

# Enigmatic Fossil Footprints from the Sundance Formation (Upper Jurassic) of Bighorn Canyon National Recreation Area, Wyoming

## Jerald D. Harris

Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, Pennsylvania, USA

## Kenneth J. Lacovara

Geology Program (CAEE), Drexel University, Philadelphia, Pennsylvania, USA

The Sundance Formation (Middle-Upper Jurassic) of Wyoming is well known for pterosaur footprints. Two new partial trackways from the upper Sundance Formation of the Bighorn Canyon National Recreation Area (BICA) of north-central Wyoming are enigmatic. The trackways are preserved in rippled, flaser bedded, glauconitic sand and mud. The deposits were laid down in tidal flats, behind barrier islands, along the mesotidal Sundance Sea.

The best-preserved print of the primary trackway possesses four impressions: three shorter digits with negative rotation and an elongate, caudally-oriented mark. The primary trackway has low pace angulation. The combination of morphology and pace angulation matches neither tracks nor body fossils of horseshoe crabs, theropod dinosaurs, pterosaurs, crocodylomorphs, "lacertoids," or mammaliforms. The secondary trackway, possibly consisting of undertracks, similarly possesses elongate caudal impressions but differs from the former by possessing four subparallel, cranially-oriented digits. These prints also do not closely resemble any of the aforementioned taxa. While the secondary trackway does not lend itself to conclusion, the primary track maker could have been either an injured, pathologic pterosaur or a pterosaurian taxon otherwise unknown from the ichnological record.

**Keywords** Sundance, Jurassic, Wyoming, Bighorn, footprint, limuloid, pterosaur, crocodylomorph, tidal, paralic

#### INTRODUCTION

Although long known for its abundance of vertebrate body fossils (Bird, 1985; Breithaupt, 1996, 1997), paleoichnological research in the vast Mesozoic exposures of the Bighorn Basin (north-central Wyoming and south-central Montana) is still in its infancy. Nevertheless, tracks have proven fairly abundant in the Basin, including recently recognized tracks made by scavenging theropods interspersed with sauropod bones at the famous Howe Quarry in the Upper Jurassic Morrison Formation (Lockley et al., 1998). Engelmann and Hasiotis (1999) reported a possible sauropod track from the Bighorn Canyon National Recreation Area (BICA, per Santucci et al. [1999]). Apart from the Morrison Formation, theropod tracks have also been reported from the underlying, Middle Jurassic Canyon Creek Sandstone Member of the Sundance Formation and the Gypsum Springs Formation (Kvale et al., 2001a, b; Mickelson, 2003). The Sundance Formation has proven to be the most ichnologically fossiliferous formation in the Bighorn Basin.

However, it is not for theropod footprints that the Sundance Formation has gained ichnological renown. Rather, the discovery of footprints made by pterosaurs in the course of terrestrial locomotion (Logue, 1977, 1994, 1996) has drawn the most attention. The first pterosaur ichnites were reported from the Morrison (or possibly Summerville, q.v. Lockley et al. [1995]) Formation of Utah (Stokes, 1957), but both these and the initial tracks reported by Logue (1977) were contested and interpreted alternatively as the traces of an indeterminate crocodyliform (Padian and Olsen, 1984). The subsequent discovery of further specimens from the Sundance Formation in the Bighorn Basin cemented the pterosaurian affinities of the ichnites (Lockley et al., 1995). Sundance pterosaur tracks formed the basis for research on tracks of similar age from France (Mazin et al., 1995) and elsewhere and proved critical to the understanding of pterosaur terrestrial locomotion (e.g., Bennett, 1997; contra Padian, 1983).

In 2001, the authors discovered some small ichnites in exposures of the upper Sundance Formation on the north side of

Address correspondence to Jerald D. Harris, Department of Earth and Environmental Science, University of Pennsylvania, 240 South 33rd Street, Philadelphia, PA 19104-6316. E-mail: jdharris@sas.upenn.edu



FIG. 1. (A) Schematic map indicating the location of BICA in north-central Wyoming. (B) North end of Sykes Mountain seen from main access road into BICA, Wyoming.

Sykes Mountain, BICA (Fig. 1). The tracks occur approximately 19.5 m below the Sundance/Morrison contact, placing the track-bearing horizon in the upper Sundance Formation. The discovery was made while investigating the stratigraphic relationship of the Sundance Formation (= Swift Formation) to the overlying Morrison Formation (the present paper preserves Wyoming stratigraphic nomenclature to facilitate comparison to tracks previously reported in this formation, but the equivalent Montana nomenclature has been used to the north of the study area). The slab (Figs. 2A–B) that preserves the right half of the primary trackway was discovered as "float" displaced down the outcrop. It was traced to its origin upslope where the left half of the main track slab, as well as two layers of undertracks from the same sequence, were preserved *in situ* (Fig. 3A). Both slabs preserve portions of two intersecting trackways. The more pronounced primary trackway on the main slab is very close to, if not on, its actual track surface, although only one print (Figs. 4A, B) is well-defined. Prints in a second, shorter trackway, are less well defined, and may be undertracks. The track bearing slabs will be reposited at the Cincinnati Museum of Natural History and Science, but do not yet bear catalogue numbers.



**FIG. 2.** Main track bearing slab. (A) Direction of track maker motion for primary (1) and secondary (2) trackways indicated by long-tailed arrows. Tracks "A" and "B" are detailed in Fig. 4, and tracks "C" and "D" in Fig. 5. Small, tailless arrow indicates vein of calcite used as tie point for all layers. (B) Main track slab, showing positions and spacing of "couplets" of indistinct paired marks (braces). Small, tailless arrows indicate ends of linear "drag" trace. Scale bars in cm.

# PALEOGEOMORPHOLOGIC SETTING, SEDIMENTOLOGY, AND DEPOSITIONAL ENVIRONMENT

During the Middle and Late Jurassic, a lobate, epeiric sea extended south from the northern Pacific and Arctic oceans to inundate vast portions of northwestern North America. The resulting "Sundance Sea," as it is known, was bound by a volcanic archipelago to the west, the Ancestral Rocky Mountain Uplift to the south, and upland, continental deposits to the east. The restricted geometry of this sea would have limited wave fetch from at least three directions and would have moderated wave climate. Paralic deposits are known from throughout the Sundance Formation. Rautman (1978) interpreted the lower Sundance Formation as a progradational barrier complex, in which he observed tidal channel and tidal flat deposits. Uhlir et al. (1988) interpreted the many coquina layers in the upper portion of the formation as channel lags resulting from the longshore migration of inlets. In addition, they described several outcrops where sand/mud couplets form spring-neap tidal bundles. The presence of mud drapes from 1–3 mm within these bundles suggests (1) mesotidal conditions and (2) attenuated wave energy.

A coastal transgression, over a gently sloping coastal plain and under mesotidal conditions, is likely to result in the formation of



FIG. 3. Lithology of track-bearing horizon. (A) *In situ* portion of track sequences showing stratigraphic relationship of track-bearing layers. Layer 3 is exposed where the displaced, main track-bearing slab originated in layer 1. (B) Undulatory to lignoid small ripples. Ripple troughs are mud-filled, forming flaser bedding; the underlying, lighter sediment is layer 3 less than 1m from the undertrack-bearing slab. Scale bars in cm.



FIG. 4. Tracks from primary trackway. (A) Stereo paired photographs of track A. (B) Enumeration of digits of track A as used in the text. (C) Stereo paired photographs of track B. (D) Enumeration of digits of track B as used in the text. Question mark refers to small impression at lower right of structure that may represent digit IV or be the proximal end of digit III. Scale bars in cm.

extensive back-barrier lagoons. The voluminous tidal prism (tidal range x lagoonal area) afforded by this configuration would have produced a large cumulative inlet cross-sectional area along the Sundance Sea coast.

