Morphology and sediment deformation
of downslope *Brasilichnium* trackways on a dune slipface
in the Nugget Sandstone of northeastern Utah, USA

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ABSTRACT

The presumed synapsid trackway known as *Brasilichnium* is known by numerous trackways from many localities throughout the eolian deposits of the Late Triassic to Early Jurassic erg that covered much of the western United States. These trackways occur primarily on the foreset beds of dunes. The overwhelming majority of the trackways were made by animals traveling up slope. A slab of Nugget Sandstone exhibited in the Department of Geology and Geophysics at the University of Utah preserves at least 17 *Brasilichnium* trackways, 13 going up slope and four going down slope. The downslope tracks have a distinctive morphology consisting of a raised anterior pressure pad ahead of, and a posterior collapse depression behind, a small, poorly preserved impression of the foot. The anterior pressure pad can be explained as a low angle thrust driven forward by the impact of the foot, whereas the posterior depression is a downslope slump as the foot was withdrawn. This interpretation is supported by the observation on an outcrop in Dinosaur National Monument of similar features in a *Brasilichnium* trackway that traverses the slope, and by studies of tracks made by other vertebrates in eolian sands. The enormous preponderance of upslope over downslope trackways in eolian sandstones remains an open question. The distinctiveness of the downslope track morphology and the fact that they are well preserved in the studied material, however, suggests that the answer is something more than coincidence or preservation bias.

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INTRODUCTION

During the Late Triassic through Early Jurassic, the western United States was covered by a vast erg system, with an estimated extent of 2.2 million km^2 and a total dunefield area larger than that of the modern day Sahara (Kocurek and Dott, 1983; Milligan, 2012). The source for the sand was deflating floodplains associated with an Amazon-like transcontinental river originating in the Appalachian Mountains and terminating in western Canada (Dickinson and Gehrels, 2010). Sediments of this erg system are known as the Nugget, Navajo, or Aztec sandstones depending on their geographic location.

Despite a seemingly inhospitable environment, both trace and body fossils indicate that life could be locally diverse and abundant (Chure et al., 2014). Skeletal remains are known from interdunal deposits, but the fossil record in the dunes consists solely of trace fossils. *Brasilichnium*, a track attributed to tritylodonts (Rowland and Mercadante, 2014), is by far the most common vertebrate ichnofossil in dune sediments of the Late Triassic–Early Jurassic erg deposits of the Nugget Sandstone and its equivalents, the Navajo and Aztec sandstones. It is widespread both geographically and stratigraphically (Buss, 1921; Faul and Roberts, 1951; Albers, 1975; Lockley and Hunt, 1995; Rainforth and Lockley, 1996; Rainforth, 1997; Lockley, 2005; Reynolds, 2006a, 2006b; Engelmann et al., 2010; Engelmann and Chure, 2011; Lockley, 2011; Lockley et al., 2011; Chure et al., 2014; Good and Ekdale, 2014; Rowland and Mercadante, 2014; Rowland et al., 2014) and is the namesake of the *Brasilichnium* dune ichnofacies (Lockley et al., 1994, 2011; Rainforth and Lockley, 1996; Hunt and Lucas, 2007; Lockley, 2007). In spite of the abundance of *Brasilichnium*, skeletal remains of the putative trackmaker, tritylodonts, are exceedingly rare in these erg deposits (Winkler et al., 1991).

Although numerous *Brasilichnium* trackways are known, nearly all record the trackmaker moving up slope on the lee side of a dune. This is true regardless of the number of trackways at a site, even when individual *Brasilichnium* tracks number in the hundreds (Lockley, 1991, figure 10.2; Engelmann et al., 2010; Engelmann and Chure, 2011; Rowland and Mercadante, 2014). The reasons for this apparent lack of downslope trackways are uncertain; however, a slab at the University of Utah (UUIC 1873) clearly records multiple *Brasilichnium* trackways traveling down slope that exhibit distinctive and characteristic sediment deformation. Here we describe the slab, the associated deformation, and a trackway from Dinosaur National Monument showing similar features.

INSTITUTIONAL ABBREVIATIONS

BYU, Brigham Young University, Provo, Utah, USA; DINO, Dinosaur National Monument acronym for museum specimens; UUIC, Ichnology Collection, Department of Geology and Geophysics, University of Utah, Salt Lake City, USA.

DESCRIPTION

UUIC 1873

UUIC 1873 is a slab of reddish sandstone with maximum measurements of 121 cm x 141 cm and bearing abundant track impressions. It is currently on exhibit on the second floor of the Frederick Albert Sutton Building, home of the Department of Geology and Geophysics at the University of Utah in Salt Lake City, Utah (Figure 1, Appendix 1).

The provenance of the slab is somewhat problematic. It was being stored in a basement room of the old Utah Museum of Natural History at the University of Utah campus when A.A. Ekdale arrived as a faculty member in 1974. How long it had been there is unknown. There were no data associated with it, and it was not accessioned and catalogued in the UUIC until sometime after 1974 (Ekdale personal commun., 2015). The grain size, color, and bedding are consistent with other footprint-bearing slabs from the Nugget Sandstone. The Nugget is a source of building stone that has been widely used in Salt Lake City and on the University of Utah campus, and there have been numerous nearby Nugget stone quarries in the Wasatch Mountains (Red Butte Canyon, Parley's Canyon, and around the city of Heber). Many of these quarries produced vertebrate and invertebrate ichnofossils (Albers, 1975; Stokes, 1978; Chure et al., 2014)

The UUIC contains about two dozen specimens of the Nugget Sandstone bearing vertebrate and invertebrate ichnofossils from the American Stone Quarry near Heber, UT, that were collected as part of a 1975 Master's thesis (Albers, 1975; Chure et al., 2014). Although UUIC 1873 was not specifically mentioned by Albers, her specimens (both the rock and the traces) compare well with UUIC 1873. We have visited exposures of the Nugget near the American Stone Quarry and have observed a strong similarity between the lithology at that quarry and UUIC 1873. We are confident that UUIC 1873 is from the Nugget Sandstone and
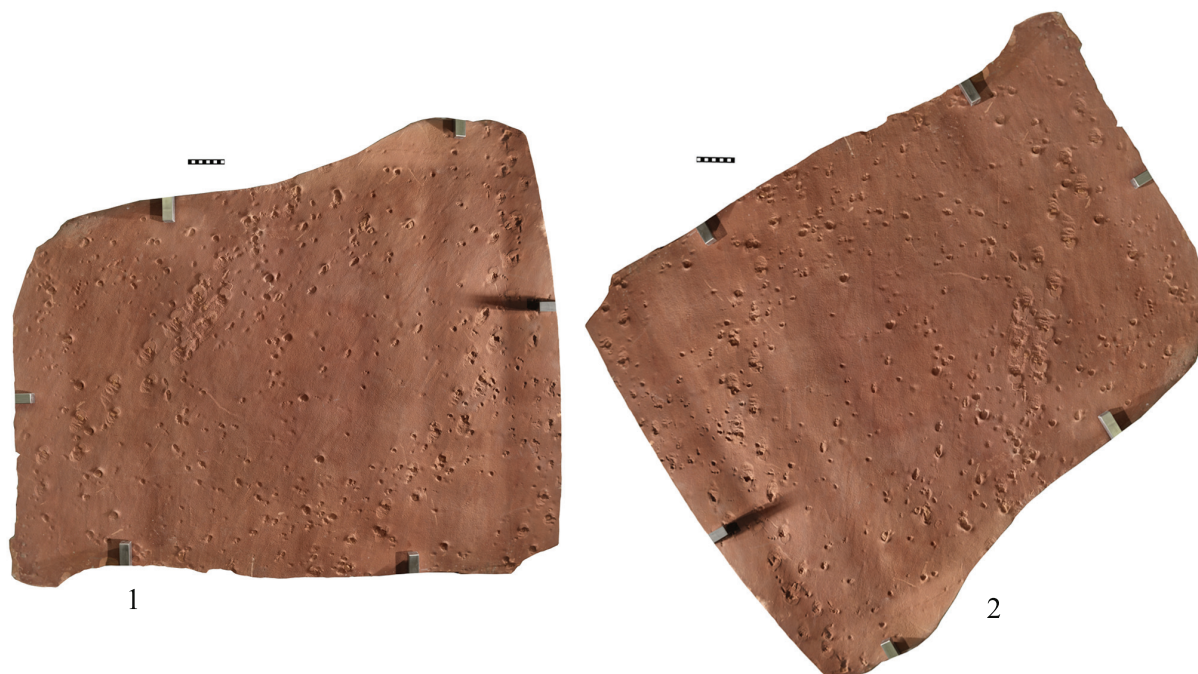
FIGURE 1. UUIC 1873, slab of Nugget Sandstone bearing multiple trackways. **1,** the slab as it is exhibited in the halls of the Frederick Albert Sutton Building of the University of Utah in Salt Lake City. **2,** image of the slab rotated 150º clockwise to show the trackways in their original orientation. Scale bars equal 10 cm.

