Cretaceous Research (1997) **18**, 849–864

Bird and dinosaur footprints in the Woodbine Formation (Cenomanian), Texas

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Revised manuscript accepted 27 May 1997

The ichnofauna of the Woodbine Formation (Cenomanian), Denton County, Texas includes bird and dinosaur tracks. A new bird trackway, *Magnoavipes lowei* ichnogen. et ichnosp. nov., appears to represent the largest bird tracks known from the Mesozoic. A theropod trackway, *Fuscinapedis woodbinensis* ichnogen. et ichnosp. nov., is characterized by long digits of uniform width and pointed small claws. Six hadrosaurid trackways, *Caririchnium protohadrosaurichnos* ichnosp. nov., are the oldest hadrosaurid tracks associated with skeletal elements. They include one isolated small footprint, a medium-sized quadrupedal, and five large bipedal hadrosaurid trackways.

KEY WORDS: ichnology; bird; dinosaurs; *Magnoavipes*; *Fuscinapedis*; *Caririchnium*; Woodbine Formation; Cenomanian; Texas.

1. Introduction

Dinosaur tracks are abundant in the Lower Cretaceous beds of the Gulf Coastal Plain in Texas. Most sites occur in the Glen Rose Formation (early Albian) of the Trinity Group, including famous sauropod and theropod trackways in the bed of the Paluxy River near Glen Rose, Texas (e.g., Bird, 1985). Dinosaur tracks have been discovered in the Woodbine Formation (Upper Cretaceous) in a stratigraphic interval that is different from that yielding more common Texas tracks. The purpose of this paper is to document vertebrate tracks from the Woodbine Formation and to discuss the importance of their stratigraphic occurrence.

According to local newspapers, the first recognized dinosaur tracks in the Woodbine Formation were discovered by a local resident, Julie Tyler, below the spillway of the dam at Grapevine Lake, Texas, in March 1981 (Figure 1). There were twelve large ornithopod dinosaur footprints. A few casts of them were sent to Brookhaven College, Dallas (Gillette, pers. comm., 1995). Unfortunately, this site was destroyed without having been studied scientifically. In 1989, other dinosaur tracks were discovered at Murrell Park, Lake Grapevine, by reservoir managers and rangers of the US Army Engineers District, Fort Worth Corps of Engineers (Figure 2A). This site was first mapped by John Congleton, Dale Winkler, and Fidelis Morocco who were researchers from Southern Methodist University. They recognized four ornithopod trackways (track numbers 10 to 14 of trackway 3, 1 to 5 of trackway 4, and trackways 7 and 8 of this study). More tracks were found by further excavation by crews from the Dallas Museum of Natural History. They include bird, theropod and ornithopod trackways (Figure 3). The Woodbine tracksite is similar to those in the Dakota Group at a location near Golden, Colorado, and the Jindong and Uhangri formations, Korea

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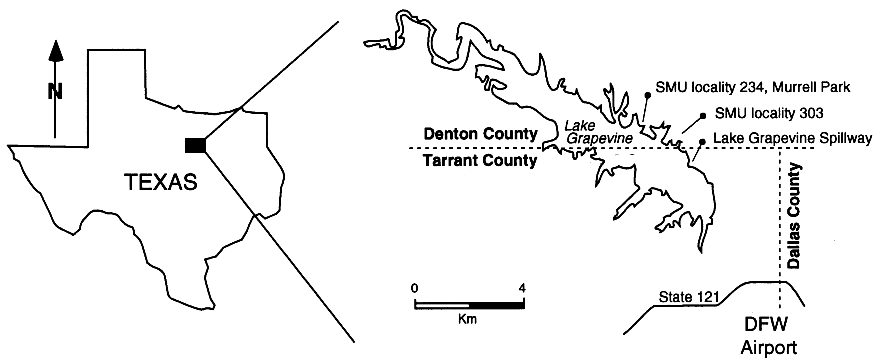

Figure 1. SMU localities near Grapevine Lake, Texas.

in that dinosaur tracks and bird footprints occur on the same surface (Lockley *et al.*, 1989, 1992; Yang *et al.*, 1995).

2. Geological setting and palaeoenvironment of the tracksite

The Woodbine Formation, named by Hill (1901) for a small town in east-central Cooke County, Texas, is the basal formation of the Gulf Series. It unconformably overlies the Grayson Marl, the uppermost formation of the Washita Group, and is unconformably overlain by the Eagle Ford Group. Two major members are widely recognized in the Woodbine Formation. They are the Dexter Member (lower sandstone) of Taff (1893) and the Lewisville Member (upper shale) of Hill (1901). In Tarrant County, Dodge (1968) proposed four rock units, in ascending order: the Rush Creek, Dexter, Lewisville, and Arlington members. Most archosaur fossils including crocodiles, and theropod, nodosaurid, and hadrosaurid dinosaurs, are known from the Arlington Member of Tarrant and Denton counties (Lee, 1997). The Arlington Member was deposited along a low-lying coastal plain (Powell, 1968).

The unit which contains the principle footprints at the tracksite consists of a fine-grained, well-sorted light grey sandstone within the lower Arlington Member (Figure 4). The heavily dinoturbated surface is found near the top of this unit (Figure 2B). At the well-defined ichnofossil level, none of the tracks appears to be undertracks but true natural impressions on a mud film overlying sand. This is supported by large ornithopod tracks showing a delicate mound of pushed-up sediment at the metatarsal-phalangeal pad, indicating that the mud horizon was partially dewatered to a cohesive, not soupy, state (Laporte & Behrensmeyer, 1980). Irregular patches of wave ripple marks on the surface are evidence that at least some of the track area was under shallow water at some point. Invertebrate traces and syneretic mud cracks are also observed on the surface. Invertebrate traces are represented by *Skolithos* associated with algal mats, which are indicative of shoreline facies (Chamberlain, 1976; Lockley *et al.*, 1994). Well preserved tracks often occur at mud-sand interfaces and clay-drape horizons (Lockley & Conrad, 1989). The quality of preservation is relatively good at this site showing toe, claw or pad impressions.

