# Newly Discovered Sauropod Dinosaur Tracks with Skin and Foot-Pad Impressions from the Upper Jurassic Morrison Formation, Bighorn Basin, Wyoming, U.S.A.

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*A recently discovered dinosaur tracksite from the Upper Jurassic Morrison Formation, Bighorn Basin, Wyoming, contains abundant sauropod tracks that exhibit varying degrees of preservation. Most of these tracks appear as indistinct bulges on the bottoms of sandstone beds, but several are well preserved and show foot-pad and skin impressions. Three track morphotypes are recognized: a sauropod pes print, a* Brontopodus*-like manus print, and a diplodocid manus print. The* Brontopodus*-like manus print most likely represents the footprint of a brachiosaur. This morphotype also contains evidence of phalangeal nodes—the first reported for a sauropod manus. The diplodocid manus print is unique because it contains impressions of a substantial ungual on digit I and a heel pad. A partial sauropod track cast also contains an impression of interlocking, polygonal scales. This is only the second known North American sauropod footprint that contains skin impressions.*

*The spectrum of preservational quality of the tracks and associated trace fossils is used to infer the relative moisture content of the original substrate. Moisture content of the original substrate is estimated to have been moist to borderline saturated. Observations of the tracks at the study areas also are used to establish a list of features that can be used to distinguish deep vertebrate tracks from load casts resulting from gravity-induced soft-sediment deformation.*

## INTRODUCTION

The purpose of this paper is to describe several newly discovered sauropod tracksites from the Upper Jurassic Morrison Formation, Bighorn Basin, Wyoming, USA, and to use their morphologies and preservation to reconstruct sauropod-foot morphology and original substrate consistency. These features, combined with characteristics of the beds in which they are preserved, can help distinguish deep sauropod tracks from load casts.

Most of the tracks in the study areas appear as rounded bulges protruding from the bases of sandstone beds, but some are very well preserved and can be assigned to distinct track morphotypes based on their morphology. A few tracks also contain rare textures that likely represent impressions of foot pads and skin (integument). These textures are compared to similar impressions in known sauropod tracks.

The range of preservation of these sauropod tracks likely represents variations in original substrate conditions. The spectrum of preservation is considered and related to factors affecting the appearance of modern vertebrate tracks, focusing in particular on original moisture content of the substrate. Several ways to distinguish sauropod tracks from load casts are discussed. These are important because load casts are similar in appearance to tracks, but are completely abiotic in origin.

## BACKGROUND

Sauropod tracks are known from the Early Jurassic through the Late Cretaceous on all continents except Antarctica (Farlow, 1992; Lockley et al., 1994b), and are recognized in part by their distinct morphology. Sauropod pes tracks typically are sub-circular or elliptical in shape, with well-preserved examples showing evidence of up to five anterolaterally directed digits and a large, rounded heel (Farlow et al., 1989; Thulborn, 1990; Farlow, 1992). Sauropod manus tracks are smaller than associated pes tracks, and typically appear as posteriorly concave, crescent shapes with no distinct digit impressions except for rare pollex claw marks (Thulborn, 1990; Farlow, 1992). Other important identifying features that are discernable where whole trackways are preserved include placement of the manus relative to the pes (Farlow, 1992), trackway gauge (the lateral position of the tracks relative to the trackway midline; Farlow et al., 1989; Farlow, 1992; Lockley et al., 1994a), and heteropody (manus-pes area ratio; Lockley et al., 1994a).

The presence of sauropod footpads has been inferred from skeletal foot and footprint morphology (Gallup, 1989; Farlow et al., 1989; Thulborn, 1990; Upchurch, 1994), but detailed impressions of the palmar surfaces of sauropod feet are rare (Gallup, 1989; Farlow et al., 1989; Thulborn, 1990). Well preserved *Brontopodus* manus prints show distinct pads, with one crescent-shaped, anterior pad encompassing digits II to IV, and separate posterior pads associated with digits I and V (Farlow et al., 1989). Possible

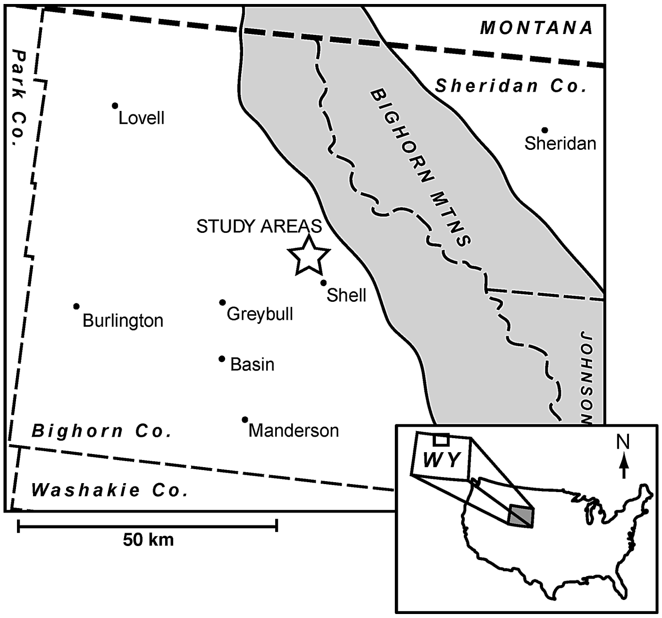


**FIGURE 1**—Inset map of the USA showing location of Wyoming; larger map shows location of the study areas in Wyoming.

phalangeal and footpads also have been described from sauropod pes prints (Gallup, 1989; Romano et al., 1999), but these do not show the distinct nodes present in some tracks attributed to other saurischian dinosaurs (e.g., Hitchcock, 1858; Rainforth, 2003).

Dinosaur tracks with skin-impressions are very rare (Currie et al., 1991; Lockley, 1991; Lockley et al., 1992; Lockley and Hunt, 1994; Gatesy, 2001), and only a small number are attributed to sauropods. One example, from the Upper Jurassic Tidwell Member of the Morrison Formation in Utah (Peterson, 1994), consists of a large oval pes print containing interlocking polygons, mostly hexagonal in shape, that measure approximately 0.5 cm along their longest axes (Lockley et al., 1992, 1998). This skin-impression-bearing track was attributed to a sauropod (Lockley et al., 1992), but reexamination of the overall morphology and skin-texture pattern has lead to a re-evaluation of this interpretation (Lockley, pers. comm., 2004). Sauropod tracks with skin impressions are known from the Jurassic of Asturias, Spain, and contain polygonal patterns of hexagons that range from 0.5 to 2 cm in diameter (García Ramos et al., 2002; Lockley, 2002; Lockley et al., in press). A regular pattern of 2-cm-diameter hexagons from the Lower Cretaceous Haman Formation originally described as the invertebrate ichnofossil *Paleodictyon* (Yang et al., 2003) has been recently recognized as the skin impression of a sauropod pes (Lockley et al., in press).