likely came from one of the quarries in the Heber area.

UUIC 1873 was deposited on the lee slope of a sand dune. Push-up rims along the posterior margin on many of the tracks on the slab support the interpretation that the sand layers maintained a primary slope at the time the tracks were made. UUIC 1873 also bears low amplitude wind ripples across its surface. The crests of these ripples were oriented parallel to dip direction of the original lee surface. Using the push-up rims and wind ripples, we can establish the original orientation of sediments on the slope which is different from the way the slab is mounted for exhibit. To place the slab in its depositional orientation it should be rotated about 150º clockwise (Figure 1.2). Throughout this paper we will describe and refer to the slab and tracks in terms of their original depositional orientation.

Nearly 400 tracks are preserved on the UUIC 1873 (Figure 2, Appendix 2); all preserved trackways terminate abruptly at the slab's margins. This is the densest occurrence of vertebrate tracks from Nugget dune foreset beds that we are aware of, being approached only by a site near Dinosaur National Monument (Engelmann and Chure, 2011).

Only one trackway is not of vertebrate origin. On the left side of the slab there is a partial trackway consisting of two parallel rows of groups of three or four closely spaced impressions (Figures 2, 3). We refer this trackway to the ichnogenus *Paleohelcura*, a trace made by both scorpions and spiders (Sadler, 1993; Braddy, 1995; Davis et al., 2007). *Paleohelcura* is a common arthropod trace fossil on dune foreset beds in Permian through Early Jurassic erg deposits, including the Nugget (Lockley et al., 1995; Chure et al., 2014).

All other traces on UUIC 1873 are of vertebrate origin and referable to *Brasilichnium*, a common trackway on dune foreset beds in the Nugget, its equivalents, and other Mesozoic eolianites (Reynolds, 2006a, 2006b; Lockley, 2011; Chure et al., 2014; Rowland and Mercadante, 2014) that is attributed to therapsids. *Brasilichnium* is a quadrupedal trackway lacking a tail drag with manus impressions smaller than pes impressions; both manus and pes prints are wider than long, with rounded heel margins (Haubold, 1971; Leonardi, 1981; Fernandes and Carvahlo, 2008; Lockley, 2011). In UUIC 1873 pes prints have three, or sometimes four, short and stubby digit impressions. This difference in digit count reflects the sub-
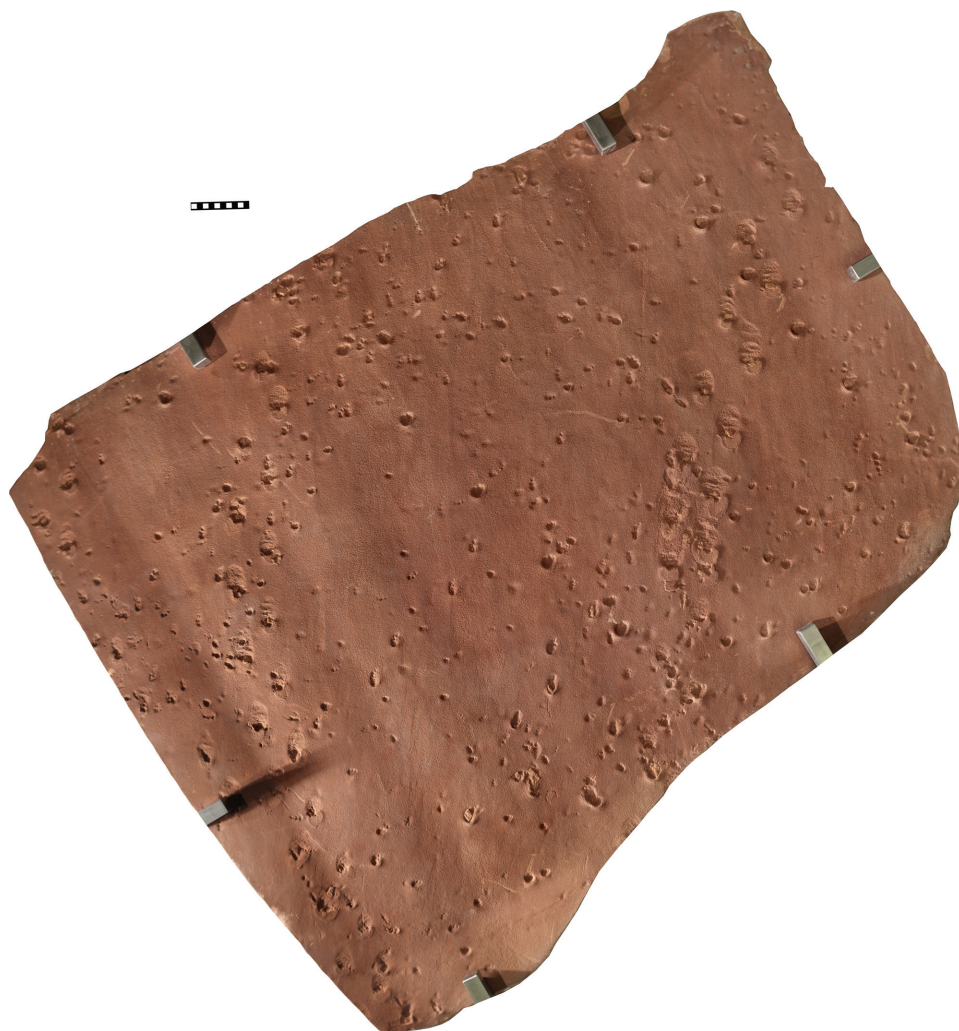
FIGURE 2. High resolution image of UUIC 1873. Scale bar equals 10 cm.

optimal nature of vertebrate tracks found in eolian deposits (Haubold et al., 1995; Morales and Haubold, 1995). Manus impressions are rare on UUIC 1873, but that is a common absence in many occurrences of *Brasilichnium* and is attributable to factors such as: 1) the small size of the manus and its shallower impressions; 2) that most trackways are probably undertracks with less potential to show the shallower prints in a trackway; 3) overprinting of manus tracks by the pes; and 4) differences in gait (Leonardi, 1981; Lockley and Hunt, 1995, figure 4.23; Lockley, 2011; Chure et al., 2014; Rowland and Mercadante, 2014).