The relative proportion of tide versus wave energy largely determines the morphodynamic behavior of a barrier coast (Davis and Hays, 1984). Under tide-dominated conditions, (1) barrier islands are relatively short and "drumstick" shaped, and (2) inlets are deep and numerous. Thus, Uhlir et al.'s (1988) interpretation of the numerous coquina layers as inlet channel lags is consistent with the presence of mesotidal indicators, such as mud drapes and tidal bundles.

The tracks discussed herein involve three layers: the main track layer (layer 1), an underlying middle layer (layer 2), and a third, undertrack layer (layer 3) (Fig. 3A). Of these, layer 1 of

the right side of the primary trackway and the undertrack layer form the focus of this discussion, though layer 2 from the right side was also recovered. Layers 1 and 2 are very thin (5 mm) slabs of lithified, fine-grained, calcite/limonite cemented, glauconitic, quartzose sandstone.

The surfaces of these slabs are formed by undulatory to lignoid small ripples (*sensu* Reineck and Singh, 1973), indicating low to moderate, variable current velocities (Fig. 3B). Mud is deposited in the ripple troughs and, together with the sand ripples, forms flaser bedding. Along exposed edges, the mud portion is often weathered out (Fig. 3A). Fresh surfaces of this outcrop, however, show the muddy trough-fill in plan view (Fig. 3B). Flaser bedding is only known to occur under the influence of oscillating tidal currents (Reineck and Wunderlich, 1968) and can be taken as inarguable evidence of a paralic environment. In addition, the presence of tracks across these rippled surfaces indicates intermittent subaerial exposure. Thus, the track-bearing facies represents a tidal flat.

The third layer, which preserves the longest trackway sequences as undertracks, is similar in composition to the two overlying layers, although weathering has removed much of the cement, rendering the slab much softer and somewhat fissile.

Layers 1 and 2, while not fitting tightly to each other or to layer 3 due to weathering-induced distortion, can be correlated using a thin vein of calcite that runs through one end of each slab (Figs. 2A, 6A).

#### **METHODS**

In a broad sense, fossil footprints can preserve characteristics that allow them to be attributed specifically to one group of organisms, if not to specific lower-level taxa. However, when such features are lacking, the only recourse is to resort to the process of elimination. In an era when detailed systematic approaches center on the recognition of taxon-specific features (autapomorphies), this is an unpopular practice. Because the tracks described herein are unusual, potentially diagnostic characters are ambiguous and have more than one possible interpretation. We thus also employ basic comparative techniques in attempting to identify the track makers, and this necessarily entails detailing reasons for ruling out certain taxa.

#### **DESCRIPTION OF TRACKS**

#### Primary Trackway, Main Slab (Layer 1)

Though only one print (track A, Fig. 2A) is distinct, the primary trackway preserves a repeating, evenly spaced pattern of indentations (Fig. 2B). These indentations occur in "couplets" (paired sets of unconnected but associated impressions averaging 65.3 mm long) consisting of smaller, circular cranial and larger, irregular (but generally linear, parallel to the trackway axis) caudal impressions. Within each couplet, the distance between the cranial- and caudalmost impressions is slightly larger than the length of the distinct print (track A, below) at the front of the trackway (65.3 mm). Thus, the less distinct couplets likely reflect the morphology of track A.

*Track A:* The lone, well-preserved track in the primary trackway (Fig. 2A), from the right side, is of unusual morphology. It appears to be either tetradactyl or tridactyl with an elongate "heel" mark (see discussion below); for ease of reference, the impressions are numbered I–IV (as would be digits) as in Fig. 4B. Measurements are given in Tables 1 and 2. Digits III and IV roughly parallel the trackway axis (determined from the undertracks); digits I–II show pronounced negative rotation (= medial, toward the trackway axis, *sensu* Lockley et al. [1995]; Unwin [1996]; contra Thulborn [1990:88]).

All digits, especially digits III and IV, present marked positive relief, though the distal end of digit II converts to negative relief. All other tracks on the slab have negative relief. The reason for this discrepancy in topography is unclear. Possibly the positive relief of track A is the result of sediment pull-up: if the weight of the track maker was concentrated in these two digits, then perhaps their extraction from the (presumably wet) substrate pulled sediment up from within a former impression. Digits I and II were not as deeply impressed and did not adhere as strongly to the substrate upon extraction.

Digits III and IV are broad mediolaterally, but digits I and II are, in contrast, very narrow. Digit II terminates indistinctly in a shallow depression; the distal end of digit I is parabolic and only slightly pointed. Digit III is broad and triangular, tapering distally. No clear ungual mark is preserved on any digit. The extremely elongate digit IV is roughly parallel-sided for most

TABLE 1

Measurements of tracks A–D as preserved. In entries with two numbers, the first number measures from tip of impression to the most distal point on the lateral bulge where all digits converge (method b in Fig. 4b of Thulborn [1990: 82]); the second number measures from the tip of the impression to the intersection with a hypothetical line tangential to the adjacent hypex and perpendicular to the digit axis (method c in Fig. 4.9 of Thulborn [1990: 83]). All values given in mm.

	Max. Length	Max. Width	Length					
			Digit I	Digit II	Digit III	Digit IV	Digit V	
Track A	57.2	21.3	21.8/10.6	29.8/14.8	21.4/11.3	31.4/33.8	n/a	
Track B	57.4	~26	10.8	37.4	35.6 (21.3)*	n/a	n/a	
Track C	30.1	17.0	14.4/8.0	13.0/5.9	9.9/3.3	3.0/2.2	19.1/19.1	
Track D	39.3 (44.4) <sup>†</sup>	19.0	11.0?/4.7?	14.1 (21.9) <sup>†</sup> /3.5	13.7 (20.5) <sup>†</sup> /4.4	10.2/3.7	21.6/21.6	

n/a = Not applicable.

\*Parenthetical value denotes measurement of positive relief portion of impression, which is separated from the main body of its print by a featureless gap.

<sup>†</sup>Parenthetical value incorporates linear mark extending from end of digit impression. See text for details.

 TABLE 2

 Angles of divarication between digits in tracks A, C, and D.

	Angle of Divarication							
	Digit I–II	Digit II–III	Digit III–IV	Digit IV–V	Digit I–IV	Digit I–V		
Track A	33°	28°	177°	n/a	238° (outward)/122° (inward)	n/a		
Track C Track D	49° 26°	49° 22°	52° 15°	64° 146°	150° 63°	214° 209°		

n/a = Not applicable.

of its length and tapers to a blunt, parabolic point at its distal end. It gently curves laterally. Topographic relief in each digit increases toward its respective long axis, though there is a small concavity toward the lateral side of digit III.

*Track B:* The primary trackway preserves a second set of topographic marks (Figs. 4C, D) that may represent a single track of differing morphology from track A. The location of the print directly in front of track A implies that it also pertains to the right side. Measurements are given in Table 1. Track B consists of a series of three low, positive relief, subparallel, linear marks. The base of a possible fourth digit may be represented on the structure's lateral margin by a low, ovoid mark. Alternatively, this may be the base of digit III; the more proximal portion of the structure labeled digit III is not preserved but also lies along a slightly different axis than the questionable mark. If indeed this entire structure represents a track, its positive relief may be the result of the same processes outlined above for track A.

All three subparallel marks are mediolaterally narrow and have more or less parallel sides. All three display negative rotation with respect to the trackway axis. The two lateralmost structures are subequal in length. The elongate, ovoid, discontinuous portions of digits I and III may represent digital pads. The heel area of the print is indistinct and probably incomplete. It consists largely of a caudally-oriented, arcuate bulge behind digit III and the questionable digit IV impressions, and a much less pronounced swelling behind digit II.

