Walk, Wade, or Swim? Vertebrate Traces on an Early Permian Lakeshore

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A new vertebrate track site in the Lower Permian Wellington Formation in north-central Oklahoma is described wherein tracks are found on a single dolomite bedding plane that can be traced along more than 1.6 km of disconnected outcrops. In excess of 1,400 tetrapod tracks, including 16 trackways, are documented. Because of extramorphological factors, it was not possible to identify ichnogenera with certainty, but five distinct morphotypes are described, and their possible affinities with known Permian ichnotaxa are given. All tracks appear to be undertracks of vertebrates walking on all fours, wading on their back legs, or swimming. It is proposed that one of these morphotypes was made by a web-footed trackmaker. Aspects of the ichnofauna and lithologic features suggest a lacustrine paleoenvironment for the track site, and could warrant further subdivision of the redbed ichnofacies.

INTRODUCTION

Recent work in vertebrate ichnology has increased greatly the number of described Early Permian vertebrate track sites (Lucas and Heckert, 1995), consolidated the taxonomy of these ichnofossils (Haubold and Lucas, 1999), and provided a basis for understanding the relationships of Permian vertebrate ichnofaunas with their depositional environments (Lockley et al., 1994). The bulk of this research has concerned ichnofaunas from Arizona and New Mexico (Lucas and Heckert, 1995; Hunt et al., 1995a) and Europe (Haubold, 1971, 1984; Lockley and Meyer, 2000, for English summary).

The ichnofauna described herein was discovered in 1998, southeast of the town of Billings in north-central Oklahoma (Fig. 1). This occurrence of abundant tracks on a single dolomite bedding plane within the Wellington Formation constitutes the first significant track site known from the Early Permian of Oklahoma. The unique depositional features of the site, and its association with a new vertebrate body-fossil and plant-fossil locality, allow an interpretation of the local Wellington paleoenvironment. The location and fauna of the site also invite comparisons with described Permian vertebrate ichnofacies.

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SITE DESCRIPTION

Geological Setting

This study was undertaken during 1998 and 1999 at a locality in the NW1/4 Sec.14 T23N R2W southeast of the town of Billings in Noble County, Oklahoma. The track-producing layer lies near the middle of the Wellington Formation. The Wellington Formation of Oklahoma and Kansas has been correlated to the Admiral and Belle Plains Formations (lower Wichita Group) of northern Texas. Recent revisions of Texan stratigraphic nomenclature have placed the Admiral and Belle Plains Formations as part of the Nocona, Petrolia, and Waggoner Ranch Formations of the Wichita Group (Hentz, 1989). Similar ichnofaunas have been described from the Early Permian (Wolfcampian) Abo and Cutler Formations of southern and northern New Mexico, respectively (Lucas and Heckert, 1995).

The depositional history of the Billings site is distinct from other known Early Permian trackway localities in both North America and Europe. The Wellington Formation exposed north of Perry, Oklahoma, and extending into Kansas is dominated by evenly bedded shales, dolomites, and lenticular sandstones that are predominantly gray or green in contrast to the fluvial redbed facies typical of the Wellington to the south and younger sediments to the west of this area. The gray sequence contains abundant evidence of very shallow water, such as mud cracks and algal structures. It is occasionally cut by channels filled with coarser clastics that have yielded vertebrate body fossils and plants (see Olson, 1970). At the Billings site, the sequence is topped by a red, cross-bedded sandstone–the basal Billings Pool Member–15 meters below the base of the Garber Formation, representing an influx of terrestrial sand. The gray sequence is sparsely fossiliferous, but a few horizons have yielded spectacular concentrations of insects and conchostracans (Carpenter, 1947; Tasch and Zimmerman, 1962). Carlson (1968, 1987, 1999) has described lungfish and amphibians from the dolomites of this sequence; no marine fossils have been collected. The gray sequence in the Wellington Formation has been interpreted as a saline tidal flat environment with interspersed channels, lakes, and ponds (Shelton, 1979; Schultze, 1985). The fauna and lithology at the Billings site suggest a lacustrine depositional environment, perhaps fluctuating between fresh and saline conditions, as Raasch (1946) and Olson (1970) have suggested. The sequence appears to show cyclic stratification consistent with fluctuations of the Permian sea to the west.

Taphonomic and Sedimentologic Considerations

More than 1,400 individual foot prints were documented on a 63.3 m^2 bedding plane exposure at the Billings site

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FIGURE 1—Map showing the location of the Billings site in Noble County and the occurrence of Lower Permian sediments in Oklahoma.

(Fig. 2). These include 16 distinguishable trackways, 12 of which were assigned to five morphotypes. The longest trackway (trackway 4) included 103 prints and extended 11.4 m. Tracks are observed easily on the surface and exhibit an average density of 22 tracks/m^2 at the study site. The abundant tracks and the occurrence below a distinctive dark shale make it possible to trace the track-producing layer along interrupted outcrops for more than 1.6 km.

The occurrence of tracks on a dolomite is unique for Early Permian trackway sites. The dolomite is light gray, fine-grained, and lacks any internal sedimentary structures, invertebrate epifaunal or infaunal traces, toolmarks, or rainprints. Irregularly occurring sub-parallel depressions, 3–6 cm wide and 0.5 cm deep, may represent remnants of ripple troughs. Six of the 16 trackways are aligned parallel to these depressions. The dolomite also has a distinctive undulating surface with fractures apparently enlarged by post-depositional solution.