A number of *Brasilichnium* tracks on UUIC 1873 consist solely of small, circular toe impressions of the pes, sometimes in a slightly arched arrangement. These are deep undertracks where only the toe impressions are present, some still filled with matrix. Individual *Brasilichnium* track sizes on the slab range from a pes width of 7 mm to 32 mm. The former is among the smallest therapsid/mammaloid tracks reported from the Jurassic (Lockley et al., 2011).

At least 17 trackways can be identified on UUIC 1873, 13 of which are going up slope (Figures 2, 3). In addition to these trackways, there are numerous other tracks in isolation, which are probably deeper undertracks from a stratigraphically higher level above the preserved surface of the slab. Four trackways are unusual in being made by therapsids traveling down slope and show sediment deformation distinctly different than that seen in upslope trackways.

FIGURE 3. Map of tracks and trackways on UUIC 1873. Scale bar equals 10 cm.

The entire UUIC 1873 slab is represented by a Gigapan image that is a composite of 80 close-up photographs. This Gigapan image formed the basis for images of the slab presented in Figures 1 and 2. These images show regularly spaced bands of tonal variation across the surface of the slab, which are artifacts of the process of compiling many images with slight differences in exposure across the subject. See Appendix 1 for information about a larger version of this image.

Transverse Trackway, Dinosaur National Monument Locality 490

Dinosaur National Monument paleontological locality 490 (Figure 4) is located in the Nugget Sandstone in the Utah portion of Dinosaur National Monument (site details are in the locality files at Dinosaur National Monument). It preserves multiple vertebrate (*Brasilichnum*) and invertebrate (*Octopodichnus*, *Paleohelcura*) trackways (Figures 5 and 6, Appendices 3 and 4). The track-bearing bedding surface is about 4 m^2. The tracks are in dune foreset beds bearing faint wind ripples oriented parallel to dip direction of the original lee surface. Nugget outcrops are discontinuous in the area of locality 490, so the site's stratigraphic level is somewhat uncertain; however, the locality is from the middle 50% of the Nugget, the part of the section dominated by dune deposits.

Most of the trackways are heading up slope, showing push-up rims along their posterior margins. An exception is a single trackway, 2.7 m in

FIGURE 4. Distant and near views of locality DNM 490. **1,** site as approached from the southeast. Arrow points to track bearing surface. **2,** the track surface of 490 is the large bedding plane surface on the erosional remnant of Nugget Sandstone.

length, which traverses the surface at a high angle to the original dip direction. This transverse trackway (Figures 5-10, Appendices 3-5) shows a number of peculiar features that complement our observations on the downslope trackways on UUIC 1873. Our description, observations, and images are based on the outcrop and original fossils. The nature of the outcrop, however, is such that collecting specimens is not possible. In lieu of collecting, we have molded the entire length of the transverse trackway, and a cast (DINO 40699) has been deposited in the monument's museum collection.

ANALYSIS OF DOWNSLOPE TRACKWAYS

Track Morphology and Dynamics of Track Formation

Two relatively long trackways on UUIC 1873 and two shorter ones show a distinctive morphology compared to the more abundant tracks made by animals traveling up slope. We interpret these trackways as the traces left by animals travelling down slope.

Individual tracks made by animals travelling up slope often show toe or claw impressions more or less distinctly preserved on the upslope margin

FIGURE 5. Composite photograph of the track-bearing surface of DNM 490. The crests of wind ripples are evident, especially near the center of the image, and provide a good indication of the primary dip direction of the slope of the dune. Scale bars equal 10 cm. Center scale bar distorted by photo stitching process.
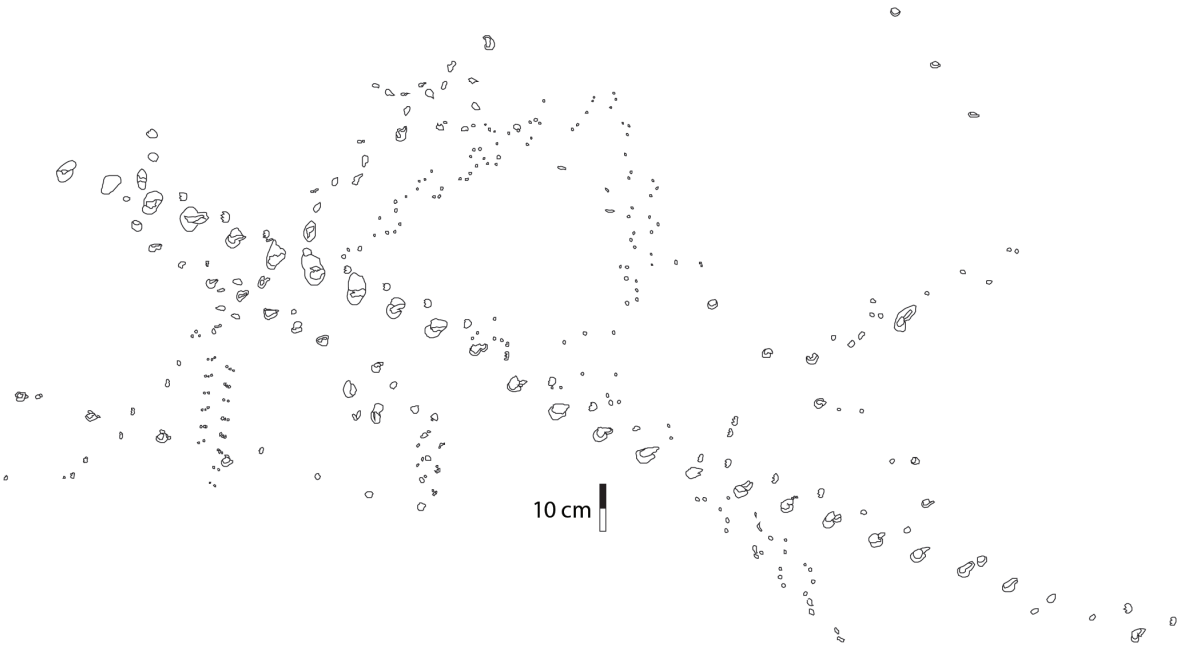

