Ichnos, 11:229–249, 2003

ISSN: 1042-0940 print / 1563-5236 online
DOI: 10.1080/10420940490428625

A Diverse Dinosaur-Bird Footprint Assemblage from the Lance Formation, Upper Cretaceous, Eastern Wyoming: Implications for Ichnotaxonomy

Martin G. Lockley
Geology Department, University of Colorado at Denver, Denver, Colorado, USA

Gregory Nadon
Department of Geological Sciences, Ohio University, Athens, Ohio, USA

Philip J. Currie
Royal Tyrrell Museum, Drumheller, Alberta, Canada

A diverse assemblage of dinosaur and bird tracks from Niobrara County, Wyoming, represents the first vertebrate ichnofauna reported from the bone-rich Lance Formation (Maastrichtian, Upper Cretaceous). The ichnofauna includes a hadrosaur track with skin impressions; three theropod track types, including the tetradactyl track *Saurexallopus zerbsti* (ichnosp. nov.); a tridactyl dinosaur footprint with a fusiform digit III; possible *Tyrannosaurus* tracks; four distinctive avian ichnites; and invertebrate traces. The footprints are generally well-preserved and so offer a unique insight into the ecology of a small river valley during the Maastrichtian.

***Saurexallopus zerbsti* ichnosp. nov. from the Lance is similar to *Saurexallopus lovei* recently reported from the Maastrichtian, Harebell Formation, of northwestern Wyoming, but is represented by much better material, facilitating amendment of the ichnogenus. Skeletal equivalents for *Saurexallopus* are not currently known. Similarly, the tridactyl track with fusiform digit III is similar to footprints reported from the coeval Laramie Formation of Colorado and may also be similar to ichnogenus *Ornithomimipus* from the Edmonton Group of Alberta (though not necessarily of ornithomimid affinity). The hadrosaurian track with the skin impression is reminiscent of a similar ichnite reported from the Maastrichtian, St. Mary River Formation in Alberta, which is herein named *Hadrosauropodus langstoni* as part of a reassessment of Cretaceous ornithopod track ichnotaxonomy. Such correlations demonstrate the utility of tracks for local or regional biostratigraphy (palichnostratigraphy) in western North America. It is also clear that tracks add to our knowledge of the composition and distribution of dinosaurian and avian components of Maastrichtian faunas. In particular the bird tracks indicate a diversity of at least four species, one of which was a semi-palmate form, hitherto unknown in the ichnological record and named *Sarjeantichnus semipalmatus*.**

Keywords Upper Cretaceous, Lance Formation, hadrosaur tracks, shorebird tracks

INTRODUCTION

The Lance Formation of eastern Wyoming is well-known as a rich source of dinosaur and other vertebrate body fossils and has a special place in the paleontological history of western North America (Weishampel et al., 1990; Derstler, 1996). Until now, however, it has not yielded any significant reports of footprints. The discovery of a diverse assemblage of well-preserved footprints in northern Niobrara County, therefore, presents us with an opportunity to compare the track and bone records. In so doing, we can establish that the dinosaur tracks are easily differentiated into distinctive morphotypes that can be correlated with potential trackmakers at a low taxonomic level. Similarly, the bird footprints are easily differentiated into distinct morphotypes but may be harder to correlate with identifiable trackmaker equivalents in the body fossil record. The purpose of this paper, therefore, is to describe the first reported vertebrate ichnofauna from the Lance Formation. The ichnofauna also affords the opportunity for broader comparisons with track (and skeletal) records in the late Maastrichtian and assessment of the degree to which the track record adds to our knowledge of vertebrates in the region.

GEOLOGICAL SETTING

The Lance Formation consists of non-marine, primarily fluvial, sediments that outcrop in Colorado, Wyoming, and Montana. The Lance represents the terminal Cretaceous

---

Address correspondence to Martin G. Lockley, Geology Department, University of Colorado at Denver, P.O. Box 173364, Denver, CO 80217-3364. E-mail: mlockley@carbon.cudenver.edu

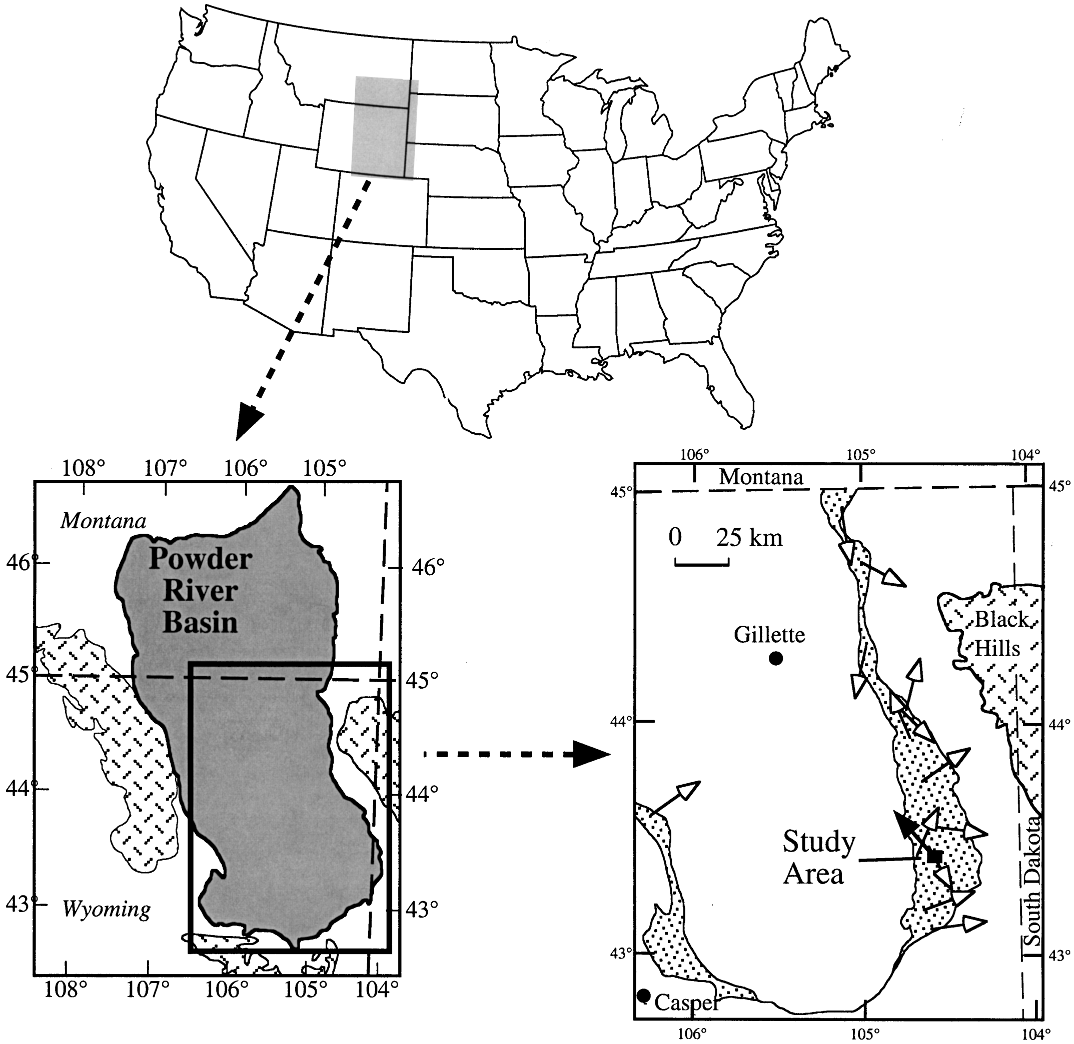

FIG. 1. Location map for the track beds at the Zerbst Ranch. The stippled area in the detailed map section indicates the outcrop pattern on the Lance Formation (after Seeland, 1988). Open arrows show averaged paleoflow directions (from Seeland, 1988). The dark arrow shows paleoflow at the track site.

sediments in the Powder River basin of Wyoming (Fig. 1) and is overlain by the Paleocene fluvial sediments of the Tullock Member of the Fort Union Formation (Conner, 1991; Nichols and Brown, 1992). The deposits in the eastern Powder River basin are characterized by thick (> 10 m) channel sandstones interbedded with floodplain mudstones and thin sandstones (Seeland, 1988; Conner, 1991). Regional petrographic and paleocurrent reconstruction in Wyoming suggest a general eastward flow direction for channel deposits during deposition of the Lance with a source near the present Wind River Mountains (Conner, 1991). The first influence of the rising Black Hills occurs in the overlying Tullock Member, which indicates paleoflow to the west and north through the basin axis into Montana (Flores and Ethridge, 1985; Seeland, 1988).

Detailed Location Description

The tracksite is located on private land (the Zerbst Ranch). Therefore, in order to protect the site precise geographical coordinates are not given. The tracks described occur at the top of a limited exposure of sandstone that fines upward from fine-grained trough crossbedded sandstone to rippled very fine-grained sandstone and siltstone (Fig. 2). Paleoflow at the site averaged 319°, which is similar to other sandstones above this interval at this location. The main track bed occurs at the top of the rippled very fine-grained sandstone. Bird tracks and raindrop impressions were also found as casts on the lower surface of slabs of a 0.1 m thick fine-grained sandstone that was removed during excavation of the main site (Lockley and Rainforth, 2002).

Interpretation

The fine-grained nature of the sediments below the main track horizon is consistent with deposition at the top of a channel sandstone. The paleoflow direction of this sandstone and the other channel sandstones above are opposite to the regional trends indicated in previous studies (e.g., Seeland, 1988; Conner, 1991).

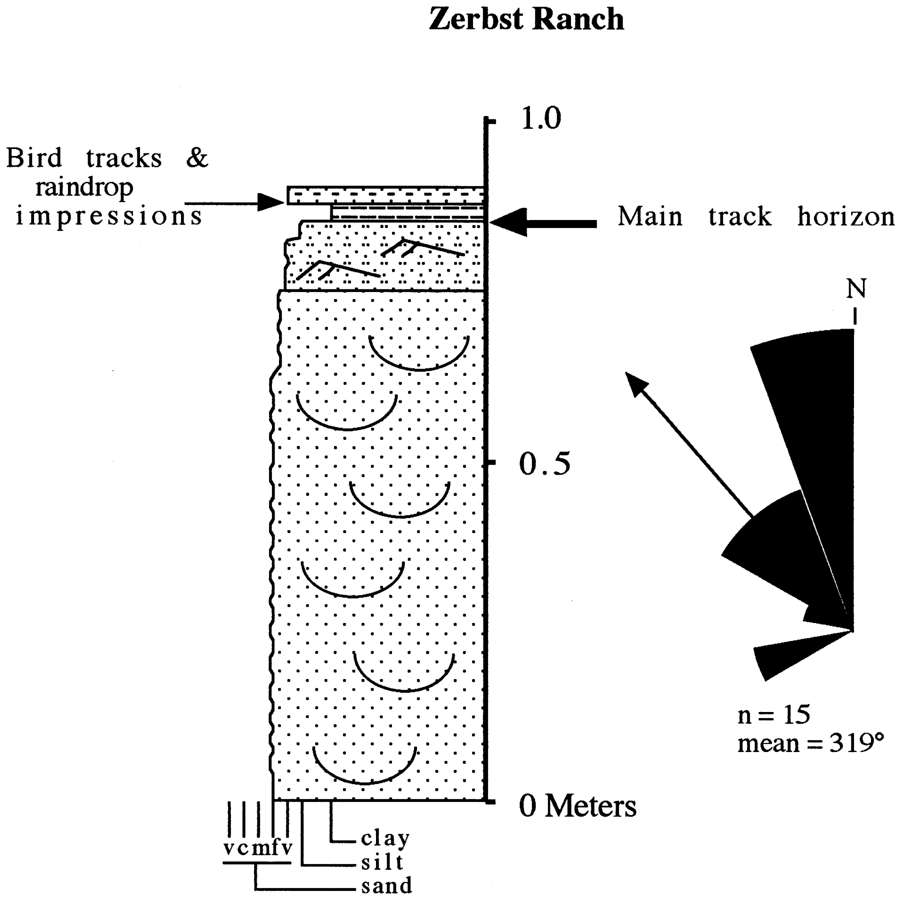

FIG. 2. Detailed vertical section at the Zerbst track site. Paleoflow was measured from the small-scale trough crossbeds below the rippled horizon.

There are too few data to determine if this is due to a local perturbation or truly is a result of an early shift in paleoflow patterns caused by the rise of the Black Hills. However, the data are consistent with reconnaissance observations made in adjacent sandstones.

The mud-draped ripples on which most of the tracks were made suggest the presence of a short-lived pond or slough with a long axis oriented roughly parallel to the paleoflow direction. The presence of the casts of bird tracks and the raindrop impressions on the thin sandstone suggests the bed was a product of the abandonment phase of channel sedimentation. The detailed and shallow nature of the tracks on both horizons is a function of the fine-grained nature of the sediments and the episodic subaerial exposure of the sediments that allowed at least partial dewatering and compaction (Laporte and Behrensmeyer, 1980; Nadon and Issler, 1997).

DESCRIPTION OF TRACKSITE

The outcrop of track-bearing bedding plane has a maximum east-west length of 13 meters and is up to 5 meters from north to south (Fig. 3). Most tracks are found in the southern sector of the site where the surface consists of a light grey, silty, fine-grained sandstone, whereas to the north this surface is overlain by beds of a brown-weathering, trough cross-bedded sandstone that results in a rough undulating exposure. Thus the track-bearing surface is no more than 20–25 m^2 in area. When first discovered in the early 1990s, only a few tracks were visible. Subsequently, the late Leonard Zerbst, the landowner, used heavy equipment to excavate the surface that is currently exposed. During the excavation sandstone overburden was removed down to a 0.5 cm thick mudstone layer directly overlying the track-bearing layer.