The preservational quality and the extramorphological characteristics of the tracks allow an interpretation of the substrate conditions. Mud globs are present on the posterior margin of many individual tracks and are useful indicators of the direction of movement. Large tracks were impressed up to 3 cm into the dolomite, nearly the thickness of the bed. However, there is no record of these prints on lower units. These qualities indicate a water-saturated carbonate mud substrate that was firm enough to preserve distinct prints. Several factors suggest that the prints are undertracks impressed in the carbonate mud through some thickness of the overlying clay. These include the incompleteness of the tracks (i.e., reduction of tracks to two or three digits), apparent digitigrady, apparent bipedalism, and the absence of tail drags. A distinctive feature of the Billings site is the absence of small tracks of vertebrates or traces of invertebrates. The selective preservation of isolated large (greater than 3 cm wide) tracks suggests that some animals may have been too lightweight to impress tracks through the overlying clay layer or that the water was, at times, deep enough to allow smaller tetrapods to swim above the substrate.

METHODS

A well-situated outcrop allowed convenient access to an 18 x 6-m area of the track-bearing surface after removing up to 30 cm of overlying black fissile shale. Figure 3 shows this outcrop. Once exposed, a grid of 1 x 1-m squares was used to record the location of the tracks and trackways. Latex molds were made of significant sections of the track surface. Photographs of individual tracks as well as trackways were made, and representative tracks from each trackway were collected. The tracks and molds are in the vertebrate paleontology collections of the Sam Noble Oklahoma Museum of Natural History in Norman, Oklahoma. The track specimen numbers are OMNH 57012 through OMNH 57036, a total of 25 specimens (a portion of the molds was used to form the base of the new Permian vertebrate exhibit at the museum). The three-dimensional latex molds, plots of the tracks and trackways, photographs, and track specimens constitute a reasonably complete record of the site.

In addition to plotting track occurrence, applicable measurements, orientations, and descriptions were made for each trackway following the conventions of Leonardi (1987). Trackway measurements included stride, pace, gleno-acetabular length, pace angulation and width (Fig. 4). Individual track data included width, length, and number of digits for both the pes and manus.

ICHNOLOGY

All the tracks at the Billings site are underprints. They could not be identified with confidence, because they are extreme extramorphological variants of Permian ichnotaxa. Five distinctive tracks and trackways are described as morphotypes. Trackways are shown in Figure 2, a partial map of the site; all measurements are listed by morphotype in Table 1.

Morphotype A—Paired Crescentic Tracks

This morphotype was seen in trackway 4 and possibly 9, and is shown in Figures 5, 6A, and 6B. A referred specimen is OMNH 57012. Morphotype A consists of crescent shaped digitigrade tracks creating the artificial appearance of hoof-prints. Four or five digits are present in the manus and five in the pes, all shallowly impressed and oriented anteriorly. The pes is wider than the manus with its axis parallel to the midline. There is a strong pairing of the pes and manus in the trackway pattern, with the pes placed behind and slightly lateral to the manus. These tracks suggest an affinity with the ichnogenus *Limnopus* (Marsh, 1894), based on the strong pairing and relative position of the pes and manus. The unique hoof-print form, possible foot morphology, and extramorphologic influences are discussed below.

Morphotype B—Short Toed Tracks

Morphotype B was seen in trackway 3 and is shown in Figures 6C and 6D. Referred specimens are OMNH 57017 and OMNH 57018. This morphotype appears to be a trackway of a relatively large animal with only the pes tracks preserved. Four digits are apparent, perhaps a fifth in the large digit IV impression. The track axis is parallel to the midline. These tracks are impressed deeply (~20 mm), showing a wide, rounded, short posterior margin (possibly a heel). Most prints display rounded digits, though a few show evidence of elongation. An affinity of specimens OMNH 57017 and OMNH 57018 with the ichnogenus *Baropezia* is based on the large size, morphology (short, wide impressions), and rounded digits. The absence of known large bipedal Permian vertebrates suggests that these may be the pseudo-bipedal variants of another large ichnogenus such as *Limnopus*.

Morphotype C—cf. *Gilmoreichnus* Haubold, 1971

Morphotype C was seen in trackways 5, 6, and 8, and is shown in Figures 6E and 6F. Referred specimens are OMNH 57014–57016. The trackways from which these specimens were taken display a consistent digitigrade pattern with the pes preserved only as digit tips. Manus digits III-V curve inward distally; digits I and II are straight, shorter and less deeply impressed. No tail drag is evident. The morphology of specimens OMNH 57014–57016 resembles "*Hylopus hermitanus*" Gilmore (1927) renamed by Haubold (1971) as *Gilmoreichnus hermitanus*.

Morphotype D—Parallel Tridactyl Traces

This morphotype was seen in trackway 15 and is shown in Figures 7A and 7B. A referred specimen is OMNH 57020. The trackway consists of three consecutive three-digit claw marks. The tracks are approximately 10 cm wide, parallel to one another, slightly s-shaped, and have tapered tips with blunt posterior ends. The size of both the track and trackway are indicative of a large swimming trackmaker with long slender toes and claws. A reasonable affinity would be with *Dimetropus* (Romer and Price, 1940).

Morphotype E—L-Shaped Traces

Morphotype E was seen in trackway 17, and is shown in Figures 8A and 8B. A referred specimen is OMNH 57013. Tracks consist of L-shaped impressions with the long margin proximal and parallel to the midline. The medial digit is longest, although distinctions between digits are not clear on most prints. The posterior medial margins of the tracks are deep, shallowing anterolaterally. Three digits are distinguishable on some prints; all are parallel and directed forward. Nail drags are very apparent anterior to many prints. Manus and pes impressions are nearly identical; the manus is somewhat smaller. An affinity with *Dromopus* Marsh (1894) is very tentative due to the poor preservation of these tracks. Haubold et al. (1995) described the variations in expression of *Dromopus* tracks when there is great substrate influence. Primary alterations of track morphology consist of reduced digits and increased digitigrady. OMNH 57013 could be interpreted as a poorly preserved example of *Dromopus* lacking pad impressions and with a reduced number of digits represented. Specimens of *Dromopus* that closely resemble those at the Billings site are found in the collections of the Science Museum of Minnesota. Specimens PMG87B10AZ0030 and PMG87B10AZ0026 from the Coconino Sandstone in the Permian of Arizona represent *Dromopus* tracks in the *Chelichnus* (eolian) ichnofacies. These tracks, made in a clearly different environment, are remarkably similar to the L-shaped tracks identified as Morphotype E from the Billings site. They are depressions with the pad implied at the posterior margin. Only two digits are represented, parallel and facing anteriorly, the medial one being longer and deeper with the print shallowing laterally.