## GEOLOGIC SETTING

The study areas are located in the Bighorn Basin, near the town of Shell, Wyoming (Fig. 1). In these areas, the Morrison Formation is ~57 m thick (Moberly, 1960), overlies the Middle Jurassic Sundance Formation, and is overlain by the Early Cretaceous Cloverly Formation. The Morrison Formation locally is dated at 155 to 144 Ma (Tithonian–Kimmeridgian; Swierc and Johnson, 1996).

In the study areas, the Morrison Formation is divided informally into two parts based on the dominant lithologies (Fig. 2). The lower part of the Morrison Formation consists of trough-crossbedded, fine-grained quartz arenite interbedded with thin siltstone and mudstone. The upper part of the Morrison is dominantly interbedded reddish brown and grayish green siltstone and mudstone interfingered with thin beds of sandstone and siltstone (Kvale et al., 2001). These lithologies are interpreted as the deposits of an alluvial system (Kvale et al., 2001; Platt and Hasiotis, 2003a, 2003b; Platt et al., 2004).

Siltstone and mudstone contain abundant carbonate nodules, rhizoliths, and invertebrate ichnofossils. Most layers break into small- to moderately sized, rounded to angular blocks, many with slickensides, and manganese and hematite staining. Red-, green-, and purple-mottled, redoximorphic colors are common also, with rhizoliths and burrows surrounded by green reduction halos. These features are consistent with the properties of paleosols, suggesting that these mudstones represent pedogenically modified floodplain deposits.

Various vertebrate and invertebrate ichnofossils are preserved within and on bedding planes between the mudstone and sandstone. Invertebrate trace fossils are interpreted as crayfish, soil-bug, and beetle burrows, bee and termite nests, gastropod-resting traces, and bivalve-dwelling burrows (Kvale et al., 2001; Platt and Hasiotis, 2003b; Platt et al., 2004). Tridactyl footprints 10 to 50 cm long are attributed to ornithopods and theropods. These footprints occur with larger, pentadactyl to amorphous footprints interpreted as sauropod tracks.

The tracks typically are associated with fine-grained, ripple- to climbing ripple-laminated quartz arenites that grade upward to planar-laminated beds with primary current lineations. These beds are interpreted as resulting from rapid deposition in longitudinal or side-accreting bars in a shallow-channel crevasse-splay system (Kvale et al., 2001). The stratigraphic relationship between crevasse-splay sandstones and paleosols is interpreted as representing several avulsion events (Platt and Hasiotis, 2003b; Platt et al., 2004).

## MATERIALS AND METHODS

Most vertebrate traces in the study areas are preserved in convex hyporelief on the undersides of crevasse-splay sandstone beds (Fig. 3A–C), weather out as natural casts, and accumulate in talus slopes. Unfortunately, this makes *in-situ* observations of the tracks nearly impossible, but it does allow for observation of the tracks in three dimensions. Because of this mode of preservation, no complete trackways are evident in the study areas. Most of the tracks are poorly preserved and appear as rounded, amorphous bulges. However, some retain evidence of the external foot morphology of the tracemaker.

Tracks were measured according to the guidelines in Leonardi (1987). Because of the isolated nature of most of the tracks, trackway measurements were not obtainable. Footprint length (FL) and footprint width (FW) were measured after interpreting and orienting the trace through comparison with similar tracks contained in complete trackways described in the literature. Where digits were preserved, measurement of digit length and divarication

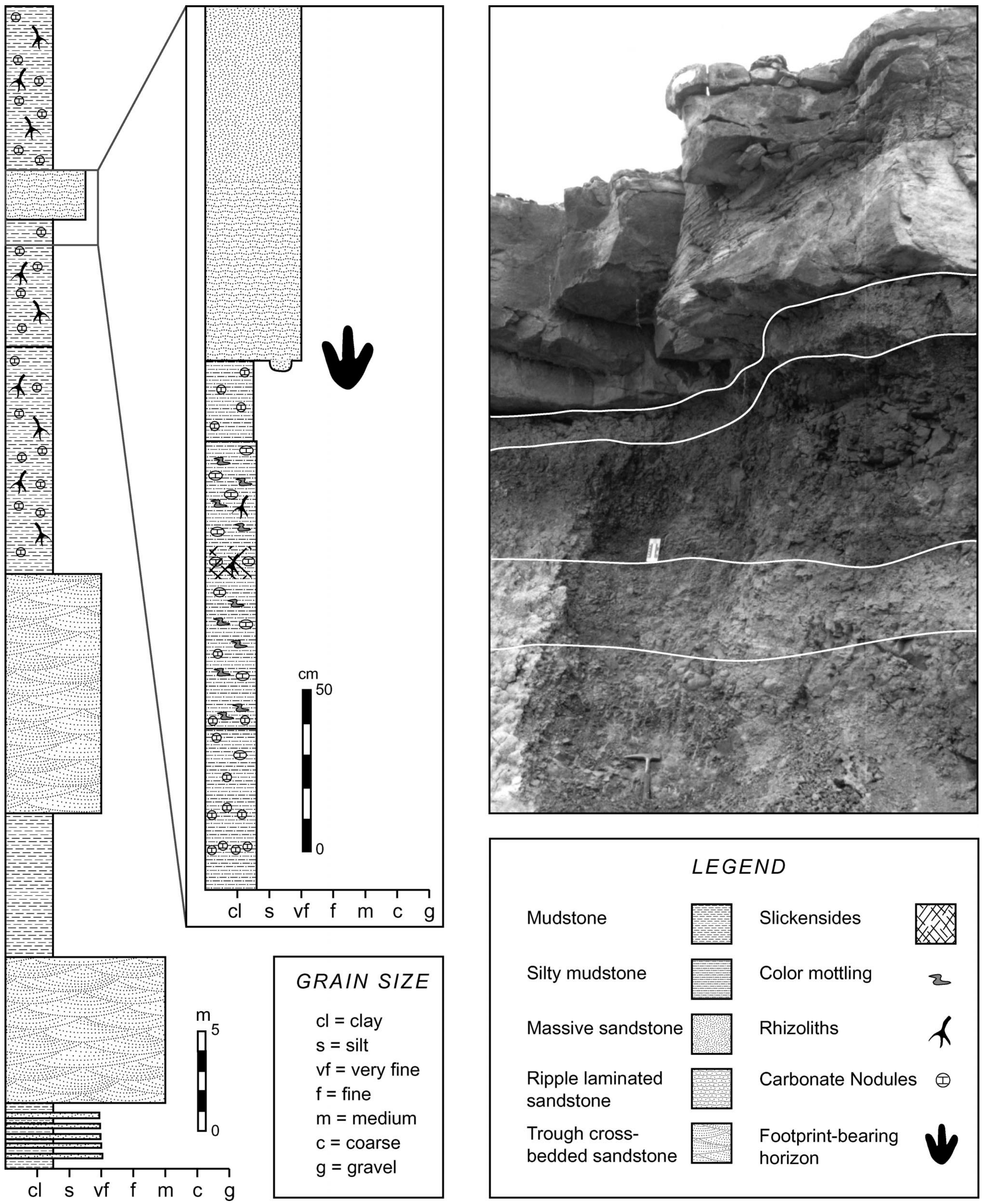


**FIGURE 2**—General measured section for the study areas and detailed section through the upper Morrison Formation. White lines on photograph delineate different paleosol horizons.

