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ORNITHOPOD TRACKWAYS FROM THE LOWER CRETACEOUS OF CANADA

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The most common ichnogenus in the Peace River Canyon is *Amblydactylus*, a large bipedal herbivore. The morphology of the hand and footprints suggest that the tracks and trackways might have been made by hadrosaurs; the ichnites may represent the earliest record of these dinosaurs. *Amblydactylus* tracks were made in a wide variety of depositional environments, including the mud beneath several metres of water. Juveniles were gregarious and probably stayed together after hatching until they were large enough to join herds of more mature animals. Individuals in herds appear to have walked side by side, seldom crossing paths, although there was little structure to the herds when they were in the water and/or feeding. Calculations of the walking speeds indicate that the herbivores were generally slower than the carnivores.

INTRODUCTION

Dinosaur footprints were first discovered in the Peace River Canyon of British Columbia in 1922 (McLearn, 1923). Expeditions by the National Museum of Canada (now the Canadian Museum of Nature) in 1930 (Sternberg, 1932), the Royal Ontario Museum (1965) and the Provincial Museum of Alberta (1976, 1977, 1978, 1979; collections now in the Royal Tyrrell Museum of Palaeontology) recovered dinosaur footprints throughout the 500 metres of strata of the Gething Formation (Aptian-Albian, Lower Cretaceous; Stott, 1975). More than 1,700 footprints were documented, 90 specimens were collected, casts were made of 200, almost 1,000 footprints in more than 100 trackways were measured, and more than 1,000 tracks were mapped during the course of the Provincial Museum of Alberta expeditions (Sarjeant, 1981; Mossman and Sarjeant, 1983).

Sternberg (1932) described six genera and eight species of dinosaur footprints from the canyon, including *Amblydactylus gethingi*. A second species of *Amblydactylus* (Currie and Sarjeant, 1979), the earliest known record of bird footprints (Currie, 1981) and mammal footprints (Sarjeant and Thulborn, 1986) have increased the diversity of the fauna. Foot structure is usually conservative; each ichnospecies could represent many biological species of closely related animals.

The fauna of the ancient Gething Delta is different from those of contemporary faunas in Brazil (Leonardi, 1989), Morocco (Dutuit and Ouazzou, 1980) and the United States (Farlow *et al.*, 1989; Pittman, 1989, Pittman and Gillette, 1989), where the Early Cretaceous footprint faunas were composed mostly of sauropods. Footprints of ornithopods are rare at these sites, whereas they dominate the Peace River fauna. Early Cretaceous ornithopod dominated faunas have been described from Brazil (Leonardi, 1989), Chile (Casamiquela and Fasola, 1968), England (Woodhams and Hines, 1989), Spain (Moratalla *et al.*, 1992) and the United States (Lockley, 1987; Lockley *et al.*, 1992; Lucas *et al.*, 1989). Relatively few sites have both ornithopod and sauropod trackways (Antunes, 1976, Leonardi, 1989; Lim *et al.*, 1989; Pittman, 1989), but these do demonstrate that overlapping habitat preference was possible.

Abbreviations

CMN, Canadian Museum of Nature, Ottawa; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller.

PEACE RIVER ORNITHOPODS

The species *Amblydactylus gethingi* was established on the basis of a single footprint (CMN 8555). The original specimen had to be left in the canyon because it was in very hard rock. Efforts to relocate the specimen failed until the last expedition in 1979, when it was spotted underwater from a helicopter. Three attempts were made to produce a new and better cast of the holotype when the levels of the Peace River were low enough, but they failed because the river level never stayed down for more than a few hours. It is an extremely important and well-preserved specimen (comparison with Sternberg's photograph shows that there was no significant erosion of the specimen after fifty years); unfortunately, the water levels and the hardness of the rock prevented any attempt to excavate it. This specimen and most others in the canyon are now inundated by a reservoir behind the Peace Canyon Dam.

The second species of *Amblydactylus*, *A. kortmeyeri*, was established on the basis of a well-preserved natural mould of a footprint (Currie and Sarjeant, 1979). It differs from *A. gethingi* in its length to width ratio and in the outline of the footprint itself. Although it was possible to distinguish species in well-preserved specimens, specific identification was not possible for the majority of *Amblydactylus* tracks. Because both species of footprint seem to represent the same general type of animal (a large, plant eating biped), they will be treated together in this paper.

Sternberg collected a trackway of four footprints that he described as *Irenesauripus occidentalis*. The impressions are very shallow and the outlines are poorly defined. The relative width of the footprints, the width of the trackway and the shortness of stride are different from *Irenesauripus mclearni* and *I. acutus*. Sternberg felt the different characters of the trackway might be partly due to the slow movement of the animal making the tracks. However, it is more likely that these four prints are synonymous with *Amblydactylus*. The divarication of digits II and IV is 73, much higher than that of *I. mclearni* and *I. acutus* but within the range for *Amblydactylus*. As in *Amblydactylus*, the width of the foot is almost as great as the length. The average length to width ratio for the four tracks is 1.05, which is significantly less than the 1.2 or greater ratio of theropods (Moratalla *et al.*, 1988). The stride length and width of the trackway are well within the range expected for *Amblydactylus*. Finally, it is worth pointing out that no other tracks were found that fit the description of *Irenesauripus occidentalis*, whereas *Amblydactylus* footprints are very common.

