al., 2004b). During December–January–February, the winds driving the dunes would have crossed the arid interior of Pangea prior to reaching the sand sea, and thus would have carried little moisture (Loope et al., 2004a).

TRACKS

Discussion

Seven vertebrate ichnogenera have been described from the Navajo Sandstone (Lockley and Hunt, 1995; Lockley, 1998; Rainforth, 2001): *Grallator*, *Brasilichnium*, *Oto-*

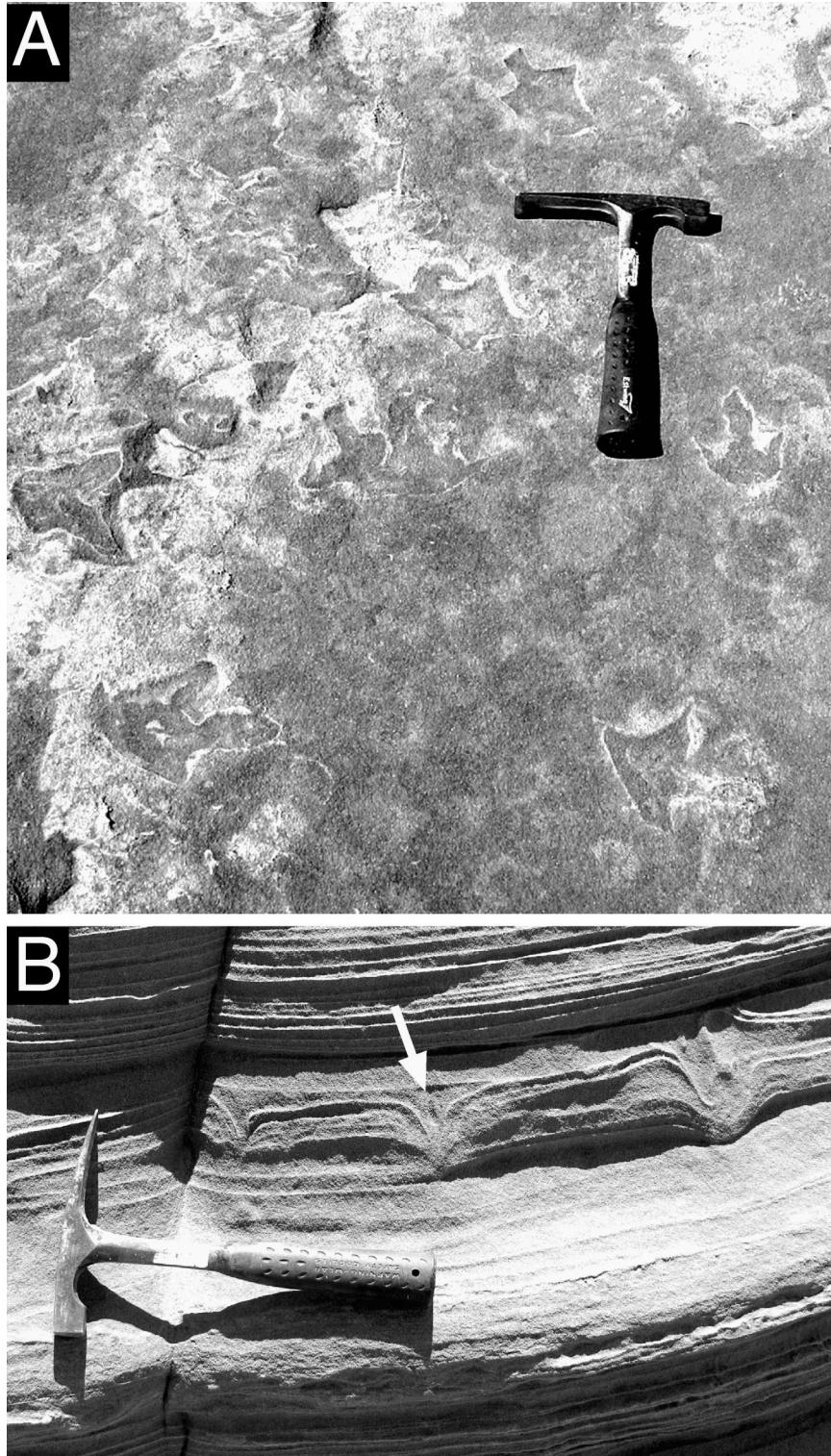


FIGURE 2—Theropod tracks (*Grallator*). All tracks are in thin grainflows that are delineated by basal pin stripes; hammer for scale; ~28 cm in length. (A) Plan view. (B) Cross-sectional view, down the dip of angle-of-repose cross-strata, interpreted as the trackway of a single animal moving left to right along, not down, the dune slope. Large amplitude of folds shows that the trackmaker's feet sunk deeply into soft sand. The two tracks on the left are older than the pin stripe (white arrow) that truncates them. This pin stripe is folded by the younger track on the right. Thus, these tracks and grainflows record a few seconds of dynamic animal/substrate interaction..