Swimming Traces

These traces are shown in Figure 7, and occur in trackways 12, 14, 15, as well as numerous individual tracks. Referred specimens are OMNH 57026, OMNH 57031, OMNH 57032, and OMNH 57036. The referred specimens are examples of the myriad of incomplete traces ranging in size from 3 to 10 cm wide; they most commonly consist of tridactyl claw marks. These traces are hypothesized to represent animals either using the substrate as a method of propelling themselves forward while swimming (especially when posterior mud gobs are present) or simply dragging their claws as they swam in relatively shallow water. Brand (1996) found that modern salamanders, when partially buoyed by water, tended to produce parallel scratch marks rather than toe impressions. An alternate interpretation is that these are undertracks made when the mud layer above the dolomite was thicker. None of these specimens exhibits a diagnostic morphology that can be used for identification. However, on the basis of size, OMNH 57020 might be attributed to a large pelycosaur.

DISCUSSION

Identification of Trackmakers

Schult (1994) and many others have noted the difficulties of attempts to pair tracks and trackmakers. Haubold (1996, table 3) has proposed taxonomic groups of body fossils generally equivalent to ichnogenera. The identifications made here generally follow previous work with some correspondence to a nearby body fossil fauna.

Morphotypes A and B (assuming the proposed affinities with *Limnopus* and *Baropezia* are correct) are considered to be of temnospondyl amphibian origin. Morphotype A may represent the trackway of *Trimerorhachis*, which is of appropriate size. Lateral line canals and evidence of perennibranchiate gills (Olson, 1979) suggest that *Trimerorhachis* spent most of its time in the water. This corresponds well with the webbed foot structure (proposed below) for the origin of these tracks and the lacustrine interpretation of the depositional environment. *Trimerorhachis* is a very common element in the fauna recovered from the nearby channel-fill deposit that intersects the track layer (pers. observ.).

The reptile tracks at the Billings site are Morphotypes C (cf. *Gilmoreichnus*), D, and E (assuming the proposed affin-

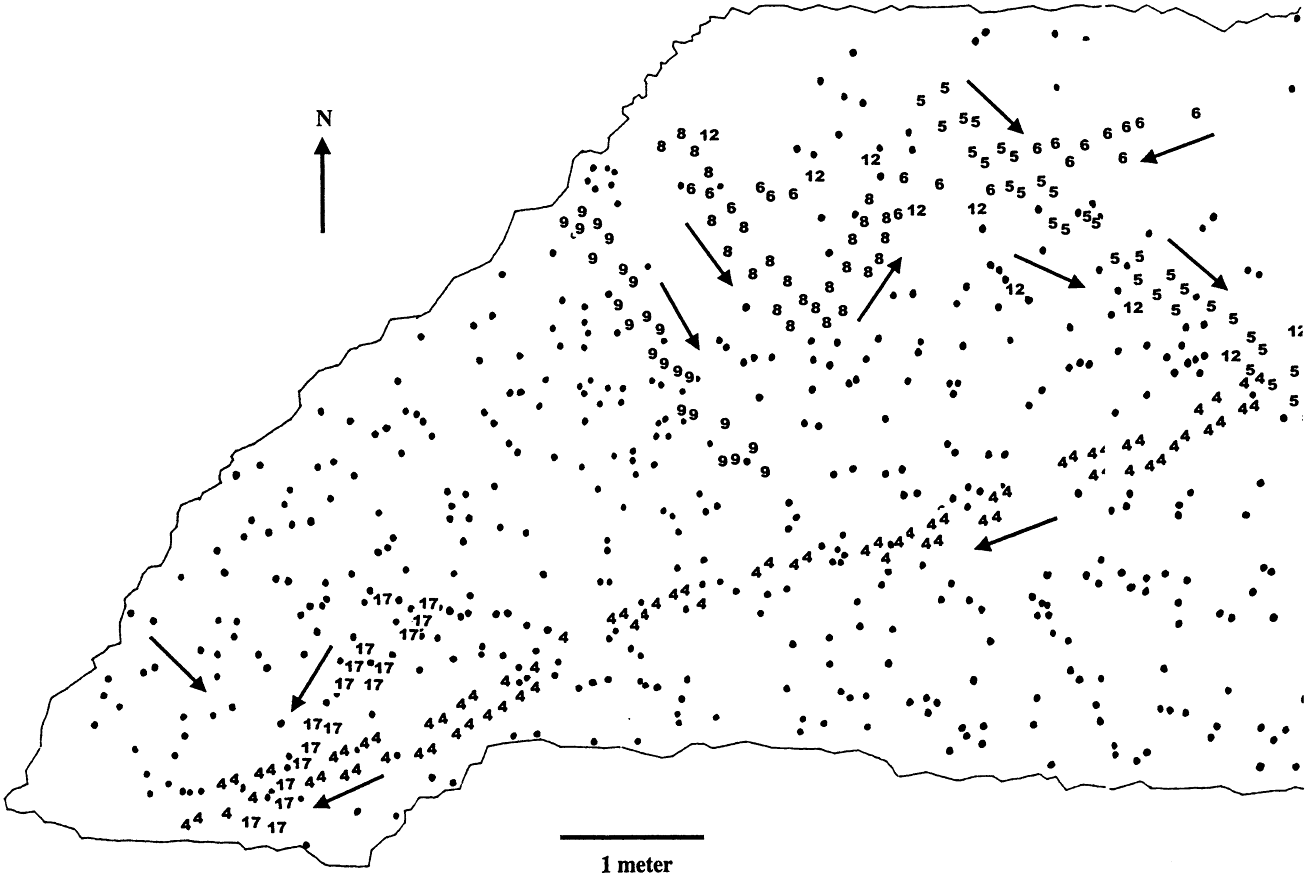

FIGURE 2—Map of the track site. Dots represent tracks; numbers associated with arrows indicate trackways. Trackways 4 and 9 are Morphotype A; 3 is Morphotype B; 5, 6, 8, and 9 are Morphotype C; 15 is Morphotype D; 17 is Morphotype E. Trackways numbered 1, 2, 7, 10–14, and 16 are indeterminate.