The possible significance of track B is discussed below.

#### Secondary Trackway, Main Slab (Layer 1)

*Tracks C and D:* The first visible track in the shorter, secondary trackway on the main slab (track C, Fig. 2A) preserves the greatest amount of morphological detail in its sequence (Fig. 5A). As with track A, it is unclear whether or not the track is pentadactyl or tetradactyl with an elongate "heel" impression. Again, for the sake of descriptive convenience, the impressions are numbered I through V (Fig. 5B) as a right appendage. Unlike track A, only one digit (I) is directed toward the trackway axis; digits II and V roughly parallel the axis, and digits III and IV are oriented outward.

All impressions are essentially linear depressions, V-shaped in cross section, and do not display any individual digit morphology. Digits I, II, and V are longer and deeper than the barely discernible III and IV. Digits I–IV radiate from a common depression, but digit V is separated from that depression by a comparatively elevated area of sediment.

A second print (track D, Figs. 2A, 5B), located cranial to the first, is of similar morphology as track C; except for the distal end of digit I, it is of positive relief rather than an impression. Its long axis is set at a low angle to that of track C, but it is offset sinistrally rather than in line with its precedent. This gives the impressions both that the print represents the left side (and is numbered as such in Fig. 5D) as well as that the track maker was bipedal. Alternatively, tracks C and D represent the left manus and pes of the track maker, where the right side would have been present on eroded outcrop adjacent to the recovered slabs. Unlike track C, digits I-IV all appear to be oriented more or less cranially and at substantially lower angles of divarication from one another, though the overall angle of divarication from digits I-V is similar to track C. These impressions in track D are narrow, short, and taper to points, but there are elongate, shallow, linear grooves extending from digits I and III. Whether these impressions represent undertrack marks of longer digits or are drag marks from the tips of their respective digits upon extraction from the sediment is unknown. Unlike track C, the elongate "digit V" mark is both connected to the central "sole" impression from which all other digits radiate, recalling more a heel than a digit impression.

Tracks C and D are somewhat similar to track A in the sense that they too possesses elongate, caudally-oriented digit or heel marks, though in track C it is not connected to the remainder of the print. Track C also differs from track A in its larger number of digit impressions as well as the positive rotation of most of its digits. The digit V impression is somewhat wider than those of the other digits.

### Undertracks (Layer 3)

Though lacking discernible morphology, the undertrack layer (Figs. 6A, B) preserves important information concerning the track makers of both the primary and secondary trackways, as well as preserving traces of a ternary trackway. It is only on this slab on which both right and left halves of the primary trackway can be seen. As on the main slab, coupled indentations with roughly uniform spacing (mean = 58.4 mm on the right side and 64.1 mm on the left side) are visible at intervals (mean = 39.9 mm on the right side and 37.4 mm on the left side). Both correspond to the prints and couplets seen on the main track slab. The right and left sides of the trackway are almost uniformly 95–100 mm apart throughout the preserved portion of the trackway.

Only a single possible print is preserved in line with the undertracks of the secondary trackway (track E, Fig. 6A). It is unremarkable and contributes no further information about the secondary track maker.



FIG. 5. Tracks from secondary trackway. (A) Stereo paired photographs of track C (stereo image intentionally exaggerates actual topographic relief of print to emphasize faint marks). (B) Enumeration of digits of track C as used in the text. (C) Stereo paired photographs of track D. (D) Enumeration of digits of track D as used in the text. Scale bars in cm.

Faint undertracks, displaying no remarkable morphology, of a ternary trackway (Fig. 6A) are preserved to the left of the primary trackway. Except for the fact that each impression is close together and that the apparent pace angulation is high, few conclusions can be drawn from this trackway.

## DISCUSSION

### Tracks A and B

Identifying a potential track maker taxon for the primary trackway requires first resolving whether or not the maker was a vertebrate (a tetrapod) or an invertebrate. Most invertebrate ichnites consist of burrows, but epifaunal trackways are also known for a variety of arthropods. Trackways made by arachnids, myriapods, hexapods, and most chelicerates are readily distinguished from the Sundance Formation tracks because they consist of numerous small dimples, not elongate digits. Trackways of some other chelicerates, however, mimic those of tetrapods because some of their appendages possess separate "digits." Given the tidal environment in which the Sundance Formation tracks were made, primary candidates for investigation would be limuloid xiphosurans (horseshoe crabs, Figs. 7A–B), which are known to have inhabited shallow marine facies in the Jurassic (Romano and Whyte, 2003). Limuloid tracks (e.g., *Kouphichnium*, Fig. 7C) have been mistaken for those of tetrapods in the past (Caster, 1941; Malz, 1964). Limuloid tracks are fairly common in Mesozoic, and especially Jurassic, sediments (Caster, 1941; Malz, 1964; Goldring and



FIG. 6. Undertracks on layer 3. (A) Positions of tracks; notation same as Fig. 2, except ternary trackway (3) also denoted. Small, tailless arrow indicates calcite vein. (B) Pace angulation of primary trackway, drawn using smaller, caudal marks (circled) of each couplet (denoted by braces).

Seilacher, 1971; Hunt et al., 1993; Mazin et al., 1997; Romano and Whyte, 2003).

Aside from the chelicerae, the four cranialmost pairs of limuloid locomotory appendages terminate in pincer-like chelae (dactyli) that, as ichnites, usually form a single indentation, but occasionally a paired indentation, often with drag marks (Goldring and Seilacher, 1971). The last pair of appendages (the "pusher" legs), however, are enlarged and possess several distal processes, including a hyperelongate one (Fig. 7A). These "feet" leave tracks with multiple, digit-like impressions stemming from a common, elongate central axis (Malz, 1964; Goldring and Seilacher, 1971). Some of the digits can be negatively rotated or even caudally oriented with respect to the track axis, and tracks can appear tridactyl or tetradactyl (Figs. 7B, C). Limuloid tracks, however, can also appear irregular in shape owing to frequent smearing as the carapace and limbs drag over preexisting prints. Limuloid trackways are usually accompanied by a shallow, linear, midline telson (tail) drag trace. Well preserved *Kouphichnium* tracks from the Solnhofen of Germany are characterized by a series of three or four foreleg dimples between each "pusher" leg impression (Fig. 7C; Goldring and Seilacher, 1971); these dimples are distributed mediolaterally within a narrow band rather than falling along a single craniocaudal axis. Limuloid trackways are symmetrical about the usually present telson drag—there is no offset between tracks of the right and left sides, as one might expect from a tetrapod trackway.

Several aspects of the Sundance Formation tracks preclude their assignment to limuloids.

 They are much larger in size and would imply a limuloid of gigantic proportions unknown in the Jurassic. Limuloid "pusher" leg tracks from the Late Jurassic of France are around 3 mm long (Mazin et al., 1997); those from the Upper Jurassic Solnhofen Limestone of Germany range from 9–19 mm (Malz, 1964). However, much older



FIG. 7. Limuloid anatomy and tracks. (A) Ventral view of horseshoe crab *Limulus*, showing arrangement of appendages. Close-up details locomotory posture of "pusher" leg and foot. (B) Idealized *Limulus* trackway. (C) Schematic diagram of *Kouphichnium* trackway from the Solnhofen Limestone of Germany. Note the tail drag demarcating the trackway axis and the symmetry of the appendage impressions on either side. (All modified from Malz [1964].)

limuloid tracks from the Carboniferous of Italy are nearly as large (39.9 mm) as Sundance Formation track A, though most are around 25 mm (Conti et al., 1991).