Ornithopod footprints from Brazil (Leonardi, 1984) and Colorado (Lockley *et al.* ,1992), referred to the ichnogenus *Caririchnium*, are diagnosed as distinct from *Amblydactylus* by the presence of bilobed heel impressions. Well-preserved specimens of *Amblydactylus*, and hadrosaur footprints from Upper Cretaceous strata (Currie *et al.*, 1991), have bilobed heel impressions. *Caririchnium* footprints are always associated with handprints, but this characteristic cannot be used by itself to distinguish them from *Amblydactylus*. The handprints figured by Leonardi (1984) seem to be larger and rounder than the crescentic handprints of *Amblydactylus*. Otherwise, it is very difficult to distinguish the two ichnogenera (as was also suggested by Lockley *et al.*, 1992). It is probable that *Caririchnium* is a junior synonym of *Amblydactylus*. Similarly,
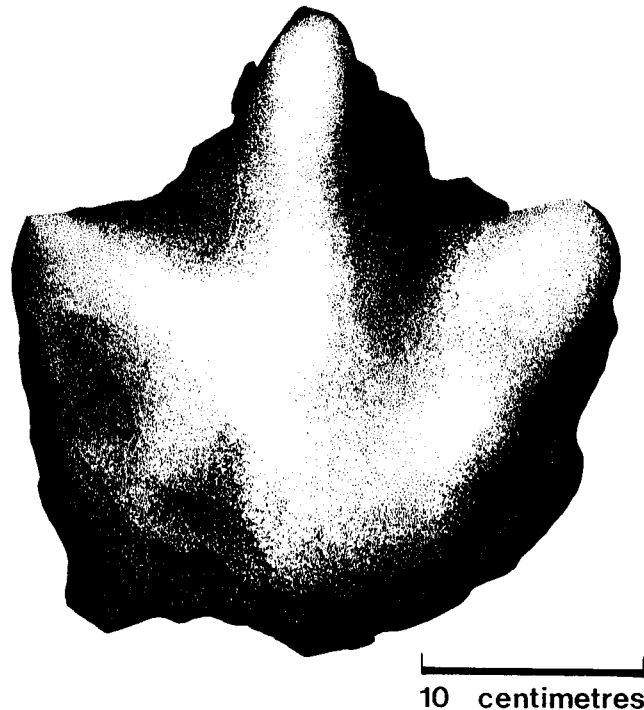
10 centimetres

Figure 1 *Amblydactylus* sp., RTMP 77.17.1. Natural mould of a large ornithopod footprint (or a natural cast of the foot) from the Peace River Canyon of British Columbia.

Hadrosaurichnus and *Ornithopodichnites* should also be regarded as junior synonyms (Lockley, 1987).

As the hoof-like ends of the toe impressions of the type specimen of *Amblydactylus gethingi* were sharper than expected for a hadrosaur track, Sternberg (1932) suggested that they more closely resembled a footprint of *Iguanodon*. At present *Iguanodon* is the only large three-toed ornithopod known from the Lower Cretaceous of North America (Galton and Jensen, 1979; Weishampel and Bjork, 1989), so it is a logical maker of *Amblydactylus* tracks. However, the majority of *Amblydactylus* tracks appear to have blunt hooves (Fig. 1) and are relatively shorter and broader than *Iguanodon* tracks from England (Beckles 1856). The type specimen of *Amblydactylus kortmeyeri* is almost identical to hadrosaur footprints from the Upper Cretaceous of Alberta (Langston, 1960; Currie *et al.*, 1991). A few of the *Amblydactylus* footprints from the Peace River Canyon have tapering toes (Currie, 1989), whereas in the majority of *Iguanodon* tracks the toe impressions are pointed (Beckles 1856; Dollo, 1905; Tylor, 1862).

A trackway worked on by staff of the Royal Ontario Museum and numerous trackways collected for the Royal Tyrrell Museum of Palaeontology had handprints associated with the footprints of *Amblydactylus*. There is no evidence of the specialized "spike" on the hand which is characteristic of *Iguanodon*. Manual digit I is very short in iguanodontids (Norman, 1980) and therefore would only have shown in the deepest handprints. However, many of the Peace River handprints were deeply impressed in
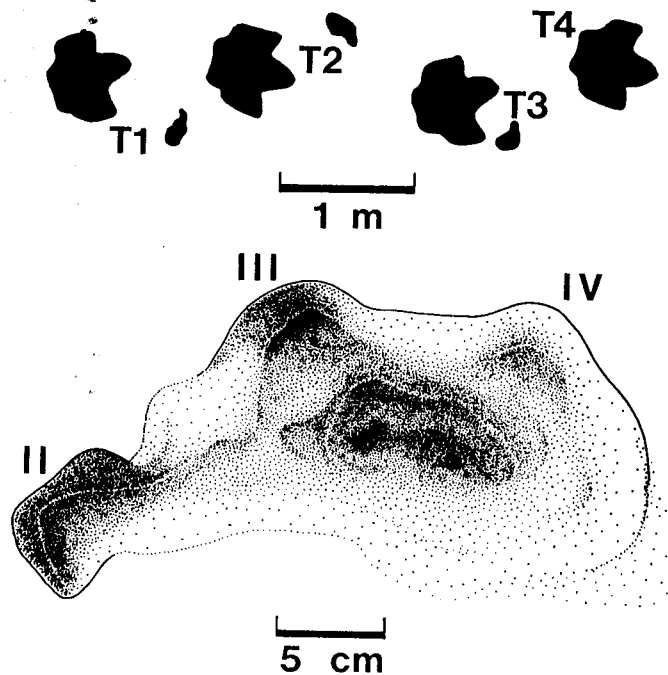
Figure 2 *Amblydactylus* sp. Above, footprints and handprints from Site 8a, Trackway T; below, enlargement of T1 handprint (RTMP 79.23.29). Footprint T1 (RTMP 79.23.24) and handprint T2 (RTMP 79.23.65) were also collected.

soft mud, yet still show no evidence of a first digit. The handprints are roughly crescent-shaped (Fig. 2) and are remarkable for the lack of details indicating separation of fingers, no matter how well the associated footprints are preserved. RTMP 79.23.29 (Fig. 2) is a well-preserved right manus impression associated with a footprint (trackway T at Site VIII). Three digits (II, III and IV) were involved in making the impression; the innermost one was somewhat independent of the two outer digits (III and IV) even though it was still connected to them by a web of skin. The impression of the third digit is deepest, followed by that of the fourth. That of the second digit is most sharply defined, even though it has the shallowest impression. This handprint and others from the Peace River Canyon are the shapes one would expect to find in hadrosaurs and compare favourably with unquestionable hadrosaur handprints from the Late Cretaceous (Currie *et al.*, 1991; RTMP 87.76.7). It is known from "mummified" specimens (Osborn, 1912; RTMP P80.23.2) that fingers II, III and IV of hadrosaurs were encased in a sheath of hide and were capable of only limited independent motion.