The Woodbine Formation is Cenomanian in age but it does not embrace the whole of this age because the upper part of the underlying Washita Group (Gray-

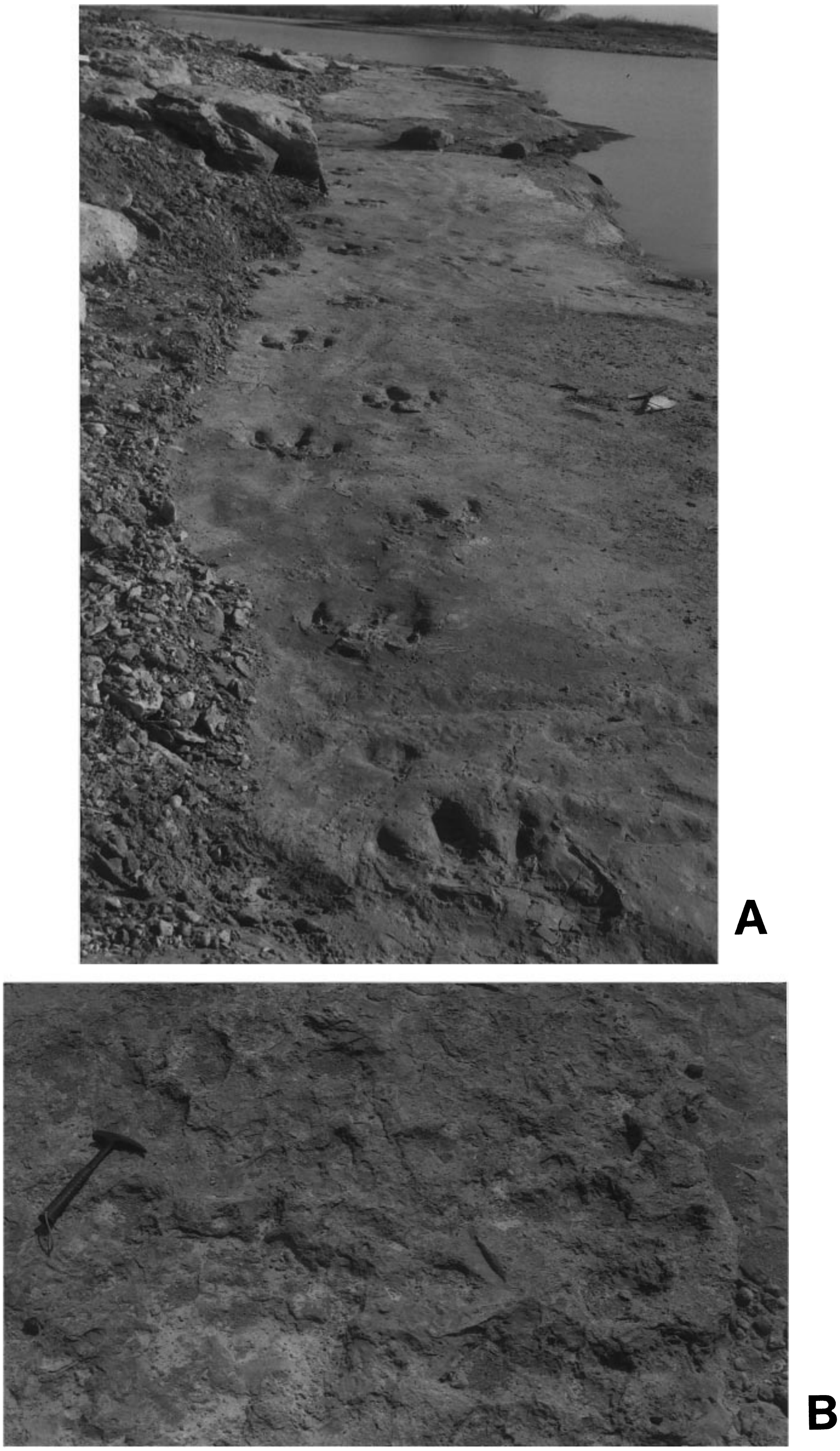

Figure 2. A, Trackways in the Woodbine Formation at SMU locality 234, Grapevine Lake, Texas; B, Dinoturbation horizon above the track level.