- 2. Despite the regular spacing of the coupled impressions, there are neither intermediary indentations, as would be expected from the other appendages, nor "smudges" where foot dragging obliterated intermediary impressions (though both could have been removed by prepreservational erosion).
- Limuloid "pusher" foot impressions are generally somewhat symmetrical about their own axes; ichnotaphonomic conditions that would preferentially enhance the inward facing digits are difficult to envision.

- 4. Limuloid tracks are symmetrical about the trackway axis (i.e., a line drawn connecting common appendage impressions would be perpendicular to the trackway axis; Fig. 7C), but the undertrack layer from the Sundance Formation demonstrates that this is not true of the primary track maker.
- 5. It is unclear whether or not the mass of a limuloid would permit either the formation of undertracks through a post-compactional 10 mm of sediment or prints formed via sediment pull-up, although if one were large enough to have made the Sundance Formation tracks, it may have possessed the necessary mass. Despite this, the distinctive "pusher" foot does not impress as deeply as the forelimbs; thus, in an undertrack layer, one would expect more distinct preservation of the chelae impressions that of the "pusher" foot (Goldring and Seilacher, 1971).

In general, limuloid undertracks tend to preserve more pristine morphology than do the actual track layers themselves (Goldring and Seilacher, 1971), which is not the case with the Sundance tracks.

As tracks of both theropod dinosaurs and pterosaurs are already known from the Sundance Formation, it is appropriate to make comparisons to those two taxa. Excepting the elongate "fourth digit" of track A, the morphology of the track does resemble the generalized morphology of theropod dinosaur hind footprints, including having the longest cranially-oriented digit mesaxial (in which case the numbering in Fig. 4B would convert so that  $I \rightarrow II$ ,  $II \rightarrow III$ ,  $III \rightarrow IV$ , and  $IV \rightarrow I$ ). Some theropod and primitive ornithischian prints (including those of presumably primitive avians) also demonstrate negative rotation (e.g., Hyphepus [Haubold, 1971: 72]; Anomoepus [Lockley and Hunt, 1995: 125]; Ignotornis [Mehl, 1931: 446]; unnamed tracks from the Late Triassic of Argentina [Melchor et al., 2002: 937]). However, even when these taxa possess elongate, incumbent halluces that create impressions at large angles to the remaining digits, the hallux impression is never longer than the remaining digits nor, as in the digit numbered IV of the Sundance Formation track, is it more than half the length of the entire print. Some theropod and early ornithischian tracks do possess elongate heel impressions that often surpass the pes proper in length (e.g., some Anomoepus trackways). Nevertheless, in these ichnites, the heel impression invariably lies on or very near, and extends from, the long axis of the mesaxial digit, unlike digit IV in track A. The regular coupling of impressions behind track A demonstrates that the elongate impression in track A is not a taphonomic fluke created by a dragged toe, although it remains conceivable that the track maker was injured and repeatedly created abnormal tracks as a result of pathological interference with its typical gait.

Morphologically, track A bears some resemblance known manus prints of pterosaurs, specifically species of *Pteraichnus* and several unnamed pterosaur tracks from Crayssac, France (per Mazin et al., 2001a), and more distantly *Purbeckopus* and

*Haenamichnus*, all of which are thought to represent pterodactyloid pterosaurs (Unwin, 1996) except for four features: (1) it possesses impressions of four, rather than three, digits; (2) the dominant orientation for the print is strongly *negatively* rotated, rather than positively (*sensu* Lockley et al., 1995; Unwin, 1996; contra Thulborn, 1990: 88); (3) digit II is longer than either digit I or digit III; and (4) it shows low pace angulation (*sensu* Thulborn 1990: 86; Fig. 6B).

Pterosaur manus prints displaying impressions of four manual digits are extremely rare but include an unnumbered Pteraichnus sp. track from Crayssac, France (Mazin et al., 1995: Fig. 3a), Purbeckopus track M1 of Wright et al. (1997: Figs. 3, 5), and one manus impression of Haenamichnus (Hwang et al., 2002: Fig. 6c). In the Crayssac track and Haenamichnus, the impression of the fourth digit protrudes caudomedially at an obtuse angle to both digits I and II from the palmar region in which all digits meet; the possible fourth digit impression in the Purbeckopus track is obtuse to digit I, lies at nearly right angles to digits II and III, and protrudes primarily caudally. The Purbeckopus print is not preserved in a trackway, but digits I-III of the Crayssac print, as in all pterosaur manus prints known from trackways, display strong positive rotation with respect to their trackway axes (e.g., Stokes, 1957; Lockley et al., 1995; Mazin et al., 1995; Meijide Calvo and Fuentes Vidarte, 1999), unlike Sundance Formation track A. Mazin et al. (1997, 2001b) briefly discussed possible "rhamphorhynchoid" ichnites from Crayssac in which, unlike the purported pterodactyloid prints above, the manual digits are pointed forwards. The manus impression of this ichnotaxon (Mazin et al., 1997: Fig. 2d) resembles neither that of any pterodactyloid ichnotaxon nor Sundance Formation track A, but it does illustrate that the locomotory postures and resultant paleoichnological diversity of pterosaurs may be underappreciated at present. Thus, it is also conceivable that Sundance Formation track A was pterosaurian but belonged to a different clade than other pterosaur track makers.

Debate has centered on the identity of the digits responsible for the impressions in tridactyl pterosaur manus impressions (either I-II-III or II-III-IV). Both models explain the lateral increase in digit impression length observed in the bulk of all pterosaur manus impressions because it reflects the osteological increase in digit length in pterosaur skeletons (Lockley et al., 1995). The aforementioned Crayssac tracks were cited by both Mazin et al. (1995) and Unwin (1996) as evidence for the I-II-III interpretation, despite a problem between the ichnological and osteological proportions of digits II and III (see Unwin [1996] for review). Taphonomic conditions (stance, gait, nature of the substrate, etc.) frequently conspire to distort known osteological proportions in some pterosaur manus prints, such that the two cranialmost impressions are subequal, but the second digit is never longer than the third in any known track. The long, narrow, delicate impressions of digits I and II in track A argues against sloppy substrate conditions that might alter the track's reflection of the track maker's anatomy, but the preserved relative dimensions argue against a pterosaurian track maker. It is conceivable that the entirety of digit III in track A was either not impressed, pathologically shortened in the individual track maker, or affected by some indeterminate factor concerning the track maker's stance at the time track A was created.

As determined from the undertracks (Fig. 6B), the pace angulation of the primary track maker is far lower than in any described pterosaur trackway, averaging 49°, versus 110° in *Pteraichnus saltwashensis*, 90° in *P. stokesi* (Lockley et al., 1995), 150° in *P. manueli* (Meijide Calvo, 2001), 108° in *P.* sp. from the Late Cretaceous of Argentina (Calvo and Lockley, 2001), and 118° in *P. palacieisaenzi* (Arribas and Pérez, 2000).

Interestingly, track B may support interpretation for track A as a pterosaur manus print. Although it is poorly preserved, both its proximity to, and position in front of, track A, as well as its long, narrow, subparallel digits recall pedal impressions of Pteraichnus saltwashensis (Stokes, 1957) and P. palacieisaenzi (Arribas and Pérez, 2000). It less closely resembles some other pterosaur foot prints (e.g., Pteraichnus stokesi [Lockley et al., 1995], Pteraichnus sp. [Calvo and Lockley, 2001]), in which the axis of the pes print is markedly offset from that of the manus print. It is very unlike Pteraichnus manueli (Meijide Calvo, 2001), Purbeckopus (Wright et al., 1997) and unnamed pterosaur prints from Crayssac, France (Mazin et al., 1995), in which the pes impressions are set far closer to the trackway midline than the manus prints. The less pronounced relief of track B may also reflect the characteristic weight concentration on the manus of pterosaurs. Both the measurements of tracks A and B, as well as the ratio of their (preserved) lengths, fall in the range of known pterosaur tracks (Table 3). However, like track A, track B also displays negative rotation with respect to the trackway axis, which is unknown in any pterosaur trackway.

