PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2008, v. 23, p. 3–13
Research Article
DOI: 10.2110/palo.2006.p06-111r

1926 SEPM Society for Sedimentary Geology

A NEW SYSTEM FOR DESCRIBING AND CLASSIFYING TETRAPOD TAIL TRACES WITH IMPLICATIONS FOR INTERPRETING THE DINOSAUR TAIL TRACE RECORD

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ABSTRACT

We introduce new terminology and a new classification scheme for describing tetrapod tail traces, focusing on the interpretation of dinosaur tail traces. Our classification divides tail traces into (1) tail impressions—there is no evidence of forward motion; (2) protracted tail traces—they persist for at least one stride length; and (3) abbreviated tail traces—they persist for less than one stride length. Protracted tail traces are simple or compound, based on the amount of interruption of the tail trace, which we quantify by the percent interruption metric (PIM). Abbreviated tail traces are also simple or compound. Classifications are modified further by sinuosity, which we describe as low or high. The PIM approximates vertical tail motion, and sinuosity approximates lateral tail motion. Sediment variations, preservation, and lateral motion resulting from locomotion must be taken into consideration when interpreting tail traces. This new classification scheme is applied to a partial theropod trackway with associated tail trace from the Upper Jurassic Morrison Formation, Bighorn Basin, Wyoming, United States. The tail trace is protracted and simple with low sinuosity and a low PIM; we interpret this as the result of relatively low tail motion. We hypothesize that significant differences exist between ornithopod and theropod tail trace patterns. We also suggest that protracted tail traces associated with bipedal dinosaur trackways are not the result of the use of the tail as a stabilizing third leg; some may represent incidental contact of the sediment by the tail owing to backward rotation about the pelvis during deceleration.

INTRODUCTION

The purpose of this paper is to establish a standard system for the description and classification of tetrapod tail traces that can be used to aid interpretations of locomotive behavior. One of our goals in creating this system is to better understand the behaviors represented by dinosaur tail traces. The classification scheme and terminology developed here are applied to published tetrapod tail traces and a new partial theropod trackway with an associated tail trace from the Upper Jurassic Morrison Formation, Bighorn Basin, Wyoming, United States. The scheme is not intended to describe and measure fish-swimming traces.

The fossil record contains many examples of vertebrate tail traces attributable to fish (e.g., Anderson, 1976; Gibert et al., 1999; Trewin, 2000; Soler-Gijón and Moratalla, 2001; Haubold et al., 2005b; Martin and Pyenson, 2005), amphibians (e.g., Kohl and Bryan, 1994; Foster, 2001; Pyenson and Martin, 2001; Haubold et al, 2005a, 2005b; Martin and Pyenson, 2005), reptiles (e.g., Chesnut et al., 1994; Foster and Lockley, 1997; Avanzini and Renesto, 2002), and synapsids (e.g., Casamiquela, 1964; Lockley, 2004b). Most of these ichnofossils pose no great challenge to interpretation because modern analogs are readily available. Dinosaur tail traces, however, are poorly understood because no modern animals can accurately reproduce dinosaur locomotion with long, narrow tails (Alexander, 1985; Gatesy, 1990; Carrano and Biewener, 1999). Studies of tetrapod tail traces are also important for understanding behaviors that contributed to the evolution of lifestyles relying heavily on use of the tail for locomotion, that is, aquatic and limbless forms.

BACKGROUND

Observations of modern tetrapods that drag their tails regularly show that tail traces produced during a normal, quadrupedal walking gait are typically long—that is, continuous—and straight to sinuous (e.g., Peabody, 1948; Brand, 1979, 1996; Farlow and Pianka, 2000; Jaeger, 2001). Changes in direction, gait, and movement of the tail cause interruptions and overlaps within the tail trace (e.g., Farlow and Pianka, 2000; Jaeger, 2001). Behaviors, such as resting and jumping, create short tail traces and are common among some extant mammals (Jaeger, 2001). Some macropods (e.g., kangaroos) also use their tails for pentapedal locomotion at low speeds (Baudinette, 1994).

Early reconstructions of dinosaurs depicted passive tail dragging as ubiquitous among most major taxa, contrary to ichnological evidence (Marsh, 1896; Wade, 1989). The paucity of tail traces at dinosaur track sites was explained initially as the result of floatation of the tail or of the entire body during locomotion in shallow water (e.g., Hitchcock, 1858; Bird, 1954). Subsequent functional studies, however, revealed that the correct position of the dinosaurian tail was near horizontal and well off the ground (Galton, 1970; Newman, 1970; Coombs, 1975), an orientation that was important for balance, especially in bipedal forms (Galton, 1970; Gatesy, 1991; Farlow et al., 2000). Dinosaur tail traces, therefore, can be viewed as representing deviations from normal locomotor patterns in response to unique biological or external environmental factors.

Widely cited examples of dinosaur tail traces have been attributed to three major groups on the basis of associated footprint morphology: sauropodomorphs (prosauropods and sauropods), theropods, and ornithopods. Known examples for each group are discussed briefly and, in conjunction with observations of modern and ancient tetrapod tail traces, form the basis for the classification scheme proposed in this paper.

Sauropodomorph Tail Traces

Sauropodomorph tracks are very rarely associated with tail traces. A short tail trace is associated with one specimen of the ichnogenus *Otozoum caudatum* (syn. *O. moodii*) and is attributed to a prosauropod (Rainforth, 2002, 2003). Tail trace–bearing *Gigandipus caudatus* trackways have been attributed to prosauropods (Weems, 1992, 2003) but have also been interpreted as theropod trackways (Olsen et al., 1998; Rainforth, 2003; Smith and Farlow, 2003).

Sauropod tail traces have been reported from the Lower Cretaceous Glen Rose Formation at the Paluxy River track site, Texas, United States (Bird, 1941, 1944, 1954). These traces, however, are indistinct and weathered (Bird, 1954) and may actually be tool marks or toe drags (Kuban, 1989). Possible sauropod tail traces are also reported from the Jurassic d'El Mers Formation in Morocco (Jenny et al., 1981) and in association with *Titanosaurimanus nana* tracks in Croatia (Dalla Vecchia and Tarlao,

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2000). A sauropod trackway from the upper member of the Middle Jurassic Entrada Sandstone, Utah, United States, contains a wide, sinuous groove interpreted as a tail trace (Foster et al., 2000; Kirkland, 2001; Breithaupt et al., 2004).

Theropod Tail Traces

The ichnotaxa *Gigandipus caudatus*, *Selenichnus falcatus*, *S. breviusculus*, and *Hyphepus fieldi* are attributed to theropods and are relatively thin, slightly sinuous, and uninterrupted to slightly interrupted; some are associated with pes prints that contain impressions of digit I (Hitchcock, 1858; Lull, 1953). There is disagreement, however, about the interpreted trace makers of the ichnogenera *Gigandipus* and *Selenichnus*, which have also been attributed to a prosauropod (Weems, 2003) and a crocodylomorph (Lockley et al., 2004a), respectively. Isolated, sinuous grooves associated with both theropod and ornithopod tracks in the Upper Cretaceous Toreva Formation in northeastern Arizona, United States, are likely tail traces but cannot be attributed with certainty to either group (Irby and Albright, 2002).