ities with *Dimetropus* and *Dromopus*, respectively). Haubold (1971) correlated *Gilmoreichnus* with ophiacodont pelycosaurs on the basis of foot morphology. A reasonable correlation for Morphotype D is a large sphenacodont pelycosaur, such as *Dimetrodon*. The Morphotype E track maker is considered an araeoscelid primarily because of its lacertoid morphology (Gilmore, 1926). Haubold (1971) has associated the gracile digits apparent in *Dromopus* with the genus *Araeoscelis*. *Dictybolos* (Olson, 1970) is similar in body plan to *Araeoscelis*, although the limb structure is understood poorly. *Dictybolos* is also common in the nearby channel-fill quarry (pers. observ.). An articulated string of vertebrae recovered from this quarry indicates a gleno-acetabular length of 24 cm, which matches closely the gleno-acetabular length of 24.5 cm estimated from the Morphotype E trackway at the Billings site. Olson (1970) proposed an aquatic lifestyle for *Dictybolos* based on the long, slender teeth, nostril placement, kinetic skull structure, and the cartilaginous nature of its limb joints.

The aforementioned channel-fill quarry is located 30 m southwest of the trackway exposure and appears to intersect the track-bearing layer. This site has yielded a number of plant and vertebrate fossils. The fauna recovered there, in addition to *Trimerorhachis* and *Dictybolos*, includes the lungfish *Gnathorhiza* and other as yet undetermined fish, amphibians, and reptiles.

The Foot Morphology of the Morphotype A Trackmaker

Trackway number 4 (OMNH 57012, Figs. 5, 6) is the most distinctive and interesting of those preserved at the Billings site. Each track is clearly an underprint with a convex-forward arc-shape, with four or five digit-tip impressions observed in the manus, five in the pes. Pes arcs are distinctly wider than the manus. Trackway 4 extends for 11.4 m in a straight line, and consists of tightly coupled manus and pes pairs. A large section of this trackway was molded in latex and is in the collections of the Sam Noble Museum of Natural History. The trackway width, stride, pace angulation, and gleno-acetabular length are given in Table 1 and are reasonably consistent along the length of the trackway. Drag marks and mud gobs that commonly are associated with tracks at this site are not found along this trackway. None of the impressions shows evidence of lateral movement along the curved direction of its arc form, implying that either such movement was not recorded by the undertrack layer or that the trackmaker did not rotate its appendages along the side of its body. The long and consistent trackway suggests that the trackmaker was walking either subaerially or in very shallow water.

These arc-shaped tracks are unlike the digit-tip and scratch-like impressions that are so abundant at the Billings site, and appear unique among described Permian

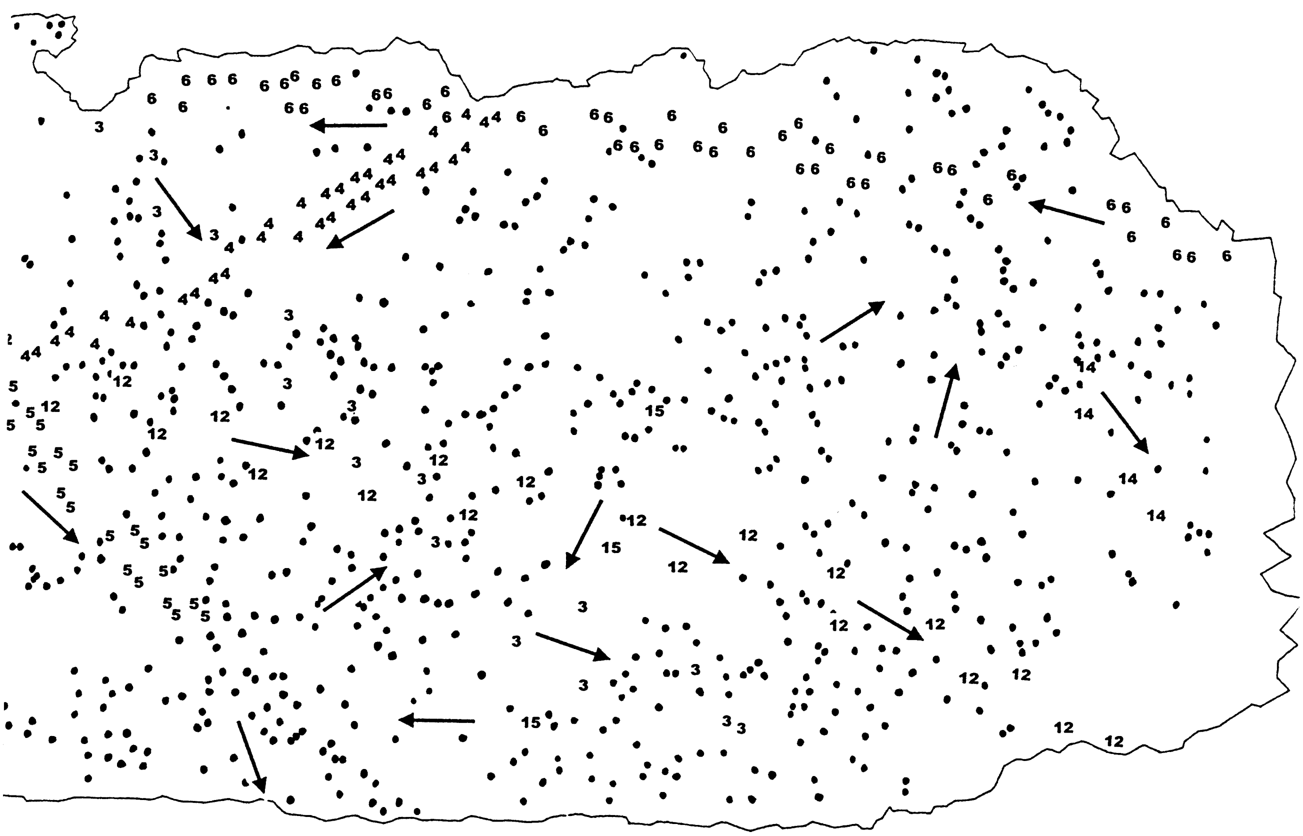

FIGURE 2—Continued.