Subsequent study of slabs of sandstone removed as overburden reveals that they contain abundant raindrop impressions and the majority of the bird tracks. These are preserved as natural casts and originate from the interface between the upper surface of the thin (0.5 cm) mudstone unit and the overlying sandstone. Additional large tracks were made on surfaces within the overlying sequence of sandstone and were transmitted through to the main surface as underprints. The well preserved tracks on the main surface were evidently made by animals that stepped into mud before the deposition of any of the overlying sandstone. The presence of skin impressions preserved as a compacted layer of mudstone adhering to footprints on the main surface appears to support this interpretation of the timing of trackmaking activity.

The main track surface has yielded a total of only about 20 individual footprints belonging to a minimum of 8 individuals.

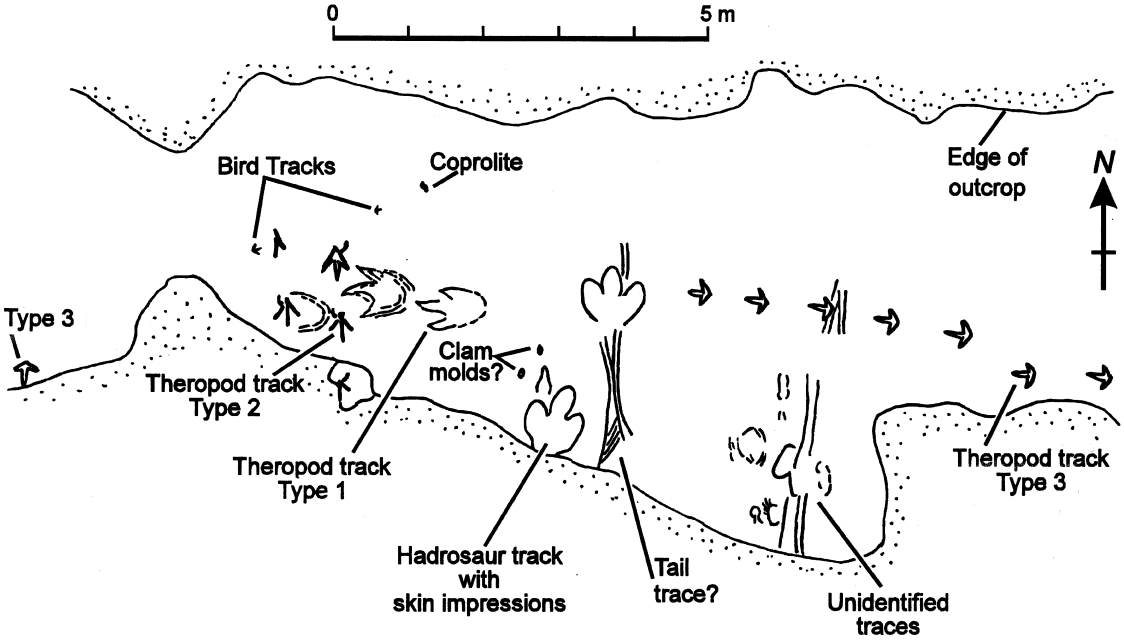

FIG. 3. Map of Zerbst ranch tracksite, in Lance Formation.

Despite the relatively small size of this sample, the tracks unequivocally represent at least four different types of dinosaurs and two different avian morphotypes. In addition at least two avian ichnotaxa are represented in slabs retrieved from the sandstone overburden. This results in a total diversity of at least eight ichnotaxa, of which four are avian and four dinosaurian. It is evidently no coincidence that these additional taxa, not represented on the main surface, are the smaller bird tracks imprinted in the top of the mudstone layer and preserved as natural casts in the overlying sandstone. Such tracks are too small and delicate to register directly on the main sandstone surface. Thus, the assemblage is divided by preservational factors into two main components—a dinosaurian sub-assemblage on the main surface and an avian sub-assemblage 0.5 cm above on the upper surface of the mudstone (and preserved as natural casts). Dinosaurs also registered tracks at higher stratigraphic levels, but only large footprints are identifiable as transmitted underprints on the main sandstone surface.

The track assemblage can be regarded as a single ichnocoenosis even though it is technically registered on more than one stratigraphic level. Its composition can be summarized as follows. Tracks attributed to dinosaurs include a partial hadrosaur trackway with skin impressions, a trackway of a large theropod preserved as underprints, and trackways of two additional and highly distinctive medium-size tridactyl trackmakers, all described in detail in the systematic section below. Bird tracks can be separated into four morphotypes, including a large variety with a partial web and hallux, herein named *Sarjeantopodus semipalmatus,* a medium-size variety with hallux, and two small varieties—one with a hallux and one without.

During the course of our study we replicated representative bird and dinosaur tracks and an enigmatic trail of probable invertebrate affinity. These are curated as rubber molds, plaster and fiberglass replicas in the University of Colorado at Denver collection under the series CU-MWC 224.1–224.11. In 2002 a large section of the track-bearing surface was also replicated by the Black Hills Institute of Geological Research.

SYSTEMATIC ICHNOLOGY

Preliminary Observations

Although vertebrate ichnology has witnessed a significant revival in recent years, especially in western North America, there have not been many reports of Upper Cretaceous tracks. Indeed, Lockley and Hunt (1995a, p. 236) noted that “the paucity of tracks in bone-rich strata of . . . Wyoming and Montana is puzzling.” especially when considering the “abundance of skeletons of Late Cretaceous dinosaurs.” This is most easily explained by the lack of suitable facies for track preservation in these areas. Purported ornithomimid tracks were reported from the Edmonton Formation of Alberta (Sternberg, 1926)—now known as the Horseshoe Canyon Formation—and a hadrosaur track was described from the St. Mary River Formation of Alberta (Langston, 1960). Recent studies of Maastrichtian ichnofaunas deal with the Laramie Formation of Colorado (Lockley and Hunt, 1995b: Lockley and Foster 2003), the Raton Formation of New Mexico and Colorado (Lockley and Hunt, 1994, 1995a), the St Mary River Formation of Alberta (Currie et al., 1991; Nadon, 1993), and the Harebell Formation of Wyoming (Harris et al., 1996). Tracks from the Hell Creek Formation of South Dakota (Triebold et al., 1999) have yet to be described in detail. Tracks

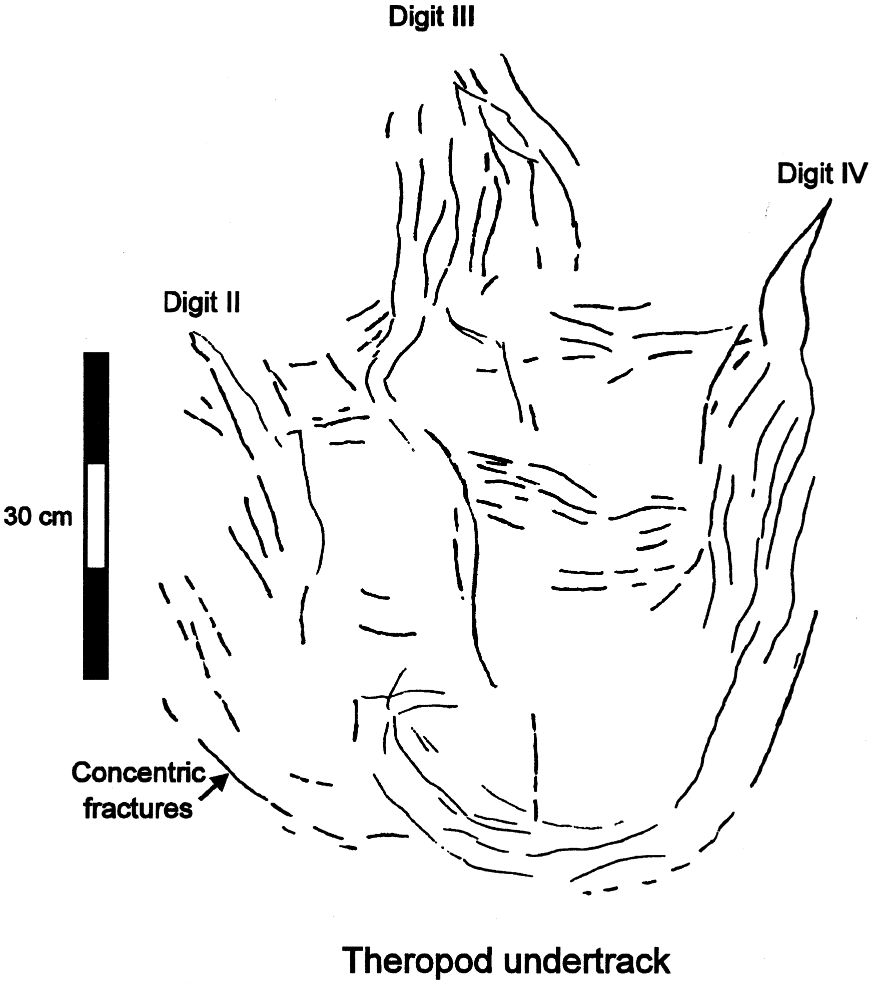

FIG. 4. Tracing of a large tridactyl track (type 1), possibly attributable to *Tyrannosaurus*.

of similar age and type have been described from Mongolia (Currie et al., 2003).

Theropod Tracks

We recognize at least two theropod track morphotypes in the Lance trackway assemblage. The largest morphotype (Fig. 4) is probably of tyrannosaurid affinity but is not well preserved. The smaller morphotype, however, shows remarkable preservation and a highly distinctive tetradactyl morphology that allies it to the ichnogenus *Saurexallopus* (Fig. 5).

Theropod Track Morphotype 1

Theropod track Morphotype 1 is the largest theropod track type found at the site. It is represented only by underprints, and so cannot be subjected to detailed morphological analysis. Based on size alone (length about 80 cm; width about 60 cm), the track is probably attributable to a tyrannosaur. A footprint, attributed to *Tyrannosaurus* and named *Tyrannosauripus pillmorei*, was recently reported from the Maastrichtian portion of the Raton Formation in New Mexico (Lockley and Hunt, 1994). The Lance and Raton tracks are similar in size. The track (Fig. 4) appears to be part of a trackway, though this is not certain. If the footprint is part of a trackway segment, and not the result of the juxtaposition of footprints from different trackways, then this is the first reported segment of a *Tyrannosaurus* trackway. Moreover, a short step is indicated, suggesting slow speed progression. Such information supports those who argue that *Tyrannosaurus* moved slowly (Alexander, 1991; Farlow et al., 1995), though such conclusions are tenuous when considering the scarcity and ambiguity of the evidence. Larson (2003) also mentions this track type, recording its foot length up to 78 cm, and assigning it to the ichnogenus *Tyrannosauripus* that he considers consistent with a *Tyrannosaurus rex* trackmaker.

Theropod Track Morphotype 2

Theropod track Morphotype 2 preserved as CU-MWC 224.2 (Figs. 5–7) is a highly distinctive, and well-preserved tetradactyl ichnite that resembles *Saurexallopus lovei,* described by Harris et al. (1996) from the Maastrichtian Harebell Formation of northwestern Wyoming (Fig. 5). Based on both morphological and

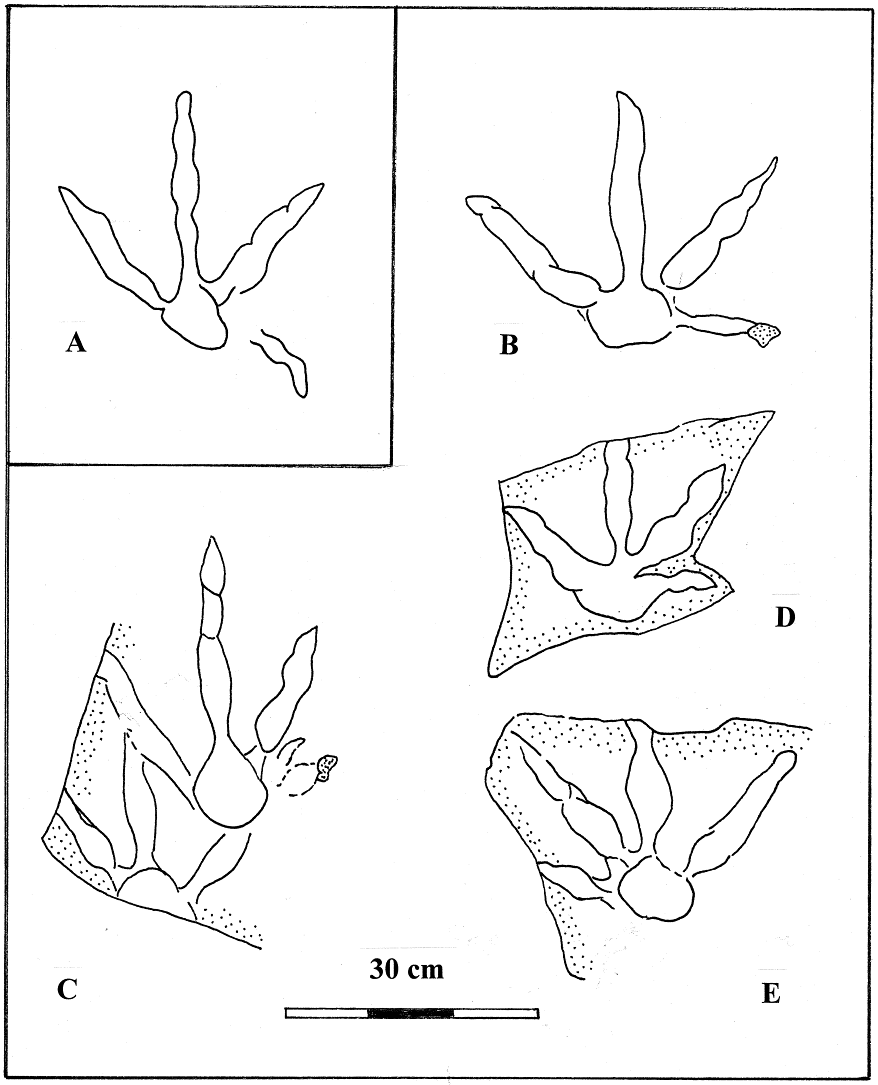

FIG. 5. Comparison of **A**: type of *Saurexallopus zerbsti* ichnosp. nov. (CU-MWC 224.2) a left footprint from the Lance Formation, with **B**: type of *Saurexallopus lovei* (DMNH 5989) a left footprint from the Harebell Formation, and other specimens (C–E) from the Harebell. **C**: DMNH 5993, a left above a right footprint, **D**: DMNH 9150-3, a left footprint, and **E**: DMNH 5996, a right footprint.

age similarities we suggest the Lance tracks are assignable to the ichnogenus *Saurexallopus*. Larson (2003) agrees with this identification as we reported to him while this paper was in review. There are, however, some differences between the Lance and Harebell ichnites that warrant discussion and suggest that the tracks might be assigned to a distinct ichnospecies. Some of these differences are extramorphologic, and attributable to preservation, but others may be genuine morphological differences.