10 cm

FIGURE 6. Map of 490, based on composite photo in Figure 5. Scale bar equals 10 cm in 5 cm increments.
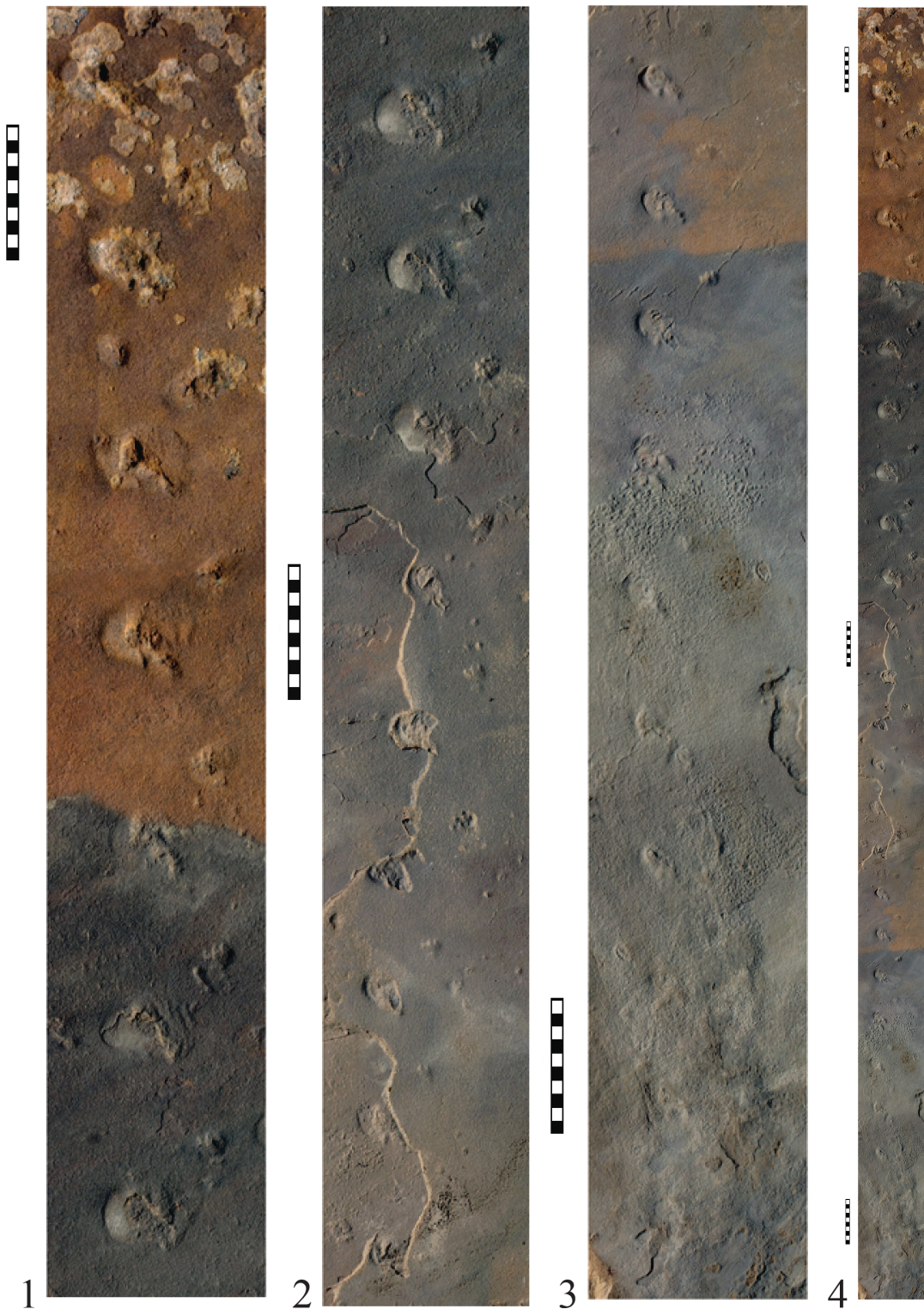
FIGURE 7. Composite image of the long transverse trackway at DNM 490 presented in 3 parts and the entire trackway. In each case, the trackway is oriented so that left (west) end is to top of page and upslope is to right of page. **1,** left (west) end of the trackway. **2,** section of the trackway adjacent to and to the right (east) of the section in Figure 7.1. **3,** section of the trackway adjacent to and to the right (east) of the section in Figure 7.2. **4,** the entire composite image of the trackway. Scale bars equal 10 cm.
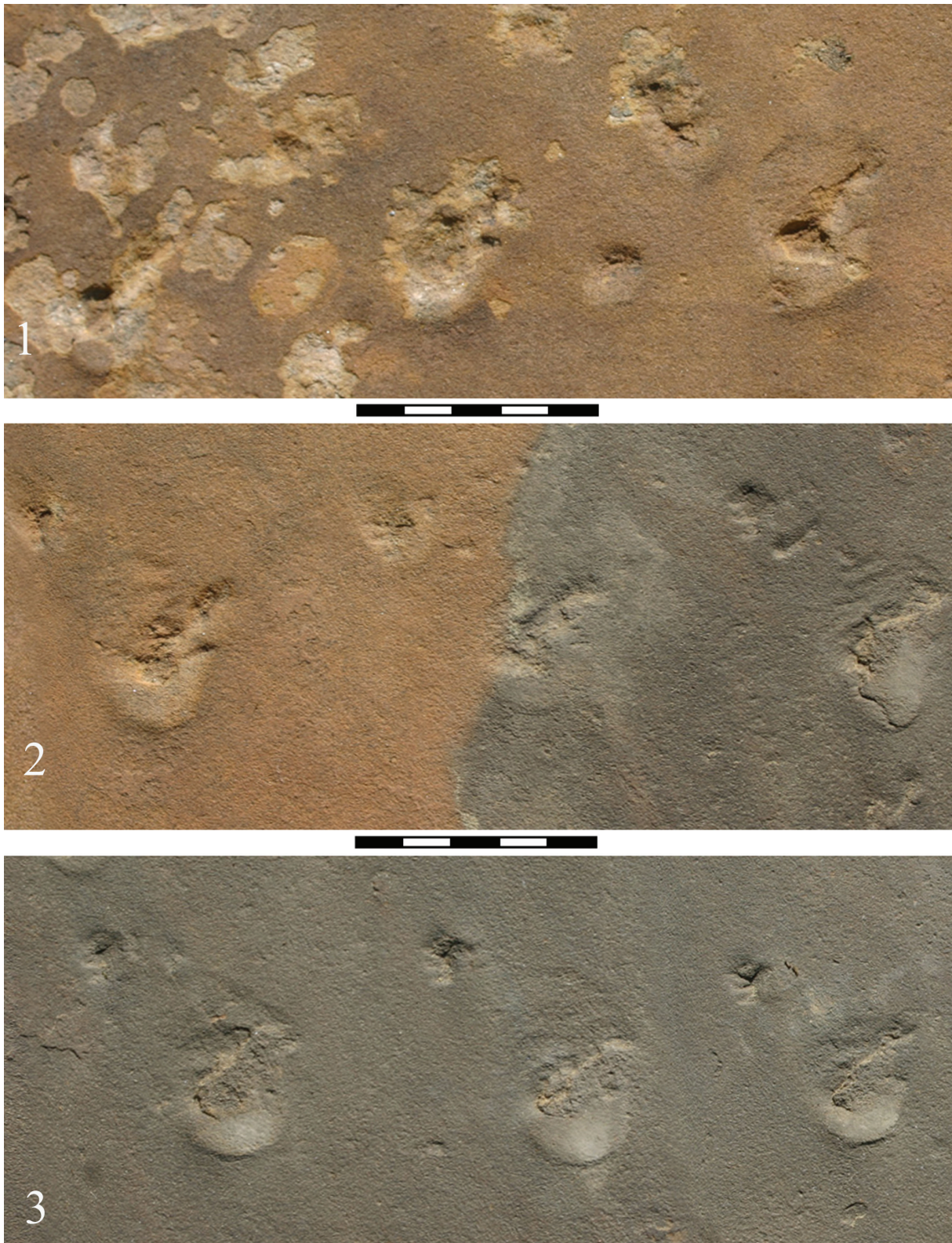
FIGURE 8. Transverse trackway from locality 490, in sections. These are enlargements of sections of the composite photo in Figure 7. Sections do not overlap, but do abut one another. **1,** left side of trackway (cf. with Figure 6) is the top section. **2,** the next section in the trackway, adjacent to and to the right of Figure 8.1. **3,** the next section in the trackway, adjacent to and to the right of Figure 8.2. Scale bars equal 5 cm.