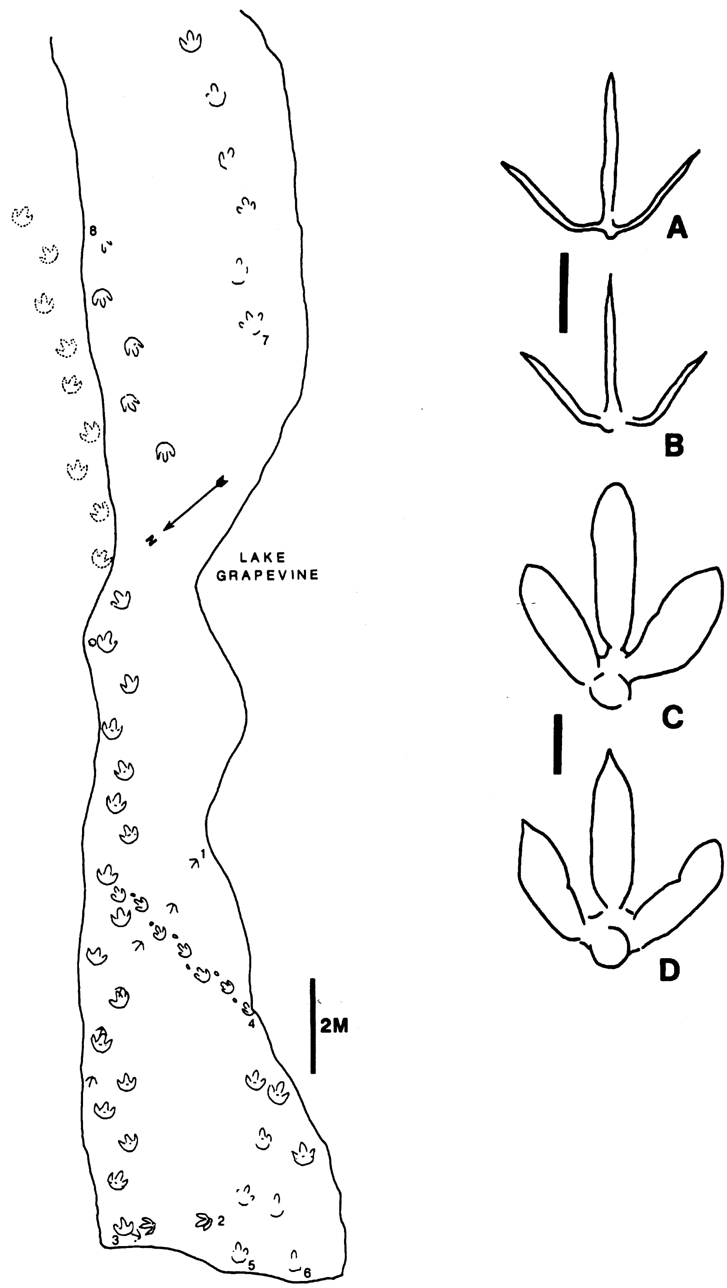

Figure 3. Map showing the distribution of trackways in the Woodbine Formation at SMU locality 234, Grapevine Lake, Texas. Stippled footprints were mapped by staff of the Dallas Museum of Natural History. A, *Magnoavipes lowei*, holotype (DMNH 918); B, *Magnoavipes lowei*, paratype; C, *Fuscinapedis woodbinensis*, holotype (SMU 74651); D, *Fuscinapedis woodbinensis*, paratype. Scale bars = 10 cm.

son Marl) and the basal unit of the Eagle Ford Group are also included in the Cenomanian. The uppermost Arlington Member yields a *Conlinoceras tarrantense* Zone ammonite fauna, which represents the lower middle Cenomanian (Kennedy

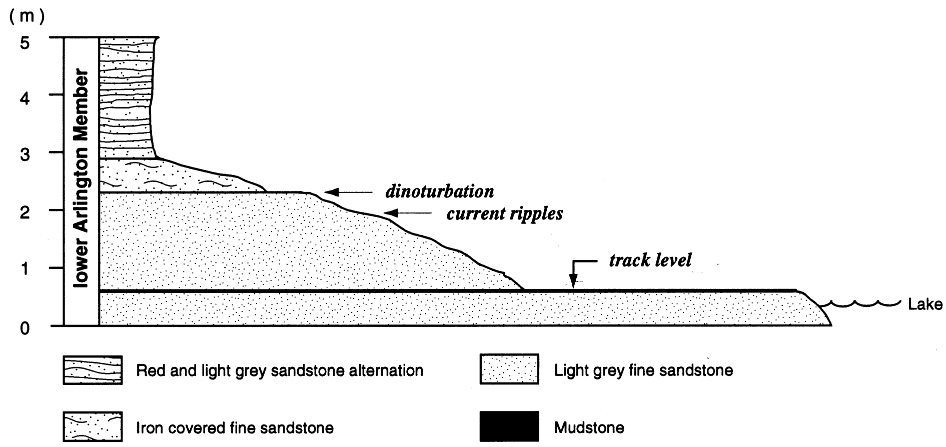

Figure 4. Stratigraphic section of the Woodbine Formation showing track-bearing horizons exposed at Grapevine Lake, Texas (SMU locality 234).

& Cobban, 1990). Therefore, the Woodbine tracks are not younger than early middle Cenomanian (approximately 95 Ma).

2. Systematic descriptions

Class Aves Linnaeus, 1758

Ichnofamily uncertain

Magnoavipes, ichnogen. nov.

Etymology. L. *magnus*, large; *avis*, bird; *pes*, foot.

Diagnosis. Large asymmetric aviform tracks with tridactyl slender pedal digits. A posteriorly-directed small 'heel' impression is present at the base between digit II and digit III impressions. Footprints range from 19 cm to 21 cm in length. Track width greater than length. Divarication between digits II and IV high (average 110°); divarication of digits II and III greater than III and IV. Digit impressions very slender (average 1 cm in width). Sharp claw impression on each digit. Trackways with long steps (about ten times foot length) and slightly outward (positive, *sensu* Leonardi, 1987) rotation of foot.

Magnoavipes lowei, ichnosp. nov.
Figures 3A, 5A

Etymology. In honor of Bill Rowe, whose mapping of the tracksite provided the basic framework for this study.

Holotype. Artificial cast of right print, number 3 in trackway 1 (DMNH, Dallas Museum of Natural History 918).

Paratypes. Left print, number 6 in trackway 1 (Figure 3B).

Horizon and locality. Woodbine Formation, Cenomanian, Denton County, Texas (Southern Methodist University locality 234, exact location on file at SMU).

Diagnosis. Type and only known ichnospecies of ichnogenus as diagnosed above.

Description. A trackway containing six footprints was found on a single bedding plane with dinosaur footprints. Although details of the phalangeal and pad organization are not evident, entire outlines can be seen clearly in most tracks. The holotype is 21 cm long and 25 cm wide (distance between toe-tip impression of digit II and digit IV). The length of digit impressions II, III, and IV is 16 cm, 19.7 cm, and 13 cm, respectively. The width of digit III impression is greater (1.5 cm) than digit IV (0.5 cm). The sharp claw impression is straight or slightly curved away from the central axis of foot in digits II and IV. Divarication of digit II and IV impressions ranges from 109° to 118°; digit divarication between II and III is 60°, which is 10° greater than between III and IV (50°). The proximal portion of digits II and IV are curved toward the central axis of digit III, forming a straight base of the foot perpendicular to digit III (10 cm in length). A posteriorly-directed small 'heel' impression, probably made by the metatarsus, lies medially behind digit III. There is no indication of hallux, nor of webbing between the toes. The pace, stride, and step angle are basically constant in the trackway. The average pace is 105 cm. Strides fall between 200 cm and 217 cm (average 208 cm), which is 10.1 times the average length of the footprints. The step angle ranges from 163° to 178°. The longitudinal axes of the footprints in the trackway are directed slightly anterolaterally (positive rotation).