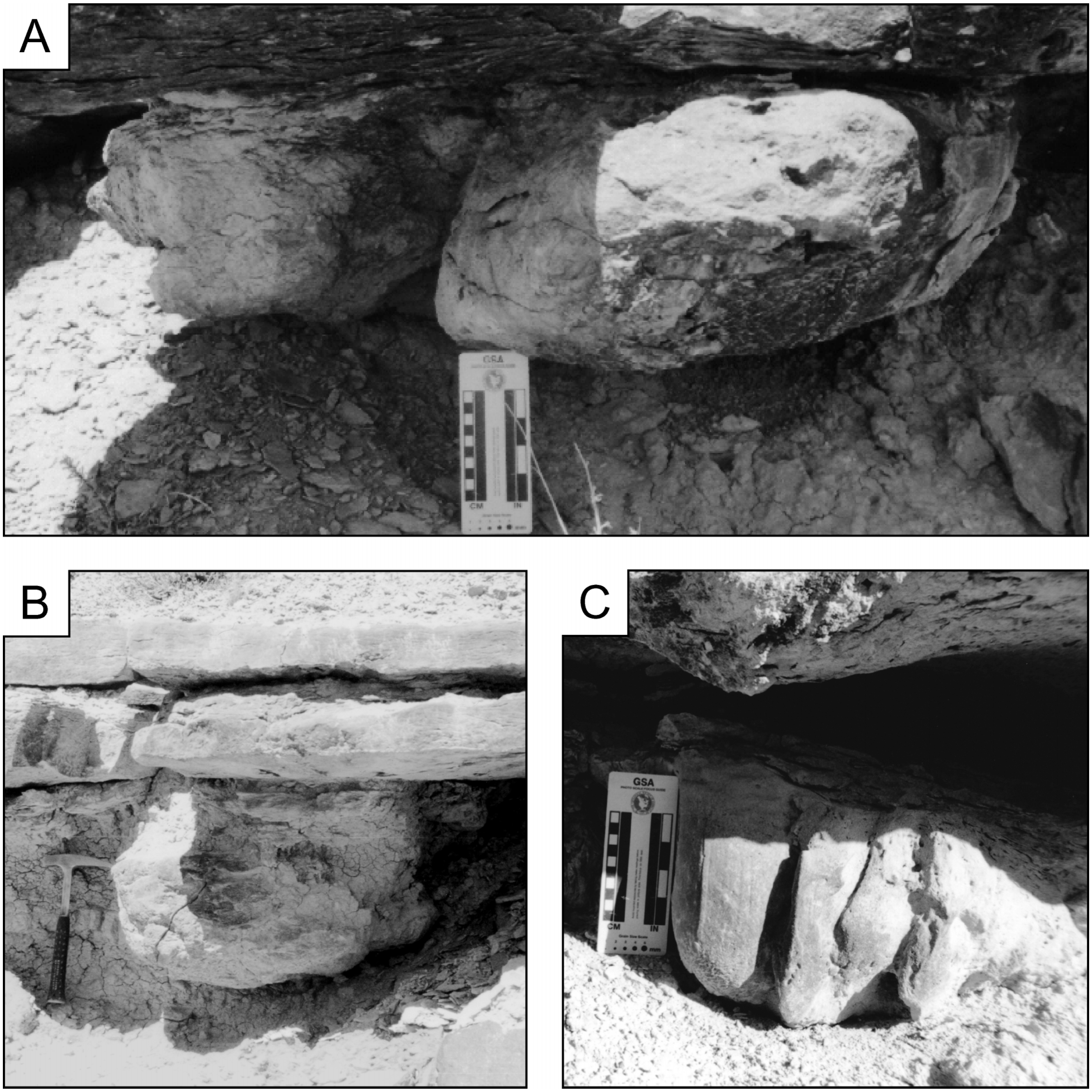


**FIGURE 3**—Field photographs of bulges in sandstone beds interpreted herein as tracks. All tracks shown in vertical profile view; scale in centimeters except for B; rock hammer is 32 cm long. (A) Bulges on the bottoms of sandstone beds interpreted as sauropod tracks. (B) Bulge on bottom of sandstone bed. (C) Sauropod track with evidence of digits. Note the vertical parallel striations on the track.

was not possible because of the highly curved nature of the digits. Where a manus-pes set was present, heteropody was estimated by using figure 2 of Lockley et al. (1994a).

## TRACK MORPHOTYPES

### Morphotype 1: Sauropod Pes Print

This trace consists of an 18-cm-thick sandstone cast containing a clear impression of the palmar surface of a footprint bearing four distinct digits and a large, rounded heel (Fig. 4). Proximally, the trace is indistinct and bulges outward, especially laterally and anteriorally. FL is 38 cm and FW is 29 cm. The digits project obliquely from the foot, giving the anterior margin of the print a step-shaped appearance. There are two vertical grooves in the proximal portion of the track that are aligned with the middle two digits (Fig. 4).

Based on footprint morphology, this track is interpreted as the right pes print of a small sauropod. The four visible digits most likely are digits I through IV (Fig. 4B, D). Digit V likely was not expressed externally on the pes of the