It is possible that iguanodontids also encased the second to fourth manual digits in skin. Manual ichnites from the Aptian-Albian of Spain described by Moratalla *et al.* (1992) were identified as *Iguanodon* tracks and were apparently made by mani that lacked free digits. In the Peace River ichnites, the impression of the second digit is shallower and much smaller in area than those of either digits III and IV. The facts that digit II is as long as digit III in *Iguanodon bernissartensis* (Norman 1980) and has a larger ungual hoof suggest that the Canadian handprints were not made by this dinosaur.

The shapes of manual and pedal ichnites led Currie (1983) to conclude that *Amblydactylus* might represent a hadrosaurian dinosaur. The earliest unquestionable records of duckbilled dinosaurs from North America are Santonian in age (Kaye and Russell, 1973), whereas the beds in the Peace River Canyon are Aptian-Albian. Asian records are as old as Cenomanian (Currie and Eberth, 1993) and show that hadrosaurs had already differentiated into two lineages (hadrosaurids and lambeosaurids), which suggests that their origins are much older. Galton and Jensen (1979) described a hadrosaurian femur from the Cedar Mountain Formation (Albian) of Utah which, if correctly identified, shows that the presence of hadrosaur footprints in Aptian-Albian beds of the Peace River Canyon is not impossible.

Sternberg (1932) described only a single specimen of *Amblydactylus* and did not refer to any trackways. This leaves the reader with the impression that it must be a rare genus. However, 50% of the trackways discovered, and 90% of the isolated footprints observed, are attributable to *Amblydactylus*.

Amblydactylus footprints of the Peace River Canyon were preserved in several types of depositional environments. At Site 1 (Currie, 1980), the tracks are found in a grey, fine-grained sandstone. Rootlets and bioturbation are evident in overlying layers; the variety of footprint types and sizes suggest that the dinosaurs were walking on the muddy margin of a quiet body of fresh water. The major footprint bearing level at Site 3 is a grey, ripple-marked sandstone with rootlets and bioturbation. There are many footprints of small dinosaurs and it seems probable that the site was a soft, flat expanse of mud at the edge of a body of quiet water, although perhaps covered to a depth of a couple of centimetres. At Site 4, a trackway of *Amblydactylus* (Fig. 3) is found in a ripple-marked, ferruginous sandstone. The pattern of the tracks at this site suggests that the animal was partially floating when the trackway was made, and that the footprints were impressed into the muddy bottom of a quiet body of water that was about two metres in depth.

Numerous other sites in the canyon appear to have been underwater when the footprints were made. A large block was found on the talus slope near Site 5 with three large negative footprints of a single *Amblydactylus*. On the other side of the slab were invertebrate trace fossils of a type known as *Rhizocorallium*, indicating that shortly after the dinosaur walked over the mud, additional sediments accumulated in a body of brackish water. The dinosaur must have been walking very close to the shore of that time. The ornithopods that left their footprints at the main level of Site 8 (Fig. 4) were walking across a crevasse splay. A single footprint was recovered from Site 10 from a course-grained, cross-bedded channel sandstone, showing that *Amblydactylus* would cross rapidly flowing rivers. Footprints at Site 15, including the type specimen of *Amblydactylus gethingi* were made in water covered sediments at the edge of a sandbar. Another footprint recovered from the talus slope above Site 15 appears to have been made in a very organic layer of mud. In summary, the ornithopods of the ancient *Gething Delta* appear to have lived in proximity to almost all of the available depositional environments.

Amblydactylus trackways are well represented. In most cases, neither handprints nor tail drag marks are preserved with the footprints, suggesting the possibility that some of the animals were floating or swimming. Handprints are associated with the footprints in at least six of the *Amblydactylus* trackways, indicating that the animals were facultative and not obligatory bipeds. The juveniles do not show any signs of having used their hands in supporting their bodies even though their footprints were found at Site 3, where there appears to have been little or no water to support them. The tail was used as a counterbalance when the animal walked and was never dragged.
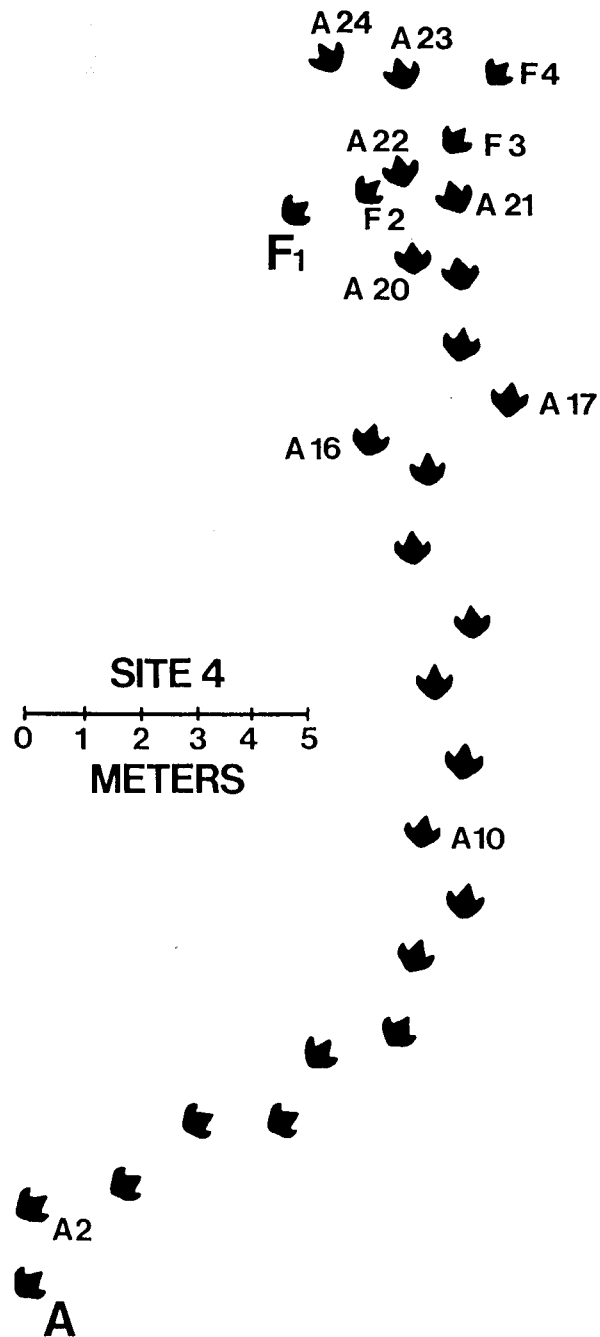
Figure 3 *Amblydactylus* sp. Trackway map for Site 4. Note pronounced lateral shift of centre of trackway to the right between tracks A16 and A17.