Discussion. Except for *Trisauropodiscus*, a Jurassic bird ichnogenus (Ellenberger, 1972; Lockley *et al.*, 1992), most Mesozoic bird ichnotaxa are known from mid-Cretaceous deposits of North America and Korea. They include *Ignotornis mcconnelli* (Mehl, 1931), and *Aquatilavipes swiboldae* (Currie, 1981) from North America, and *Koreanaornis hamanensis* (Kim, 1969), *Jindongornipes kimi* (Lockley *et al.*, 1992), and *Uhangrichnus chuni* and *Hwangsanipes choughi* (Yang *et al.*, 1995) from Korea. These bird tracks range from 2 cm to 7.5 cm and seldom exceed 10 cm in length. Therefore, *Magnoavipes* is unique among Mesozoic bird tracks in its size. It is three times longer than *Jindongornipes kimi*, which was previously the largest Mesozoic bird track.

Among these Cretaceous ichnotaxa, *Magnoavipes lowei* is similar to *Aquatilavipes swiboldae* from the Gething Formation (Aptian–Albian) in the Peace River Canyon of western Canada in having no indication of a hallux. This taxon shows size variation with lengths ranging from 2 cm to 4.4 cm based on 200 footprints. Thus, *Magnoavipes* is five times larger than *Aquatilavipes*. The stride to foot length ratio of *Magnoavipes* is much greater (average 10.1) than that of *Aquatilavipes* (average 4.0). *Magnoavipes* is typical of avian footprints judging from its wide divarication angle (110°) between digits II and IV, slender digit impressions (ranging from 0.5 cm to 1.5 cm), slender claws, distal curvature of outer (digits II and IV) claws away from the central axis of the foot (Lockley *et al.*, 1992), and width greater than length (Currie, 1981). In addition, it is notable that an unnamed large track (less than 25 cm in length) from the lower Cenomanian of Israel interpreted as a theropod manus print by Avnimelech (1966) was recently suggested to be a bird track (Lockley *et al.*, 1992).

Trackmakers of other Cretaceous ichnotaxa (*Ignotornis*, *Koreanaornis*, *Aquatilavipes*, *Jindongornipes*, *Uhangrichnus*, and *Hwangsanipes*) are interpreted as plover-like birds (Charadriiformes) because of their small size and high density of preserved tracks (Lockley *et al.*, 1992). *Magnoavipes*, based on one trackway of six steps, differs from them in size and occurrence. Long stride length suggests that

Magnoavipes was a long-legged wading bird adapted to shallow waters, like modern cranes (Gruiformes). It is possible that a crane-like bird left *Magnoavipes* because cranes are the tallest flying birds and have a relatively small hallux. Such a large bird taxon is not known from skeletal elements in the Mesozoic.

Suborder Theropoda March, 1881

Ichnofamily uncertain

Fuscinapedis, ichnogen. nov.

Etymology. L. *fuscina*, three prolonged fork; *pedis*, foot.

Diagnosis. Bipedal tracks with three long, slender functional pedal digit impressions, a small circular metatarsal impression, and no trace of the hallux. Footprint length greater than width. Digit impressions of uniform width; digit II width greater than digit III and IV. Phalangeal pads not well defined, but at least two pad impressions in digit II. Claw impression on each digit. Average divarication of digits II and IV is 70°.

Fuscinapedis woodbinensis, ichnosp. nov.
Figures 3C, 5B

Etymology. Named after the Woodbine Formation, which yielded the holotype.

Holotype. Artificial cast of left print, number 1 in trackway 2 (SMU, Shuler Museum of Paleontology, Southern Methodist University 74651).

Paratype. Right print, number 2 in trackway 2 (Figure 3D).

Horizon and locality. Woodbine Formation, Cenomanian; found on the north shore of Grapevine Lake, Denton County, Texas (SMU locality 234).

Diagnosis. Type and only known ichnospecies of ichnogenus as diagnosed above.

Description. Although phalangeal pads are not well defined, two footprints show the outline clearly. The holotype is 38 cm long and 35 cm wide. The length of digits II, III, and IV is 22 cm, 29 cm, and 19 cm, respectively. The digit impressions are well separated from each other and terminate in pointed small claw impressions. Digit II tends to be wider than digits III and IV. Divarication of digits II and IV is 69°. The metatarsal pad makes a distinct circular impression on the posterior margin whose diameter is 6.7 cm. The pace is 120 cm, which is approximately 3.3 times the length of the footprint. The trackway is narrow and almost in a direct line. The footprints show slightly anterolateral rotation (positive).

Discussion. Mid-Cretaceous theropod tracks in North America are known from the Dakota Group (Aptian–Cenomanian), Colorado and New Mexico, and the Gething (Aptian–Albian) and Dunvegan (Cenomanian) formations, Canada. *Fuscinapedis* differs from two unnamed theropod tracks from the Dakota Group (Gillette & Thomas, 1985; Lockley, 1985; Markman, 1938), which have digits tapering to a point. *Irenesauripus* and *Columbosauripus* from the Gething and Dunvegan formations, Canada, are easily distinguished from *Fuscinapedis* in having large metatarsal pads (Sternberg, 1932; Storer, 1975). The digit II impression of *Irenichnites* from the Gething Formation is uniquely separated from digits III and IV (Sternberg, 1932). Theropod teeth similar to *Richardoestesia gilmorei* are known from the Woodbine Formation (Lee, 1997), but it is not certain that it was a trackmaker for *Fuscinapedis*.

According to Thulborn's formula (1989) for hip-height ratio (h = 4.9 X foot length) and Alexander's formula (1976) for the speed estimate, this animal was walking (stride/hip-height = 1.3) at 6 km/hr.