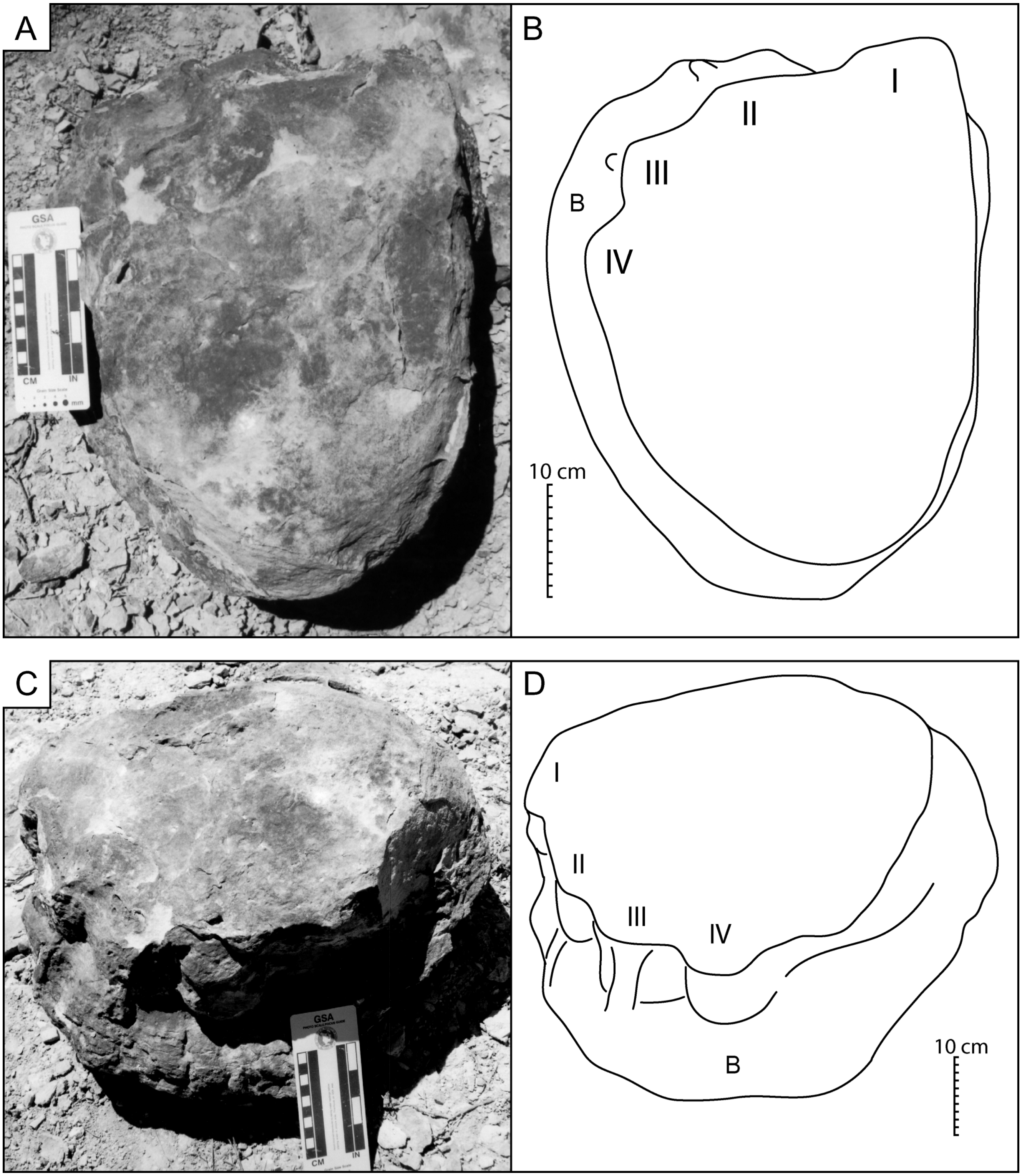


**FIGURE 4**—Sauropod track morphotype 1. Letter B in (B) and (D) refers to anterolateral bulge. (A) Palmar view of natural cast of sauropod pes. (B) Interpretation of track pictured in A. (C) Oblique view of same trace. (D) Interpretation of track pictured in C.

trackmaker (Farlow et al., 1989). The vertical grooves associated with digits II and III are interpreted as claw marks. The lack of a claw mark associated with digit I likely is due either to weathering or to non-preservation (i.e., the substrate was moist enough so that any marks made by the claw were obliterated). The anterior surface of digit IV does not appear to be broken, but it is possible that a claw mark was created and not preserved. The anterolateral bulge in the shallow portion of the track suggests motion either in a posteromedial direction as the foot entered the substrate, or in an anterolateral direction as the foot was removed from the substrate. The fairly uniform thickness of this bulge and the straight nature of the claw marks indicate that rotation of the foot was not employed during the formation of this track. Because of the lack of significant detail within the track and the absence of additional trackway data, this footprint cannot be attributed accurately to a trackmaker, nor can it be assigned to an ichnogenus.

### Morphotype 2: Sauropod Manus Print, cf. *Brontopodus birdi*

This morphotype is roughly circular in shape, with two concave-inward directed sides opposite each other (Fig. 5A). Because the track is not associated with a trackway, its orientation is not immediately clear, making the measurement of length and width difficult without further interpretation. The track penetrated to a maximum depth of 25 cm below the original surface and appears to be composed of multiple areas depressed to different depths. The largest and most deeply impressed surface is roughly kidney-shaped. Adjacent to the concavity in this surface is a smaller, less deeply impressed triangular area flanked on two sides by smaller, rounded lobes that extend outward 10 cm and 20 cm. The larger lobe is more deeply depressed. There is no evidence of claw impressions. The surface of the track also shows a texture of elongate creases or cracks. These are most prominent on the kidney-shaped portion, where they are arranged in subparallel orientations. The rock is well cemented and appears freshly exposed with no evidence of fractures or significant weathering.

This track is interpreted as a sauropod manus print, similar to *Brontopodus birdi* (Farlow et al., 1989). According to this interpretation, the kidney-shaped region represents the anterior of the foot and is the impression of digits II, III, and IV, which were bound together into one pad (Fig. 5B; Farlow et al., 1989). A closer examination of this pad reveals subtle differences in relief accentuated by creases that define the individual digits (Fig. 5C, D). The two posterior lobes represent digits I and V. The larger and deeper example of the posterior lobes is interpreted as digit I and the smaller as digit V because sauropod manus are characterized by reduction of digits II through V and a substantial pollex claw on digit I (Upchurch, 1994). This also is the pattern seen in manus prints from *Brontopodus* trackways (Farlow et al., 1989). With the proper orientation of the footprint established, FL and FW are measured as 46 cm and 50 cm, respectively. The proximity of FW to FL is significant because sauropod manus tracks typically are substantially longer than they are wide (e.g., Thulborn, 1990; Farlow, 1992; see also Morphotype 3). This raises the question of whether sauropod manus tracks typically represent only digits II–IV. This may indicate that digits I and V did not bear a significant amount of weight of the sauropod. Further paleontological investigation is required to resolve this matter.

The apparent conformation of the creases to the flexures between digits likely represents folds in the soles of the pads. According to this interpretation, the folds between digits opened as the pad expanded laterally under the weight of the animal during mid-stance (Gatesy, 2001). A similar expansion occurs in the feet of elephants during locomotion (Sikes, 1971). There are no integumentary impressions present on the track, but digit I contains possible digital-node impressions (Fig. 5E, F). The distal end of the digit is broken, but the proximal portion appears to be composed of two nodes separated by a thin, constricted segment of skin. These features tentatively are interpreted as the impressions of arthral nodes (nodes or pads that enclose the joints) (Thulborn, 1990). According to this interpretation, the proximal node represents the metacarpophalangeal joint, the distal node represents the joint between the phalanges, and the broken tip represents the partial impression of the ungual. Alternatively, the creased texture of the palmar surface may be a preservational artifact resulting from a partially dewatered or desiccated substrate (Lockley et al., 1989; Nadon, 1993); however, the subparallel creases do not radiate from the center of the track and likely are not the result of loading or desiccation.

Sauropod manus tracks that show an anterior pad representing digits II–IV, a posterolateral digit-V pad, and a posteromedial digit-I pad typically are associated with wide-gauge trackways attributed to titanosaurs (Wilson and Carrano, 1999). Based solely on manual footprint morphology, however, tracks of this type may be attributed to any of the Titanosauriformes (Farlow, 1992), which comprises titanosaurs and brachiosaurs (Salgado et al., 1997; Wilson and Sereno, 1998; Wilson and Carrano, 1999). Skeletal remains of brachiosaurs are known from the Morrison Formation (Riggs, 1903; Jensen, 1985, 1987; Paul, 1988), but the earliest skeletal material of North American titanosaurs comes from the Lower Cretaceous Cedar Mountain Formation (Britt et al., 1996, 1998; Tidwell et al., 2001; Tidwell and Carpenter, 2003). Based on morphology and age, this track most likely represents the footprint of a brachiosaur. The possibility cannot be ruled out, however, that this footprint represents the presence of titanosaurs in North America in the Late Jurassic. At this time, the track is not assigned to an ichnogenus because it is an isolated example.