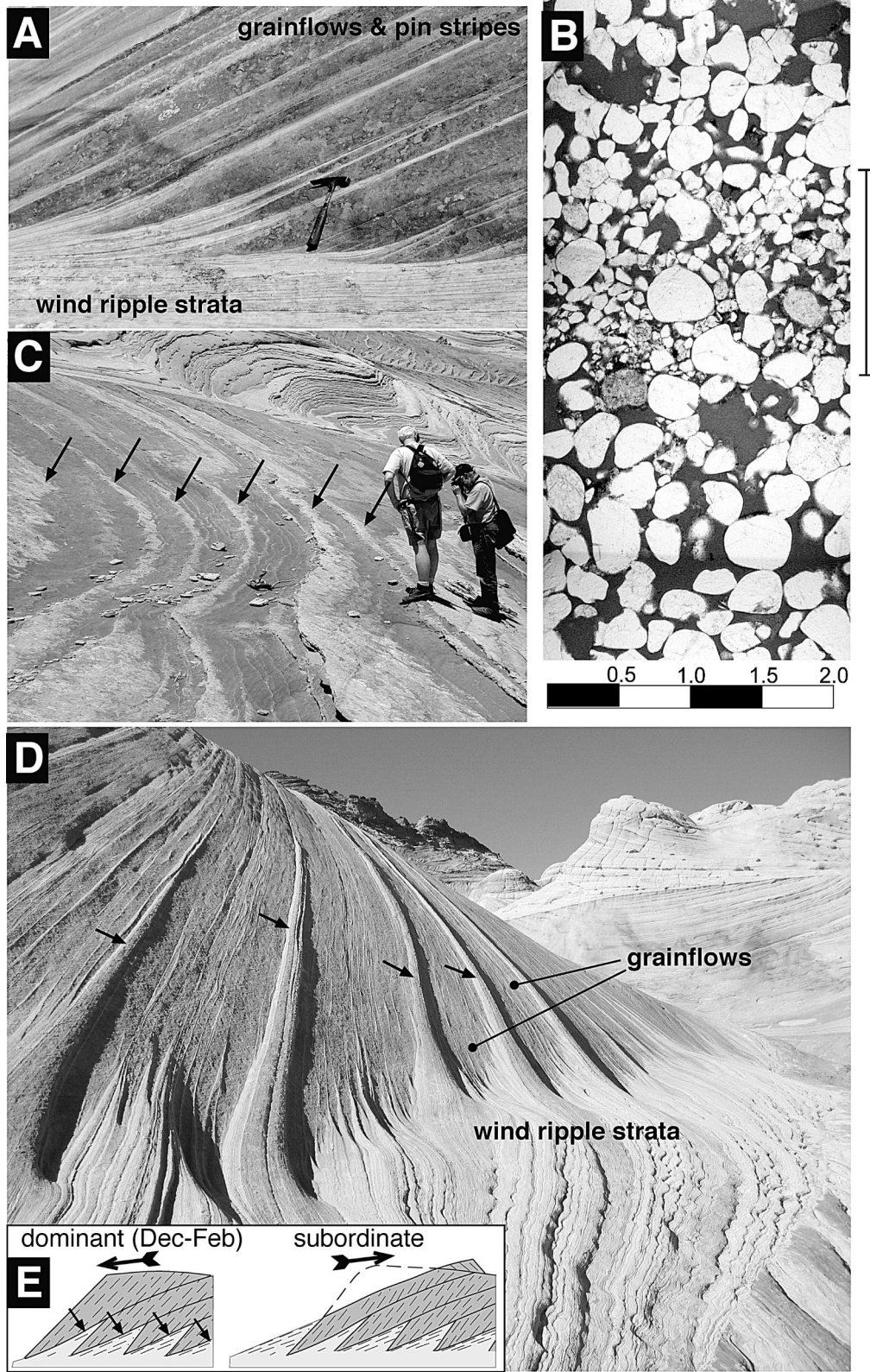


FIGURE 3—Physical sedimentary structures in the Navajo Sandstone. (A) Wind-ripple strata interbedded with thick grainflows at the base of the paleo-slipface; near east entrance of Zion National Park. Hammer for scale; ~28 cm in length. (B) Pin stripes; these delineate individual grainflows and are composed of very fine sand and coarse silt that accumulated along the shear plane at the base of the grainflow (line at right delineates pin stripe). Arrows in C–E mark the top of the wind-ripple wedge and the base of grainflow deposits; this change marks the beginning of the dry season. (C) Depositional cycles in eolian cross-strata with abundant tracks. (D) Depositional cycles in eolian cross-strata without tracks. (E) Grainflow-dominated packages deposited by the dominant (northwesterly) cross-equatorial winds that blew during the northern hemisphere winter; diagram modified from Hunter and Rubin (1983). Wind-ripple strata were banked against the slip face during the rest of the year by subordinate winds (Loope et al., 2004a).

TABLE 1—Grainflow thicknesses. (A) A continuous series of grainflows in which tracks are absent, and (B) a continuous series in which tracks are abundant. Data are from adjacent sets of cross-strata: the trackless grainflows (Fig. 3D) lie directly above the grainflows with abundant tracks (Figs. 2B and 8). A thick grainflow can be deposited only if a large volume of sand is stored on the dune lee slope before the flow is triggered. Animal activity on the lee slope caused frequent avalanching, leading to deposition of thin grainflows.

		Mean grainflow thickness	Number of measurements	Standard deviation
A	No tracks	3.19 cm	127	1.88
B	Abundant tracks	1.18 cm	175	0.93

zoum, *Eubrontes*, *Anchisauripus*, *Anomoepus*, and *Batrachopus*. Only the first three, interpreted respectively as tracks of small theropods, tritylodont therapsids, and prosauropods, are discussed here.

The tracks are present throughout the vertical extent of individual sets of cross-strata. No concentration toward the base of slope has been noted, and, in respect to track orientation in plan view, no preferential preservation has been noted (Fig. 2A).

Cross-sectional views of the tracks show that pin stripes were strongly down-folded (but very rarely broken) as the animals' feet penetrated the loosely packed grainflows; wind-ripple strata provided a firmer, much less deformable substrate (Figs. 2B, 4). In grainflows, *Grallator* and

Brasiliichnium tracks show fold amplitudes as great as 10 cm. On one horizontal bounding surface, *Otozoum* tracks penetrate more than 30 cm into underlying grainflows (Fig. 4B). In contrast, within an *Otozoum* trackway exposed on an adjacent bounding surface that is underlain by wind-ripple strata, tracks downfold laminae less than 2 cm (Fig. 4A).