A trackway at Site 4 appears to indicate that hadrosaurs were efficient swimmers (Fig. 3). Here an animal was walking on the muddy bottom of a quiet body of water. As the water became deeper, its stride decreased and, since the mark for the heel pad is shallow and poorly defined, it appears to have been pushing off the bottom with its toes. At one point (between footprints A16 and A17, Fig. 3), the midline of the trackway shifts more than metre to the right; several steps later (between A22 and A23), it shifts to the left again. It would be difficult to explain these shifts unless the three or four tonne weight of the body was buoyed up by water. Furthermore, there are other isolated but clearly defined tracks at Site 4 which suggest that animals were swimming, only occasionally putting a foot down to push off the muddy bottom.

There are many other sites in the canyon where clearly defined *Amblydactylus* footprints are not associated in trackways, even though individual tracks cover the entire bedding plane. The best explanation for the lack of continuous trackways is that the animals were in water deep enough for swimming. Finally, it should be pointed out that at many of the sites only the footprints of large animals were found, suggesting that either the water was too deep for small animals, or that the smaller dinosaurs were swimming close to the surface. Bird (1944) was the first to describe trackways that he felt were made underwater, although his conclusions have been disputed by Lockley and Rice (1990). Track evidence has been used to suggest that footprints at other localities were made while dinosaurs were in the water (Ishigaki, 1989; Lockley, 1987; McAllister, 1989).

Juvenile *Amblydactylus kortmeyeri* footprints were found at Site 7 (Currie and Sarjeant, 1979) and Site 3. Using calculations provided by Carpenter (1992), the trackmakers at Site 7 would have been about two metres long. In both cases, pairs of animals of approximately the same size were moving in the same direction, suggesting that juveniles were gregarious and stayed together after hatching until they were large enough to join herds of more mature animals. Evidence from hadrosaur trackways in Upper Cretaceous strata seem to show the same separation between juveniles and mature animals, although Carpenter (1992) has argued in favour of a preservational bias.

Trackway series of numerous animals of the same type proceeding in one direction have been reported for numerous sites in the world and have been cited as evidence that dinosaurs were gregarious (Ostrom, 1972; Lockley *et al.*, 1983). Carpenter (1992) has even suggested that unidirectional hadrosaur trackways from the Upper Cretaceous may indicate that the herds were migrating. Site 8 (Fig. 4) in the Peace River Canyon could be one of the best sites anywhere to demonstrate that at least some species of dinosaurs were herding animals, because their trackways each turn in the same direction. Nine or ten individuals were walking across a crevasse splay. The more northerly footprints must have been made in very soft mud, since they are deeply impressed and there was considerable fluid mud flow after the dinosaurs walked onward. The footprints are shallower and better defined towards the end of the series, suggesting that the mud was firmer in this area. Ripple marks on the bottoms of these shallow footprints might indicate that the river was in flood when the tracks were made.

Trackways C, D, E and F at Site 8 were made by animals that must have been walking side by side. The four trackways follow the same sinuous curves, although the curvature of the path is stronger in F. The trackways are close together at several points, but do not intersect. One possible interpretation is that the four animals were walking so close together that when F changed direction suddenly, the courses of the remaining three animals were altered to avoid collision.

The evidence at Site 8, and an unmapped series of nine trackways at Site 5, indicate
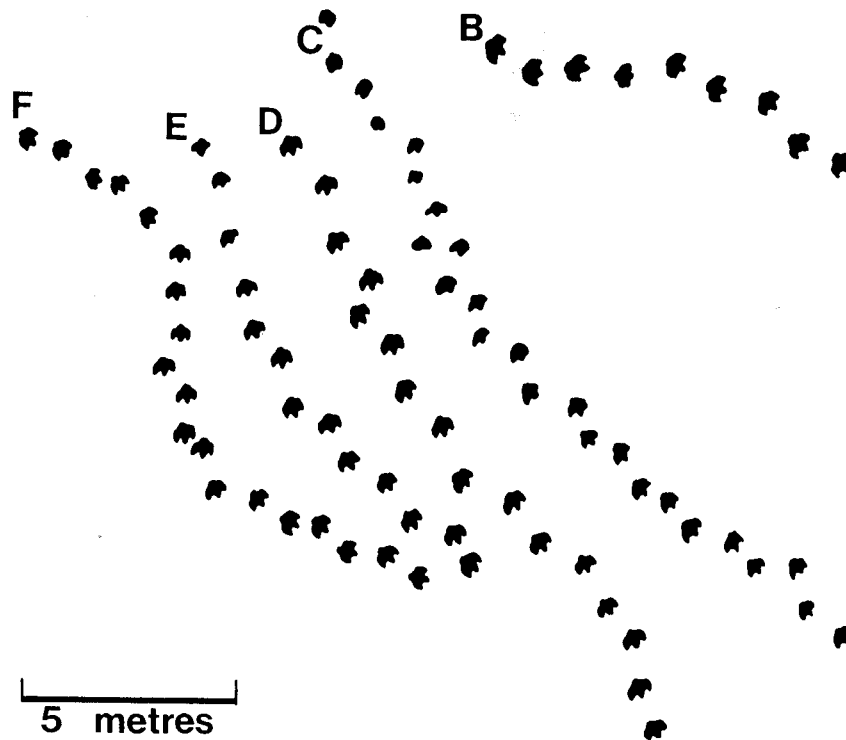
Figure 4 Map of a portion of Site 8 in the Peace River Canyon, showing trackways of *Amblydactylus gethingi* (B, C, D, E, F). All footprints were mapped in the field. Because of the reduced scale and the complexity of the drawing, a standard outline has been used for the *Amblydactylus* footprints (except for trackway C). North is towards the top of the drawing.

that ornithopod herds were spread out on a wide front and that the animals were walking side by side, seldom crossing paths. However, an *Amblydactylus* trackway at Site 3c is overlain by a second trackway made by an animal of the same species and of a smaller size. This shows that they did not always walk side by side when proceeding in the same direction. Other sites in the canyon with deep-water depositional environments show random distribution and orientation of the *Amblydactylus* tracks, suggesting that there was little structure to a herd of ornithopods that was in the water and/or feeding.