### Morphotype 3: Diplodocid Manus Print

This morphotype is a trace that is *in situ*, and has a rounded anterior margin with no discernable digits, a sharp, convex heel, and an approximately 15-cm-long, blunt-tipped, anteromedially directed digit; FL is 32 cm and FW is 55 cm (Fig. 6). The track is associated with a larger, anterolaterally oriented track similar in shape to morphotype 1, but no other associated tracks are evident. The larger track partially overlaps (*sensu* Leonardi, 1987) the smaller track and is not as deeply impressed. The orientation of the tracks suggests that the trackmaker was traveling in a direction of approximately 210° azimuth. The smaller track shows no evidence of significant deformation from being overstepped.

The smaller, more deeply impressed track is interpreted as a sauropod manus print because its shape most closely matches the skeletal morphology of a sauropod manus, with digits II through V tightly bundled into a tubular column and an elongate, anteromedially directed pollex claw on digit I (Upchurch, 1994; Bonnan, 2003). This track differs from most sauropod manus tracks, which rarely con-

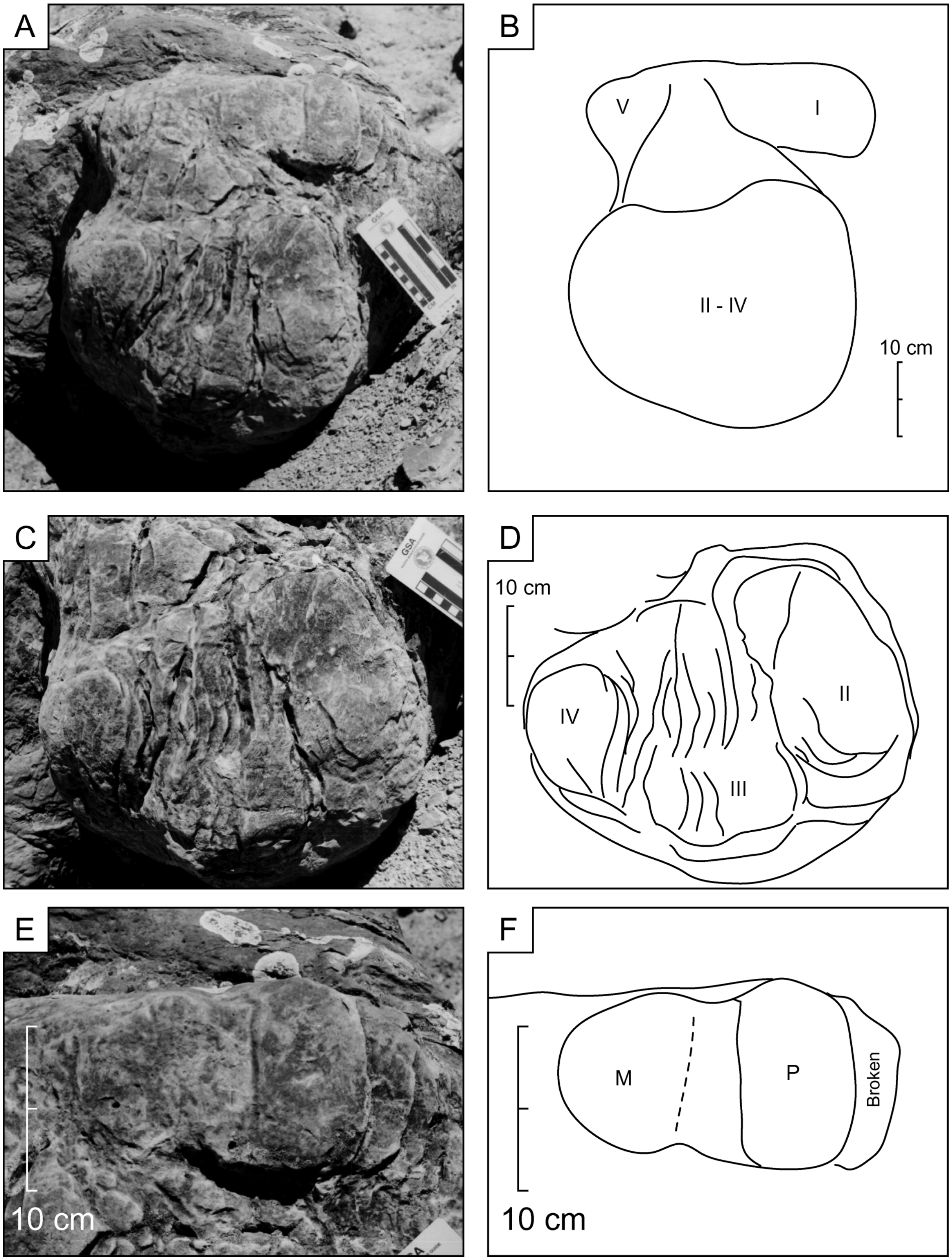


**FIGURE 5**—Sauropod track morphotype 2. (A) Palmar view of sauropod manus. (B) Interpretation of track pictured in A with digital pads labeled. (C) Close up of anterior foot-pad. Note the anterior-posterior oriented creases. (D) Interpretation of anterior foot pad pictured in C with digits II, III, and IV labeled. (E) Close up of posteromedial portion of the track interpreted as digit I. Note the presence of digital nodes. (F) Interpretation of nodes of digit I pictured in E. M and P refer to the inferred metacarpophalangeal and phalangeal-phalangeal joints, respectively.

tain impressions of digit I and a heel (Farlow, 1992; Farlow et al., 1989; Thulborn, 1990; Upchurch, 1994). The width of the impression of digit I relative to the width of the phalanges in digit I suggests that the digit was enveloped by a significant amount of tissue that expanded laterally during locomotion. The length of the impression of digit I is substantial enough to suggest that all of the phalanges of digit I are represented, implying that the ungual may have been enveloped in tissue. The convex posterior seems to represent the impression of a spongy, heel-like pad, like that of the pes. However, this track differs from other sauropod tracks with posterior convexities in that FW is greater than FL (Lockley et al., 1986; Mohabey, 1986).

Assuming the manus and pes prints are from the same animal, heteropody appears to be greater than 1:2. Because the manus and pes have similar areas and the manus is deeper than the pes, a greater amount of the weight of the tracemaker likely was borne by the front feet. It is possible that the manus print could be attributed to a diplodocid sauropod based on anterior footprint morphology and the substantial pollex claw; however, the heteropody is not consistent with this interpretation. At this time, the track is not assigned to an ichnogenus.