In his discussion of the structural elements of tracks in cross-section, Allen (1989) referred to the central axis of the track as the shaft, and described a marginal upfold that is generated as material is pushed up and out of the shaft (Fig. 5). If the shaft of the track remains open after the foot is withdrawn, commonly, it is filled by material with a texture that is distinct from that of the folded substrate. In none of the tracks described here is a distinct shaft fill discernable. However, a marginal upfold is commonly seen, and the upper part of this structure typically is truncated by the pin stripe at the base of the next higher grainflow (Fig. 2B).

Although breakage of pin stripes within tracks is relatively rare, a few tracks exposed at the base of the slip face (in the zone of interbedded grainflows and wind-ripple deposits) are defined by circular to oval structures generated by mm-scale displacements of pin stripes (Fig. 6). Large-scale displacement and brecciation was observed in one *Otozoum* trackway. In this case, brecciated pin stripes lie directly below a thin, disrupted wedge of wind-ripple laminae (Fig. 7).

In cross-sectional views of closely spaced tracks, strati-

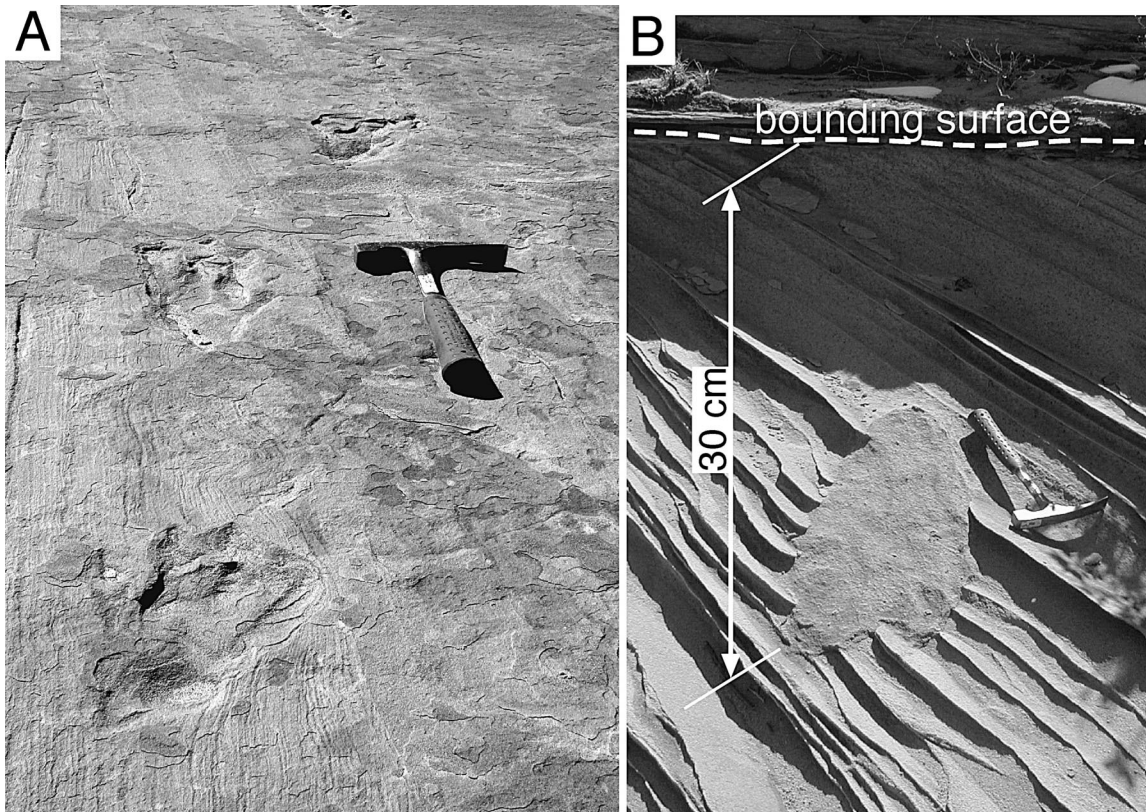


FIGURE 4—*Otozoum* (prosauropod) tracks on near-horizontal bounding surfaces. Tight packing of wind-ripple deposits makes them firm underfoot, but animals sink deeply into looser-packed grainflows. Hammer for scale; ~28 cm in length. (A) Bounding surface underlain by wind-ripple strata that dip to the left at about 15°. (B) Bounding surface underlain by grainflow strata.

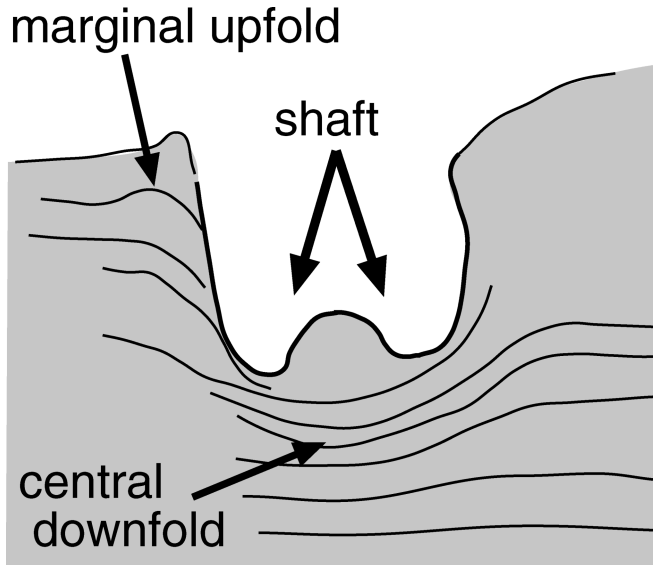


FIGURE 5—Terminology for features of tracks in cross-section (based on Holocene bison track, Loope, 1986; modified from Allen, 1989).

graphic relationships commonly show that the structures are diachronous—a pin stripe that truncates one track may be folded in the adjacent track (Figs. 2B, 8).