tracks. The arc shapes with the digit tips are explained best as the impressions made by digits connected by skin, indicating a web-footed trackmaker. To date, there is no evidence for webbed feet among Permian tetrapods. But, this innovation hardly seems surprising given the frequency with which this structure appears in aquatic forms of major tetrapod groups.

Locomotion Styles

The range of morphology and preservational features of the tracks and trackways argues for an extended period during which tracks were made by walking, wading, and swimming tetrapods. The clay above the track layer may have been deposited in water that varied in depth. Variation in water depth would result in different locomotion styles in the trackmakers.

Walking

Long and continuous trackways with regular manus and pes pairs, such as trackway 4 (Morphotype A), suggest an animal walking either through shallow water or on a thin clay drape that covered the carbonate layer. In either case, the result would be a long and regular trackway. Less regular trackways (such as trackways 5, 6, and 8; Morphotype C), where the manus is digitigrade and pes impressions show only digit tips, reflect a walking animal either partially buoyed up by water or walking on a thicker clay drape that limited the penetration of feet into the underlying carbonate.

Wading

The deeply impressed and regular tracks as in trackway 3 (Morphotype B) could be interpreted as the result of animals acting as bipeds, wading on their hind legs with their heads at the surface and their front limbs held above the substrate. This locomotion style was first noticed in an underwater film of crocodiles in a David Attenborough video, but other paddling quadrupeds adopt this locomotion at water depths where their hind feet reach the bottom.

Berman et al. (2000) described *Eudibamus*, a small bolosaurid reptile from the Lower Permian of Germany, and interpreted its locomotion as parasagital, digitigrade, and bipedal at high speeds. The pes of *Eudibamus* is laterally compressed with elongated digits 3–5, and could not have left traces similar to Morphotype B. To date, large, fully terrestrial bipeds have not been reported from the Lower Permian.

Swimming

The majority of tracks at the Billings site consist either of isolated digit tip and scratch-like claw impressions or short and irregular trackways (trackways 12 and 14). These largely isolated traces may have been made by

FIGURE 3—The Billings track site. The track bearing dolomite surface exposed by the removal of the overlying shale.

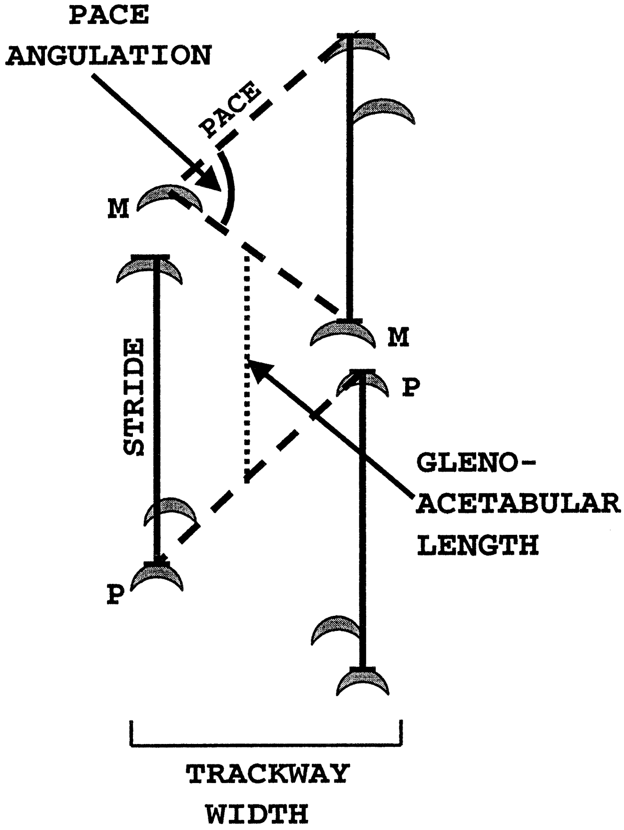

FIGURE 4—Trackway measurements. Data are in Table 1. After Leonardi (1987).

swimming animals that occasionally used their feet to propel or maneuver their way along the water-substrate interface. Brand (1996) showed that partially buoyed salamanders tended to produce parallel scratch traces with reduced numbers of digits. Alternately, these may be impressions made through a thicker or drier clay layer.

Track Density and Form

The exposure of abundant tracks on one large continuous bedding surface affords an unusual opportunity to analyze their origin. The average track density is 22 prints/m^2, with a maximum of 39 and a minimum of 8/m^2. At least two factors may have contributed to this high density: (1) The carbonate mud that preserved the tracks remained in an impressionable state for a long period of time below the dark clay of the overlying layer, or (2) the aquatic environment attracted large numbers of tetrapods. Although preservational factors limited the list of described

TABLE 1—Track and trackway measurements. Measurements are in mm. Measurements are averages taken from individual tracks or trackway. * = partial tracks. # = pseudobipedal tracks with no manus prints. /\ = All tracks were from one side of the body.