Theropod pes and tail traces associated with manus, ischial, and metatarsal impressions are interpreted as resting traces (e.g., Lockley et al., 2003). Examples are *Agialopous* (Breithaupt and Matthews, 2004), which may be a junior synonym of *Grallator* (Heckert and Lucas, 1998), *Eubrontes* (Gierlinski et al., 2004; Matthews et al., 2004; Milner et al., 2004), and *Chonglongpus* (Lockley et al., 2003). Note that *Eubrontes* has been attributed also to an ornithopod dinosaur (Weems, 2003). Y-shaped furrows associated with theropod tracks in the Lower Cretaceous Glen Rose Formation, Texas, United States, are interpreted as the result of double contact of the tail of one individual (Kuban, 1989).

Ornithopod Tail Traces

Elongate, sinuous tail traces, many with interruptions, are known from trackways attributed to ornithopod dinosaurs, including *Moyenisauropus* (Ellenberger, 1974; Thulborn, 1990), which may be a junior synonym of *Anomoepus* (Olsen and Rainforth, 2003), and from various trackways not assigned to ichnogenera (Viera et al., 1984; Gillette and Thomas, 1985; Irby and Albright, 2002; Getty, 2004; Hunt and Lucas, 2004). Some ornithopod tail traces are associated with crouching or resting traces that include impressions of the metatarsals, manus, chest, or ischia. Examples include *Anomoepus* (Hitchcock, 1865; Lull, 1953; Olsen and Rainforth, 2003; Kundrát, 2004), *Jialingpus yuechiensis* (Zhen et al., 1983), and *Moyenisauropus* (Ellenberger, 1974).

CLASSIFICATION AND MEASUREMENT OF TETRAPOD TAIL TRACES

Tail Trace Terminology and Measurements

The cross-sectional profiles of well-preserved tail traces are described commonly as U- or V-shaped (e.g., Kohl and Bryan, 1994; Irby and Albright, 2002). Some tail traces contain a deep, central furrow referred to as a ventral keel, which is interpreted as the impression of a dermal projection along the ventral midline of the tail (Rainforth, 2002). Many tetrapod tail traces also contain raised ridges along the lateral borders of the tail trace that resulted from displacement of sediment during lateral movement by the tail. These ridges can vary in thickness along the length of a tail trace and are referred to as expulsion rims (Irby and Albright, 2002).

Tail Trace Width.—The width of the tail trace is the distance between the lateral margins of the trace, excluding expulsion rims, measured

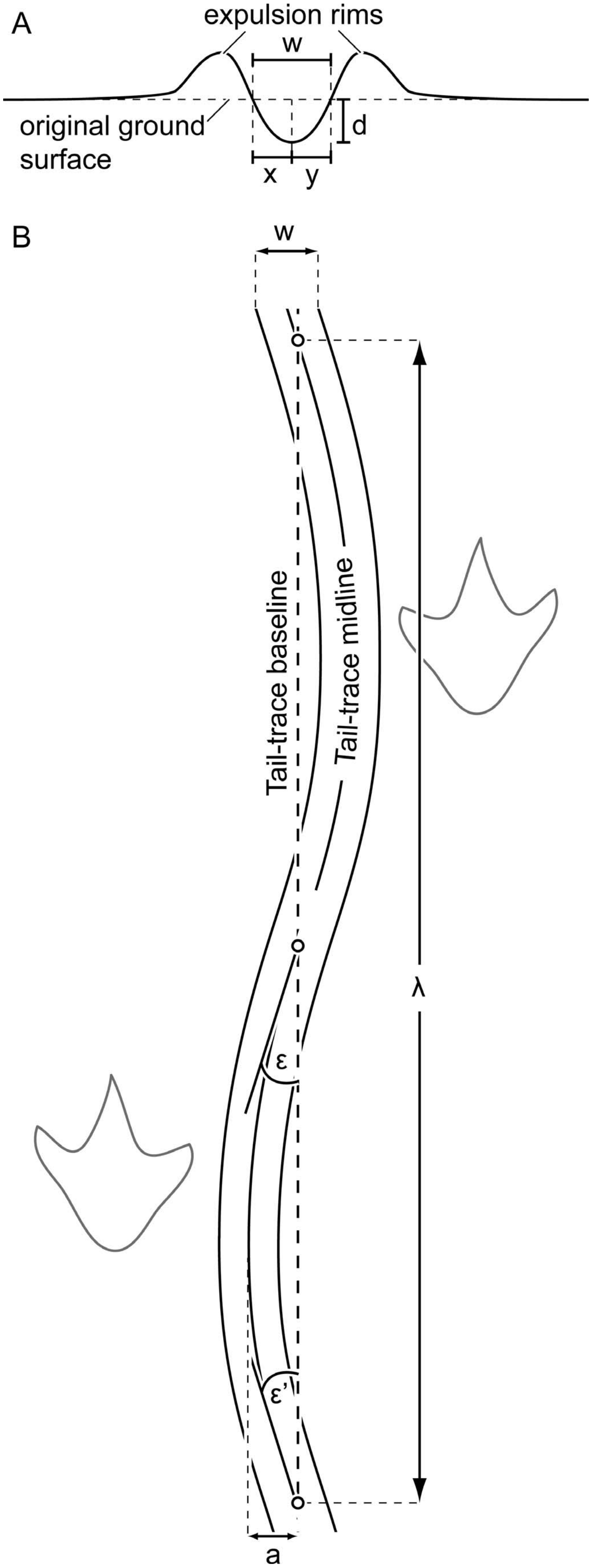

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FIGURE 1—Tail trace measurements. A) Cross-sectional profile view of a tail trace with expulsion rims; if x = y, then the tail trace is symmetrical; otherwise it is asymmetrical. B) Plan view of tail trace. a = amplitude; d = depth; w = width; ε, ε′ = divarication of tail trace midline from baseline; λ = wavelength.