Interpretation

Dry Grainflows: Both dry and water-saturated sand are non-cohesive, and can generate grainflows. The abundant wind-ripple lamination (Hunter, 1977) closely associated with the tracks and grainflows (Fig. 3A, C–E) is the best single line of evidence against a subaqueous origin for the cross-strata of the Navajo Sandstone. The thin, tabular grainflows that contain the tracks were deposited in a dry condition, and, after the tracks were formed, the surface was buried by dry sand of the next grainflow. Dune lee slopes can become water saturated during heavy rainfall events (Loope et al., 1999; Loope et al., 2001), but it is unlikely that many tracks would be emplaced during such brief events.

No Distinct Shaft Fill: The absence of shaft fills with textures distinct from the surrounding, folded sediment suggests that track shafts were not left open, but instead were filled immediately by surrounding, non-cohesive sediment upon removal of the animals' limbs. If the sand had been cohesive (as when moist), the shafts would have remained open (Fig. 9), and the declivities could have been filled by a distinct sediment—in this case, perhaps, the rainout of fine-grained, distal grainfall sand and silt (which is not seen).

Folded, Not Broken: Tracks in moist sand break lamination and generate abundant breccia blocks (Fig. 9). Dry, cohesionless sand folds smoothly below a trackmaker's foot because each grain is free to rotate relative to its neighbors (Doe and Dott, 1980). Any water applied to the surface of the ancient slip face would have moved quickly from the medium sand at the surface to become concentrated in the finer-textured pin stripes (Stephens, 1996), making them especially cohesive. Loading of a moistened sediment surface would have broken (brecciated) the pin

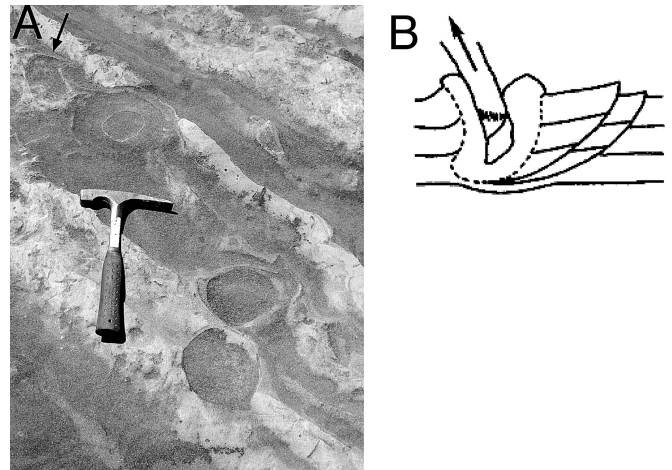


FIGURE 6—Circular structures interpreted as microfaults generated beneath trackmaker's foot by propulsive, rotational movement. Hammer for scale; ~28 cm in length. (A) Three circular structures and a *Gallator* footprint (arrow) with two discernable digits; grainflows in Navajo Sandstone near base of slip face. (B) Interpretive diagram showing rotation of an animal's foot generating microfaults (modified from fig. 21 of Fornos et al., 2002).

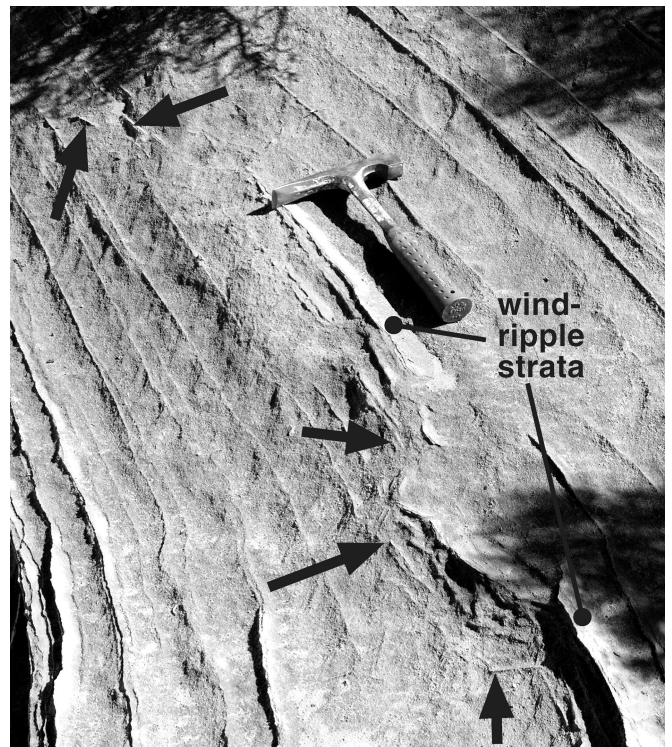


FIGURE 7—*Otozoum* tracks with brecciated pin stripes; arrows mark breccia blocks. In this study, this is the only clear example of tracks made in a moist-sand substrate. Note that the animal stepped on a wedge of wind-ripple strata near the base of the slip face, therefore, the track was not made during the dry season when the dominant winds generated the grainflows (see Fig. 3D). Hammer for scale; ~28 cm in length.