## SAUROPOD SKIN IMPRESSION

In addition to the well-preserved sauropod tracks described above, one partial track cast was found that preserves a small area with a polygonal texture. The specimen was found in float in an area with many large, deep tracks, only one of which has a clear shape (Morphotype 3). Neither the remainder nor the original location of the partial track could be located. Because so much of the track is missing and there are no clear digit impressions, it is difficult to identify and orient. One surface is relatively flat and smooth, and matches the broken upper surfaces of other fallen track casts where they have detached from the horizontal bedding plane. Opposite this surface is the inferred palmar surface, which has a wrinkled texture (Fig. 7A) similar to that of Morphotype 2 (Fig. 5A, B). A different texture, not observed in any other tracks at the site, is present on an upward-curved margin of the track. The texture is composed of many raised polygons with maximum widths ranging from 0.75 cm to 1.2 cm. Polygons are separated by recessed grooves that are V-shaped in profile. The best-preserved portions of the pattern show raised hexagonal surfaces arranged in rosettes, where any one polygon is in contact with five to seven other polygons (Fig. 7B, C).

The pattern is interpreted as the impressions of individual integument tubercles on the tracemaker's foot. The tubercles are similar in size and arrangement to other known sauropod tracks with skin impressions (Lockley et al., 1992; García Ramos et al., 2002; Yang et al., 2003; Lockley et al., in press). The pattern also is similar to that of sauropod body skin (Czerkas, 1994).

An interpretation of the polygonal pattern as mud cracks is rejected because mudcracks would be preserved as positive features in a cast (Fig. 8). The skin pattern probably is restricted to such a small area because of substrate variation or obliteration of the impression during removal of the foot from the substrate. The position of the

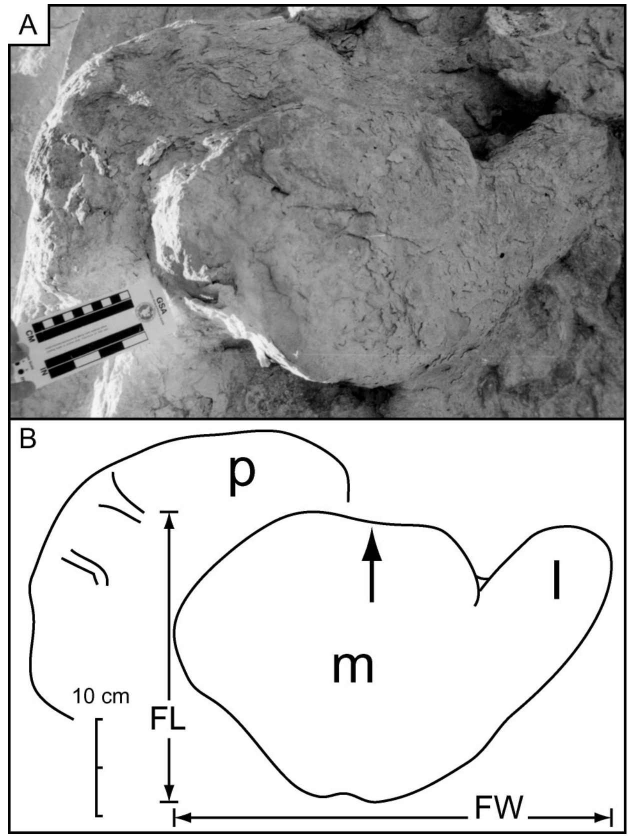


**FIGURE 6**—Sauropod track morphotype 3. (A) Palmar view of sauropod manus and pes prints. Note the thumb like projection and heel impression in the manus. (B) Interpretation of tracks pictured in A; p = pes, m = manus, I = digit I, FL = footprint length; FW = footprint width; arrow indicates anterior of manus.

skin impression suggests that it represents pad deformation during the mid-stance phase of locomotion (Gatesy, 2001, Fig. 5). This implies that the impression is not a perfect facsimile of the actual skin texture (Gatesy, 2001).

## INTERPRETATION OF SUBSTRATE

Despite modern and theoretical studies, original substrate consistency is extremely difficult to interpret. This is due, in part, to the extreme uncertainty regarding original moisture content and cohesion of the substrate (Laporte and Behrensmeyer, 1980; Nadon, 1993; Allen, 1997). Laporte and Behrensmeyer (1980) outlined the elements necessary for preservation of vertebrate tracks, and plotted their observations on a qualitative graph with water content and sediment texture as axes. Because grain size of the track-bearing Morrison rocks is known, a zone can be plotted on the graph to encompass the range of possible original moisture content of the substrate (Fig. 9). This range can be narrowed down through combining observations of the morphology and nature of the tracks and associated ichnofossils.

The depths of the traces and presence of striations suggest that the substrate was relatively moist, allowing the tracemakers' feet to penetrate a substantial distance with relative ease. Once the foot was removed, the depressions must have maintained their shape without collapsing or

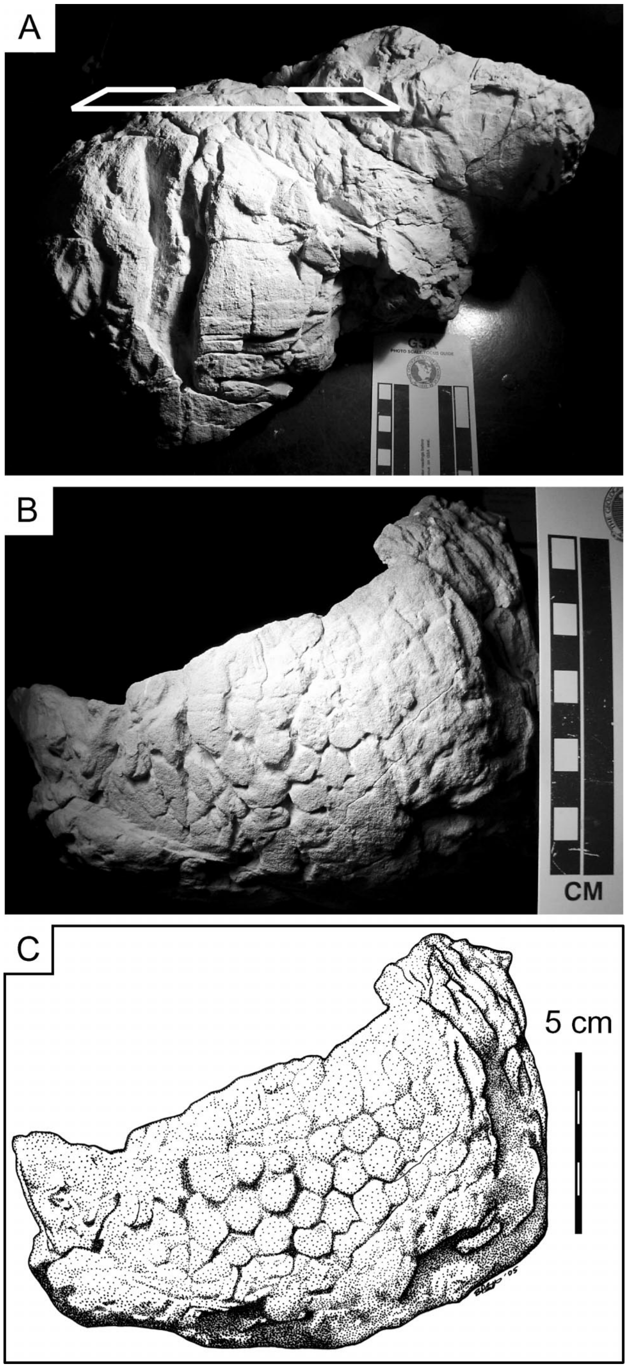


**FIGURE 7**—Sauropod skin impression. (A) Inferred palmar surface of sauropod track (KUMIP 311151) showing creased texture. Note the similarities between this texture and that pictured in Figures 5A and C. White trapezoid represents view of track in B. (B) Inferred side view of sauropod track showing skin-impression. Note the interlocking polygonal scales arranged in rosettes. (C) Artistic interpretation of skin pattern.

deforming, implying a cohesive substrate that was moist, but not saturated. None of the tracks contains evidence of desiccation, so it is inferred that the substrate remained moist until burial, which likely was rapid, thus contributing to their exceptional preservation (Laporte and Behrensmeyer, 1980).