If the maker of the primary trackway was pterosaurian, then it displays an unusual mode of locomotion. Possibly the track maker suffered an injury or other pathology that deformed the right arm in the region of the wrist and manus, twisting it inward from its normal orientation. The inflated impressions of digits III and IV and the foreshortened digit III might also be relics of an injury. An injury to the fourth (wing) digit may have twisted the track maker's arm such that it was forced to drag part of its wing membrane on the substrate, and this might be evidenced by the shallow, linear mark that lies lateral to track A (Fig. 2B). Linear features lateral to Pteraichnus saltwashensis tracks from the southern Bighorn Basin were also interpreted as wing marks by Logue (1996). Such an injury might also be responsible for the low pace angulation. The negative rotation of the pes in the Sundance Formation track is more difficult to explain unless the aforementioned hypothetical pathology afflicted *both* the right limbs or unless the animal turned sinistrally at the preserved terminus of the track slab. While this sounds like "special pleading" to invoke unlikely circumstances, osteological pathologies are actually moderately

	Manus Max.	Pes Max.	Manus:		
	Length	Length	Pes Ratio	Age	Reference
Sundance Tracks A + B	57.2 (Track A)	57.4* (Track B)	0.99*	Late Middle or early Late Jurassic	This paper
Pteraichnus saltwashensis	$83.0^{*}$	76.2†	1.09	Late Jurassic	Stokes, 1957
Pteraichnus stokesi	56.5 <sup>‡</sup>	801	0.71 <sup>‡</sup>	Middle Jurassic	Lockley et al., 1995
Pteraichnus sp.	28-44	28-42	~1	Late Jurassic	Mazin et al., 1995
Pteraichnus cidacoi	30-60	?	?	Early Cretaceous	Fuentes Vidarte, 2001
Pteraichnus vetustior	$70^{\dagger}$	115†	0.61	Early Cretaceous	Meijide Fuentes, 2001
Pteraichnus manueli	25.3 <sup>†</sup>	$21.0^{\dagger}$	1.20	Early Cretaceous	Meijide Calvo, 2001
Pteraichnus palacieisaenzi (SCY specimens)	146.5†	106.8 <sup>†</sup>	1.37 <sup>†</sup>	Early Cretaceous	Arribas and Pérez, 2000
Pteraichnus sp.	86.7 <sup>†</sup>	100	0.87	Late Early or early Late Cretaceous	Calvo and Lockley, 2001
Pteraichnus sp.	40-50	70	0.57–0.71 <sup>¶</sup>	Late Cretaceous	Lockley, 1999
Purbeckopus pentadactylus	187-225 <sup>§</sup>	187-225	~1§	Early Cretaceous	Wright et al., 1997
Haenamichnus uhangriensis	$202.7^{\dagger}$	211 <sup>†</sup>	0.96	Late Cretaceous	Hwang et al., 2002

 TABLE 3

 Comparative metrics of purported pterosaur manus and pes prints. Measurements given in mm.

\*Track incomplete; †Value averaged from many tracks; ? = Tracks not preserved, values unknown.

<sup>‡</sup>Lockley et al. (1995) did not provide explicit measurements for the lengths of the manus prints in the holotype of *Pteraichnus stokesi*, and did not provide a scale in their Fig. 1 for the holotype. Measurements used here are taken from their Fig. 6a (middle fig.), assuming their scale bar = 1 cm, as no scale was specified. This assumption is supported by using the same assumption for the scale provided for the figured pes print from the same trackway (Fig. 6c, bottom), which, when applied to the figured pes print, provides a length of 78.2 mm, close to the 80 mm length stated in their diagnosis for the ichnospecies. Using the diagram and scale provided by Bennett (1997), however, the pes prints average 77.9 mm while the manus prints average about 66 mm, providing a ratio of 0.85.

<sup>¶</sup>Manus and pes prints not from same trackway and almost certainly made by different individuals, so ratio does not necessarily represent true proportions of tracks.

<sup>§</sup>Wright et al. (1997) do not provide specific measurements for *Purbeckopus* manus prints, but do state that they are all subequal to the pes in length. However, applying the scale given in their Fig. 3b, the average manus length (using tracks M1 and M2) is 151.0 mm and the average pes length is 196.5 mm, giving a ratio of 0.77. Presumably measurements from specimens discussed but not Fig. d by Wright et al. (1997) were included in drawing their stated conclusion of approximate equality.

common in the Mesozoic tetrapod record (e.g., Tanke and Rothschild, 2002), though thus far underreported in pterosaurs (but see Bennett [2003]).

Some or all digits of one or both limbs in tracks (and, more often, presumed tracks) of various amphibians, squamates, and crocodylians frequently display varying degrees of negative rotation. This is evident in modern observations and experimentally generated data (e.g., Leonardi, 1975; Farlow and Pianka, 2000) and is common in numerous Paleozoic and Mesozoic tracks, including some ichnospecies of *Attenuosaurus* (Schult, 1995), *Batrachichnus* (Haubold et al., 1995), *Amphisauroides, Lacertipus*, *Rotodactylus* (Haubold, 1971), *Dolichopodus* (?= *Lacertipus*) (Lockley and Hunt, 1995), and *Crocodylopodus* (Fuentes Vidarte and Meijide Calvo, 1999). When well preserved, most of these prints differ from Sundance Formation track A in possessing pentadactyl mani and pedes plus frequent preservation of distinctive, axial tail drags:

 Tetradactyl *Dolichopodus* pes print digits *decrease* in size caudally (Lockley and Hunt, 1995: Fig. 4.24), unlike those of track A. *Crocodylopodus* manus prints (Figs. 8A, B) from the Early Cretaceous of Spain, which do bear marked similarity to print of the modern *Caiman* (Harris, 1998: Fig. 2d), are of particular interest: although none are preserved in quite this fashion, removal of one digit impression (usually the fourth) in some of the pentadactyl manus prints would produce a print similar to Sundance Formation track A. Such removal would also force the perspective that the print was negatively rotated, when in reality it is positively rotated (Figs. 8A, B).

- 2. *Crocodylopodus* manus tracks fall within the size range (12–24 mm) of smaller pterosaur tracks (Table 3). The pes, however, is substantially larger (30–70 mm), creating manus:pes ratios (as determined from published trackway figs. in Fuentes Vidarte and Meijide Calvo [1999]) ranging from 0.58–0.69, smaller than that between tracks A and B, although again B may be incomplete.
- 3. *Crocodylopodus* pes tracks are located immediately caudal to the manus prints; this is also true of modern *Caiman* prints (Harris, 1998).
- 4. *Crocodylopodus* prints, like the pterosaur prints, also show a much larger pace angulation than the Sundance Formation prints.

5. While *Crocodylopodus* prints from Spain do not preserve one, trackways of modern crocodylians typically leave a tail drag (Reineck and Howard, 1978).