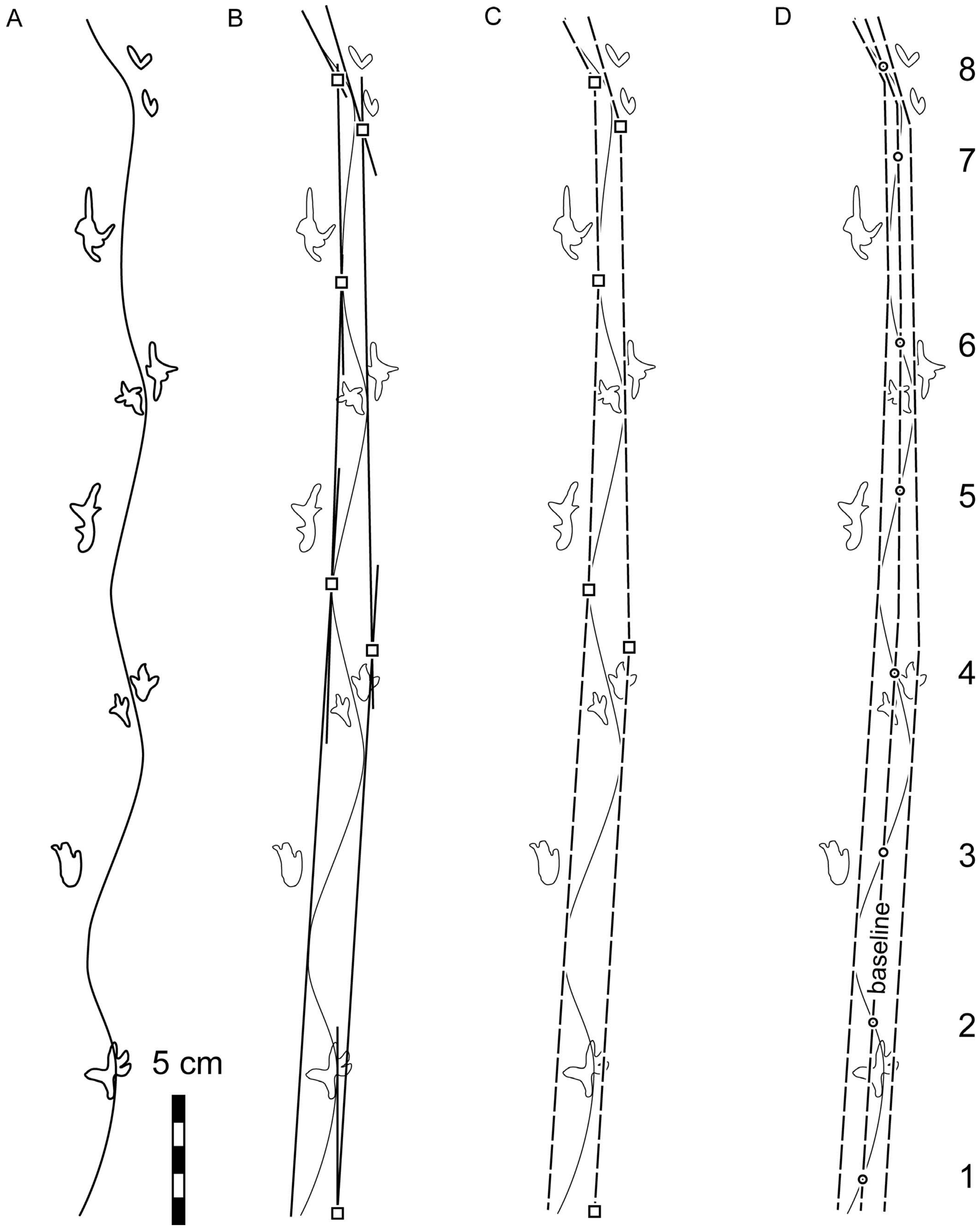

FIGURE 2—Suggested method for taking tail trace measurements. A) Example of method for establishing tail trace baseline; trackway is *Macropterna vulgaris* (redrawn from Hitchcock, 1858). B) Tangents drawn at each crest and trough, squares mark intersections of tangents. C) Dashed lines connect tangent intersections. D) Tail trace baseline is equidistant from the dashed lines in C. Nodes are numbered 1–8 and represent intersections of baseline and midline. Nodes mark points of inflection and are used for measuring wavelength.

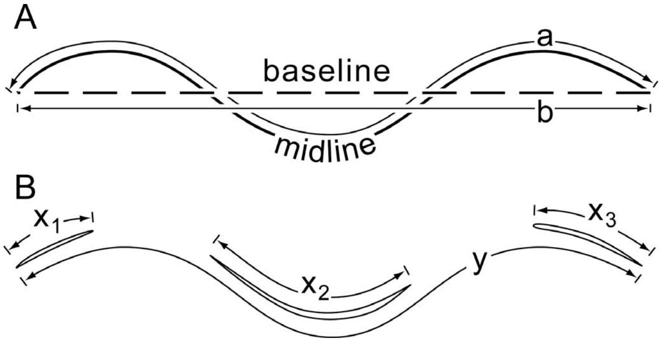

FIGURE 3—Measurement of tail trace sinuosity and percent interruption metric (PIM). A) Sinuosity = a/b. B) Example of PIM calculation: PIM = $100\ y^{-1}\ (y - (x_1 + x_2 + x_3))$. a = length of tail trace midline; b = length of tail trace baseline; x_1, x_2, x_3 = lengths of segments of tail trace; y = total length of tail trace midline.

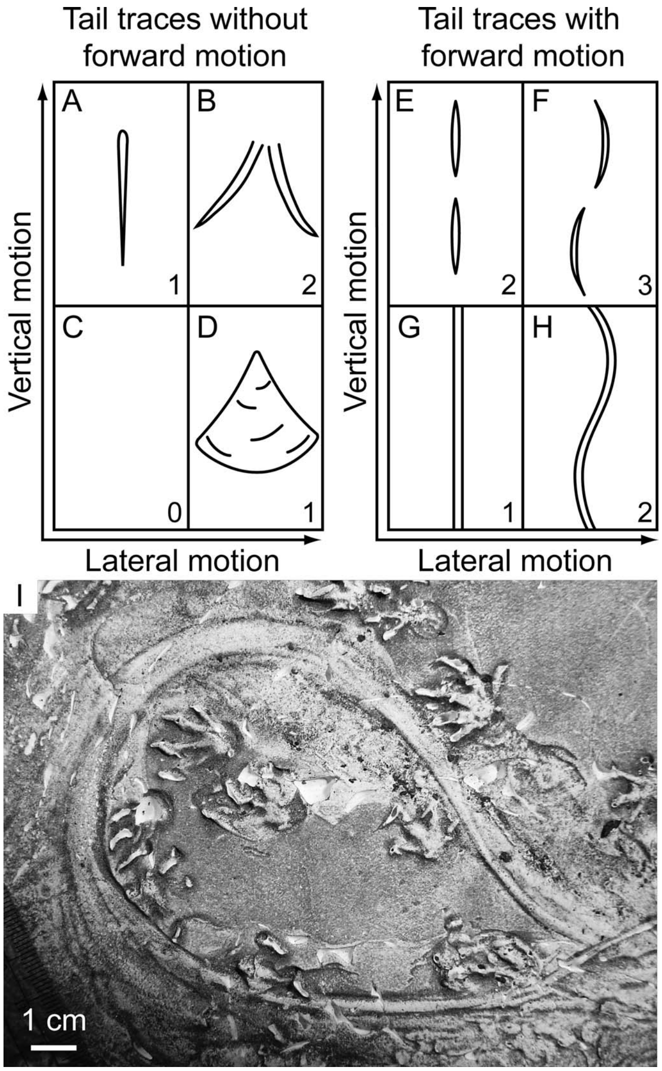

FIGURE 4—Tail trace patterns (in plan view) with varying amounts of motion in three dimensions. A–H) Theoretical patterns showing active tail motion while the trace maker remains stationary (A–D) and tail ground surface contact during forward locomotion (E–H). Numbers in the lower right-hand corners = number of vectors represented by each trace. A) Tail impression produced from vertical motion only. B) Abbreviated, compound tail trace produced from both lateral and vertical movement of the tail without any forward motion. C) No tail motion in any direction. D) Wide, fanlike trace produced by lateral motion without vertical motion. E) Vertical tail motion during locomotion produces a straight, interrupted tail trace. F) Vertical and lateral motion during locomotion produces a sinuous, interrupted tail trace. G) Forward motion with no active tail motion produces a straight, uninterrupted tail trace. H) Lateral tail motion during locomotion produces a sinuous, uninterrupted tail trace. I) Plaster cast of tail trace produced by tiger salamander (*Ambystoma tigrinum*) in moist sediment of very fine sand, silt, and clay (<0.125 mm). Note increase in tail trace width associated with the turn in the trackway.

perpendicularly to the long axis of the trace (Figs. 1A–B). Tail trace width represents the width of the widest part of the tail in contact with the sediment and can be used to calculate minimum tail radius (Kohl and Bryan, 1994). Thin tail traces may represent only the ventral keel of an animal (Rainforth, 2002). Avanzini and Renesto (2002) related *Rhynchosauroides tirolicus* tail trace width to the distance to the height of the trace maker above the ground.