Harris et al. (1996, p. 381) reported that "no clear trackways are available." This situation is rectified in the Lance assemblage (Fig. 6) where we have identified two trackways, one consisting of three consecutive footprints (two steps) and the second consisting of two footprints (one step). Second, the Harebell tracks are "all natural casts" (op. cit., p. 391), whereas the Lance tracks are all impressions. Harris et al. (1996) stated that the Harebell tracks are "not so well-defined that digital nodes ('pads') can be distinguished." Based on our examination of the Harebell material in the Denver Museum of Natural History collections, we are able to distinguish digital pad traces (Fig. 5) in several specimens. The Lance tracks also reveal clear digital pad impressions.

Harris et al. (1996) named their new ichnospecies on the basis of material in which diagnostic trackway parameters and digital pad morphologies were not identified. Their original ichnogenus "*Exallopus*" was a junior synonym of an extant polychaete worm (Fauchauld, 1977) and so was renamed *Saurexallopus* (Harris, 1997). Despite these problems, we tend to agree with these authors that "the tracks display a suite of characteristics that is unique among known theropod tracks" (op cit.,

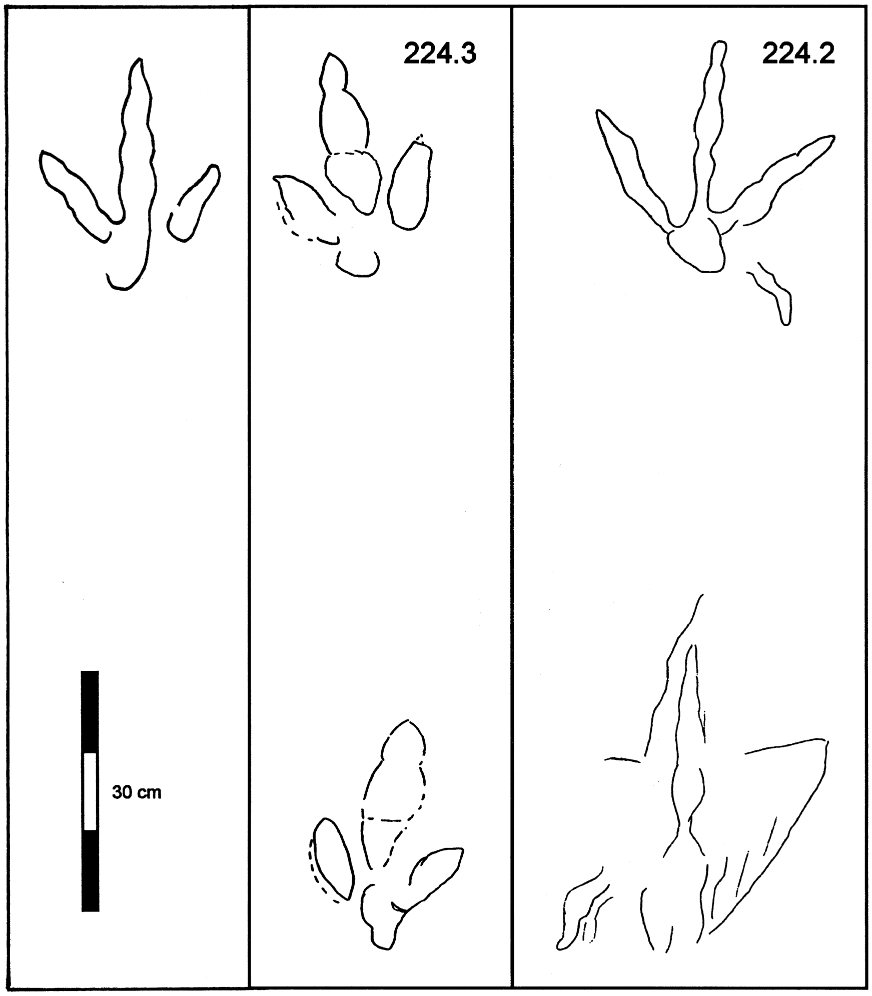

FIG. 6. **Left**: line drawings of *Ornithomimipus* (left) after Sternberg (1926). **Middle**: two sequential unnamed tridactyl theropod tracks type 3 from the Lance Formation (compare with Figure 3); second is CU-MWC 224.3. **Right**: two sequential tracks of *Saurexallopus zerbsti*; second is CU-MWC 224.2.

p. 391). Regardless of the quality of the Harebell material, the Lance material is of better preservational quality and allows us to give the emended diagnosis of *Saurexallopus* presented below.

The Lance and Harebell tracks evidently display a significantly different hallux configuration. The Harebell tracks are diagnosed as having a hallux that is not reversed. In other words, it is directed along or slightly to the anterior of the medio-lateral line (Figs. 5 and 6), whereas the Lance tracks display a much more posteriorly directed hallux. Moreover, the Harebell specimens display a hallux that is relatively straight, “impressed along the entirety of the digit,” and it is described as radiating “directly from the forward margin of the metapodial impression.” (This description is questionable. The hallux apparently radiates from the medial rather than the forward margin of the metapodial impression). By contrast the Lance track reveals a curved hallux that is not impressed along the entirety of the digit, and radiates from the posteromedial margin of the metapodial impression. The Lance tracks reveal this distinctive hallux configuration in both trackways and in both left and right footprints. Finally we note that there is some suggestion that the Harebell tracks might reveal traces of webbing. No such traces exist in the Lance ichnites, even though they are much better-preserved.

Based on these morphological differences we suggest that the Lance tracks should be assigned to a different ichnospecies within the ichnogenus *Saurexallopus*. It could be argued that the differences in hallux configuration are related to differences in preservation, or to the dynamic emplacement of the foot during footprint registration (cf. Gatesy et al., 1999). In the final analysis, however, the Lance specimens do not conform to the diagnosis and description of *Saurexallopus*, which is quite specific about the hallux not being reversed. Thus it is impossible to demonstrate that the Lance tracks are identical to *Saurexallopus lovei*. Differences in the hallux configuration are not considered sufficient to warrant the establishment of a new ichnogenus to distinguish the Lance material from *Saurexallopus*. We have therefore amended the diagnosis of this ichnogenus to

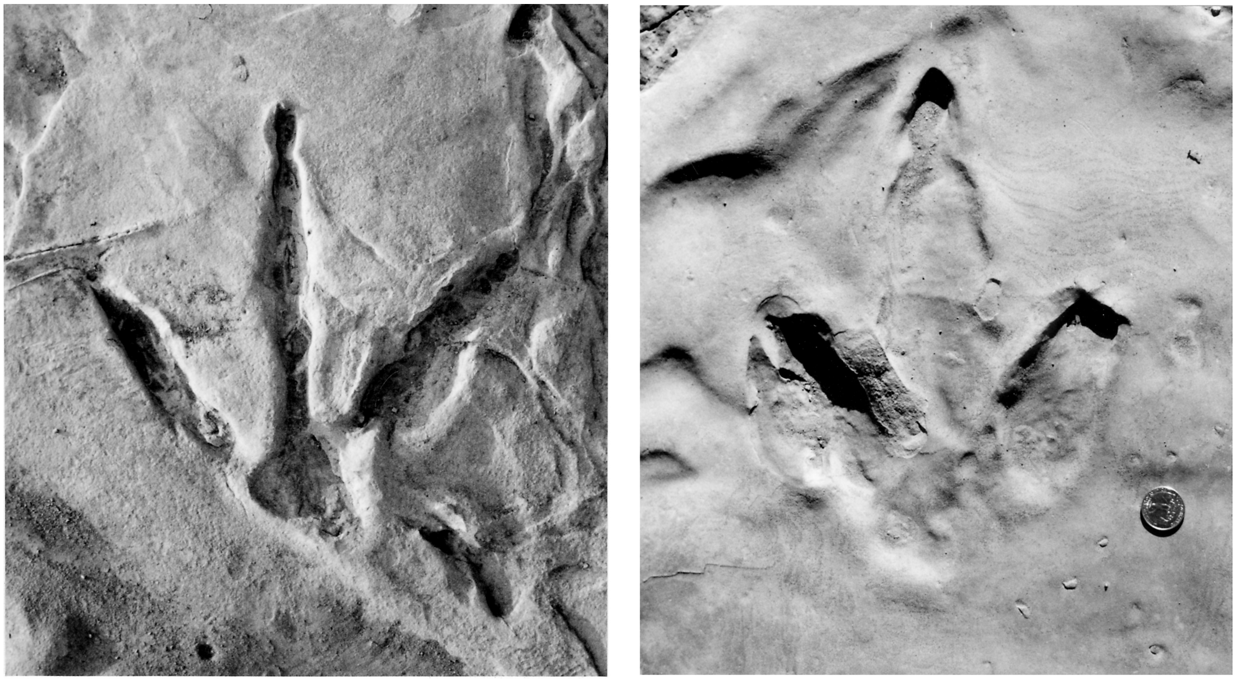

FIG. 7. Photographs of *Saurexallopus zerbsti* ichnosp nov. (left, CU-MWC 224.2) and unnamed tridactyl dinosaur track (right CU-MWC 224.3). Compare with Figure 6 for scale.

accommodate the new information provided by the Lance footprints and assigned them to a new ichnospecies (*Saurexallopu zerbsti*).

Tridactyl Dinosaur Track Morphotype 3

Tridactyl dinosaur track Morphotype 3 (CU-MWC 224.3, Figs. 6 and 7) are similar to a medium-size footprint illustrated by Lockley and Hunt (1995b) and assigned to the informal category of theropod "morphotype E" from the Maastrichtian of Colorado (op. cit., Figs. 8 and 11H, and Lockley and Hunt, 1994, Fig. 27). The Wyoming example described herein (CU-MWC 224.3) has a very long fusiform middle toe impression and is about 29 cm long by 30 cm wide. The medial and lateral digits (II and IV) are short and quite widely divergent. The trackway is narrow with a relatively long step (85 cm) and stride (about 170 cm). Foot length/pace length ratio 1: 2.8.

The only named track from the late Cretaceous that compares with this morphotype is *Ornithomimipus angustus* from the Edmonton (now Horseshoe Canyon) Formation of Alberta (Sternberg, 1926), which is 28 cm long and 20 cm wide, with a stride of 94 cm. (Foot length/pace length ration 1: 3.3). These measurements are similar to those recorded for the Wyoming trackway. Another feature of specimen CU-MWC 224.3 that resembles *Ornithomimipus* is the impression of digit II that is "separated from the rest of the foot" (Sternberg, 1926, p. 87). We tentatively conclude that the Wyoming track is similar to ichnogenus *Ornithomimipus*. This does not imply, however, that we agree with Sternberg that this "leaves very little doubt" that the tracks were made by the genus *Ornithomimus* or another member of the family Ornithomimidae. Following our suggestion, Larson (2003) uses the label ornithomimid for these tracks, and Farlow (written communication, 2003) also concurs that this interpretation is reasonable. Further study of well-preserved material, and ornithomimid feet, is necessary before drawing further conclusions about the affinity of the trackmaker.

General Observations on Hadrosaur Tracks

Revision of the ichnotaxonomy of hadrosaur tracks, and the tracks of large Cretaceous ornithopods in general, is long overdue. Ever since their discovery, in Lower Cretaceous strata in England, in the early part of the nineteenth century, large ornithopod footprints have routinely been referred to as *Iguanodon* tracks. This casual usage of a generic name, based on osteological material, is an archaic practice that departs from normal ichnological procedure. Consequently the name *Iguanodontipus* has recently been proposed (Sarjeant et al., 1998). A similar situation appears to exist with Upper Cretaceous tracks. Although abundant examples of Upper Cretaceous hadrosaur tracks are known from North America (Langston, 1960; Currie et al, 1991; Lockley et al., 1993; Nadon, 1993; Lockley and Hunt, 1995; Lockley and Wright, 2001), none has been named as a result of these studies. Lockley (1991, p. 57) concluded that "hadrosaur tracks . . . have yet to be adequately and systematically described." Unfortunately, however, several tracks have been named as if to imply hadrosaur affinity (e.g., *Hadrosaurichnus* and *Hadrosaurichnoides*) even though it is highly probable that they are *not* of hadrosaur affinity.