Suborder Ornithopoda Marsh, 1881

Ichnofamily uncertain

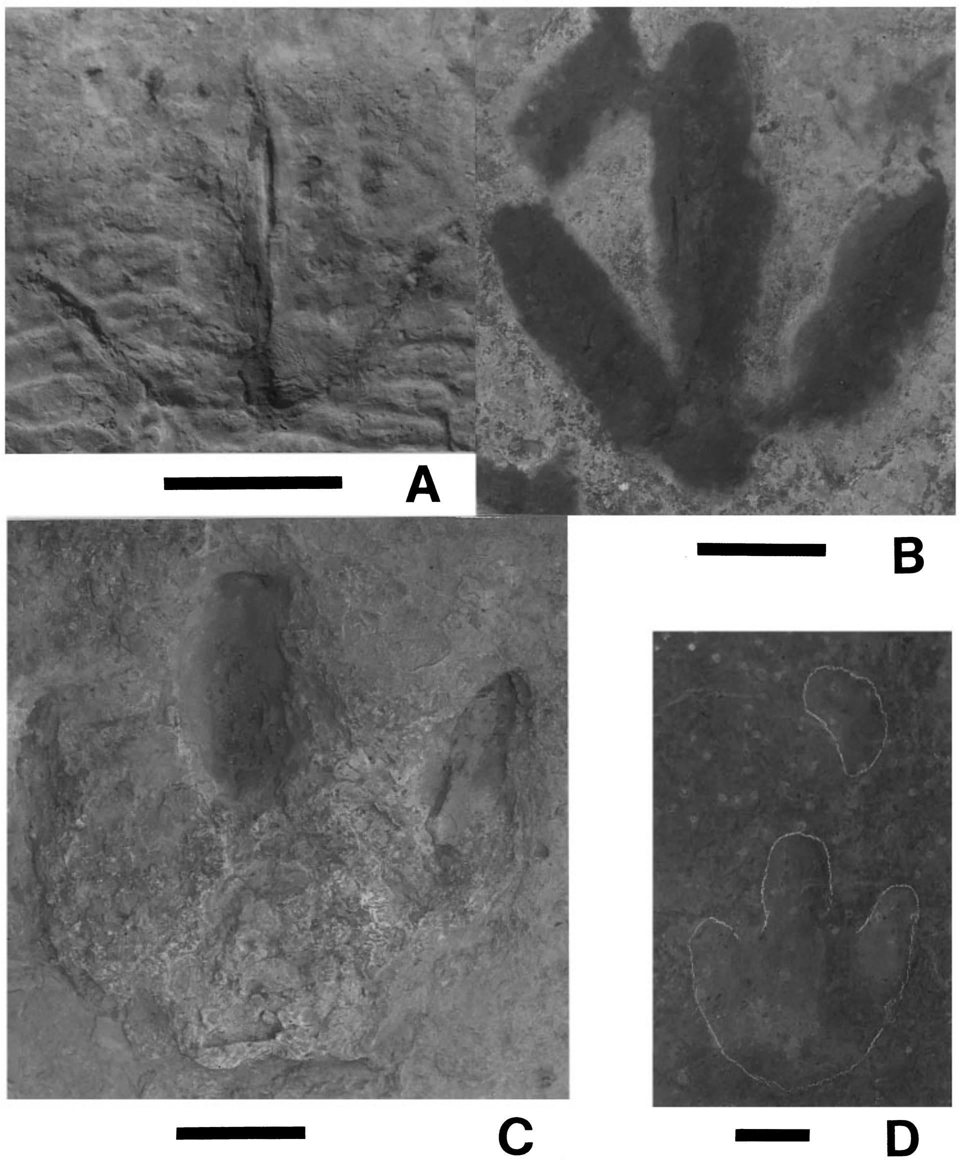

Figure 5. A, *Magnoavipes lowei*, holotype (DMBH 918); B, *Fuscinapedis woodbinensis*, holotype (SMU 74651); C, *Caririchnium protohadrosaurichnos*, holotype (SMU 74652, bipedal footprint); D, *Caririchnium protohadrosaurichnos*, holotype (SMU 74653, quadrupedal footprint). Scale bars = 10 cm.

Ichnogenus *Caririchnium* Leonardi, 1984.

Type ichnospecies. *Caririchnium magnificum* Leonardi, 1984

Emended diagnosis. Quadrupedal trackway with small elongate manus and large tridactyl plantigrade pes impressions. Bipedal trackway with large tridactyl footprints and wide trackway width. Pace angulation of quadrupedal trackway higher than bipedal. Negative rotation in both manus and pes impressions.

Caririchnium protohadrosaurichnos, ichnosp. nov.
Figure 5C, D

Etymology. Gr. *protos*, first; *hadros*, sturdy; *sauros*, lizard; *ichnos*, footstep.

Holotype. Artificial casts of left footprint, number 4 in trackway 3 (SMU 74652), and right manus and pes prints, number 4 of trackway 4 (SMU 74653).

Horizon and locality. Woodbine Formation, Cenomanian; found on the north shore of Grapevine Lake, Denton County, Texas (SMU locality 234).

Diagnosis. In quadrupedal tracks, small elongate manus impression located anteriorly between digits III and IV of the pes impression. Long axis of manus print directed slightly anteromedially. Outer margins of digit II and IV impressions within an angle of approximately 10°. Foot length greater than width. Divarication of digits II and IV is 56°. In bipedal tracks, digits II and IV claw impressions pointed, unlike blunt digit III. Foot width is greater than length. Divarication of digits II and IV is 64°. Negative rotation in bipedal trackway stronger than in quadrupedal.

Description. *Caririchnium protohadrosaurichnos* is based on six trackways including an isolated small footprint, a medium-sized quadrupedal trackway, and five large bipedal trackways. A right (?) small foot impression is present next to the sixteenth footprint of trackway 3. It is 13 cm long and 12 cm wide. The metatarsal-phalangeal pad is more deeply impressed into the sediments than all digits. There is no indication of interdigital webs or interphalangeal constrictions in wide digital pads. Compared with a pointed digit II impression, the digit III impression has a distinctly broad anterior outline indicating a distally blunt ungual. The medial outline of digit II is nearly parallel to the longitudinal axis of digit III.

A quadrupedal trackway consists of five manus and six pes impressions. The pes prints average 32.6 cm long and 30.1 cm wide, which is larger than the small track but considerably smaller than large trackways 3 and 5 to 8, ranging from 38.8 to 46.6 cm in length. Although all digit and the metatarsal-phalangeal impressions are relatively shallow, the outline of the footprint is easily traced in the field. Distally blunt digits are well separated from each other. One faint interphalangeal constriction is observable in digit IV. Divarication from the most posterior point of the footprint to the tips of digits II and IV is 56°. The longitudinal axes of digits II and IV are roughly parallel to that of digit III, and interdigital angles do not exceed 15°. Manus impressions are ellipsoidal in shape; average length and width is 11.5 cm and 6.7 cm, respectively. The long axes of manus impressions are directed anteromedially except for manus print number 5, which is oriented transversely. They are all located anterior to and between digits III and IV of the pes impression. The distance from the tip of digit III of the pes to the posterior margin of the manus ranges from 10 to 15 cm. There is no evidence of scraping marks. The trackway is wider across the manus than the pes impressions so that the pace angulation of the manus (121°) is smaller than that of the pes (141°). The stride averages 120.8 cm for manus and 125 cm for pes impressions. The glenoacetabular distance of this animal is about 205 cm based on the position of manus and pes impressions (Figure 6).