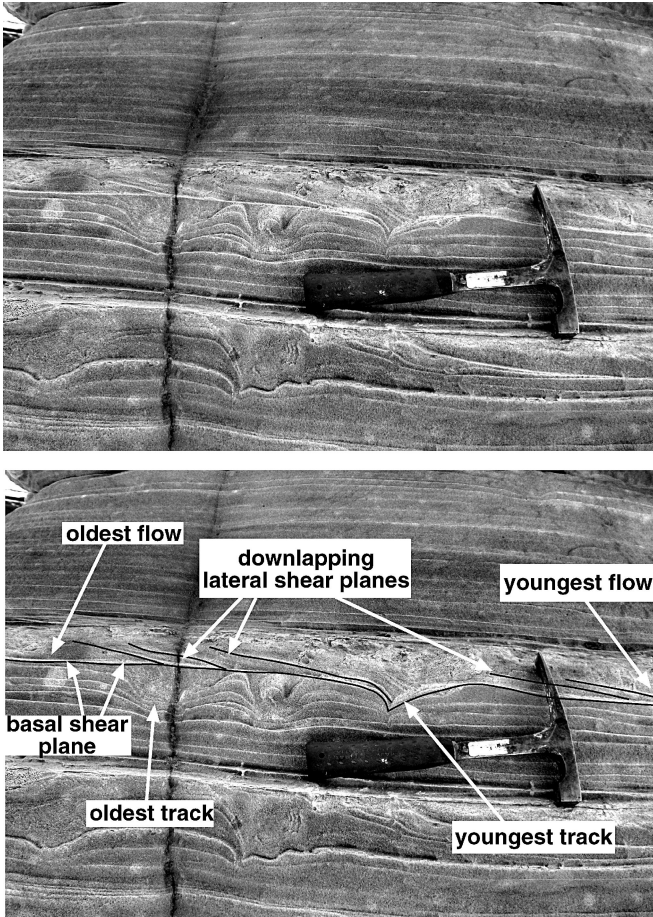


FIGURE 8—Stratigraphic relationships between tracks and surrounding strata, interpreted as a trackway of a theropod dinosaur that moved across the slope, triggering and trampling avalanches. View is down the dip of the cross-strata. The downlap of pin stripes onto a basal shear shows that grainflows young from left to right, along the strike of the ancient slip face. Stratal relationships also show that the two tracks on left are older than the track on right. Hammer for scale; ~28 cm in length.

stripes. Instead, loading produced smooth folds involving both coarse and fine laminations, indicating a cohesionless substrate. The only tracks showing brecciation of pin-striped grainflows (Fig. 7) are directly below a thin, ruptured wedge of wind-ripple deposits. According to the paleoclimatic interpretation of the annual depositional cycles (Loope et al., 2004b), the wind-ripple wedges accumulated during the nine-month period when the dominant cross-equatorial winds did not drive the dunes toward the southeast (Fig. 3E). Because they deform the wind-ripple wedge, and because they record moist sand conditions, these brecciated tracks are interpreted as wet-season traces.

Truncated Marginal Upfolds: Grainflows on the lee slopes of dunes are erosive near their point of origin, but become depositional down-dip (Hunter, 1977). Although most grainflows are initiated on the upper- or middle-lee face, the erosion surfaces truncating the Navajo tracks indicate that the thin grainflows originated near where the tracks were emplaced, and, in many cases, this was very near the base of the slip face. Animals on slip faces pro-



FIGURE 9—Trackway of booted human across slip face underlain by moist sand, Coral Pink Sand Dunes, Utah. Note the breccia blocks and open shaft at each track.

duce grainflows in two places: (1) immediately downslope from their footfalls; and (2) above their footfalls, as a small scarp rapidly retreats upslope (Fig. 10B). The erosive surfaces that truncate the marginal upfolds of many tracks probably were generated by the grainflows sourced by scarps retreating upslope from the track maker.

Animal activity commonly generates thin avalanches on the dune slip face that obliterate all surface expression of tracks. Tracks will be preserved, however, if the animals' feet disturb laminae beneath the dune slope to a depth greater than the scour depth of the small avalanches (Fig. 10D).

Firm and Soft Substrates: The 10-cm amplitude of the folds (Fig. 2B) shows that a soft dune slope was deeply penetrated by the track makers' feet. The deposits of wind ripples and of grainflows provided remarkably distinct substrates to animals of the Navajo sand sea (Fig. 4). Observed track depths are fully consistent with Bagnold's (1954) well-known observations on North African dunes. He showed that tightly packed deposits of wind ripples provide firm support for wheeled vehicles, but the same vehicles sink deeply when the dune surface is underlain by highly porous grainflows (Bagnold, 1954, p. 236–237).

Circular to Oval Structures: From Pleistocene eolianites preserved on the island of Mallorca, Fornos et al. (2002) interpreted circular structures identical to those preserved in the Navajo (Fig. 6) as microfault-bounded masses of sand that were generated within the substrate by rotational movement of a trackmaker's foot. They argue that similar structures in other strata have been misinterpreted as small avalanches or "sand crescents" (Fornos et al., 2002, p. 287). It seems unlikely that this structure can form in dry, cohesionless sand. The observed concentration of these relatively rare structures within the area