Since less weight is borne on the substrate by the tail than by the appendages, tail drags are less likely to be preserved as undertracks; Fuentes Vidarte and Meijide Calvo (1999) neither discuss the absence of a tail drag nor mention whether or not the Spanish *Crocodylopodus* specimens are undertracks. A track maker similar to that which produced *Crocodylopodus* cannot be fully ruled out for the Sundance Formation tracks,



**FIG. 8.** Crocodylomorph and mammaliform tracks. (**A** and **B**) Two sets of *Crocodylopodus* manus and pes prints from the Lower Cretaceous of Spain. Selected right manus prints (circled) shown with hypothetical removal of one digit impression (digit IV in both instances) to produce artificial, tetradactyl tracks (arrows). Compare with Fig. 4. Scale bars are 5 cm. (**C**) Unnamed mammaliform footprints from the Lower Jurassic Botucatu Formation of Brazil probably made by a saltating animal. Compare with Fig. 4. Scale in cm. (**D**) *Ameghinichnus patagonicus* tracks from the Middle Jurassic La Matilde Formation, also presumed to have been made by a mammal or advanced therapsid. (**E**) Purportedly mammaliform tracks from the Late Triassic or Early Jurassic of Lesotho. (A–B modified from Fuentes Vidarte and Meijide Calvo, 1999; C–D from Rainforth and Lockley [1996]; E from Sarjeant [2000].)

but a scenario selectively removing one entire digital impression (barring pathology in the track maker's appendage) is difficult to imagine. Combined with the reversed association between manus and pes prints between *Crocodylopodus* and tracks A and B (presuming track B is indeed a pes print), this renders a crocodylian interpretation for the Sundance Formation track maker unlikely.

A mammaliform (or advanced therapsid, e.g., tritylodontid) track maker must also be considered. Early and Middle Jurassic, probably mammaliform prints from South America were reviewed by Rainforth and Lockley (1996). Tiny (20 mm, about one-third the size of track A), long tracks of a saltating animal from the Botucatu Formation in Brazil (Fig. 8C) do bear some similarity to track A. These unnamed tracks were originally attributed to a small, hopping theropod but were considered by Rainforth and Lockley (1996) to be mammaliform. Like track A, they are tridactyl and possess an elongate, caudally-oriented "heel" impression. At least one of these tracks (the right in the close-up, Fig. 8C) displays a pronounced angle between the elongate heel impression and the mesaxial, cranially-oriented digit, similar to (though less negatively rotated than) track A. However, saltating locomotion produced tracks that, like those of limuloids, are symmetrical about the trackway axis, unlike the Sundance Formation prints. Other Mesozoic mammaliform tracks (e.g., Ameghinichnus from the Middle Jurassic of Argentina [Fig. 8D] and many others; see review in Sarjeant [2000]) are much more distinctive than the Botucatu Formation prints by lacking an elongate heel impression and/or possessing five digits. If the Botucatu Formation prints are correctly attributed, then a mammaliform track maker for the primary trackway cannot be ruled out, although it seems unlikely.

### Tracks C and D

Most of the comparisons above for track A also apply to tracks C and D. Many of the distinctive features of these prints, however, imply that the track maker of the secondary trackway differed from that of the primary trackway. Foremost, they are either pentadactyl or, more likely, tetradactyl with an elongate heel impression. The pattern of digital impressions in track C is vaguely similar to those of limuloids, but the closer clustering in track D render such an assignment unlikely. They resemble neither tridactyl theropod pes nor pterosaur manus prints, but they are reminiscent of crocodylian and some "lacertoid" prints. The lack of detail in the impressions of the digits, however, makes it difficult to attribute them to a specific clade. That they appear bipedal but possess a tetradactyl configuration seems contradictory since the only known Middle Jurassic habitual makers of tetradactyl prints have shortened halluces that, if making an impression, always protrude caudomedially, unlike track D. As with track A, it is possible that they represent a pterosaurian track maker hitherto unrecognized in the track record. In particular, anurognathid pedes are unusual in possessing digits apparently capable of fairly wide angles of divarication

(Wellnhofer, 1975: Fig. 37). The especially long fifth digit probably projected caudally during terrestrial locomotion (D. Unwin, pers. comm., 2003), though it is uncertain if it would have been capable of making a centrally-located impression directly connected to the remainder of the pes. At any rate, the apparently bipedal nature of the track maker would also be surprising for a pterosaur of any sort (but see Padian [1983]), although pterosaurs may have progressed bipedally for short distances during take-off and landing (D. Unwin, pers. comm., 2003).

Except for being tetradactyl and for their elongate heel impressions, tracks C and D bear some similarity to most mammaliform footprints (Figs. 8D, E). These Late Triassic and Early Jurassic mammaliform tracks are tetradactyl, but except for the unnamed tridactyl prints from Brazil (Fig. 8C), none possess an elongate heel impression. However, tracks C and D could represent a mammaliform during an unusual mode of locomotion. Alternatively, if they represent undertracks, an outer digit bearing little weight although present in the track maker, may not be preserved.

In terms of the short, forward-pointing digits I–IV separated by low angles of divarication, tracks C and especially D are not unlike tetradactyl, purported chelonian tracks from the Morrison Formation of Utah (Foster et al., 1999) or the Upper Cretaceous Laramie Formation of Colorado (Wright and Lockley, 2001). Some of the Laramie Formation tracks, as well as tracks from the Late Jurassic of France (Bernier et al., 1982), were made by partially buoyed turtles while swimming and possess narrow, elongate claw marks extending from the tips of the digits, as in track D. However, none of these tracks possesses the elongate, caudal impression seen in the Sundance Formation tracks, and it is difficult to envision a claw capable of producing this mark (wider than those at the digit tips) without also crossing the broader heel impression from which all digit impressions radiate. A chelonian track maker is not indicated.

### CONCLUSIONS

Because of the highly unusual morphology of the Sundance Formation tracks, attempts to identify the track makers are more processes of elimination than of the identification of diagnostic characters. All of the common potential track making animals of the western American Middle Jurassic (limuloids, small dinosaurs, pterosaurs, "lacertoids," crocodylians, or chelonians) produce less-than-satisfactory matches for the Sundance Formation track morphologies without resorting to "special pleading" to manufacture circumstances rare enough in life that they are highly unlikely to be preserved. Yet the prints do not clearly match either known prints or known appendages of potential track makers. So perhaps, to paraphrase Sir Arthur Conan Doyle's detective Sherlock Holmes, when the impossible has been excluded, "whatever remains, however improbable, must be the truth."

Of the scenarios discussed, a pathologic pterosaur perhaps provides the most satisfactory solution for track A and the primary trackway inasmuch as it satisfies the largest number of criteria and would explain the largest number of preserved ichnological features, but it is not a powerful case. A pterosaurian interpretation would explain the number of digits, the elongate, caudal impression, the drag mark lateral to the print, and possibly the existence of track B and its relative position to track A. Arguing against this assignment are the negative rotation of the digits and the low pace angulation. Track A is less like theropod, crocodylian, or mammaliform prints in the preserved morphology. It seems less plausible to invoke such things as selective non-preservation of a single digit than a pathologic track maker. Tracks C and D do not appear to have been made by the same track maker as the prints in the primary trackway and are, in their own way, as enigmatic as track A. They are probably not pterosaurian; they preserve some features reminiscent of crocodylians and turtles, but neither argument is compelling. Of course, it remains possible that the track makers of both the primary and secondary track ways were either taxa unrecognized in the ichnological record or entities currently unknown from body fossils, or that these tracks may have been made by known taxa during complex patterns of locomotion. Future discoveries of tracks of similar morphologies will help elucidate the nature of the Sundance Formation tracks.

### ACKNOWLEDGEMENTS

It is a pleasure to be able to contribute this work in honor of Dr. Bill Sarjeant, whose seminal and copious paleoichnological work paved the way for all future research. The footprints described herein were discovered during the course of research with Drs. Peter Dodson and Bill Donawick (University of Pennsylvania) involving the stratigraphic setting of a sauropod specimen from the Morrison Formation in Montana. Paleoichnological conversations with Dr. Glen Storrs (Cincinnati Museum of Natural History and Science) were enlightening. Comments on earlier versions of this manuscript by Dr. Peter Dodson, Barbara Grandstaff, and Matt Lamanna (University of Pennsylvania) were very helpful and greatly appreciated. Review comments by Debra Mickelson (University of Colorado, Boulder) and discussions with Dr. David Unwin (Museum für Naturkunde, Berlin) greatly improved the manuscript. We thank Bonnie Winslow and Jim Stabler (BICA) for their interest, understanding, and assistance in obtaining the collection permit. Partial funding for the discovery expedition was graciously provided by Emilie deHellebranth.

