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LOWER CRETACEOUS DINOSAUR FOOTPRINTS FROM THE PEACE RIVER CANYON, BRITISH COLUMBIA, CANADA

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ABSTRACT

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During a series of three expeditions to a part of the Peace River valley of eastern British Columbia shortly to be submerged by a reservoir, a rich assemblage of dinosaur footprint tracks has been recovered. These include a new type. *Amblydactylus kortmeyeri* sp. nov. comprises tridactyl impressions considered to be those of a hadrosaurid ornithopod; these footprints include those of juveniles, as well as of adults, and provide some suggestions of gregarious behaviour among these herbivorous reptiles.

INTRODUCTION

Dinosaur footprints were first discovered in the Peace River Canyon of British Columbia in 1922 by F. H. McLearn (1923), a geologist with the Geological Survey of Canada. The site was not investigated until 1930, when Charles M. Sternberg made plaster moulds and collected specimens and data for the National Museum of Canada. Sternberg (1932) observed more than 400 footprints at different points along the outcrops in the canyon; on the basis of the material cast or collected, he established six new ichnogenera containing eight new ichnospecies. During the construction of the W.A.C. Bennett Dam (1961—68), more dinosaur footprints were discovered upstream from the original site. Members of an expedition from the Royal Ontario Museum made latex moulds of two trackways before they were covered by the earth-fill of the dam.

In 1975, construction started on a second dam downstream from the footprint localities. John A. Sulek, who saw some of the dinosaur trackways while on a fishing trip, was concerned that the footprints would be inundated before palaeontologists were aware of the situation; he therefore approached a number of institutions in the hope of initiating a salvage

operation. The Provincial Museum of Alberta, assisted financially by Imperial Oil of Canada, responded by sending an expedition into the Peace River Canyon in 1976. Sternberg's primary trackway site, near Ferro Point, could no longer be seen because of high water levels, but the expedition was successful nevertheless. One of the more spectacular discoveries was a single bedding plane, 12 m long by 5 m wide, with over one hundred dinosaur footprints preserved on it.

Fig.1. North wall of Peace River canyon west of Grant's Flat. Footprints of juvenile specimens of *A. kortmeyeri* were found among large blocks at the base of the exposures.

The Provincial Museum of Alberta returned to the Peace River Canyon in 1977 and 1978, assisted by generous grants from British Columbia Hydro. Rubber moulds were made of some trackways and individual ichnites, other trackways were mapped and photographed and, wherever possible, actual specimens were extracted.

Among the new trackways discovered in the Peace River Canyon, evidence

of juvenile dinosaurs was found. Their discovery is considered significant because of the scarcity of evidence for young dinosaurs in the fossil record (Jepson, 1964; Richmond, 1965). This paper includes the description of a new ichnospecies; a fuller account of the discoveries is in preparation.

For recent discussions of the stratigraphical setting of these discoveries, reference should be made to Stott (1972, 1975).

SYSTEMATIC PALAEONTOLOGY

CLASS REPTILIA
SUBCLASS ARCHOSAURIA
Order Ornithischia
Suborder Ornithopoda
Family Hadrosauridae Cope, 1869

Amblydactylus Sternberg 1932, emend. Currie and Sarjeant, herein.

1932 *Amblydactylus* Sternberg, p. 72
1955 *Amblydactylus* Sternberg. Lessertisseur, p. 114
1958 *Amblydactylus* Sternberg. Kuhn, p. 27
1963 *Amblydactylus* Sternberg. Kuhn, p. 106
1971 *Amblydactylus* Sternberg. Haubold, p. 88

Type species: Amblydactylus gethingi Sternberg 1932, p. 72.
Emended diagnosis: Bipedal, with three functional pedal digits. The outer contours of digits II and IV diverge at low angles from the longitudinal axis of the ichnite. A distinct posterior impression is produced by a metatarsal-phalangeal pad. Interdigital webs link the proximal portions of the fleshy digital pads; the digits end in blunt claws or pointed hooves. The ichnite is almost as wide as, or wider than, it is long.

Amblydactylus gethingi Sternberg 1932

1932 *Amblydactylus gethingi* Sternberg, pp. 72—73, pl. 4. fig.2, text-fig.8
1955 *A. gethingi* Sternberg. Abel, p. 150, fig.127
1958 *A. gethingi* Sternberg. Kuhn, p. 26, pl.12, fig. 10
1963 *A. gethingi* Sternberg. Kuhn, p. 106
1971 *A. gethingi* Sternberg. Haubold, p. 88, fig. 54, no. 7

Diagnosis: Tridactyl pedal impressions, each longer than it is broad; no evidence of separate phalangeal pads. The divarication of digits II to IV is 56°. Each digital impression tapers distally to a point, corresponding to a pointed hoof, which is in line with the longitudinal axis of the digit. (Abbreviated from Sternberg, 1932, pp. 72—73.)
Discussion: During the investigations we have made in the Peace River Canyon, no further footprints of this type have so far been recovered. The holotype was discovered at a stratigraphical level now generally submerged beneath the Peace River.