Tail Trace Symmetry.—Tail trace symmetry is determined by comparing the distances between the point of maximum depth of the tail trace and each lateral margin of the trace in cross section (Fig. 1A).

Tail Trace Depth.—The depth of the tail trace is measured vertically from, and perpendicularly to, the original ground surface (Fig. 1A), disregarding expulsion rims, to the maximum depth of the trace (Kohl and Bryan, 1994, fig. 7).

Tail Trace Midline.—The tail trace midline is the line connecting all points that are equidistant from the lateral margins of the tail trace (Fig. 1B). The midline is especially important for measuring wide tail traces.

Tail Trace Baseline.—The baseline is a reference line for measurements drawn to account for turns in the track maker's path. A baseline is established easily for curved and sinuous tail traces (e.g., Fig. 2A) by first drawing tangents to each crest of the tail trace midline (Fig. 2B) and then connecting the intersections of the tangents on each side of the midline; this will create two lines that bracket the tail trace (Fig. 2C). The baseline is the line equidistant between these two lines (Fig. 2D). The tail trace baseline can be easily superimposed on a trackway photograph with vector graphics software by using such tools as the blend feature in Adobe Illustrator CS2 (Adobe Systems, 2005). The baseline will intersect the points of inflection, which we refer to as nodes, in the tail trace midline. This method is necessary in order to standardize the construction of the tail trace baseline, and it ensures that tail trace measurements are repeatable when the same trace is measured by different workers.

Tail Trace Wavelength.—Many tail traces resemble transverse waves. Wavelength is used to refer to the distance between two crests or troughs on an individual tail trace (e.g., Foster and Lockley, 1997; Gibert et al., 1999; Trewin, 2000; Soler-Gijón and Moratalla, 2001). The distance between every three nodes is measured to determine tail trace wavelength because sinuous tail traces are not perfect waves (Fig. 1B). Tail trace wavelength represents tail motion in the lateral plane. If enough data are collected to relate wavelength and stride length, the two may be able to aid in track-maker identification and estimation of tail motion.

Tail Trace Amplitude.—Amplitude is used as a descriptive term in the literature for sinusoidal tail traces (e.g., Gibert et al., 1999; Farlow and Pianka, 2000; Soler-Gijón and Moratalla, 2001). Here we formalize the definition of tail trace amplitude as the maximum distance between tail trace baseline and midline in each crest or trough (Fig. 1B). Amplitude, like wavelength, is related to lateral tail motion.

Divarication of Tail Trace Midline from Baseline.—Tail traces can be described by the angles with which the midline intersects the baseline, similar to the attitude angle of fish trails described by Soler-Gijón and Moratalla (2001). This is done by constructing a tangent to the midline and measuring the angle created where midline intersects baseline at each node (Fig. 1B). We refer to the angle at which the trace departs from the midline as ε, and the angle at which the same excursion reenters the tail trace midline as ε'. We chose this letter because Leonardi (1987) has already assigned the letters α through δ to different trackway angles.

Tail Trace Sinuosity.—Sinuosity can be a simple and convenient way to describe tail traces, just as it is for characterizing meandering rivers. To calculate tail trace sinuosity, divide total tail trace length, measured along the midline, by the length of the corresponding tail trace baseline

TABLE 1—Application of measurement and classification systems to examples of tetrapod tail traces from the literature; all examples represent protracted, simple traces. a = average amplitude; PIM = percent interruption metric; S = sinuosity; λ = average wavelength.

								Classification all protracted, simple	
Reference	Ichnotaxa	Trackmaker	PIM	S	λ (cm)	a (cm)	λ/a ratio	PIM	Sinuosity
Hitchcock, 1858, pl. 35, fig. 9	*Macropterna vulgaris*	amphibian	0	1.08	12.4	0.8	15.5	low	high
Peabody, 1948, p. 461, pl. 42A	—	*Gerrhonotus coeruleus*	0	1.02	5.5	0.2	27.5	low	low
Lull, 1953, p. 160, fig. 33	*Selenichnus*	theropod or crocodile[1]	0	1.01	20.7	0.2	103.5	low	low
Lull, 1953, p. 184, fig. 52	*Gigandipus caudatus*	theropod or prosauropod[2]	0	1.02	14.8	0.3	49.3	low	low
Lull, 1953, p. 186, fig. 54	*Hyphepus*	theropod dinosaur	0	1.03	38	2.5	15.2	low	low
Gillette and Thomas, 1985, p. 284, fig. 3	—	ornithopod dinosaur	23.5	1.09	360	37.5	9.6	high	high
Thulborn, 1990, p. 94, pl. 6	*Moyenisauropus longicauda*	ornithopod dinosaur	9.7	1.02	44.3	0.8	55.4	high	low
Farlow and Pianka, 2000, p. 241, fig. 6A	—	*Varanus eremius*	8.5	1.10	16.5	1.8	9.2	high	high
Farlow and Pianka, 2000, p. 243, fig. 7	—	*Varanus tristis*	0	1.07	16.8	0.7	24	low	high
Foster et al., 2000, p. 173, fig. 5	cf. *Brontopodus*	sauropod dinosaur	7.3	1.03	450	30	15	high	low
Irby and Albright, 2002, p. 518, fig. 3, no. 2	—	ornithopod or theropod	0	1.06	163.3	6.4	25.5	low	high

[1] See Lockley et al. (2004a).

[2] See Weems (2003).

(Fig. 3A). The result is a dimensionless number that will always be ≥1—the larger the number, the more sinuous the tail trace. Tail trace sinuosity is related to the amount of lateral tail motion. Further studies of tail traces may reveal a relationship between tail trace sinuosity and gait.

Percent Interruption Metric.—Tetrapod tail traces are described typically as continuous or discontinuous (e.g., Lull, 1953; Farlow and Pianka, 2000; Irby and Albright, 2002). These terms are dependent, however, on the length of trackway exposed. Any dinosaur tail trace, for example, should be discontinuous in a long enough trackway based on the normal horizontal position of the tail (Galton, 1970; Gatesy, 1991; Farlow et al., 2000). We propose that tail traces be viewed in terms of continuity relative to the total length of the tail trace. This can be quantified by calculating the percent interruption metric (PIM):

$$\mathrm{PIM} = 100 \times y^{-1}\left(y - \sum x_n\right),$$

where n = number of tail trace segments, x = length of each segment, and y = total length of the trace. Most tail traces range from 0% interruption (truly continuous) to <100% interruption. If the tail struck the ground more than once along the forward path of motion (Farlow and Pianka, 2000, fig. 6), however, segments of the tail trace will overlap, and the sum of segment lengths (Σx_n) will exceed the total length (y), yielding a negative PIM.