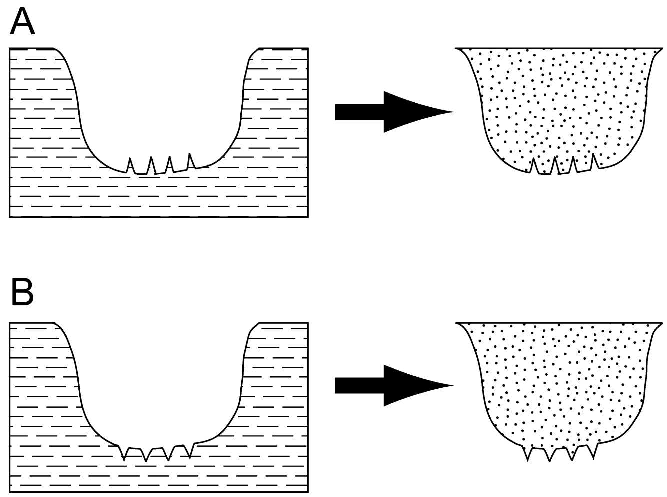


**FIGURE 8**—Comparison between casts of skin impressions and desiccation cracks. (A) Cross-sectional representation of impression made by footprint in substrate that preserves skin-impressions and the corresponding natural sandstone cast. (B) Cross-sectional representation of footprint with superimposed desiccation cracks and the corresponding natural sandstone cast. Footprints are not to scale. Skin-impressions and mud cracks are exaggerated to illustrate their differences.

Additional evidence for original substrate consistency comes from the ichnofossil associations in the track-bearing rocks. Trace fossils attributed to wasps, orthopterans, and termites, and relatively deep vertical burrows and root traces are all found in close proximity to each other and to the vertebrate tracks in the same stratigraphic interval. These traces suggest relatively low moisture and water tables. These same beds grade laterally into areas that contain shallow, vertical burrows and U-shaped tubes and surficial traces, such as *Cochlichnus* and *Pelecypodichnus*, which indicate relatively high-moisture environments (Hasiotis, 2002). These areas contain very few preserved vertebrate tracks. These assumptions about ichnofossil assemblages can be made because it is thought that these beds were deposited and buried relatively rapidly.

All of this information narrows the choice of the zone on Laporte and Behrensmeyer's (1980) graph of substrate consistency to which this track-making activity should be assigned. It has been associated here with the mid- to upper-moisture regime for mud-sized particles (Fig. 9 A–D). Examples of deep sauropod tracks from coarser-grained substrates are provided for comparison (Fig 9 E–F).

## DISTINGUISHING BETWEEN DEEP SAUROPOD TRACKS AND LOAD CASTS

Indistinct bulges protruding into underlying beds historically have been interpreted as load casts, which result from gravitational instability when a layer of material lacks the strength to support an overlying layer (Allen, 1982). In such cases, soft-sediment deformation is initiated by liquefaction (Sims, 1973, 1975) or unequal sediment loading (Shrock, 1948; Kelling and Walton, 1957). Load casts are most common in turbidites, but also are known from fluvial deposits (Allen, 1982 and references therein).

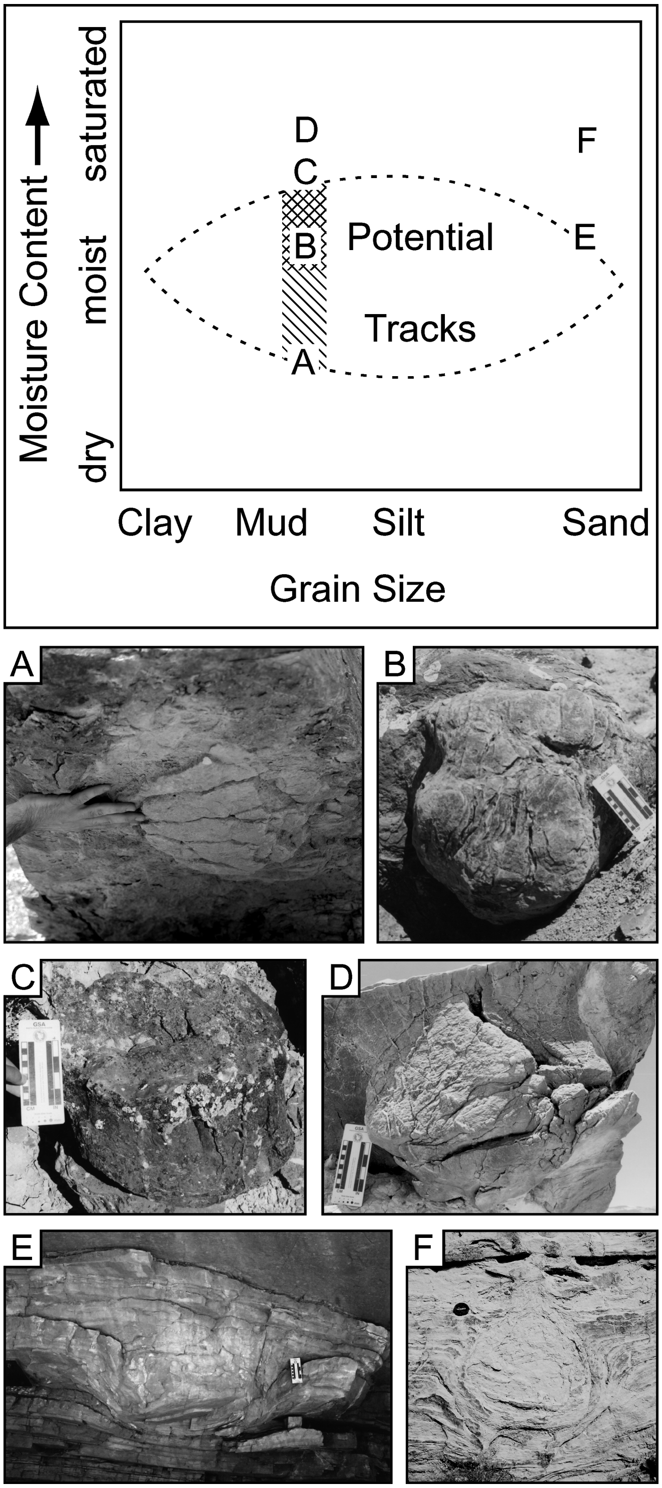


**FIGURE 9**—Top of figure is a graph showing ideal conditions for preservation of vertebrate footprints (modified from Laporte and Behrensmeyer, 1980). The hatched interval represents the zone in which the tracks in the study area could fall, based on grain size. The cross-hatched area represents the relative amount of moisture in the original substrate where the best-preserved tracks were created. Letters on the graph correspond to the hypothesized condition of the substrate when the footprints pictured below in photos A–F were made. Hand for scale in (A); scale in photos (B–E) is in cm; lens cap for scale in F. (B, C) represent tracks created in overly moist substrates; (D) represents the ideal substrate; (E) represents a deep sauropod track