FIGURE 9. Transverse trackway from locality 490, in sections. These are enlargements of sections of the composite photo in Figure 7. Sections do not overlap, but do abut one another. **1,** the next section in the trackway, adjacent to and to the right of Figure 8.3. **2,** the next section in the trackway, adjacent to and to the right of Figure 9.1. **3,** the next section in the trackway, adjacent to and to the right of Figure 9.2. Scale bars equal 5 cm.
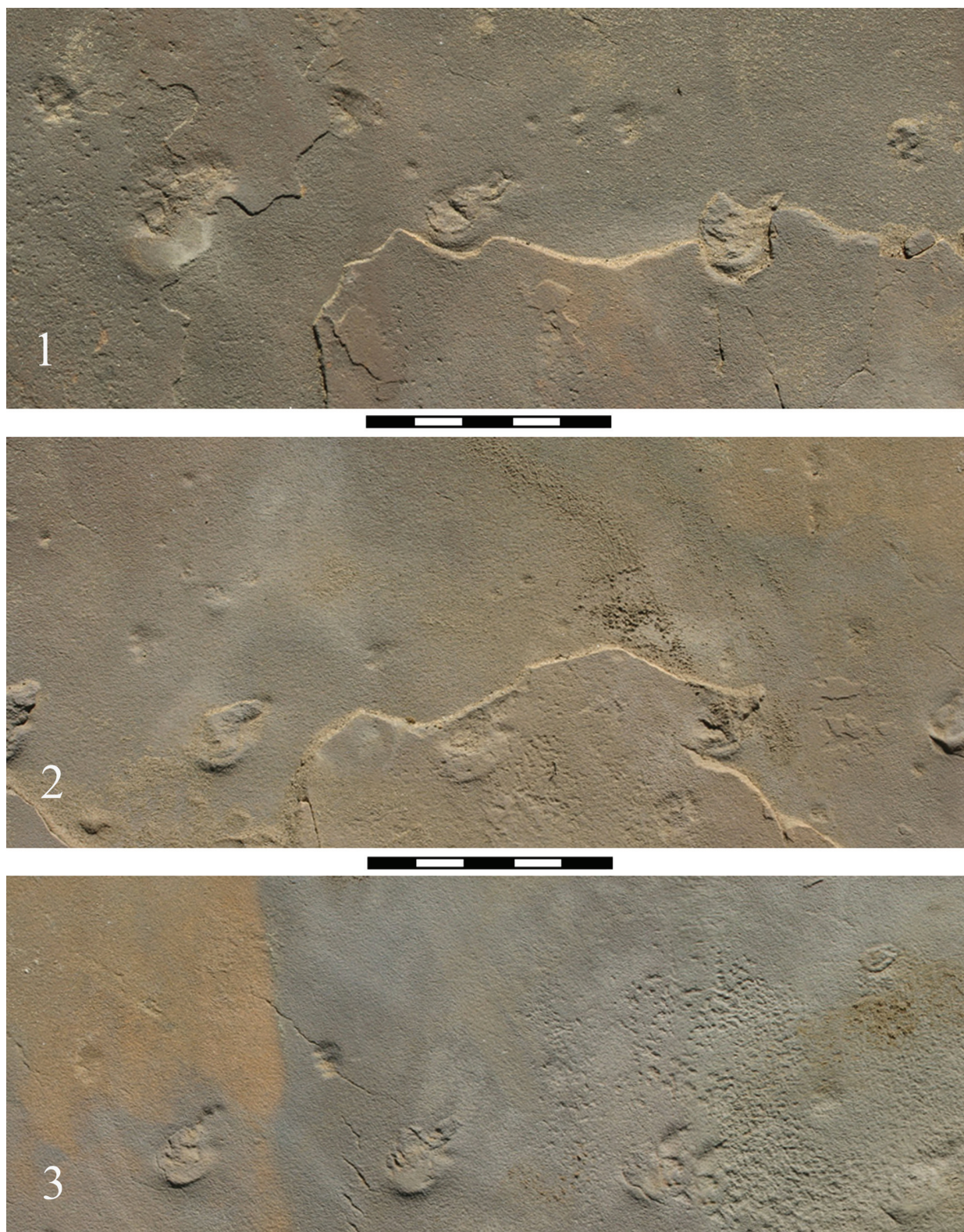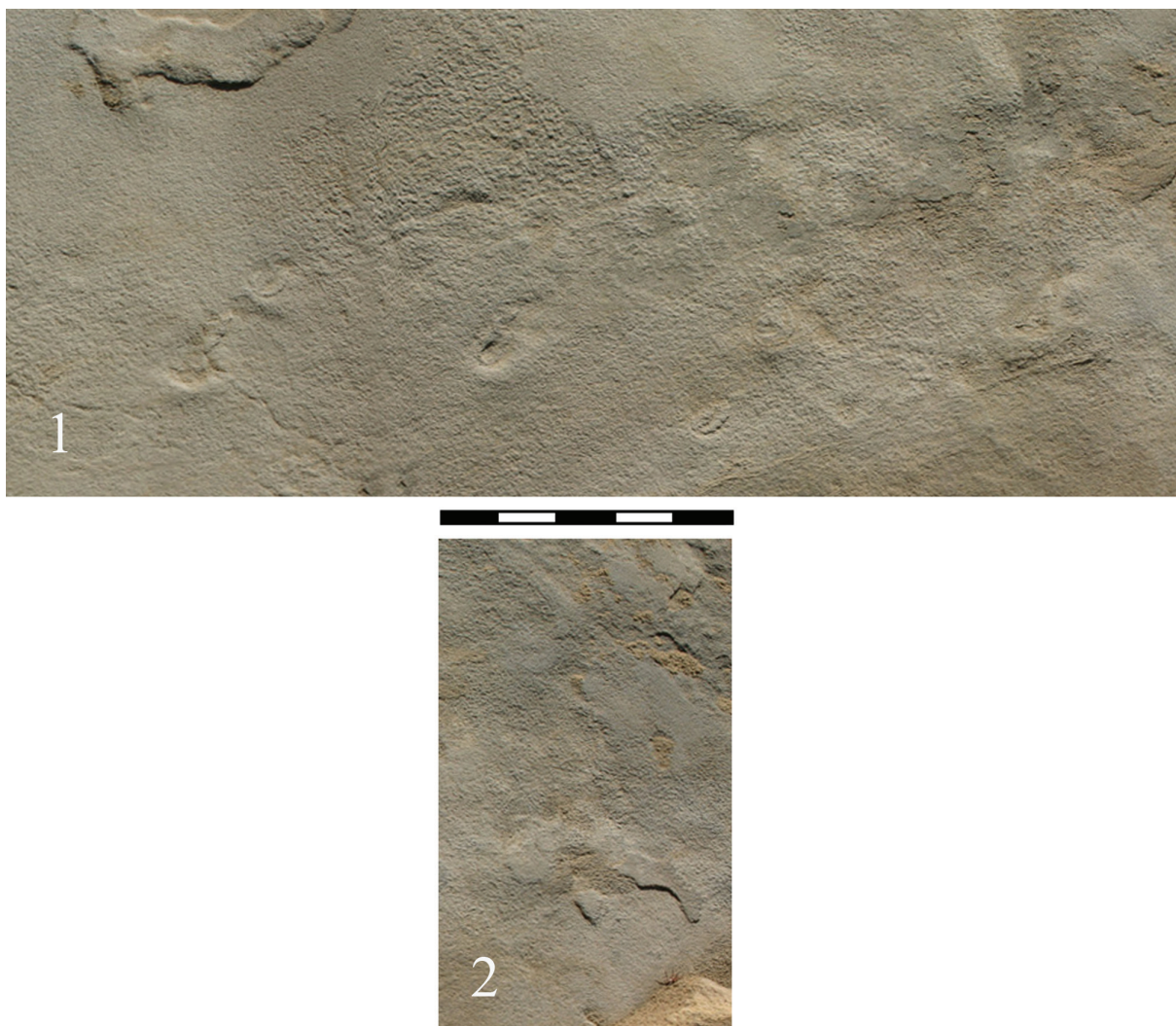
FIGURE 10. Transverse trackway from locality 490, in sections. These are enlargements of sections of the composite photo in Figure 7. Sections do not overlap, but do abut one another. **1,** the next section in the trackway, adjacent to, and to the right of Figure 9.3. **2,** the next section in the trackway, adjacent to and to the right of Figure 10.1. Scale bar equals 5 cm.