There is an interesting association between the trackways of *Amblydactylus* and the large carnivore *Irenesauripus acutus*. At Site 8, three trackways (J, K and L) of the theropod appear toward the end of a series of hadrosaur footprints (Currie, 1983). Trackways of *I. acutus* are also found in some (Sites 3d and 8a) of the deep water environments in association with *Amblydactylus* tracks. The large carnivores of the Gething Delta were apparently not adverse to walking in relatively deep water, although no evidence has been found to suggest that they swam, as one of the Early Jurassic theropods did (Coombs, 1980).

Alexander (1976) developed a formula from which the speed of a dinosaur can be calculated from a dinosaur trackway. The speeds of movement of the Peace River dinosaurs have been calculated using this formula (Kool, 1981; Table 1). Although

Table 1 Speeds of dinosaurs calculated from trackways in the Peace River Canyon
L = average length of foot (in metres)

Trackway Number	Identification	L	Aver.	Min. Speed (m/sec)	Max.	Aver.	Min. Speed (km/hr)	Max.
III-B	cf. *Columbosauripus ungulatus*	.307	2.26	2.12	2.34	8.15	7.64	8.42
III-C	Theropod	.343	2.90	2.84	2.96	10.44	10.21	10.66
III-D	cf. *Columbosauripus ungulatus*	.259	2.33	----	----	8.38	----	----
III-E	Theropod?	.285	2.28	----	----	8.21	----	----
III-F	Theropod?	.292	2.58	2.43	2.68	9.30	8.76	9.64
III-H	Theropod?	.293	2.13	----	----	7.66	----	----
III-I	*Irenesauripus mclearni*	.318	1.86	1.56	2.08	6.71	5.62	7.48
III-J	*Amblydactylus* sp.	.140	.84	.63	1.00	3.04	2.27	3.59
III-K	cf. *Gypsichnites pacensis*	.283	1.70	1.36	1.99	6.12	4.90	7.18
III-L	*Irenesauripus acutus*	.419	1.83	1.52	2.09	6.60	5.48	7.54
III-M	*Irenesauripus mclearni*	.365	1.67	1.45	1.85	6.01	5.23	6.64
III-N	*Irenesauripus mclearni*	.326	2.94	2.86	3.06	10.57	10.31	11.01
III-O	cf. *Gypsichnites pacensis*	.295	2.74	2.59	2.86	9.86	9.32	10.29
III-P	cf. *Gypischnites pacensis*	.246	1.98	.91	2.59	7.12	3.26	9.32
III-Q	*Irenesauripus mclearni*	.288	4.56	4.10	4.89	16.43	14.78	17.61
III-R	*Irenesauripus mclearni*	.334	3.21	2.34	4.19	11.55	8.42	15.07
III-S	cf. *Gypsichnites pacensis*	.292	2.04	1.82	2.20	7.34	6.56	7.91
III-T	cf. *Gypsichnites pacensis*	.294	2.15	2.08	2.23	7.75	7.47	8.04
III-V	*Irenesauripus mclearni*	.339	2 36	1.98	2.63	8.51	7.13	9.47
III-W	*Irenesauripus mclearni*	.334	1.69	1.50	1.85	6.10	5.40	6.65
III-X	Theropod?	.268	1.59	1.50	1.73	5.73	5.40	6.23
III-Z	*Irenichnites gracilis*	.147	1.89	1.77	2.03	6.80	6.38	7.30
III-AA	cf. *Irenesauripus mclearni*	.274	2.12	1.87	2.40	7.62	6.75	8.65
III-BB	*Irenesauripus mclearni*	.365	2.30	----	----	8.30	----	----
III-CC	*Irenichnites gracilis*	.157	1.97	1.88	2.06	7.09	6.76	7.42
III-DD	*Irenesauripus acutus*	.370	.83	.75	.99	2.97	2.69	3.58
III-EE	*Irenesauripus mclearni*	.275	3.02	----	----	10.87	----	----
IIIa-A	*Amblydactylus* sp.	.542	1.63	1.38	1.75	5.85	4 98	6.32
IIIa-B	*Amblydactylus* sp.	.382	1.63	1.24	1.94	5.88	4.45	6.99
IIIa-C	*Amblydactylus* sp.	.513	1.38	----	----	4.95	----	----
IIIa-E	*Amblydactylus* sp.	.560	1.12	----	----	4.03	----	----
IIIc	*Irenesauripus mclearni*	.300	2.45	1.61	3.42	8.81	5.79	12.32
IIIc-A	*Irenesauripus mclearni*	.291	2.37	2.26	2.56	8.55	8.14	9.20
IIIc-B	*Irenesauripus mclearni*	.333	1.49	1.36	1.91	5.37	4.88	6.87
IIIc-C	*Irenesauripus mclearni*	.256	2.63	2.48	2.84	9.47	8.93	10.22
IIIc-D	*Amblydactylus* sp.	.275	2.05	1.24	2.38	7.36	4.47	8.56
IIIc-E	*Irenichnites gracilis*	.160	2.31	2.23	2.37	8.31	8.03	8.52
IIIc-F	*Irenesauripus mclearni*	.266	1.97	1.81	2.16	7.10	6.51	7.78
IIIc-G	*Irenesauripus mclearni*	.197	3.08	2.73	3.23	11.08	9.84	11.64
IIId-A	*Irenesauripus acutus*	.578	1.78	1.58	1.99	6.41	5.68	7.18
IIId-B	*Amblydactylus* sp.	.466	1.77	1.58	2.04	6.38	5.70	7.36
IIId-C	*Amblydactylus* sp.	.505	1.33	----	----	4.79	----	----
IIIe-A	*Amblydactylus* sp.	.430	1.88	1.59	2.11	6.76	5.74	7.60
IIIe-C	*Amblydactylus* sp.	.265	1.34	1.30	1.37	4.82	4.70	4.95
IIIe-D	*Amblydactylus* sp.	.371	1.32	1.14	1.81	4.75	4.09	6.52
IV-A	*Amblydactylus* sp.	.543	.94	.44	2.18	3.39	1.59	7.84
IV-F	*Amblydactylus* sp.	.510	1.39	1.02	1.79	5.00	3.68	6.46
V-A	*Amblydactylus* sp.	.550	1.35	1.32	1.38	4.87	4.76	4.98
V-B	*Amblydactylus* sp.	.580	1.19	----	----	4.29	----	----
V-C	*Amblydactylus* sp.	.547	1.53	1.29	1.80	5.50	4.66	6.47
V-D	*Irenesauripus acutus*	.416	2.35	2.29	2.41	8.45	8.25	8.66
V-E	*Amblydactylus* sp.	.420	2.16	----	----	7.79	----	----