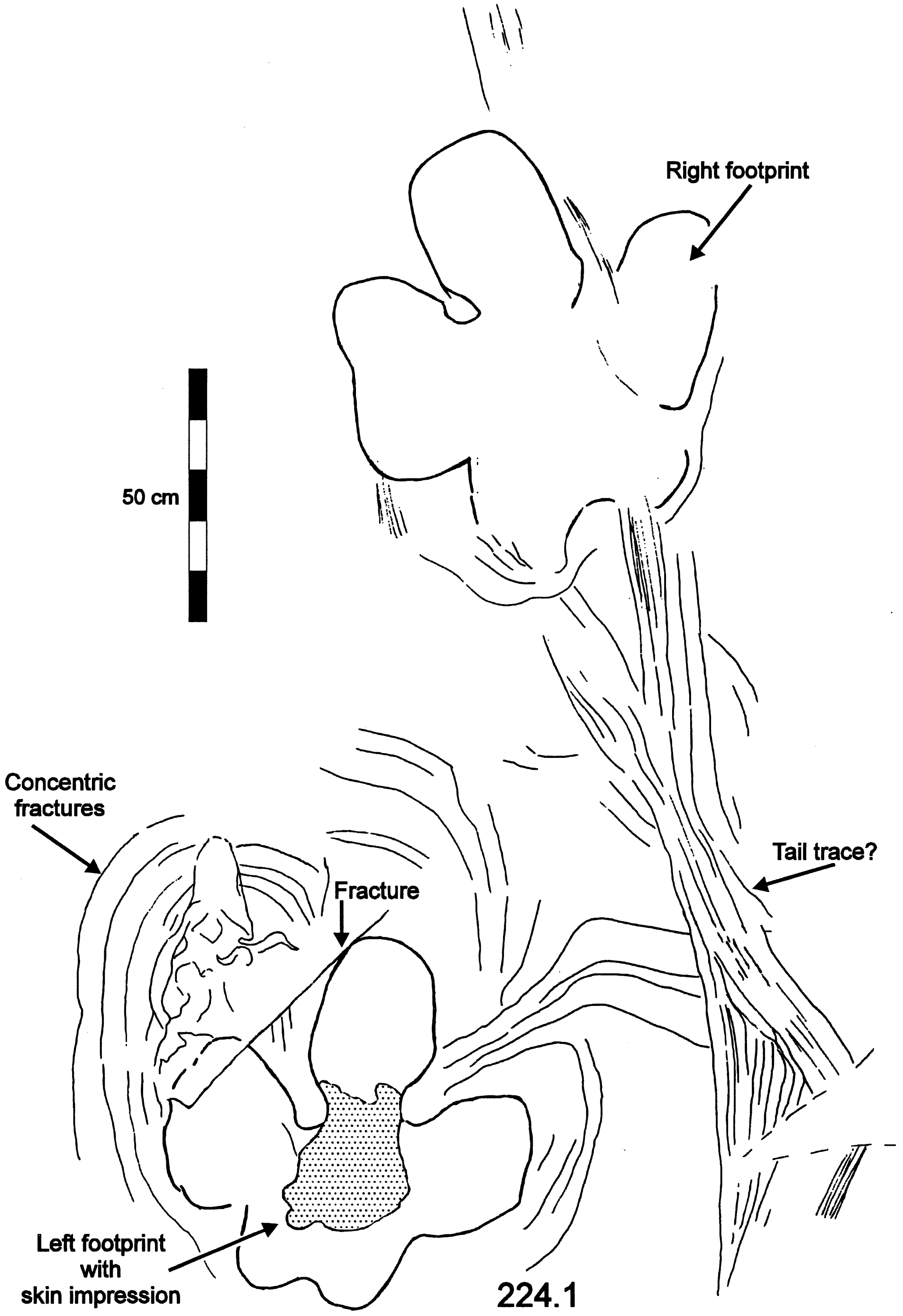

FIG. 8. Tracing of hadrosaur trackway with probable tail trace. Stippled area indicates general location of skin impressions.

Table 1 lists, in publication order, purported Cretaceous ichnogenera assigned to large ornithopods, with probable trackmakers, and clearly indicates the extent to which the ichnotaxonomy is confused. Only three tracks are unequivocally those of large ornithopods, and all these are of Lower Cretaceous origin, and therefore probably not of hadrosaurian affinity.

Several of these ichnogenera were only casually described, usually with limited explanation as to why affinity with large ornithopods such as iguanodontids or hadrosaurids was proposed. We therefore look briefly at each of these examples in an attempt to determine the status of the ichnotaxon, and its utility for comparison with hadrosaurian ichnites from western North America.

Camptosaurichnus. Casamiquela (1968) was originally described as a Lower Cretaceous ornithopod track from Chile. However, based on descriptions and information provided by

TABLE 1

Named ichnogenera of purported hadrosaur, or other large ornithopod tracks. Only those indicated in ***bold*** are herein considered of large ornithopod affinity.

Ichnogenus and author(s)	**Probable Trackmaker**
Camptosaurichnus Casamiquela (1968)	Theropod
Iguanodonichnus Casamiquela (1968)	Sauropod (Santos et al., 1992; Sarjeant et al., 1998).
Amblydactylus Sternberg (1932)	Ornithopod
Hadrosaurichnus Alonso (1980)	Theropod
Ornithopodichnites Llompart (1984)	Theropod (Lockley and Meyer, 2000)
Orcauichnites Llompart (1984)	Theropod (Lockley and Meyer, 2000)
Caririchnium (Leonardi, 1984)	Ornithopod (Lockley, 1987)
Hadrosaurichnoides C-Cladellas et al. (1993)	Theropod
Iguanodontipus (Sarjeant et al., 1998)	Iguanodontid

Karen Moreno (written communication, 1998), Sarjeant et al. (1998) suggested that the tracks may be of theropod origin and of Late Jurassic age. They are not well-preserved, and in our opinion are undiagnostic of any category of dinosaurs more precise than tridactyl biped. Nonetheless, the name has been retained in a recent restudy of the type locality (Moreno and Pino, 2002), as has the claim that the affinity of the tracks is ornithopodan. However, the age of the tracks as Late Jurassic has been confirmed.

Iguanodonichnus. Casamiquela (1968) was originally described as at lower Cretaceous ornithopod trackway from Chile. However, based on analysis of the trackway parameters it was reinterpreted as a sauropod trackway (Santos et al., 1992; Sarjeant et al., 1998). Descriptions and information provided by Karen Moreno (written communication, 1998) and Moreno and Pino (2002) confirm this and place it, with *Camptosaurichnus*, in the Late Jurassic. It is not well-preserved, and is undiagnostic of any grouping of dinosaurs more precise than sauropod, and we therefore consider it a *nomen dubium*.

Amblydactylus. Sternberg 1932, Currie and Sarjeant (1979), is an ornithopod track from the Aptian-Albian of western Canada, and, based on age, is could be of iguanodontid affinity, but as noted by (Currie, 1983, 1995) a hadrosaurian origin is also possible, based in part on manus morphology. The material is well preserved, adequately described, and diagnostic of large ornithopods with well padded feet. Manus tracks are associated in some cases. We therefore consider the material diagnostic and the name valid. It is even possible that *Caririchnium* is a junior synonym of *Amblydactylus* (Currie, 1995).

Hadrosaurichnus. Alonso (1980), as the name implies, is supposed to suggest a Late Cretaceous hadrosaur from Argentina. *Hadrosaurichnus* (sensu Alonso, 1980) is characterized by an elongate foot (length 37 cm; width 28 cm) with relatively slender, tapering digit impressions, where seen. The trackway is relatively narrow, with a pace angulation of 145–150 degrees, and the step is 107 cm, or approximately three times foot length. This is typical of a theropod trackway, we therefore disagree with Thulborn (1990, p. 97) who stated that "the name *Hadrosaurichnus* may well signify a hadrosaur track." As noted by Lockley (1991, p. 57), "A number of names have been proposed [for hadrosaur tracks] but as is sometimes the case, these names, including *Hadrosaurichnus*..., have been proposed for poorly preserved footprints, whereas well-preserved tracks that have more frequently come to light remain unnamed." *Hadrosaurichnus* is, in our opinion, diagnostic of theropod track morphology. An excellent picture can be found in Psihoyos and Knoebber (1994, p. 148) where a paratype trackway is identified as those of a "carnivorous dinosaur." Clearly one cannot justify a type specimen of purported ornithopod affinity, and a paratype (or paratypes) of theropod affinity!

Ornithopodichnites. Llompart (1984), from the Late Cretaceous of Spain, as noted by Lockley and Meyer (2000), is probably a theropod track, being considerably longer than wide. It is not well-preserved, and is undiagnostic of any grouping of dinosaurs more precise than theropod or tridactyl biped, and we therefore consider it a *nomen dubium*.

Orcauichnites. Llompart (1984), from the Late Cretaceous of Spain, as noted by Lockley and Meyer (2000), is probably a theropod track, being considerably longer than wide. It is not well-preserved, and is undiagnostic of any grouping of dinosaurs more precise than theropod or tridactyl biped, and we therefore consider it a *nomen dubium*.

Caririchnium. (Leonardi, 1984), from the Lower Cretaceous of Brazil, was originally described as a possible stegosaur track, but is now interpreted as an ornithopod track type (Lockley, 1987; Leonardi, 1994). Two ichnospecies are known, one form Brazil, the other from Colorado, Oklahoma, and New Mexico. The material is well preserved, adequately described, and diagnostic of large ornithopods with well-padded feet. Manus tracks are also associated in some samples. We therefore consider the material diagnostic and the name valid. (Lee, 1997) described a new species of *Caririchnium* as *C. protohadrosaurichnus*, from the Cenomanian Woodbine Formation of Texas. The justification for inferring that the trackmaker was a hadrosaur seems to be based on the age of the tracks.

Hadrosaurichnoides. Casanovas-Cladellas et al. (1993) is a Lower Cretaceous track from Spain, and therefore unlikely to be of hadrosaurian affinity. The foot is described as longer than wide, in both the holotype and the paratype, and is therefore more characteristic of a theropod than an ornithopod. In addition they describe the pace angulation as "relatively high" and the trackway as "narrow" again indicating theropod affinity in our opinion. The tracks also occur in limestones, which is a somewhat unusual facies association (Wright, 1996).

Although these authors made an attempt to compare the Spanish ichnites with *Amblydactylus, Caririchnium and Hadrosaurichnus*, and even suggest that the tracks show wide hoof marks (not narrow claw marks) we do not agree with their conclusions. For example, they interpret the tracks as showing evidence of webbing. This indicates, we believe, a misinterpretation of the preservation of these tracks. To date there have been no convincing reports of footprint evidence for webbing among ornithopods or any other group of dinosaurs. Indeed reports of "web-footed theropods from the Cretaceous of New Mexico, were reinterpreted as ornithopod tracks that had caused the substrate to bulge and exfoliate around the anterior margin of the tracks (Lockley and Hunt, 1995, fig. 5.25). Moreover, Casanovas Cladellas et al. (1993) present a number of inconsistent arguments to suggest that hadrosaurs might be known from the Lower Cretaceous, or that web-footed forms might be found in "a transition species between iguanodontids and hadrosaurs." They then undermine their own unconvincing argument for hadrosaur affinity of these tracks by stating that the tracks could be those of iguanodontids such as *Probactrosaurus* or *Ouranosaurus*. The Spanish *Hadrosaurichnoides* is not well-preserved or well-illustrated, and is undiagnostic of any grouping of dinosaurs more precise than theropod or tridactyl biped, and we therefore consider it a *nomen dubium*.

Iguanodontipus. (Sarjeant et al., 1998) The material is moderately well preserved, adequately described, and diagnostic of large ornithopods with well padded feet. We therefore consider the name valid. However, not all large Lower Cretaceous tridactyl tracks from Britain are of ornithopod affinity. For example, one trackway specimen (GLAHM X 1101) from the Hunterian Museum (Glasgow University) assigned to *Iguanodontipus* by Sarjeant et al. (1998), is evidently of theropod affinity (Wright, 1996). This error has been known to the senior author for sometime but was not corrected during the lifetime of W.A. S. Sarjeant.

Hadrosaur Tracks from North America

.

Alonso (1980) noted that the ichnological record of hadrosaurs was so poor that only one footprint was then known, from North America (i.e., from the St. Mary River Formation of Alberta: Langston, 1960). He also noted that hadrosaurs are scare in South America (until Maastrichtian times) and poorly known (Brett-Surnam, 1972, 1979; Weishampel et al., 1990). Such considerations would seem to argue against inferring that South American tracks are hadrosaurian. Indeed, in the most recent study of a large South American ichnofauna (Lockley et al., 2002) large ornithopod tracks were rare and of an ambiguous nature, possibly indicating an indigenous taxon. By contrast we now know that hadrosaurian tracks are abundant in the Upper Cretaceous of North American and often found in close association with skeletal remains that match track morphology in all essential details.

The discovery of more well-preserved hadrosaur tracks in the St. Mary River Formation of Alberta that display skin impressions and occur in a sample with multiple manus-pes sets and trackway segments (Currie et al. 1991) has prompted us to describe what we consider to be the best hadrosaur tracks currently known. In making these the type of a new ichnospecies *Hadrosauropodus langstoni*, we hope to bring some semblance of order to the disorderly field of ichnotaxonomy of large Cretaceous ornithopods. We also demonstrate that similar tracks (with comparable skin impressions) also occur in the Lance Formation of Wyoming.

In addition we establish a modicum of historical continuity by connecting our studies with the "hadrosaurian ichnite" described by Langston (1960) from the same formation. We also stress the need for an appropriate label for well-preserved and diagnostic hadrosaur tracks, and emphasize the severe inadequacy of all existing descriptions of purported hadrosaur tracks by relegating them to the category of *nomina dubia*, as argued above.

Bird Tracks

It is outside the scope of this paper to describe all the bird tracks found at the Zerbst Ranch site in detail, or to attempt to correlate them with known skeletal remains from the Maastrichtian. The tracks were first illustrated by Lockley and Rainforth (2002) with brief descriptions. This material is also illustrated herein with modification and supplemental photographs. However, the most distinctive, semi-palmate track is described in detail, below, and assigned to the new ichnospecies *Sarjeantopodus semipalmatus*.