of the track. A push-up rim with a short, curved pro-file defines the downslope margin of the track. Such tracks are typical of those found on track surfaces and comprise the majority of tracks on UUIC 1873.

In contrast, the tracks we interpret as having been made during downslope travel rarely preserve any details of foot morphology, and the greater part of the track consists of two distinctive features developed marginal to the actual impression of the foot. The first is a flat-topped raised, arcuate platform we shall refer to as a pressure pad, following the use of Fornos et al. (2002), which extends from the downslope margin of the depression made by the foot. The second is a shal-low depression with an arcuate margin and congruent crescentic ridges across its surface as the upslope part of the track. In UUIC 1873, the features of the tracks are preserved in deep red sandstone; the small depressions left by the removal of the animals' feet in the downslope tracks, however, are filled by lighter colored sand, making them clearly distinguishable. In at least two of these tracks, the impression of digits along the anterior margin of the foot impression is consistent with our interpretation of the orientation of these tracks. This morphology is very consistent through all the tracks in the downslope trackways. Because the greater part of the track is the result of disturbance around the actual impression of the foot, the tracks

FIGURE 11. Detail of a track from the downslope trackway along the right side of UUIC 1873. The location of this figure is indicated by the small rectangle in Figure 3. Note the anterior platform, the posterior, slumped depression, and the small space for the foot filled with lighter colored sand.

vary somewhat in size, especially as measured along the long axis of the track, and in relative proportions of the different elements of the track. One track that is well preserved and clear of interference with other traces (Figure 11) is 65 mm total length along its longest axis, 19 mm along the anterior/downslope pressure pad, 11 mm along the depression left by the foot, and 35 mm along the posterior/upslope depression.

One of the two longer downslope trackways (right side of the slab) exhibits a change of gait and shortening of the stride evident in a section in the middle of the trackway (Figures 2, 3, 12). From the point where the trackway enters the slab surface, there are eight (four left, four right) steps that are equally spaced. Then there is an abrupt shortening of stride length for 2.5 paces (two left, three right) before the trackway continues with lengthening strides. Not only are these five tracks more closely spaced, but it is also among these tracks that impressions of the digits are preserved, and manus tracks can be distinguished by small anterior pressure pads anterior to the pressure pads of the pes (Figure 12).

FIGURE 12. Segment of the trackway along the right side of UUIC 1873 that shows closely spaced tracks. The location of this figure is indicated by the large rectangle in Figure 3. Note also the impressions of digits on two of the tracks and the smaller anterior platforms of the manus tracks immediately anterior to the pes tracks.

We interpret the parts of the downslope tracks described above as the result of a two-step process driven by the animal planting and withdrawing its foot. First, as the foot is planted, a mass of sand is displaced forward and upward along a low-angle slip surface (a thrust fault). The sand is lifted up slightly to create the flat-topped pressure pad, the anterior or downslope part of the track. Second, as the foot is withdrawn, the sand up slope from the foot impression loses its support and collapses as a small scale mass wasting event in which the sand slumps, rotating along curved slip planes. The resulting depression crossed by crescentic ridges that mark the slip surfaces forms the posterior/upslope part of the track. The impression of the foot itself usually does not reveal a clear outline because the anterior margin, which would show the digits is the deepest part of the track and perhaps extends under the edge of the pressure pad of displaced sand, and the posterior part is buried

by the slumping sand. A few tracks, however, do show features that look like the impressions of toes along the anterior margin of the foot impression (Figure 10), corroborating our interpretation of the direction of travel.

Related Studies

The anterior pressure pad is attributed to displacement of a mass of sand forward and slightly upward along a low angle slip surface. This feature is seldom seen and has not been reported in track literature, although there have been reports of similar features produced by related processes. Fornos et al. (2002) described trackways of *Myotragus* preserved in Pleistocene dune sands. The morphology of these tracks is diverse, but none duplicates the features observed on the downslope tracks of UUIC 1873. There are, however, some similar features. Fornos et al. (2002) used the term "pressure pads" for features that share some characteristics with the features we have observed in the downslope *Brasilichnium* tracks and are probably formed by related processes. Therefore, we have followed this usage in referring to them as anterior pressure pads. Like the anterior pressure pads, the pressure pads associated with the *Myotragus* tracks are small masses of sand displaced upward and outward along curving slip surfaces in response to the forceful intrusion of the hoof of the animal into the sand. Unlike the anterior pressure pads, however, the *Myotragus* pressure pads usually occur as several, narrow ridges separated by the curved slip surfaces along which they moved. These pressure pads may form symmetrically around tracks made on a level surface, but are preferentially developed on the downslope side of tracks made on a slope, regardless of the direction of travel. One reason for the typical occurrence of multiple pressure pads appears to be the steeper angle of the slip surfaces that separate them and the resulting tendency of the plane of thrusting to step outward as the foot was forced deeper into the sand. In contrast, the single, anterior pressure pad appears to be the result of displacement along a single, low-angle slip surface driven by a shallower penetration by the foot, which delivered a force directed more tangentially to the surface. These differences could be the result of the great difference in the size of the trackmakers and, perhaps especially, the difference in the shape of the foot and resulting force per unit area delivered to the substrate. In other words, the *Myotragus* feet were driven more deeply and more forcefully into the sand, in both absolute and relative terms.

Theropod dinosaur tracks studied by Graversen et al. (2007) also show features that indicate a process similar to that which produced the anterior pressure pads in UUIC 1873. By identifying slip planes and the masses of sand bounded by them, they were able to recognize disturbed areas which they called thrust ramp systems that extended posterior to the posterior margin of the foot impression itself some considerable distance. These thrust ramp systems represent masses of sand that have been displaced backward (horizontally) and slightly upward along low angle thrust faults in response to a largely horizontally directed force. This is somewhat comparable to the mechanics of the formation of the anterior pressure pad in the UUIC 1873 tracks, but in this case the horizontal thrust results from the propulsive phase of the stride of the theropod walking on a level surface, creating the thrust ramp systems on the posterior margin of the track. Because the theropod tracks studied were undertracks, the surface morphology was not preserved and cannot be compared with the Nugget tracks. But in their reconstruction of the track development, it seems likely that there were at least two disks of displaced sand, making them more like the concentric pressure pads described by Fornos et al. (2002). Graversen et al. (2007) interpreted the progressive increase in propulsive force as the cause of development of successive thrust faults. This may be an important difference from the sudden application of force in the impact of the downhill footfall of the Nugget trackmaker.