Ideally, PIM represents tail motion in the vertical (i.e., sagittal) plane but can vary as a result of preservational factors. Nonpreservation of portions of the tail trace because of changes in sediment consistency, bioturbation, and weathering can artificially increase the PIM. This must be taken into account when interpreting the amount of tail motion represented by a tail trace.

Application of Measurement Methodology

We have applied our measuring methods to several tetrapod tail traces in the literature (Table 1). The measurements are taken from published figures using the associated scale bars. This has reduced precision, but it provides an idea of the variation of these values, which is used in the construction of the classification scheme. Wavelength and amplitude are highly variable and appear to be related to the size of the trace maker. The effects of size can be negated by using a ratio of wavelength to amplitude in comparing tail traces, which is similar to that done in studies of fish swimming traces (e.g., Gibert et al., 1999; Trewin, 2000) and the sinuous invertebrate trace fossil *Cochlichnus* (e.g., Uchman et al., 2004).

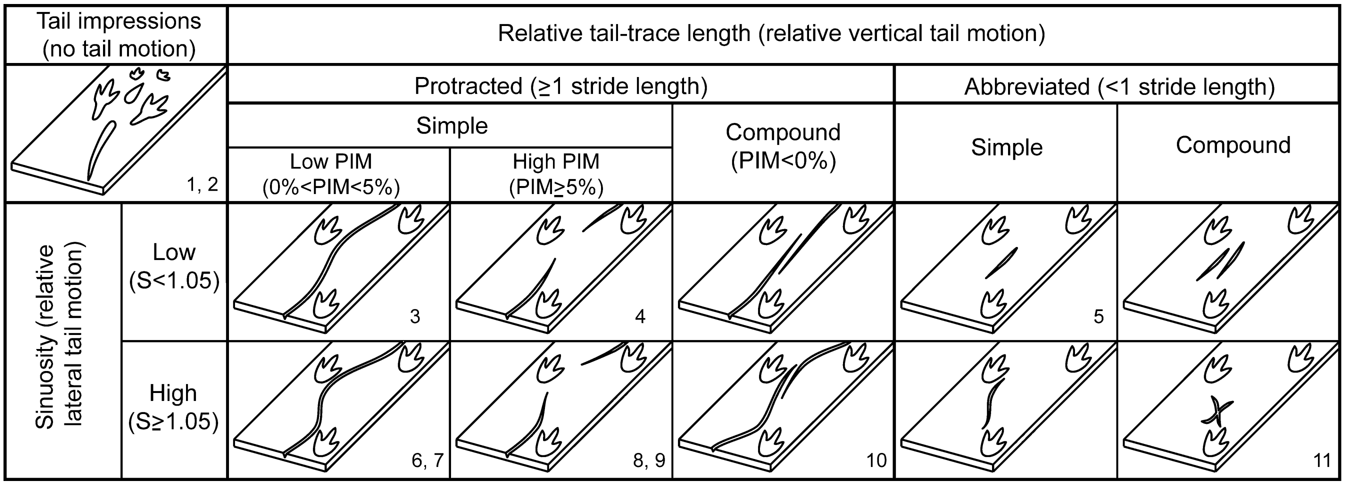

FIGURE 5—Summary of proposed tail trace classification scheme, pictured for bipedal trackways but applicable to all tetrapod trackways. Numbers in lower right-hand corner of boxes refer to literature examples: 1 = Olsen and Rainforth (2003, fig. 19.5B); 2 = Olsen and Rainforth (2003, fig. 19.25V–W); 3 = Peabody (1948, pl. 42A); 4 = Foster et al. (2000, fig. 5); 5 = Rainforth (2003, fig. 5E); 6 = Farlow and Pianka (2000, fig. 7); 7 = Hitchcock (1858, pl. 35, fig. 9); 8 = Viera et al. (1984, fig. 5); 9 = Gillette and Thomas (1985, fig. 3); 10 = Farlow and Pianka (2000, fig. 6, right); 11 = Kuban (1989, fig. 7.7).