SYSTEMATIC DESCRIPTIONS
DINOSAURIA
?THEROPODA
Ichnogenus *Saurexallopus* Harris, 1997

Amended Diagnosis

Tetradactyl track with slender toe impressions, and prominent hallux trace extended medially to postero-medially. Formula for digital pad impressions is 2,2,3,?4 corresponding to digits I–IV, respectively. Metapodial impressions subtriangular and slightly asymmetric with anterior apex converging with proximal portion of digit three. Digit IV connected to metapodial proximally, whereas digit II connects distally. Trackway narrow with relatively short step.

Synonymy

Exallopus lovei Harris et al., 1996

Saurexallopus Lockley and Peterson, 2002, p. 77, 99.
Type ichnospecies
Saurexallopus lovei Harris, 1997

Saurexallopus zerbsti ichnospecies nov.
Figs. 5–7

Holotype
CUMWC 224.2
Etymology
see Harris (1997) for ichnogenus.

Ichnospecies named in honor of the late Leonard Zerbst, Arlene Zerbst and their family
Locality
The Zerbst Ranch, Niobrara County, Wyoming
Horizon
Lance Formation
Age
Late Cretaceous (Maastrichtian)
Description

Tetradactyl track with very slender toe impressions, and prominent hallux trace extended medially. Holotype 35 cm long including hallux and 30 cm wide. Length 30 cm excluding hallux. Metapodial impressions sub-triangular and slightly asymmetric with anterior apex converging with distal portion of digit three, and posteromedial corner oriented toward hallux impression: posterolateral corner of metapodial impression connects proximally with digit IV, whereas digit II connects distally, resulting in a much deeper posterior recess (hypex) for the interdigital angle between III and IV than between II and III. Trackway narrow with relatively short step (78 cm). Foot length/pace length ratio about 1:2.5.

Discussion

These tracks have been casually described as heron- or stork-like (Lockley and Peterson, 2002), while nonetheless being attributed to a bird-like, theropod dinosaur rather than a bird. The true affinity of these tracks is unknown. Ornithomimid dinosaurs tend to have long slender toes, probably with wide digit divarication angles in life. They also lacked a hallux. For example *Magnoavipes* is somewhat similar in size to *Saurexallopus* but quite distinct in its lack of a hallux. It has been interpreted as a bird (Lee, 1997) but also as an ornithomimid dinosaur (Lockley et al., 2001). The hallux of *Saurexallopus* seems to rule out the likelihood of an ornithomimid trackmaker.

DINOSAURIA
HADROSAURIDAE
Hadrosauropodus ichnogen nov.

Synonymy
Langston, 1960
Currie et al., 1991. Figs. 5 and 6
Lockley, 1991, Fig 5. 3 (part)
Holotype
TMP 87.76.7
Etymology
meaning footprint of a hadrosaur
Locality
St.Mary River valley, about 20 km SSW of Lethbridge, Alberta (Currie et al., 1991, fig. 1)
Horizon
St. Mary River Formation
Age
Late Cretaceous (Maastrichtian)
Diagnosis

Trackway of a large three-toed biped. Tracks as wide or wider than long. Each toe impression consists of an oval pad with long axis parallel to track axis. Track axis rotated inward relative to trackway mid line. Step short, about 2 × foot length. Heel rounded, transverse or posteriorly concave with bilobed posterior margin. May be associated with small manus tracks.
Type ichnospecies
Hadrosauropodus langstoni

Hadrosauropodus langstoni Ichnospecies nov.
Figs. 8–12

Holotype

TMP 87.76.7, a pes track found with associated manus and topotype/paratype trackway segments on the same surface (Currie et al., 1991, fig. 5).
Etymology

Meaning hadrosaur track named in honor of Wann Langston, who first identified such tracks from the St. Mary River Formation.
Locality
As for ichnogenotype
Horizon
St. Mary River Formation
Age
Late Cretaceous (?Campanian-Maastrichtian)
Description

Pes tracks wider than long (55 cm long and 60 cm wide), with a wide bilobed heel, about 35 cm in maximum width near the posterior margin. Heel and toes characterized by polygonal skin impressions. Track is sub symmetrical with tear drop shaped pads on all digits, which are separated from the much larger heel pad by well-defined creases. Associated subtriangular manus impression situated anterolateral to the impression of pes digit III. Manus wider than long (about 25 by 15 cm) with long axis oriented at about 45° to the trackway mid line The step short, measuring little more than two foot lengths (1.2–1.3 m). Pes axis rotated inwards at about 20° to the trackway midline.

Skin impressions consist of honeycomb-like mosaic of tightly packed sub hexagonal polygons ranging from about 0.3–0.8 mm in diameter. Pattern more or less regular over large areas of the foot. Size and packing pattern may vary among individuals.

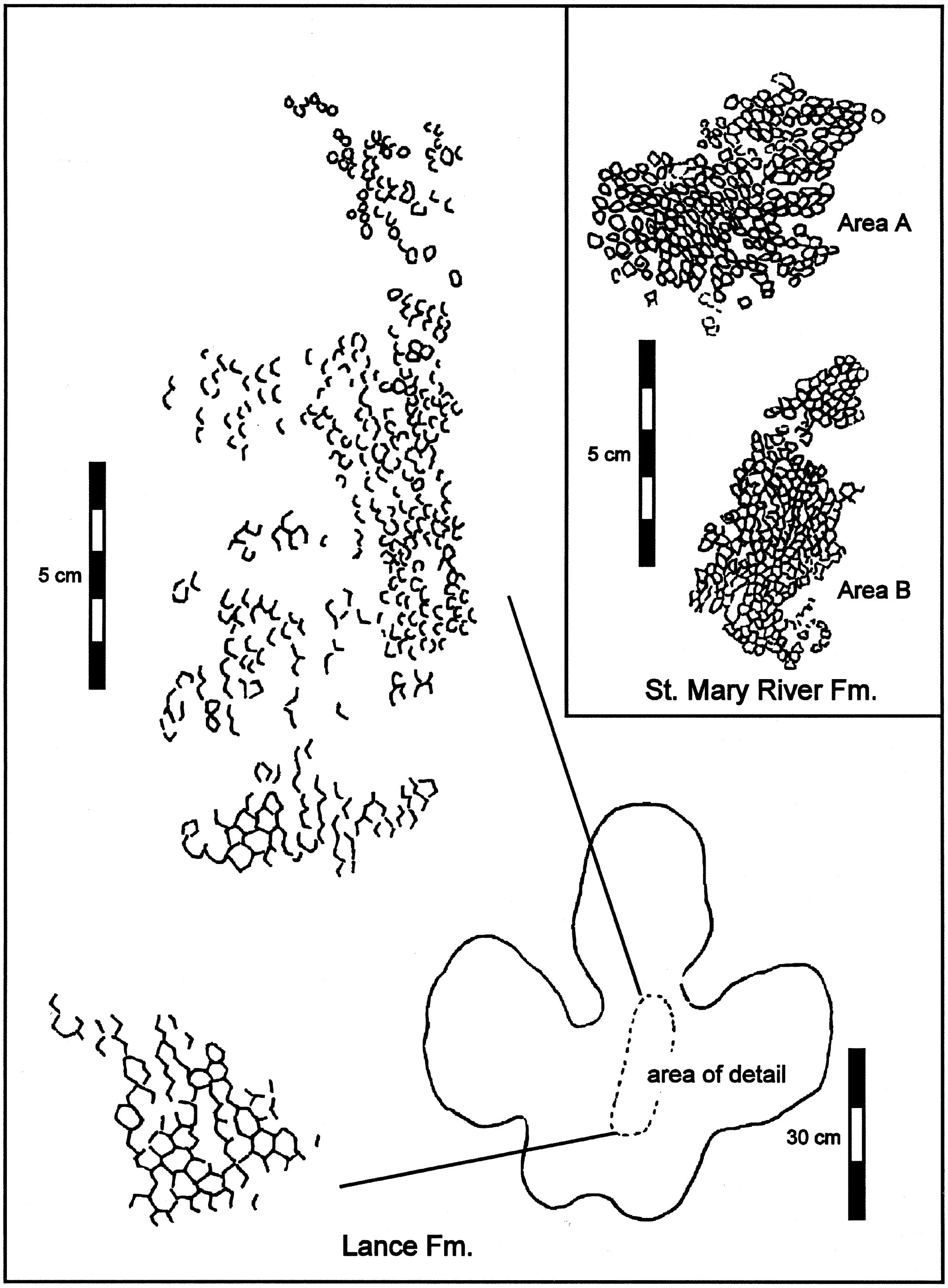

FIG. 9. Tracing of skin impressions from hadrosaur tracks in Lance Formation with inset showing comparable patterns from type specimen (TMP 87.76.6) of *Hadrosauropdus langstoni* drawn to same scale. Compare with Fig. 11.

Comparisons Between Trackways from the Lance and St. Mary River Formations (Fig. 11)

Although only one segment of hadrosaur trackway is known from the Lance site under discussion (Figs. 3, 8), it is a trackway of considerable significance. Firstly it reveals, well-preserved skin impressions (Figs. 9 and 10) that allow the integument pattern to be compared with hadrosaurian tracks with skin impressions from the St. Mary River Formation (Currie et al., 1991). The trackway is also associated with a possible tail drag impression (Fig. 8).

The two tracks are similar, except for the width of the bilobed heel impression, which is significantly wider in the St. Mary

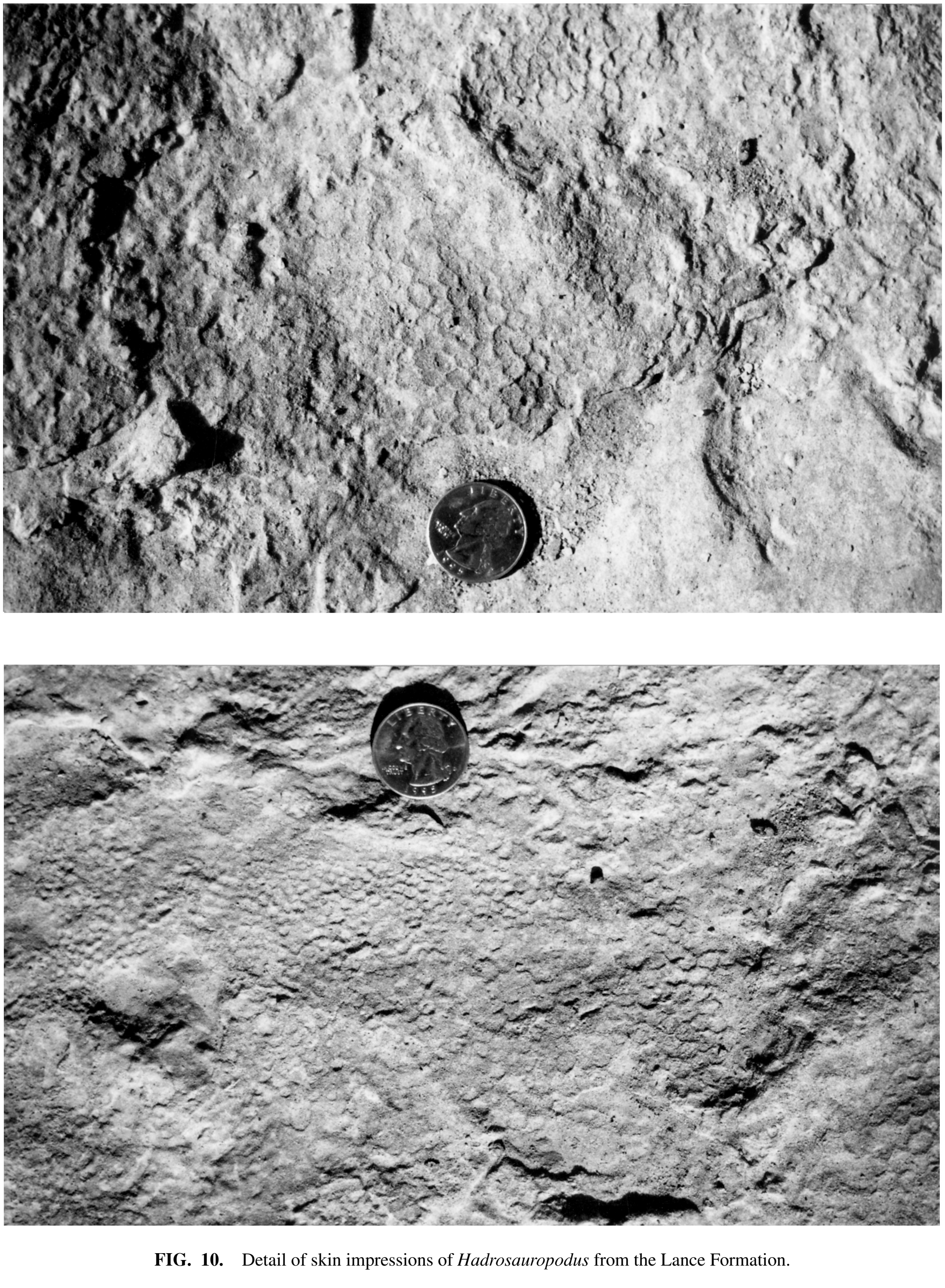

FIG. 10. Detail of skin impressions of *Hadrosauropodus* from the Lance Formation.

River Formation example. This could represent individual, specific, generic, or dimorphic differences in the trackmaker, and so could be sufficient justification for naming the Lance specimen as a different ichnospecies. We prefer to err on the side of caution and simply refer to the Lance specimen as *Hadrosauropodus* sp. Nonetheless, the St. Mary River specimen is a natural cast with substantial relief, whereas the Lance specimen is an impression with little relief. Differences in heel width may be due, in part, to dynamic movement of the foot resulting in different preservation. However, given the presence of clear skin impressions, we assume minimal distortion of the original foot morphology.