Five trackways are exclusively large bipedal tracks. Trackway 3 containing 26 consecutive footprints turns slightly to the left from footprint number 18. The footprints average 40.2 cm long and 41.9 cm wide in trackway 3. They are slightly larger than the average value of trackway 8, but smaller than those of trackways 5–7, ranging from 44.5 to 44.9 cm in length. Although there are size variations and differences in preservation, these trackways have similar footprint morphologies. The footprints have well-developed digital pads. The outer margins of digits II and IV are nearly parallel to the longitudinal axis of digit III within an angle of approximately 10°. All digit impressions are well separated from each other with no interdigital web. Interphalangeal constriction is not clearly defined. The broad and rounded anterior outline of digit III forms a deeply impressed elongate digital pad in the middle of the footprint. Digit IV (average length = 18.5 cm) is slightly longer than digit II (average length = 16.5 cm), but both are much shorter than digit III (average length = 23.8 cm), which exceeds one half of the footprint length. The outlines of the impressions of digits II and IV are teardrop-shaped with an anterior point made by a sharp claw. The impressions of the claw marks are shallower than those of the digital pads. In both digits II and IV the median margins are straight compared with the outer margins. Divarication of digits II and IV is 64°. The metatarsal-phalangeal pad occupies a small portion of the posterior to the well-developed digital pads. Contrasting with the deeply impressed digital pads, a distinct, irregular, raised region (average 2.5 cm high) is present in the center of the metatarsal-phalangeal pad. In most, this forms a U-shaped area of relief near the posterior margin of footprint. This feature was obviously made when layers of sediment adhered to the metatarsal-phalangeal pad as the animal took its foot off the substrate, pulling up the heel and pushing down digits into the substrate. Although the posterior margin of the foot is not well defined in most footprints because of the deformation of the metatarsal-phalangeal pad impressions, a faint concave outline is observable in footprint number 14 in trackway 3.

Discussion. Ichnotaxa of iguanodontid-hadrosaurid grade are represented by four ichnospecies from Early Cretaceous and Cenomanian sediments of North America. They are *Amblydactylus gethingi* (Sternberg, 1932) and *A. kortmeyeri* (Currie & Sarjeant, 1979) from the Gething Formation, British Columbia, *Caririchnium leonardii* (Lockley, 1987) from the Dakota Group, Colorado, and *C. protohadrosaurichnos*. *Caririchnium* is easily distinguished from ichnogenus *Amblydactylus* in having well-developed digital pads and no interdigital web (Currie & Sarjeant, 1979). Ichnogenus *Caririchnium*, as ornithopod trackways, consists of three ichnospecies. They are *C. magnificum* from the Rio do Peixe Group of Brazil (Leonardi, 1984), *C. leonardii* from the Dakota Group of eastern Colorado (Lockley, 1987), and *C. protohadrosaurichnos*. Manus impressions of *C. magnificum* are irregular in shape and positioned anterior to digit III or between digits II and III of the pes impression. Both manus impressions of *C. leonardii* and *C. protohadrosaurichnos* are located anteriorly between digits III and IV of the pes impressions. However, the elongate manus of *C. protohadrosaurichnos* differs from that of *C. leonardii*, which shows the medially directed impression of a digit. In addition, ornithopod tracks known from the Glen Rose Formation, Texas differ from *C. protohadrosaurichnos* in having a distinct 'heel' pes and double manus impressions (Pittman, 1989). With no body fossils, trackmakers of these ichnotaxa have been alleged to be hadrosaurids or iguanodontids based only on the footprint morphology (see Sternberg, 1932; Currie & Sarjeant, 1979; Currie, 1983; and Paul, 1987, for *Amblydactylus*, and Lockley, 1985, 1986, 1987 for *Caririchnium*).

3. Discussion

The theropod trackway is perpendicular to hadrosaurid trackway 3. The fourth bird track is superimposed on the sixth footprint of ornithopod trackway 3. Trackway 7 may be a continuation of trackway 6 because these have the same footprint size, stride, and direction (Table 1). Except for trackway 8, all large ornithopod trackways trend southeast (Figure 3). They were probably made simultaneously because the depth of track impressions is nearly constant (5.6 cm deep). If these trackways were made at the same time, they indicate that a herd of gregarious ornithopods were moving in a preferred direction, parallel to the palaeo-shoreline along the east of the Western Interior Seaway. Using Thulborn's formula (1989) for hip-height ratio (h = 5.9 X foot length) and Alexander's formula (1976) for