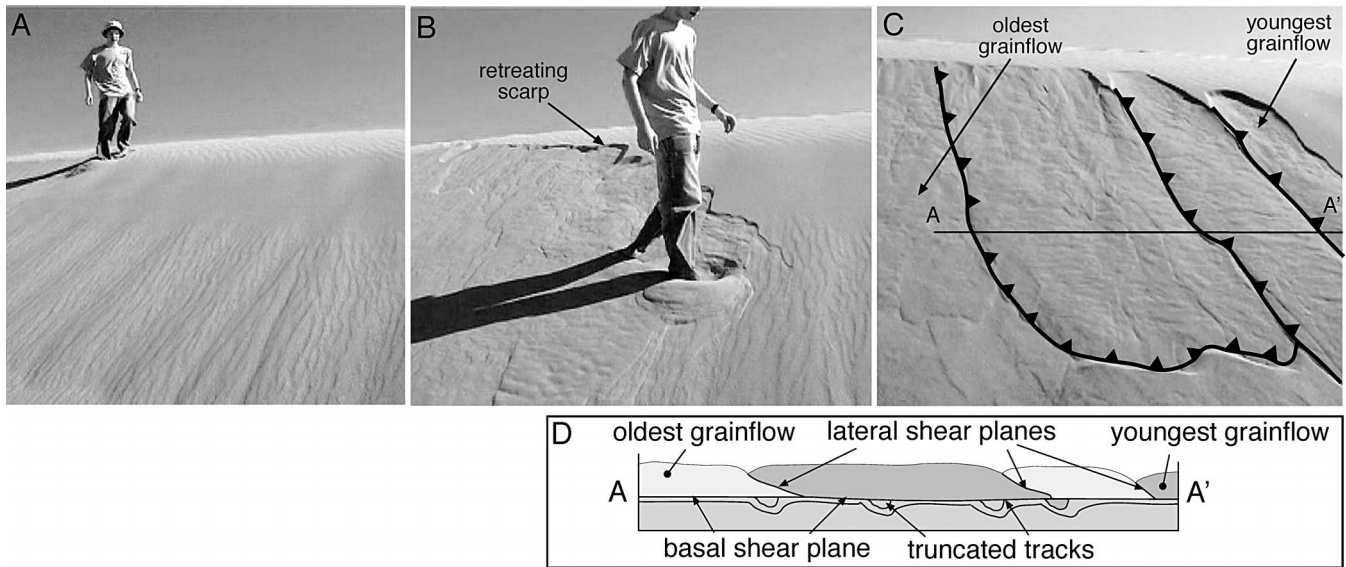


FIGURE 10—Time sequence (A-B-C) of animal-triggered avalanching at Killpecker Dunes, Wyoming. Note that grainflows are generated both below and above each footfall as scarps retreat upslope. No surface expression of tracks is visible after avalanching. (D) interpretive diagram, showing that lower portions of tracks can be preserved below the basal shear plane of the grainflows. Diagram also shows how the strike-parallel downlap of grainflows preserves the sequence of animal-triggered avalanching.

near the toe of the slip face suggests that they may not have originated while grainflows were actively accumulating (i.e., like the tracks shown in Fig. 7, they may not have been made during the dry season; see Paleoclimate discussion, below).

Diachroneity of Adjacent Tracks and the Triggering of Avalanches: When large (>100 g) animals step on the dry, angle-of-repose slopes of active dunes, they cause avalanching (McKee, 1947; Fig. 10). Although the arguments presented here that are based on track morphology are consistent with the principles of soil mechanics, the most definitive evidence for a dry-sand origin for the Navajo tracks comes from microstratigraphy. No two tracks in a trackway are of precisely the same age. Close inspection of the relationships between tracks and grainflows indicates a dynamic interaction: as animals walked along the slip face, they triggered grainflows, and then stepped on the new deposits. In Figure 8, the lateral margins of a series of grainflows downlap onto a basal shear. The oldest grainflow is shown on the left and progressively younger ones to the right. The two tracks on the left lie beneath the shear. The track on the right folds the shear plane, indicating that it is the youngest track of the three. Similarly, in Figure 2B, the two tracks on the left are older than the one on the right, which deforms the grainflow that truncated and buried the others. These stratal relationships require an intimate spatial and temporal relationship between avalanching and animal movement, and the idea that the animals triggered the avalanches is by far the simplest explanation. On slip faces underlain by moist sand, animals can produce short grainflows with abundant breccia blocks (Fig. 9), but the thin, tabular grainflows shown here require that the tracked surface was dry when it was disturbed.

In his experiments with animals in a lab setting, McKee (1947) found that only the animals walking on dry sand generated clear tracks resembling those in the rock record

(contrary to the views of McKee, 1991). However, when he enticed a 132-g chuckwalla lizard (*Sauromalus*) to climb up and down dry-, moist-, and wet-sand slopes of 12°, 28°, and 33°, the tracks made on the dry, angle-of-repose slopes either were destroyed or partially destroyed by avalanching, as were the tracks going down the 28° slope. Although avalanching destroyed the surface expression of the chuckwalla tracks, it is unclear whether the full thickness of the tracks was destroyed. Future experiments should give greater emphasis to the depth of tracks in cross-section and their position relative to the shear plane of the overlying grainflow. Many of the tracks described here are in erosional contact with overlying grainflows, but, typically, only the uppermost portion of each track was truncated by the erosive event.

Thin Grainflows: The tracks at Coyote Buttes are preserved in grainflows that are much thinner than most other grainflows in the Navajo Sandstone. Grainflows in crossbed sets that lack tracks have a mean thickness nearly three times that of grainflows within sets with abundant tracks (Table 1). The evidence for frequent animal activity of the slip face helps to explain the unusually thin grainflows associated with the tracks. Grainflows are mass movements of sediment that was temporarily stored on the lee face after transport over the stoss slope and dune crest by saltation and grainfall. Thick grainflows require that a large volume of sand was stored before slope failure. Frequent animal activity would have precluded storage of a large sediment volume, and would have generated numerous thin, low-volume grainflows.