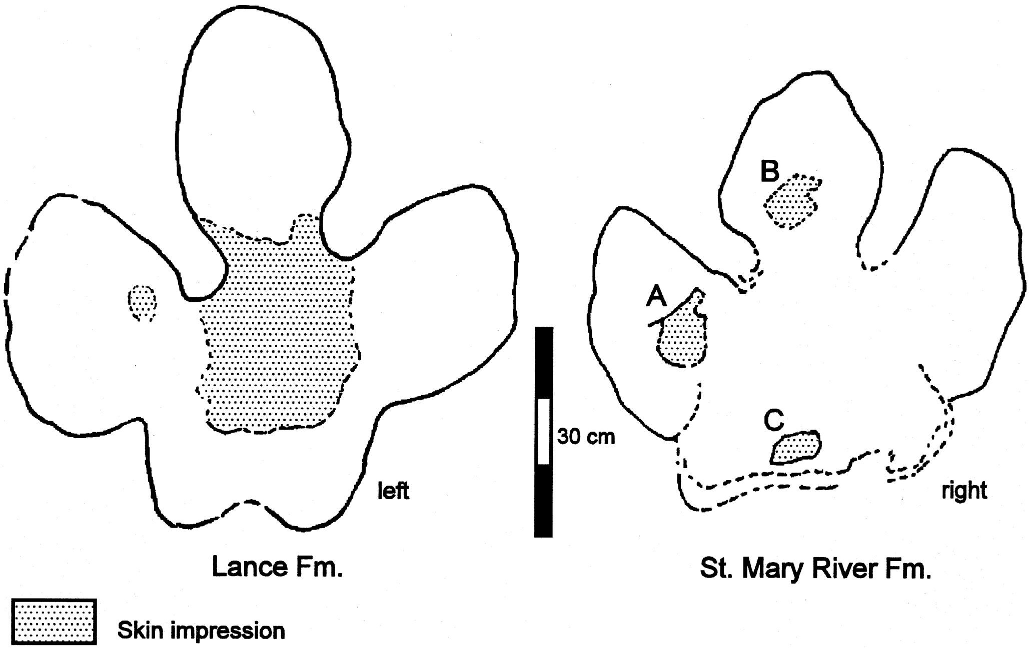

FIG. 11. Comparison of hadrosaur tracks with skin impressions from the Lance (left) and St. Mary River Formations (right) Areas A and B on the type specimen (TMP 87.76.6) of *Hadrosauropodus langstoni* correspond to details shown in Fig. 9.

Skin Impressions

Foot pad skin impressions are similar in both the Canadian and Wyoming examples (Figs. 9 and 11), and both tracks are similar in size, though the Lance footprint is somewhat larger (length and width about 75 cm, compared with 55–60 cm for the Canadian specimen). The skin traces are also located in the central portions of the plantar surface of the broad toe impressions and in the central region of the metatarsal impression. There are no obvious differences in the pattern of skin impressions between the two specimens, nor is there an obvious difference in the polygonal pattern of tubercles. In both specimens the tubercles appear larger toward the posterior region of the metatarsus impression, and appear smaller in more distal locations. Close examination of the tubercles suggests that they vary in shape from hexagonal to pentagonal to rounded. Apparently such shapes varied, presumably owing to the flexibility of the integument, for in some areas the tubercles all show similar patterns of compression.

Possible Tail Trace

Tail traces are rare for dinosaurs in general (cf. Foster et al., 2000); thus, characteristic features have not been described. The Lance trace consists of an hour-glass shaped trace extending for about 2.5 meters from the right-hand side of the first (left) footprint in the sequence as far as the heel of the next (right) footprint. The trace then evidently disappears under this second footprint but reappears in front of the second track (Fig. 8), as if the track had overprinted the tail trace. Given that one would expect the tail trace to over lap the track (not vice versa) this interpretation is subject to criticism. However, Farlow (written communication, 2003) points out that a similar situation is seen in the Lower Jurassic trackway *Gigandipus* from the Connecticut valley. He suggested that the tail trace may not register because the footprint is impressed deeply below the substrate surface. In the Lance ichnites, however, the footprints are very shallow. Other possibilities are that the tail trace did not impact the track, because the substrate had already been made firm by the footprint. Alternatively the tail trace may have been made by another animal that passed previously. It appears that the longest continuous part of the tail trace (about 1.5 meters) consists of a slightly convex-left series of curved lineations that overlaps a similar slightly curved convex right series. The symmetry suggests the sinuous motion of a tail leaving overlapping traces. There is a definite impression of dynamic motion, and moreover there is a another set of linear traces about 2 meters to the east (Fig. 3) of those illustrated in Fig. 3. However, in the final analysis, one can not rule out the possibility that this is some kind of trace/impression of something other than a tail in motion, e.g., a plant stem.

Larson (2003, p. 70A) referred to the ornithopod trackway as that of a "very large quadrupedal edmonosaurine" and inferred that " the most parsimonious interpretation for a . . . trail drag . . . is injury, most likely inflicted by a *T. rex*-sized predator," thus giving us "new information on behavior in *Tyrannosaurus rex*." We did not observe evidence that the ornithopod was progressing quadrupedally. The possibility that the trail drag indicates injury is interesting but conjectural. We infer that the ornithopod track can not be directly connected with the probable tyrannosaurid tracks (theropod track type 1) as the latter

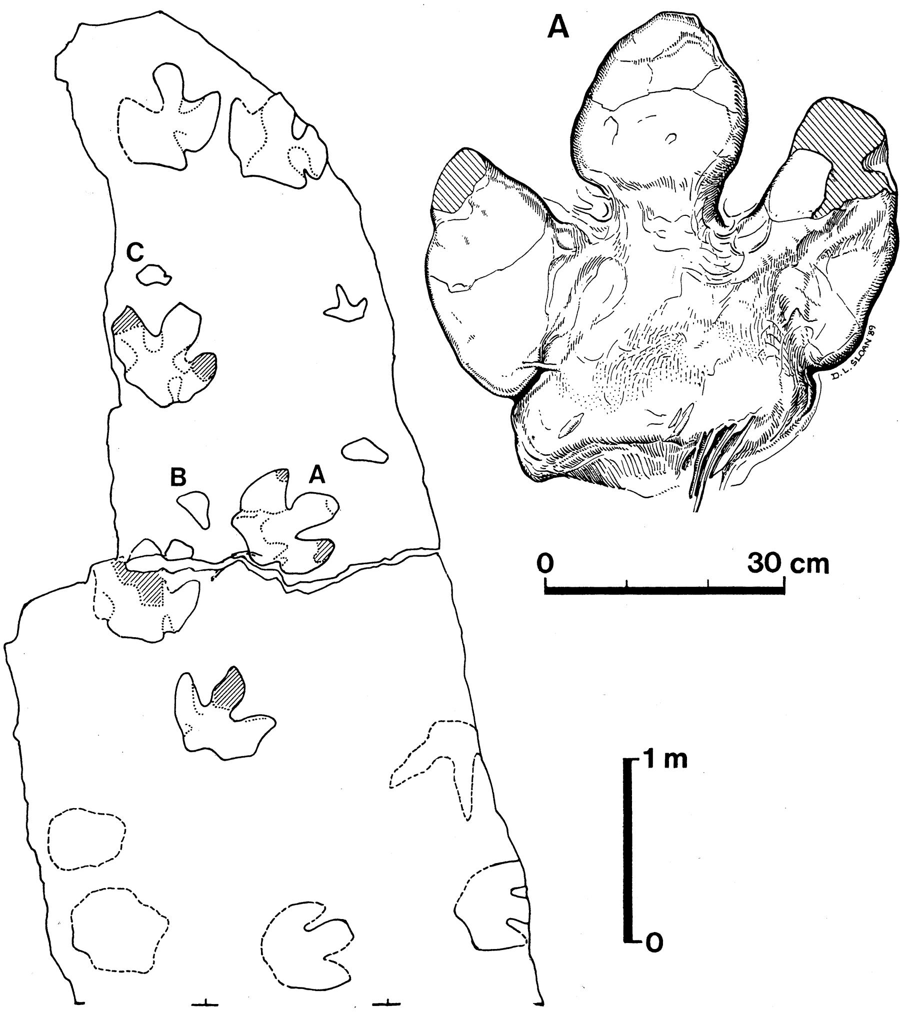

FIG. 12. Type specimen (TMP 87.76.6) of *Hadrosauropodus langstoni* (top left) shown in relation to hadrosaur track assemblage, manus tracks and partial trackway segments. After Currie et al., 1991. See text for details.

appear to be underprints made on a younger layer of sediment. They are not well-defined and lack skin impressions. Thus, they represent an animal that passed by sometime after the hadrosaur.

Concentric fractures are noted around the hadrosaur tracks. It looks as if the upper 2 cm of sand was easily penetrated, but the foot then came to rest on very firm substrate. This may be why the tracks are so well-preserved, and may explain why the inferred tail trace moved the upper 2 cm of sand so easily. The overlying mud probably played an important role in preservation of these tracks. One can envisage the registration of the hadrosaur foot through the thin layer of mud onto a firmer sandy substrate. As the sand was competent it resisted penetration about 2 cm below the mud-sand interface. At that point the impact of the hadrosaur foot would presumably have "molded" or pressed a thin layer of mud on to the surface of the sand. It is probably this process that has helped preserve such clear skin impressions.

Class AVES
?Order CHARADRIIFORMES
Sarjeantopodus ichnogen. nov.

Figs. 13–15

Holotype

CUMWC 224.4 (Figs. 12 and 14)

Etymology

Footprint named in honor of William (Bill) A. S. Sarjeant, a renowned professional paleoichnolgist and keen ornithologist.

Locality

The Zerbst Ranch, Niobrara County Wyoming

Horizon

Lance Formation

Age

Late Cretaceous (Maastrichtian)

FIG. 13. Photograph of semipalmate bird track morphotype A: the type specimen of *Sarjeantopodus semipalmatus*. (CU-MWC 224.4). Coin diameter 2.3 cm: compare with Fig. 15 for scale.

Diagnosis. Medium-size, semipalmated, charadriiform-like bird track with well developed hallux. Web extends for more than half the lengths of digits III and IV.

Sarjeantopodus semipalmatus ichnosp. nov.
Figs. 13–15

Description

Natural cast of medium-size right footprint (9.5 cm long, including hallux, by 9.2 cm wide). Toes narrow without distinct phalangeal pad impressions, terminating in blunt points, without distinct claw impressions. Web between digits III and IV connects to digits about 1.5 cm from their distal ends. Web between digits II and III connects proximally at 3 and 4 cm, respectively, from the their distal ends. Divarication between digits II and IV is 150° (i.e., 95° between digits II and III, and 50° between digits III and IV). Hallux, medium length, rotated

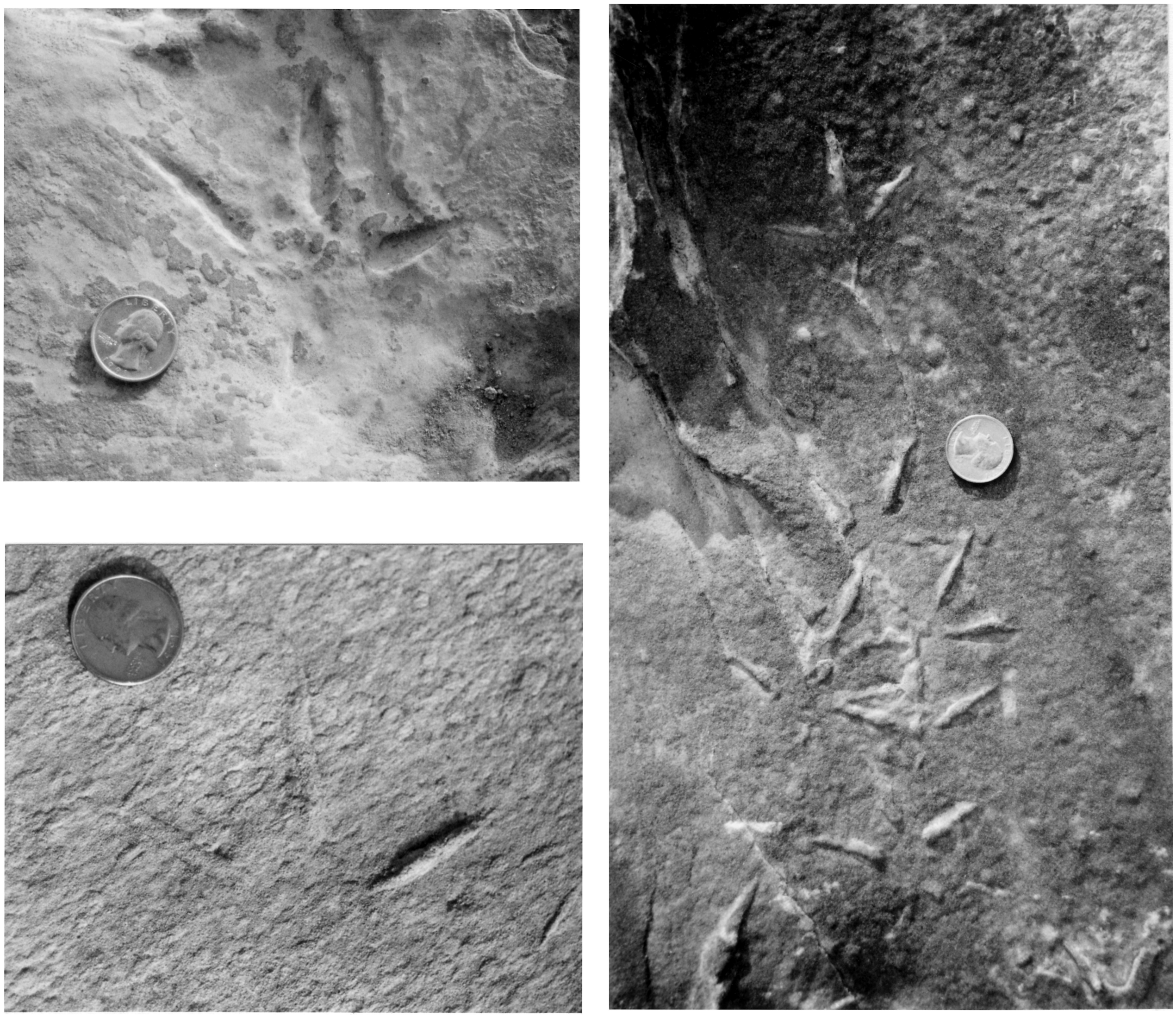

FIG. 14. Photographs of other bird tracks. **Top left**: *Sarjeantopodus semipalmatus*. (CU-MWC 224.5); **bottom left**: tridactyl track with high density of rain drop impressions; right: morphotype B (CU-MWC 224.6). Coin diameter 2.3 cm: compare with Fig. 15 for scale.