Characteristic	Morphotype				
	Morphotype A	Morphotype E	Morphotype B	Morphotype C	Morphotype D
Specimen:	57012	57013	57017, 57018	57014–57016	57020
Trackway	4, 9	17	3	5, 6, 8	15
Stride of pes:	230	225	556	325	
Stride of manus:	240	220	#	310	#
Pace:	160	175	376	220	/\
Pace angulation:	98°	83°	98°	94°	/\
Pes length:	5*	67	42	29	105
Pes width:	45	35	70	52	100
Manus length:	5*	70	#	27	#
Manus width:	29	3	#	50	#
Trackway width:	154	160	310	235	/\
Gleno-acetabular length:	180	245	#	290	/\

FIGURE 5—Morphotype A. A portion of trackway 4.

morphotypes to five, indeterminate traces suggest a larger fauna. As Farlow and Pianka (2000) and others have noted, trace fossil diversity is likely to under-represent zoological diversity.

Permian tetrapods presumably frequented aquatic environments for several reasons. Some forms, such as *Trimerorhachis*, were entirely aquatic (Olson, 1979). But upland forms also may have been attracted to water areas for feeding, protection from predation, thermoregulation, or reproduction. However, there is no compelling evidence in these trackways, the dolomite, or the overlying shale for any of these behaviors. For example, no invertebrate body fossils suggesting a food chain are preserved in these layers, although conchostracan, insect, and fish remains are abundant elsewhere in the sequence. However, the negative evidence of the lack of body fossils never makes a strong argument for the absence of a fauna, because the occurrence of tracks and body fossils often is mutually exclusive.

Ichnofacies Placement

Lockley et al. (1994) defined the ichnofacies concept as the recurrence of key vertebrate tracks that are found in association with a particular sedimentary facies. This classification scheme is similar to the ichnofacies system used for invertebrate trace fossils, in that both recognize the distribution of ichnofossils in space and time as controlled largely by geographic and sedimentologic factors. The ichnofacies concept attempts to explain the relationship between track occurrence and paleoenvironment for diverse and widely distributed ichnofaunas. In addition, the recognition of ichnofacies allows the use of distinctive vertebrate tracks to establish higher resolution biochronologies than can be provided by invertebrate ichnofacies alone (Lockley et al., 1994).

Two ichnofacies are recognized from the early Permian: the *Chelichnus* ichnofacies and a subdivided redbed ichnofacies (Lockley et al., 1994; see also Lockley and Meyer, 2000). These were defined on the basis of Permian faunas and sediments of western North America, and now are used to recognize paleoenvironment-track relationships worldwide. The *Chelichnus* ichnofacies is an association of a restricted desert fauna within an eolian lithofacies (McKeever and Haubold, 1996). The redbed ichnofacies represents a variety of fluvial, deltaic, lacustrine, and marginal marine environments. Haubold and Lucas (1999) restricted the number of Permian redbed ichnogenera to *Dromopus*, *Gilmoreichnus*, *Batrachichnus*, *Hyloidichnus*, *Dimetropus*, *Amphisauropus*, *Ichniotherium*, *Limnopus*, and potentially two or three more (Haubold et al., 1995).

The depositional history of the Billings site is distinct from other described Early Permian trackway localities in both North America and Europe. The dolomite track layer and the lithologic features of the dolomite-and-shale sequence of this part of the Wellington Formation, along with its vertebrate, insect, and conchostracan fauna, all suggest a lacustrine environment. Assuming the affinities proposed for Morphotypes A, C, and E (*Limnopus*, *Gilmoreichnus* and *Dromopus*), their presence at the Billings site corresponds well with the redbed ichnofacies. Hunt et al. (1995b) subdivided the redbed ichnofacies into an *Ichniotherium-Parabaropus* facies representing inland environments, and a *Dimetropus-Batrachichnus* facies representing coastal and fluvial environments. Morphotypes A, C, and E of the Billings site appear in both of these subfacies. Hunt et al. (1995b) suggest that the occurrence of *Limnopus* indicates a more inland environment, as it was found to be rare in coastal environments in New Mexico, but the limited occurrence of Morphotype A at Billings is not seen as diagnostic. The interpretation of this site as a lacustrine environment may warrant the further subdivision of the redbed ichnofacies.