Table 1 *Continued*

Trackway Number	Identification	L	Aver.	Min.	Max.	Aver.	Min.	Max.
			Speed (m/sec)			Speed (km/hr)		
VI-A	*Amblydactylus* sp.	.530	1.80	----	----	6.48	----	----
VI-B	*Amblydactylus* sp.	.466	.94	.82	1.13	3.38	2.95	4.07
VIa-A	*Amblydactylus* sp.	.410	1.47	----	----	5.28	----	----
VIa-B	*Amblydactylus* sp.	.577	.51	.48	.57	1.85	1.73	2.04
VIII-A	*Amblydactylus* sp.	.529	1.05	.90	1.24	3.78	3.24	4.45
VIII-B	*Amblydactylus* sp.	.628	1.02	.82	1.75	3.67	2.95	4.52
VIII-C	*Amblydactylus* sp.	.458	.83	.24	1.25	3.00	.87	4.50
VIII-D	*Amblydactylus* sp.	.430	1.48	.92	1.80	5.33	3.33	6.46
VIII-F	*Amblydactylus* sp.	.413	1.02	.60	1.30	3.68	2.15	4.69
VIII-G	*Amblydactylus* sp.	.492	.68	.30	1.10	2.44	1.07	3.96
VIII-I	*Amblydactylus* sp.	.594	.97	.80	1.14	3.49	2.88	4.11
VIII-J	*Irenesauripus acutus*	.508	1.83	1.72	1.91	6.60	6.19	6.88
VIII-K	*Irenesauripus acutus*	.551	2.37	1.60	3.38	8.53	5.76	12.17
VIII-L	*Irenesauripus* cf. *acutus*	.394	2.19	1.14	2.61	7.87	4.09	9.39
VIII-N	*Amblydactylus* sp.	.500	1.10	1.04	1.16	3.96	3.75	4.18
VIII-O	*Irenesauripus acutus*	.542	1.72	1.45	2.06	6.18	5.21	7.41
VIII-P	*Irenesauripus acutus*	.560	2.28	2.21	2.35	8.21	7.97	8.46
VIIIa-T	*Amblydactylus* sp.	.617	1.35	1.33	1.37	4.87	4.79	4.95
VIIIa-U	Theropod? n. gen, n.sp.	.332	1.80	1.65	1.89	6.49	5.95	6.81
VIIIa-V	Theropod? n. gen, n.sp.	.194	1.47	1.21	1.72	5.29	4.37	6.17
VIIIa-W	Theropod? n. gen, n.sp.	.247	1.78	1.72	1.85	6.42	6.19	6.66
VIIIa-X	Theropod? n. gen, n.sp.	.267	1.76	1.70	1.88	6.34	6.14	6.76
VIIIa-Y	Theropod? n. gen, n.sp.	.310	1.16	1.08	1.23	4.17	3.89	4.43
VIIIa-Z	Theropod? n. gen, n.sp.	.300	2.07	1.85	2.32	4.44	6.64	8.36
IX-A	Theropod? n. gen, n.sp.	.315	2.09	----	----	7.53	----	----
IX-B	*Irenesauripus mclearni*	.237	1.26	1.19	1.32	4.53	4.29	4.76
IX-C	*Irenesauripus mclearni*	.310	2.19	1.97	2.32	7.90	7.08	8.35
IX-D	*Amblydactylus* sp.	.425	1.44	----	----	5.18	----	----
XII-A	*Amblydactylus* sp.	.640	1.15	.98	1.41	4.14	3.51	5.08
XIII-A	*Amblydactylus* sp.	.355	2.15	----	----	7.73	----	----
XIII-B	*Amblydactylus* sp.	.434	1.46	1.40	1.52	5.26	5.06	5.47
XIV-A	*Amblydactylus* sp.	.594	1.62	1.61	1.64	5.82	5.79	5.91
XIV-B	*Amblydactylus* sp.	.730	1.77	----	----	6.39	----	----
NMC 8548	*Irenesauripus mclearni*	.323	.88	----	----	3.15	----	----
NMC 8550	*Irenesauripus occidentalis*	.464	1.22	1.21	1.24	4.40	4.35	4.45
NMC 8552	*Irenichnites gracilis*	.156	2.47	2.24	2.75	8.90	8.07	9.89
NMC 8556	"*Tetrapodosaurus borealis*"	.280	1.11	1.10	1.12	3.98	3.94	4.02
NMC 8558	*Irenichnites gracilis*	.158	1.47	----	----	5.31	----	----
NMC 8561	*Irenesauripus mclearni*	.281	2.06	1.95	2.13	7.40	7.01	7.68
NMC 8562	*Irenesauripus mclearni*	.297	2.21	2.16	2.28	7.96	7.79	8.20
NMC 8563	*Irenesauripus mclearni*	.257	1.82	----	----	6.55	----	----

there are some problems associated with the use of this formula (see Demathieu, 1984 for examples), it is probably accurate enough for comparing the relative speeds of two types of fundamentally bipedal dinosaurs (theropods and ornithopods).