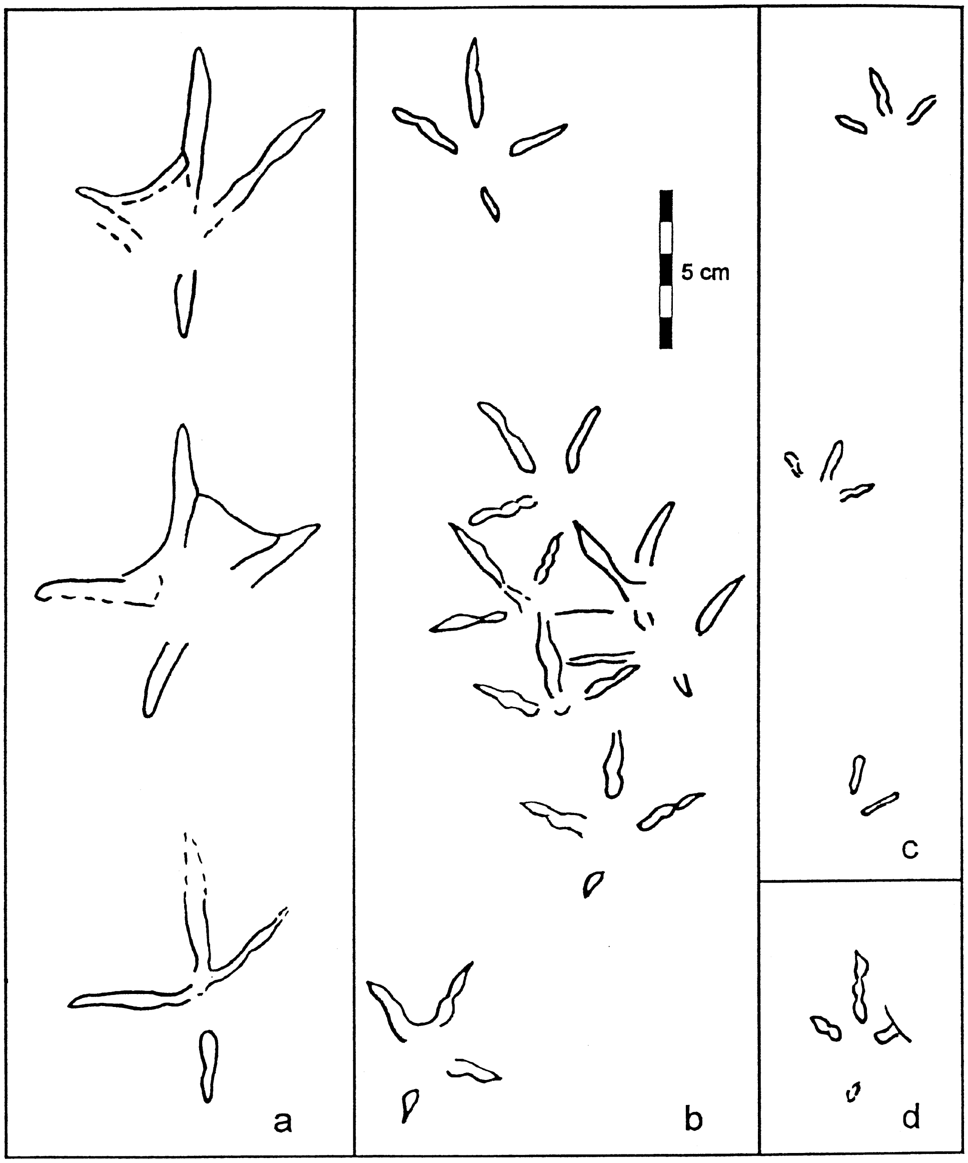

FIG. 15. Line drawings of bird tracks from the Lance Formation after Lockley and Rainforth (2002). Tracks a-d correspond to morphotypes A–D respectively. Compare with Figs. 13 and 14. Middle track in box a is holotype of *Sarjeantopodus semipalmatus* (CU-MWC 224.5): compare with Fig. 13.

posterior-medially: i.e., subtending a 165° angle to digit III. Trackway unknown.

Discussion

Shorebird or charadriiform-like bird tracks are common in the Cretaceous. However, this is the first North American Cretaceous report of a well-preserved semipalmated form, and as such it is a unique morphology that merits separate diagnosis as a new ichnogenus and ichnospecies. We name it in honor of the late Bill Sarjeant, who himself named several fossil bird track species, and who was an avid ornithologist. For clarification the term "semipalmated" refers to partial webbing between digits II and IV, and not to the asymmetry of webbing seen in *S. semipalmatus* and similar modern forms. In fact asymmetry of webbing in semiplamated forms is the rule, and invariably involves greater web development between digits III and IV than between II and III.

Late Cretaceous shorebird tracks almost all lack preserved webbing impressions (Lockley et al., 1992; Lockley and Rainforth, 2002). Only two webbed forms have been reported (Yang et al., 1995), one of which reveals a symmetrical (i.e., palmated) morphology. The second form (*Hwangsanipes*) is much smaller than *Sarjeantopodus* (by about 32%) and appears to be asymmetrical and semipalmated, though this characteristic is not brought out clearly in the original descriptions (Yang et al., 1995). Size is also an important morphological criterion among birds because most species are fully grown when they leave the nest; thus, *Hwangsanipes* can not be considered the track of a juvenile of *Sarjeantopodus* trackmaker. *Hwangsanipes* is similar to *Sarjeantopodus* in shape and hallux length, but has a more developed web between digits II and III. Although not of immediate taxonomic concern, *Hwangsanipes*is is probably about 15 million years older than *Sarjeantopodus* and is found on a different continent, at a different latitude (Hwang et al., 2002).

A similar web trace situation pertains in the Tertiary, where most tracks lack web traces, or have fully developed webbing (palmation) as in ducks, geese and their relatives (e.g., Lockley and Hunt, 1995). Preservational factors play a role in whether or not web traces are preserved in fossil footprints. Thus duck and geese tracks may lack obvious web traces in some examples, as can also be seen among modern tracks under certain substrate conditions. However, in this case the holotype (CU-MWC 224.4) is remarkable well preserved. There is sufficient relief to prevent any ambiguity in interpretation and, moreover, raindrop impressions are preserved both within the track (web trace) area and on the surrounding substrate. This suggests that the rain drop traces were made after, not before, the tracks. Indeed it could have been raining as the trackmaker crossed this area, causing the rain drop impressions to form immediately afterwards.

According to Kochan (1994) semipalmate feet are found in avocets, dotterels, willets, semipalmated plovers, certain other plover and sandpiper species, and certain herons. However, in some of these species the webbing is only slightly developed in the proximal region. The closest match for *S. semipamatus* would be among birds in which webbing is well developed towards the distal end of the foot, especially asymmetrically between digits III and IV. This situation is approached in the American avocet, though the webbing between digits II and III is more highly developed (Jaeger, 1948; Brown et al., 1984, 1987; Elbroch and Marks, 2001), and in the Curlew (Brown et al., 1987), though both these forms lack a well developed hallux. Conversely in a bird like the black-necked stilt the webbing between digits II and IV is less well developed (Elbroch and Marks, 2001: *contra* Jaeger, 1948).

Other Bird Tracks

As noted by Lockley and Rainforth (2002), there are at least four bird track morphotypes (Figs. 12–14) in this assemblage. They have been assigned CU-MWC numbers as follow:

1) Morphotype A: large tetradactyl with semipalmate web: herein named *S. semipalmatus* (CU-MWC 224.4, 224.5)
2) Morphotype B: medium sized tetradactyl (CU-MWC 224.6, 224.7)
3) Morphotype C: small tridactyl (CU-MWC 224.8, 224.9)
4) Morphotype D: small tetradactyl (CU-MWC 224.10)

Morphotype A: *S. selmipalmatus*, is described in detail in this paper. All other morphotypes potentially warrant descriptions as new ichnotaxa. However, although comparisons with modern bird tracks are helpful, it is beyond the scope of this paper to formally name morphotypes B–D.

Morphotype B: a medium-sized morphotype (length 6.0 cm; width 5.6 cm; Fig. 13b) with a hallux that is slightly shorter than that found in morphotype A. Based on size, digit divarication and hallux configuration Morphotype B resembles that of a shorebird (Charadriformes) similar to a modern godwit, willet or curlew (Jaeger, 1948). This type has not previously been reported from the Upper Cretaceous.

Morphotype C: a small track without hallux (length 2.0 cm; width 3.3 cm; Fig. 13c) resembles the track of a modern least sandpiper or sanderling, and so is obviously representative of a Charadriiformes-like form. It is characterized by inward rotation of the foot (Digit III) in relation to the trackway axis, and is similar to unnamed tracks from the Upper Cretaceous North Horn Formation (Lockley, 1999). In ichnotaxonomic terms, the tracks are similar to the Lower Cretaceous track *Koreanornis* (Lockley et al., 1992) except that they lack the evidence of a small hallux sometimes seen in this ichnogenus.

Morphotype D: a small track with hallux (length 4.7 cm; width 3.0 cm; Fig. 13d) is represented by a single specimen, and is not easily matched with modern species. It is notable for having a rather elongate middle digit, and is not obviously representative of the Charadriiformes.

The presence of four distinct bird track morphotypes, all from the same bedding surface (Figs. 12 and 13), is suggestive of a moderate avian diversity, as already seen in Campanian deposits such as the Blackhawk and North Horn Formations (Robinson, 1991, and Lockley, 1999, respectively). The Lance Formation is one of the few Late Cretaceous deposits from which skeletal remains of birds are known; Brodkorb (1963) reported eight species. As summarized by Olson (1985: p. 173) these were “described as loons, flamingos, shorebirds and ichthyornithiforms” and included the new genus *Palintropus* (Brodkorb, 1970). According to Olson (1985: p. 173) “the entire known avifauna from the Lance Formation . . . . . . may consist of “transitional” charadriiforms.” More recently Hope (1999, 2002) has listed twenty possible avian taxa from the Lance of which nine have formal names (Hope, 2002, Table 15.2). She notes, however, that unequivocal assignment of species to Charariiformes remains problematic owing to the fragmentary nature of much material. Nonetheless she lists *Graculavus, Telmatornis, Volgavis* and *Cimolopteryx* as probable charadriiform genera, thus coincidentally matching the diversity suggested by the tracks. In any event, it is interesting that this diverse avian track assemblage has come to light because it affords us the opportunity to begin to compare the trace fossil record of birds with their body fossil record.

CONCLUSIONS

Although well known for having produced an abundance of skeletal remains, the Lance Formation was previously not known for having produced any significant footprint evidence. The Zerbst ranch site is exceptional in having revealed a diverse ichnofauna of well-preserved dinosaur and bird tracks with associated skin impressions, probable tail traces and rain drop impressions. While the hadrosaur tracks and a large theropod footprint (morphotype A) tentatively attributed to *Tyrannosaurus* represent dinosaurs well-known in this time interval, the affinity of the two other theropod tracks (Morphotype B or *Saurexallopus* and unnamed Morphotype C) remain uncertain, and perhaps as yet unmatched by any known skeletal remains. However, these latter morphotypes have been identified in coeval deposits and so appear to have some utility for local correlation and ichnofauna comparison. A similar situation pertains with the four bird track types, of which at least three probably represent Charadriiformes (shorebirds). They may correspond in a general sense with what appears to be a relatively diverse charadriiform avifauna including four genera based on fragmentary skeletal remains. However, detailed correlation between these genera and the footprints is impossible owing to the absence of articulated foot remains.

ACKNOWLEDGEMENTS

Thanks to Arlene Zerbst and the late Leonard Zerbst for access to the Lance site on the Zerbst Ranch and all their help. Thanks also to Peter Larson for making a large mold of the entire site as a means of preserving a permanent "hard copy" replica. We thank Jim Farlow, Indiana University, and Spencer Lucas, New Mexico Museum of Natural History and Science, for their helpful reviews and suggestions. Joanna Wright also read an early draft of this manuscript and offered comments.

REFERENCES

Alexander, R. Mc N. 1991. How dinosaurs ran. *Scientific American*, 264:130–136.

Alonso, R. 1980. Icnitas de dinosaurios (Ornithopoda, Hadrosauridae) en el Cretacico superior del norte Argentina. *Acta Geologica Lilloana*, 15:55–63.

Brett-Surnam, M. 1972. The appendicular anatomy of hadrosaurian dinosaurs. Thesis, University of California at Berkeley.

Brett-Surnam, M. 1979. Phylogeny and paleobiogeography of hardrosaurian dinosaurs. *Nature*, 277:560–562.