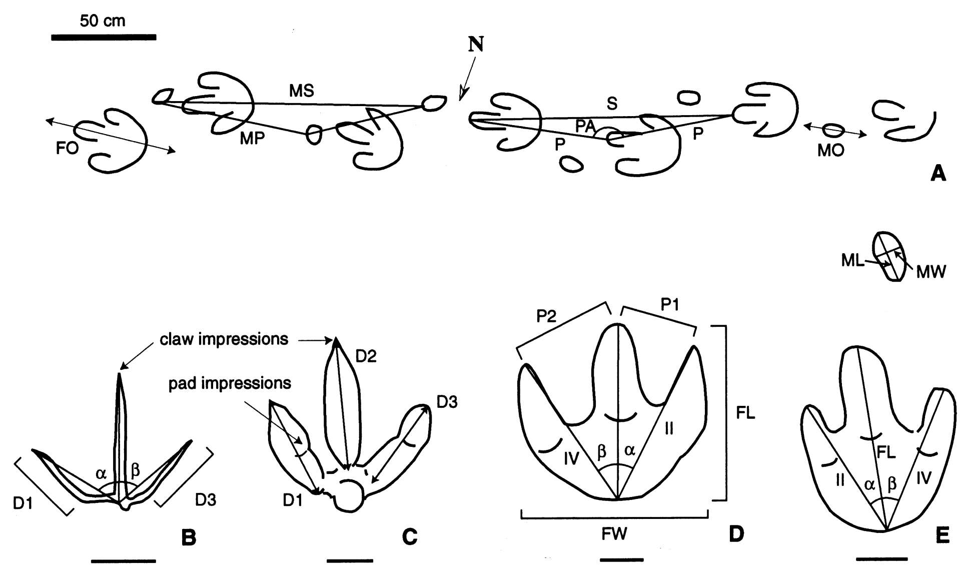

Figure 6. Measurements of tracks and trackway. A, Trackway 4; B, *Magnoavipes lowei* (DMBH 918); C, *Fuscinapedis woodbinensis*, paratype; D, *Caririchnium protohadrosaurichnos* (SMU 74652); E, *Caririchnium protohadrosaurichnos* (SMU 74653). Scale bars = 10 cm. Abbreviations: F, footprint number; FD, footprint depth (cm); FL, footprint length (cm); FO, footprint long axis orientation (degrees); FW, footprint width (cm); L/R, left or right footprint; ML, manus print length (cm); MO, manus print, long axis orientation (degrees); MP, manus pace length (cm); MS, manus stride length (cm); MW, manus print width (cm); P, pace length (cm); PA, pace angulation (degrees); S, stride length (cm); II, length from the anterior end of digit II impression to the furthest posterior point of footprint (cm); IV, length from the end of digit IV impression to the furthest posterior point of footprint (cm); D1, digit II impression length (cm); D2, digit III impression length (cm); D3, digit IV impression length (cm); P1, length between ends of digit II and III impressions (cm); P2, length between ends of digit III and IV impressions (cm); α, angle between digit II and III impressions (degrees); β, angle between digit III and IV impressions (degrees).

Table 1. Measurements of tracks and trackways illustrated in Figure 3

Trackway No.	F	L/R	S	P	PD	FL	FW	FD	FO	II	III	IV	D1	D2	D3	D4	P1	P2	II & III	III & IV	II & IV		
1	1	R	217	107	168	21	25	−0.5	10W	17.5	21	18	14.5	18	16	8	15	15	53	47	100		
	2	L	208	108	163	19	25	−0.5	28W	16	19	16	14	17	14.5	11	18	15	64	54	118		
	3	R	200	104	178	21	25	−0.5	14W	16.7	21	14.5	16	19.7	13	10	18	16	60	50	110		
	4	L	208	98	170	21	24	−0.5	35W	15.5	21	16	14	19	14	7	20	15	62	48	110		
	5	R		110		20	27	−0.5	25W	19.8	20	16	17.5	17.5	14	10	18	15	62	47	109		
	6	L				21	24	−0.5	40W	16	21	18	13.5	18	14	11	19	15	58	54	112		
average			208	105	170	20.5	25	−0.5		16.9	20.5	16.4	14.9	18.2	14.3	10	18	15	59.8	50.0	109.8		
2	1	L		120		38	35	2	20E	28	38	31	22	29	19		22	23	34	35	69		
	2	R				36	35	2	30E	28	36	28	22	27	22		24	20	35	36	71		
average						37	35	2		28	37	29.5	22	28	20.5		23	22	34.5	35.5	70		
3	1	R	183	106	140	39	41	6	60W	35	37	31	20	23	18	10	21	22					
	2	L	153	91	113	38	41	4	22W	35	36	33	20	25	22	10	19	21					
	3	R	130	93	97	37	42	3	71W	32	37	35	19	24	21	10	20	22					
	4	L	147	82	102	37	42	6.2	40W	29	36	33	15	27	18	11	21	22					
	5	R	185	108	116	39	41	3.5	60W	31	38	34	15	25	19	12	19	22					
	6	L	186	109	120	39	42	4	40W	32	38	32	17	25	15		22	22					
	7	R	170	110	110	38	42	6	73W	33	36	31	14	23	15	12	19	23					
	8	L	172	100	124	39	43	3	35W	34	38	32	17	25	19	11	23	22					
	9	R	179	97	128	40	42	5	60W	33	38	35	20	23	18	15	20	23					
	10	L	154	103	116	41	42	7.5	40W	32	39	35	17	25	24	13	22	23					
	11	R	140	78	125	40	41	4	70W	32	35	32	18	22	15	12	19	22					
	12	L	161	77	135	45	42	5	35W	33	39	37	18	23	20	15	22	22					
	13	R	197	98	131	41	41	8	72W	32	40	36	13	22	19	13	17	23					
	14	L	200	113	122	44	42	7	35W	34	43	39	16	27	23	12	22	23					
	15	R	181	106	125	42	43	6	70W	37	40	34	15	23	15		20	22					
	16	L		97		42	42	3	40W	35	40	36	11	22	20	9	22	23					
	17	R				42	43	3	76W	34	41	37	15	21	14	11	22	23					
average			169	98	120	40.2	41.9	5.0		33.1	38.3	34.2	16.5	23.8	18.5	12	21	22					
	F	L/R	S	P	PD	FL	FW	FD	FO	II	III	IV	D1	D2	D3	D4	P1	P2	MS	MP	MO	ML	MW
4	1	L	122	66	145	30	32	1	88W	26	30	25		16	15			15	128	70	78W	12	7
	2	R	120	63	141	35	29	1	67E	28	36	28	17	19	16	10	19	17	119	67	40E	12	8
	3	L	127	64	155	33	31	1	82W	26	32	27	15	16	18	10	15	18	118	67	W-E	10	5