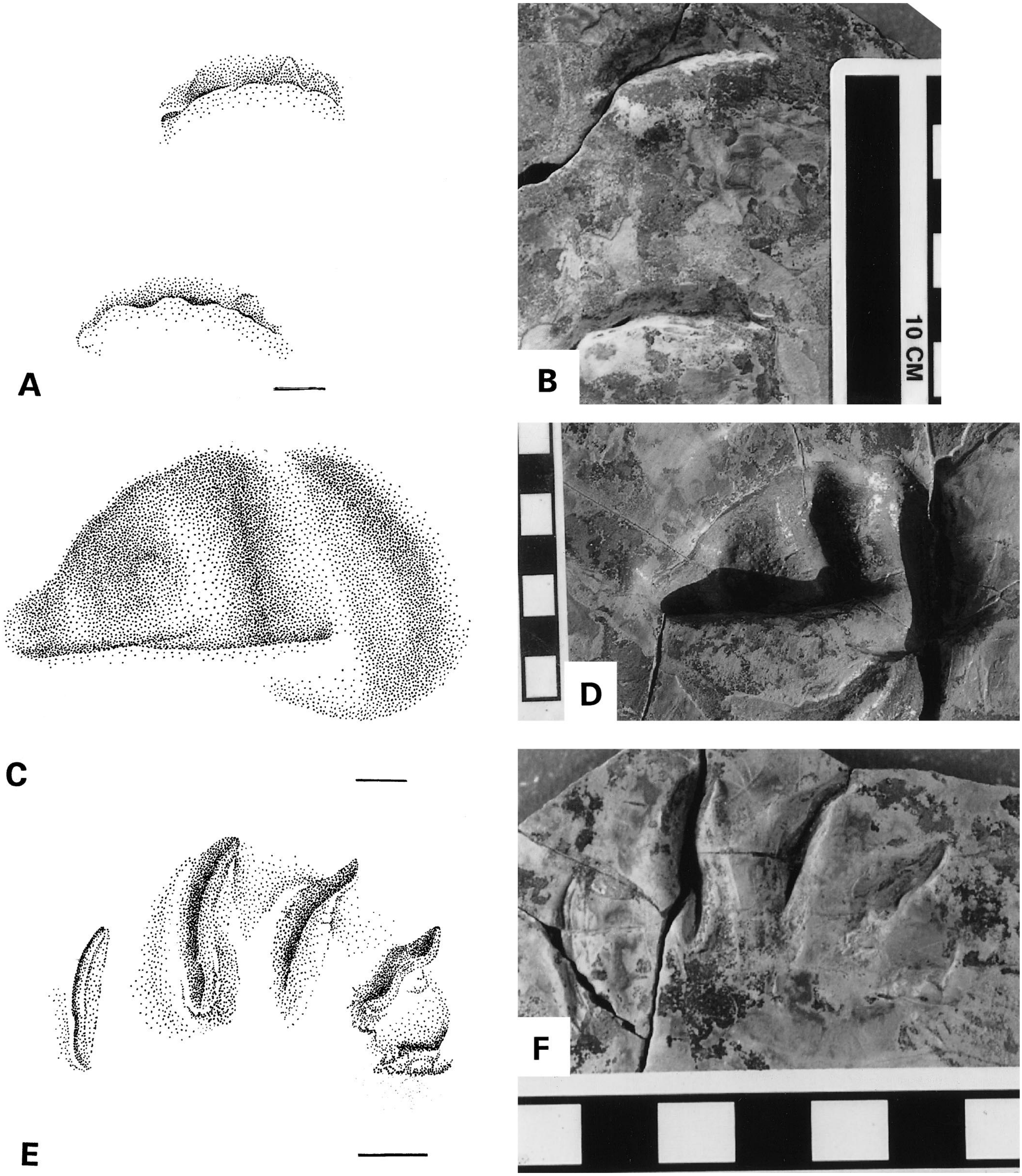

FIGURE 6—Billings site vertebrate tracks. (A, B) Left manus and pes of Morphotype A; OMNH 57012; trackway 4. (C, D) Pes of Morphotype B; OMNH 57017; trackway 3. (E, F) Manus of Morphotype C; OMNH 5716; trackway 5. Bars and rule divisions are 1 cm.

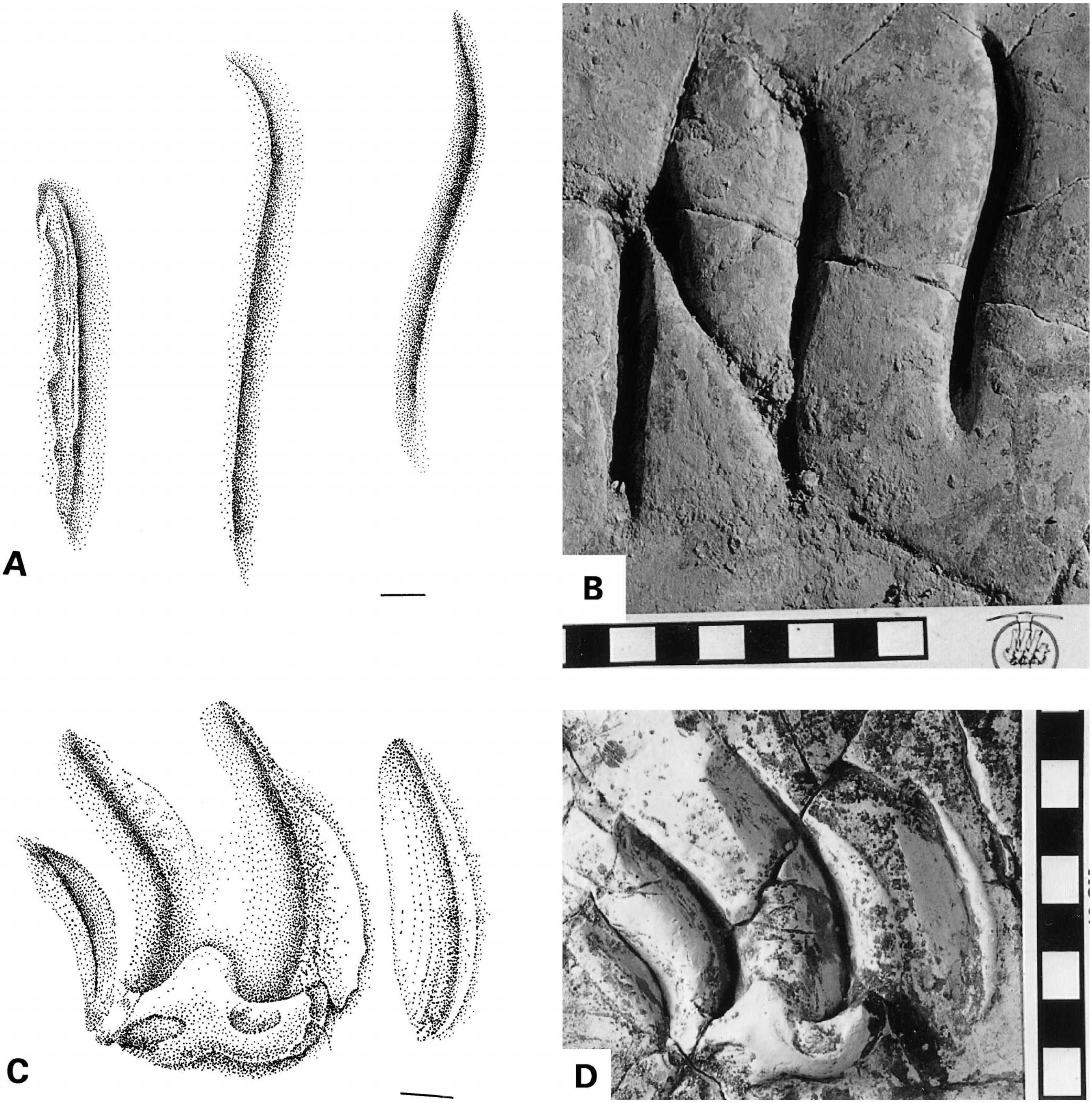

FIGURE 7—Billings site vertebrate tracks. (A, B) Three-digit impression of Morphotype D; 57020; trackway 15. (C, D) Unidentified track interpreted as a swimming impression; OMNH 57032. Note the mud gobs at the posterior of the track. Bar and rule divisions are 1 cm.