#### REFERENCES

- Arribas, C. P. and Pérez, E. S. 2000. Huellas de pterosaurios en el Grupo Oncala (Soria, España). *Pteraichnus palaciei-saenzi*, nov. ichnosp. *Estudios Geologicos*, 56:73–100.
- Bennett, S. C. 1997. Terrestrial locomotion of pterosaurs: a reconstruction based on *Pteraichnus* trackways. *Journal of Vertebrate Paleontology*, 17:104–113.

- Bennett, S. C. 2003. A survey of pathologies of large pterodactyloid pterosaurs. Palaeontology, 46:185–198.
- Bernier, P., Barale, G., Bourseau, J.-P., Buffetaut, E., Demathieu, G., Gaillard, C., and Gall, J.-C. 1982. Trace nouvelle de locomotion de chélonien et figures d'émersion associées dans les calcaires lithographiques de Cerin (Kimméridgien Supérieur, Ain, France). *Géobios*, 15:447–467.
- Bird, R. T. 1985. Bones for Barnum Brown: Adventures of a Dinosaur Hunter. Texas Christian University Press, Fort Worth: 225 pp.
- Breithaupt, B. H. 1996. The discovery of a nearly complete *Allosaurus* from the Jurassic Morrison Formation, eastern Big Horn Basin, Wyoming. *In* Hunter, R. A. (ed.). Tate '96: Paleoenvironments of the Jurassic, Field Conference, Friday, June 21–Sunday, June 23. Tate Geological Museum, Casper College, Tate Museum Guidebook 1:98.
- Breithaupt, B. H. 1997. Howe Quarry. In Currie, P. J. and Padian, K. (eds.). Encyclopedia of Dinosaurs, Academic Press, San Diego: 355–356.
- Calvo, J. O. and Lockley, M. G. 2001. The first pterosaur tracks from Gondwana. *Cretaceous Research*, 22:585–590.
- Caster, K. E. 1941. Trails of *Limulus* and supposed vertebrates from Solnhofen lithographic limestone. *Pan-American Geologist*, 76:241–258.
- Conti, M. A., Leonardi, G., Manni, R., and Venturini, C. 1991. Limuloid tracks into the Meledis Fm. (Upper Carboniferous, Kasimovian) of the Carnic Alps. *Giornale di Geologia, Serie* 3, 53:151–159.
- Davis, R. A. and Hays, M. O. 1984. What is a wave-dominated coast? *Marine Geology*, 60:313–329.
- Engelmann, G. F. and Hasiotis, S. T. 1999. Deep dinosaur tracks in the Morrison Formation: sole marks that are really sole marks. *In* Gillette, D. D. (ed.). Vertebrate Paleontology in Utah. Utah Geological Survey, *Utah Geological Survey Miscellaneous Publication*, 99-1:179–183.
- Farlow, J. O. and Pianka, E. R. 2000. Body form and trackway pattern in Australian desert monitors (Squamata: Varanidae): comparing zoological and ichnological diversity. *Palaios*, 15:235–247.
- Foster, J. R., Lockley, M. G., and Brockett, J. 1999. Possible turtle tracks from the Morrison Formation of southern Utah. *In* Gillette, D. D. (ed.). Vertebrate Paleontology in Utah. Utah Geological Survey, *Utah Geological Survey Miscellaneous Publication*, 99-1:185–191.
- Fuentes Vidarte, C. 2001. A new species of *Pteraichnus* for the Spanish Lower Cretaceous: *Pteraichnus cidacoi. Strata, Serie* 1: *Communications*, 11: 44–46.
- Fuentes Vidarte, C. and Meijide Calvo, M. 1999. Primeras huellas de cocodrilo en el Weald de Cameros (Soria, España). Nueva familia: Crocodylopodidae, nuevo icnogénero: *Crocodylopodus* nueva icnoespecie: *C. meijidei. In* Colectivo Arqueológico-Paleontológico de Salas (ed.). Actas de las I Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno. Colectivo Arqueológico-Paleontológico de Salas, Burgos: pp. 329–338.
- Goldring, R. and Seilacher, A. 1971. Limulid undertracks and their sedimentological implications. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 137:422–442.
- Harris, J. D. 1998. Dinosaur footprints from Garden Park, Colorado. In Carpenter, K., Chure, D. J., and Kirkland, J. I. (eds.). The Upper Jurassic Morrison Formation: An Interdisciplinary Study, Modern Geology, 23:291–307.
- Haubold, H. 1971. Ichnia Amphibiorum et Reptiliorum Fossilium. Handbuch der Paläoherpetologie, 18:1–124.
- Haubold, H., Hunt, A. P., Lucas, S. G., and Lockley, M. G. 1995. Wolfcampian (Early Permian) vertebrate tracks from Arizona and New Mexico. *In Lucas*, S. G. and Heckert, A. B. (eds.). Early Permian Footprints and Facies. *New Mexico Museum of Natural History and Science Bulletin*, 6:135–165.
- Hunt, A. P., Lucas, S. G., and Lockley, M. G. 1993. Fossil limuloid trackways from Petrified Forest National Park, Arizona, USA. *In Lucas*, S. G. and Morales, M. (eds.). The Nonmarine Triassic. *New Mexico Museum of Natural History and Science Bulletin*, 3:205–207.
- Hwang, K.-G., Huh, M., Lockley, M. G., Unwin, D. M., and Wright, J. L. 2002. New pterosaur tracks (Pteraichnidae) from the Late Cretaceous Uhangri Formation, southwestern Korea. *Geological Magazine*, 139:421–435.
- Kvale, E. P., Hasiotis, S. T., Mickelson, D. L., and Johnson, G. D. 2001a. Middle and Late Jurassic dinosaur fossil-bearing horizons: implications for di-

nosaur paleoecology, northeastern Bighorn Basin, Wyoming. *In* Hill, C. L. (ed.). Guidebook for the Field Trips, Society of Vertebrate Paleontology 61st Annual Meeting: Mesozoic and Cenozoic Paleontology in the Western Plains and Rocky Mountains. *Museum of the Rockies Occasional Paper*, 3:17–45.