Brodkorb, P. 1963. Catalogue of fossil birds (Archaeopterygiformes through Ardeiformes), Part 1. *Bulletin of the Florida State Museum, Biological Sciences*, 7:180–293.

Brodkorb, P. 1970. The generic position of a Cretaceous bird. *Quarterly Journal of the Florida Academy of Science*, 32:234–240.

Brown, R., Lawrence, M., and Pope, J. 1984. Animals of of Britain and Europe: their tracks trails and signs. Country Life Books, London: 236 p.

Brown, R., Ferguson, J., Lawrence, M., and Lees, D. 1987 Tracks and signs of the Birds of Britain and Europe, Helm, London: 333 p.

Casamiquela, R. 1968. Ichnolgia. *In* Casamiquela, R. and Fasola, A (1968). Sobre pisadas de dinosaurios del Cretacico Inferior de Colchagua (Chile). *Universidad de Chile Publication*, 30:13–24.

Casanovas Cladellas, M. L., Ezquerra Miguel, R., Pernandez Ortega, A., Perez-Lorente, F., Santafe Llopis, J. V., and Torcida Fernandez, F. 1993. Tracks of a herd of webbed ornithopds and other footprints found in the same site (Igea, la Rioja, Spain). *Revue de Paleobiologie*, 7:29–36.

Conner, C. W. 1991. The Lance Formation—Petrography and Stratigraphy, Powder River basin and nearby basins, Wyoming and Montana. *United States Geological Survey Bulletin*, 1917-F: 17 p.

Currie, P. J. 1983. Hadrosaur trackways from the Lower Cretaceous of Canada. *Acta Paleontologica Polonica*, 28:63–73.

Currie, P. J. 1995. Ornithopod trackways from the Lower Cretaceous of Canada. *In* Sarjeant, W. A. S. (ed.), Vertebrate Fossils and the evolution of scientific concepts. Gordon and Breach Publishers, Amsterdam: 431–443.

Currie, P. J., Badamgarav, D., and Koppelhus, E. B. 2003. The first late Cretaceous footprints from the Nemegt Locality in the Gobi of Mongolia. *Ichnos* (in press).

Currie, P. J., Nadon, G., and Lockley, M. G. 1991. Dinosaur Footprints with Skin Impressions from the Cretaceous of Alberta and Colorado. *Canadian Journal of Earth Sciences*, 28:102–115.

Currie, P. J. and Sarjeant, W. A. S. 1979. Lower Cretaceous Footprints from the Peace River Canyon, B.C., Canada. *Palaeogeography Palaeoclimatology Palaeoecology*, 18:103–115.

Derstler, K. 1996. The forgotten treasure—dinosaurs from the Lance Formation of Wyoming. *In* Wolberg, D. L. and Stump, E. (eds). Dinofest International Symposium. Program and Abstracts. Arizona State University: 44.

Elbroch, M. and Marks, E. 2001. Bird tracks and sign. Stackpole Books, Mechanicsburg, Pennsylvania: 456 p.

Farlow, J. O., Smith, M. B., and Robinson, J. M. 1995. Body Mass, bone "strength indicator," and cursorial potential of *Tyrannosaurus rex*. *Journal of Vertebrate Paleontology*, 15:713–725.

Fauchauld, K. 1977. The polychaete worms. Definitions and keys to orders, families and genera. *Natural History Museum of Los Angeles County, Science Series*, 28:1–88.

Foster, J., Hamblin, A., and Lockley, M. G. 2000. The oldest evidence of a sauropod dinosaur in the western United States and other important vertebrate trackways from Grand Staircase-Escalante National Monument, Utah. *Ichnos*, 7:169–181.

Flores, R. M. and Ethridge, F. G. 1985. Evolution of intermontane fluvial systems of the Powder River basin, Montana and Wyoming. *In* Flores, R. M. and Kaplan, S. S. (eds.), Cenozoic Paleogeography of the West-central United States, Rocky Mountain Paleogeography Symposium 3. Rocky Mountain Section, Society of Economic Paleontologists and Mineralogists: 107–126.

Gatesy, S. M., Middleton, K. M., Jenkins, F. A. Jr., and Shubin, N. H. 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature*, 399:141–144.

Harris, J. D. 1997. Four-toed theropod footprints and a paleomagnetic age from the Whetstone Falls Member of the Harebell Formation (upper Cretaceous: Maastrichtian), northwestern Wyoming: a correction. *Cretaceous Research*, 18:139.

Harris, J. D., Johnson, K. R., Hicks, J., and Tauxe, L. 1996. Four-toed theropod footprints and a paleomagnetic age from the Whetstone Falls Member of the Harebell Formation (upper Cretaceous: Maastrichtian), northwestern Wyoming. *Cretaceous Research*, 17:381–401.

Hope, S. 1999. A new species of *Graculavus* from the Cretaceous of Wyoming (Aves: Charadriformes). *In* Olsen, S. L. (ed.), Avian Paleontology at the close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington D.C. *Smithsonian Contributions to Paleobiology*, 89:231– 243.

Hope, S. 2002. The Mesozoic radiation of Neornithes. *In* Chiappe, L. and Witmer, L. M. (eds), Mesozoic Birds above the heads of dinosaurs. University of California Press, Berkeley:339–388.

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, S. W. Korea. *Geological Magazine*, 139:421–435.

Jaeger, E. 1948. Tracks and Trailcraft. Macmillan, New York: 381 p.

Kochan, J. B. 1994. Birds feet and legs. Stackpole Books. Mechanicsburg, Pennsylvania: 81 p.

Langston, W. 1960. A hadrosaurian ichnite (Alberta). National Museum of Canada Natural History papers No. 4:1–19.

Laporte, L. and Behrensmeyer, A. K. 1980. Tracks and substrate reworking by terrestrial vertebrates in Quaternary sediments of Kenya. *Journal of Sedimentary Petrology*, 50:1337–1346.

Larson, P. 2003. An important trackway site from the Lance Formation (Late Cretaceous) of Niobrara County, Wyoming, with new information on the behavior of *T. rex*. *Journal of Vertebrate Paleontology*, 23: 70A.

Lee, Y.-N. 1997. Bird and Dinosaur Footprints in the Woodbine Formation (Cenomanian), Texas. *Cretaceous Research*, 18:849–864.

Leonardi, G. 1984. Le impronte fossili di Dinosauri. *In* Sulle orme de dinosauri. Erizzo Editrice, Venice: 165–186 p.

Llompart, C. 1984. Un nuevo yacimiento de ichnitas de dinosaurios en las facies Garumnienses de la Conca de Tremp (Leida Espana). *Acta Geologica Hispanica*, 19:143–7.

Lockley, M. G. 1987. Dinosaur Footprints from the Dakota Group of Eastern Colorado. *Mountain Geologist*, 24:107–122.

Lockley, M. G. 1991. Tracking Dinosaurs: a New Look at an Ancient World, Cambridge University Press, Cambridge: 238 p.

Lockley, M. G. 1999. Pterosaur and bird tracks from a new locality in the Late Cretaceous of Utah. *In* Gillette, D. D. (ed). *Utah Geological Survey. Miscellaneous Publication*, 99–1:355–359.

Lockley, M. G. and Foster, J. 2003. Late Cretaceous Mammal tracks from North America. *Ichnos*, 10:269–276.

Lockley, M. G., Holbrook, J., Hunt, A. P., Matsukawa, M., and Meyer, C. 1992. The Dinosaur Freeway: a Preliminary Report on the Cretaceous Megatracksite, Dakota Group, Rocky Mountain Front Range and Highplains; Colorado, Oklahoma and New Mexico. *In* Flores, R. (ed.), Mesozoic of the Western Interior, Society of Economic Paleontologists and Mineralogists Midyear Meeting Fieldtrip Guidebook, 87:39–54.

Lockley, M. G. and Hunt, A. P. 1994. A Track of the Giant Theropod Dinosaur *Tyrannosaurus* from Close to the Cretaceous/Tertiary Boundary, Northern New Mexico. *Ichnos*, 3:213–218.

Lockley, M. G. and Hunt, A. P. 1995a. Dinosaur Tracks and Other Fossil Footprints of the Western United States, Columbia University Press, New York: 338 p.

Lockley, M. G. and Hunt, A. P. 1995b. Ceratopsid Tracks and Associated Ichnofauna from the Laramie Formation (Upper Cretaceous: Maastrichtian) of Colorado. *Journal of Vertebrate Paleontology*, 15:592–614.

Lockley, M. G., Matsukawa, M., and Hunt, A. P. 1993. Tracking Dinosaurs: New Interpretations Based on Footprints. An Exhibit Guidebook, University of Colorado at Denver, 68 p.

Lockley, M. G. and Meyer, C. A. 2000. Dinosaur Tracks and other fossil footprints of Europe. Columbia University Press, New York: 323 p.

Lockley, M. G., Meyer, C., Hunt, A. P., and Lucas, S. G. 1994. The Distribution of sauropod Tracks and Trackmakers. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural*, *Lisbon, Portugal*, 10:233–248.

Lockley, M. G. and Peterson, J. 2002. Fossil footprints of the world. A Lockley Peterson Publication, Boulder Colorado, Published in conjunction with the Friends of Dinosaur Ridge, Boulder: 128 p.

Lockley, M. G. and Rainforth, E. 2002. The tracks record of Mesozoic Birds and Pterosaurs: an ichnological and paleoecological perspective. In Chiappe, L. and Witmer, L. M. (eds.), Mesozoic Birds above the heads of dinosaurs. University of California Press, Berkeley: 405–418.

Lockley, M. G., Schulp, A., Meyer, C. A., Leonardi, G., and Kerumba-Mamani, D. 2002. Titanosaurid trackways from the Late Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behavior. *Cretaceous Research*, 23:383–400.

Lockley, M. G. and Wright, J. L. 2001. The trackways of large quadrupedal ornithopods from the Cretaceous: a review. In Carpenter, K., and Tanke, D. (eds.). Mesozoic Vertebrate Life. New research inspired by the Paleontology of Philip J. Currie, Indiana University Press, Bloomington: 428–442.

Lockley, M. G., Wright, J. L., and Matsukawa, M. 2001. A New Look at *Magnoavipes* and so-called "Big Bird" tracks from Dinosaur Ridge (Cretaceous, Colorado). *Mountain Geologist*, 38:137–146.

Lockley, M. G., Yang, S. Y., Matsukawa, M., Fleming, F., and Lim, S. K. 1992. The track record of Mesozoic birds: evidence and implications. *Philosophical Transactions of the Royal Society of London*, 336:113–134.

Moreno, K. and Pino, M. 2002. Huellas de dinosaurios en la Formación Baños del Flaco (Titoniano-Jurásico Superior), VI Región, Chile: paleontología y paleoambiente. *Revista Geologicia de Chile*, 29:191–206.

Nadon, G. C. 1993. The Association of Anastomosed Fluvial deposits and Dinosaur Tracks, Eggs, and Nests: Implications for the Interpretation of Floodplain Environments and a Possible Survival Strategy for Ornithopods. *Palaios*, 8:31–44.

Nadon, G. C. and Issler, D. R. 1997. The compaction of floodplain sediments: what's wrong with this picture? *Geoscience Canada*, 24:37–43.

Nichols, D. J. and Brown, D. L. 1992. Palynostratigraphy of the Tullock Member (Lower Paleocene) of the Fort Union Formation in the Powder River Basin, Montana and Wyoming. *United States Geological Survey Bulletin*, 1917–F:35 p.

Olson, S. L. 1985. The Fossil Record of Birds. *In* D. S. Farner, J. R. Kingam and K. C. Parkes, "Avian Biology volume III," Academic Press, London: 79–256.

Psihoyos, L. and Knoebber, J. 1994. Hunting Dinosaurs. Random House, New York: 267 p.

Robinson, S. F. 1991. Bird and frog tracks from the late Cretaceous Blackhawk Formation in east central Utah. *Utah Geological Association Publication*, 19:325–334.

Santos, V. F., Lockley, M. G., Moratalla, J. J., and Galopim, A. 1992. The Longest Dinosaur Trackway in the World? Interpretations of Cretaceous Footprints from Carenque, near Lisboa, Portugal. *Gaia: Revista de Geociencas, Museu Nacional de Historia Natural, Lisbon, Portugal*, 5:18–27.

Sarjeant, W. A. S., Delair, J. B., and Lockley, M. G. 1998. The footprints of *Iguanodon*: a history and taxonomic study. *Ichnos*, 6:183–202.

Seeland, D. 1988. Laramide paleographic evolution of the eastern Powder River basin, Wyoming and Montana. *Wyoming Geological Association Guidebook, 38th Field Conference*: 29–34.

Sternberg, C. M. 1926. Dinosaur Tracks from the Edmonton Formation of Alberta. *Canada Museum, Bulletins geological series*, 44:85–87.

Thulborn, R. A. 1990. Dinosaur Tracks. Chapman Hall, London: 410 p.

Triebold, M., Lockley, M. G., Janke, P., and Nystrom, C. 1999. Dinosaur Tracks from the Hell Creek Formation (Upper Cretaceous, Maastrichtian). South Dakota. *Journal of Vertebrate Paleontology*, 19: 81A.

Weishampel, D., Dodson, P., and Osmolska, H. 1990. The Dinosauria, University of California Press, Berkeley: 733 p.

Wright, J. L. 1996. Fossil Terrestrial Trackways: function, taphonomy and paleoecological significance. Unpublished Ph.D. thesis, University of Bristol: 300 p.

Yang, S.-Y., Lockley, M. G., Greben, R., Erikson, B. R., and Lim, SY. 1994. Flamingo and Ducklike Bird Tracks from the Late Cretaceous and Early Tertiary: Evidence and Implications. *Ichnos*, 4:21–34.