The posterior/upslope depressions seen in the downslope tracks of UUIC 1873 interpreted as a small scale slumps have not been previously reported. The crescentic ridges separated by parallel troughs descend stepwise from the arcuate posterior margin. It has all the characteristics of a small-scale landslide that has developed by sequential slumping. The ridges are small, rotated sand bodies, and the troughs indicate the position of the slip planes.

Insights from Locality 490

As uncommon as the morphology of the downslope tracks of UUIC 1873 appear to be, essentially the same features are present in the tracks of the long trackway at locality 490. This trackway was made by an animal that was not travelling down slope, but that traversed the slope, ascending only very gradually. In these tracks, the pressure pad is formed along the downslope margin rather than the anterior margin of the track, and the slumped depression is on the opposite, ups-

lope side of the track. The orientation of these features appears to be entirely determined by slope direction and little affected by the propulsive force of the animal's stride. As in the downslope tracks, when the downslope foot of the track maker struck the substrate, the greater part of the force was directed down slope at a low angle to the surface, producing a downslope pressure pad of sand, and as the foot was withdrawn, the destabilized slope above slumped into the track.

Some features of the long trackway at locality 490 raise interesting questions about, and perhaps provide insights into, the formation and preservation of downslope tracks such as those in UUIC 1873. The trackway crosses an interval where a sediment lamina, 2–3 mm thick, has spalled off the outcrop exposing the surface below. Most of the trackway is preserved on the uppermost layer preserved, but the portions that cross the spalled area of the outcrop represent undertracks from only a small increment of sediment below that layer. Loss of this small thickness of sediment results in a significant difference in the morphology of the tracks. The undertracks lack the flat-topped downslope pressure pad. Instead, the downslope margin of the track is marked by a push-up rim with a gently curved profile of much more limited lateral extent. This morphology is more similar to the simple push-up rims seen in most upslope tracks. In addition, there is no trace of the slumped upslope depression in the undertracks. One fact that is apparent from the difference in track morphology expressed in the different layers is that the downslope pressure pad and upslope slump depression appear to be confined to a very thin (approximately 1–3 mm) lamina.

The transverse trackway at locality 490 preserves both left (downslope) and right (upslope) tracks. The left and right tracks are strongly asymmetrical. The downslope tracks are more deeply impressed and cause greater sediment disturbance surrounding the impression of the foot. In contrast, the upslope tracks are very shallowly impressed and simple in morphology. These upslope tracks preserve only the outline of the foot with a weakly developed push-up rim that is posterior to the track rather than on its downslope margin. Because the downslope foot would have borne most of the weight of the animal, the tracks they produced would be expected to be more strongly developed than the upslope tracks. The upslope foot may have been used less for support than for balance and propulsion.

The downslope tracks preserve both manus and pes tracks. The manus and pes are not well separated, but can be readily distinguished. The pes placement is downslope and anterior to the manus, partly obscuring it. No doubt this is the result of gravitational acceleration across the line of travel, shifting the path of the animal's body as it walked. Both manus and pes tracks have downslope pressure pads and upslope slump depressions that have merged to some extent, but that can still be distinguished. For the upslope tracks, only a single track, presumably the pes impression, represents each stride. Absence of manus tracks could be explained by overprinting by the pes, but given the offset of manus and pes in the downslope tracks it seems likely that there would be separation between the manus and pes in the upslope tracks for the same reason. Another possible explanation for the absence of manus tracks in the upslope side of the trackway is that these tracks are undertracks, and the fainter manus impressions were only present in a higher layer that is not preserved. The upslope tracks exposed in the segments of the trackway where a layer has spalled off are markedly shallower and less distinct than those in the layer above, illustrating how quickly these faint impressions can fade with depth. If the upslope tracks present on the uppermost preserved layer are undertracks, then the downslope tracks must be as well. This is entirely possible, although it seems surprising that the fine detail of the surface of the slump depression and the level surface of the pressure pad do not represent the original substrate surface. It also seems surprising that the uppermost increment of sediment on which the tracks were originally impressed is nowhere preserved. One possible explanation for this is that the most superficial sediment on which the tracks were made was loose, dry sand and was removed by the wind prior to the next preserved increment. The differences in features preserved in tracks exposed on the two different laminae in this trackway show that features can be confined to very thin laminae, and that significant changes in morphology can occur from one layer to the subjacent surface. Therefore, there is some degree of independence in the response of sediment to track formation from layer to layer.

OTHER NUGGET SANDSTONE DOWNSLOPE TRACKWAYS

Another dune foreset, downslope trackway is on one of two slabs figured by Buss (1921). Both slabs are from the Nugget Sandstone in the area of

Heber, UT. At the time Buss was in the Department of Geology at Brigham Young University in Provo, UT. A search of the collections in the BYU Department of Geology and the BYU Museum of Paleontology failed to turn up either the specimens or any data associated with them, so their whereabouts are unknown. Although Buss's photographs are not of high quality (Figure 13), a few relevant observations can be made. The trackway compares quite well with the downslope tracks on UUIC 1873. The trackway consists of 12 alternating tracks, all of which appear to be pes impressions. The original (depositional) dip of the slab cannot be determined from the photos, but based on UUIC 1873, each track has a large, smooth pressure pad at its downslope margin and a pronounced depression with crescent, ridges on the upslope margin.

Lockley (2005) briefly mentioned and figured a downslope trackway from the Iceberg Canyon site in the Navajo Sandstone. However, he did not identify the track as either bipedal or quadrupedal, and the drawing of the trackway is insufficient for comparison with the sediment distortion seen in UUIC 1873 and the transverse trackway at locality 490. Finally, given the large size of those tracks it is unlikely that they are *Brasilichnium*, even if quadrupedal.

DISCUSSION

Vertebrate tracks are common fossils in eolian deposits from the Carboniferous through the Holocene (McKeever, 1991). Those on dune foreset beds are virtually all made by animals walking up slope. Gilmore (1927, p. 3) noted that of the hundreds of Coconino Sandstone tracks he had examined only three that were not upslope tracks. A similar pattern is present in the Nugget, Navajo, and Aztec sandstones (Lockley, 2005; Engelmann and Chure, 2011; Rowland and Mercadante, 2014). Fornos et al. (2002) described abundant tracks of the goat *Myotragus balearicus* in Pleistocene dune foreset beds on the island of Mallorca, but downslope tracks are rare at that site as well (Fornos, personal commun., 2013). Thus, there is a puzzling pattern of an absence of downslope trackways on dune slip faces either in isolation or on surfaces with abundant upslope trackways. This pattern holds across a wide phylogenetic and temporal scale (from Late Paleozoic synapsids/mammaloids to Pleistocene goats). Although various biological and environmental explanations for this pattern have been proposed (see discussion below), no consensus has appeared. The analysis of trackway formation and dynamics has become

FIGURE 13. Reproduction of part of the photograph from Buss (1921). The original figure has been cropped to show only the *Brasilichnium* trackway and rotated 180º to show the tracks in what we interpret to be their original vertical orientation. No scale in photo, but based on Buss' description, the block is slightly less than 1 m.

increasingly sophisticated (Milan et al., 2004; Graversen et al., 2007; Jackson et al., 2009), but much of that work focuses on dinosaur tracks and tracks in horizontally bedded sediments.