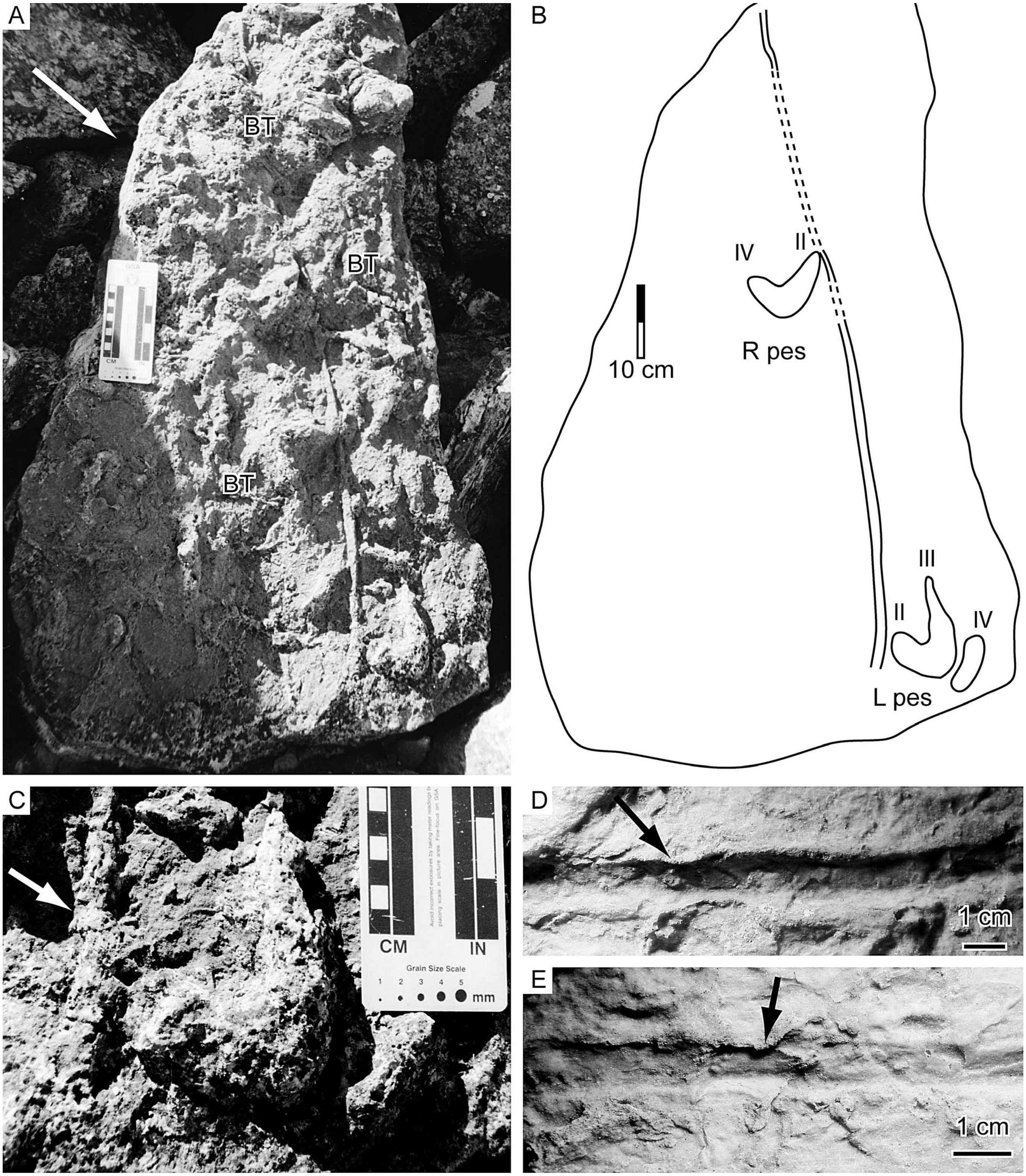

FIGURE 6—New Morrison Formation partial trackway with associated tail trace. Arrows = direction of light. A) Photograph of entire slab; BT = areas of bioturbation. B) Line drawing of partial trackway in A. C) Detail of tridactyl pes print. D) Detail of tail trace showing expulsion rims. E) Detail of tail trace showing ventral keel. Photographs A, C = natural sandstone cast; D, E = latex mold of trace (University of Kansas Museum of Invertebrate Paleontology specimen KUMIP 311150).

Classifying Tail Traces

Tail traces can be viewed as resulting from varying amounts of motion in three dimensions (Fig. 4). Motion in the vertical plane controls continuity, lateral motion controls sinuosity, and the forward motion of the animal controls length. Our classification is biased toward tail traces that show evidence of motion in all three dimensions (Figs. 4F, 4H) because this pattern is prevalent in modern and fossil tail traces. Forward and some lateral motion result from locomotion (e.g., Snyder, 1962; Gatesy, 1990) and are deemphasized in our classification to enable interpretations

TABLE 2—Measurements of new partial trackway in the Morrison Formation.

	Footprint length (cm)	Footprint width (cm)	Digit length (cm)			Digit divarication		
			II	III	IV	II–III	III–IV	II–IV
Right pes	NA	13	6.0	NA	5.6	NA	NA	85°
Left pes	13.1	12	5.5	8.7	4.7	37°	40°	87°

of active tail motion. We define active tail motion as movement of the tail that is independent of limbed locomotion. For example, the caudofemoralis muscles cause tail movement during normal locomotion of limbed tetrapods; this example is not considered active tail motion. Note also that tail trace patterns are affected by the length of the portion of the tail in contact with the sediment. We have observed in neoichnological experiments that a substantial length of tail in continuous contact with the ground surface can produce increases in tail trace width during direction change (Fig. 4I).

Tail traces are classified primarily on inferred vertical motion; these designations are supplemented by the PIM and sinuosity. This classification (Fig. 5) separates out tail traces that show no evidence of forward or lateral motion; these are referred to as tail impressions (Olsen and Rainforth, 2003). Tail impressions are diagnosed by their association with resting traces and pes prints with metatarsal impressions, their distal-tapering nature, and rare skin impressions (e.g., Olsen and Rainforth, 2003).

All remaining tetrapod tail traces presumed to have been produced during locomotion are divided into two broad categories—protracted and abbreviated—based on tail trace length relative to stride length (Fig. 5). Protracted tail traces are present, with or without interruption, for one or more consecutive stride lengths, while abbreviated tail traces persist for less than one stride length. One stride length is used as the division between protracted and abbreviated tail traces because we assume that a tail trace persisting for more than one stride length resulted from an intentional behavior that was incorporated into the track maker's gait. A tail trace present for less than one stride length and not repeated is viewed as unintentional or unnecessary for locomotive behavior because tail position is not consistent over one complete gait cycle. Protracted tail traces are subdivided into simple or compound based on the PIM. Protracted simple tail traces (Fig. 5) have a PIM between 0% and 100% and record evidence of the tail of the trace maker making one pass across the sediment. For these, a PIM of 5% is tentatively assigned as the dividing point between low and high interruption, based on the calculated mean PIM values in Table 1. Protracted compound tail traces (Fig. 5) are protracted tail traces that show overlap, and, as a result, each will have a negative PIM.

Abbreviated tail traces are divided into simple and compound (Fig. 5) based on whether they represent a single or multiple episodes of tail sediment contact at the same point. The segments of these tail traces may or may not intersect.

The primary classifications are based on inferred vertical tail motion. These are modified further by measurements of sinuosity, which describe lateral tail motion. Sinuosity will not be applicable to many abbreviated tail traces because they are too short to record a significant amount of curvature. Abbreviated, compound tail traces are considered to have high sinuosity when one or more of the tail trace segments have high sinuosity. The division between low and high sinuosity tail traces is tentatively placed at 1.05 (Fig. 5), based on the mean of calculated sinuosity values in Table 1. Using this system, several examples of published tail traces are classified in Table 1.

A NEW TAIL TRACE FROM THE MORRISON FORMATION

Trace-Fossil Description

The newly discovered slab containing vertebrate trace fossils associated with a tail trace is from the Upper Jurassic Morrison Formation, Bighorn County, Wyoming, United States. The trace fossils are preserved in convex hyporelief on the underside of a 0.5-m-thick, fine-grained, climbing-ripple-laminated sandstone bed. The sandstone overlies a red- and green-mottled, bioturbated mudstone containing carbonate nodules and rhizoliths. We interpret the sandstone as a crevasse-splay deposit and the mudstone as pedogenically modified floodplain deposits. This succession is interpreted as part of an avulsion deposit. The preservation of traces at the contact between the mudstone and sandstone suggests that the traces were created originally in the underlying mudstone (Platt and Hasiotis, 2006). The sandstone slab with the vertebrate trace fossils has weathered out, fallen from the outcrop, and is overturned relative to its original orientation. Measurement protocol is taken from Leonardi (1987).

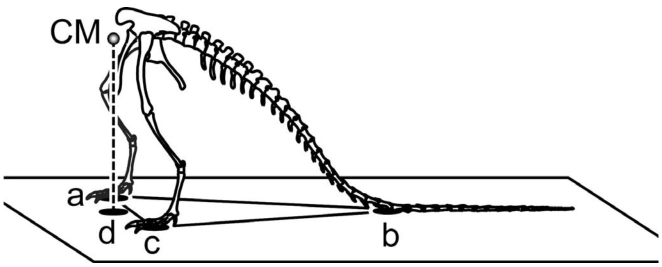

FIGURE 7—Partial *Ornitholestes* skeleton showing how tail dragging fails to increase stability in bipedal dinosaurs. The center of mass (CM) projected to a point on the ground (d) falls outside triangle created by the feet and tail (abc). Redrawn from Osborn (1903).

The slab (Figs. 6A–B) contains one well-preserved tridactyl print, a poorly preserved didactyl print, and a very slightly sinuous ridge oriented parallel to the middle digit of the tridactyl track. The tridactyl track cast is digitigrade, 13.1 cm long, 12 cm wide, and 1.8 cm thick. The track has a narrow, anterior-tapering, slightly sinuous middle digit that is 8.7 cm long, which is substantially longer than the length of the 5.5 cm and 4.7 cm outside digits (Fig. 6C). The middle digit is connected to the 5.5-cm-long digit by a hypex impression. The angles of divarication between the two connected digits, the middle digit and the unconnected digit, and the two outermost digits are about 37°, 40°, and 87°, respectively. The didactyl track cast is 13 cm wide, 1.9 cm thick, and preserves two connected digits, with lengths of ~6.0 cm and 5.6 cm. The angle between the two preserved digits is ~85°.