The ornithopods appear to have been relatively slow animals in comparison with the carnivores (*Irenesauripus*, *Irenichnites*, *Columbosauripus*), attaining a top speed of 8.5 km/hr. This figure was calculated on the basis of the total length of the foot, which includes a substantial "heel" pad. Alexander's formula is based on the distance between the distal end of the third metatarsal and the distal end of the third toe. As the pad

obscures the distal end of the third metatarsal, it is not known precisely what percentage of the length of the foot is made up by the "heel" pad. The increased length of the foot, given by inclusion of the pad, results in a significant error in the calculation of the speed. For example, the average calculated speed of trackway IIIa-A is 5.85 km/hr for the full length of the footprint. However, if we reduce the length of the track by 15% to compensate for the additional length of the heel pad, then the average speed for the same animal increases to 7.08 km/hr. The average speed for all of the carnivore trackways is 7.56 km/hr, whereas that for the herbivores is 5.18 km/hr. If we add a 20% compensation to the speed of the herbivores in response to the "heel" pad, then the average speed of the herbivores can be raised to about 6.5 km/hr, which is still significantly less than the average speed of the carnivores. All *Amblydactylus* trackways were made by animals utilizing walking gaits (λ/h less than 2.0, Thulborn, 1984).

References

Alexander, R. McN. (1976) Estimates of the speeds of dinosaurs. *Nature* **261**, 129.

Antunes, M. T. (1976) Dinossáurios eocretácicos de Lagosteiros. *Ciências da Terra* **1**, 1–35.

Beckles, S. H. (1862) On some natural casts of reptilian footprints in the Wealden Beds of the Isle of Wight and Swanage. *Quarterly Journal of the Geological Society* **18**, 443–447.

Bird, R. T. (1944) Did *Brontosaurus* ever walk on land? *Natural History* **53**, 60–67.

Carpenter, K. (1992) Behavior of hadrosaurs as interpreted from footprints in the "Mesaverde" Group (Campanian) of Colorado, Utah, and Wyoming. *University of Wyoming, Contributions to Geology* **29**, 81–96.

Casamiquela, R. M. & A. Fasola (1968) Sobre pisadas de Dinosaurios del Cretacico Inferior de Colchagua (Chile). *Universidad de Chile, Facultad de Ciencias Fisicas y Matematicas, Departamento de Geologia, Publicación* **30**, 5–24, Plates I–VII.

Coombs, W. P. (1980) Swimming ability of carnivorous dinosaurs. *Science* **207**, 1198–1199.

Currie, P. J. (1980) Palaeontological expedition to the Peace River Canyon, between Hudson's Hope and the W. A. C. Bennett Dam, 1979. Unpublished report to Heritage Conservation Branch, B.C. Provincial Government.

Currie, P . J. (1981) Bird footprints from the Gething Formation (Aptian, Lower Cretaceous) of northeastern British Columbia, Canada. *Journal of Vertebrate Paleontology* **1**, 257–264.

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

Currie, P. J. (1989) Dinosaur footprints from western Canada, pp. 293–300. In D.D. Gillette & M.G. Lockley, eds., *Dinosaur Tracks and Traces*. Cambridge University Press. Cambridge, England; New York.

Currie, P. J. & D. A. Eberth (1993) Palaeontology, sedimentology and palaeoecology of the Iren Dabasu Formation (Upper Cretaceous), Inner Mongolia, People's Republic of China. *Cretaceous Research* **14**, 127–144.

Currie, P. J., G. C. Nadon & M. G. Lockley (1991) Dinosaur footprints with skin impressions from the Cretaceous of Alberta and Colorado. *Canadian Journal of Earth Sciences* **28**, 102–115.

Currie, P. J. & W. A. S. Sarjeant (1979) Lower Cretaceous dinosaur footprints from the Peace River Canyon, British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* **2**, 103–115.

Demathieu, G. R. (1984) Utilisation de lois de la mécanique pour l'estimation de la vitesse de locomotion des vertébrés tétrapodes du passé. Géobios 17, 439–446.

Dollo, L. (1905) Les allures des Iguanodons, d'après les empreintes des pieds et de la queue. Bulletin Scientifique de la France et de la Belgique 50, 1–12.

Dutuit, J. M. & A. Ouazzou (1980) Découverte d'une piste de Dinosaure Sauropode sur le site d'empreintes de Demnat (Haut-Atlas marocain). Mémoires de la Société Géologique de France, Nouvelle Série 139, 95–102.

Farlow, J. O., J. G. Pittman & J. M. Hawthorne (1989) Brontopodus birdi, Lower Cretaceous sauropod footprints from the U.S. Gulf coastal plain, pp. 371–394. In D. D. Gillette & M. G. Lockley, eds., Dinosaur Tracks and Traces. Cambridge University Press. Cambridge, England; New York.

Galton, P. M. & J. A. Jensen (1979) Remains of ornithopod dinosaurs from the Lower Cretaceous of North America. Brigham Young University Geology Series 25, 1–10.

Ishigaki, S. (1989) Footprints of swimming sauropods from Morocco, pp. 83–86. In D. G. Gillette & M. G. Lockley, eds., Dinosaur Tracks and Traces. Cambridge University Press. Cambridge, England, New York.

Kaye, J. M. & D. A. Russell (1973) The oldest record of hadrosaurian dinosaurs in North America. Journal of Palaeontology 47; 91–93.

Kool, R. (1981) The walking speed of dinosaurs from the Peace River Canyon, British Columbia, Canada. Canadian Journal of Earth Sciences 18, 823–825.

Langston, W., Jr. (1960) A hadrosaurian ichnite. Natural History Paper, National Museum of Canada 4, 1–9.