- Kvale, E. P., Johnson, G. D., Mickelson, D. L., Keller, K., Furer, L. C., and Archer, A. W. 2001b. Middle Jurassic (Bajocian and Bathonian) dinosaur megatracksites, Bighorn Basin, Wyoming, U.S.A. *Palaios*, 16:233–254.
- Leonardi, G. 1975. Trackways of the South American lizard *Tupinambis* teguixin (Linnaeus 1758), Lacertilia, Teiidae. Anais Academia Brasilia Ciencias, 47:301–310.
- Lockley, M. and Hunt, A. P. 1995. Dinosaur Tracks and Other Fossil Footprints of the Western United States. Columbia University Press, New York: 338 pp.
- Lockley, M., Meyer, C., Siber, H.-J., and Pabst, B. 1998. Theropod tracks from the Howe Quarry, Morrison Formation, Wyoming. *In* Carpenter, K., Chure, D. J., and Kirkland, J. I. (eds.). The Upper Jurassic Morrison Formation: An Interdisciplinary Study, Part 2. *Modern Geology*, 23:309–316.
- Lockley, M. G. 1999. Pterosaur and bird tracks from a new Late Cretaceous locality in Utah. *In* Gillette, D. D. (ed.). Vertebrate Paleontology in Utah. Utah Geological Survey, *Utah Geological Survey Miscellaneous Publication*, 99-1:355–359.
- Lockley, M. G., Logue, T. J., Moratalla, J. J., Hunt, A. P., Schultz, R. J., and Robinson, J. W. 1995. The fossil trackway *Pteraichnus* is pterosaurian, not crocodilian: implications for the global distribution of pterosaur tracks. *Ichnos*, 4:7–20.
- Logue, T. 1996. Pterosaur tracks at Alcova, Wyoming. *In* Hunter, R. A. (ed.). Tate '96: Paleoenvironments of the Jurassic, Field Conference, Friday, June 21–Sunday, June 23, Tate Geological Museum Guidebook, 1:73–80.
- Logue, T. J. 1977. Preliminary investigation of pterodactyl tracks at Alcova, Wyoming. Wyoming Geological Association Earth Science Bulletin, 10:29.
- Logue, T. J. 1994. Alcova, Wyoming tracks of *Pteraichnus saltwashensis*, made by pterosaurs. *Geological Society of America Abstracts with Programs*, 26:10.
- Mazin, J.-M., Billon-Bruyat, J.-P., Hantzpergue, P., and Lafaurie, G. 2001a. The pterosaurian trackways of Crayssac (southwestern France). *Strata, Serie* 1: *Communications*, 11:54–56.
- Mazin, J.-M., Billon-Bruyat, J.-P., Hantzpergue, P., and Lafaurie, G. 2001b. Could they be the first rhamphorhynchoid tracks? Yes! Strata, Serie 1: Communications, 11:64–65.
- Mazin, J.-M., Hantzpergue, P., Bassoullet, J.-P., Lafaurie, G., and Vignaud, P. 1997. Le gisement de Crayssac (Tithonien inférieur, Quercy, Lot, France): découverte de pistes de dinosaures en place et premier bilan ichnologique. *Comptes Rendus de l'Academie des Sciences de Paris, Sciences de la Terre et des Planètes*, 325:733–739.
- Mazin, J.-M., Hantzpergue, P., Lafaurie, G., and Vignaud, P. 1995. Des pistes de ptérosaures dans le Tithonien de Crayssac (Quercy, France). *Comptes Rendus de l'Academie des Sciences de Paris, Série* IIa, 321:417–424.
- Mehl, M. G. 1931. Additions to the vertebrate record of the Dakota Sandstone. American Journal of Science (Fifth Series), 21:441–452.
- Meijide Calvo, M. 2001. Pterosaur trace in Oncala Berriasian (Soria, Spain). New ichnospecies: *Pteraichnus manueli. Strata, Serie* 1: *Communications*, 11:72–74.
- Meijide Calvo, M. and Fuentes Vidarte, C. 1999. Huellas de pterosaurios en el Weald de Soria (España). *In* Colectivo Arqueológico-Paleontológico de Salas (ed.). Actas de las I Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, pp. 397–406. Colectivo Arqueológico-Paleontológico de Salas, Burgos.
- Meijide Fuentes, F. 2001. Pterosaur tracks in Oncala Mountain Range (Soria, Spain). A new ichnospecies: *Pteraichnus vetustior. Strata, Serie* 1: *Communications*, 11:70–71.
- Melchor, R. N., de Valals, S., and Genise, J. F. 2002. Bird-like fossil footprints from the late Triassic. *Nature*, 417:936–938.
- Mickelson, D. L. 2003. Jurassic dinosaur tracksites from the American West. In Fossils in Motion: Seventh Annual Paleontological Symposium, Alberta

Paleontological Society, Alberta Paleontological Division and Canadian Society of Petroleum Geology, Calgary: 52–56.

- Padian, K. 1983. A functional analysis of flying and walking in pterosaurs. *Paleobiology*, 9:218–239.
- Padian, K. and Olsen, P. E. 1984. The fossil trackway *Pteraichnus*: not pterosaurian, but crocodilian. *Journal of Paleontology*, 58:178–184.
- Rainforth, E. C. and Lockley, M. G. 1996. Tracks of diminutive dinosaurs and hopping mammals from the Jurassic of North and South America. *In* Morales, M. (ed.). The Continental Jurassic. *Museum of Northern Arizona Bulletin*, 60:265–269.
- Rautman, C. A. 1978. Sedimentology of late Jurassic barrier-island complex; lower Sundance Formation of Black Hills. *American Association of Petroleum Geologists Bulletin*, 62:2275–2289.
- Reineck, H. E. and Wunderlich, F. 1968. Classification and origin of flaser and lenticular bedding. *Sedimentology*, 11:99–104.
- Reineck, H.-E. and Howard, J. D. 1978. Alligatorfährten. Natur und Museum, 108:10–15.
- Reineck, H.-E. and Singh, I. B. 1973. Depositional Sedimentary Environments with Reference to Terrigenous Clastics. Springer-Verlag, Berlin: 542 pp.
- Romano, M. and Whyte, M. A. 2003. The first record of xiphosurid (arthropod) trackways from the Saltwick Formation, Middle Jurassic of the Cleveland Basin, Yorkshire. *Palaeontology*, 46:257–269.
- Santucci, V. L., Hays, D., Staebler, J., and Milstein, M. 1999. A preliminary assessment of paleontological resources at Bighorn Canyon National Recreation Area, Montana and Wyoming. *In* Santucci, V. L. and McClelland, L. (eds.). National Park Service Paleontological Research. U.S. National Park Service, Geologic Resources Division Technical Paper, NPS/NDGRD/ GRDTR-99/03: 18–22.

- Sarjeant, W. A. S. 2000. The Mesozoic mammal footprint record reconsidered: with an account of new discoveries in the Cretaceous of northwestern Alberta, Canada. *In Lee*, Y.-N. (ed.). 2000 International Dinosaur Symposium for Kosong County in Korea. *Paleontological Society of Korea Special Publication*, 4:153–168.
- Schult, M. F. 1995. Vertebrate trackways from the Robledo Mountains Member of the Hueco Formation, southcentral New Mexico. In Lucas, S. G. and Heckert, A. B. (eds.). Early Permian Footprints and Facies. New Mexico Museum of Natural History and Science Bulletin, 6:115–126.
- Stokes, W. L. 1957. Pterodactyl tracks from the Morrison Formation. *Journal of Paleontology*, 31:952–954.
- Tanke, D. H. and Rothschild, B. M. 2002. Dinosores: an annotated bibliography of dinosaur paleopathology and related topics—1838–2001. New Mexico Museum of Natural History and Science Bulletin, 20:1–96.
- Thulborn, R. A. 1990. Dinosaur Tracks. Chapman and Hall, London: 410 pp.
- Uhlir, D. M., Akers, A., and Vondra, C. F. 1988. Tidal inlet sequence, Sundance Formation, north-central Wyoming. *Sedimentology*, 35:739–752.
- Unwin, D. M. 1996. Pterosaur tracks and the terrestrial ability of pterosaurs. *Lethaia*, 29:373–386.
- Wellnhofer, P. 1975. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Suddeutschlands Teil II: systematische Beschreibung. Palaeontographica Abteilung A, 148:132–186.
- Wright, J. and Lockley, M. G. 2001. Dinosaur and turtle tracks from the Laramie/Arapahoe formations (Upper Cretaceous), near Denver, Colorado, USA. *Cretaceous Research*, 22:365–376.
- Wright, J. L., Unwin, D. M., Lockley, M. G., and Rainforth, E. C. 1997. Pterosaur tracks from the Purbeck Limestone Formation of Dorset, England. *Proceedings of the Geologists' Association*, 108:39–48.