The ridge follows approximately the midline between the two tracks and is up to 1.3 cm wide and 0.5 cm thick; it has a V-shaped, cross-sectional profile and narrow grooves on the left and right margins (Fig. 6D). In some places, the ridge contains a thicker, 0.2-cm-wide protrusion parallel to its orientation at the apex of the V shape in its profile (Fig. 6E). The ridge passes close to the medial border of the tridactyl track and intersects the didactyl track.

Trace-Fossil Interpretation

We interpret the didactyl track as a poorly preserved example of a tridactyl track. The two digits of the didactyl track represent digits II and IV because their lengths and total divarication are similar to digits II and IV of the associated tridactyl track. The middle digit of the didactyl track was either not preserved owing to sediment variation or subsequent bioturbation, or it was not present because of injury. Both footprints represent two sequential pes tracks in the same bipedal trackway because of their dimensions, orientations, and positions relative to each other. According to this interpretation, the tridactyl track is a left pes and the didactyl track is a right pes (Table 2), and pace width and external trackway width are 4.9 cm and 21 cm, respectively. The next left pes print should be present based on stride length, but it may have been obliterated by subsequent bioturbation by invertebrates, was not preserved because of variation in sediment consistency, or was not placed as predicted owing to a change in the animal's gait. Supposing the right pes represents the point approximately halfway between successive left footfalls, the stride length is estimated to be ≤ 92 cm by doubling pace length.

We interpret the sinuous ridge along the partial trackway midline as the cast of a tail trace. The parallel grooves are interpreted as casts of expulsion rims, and the central protrusion is interpreted as the cast of a ventral keel impression. Assuming that a second left pes print was present but not preserved, the tail trace is classified as protracted and simple according to the classification system presented here. The tail trace has a sinuosity of 1.01 and a PIM of 34%, but most of its interruption appears to have been caused by bioturbation. Wavelength, amplitude, and divarication of tail trace from the midline cannot be measured because there is not a long enough portion of the trackway preserved.

Track-Maker Interpretation

The partial trackway is tentatively attributed to a theropod dinosaur based on the elongate, tapering, and sinuous nature of digit III and the narrowness of the digits (Thulborn, 1990; Dalla Vecchia and Tarlao, 2000). It is important to note, however, that the tracks do exhibit some ornithopod characteristics such as subequal length and width and wide digit divarication (Dalla Vecchia and Tarlao, 2000). Using the morphometric relationships of Thulborn (1989), we estimate a hip height (h) of 57.5 cm. Henderson (2003) found that morphometric formulas are the most accurate methods for estimating hip heights of small theropods. Because of the highly digitigrade nature of this track, however, this method may not produce reliable results. Geometric estimations are also inadequate because of the uncertain stride length and angle of gait. Alternatively, we applied a morphometric ratio derived by Avnimelech (1966), which states that in tridactyl, bipedal dinosaurs, the length of digit III represents 18% of the combined lengths of the femur, tibia, and metatarsus. This technique yields a value of 48.3 cm for h. Alexander's (1976) equation for calculating speed yields maximum velocities of 1.3 $\mathrm{m{\cdot}s^{-1}}$ and 1.6 $\mathrm{m{\cdot}s^{-1}}$ for each value of hip height, respectively. Note, however, that this value is based on a highly uncertain reconstructed stride length.

The firmness and consistency of the original sediment cannot be determined with certainty because these traces represent merely the infilling of the actual tracks. Using the nature of the traces to interpret original consistency, we interpret that the sediment was likely moist, allowing for penetration of the foot and tail into the sediment. The apparently undeformed and relatively well preserved nature of the dinosaur traces suggests that the sediment was also fairly cohesive. Sediment variation appears to be minimal with little variation in depth between footprints and within the trail trace. The trace maker is interpreted to have exercised relatively low tail motion while creating the interval of the trace preserved, based on the low PIM and low sinuosity of the simple tail trace.

DISCUSSION

Trace-Maker Identification

Such features as a cross-sectional profile and the presence or absence of a ventral keel may be diagnostic of certain groups of trace makers (Rainforth, 2003). We hypothesize that such features as sinuosity, amplitude, and wavelength can be used to distinguish between groups of trace makers. This can be useful where tracks are poorly preserved or absent (e.g., Irby and Albright, 2002) or with trace makers that make very similar footprints, for example, many theropod and ornithopod dinosaurs (Thulborn, 1990). We propose that theropods and ornithopods produced

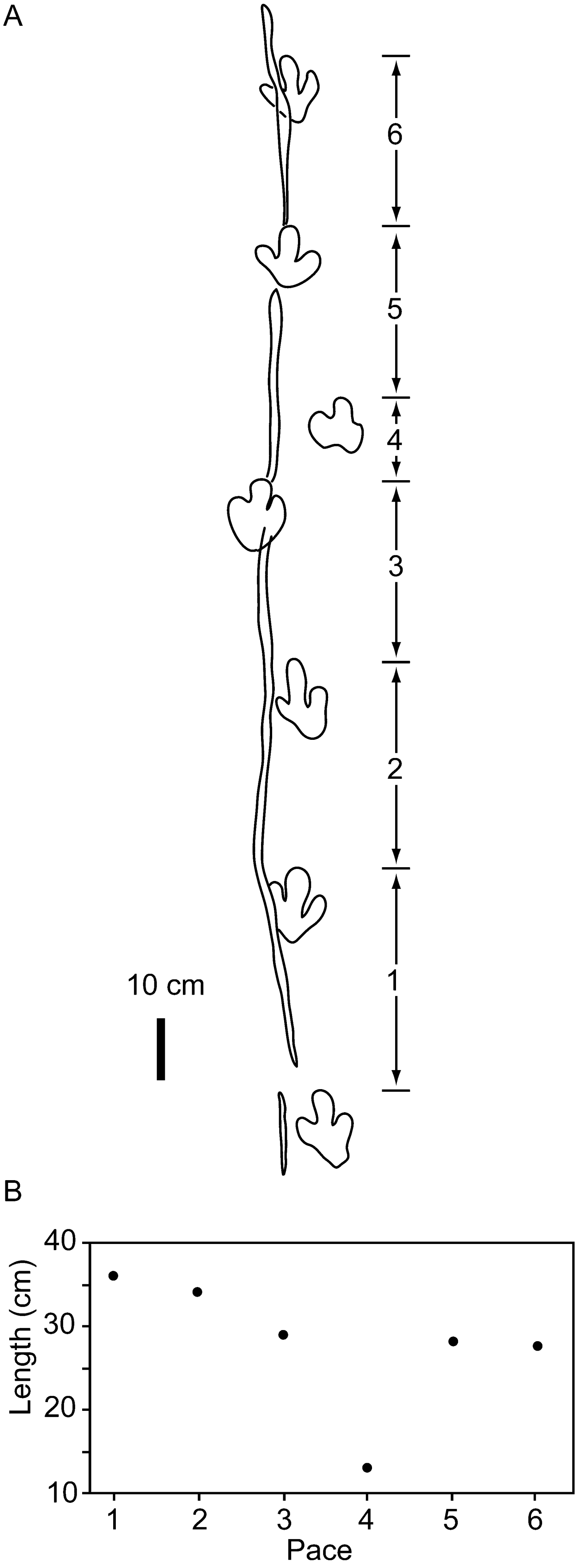

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FIGURE 8—Example of tail trace associated with deceleration in a bipedal trackway. A) *Moyenisauropus longicauda* trackway with tail trace showing decrease in pace length (1–4) interpreted as the result of a decelerating track maker. Redrawn from Thulborn (1990). B) Overall decreasing trend in pace length between successive tracks shown in A.

distinct tail trace patterns based on differences in theropod and ornithopod tail anatomy.