Significance within Texas-Oklahoma Ichnofauna

The Billings site is the first Permian track site described from Oklahoma, and provides a geographic link between the ichnofaunas of Arizona and New Mexico, and those of Europe (Lockley and Meyer, 2000). Raasch (1946) noted tracks from the Wellington of Oklahoma, but these were isolated and not identified. Schult (1994) noted eight ichnogenera that were known from isolated occurrences in Texas and Oklahoma. These consisted of putative amniote tracks *Erpetropus*, *Microsauropus*, *Dimetropus*, *Varanopus*, *Dromopus*, *Moodieichnus*, and amphibian tracks *Baropezia* and *Oklahomaichnus*. However, the Castle Peak, Texas specimen of *Moodieichnus* (Sarjeant, 1971) has been reidentified by Hunt et al. (1995c) as *Dromopus*, and *Oklahomichnus* is now considered a misidentified invertebrate trace (Lockley, 1993), reducing the number of Permian ichnogenera in Texas-Oklahoma to six. All of these ichnogenera, with the exception of the misidentified *Oklahomichnus*, are known only from Texas. The ichnofauna described here substantiates the presence of *Dromopus* and *Baropezia* in the Texas-Oklahoma region, while the possi-

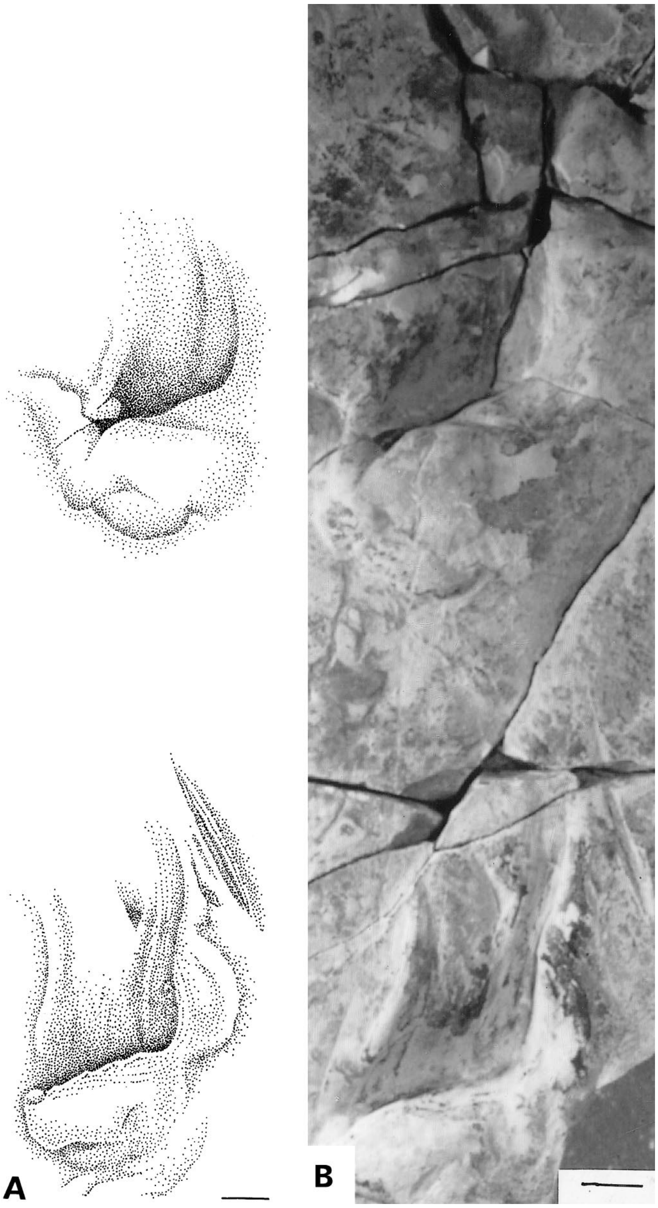

FIGURE 8—Billings site vertebrate tracks. (A, B) Left manus and pes of Morphotype E; OMNH 57013; trackway 17. Bar is 1 cm.

ble addition of *Limnopus* and *Gilmoreichnus* to this list is useful in extending comparisons of Permian ichnofaunas.

SUMMARY

As the first Permian trackway locality reported from Oklahoma, the Billings site allows a comparison with the ichnogenera and ichnofacies of Arizona-New Mexico. The wide lateral extent of this dolomite track-bearing layer, as well as the sedimentology of the associated sequence at the Billing site, suggest a lacustrine depositional environment.

Track density and diversity indicate relatively long-term accessibility of the original surface, during which putative amphibians and amniotes made the five morphotypes described here, and a number of indeterminate animals left traces on the surface. All the traces appear to be undertracks impressed through an overlying clay, and extramorphological factors also explain the pseudo-bipedalism, and the absence of both tail-drags and small tracks. Although these undertracks lack fine detail, features of the trackways suggest that the tetrapods left these traces while walking, wading on their hind legs, and swimming partially buoyed above the surface during periods of different water depths.

The ichnofauna of the Billings site places it within Lockley et al.'s (1994) redbed ichnofacies, but it can't be assigned with confidence to either of the subfacies described by Hunt et al. (1995b). Additional and better-preserved sites may call for the description of a new Permian dolomite ichnofacies.

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