The very thick grainflows present in some Navajo outcrops (Fig. 3A) are difficult to explain sedimentologically. According to modeling and process studies on small eolian dunes (McDonald and Anderson, 1995; Nickling et al., 2002), at least 85% of the sediment transported over the dune slope is deposited on the uppermost 2 m of the lee slope. Oversteepening and failure of depositional bumps

built in that restricted zone cannot account for the large volume of the grainflows seen in ancient strata (McDonald and Anderson, 1995). During flume studies, Allen (1968, 1970) observed that under low-flow conditions, small-volume avalanches sourced from the crest area of subaqueous bedforms seldom reach the base of the slip face. He noted that the flows thinned as they moved downslope, and that friction eventually stopped them as they reached the mid-slope. Build-ups of such flows are gravitationally unstable; they finally are flushed to the base of slope in a single event. Similar processes may operate on large eolian dunes, but they have not yet been observed. Unfortunately, this hypothesis for the origin of thick grainflows is difficult to test using the stratigraphic record because only the lowest parts of ancient slip faces are preserved. In any case, thin grainflows on long dune slopes are easier to explain. They form on slip faces where physical or biological processes frequently trigger avalanches.

Paleoclimate: All of the Navajo tracks discussed here lie within southeast-dipping, grainflow cross-strata deposited in an inland desert—perhaps the largest sand sea in Earth's history. If preservation of the Navajo tracks required a moist substrate, a high percentage of (dry-sand) depositional events necessarily were followed closely by rain, fog, or dew-forming episodes. Such preservation (and such conditions) would be completely inconsistent with recent interpretations of the strong seasonal changes in wind and rain during Navajo deposition (Loope et al., 2004b). The winds that pushed the large Navajo dunes more than 1 meter each season were tropical westerlies that were strong and persistent, but blew only during the winter (Loope et al., 2004b). Although the Navajo sand sea was positioned considerably farther south than the Sahara, its winter climate probably was similar to that near the Sahara's southern edge, where rainfall events are very, very rare and dew deposition is impossible. Before reaching the study site, the winter winds would have traversed not only the full N–S extent of the Navajo sand sea, but, as trade winds, also would have crossed the barren interior farther north where they picked up sand derived from streams flowing west from the Appalachian Mountains (Rahl et al., 2002; Dickinson and Gehrels, 2003, fig. 1B). Without an up-flow source of moisture or a mechanism for lift, these strong, persistent winds would have brought little or no rain to the sand sea. As at the Sahara's southern margin, the life-giving rains of the ancient sand sea instead came in summer with the arrival of the intertropical convergence zone. During long-lived pluvial episodes, wet-season rains made year-round animal activity possible (Loope and Rowe, 2003), but the bulk of the cross-strata (and all of the easily deformed grainflows—see above) were deposited during the dry season. After dry-season deposition was complete, wind-ripple strata were banked against the slip face. The brecciated *Otozoum* tracks (Fig. 7) apparently were made during the wet season. On the portion of the slip face not covered by the wedge of wind-ripple strata, summer rains would have wetted the previous winter's avalanche slope. In summer, these dune surfaces would have been accessible to animals for the brief time intervals between wetting and drying of the sand, but no tracks with distinct moist-sand features have been recognized on them.

DISCUSSION

Trace fossils vary widely in their preservation potential; those that are emplaced deep in the sediment and in low-energy settings are less likely to be obscured by other traces or to be eroded (Bromley, 1996). Although previous authors (McKee, 1947; McKee, 1991) have stressed track destruction by avalanching and the ease of reworking dry sand, an eolian grainflow is, in several ways, an especially favorable medium for preserving tracks. Of the three main types of stratification that compose sand dunes (Hunter, 1977), the grainflow is the one least likely to be subsequently eroded. These strata accumulate in the zone of flow separation; if the wind regime is dominated by a single flow direction, and the bedforms are climbing over one another, these strata (especially those portions deposited near the base of the slip face) are well protected from erosive events. An argument based on dry-sand erodibility could be used to deny that any eolian strata have been preserved in the rock record. Like all strata preserved in the rock record, ancient eolian cross-strata necessarily accumulated at sites where more sediment was deposited than was eroded. The high percentage of Navajo Sandstone that is composed of grainflows is a strong testimony to the high preservation potential of these strata. Because grainflows have high porosity, tracks made in them are deep. Concurrent avalanching erases only the uppermost portions of deep tracks; the remainders of the tracks are buried immediately and preserved.

Knowledge of the diversity and paleoecology of Early Jurassic terrestrial vertebrates in the western USA is based almost entirely on tracks. Most of the tracks (*Grallator* and *Brasilichnium*) observed at Coyote Buttes were made by small to medium-sized animals, but the tracks of much larger animals (*Otozoum*) also are present, and are known from other Navajo localities (Gilland, 1979; Lockley et al., 1998, fig. 9). Rainforth (2001) reported that although Navajo cross-strata contain only small traces (e.g., *Grallator*, *Brasilichnium*, *Batrachopus*), tracks of larger animals (e.g., *Anchisauripus*, *Eubrontes*, *Otozoum*) are recorded in flat-bedded interdune/playa deposits. Using the argument based on McKee's (1947) study, she interpreted the absence of large tracks from cross-strata to be related to non-preservation (loss by avalanching), not to the habitat preferences of the animals. The *Otozoum* tracks (Fig. 7) support her view that large animals did walk on the lee faces of Navajo dunes, but the great depth of deformation shown in these tracks makes them unlikely to be erased by avalanching. Medium-size, dry-sand tracks that display minor truncation by avalanching are abundant at Coyote Buttes; it seems very unlikely that large animals made abundant tracks that were erased completely by animal-induced avalanching.