Track formation and preservation on dune foresets, especially those in the Permian Coconino Sandstone, have long attracted the attention of paleontologists. Integral to the studies of how these tracks were formed was the explanation for the rarity of downslope tracks. McKee (1944, 1947) experimented with living side-blotched lizard (*Uta*), the spiny lizard (*Sceloporus*), and the common chuckwalla (*Sauramalus ater*) walking on variously inclined sandy slopes with varying amounts of moisture in the sand. He investigated both the best slope for preservation as well as how the tracks were preserved. Unexpectedly, McKee found that the best defined tracks were formed in dry, rather than moist sand. In his dry sand experiments he used very fine sand, but noted that other sands did not significantly change the results. Both upslope and downslope tracks were well defined at 12°, the approximate maximum angle of dune stoss slopes. At an angle of 28°, a common angle on dune lee slopes, uphill tracks were well developed, but slumping destroyed downslope tracks. At 33°, the angle of repose for the sand he was using, the slumping and sliding destroyed most upslope and all downslope tracks. Based on his experiments, McKee concluded that the predominance of upslope tracks on dune foreset beds was because they formed on slopes between 28–30° where uphill tracks are well developed and preserved but downslope tracks are obliterated by slumping.

In support of his explanation for the absence of downslope tracks, McKee (1944) cited Reiche (1938, p. 918) who observed that tracks of coyotes, rabbits, and lizards on modern dunes after a rain lead up slope "without exception," but that downslope tracks were "obscured by sliding of the surface layers of sand." Reiche offered a single example of a continuous trackway made by a rabbit ascending and descending the lee slope of a dune leaving clear upslope tracks and obscuring the downslope tracks along its path as evidence for this generalization. Reiche did not report what the dip of that dune slip face was nor how high up the tracks occurred. In addition, his observations were made after a rain, rather than in dry sand.

Based on McKee's work, we would expect that well-preserved upslope and downslope tracks would be present well out on distal regions of the foresets with an original dip of 12° or less. Vaughn (1963) described an isolated downslope trackway

from foreset beds in the De Chelly Sandstone, where the original dip of the bed was 17–18°. However, such bedding surfaces are generally unknown in Permian through Early Jurassic dune deposits, with the possible exception of UUIC 1873, but the original dip of that slab is unknown. Furthermore, we would expect to see trackways in this area of the dune face to be less likely to have a preferred orientation, i.e., trackways should run perpendicular, and at other angles, to original dip. However, such trackways are extremely rare, based on literature reports.

McKee's (1944) upslope and downslope lizard trackways were made on separate areas of the slope in his experimental setup, so it is unknown whether or not an animal coming down a slope already containing upslope tracks would destroy those upslope tracks. We expect that they would. If so, then such destruction should be seen on Nugget surfaces with numerous upslope tracks, possibly expressed as irregular blank strips running approximately parallel to dip, but it is not (Engelmann and Chure, 2011; Rowland and Mercadante, 2014).

Although McKee reported that downslope tracks made during his experiments were "destroyed," he did not publish any photos documenting the downslope track trials. We are uncertain as to whether those tracks were completely unrecognizable or that they left some disturbance of surface sediment that might be identified as a place where an animal had proceeded downhill. Furthermore, given what is known about the complexity of underprints in vertebrate trackways on dune foreset beds (Fornos et al., 2002), it is possible that while a downslope track itself might not be identifiable, its underprint might be recognizable in vertical or transverse sections.

An alternative explanation for the absence of downslope tracks is that the trackmakers came down the dune by a different path than the one they went up slope on. For example, there may be a behavioral preference for the trackmakers to descend from the dunes along the crests or the more gently sloping upwind surfaces, which are not preserved. However, that is difficult to test with ichnofossils, and we know of no reports of such behavior in modern desert vertebrates. Another way in which behavior could bias the record was suggested by Rowland and Mercadante (2014) who proposed that gregarious behavior in therapsids may account for parallel upslope *Brasilichnium* trackways. This could act as a multiplier to increase the disparity in the track record.

McKee's interest in tracks was to understand the ichnology of the Coconino Sandstone. The lizards in his experiments approximated the estimated size and weight of the Coconino trackmakers and left similar track impressions. However, lizards may not be good models for the *Brasilichnium* trackmaker. *Brasilichnium* tracks are broader than long with short stubby digits (as opposed to hands and feet longer than broad and with long, thin digits as in lizards). *Brasilichnium* trackways also differ in not showing tail drag marks. This may be a reflection of the semi-upright posture of therapsids as opposed to the sprawling posture of lizards. How these significant differences might affect track making and preservation is unknown. It may be that the more compact structure of the manus and pes in *Myotragus* and the *Basilichnium* trackmaker result in deeper penetration of sediments with greater force per unit area than in forms with a lizard-like manus/pes structure. However, the pressure pads seen in UUIC 1873 and the transverse trackway at locality 490 are not present in either Coconino tracks or McKee's experimental trackways, nor are those features seen in a 1.5 m downslope trackway described by Vaughn (1963), which has lizard like tracks with long toes. However, downslope pressure pads are present in goat (*Myotragus*) up and downslope trackways on Pleistocene dune foresets in Mallorca (Fornos et al., 2002).

Given the rarity of downslope trackways on dune lee slopes, it is ironic that the first reported vertebrate ichnofossil from the Nugget Sandstone should be of just such a trackway (Buss, 1921), although it was unrecognized as such at the time. Unfortunately that specimen cannot now be located at BYU and, despite all the subsequent ichnological field work done in the Nugget, Navajo, and Aztec sandstones, it would be almost 90 years before another such Nugget trackway was discovered, this time on display in the halls of the Frederick Albert Sutton Building at the University of Utah.

APPENDICES

Many details of the trackways described in this paper are best seen in large images, which are too big for the printable text version of this paper. We have provided full viewable Gigapan images of UUIC 1873 (Appendix 1) and the track surface at locality 490 (Appendix 3) at the Gigapan website and downloadable larger versions of Figures 2, 5, 6, and 7 as appendices.

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APPENDIX 1.

The full sized Gigapan image of UUIC 1873 (656 megapixels), presented at reduced size as Figures 1 and 2, can be viewed at the Gigapan website (http://www.gigapan.com/gigapans/174739) where the viewer can zoom to the maximum resolution at any part of the entire slab. The viewer should be aware that when viewed at this site the slab is oriented as displayed at the University of Utah.

APPENDIX 2.

The full size image reduced to create Figure 2. UUIC 1873 (824.8MB) rotated from as exhibited at the University of Utah to the orientation at the time of track formation. This file, append2.tif, can be downloaded from a folder in Box that can be reached with the link (https://unomaha.box.com/s/yqehi4vgasbsdvgpaqo72ef3m8s20ay7).

APPENDIX 3.

The full sized Gigapan image of the track bearing surface at locality 490 (284 megapixels) can be viewed at the Gigapan website (http://www.gigapan.com/gigapans/174736) where the viewer can zoom to the maximum resolution at any part of the entire slab. Discoloration of transverse trackway is artifact of molding the trackway.

APPENDIX 4.

The full size image reduced to create Figure 5 viewable with the map in Figure 6 as an overlay. Composite photograph of the track-bearing surface of DNM 490 and outlines of tracks on an overlying layer (123.7MB). This file, append4.ai, can be downloaded from a folder in Box that can be reached with the link
(https://unomaha.box.com/s/yqehi4vgasbsdvgpaqo72ef3m8s20ay7).

APPENDIX 5.

The full size image reduced to create Figure 7. Composite image of the long transverse trackway at DNM 490 (89.4 MB). This file, append5.tif, can be downloaded from a folder in Box that can be reached with the link (https://unomaha.box.com/s/yqehi4vgasbsdvgpaqo72ef3m8s20ay7).