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in a sandy substrate with high moisture (Upper Jurassic Morrison Formation, Dinosaur Ridge, Morrison, Colorado). (F) represents a deep sauropod track in a sandy substrate with very high moisture (Upper Jurassic Morrison Formation, Thermopolis, Wyoming; courtesy of Debra Jennings).

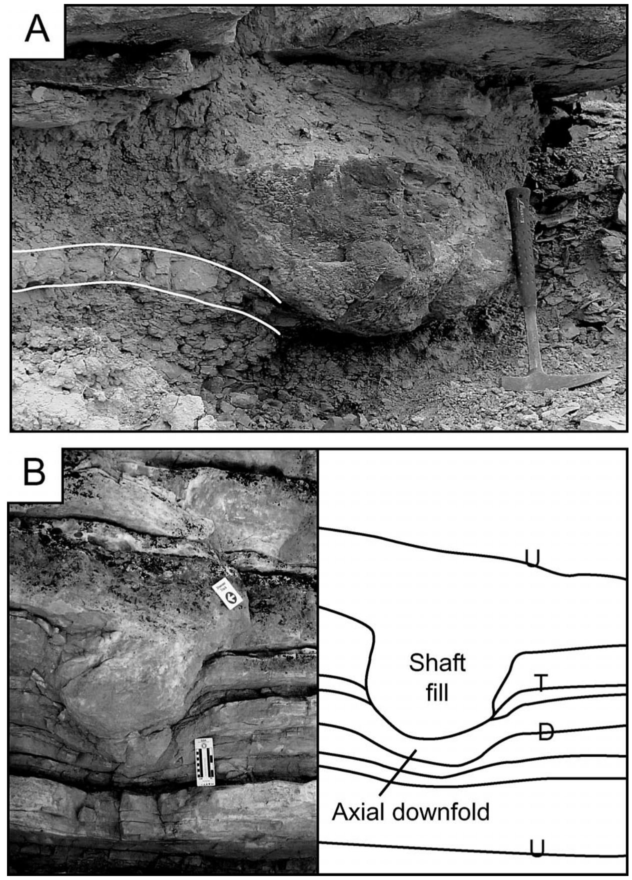


**FIGURE 10**—Features of deep sauropod tracks. (A) Deep sauropod track from the study area showing deformation of the underlying beds. Rock hammer is 32 cm long. (B) Deep sauropod track in the Morrison Formation at Dinosaur Ridge, Morrison, Colorado. Note undeformed bedding planes; U; truncated beds; T; and deformed beds; D. Additional terminology from Allen (1997).

Some load-cast-like features previously have been interpreted as vertebrate tracks (Webb, 1980; Boyd and Loope, 1984), but deep sauropod tracks similar to those described here have been recognized only relatively recently in continental rocks (Nadon, 1993; Engelmann and Hasiotis 1999; Houck, 2001; Nadon, 2001; Difley and Ekdale, 2002; Hasiotis, 2002, 2004). Because the majority of these tracks are not well preserved, it is important to be able to distinguish them from load casts so that paleoenvironments and modes of deposition are not misinterpreted. Several features of deep sauropod tracks at the study areas are inconsistent with a purely gravitational model of soft-sediment deformation (see also Nadon, 2001, for a discussion of the distinction between tracks and soft-sediment deformation).

Deformation of underlying beds associated with deep tracks is mainly directed downward (Fig. 10) with only minor upward-directed marginal deformation constrained to a narrow zone adjacent to the margin of the footprint (Allen, 1997). Many examples of load casts, in contrast, show significant injection of lower beds into overlying beds at irregular intervals (Sorby, 1908; Kelling and Walton, 1957). The tops of most of the beds that contain deep tracks are horizontal and undeformed (Fig. 3B, 10B), indicating that the depressions were present in the mudstones before the overlying sandstone was deposited. Laminae typically are well preserved within the track-bearing beds, and there is no associated convolute bedding. Deformation in the underlying mudstones is restricted to a confined zone near the track. Uppermost mudstone beds are truncated where the foot penetrated through them and subjacent beds are deformed from the weight of the trackmaker (Fig. 10B).

Another feature present in some deep tracks is a series of parallel, vertical to subvertical grooves and striations. One particularly well-preserved *in-situ* track (Fig. 3C) shows, in profile view, four vertical, asymmetrical grooves, one of which contains narrow, closely spaced, parallel, vertical striations. The grooves are interpreted as marks left by the unguals of a sauropod pes pressing down into the substrate. The smaller striations are interpreted as marks made by raised areas on the skin, imperfections on the toenails, or coarse grains in the substrate that were pushed down or pulled up along with the foot.

## CONCLUSIONS

A recently discovered dinosaur tracksite in the Upper Jurassic Morrison Formation, Bighorn Basin, Wyoming, contains many sauropod tracks, but none is associated with trackways because of their expression in the outcrop. The tracks are preserved in convex hyporelief on the bottom of crevasse-splay sandstone beds. Most appear as indistinct bulges of sandstone, but several are well preserved and show detailed features, such as pad and skin impressions. Three morphotypes of sauropod tracks are recognized. The first is a small pes print with four clear digits, and claw marks associated with digits II and III. There is insufficient evidence to attribute it to a particular group of sauropods. The second morphotype is a large *Brontopodus*-like manus track that is attributed to a brachiosaur based on morphology. Theoretically, it could be attributable to a titanosaur, but this is unlikely. The third morphotype is a sauropod manus print partially overlapped by a pes print. The manus print is distinctive in that it contains a heel and large impression of digit I with no evidence of a claw. This morphology most closely matches that of a diplodocid manus. Another partial sauropod track cast contains a skin impression composed of polygonal, interlocking integument tubercles similar to those found in a few other sparsely documented examples from Europe and Asia.

The original substrate-moisture content is estimated to have been relatively moist based on grain size, depth, and degree of preservation of sauropod tracks and associated ichnofossils. Several features were observed that distinguish these deep sauropod tracks from load casts in terrestrial deposits. Deep tracks typically deform underlying layers only in a downward direction. Beds penetrated by the tracemaker's foot are truncated. The tops of the beds that contain the tracks are horizontal and undisturbed. Primary sedimentary structures are preserved within the overlying bed, and convolution is absent.

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