Leonardi, G. (1984) Le impronte fossili di dinosauri, pp. 164–186. In J. Bonaparte, E.H. Colbert, P.J. Currie, A. DeRicqles, Z. Kielan-Jaworowska, G. Leonardi, N. Morello, & P. Taquet, Sulle Orme Dei Dinosauri. Erizzo. Venice, Italy.

Leonardi, G. (1989) Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation, pp. 165–178. In D. G. Gillette & M. G. Lockley, eds., Dinosaur Tracks and Traces. Cambridge University Press. Cambridge, England; New York.

Lim, S.-K., S.-Y. Yang & M. G. Lockley (1989) Large dinosaur footprint assemblages from the Cretateous Jindong Formation of southern Korea, pp. 331–336. In D. G. Gillette & M. G. Lockley, eds., Dinosaur Tracks and Traces. Cambridge University Press. Cambridge, England; New York.

Lockley, M. G. (1987) Dinosaur footprints from the Dakota Group of eastern Colorado. The Mountain Geologist 24, 107–122.

Lockley, M. G., A. Hunt, J. Holbrook, M. Matsukawa & C. Meyer (1992) The dinosaur freeway: a preliminary report on the Cretaceous megatracksite, Dakota Group, Rocky Mountain Front Range, and High Plains, Colorado, Oklahoma and New Mexico, pp. 39–54. In R. M. Flores, ed., Field Guidebook, Mesozoic of the Western Interior. Rocky Mountain Section, Society for Sedimentary Geology. Fort Collins, Colorado.

Lockley, M. G. & A. Rice (1990) Did "Brontosaurus" ever swim out to sea?, evidence from brontosaur and other dinosaur footprints. Ichnos 1, 81–90.

Lockley, M. G., B. H. Young & K. Carpenter (1983) Hadrosaur locomotion and herding behavior, evidence from footprints in the Mesaverde Formation, Grand Mesa Coal Field, Colorado. Mountain Geologist 20, 5–14.

Lucas, S. G., A. P. Hunt & K. K. Kietzke (1989) Stratigraphy and age of Cretaceous dinosaur footprints in northeastern New Mexico and northwestern Oklahoma, pp. 217–221. In D. G. Gillette & M. G. Lockley (eds.), Dinosaur Tracks and Traces. Cambridge University Press. Cambridge, England; New York.

McAllister, J. A. (199) Dakota Formation tracks from Kansas, implications for the recognition of tetrapod subaqueous traces, pp. 343–348. In D. G. Gillette & M. G. Lockley (eds.), Dinosaur Tracks and Traces. Cambridge University Press. Cambridge, England; New York.

McLearn, F. H. (1923) Peace River Canyon coal area, B.C. Geological Survey of Canada, Summary Report 1922 part B, 1–46.

Moratalla, J. J., J. L. Sanz & S. Jimenez (1988) Multivariate analysis on Lower Cretaceous dinosaur footprints, discrimination between ornithopods and theropods. Geobios 21, 395–408.

Moratalla, J. J., J. L. Sanz, S. Jimenez & M. G. Lockley (1992) A quadrupedal ornithopod trackway from the Lower Cretaceous of La Rioja (Spain), inferences on gait and hand structure. Journal of Vertebrate Paleontology 12, 150–157.

Mossman, D. J. & W. A. S. Sarjeant (1983) The footprints of extinct Animals. Scientific American 248(1), 74–85.

Norman, D. B. (1980) On the ornithischian dinosaur Iguanodon bernissartensis of Bernissart (Belgium). Institut Royal des Sciences Naturelles de Belgique, Mémoires 178, 1–104.

Osborn, H. F. (1912) The integument of the iguanodont dinosaur Trachodon. American Museum of Natural History, Memoir 1, 33–54.

Ostrom, J. H. (1972) Were some dinosaurs gregarious? Palaeogeography, Palaeoclimatoloy, Palaeoecology 11, 287–301.

Pittman, J. G. (1989). Stratigraphy, lithology, depositional environment, and track type of dinosaur track-bearing beds of the Gulf Coastal Plain, pp. 135–153. *In* D. G. Gillette & M. G. Lockley, eds., *Dinosaur Tracks and Traces*. Cambridge University Press. Cambridge, England; New York.

Pittman, J. G. & D. D. Gillette (1989) The Briar Site, a new sauropod dinosaur tracksite in Lower Cretaceous beds of Arkansas, USA, pp. 313–332. *In* D. G. Gillette & M. G. Lockley, eds., *Dinosaur Tracks and Traces*. Cambridge University Press. Cambridge, England; New York.

Sarjeant, W. A. S. (1981) In the footsteps of the dinosaur. *Explorers Journal* **59**(4), 164–171.

Sarjeant, W. A. S. & R. A. Thulborn (1986) Probable marsupial footprints from the Cretaceous sediments of British Columbia. *Canadian Journal of Earth Sciences* **23**, 1223–1227.

Sternberg, C. M. (1932) Dinosaur tracks from Peace River, British Columbia. *National Museum of Canada, Annual Report* **1930**, 59–85.

Stott, D. F. (1975) The Cretaceous system in northeastern B.C. Geological Association of Canada, Special Paper **13**, 441–467.

Thulborn, R. A. (1984) Preferred gaits of bipedal dinosaurs. *Alcheringa* **8**, 243–252.

Tylor, A. (1862) On the footprint of an *Iguanodon*, lately found at Hastings. *Quarterly Journal of the Geological Society of London* **18**, 247–253.

Weishampel, D. B. & P. R. Bjork (1989) The first indisputable remains of *Iguanodon* (Ornithischia: Ornithopoda) from North Amelica, *Iguanodon lakotaensis* sp. nov. *Journal of Vertebrate Paleontology* **9**, 56–66.

Woodhams, K. E. & J. S. Hines (1989) Dinosaur footprints from the Lower Cretaceous Of East Sussex, England, pp. 301–307. *In* D. G. Gillette & M. G. Lockley, eds., *Dinosaur Tracks and Traces*. Cambridge University Press. Cambridge, England; New York.