	4	R	135	67	146	36	31	1.5	84E	24	36	32	14	15	15		18	16	118	61	55E	13	8
	5	L	120	73	132	31	30	1	80W	27	32	35	16	14		11	16	17		68	35W	9	5
	6	R		55		32	29	0.7	70E	23	32	26	12	16	14		18	16			48E	13	7
	7	L				31	29	0.7	82W	25	30	25	15	15	14		16	16					
average			125	64.7	144	32.6	30.1	1.0		25.6	32.6	28.3	14.8	15.9	15.3	10	17	16	120.8	66.6		11.5	6.7
5	1	R	260	130	162	40	40	5.5	50W	32	39	32	16	21	14		25	25					
	2	L	250	130	150	41	42	6	30W	31	40	31	13	23	16		24	26					
	3	R		125		42		6	52W		45	39		24	17			22					
	4	L				42	43	7	40W	42	45	39	14	24	16		20	21					
average			255	128	156	41.3	41.7	6.1		35	42.3	35.3	14.3	23	15.8		23	24					
6	1	R	240	130	130	45		6	52W	31	43		14	20		22							
	2	L	250	130	123	47		5.5	40W		47			25									
	3	R		131		45	46	7.5	55W	37	43	42	20	25	18		27	28					
	4	L				46	46	7	28W	40	48	36		27	20		20	31					
average			245	130	127	45.8	46	6.5		36	45.3	39	17	24.3	19		23	30					
7	1	R	231	114	146	49	50	3	70W	44	52	44	18	32	22		31	25					
	2	L	228	117	143	50		5	42W		52	42		30	21			25					
	3	R	254	117	163		46	6	68W					21			21	23					
	4	L	265	138	160	44		8	40W		42	38		22	20			21					
	5	R		126		45		6	70W		44	39		27	22			22					
	6	L				45	47	6	60W	37	40	36	21	27	22		23	26					
average			245	122	153	46.6	47.7	5.7		40.5	46	39.8	19.5	26.5	21.4		25	24					
8	1	L			147				60W					24	19								
	2	R	233	120	145	39	41	6	62W	36	37	31	15	18	11		18	21					
	3	L	231	123	140	40	38	4.5	70W	34	40	35	12	21	12		19	19					
	4	R		123		38	40	4.5	73W	36	37	30	11	17	11		19	24					
	5	L				38	38	4	60W	34	39	34	12	17	11		17	21					
average			232	122	144	38.8	39.3	4.8		35	38.3	32.5	12.5	19.4	12.8		18	21					
An isolated small ornithpod track	1	R(?)				13	12	0.5	5E	11.5	12.5	10.5	6.5	7	6		6	5					

the speed, it appears that they were walking slowly (stride/hip-height < 1) at an average of 3.7 km/hr. Compared with large tracks, quadrupedal ornithopod tracks did not leave distinct prints deep into the sand below the mud flat. They are oriented east, crossing trackway 3. The shallow impressions of quadrupedal tracks were probably produced by a smaller, lighter juvenile, but it is not certain whether the juvenile tracks were made at the same time as the adult tracks. The animal was walking slowly at 1.9 km/hr, if the same hip-height ratio is applicable to quadrupedal ornithopods (Thulborn, 1989).

Facultative switching from quadrupedal to bipedal progression observed in *Amblydactylus* (Currie, 1983) and *C. leonardii* (Lockley, 1987) is not seen in the small sample of *C. protohadrosaurichnos*. All large trackways (3 and 5–8) are bipedal, but the medium-sized tracks (trackway 4) are exclusively quadrupedal. If quadrupedal posture was necessary for juveniles to hold the body balance over the narrow trackway width of the pes, compared with wide trackway width of bipedal adults, a transition from quadrupedal to bipedal habit might be an ontogenetic change in this Woodbine ornithopod. This interpretation might be supported by the same observation on small quadrupedal and larger bipedal ornithopod footprints in the Dakota Group at Mosquero Creek, New Mexico (Lockley & Hunt, 1995).

Hadrosaurid bones have been found approximately 300 m north of the *C. protohadrosaurichnos* tracksite. A femur, tibia, fibula, and astragalus were in the same horizon as the bedding plane of the track (Lee, 1997). No ornithopod body fossil is known from the Woodbine Formation except for hadrosaurid bones, which occur in three localities near Grapevine Lake (SMU localities 234, 245 and 303). Therefore, it is reasonable to conclude that one hadrosaurian species produced *C. protohadrosaurichnos*. To see phylogenetic changes in hadrosaurid footprints, *C. protohadrosaurichnos* was compared with hadrosaurid footprints in the 'Mesaverde' Group (Campanian) of Colorado, Utah, and Wyoming (Lockley *et al.*, 1983). The latter are characterized by blunt toe impressions which compare well with the broad, blunt toe bones of *Kritosaurus* (see Carpenter, 1992, fig. 5a). Pointed claw impressions in *C. protohadrosaurichnos* are supported by an ungual recently recovered with a primitive hadrosaurid skull from the Woodbine Formation exposed in Flower Mound, Denton County (SMU 74582, SMU locality 303; Head, 1996). This ungual appears to be between iguanodontids and derived post-Campanian hadrosaurids in shape. Its length/width ratio (1.13) is greater than that in *Kritosaurus incurvimanus* (= 0.79; Parks, 1920) and less than in *Iguanodon atherfieldensis* (= 1.5; Norman, 1986). Therefore, the Woodbine hadrosaurid is phylogenetically primitive based on ungual shape, as reflected in *C. protohadrosaurichnos*.

Although some differences may be the result of inadequate sampling or sampling bias, the ichnofaunal contents of the Woodbine Formation appear to be different from those of the Trinity Group (Aptian-middle early Albian) of the Gulf Coastal Plain in terms of the absence of sauropod tracks and the appearance of hadrosaurid tracks. It is supported by the record of body fossils of both the Trinity Group and the Woodbine Formation (Lee, 1995; Winkler *et al.*, 1995).

Acknowledgments

I thank Mr Bill Lowe who has long been a good collaborator in fossil hunting. He kindly provided me with field maps and photographs. I had useful discussions with Dr A. Fiorillo at the Dallas Museum of Natural History. I thank Dr D. Gillette for informing me about the Lake Grapevine spillway footprints. An original map by Mr J. Congleton was helpful in locating trackways. At Grapevine Lake, Ms Becky St. John of the US Army Corps of Engineers, Fort Worth District, allowed access to the tracksite. Acknowledgment is made to the Dinosaur Society, New York, and to The Saurus Institute, SMU, Dallas, for partial support of this research.

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