Eolian grainflows are difficult to distinguish from their subaqueous counterparts, but due to the distinctive deposits made by climbing wind ripples (Hunter, 1977; Kocurek and Dott, 1981), eolian sandstones have been identified confidently in both outcrop and core since 1977. In addition, Doe and Dott (1980) pointed out that brecciation of unlithified sand (Fig. 7) is evidence for an air-water interface within the sand, and therefore is a unique feature of moist, subaerial deposits. The present study has not yielded any new criteria for differentiating eolian and subaque-

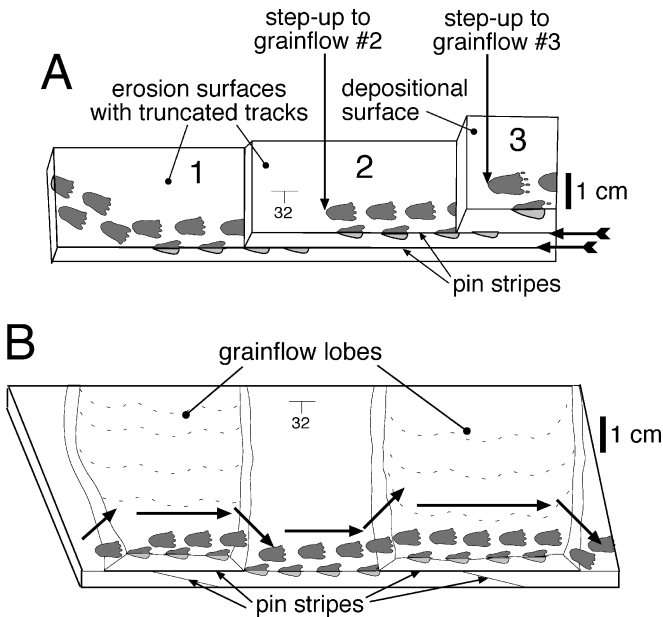


FIGURE 11—Sketches of how the trackways of small animals could become segmented by avalanching. If the strata were split along any of the bedding planes, the revealed trackways would appear to start and stop abruptly (see Brand and Tang, 1991). (A) Animal is present on slope when avalanching takes place. (B) Animal encounters grainflow lobes that were deposited previously. Note that the larger, deeper tracks described in this paper disrupt numerous grainflows, and do not show this style of preservation.

ous cross-strata, but, by demonstrating the different depths of track penetration into wind-ripple and grainflow deposits (Fig. 4), it has further corroborated Hunter’s (1977) interpretations.

Like the Navajo Sandstone, the Permian Coconino Sandstone contains numerous tracks and trackways. As is the case for the Navajo (Fig. 3A, C, D), a large portion of the Coconino Sandstone is composed of climbing translaminar stratification produced by migrating wind ripples (Loope, 1992). From experimental and field studies, however, Brand (1979) and Brand and Tang (1991) concluded that the traces (and presumably the ancient dunes) of the Coconino originated in a subaqueous environment. One of the lines of evidence used by Brand and Tang (1991) for a subaqueous origin for the Coconino Sandstone was that trackways on the smooth surfaces of individual cross-strata commonly stop or start abruptly. This was interpreted as the result of the animal alternately walking on and swimming over the substrate. Such abruptly starting and stopping trackways also could be explained if bedding planes separate along pin stripes that formed at the base of eolian grainflows that took place during the (small) animal’s traverse of the slip face (Fig. 11A) or if the animal moved up, down, and between distinct grainflow lobes, each of which was floored by a different pin stripe (Fig. 11B). In both cases, if the tracks were shallow compared to the thickness of the grainflows, the animal would leave a succession of partial trackways on adjacent, smooth bedding planes.

This study has highlighted the dynamic interplay between biological and physical processes on dune lee slopes. The exquisite outcrops at Coyote Buttes provide outstand-

ing opportunities to generate hypotheses for the origin of sedimentary structures, but full testing of these hypotheses will require laboratory experiments that fully integrate both types of processes in real time. Delicate pin stripes and porous grainflows are key elements in the Navajo’s high-quality record of biological events. For large dunes, the textural contrast between pin stripes and the remainder of the grainflow stratum (Fig. 3B) is likely to be greater than in small dunes for two reasons. Because the coarsest grains travel fastest during avalanching, they have a chance to become fully segregated from finer materials on long lee slopes. A likely source of the fine particles that percolate through grainflows to form pin stripes is distal grainfall on the lower lee slope. Because of the greater distance from crest to toe in large dunes, they probably have finer, more distinct pin stripes than small dunes. Generating grainflows with distinct pin stripes in a laboratory setting seems to be a prerequisite for realistic simulations with live animals.

CONCLUSIONS

The tracks from the Navajo Sandstone described here demonstrate that, despite numerous views to the contrary, animal tracks made on the dry slip faces of dunes can be preserved in great numbers and in considerable detail. The structural features of the tracks indicate that nearly all were impressed into cohesionless sand—an interpretation fully consistent with paleoclimatic interpretations of the prominent annual depositional cycles enclosing the tracks. Stratigraphic relationships indicate that the motion of the animals across the slip face generated small-scale avalanches that were trampled immediately by subsequent animal activity.

Nearly all of the abundant, small tracks at Coyote Buttes were made during the winter dry season (December–January–February), when the dominant, cross-equatorial winds blew out of the northwest. The tracks were made in dry, cohesionless sand that was both emplaced and buried by dry avalanching. The avalanche deposits (grainflows) that contain the tracks are dominantly composed of medium sand, and are delineated by a basal erosion surface overlain by a thin lamina of very fine sand. The track-bearing grainflows are thinner than most Navajo grainflow strata. Frequent animal activity on the slip faces apparently prevented the build-up of sand needed for large-volume grainflows. Like deep-tier traces in the marine realm, the deepest-penetrating animal tracks have the highest preservation potential. On an active dune, the softest, most easily deformed substrate underlies the slip face. Because the slip face lies within the zone of flow separation, tracks made on grainflows are better protected from wind erosion than those made on any other dune surface.

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