Most ornithopods had ossified tendons along the vertebral column that restricted motion in at least the proximal portion of the tail (Horner et al., 2004; Norman, 2004; Norman et al., 2004). These tendons restricted mostly vertical but also lateral motion. Although the amount of flexibility is uncertain (Alexander, 1989), a conservative estimate of 1° of lateral movement at each vertebral joint results in a swing of the tail tip $>50°$ (Wade, 1989).

The caudal vertebrae of most theropods show a distinct transition point marked by the distal reduction and absence of neural arches and transverse processes, L-shaped distal chevrons, and elongated prezygapophyses on the distal caudal vertebrae (Russell, 1972; Gauthier, 1986; Farlow et al., 2000). This resulted in a tail with more lateral flexibility proximally than was present distally (Newman, 1970; Holtz and Brett-Surman, 1997; Farlow et al., 2000). More tail trace data are needed ultimately to test the hypothesis that differences in theropod and ornithopod tail anatomy were sufficient to produce diagnostic tail trace patterns.

Behavioral Interpretations of Bipedal Dinosaurs

Tail traces associated with bipedal dinosaur trackways may provide important behavioral information that is not obvious from footprints alone because they represent departures from normal posture. There appear to be two different types of theropod and ornithopod tail traces based on observations of published trackways: (1) tail impressions and abbreviated tail traces associated with resting traces and (2) protracted tail traces associated with locomotion.

Tail traces associated with resting traces are interpreted most parsimoniously as the result of the tail touching the ground as the body of the animal was lowered. The behavior responsible for protracted tail traces, however, is more difficult to interpret. Gillette and Thomas (1985) and Weems (2003) hypothesized that a protracted tail trace may be the result of the use of the tail as a weight-bearing, stabilizing brace on slippery surfaces. In order to achieve maximum stability, however, an animal must keep the vertical projection of its center of mass on the ground within the polygon created by its points of contact with the ground (Alexander, 1985, 2002). Centers of mass of bipedal dinosaurs are estimated to have been located anteroventral to the hips (Alexander, 1985, 1989; Henderson, 1999). This would place the center of mass of a bipedal dinosaur using its tail as a brace anterior to the triangle created by the feet and tail during most of the gait cycle (Fig. 7). This behavior, however, is inconsistent with shallow and narrow tail traces, which should be deep and wide if the tail was supporting part of the weight of the trace maker.

Tail traces associated with bipedal trackways have also been hypothesized to be associated with slowing of the trace maker during locomotion (Lull, 1953; Getty, 2004). We suggest that these tail traces were created during backward rotation of the body about the acetabulum, which caused the distal portion of the tail, still held as a relatively straight continuation of the sacrum, to touch the ground surface passively. This interpretation is consistent with the narrow and shallow nature of tail traces and the digit I impressions that are often associated with protracted tail traces of bipedal dinosaurs, and leaning back is a behavior commonly employed by decelerating bipedal animals (Alexander, 2002). Some bipedal dinosaur trackways with protracted tail traces also show evidence of decreased stride length (Fig. 8). Tail traces are not expected to be associated with all bipedal dinosaur trackways that show evidence of slowing, however, because the angle of backward rotation and tail length differs depending on the trace maker. Environmental conditions may also play a role in the appearance and preservation of tail traces. Hunt and Lucas (2004, 2005), for example, observed that the majority of known Permian and Cretaceous tetrapod tail traces in New Mexico are preserved in nearshore, high-moisture environments. This assertion should be tempered by the fact that such moisture conditions can occur in numerous settings within eolian, alluvial, palustrine, and lacustrine environments under different climate settings and are not restricted to nearshore environments.

CONCLUSIONS

Tetrapod tail traces, like footprints, can record valuable information about behavior, locomotion dynamics, and functional morphology that cannot be studied directly elsewhere. The classification system proposed here for tetrapod tail traces is meant to represent the role of active tail motion in their formation and divides tail traces into tail impressions, protracted tail traces, and abbreviated tail traces. This new classification system is applied to tetrapod tail traces in the literature and a new partial trackway from the Upper Jurassic Morrison Formation. The new tail trace is protracted and simple, with a low PIM and low sinuosity. It has expulsion rims and a V-shaped, ventral keel impression. We attribute the trackway to a small theropod dinosaur that walked across a moist, cohesive sediment and moved its tail very slightly laterally. The trackway and sediment are part of a crevasse-splay within an avulsion deposit (Platt and Hasiotis, 2006).

Tail traces associated with trackways of bipedal dinosaurs are likely the result of deviations from normal locomotive behavior because these animals kept their tails horizontal and elevated. Most bipedal-dinosaur trackways with tail traces are attributed to theropod and ornithopod dinosaurs. We hypothesize that a significant difference exists between tail trace patterns of these two groups of dinosaurs based on differences in tail anatomy, but more data on tail traces, tail anatomy, and modeling of tail movement are needed to test this hypothesis. Two types of theropod and ornithopod tail traces are predominant in the fossil record: tail impressions associated with resting traces and protracted tail traces. Protracted tail traces associated with bipedal trackways have been interpreted as the result of use of the tail as a stabilizing third leg, but this would likely have decreased stability. We favor an interpretation of bipedal trackways with protracted tail traces as the result of incidental touching of the ground surface by the tip of the tail. This can happen when the torso and tail are rotated backward about the pelvis, a common behavior in bipedal animals when slowing during locomotion.

ACKNOWLEDGMENTS

We thank M. Fallin, J. Farlow, A. Huttenlocker, M. Kraus, and E. Kvale for their help in the field, the Iowa State University field camp for lodging accommodations, C. and R. Manuel for logistics, and D. Hansen for providing the necessary permits. J. Farlow, R. Goldstein, L. Martin, and R.E. Weems provided reviews and helpful comments on a previous version of this manuscript. Thank you to D. Gillette, M. Gingras, and A. Martin for helpful reviews and comments. This paper is part of a master's thesis conducted by B.F.P. at the University of Kansas, Department of Geology. This project was funded by the University of Kansas Geology Department and Sigma Xi. Specimens were collected under U.S. Bureau of Land Management permit PA03-WY-107 and are housed with the trace-fossil collections in the University of Kansas Museum of Invertebrate Paleontology.

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ACCEPTED FEBRUARY 16, 2007