Amblydactylus kortmeyeri Currie and Sarjeant, new species (Figs.2—7)

Derivation of name: In tribute to Carl Kortmeyer, the discoverer of the holotype.

Holotype: Provincial Museum of Alberta, PMA P76.11.11. Natural

cast in fine-grained sandstone of a single footprint, found on a talus slope on the north bank of the Peace River, approximately 275 m upstream from the point where Aylard Creek flows into the Peace River Canyon, British Columbia. *Horizon:* Gething Formation of Bullhead Group, Lower Cretaceous. *Dimensions:* Length 420 mm (measured along the longitudinal axis), breadth 430 mm (Fig.2).

Paratype I: British Columbia Provincial Museum BC719. Single footprint, found 320 m downstream from Ferro Point on the north bank of the Peace River, Peace River Canyon, British Columbia. *Horizon:* 88 m above the

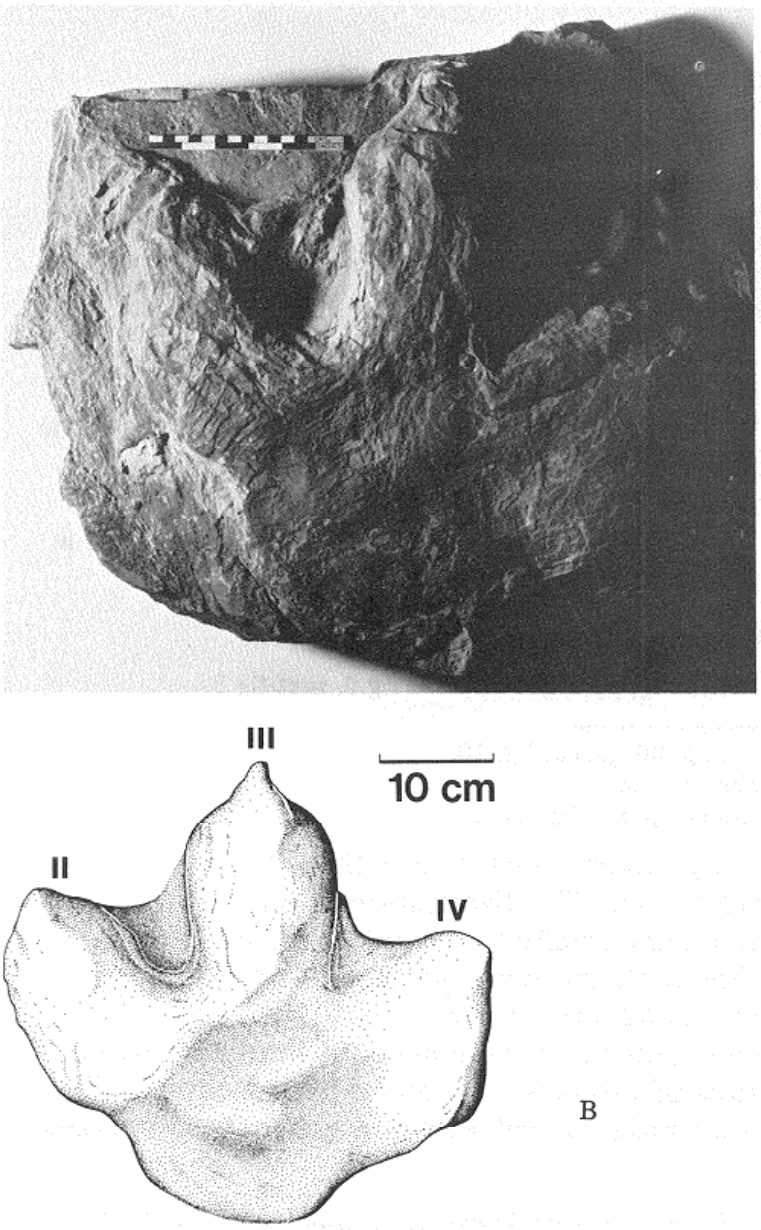

Fig. 2. *Amblydactylus kortmeyeri* sp. nov. Holotype (PMA P76.11.11). A. Photograph of specimen. B. Interpretative drawing.

Grant Coal Seam, Gething Formation of Bullhead Group, Lower Cretaceous. *Dimensions:* Length 190 mm, breadth 210 mm (Fig.3).
Paratypes II—V: BC720 — PMA P77.17.6. Natural casts of seven footprints from at least two trackways, found on three large blocks of siltstone in close proximity on talus slope 150 m downstream from Reef Point, on the north bank of the Peace River, Peace River Canyon, British Columbia. [Three ichnites were collected and the remaining four were cast.] *Horizon:* Gething Formation of Bullhead Group, Lower Cretaceous. *Dimensions:*

II — BC 720 — 112 mm long, 124 mm wide (not illustrated)
III — PMA P77.17.6a — 108 mm long, 121 mm wide (Fig.4—6; 7B)
IV — PMA P77.17.6b — 117 mm long, 123 mm wide (Fig.6A)
V — PMA P77.17.6c — 120 mm long, 120 mm wide (Fig.6A)

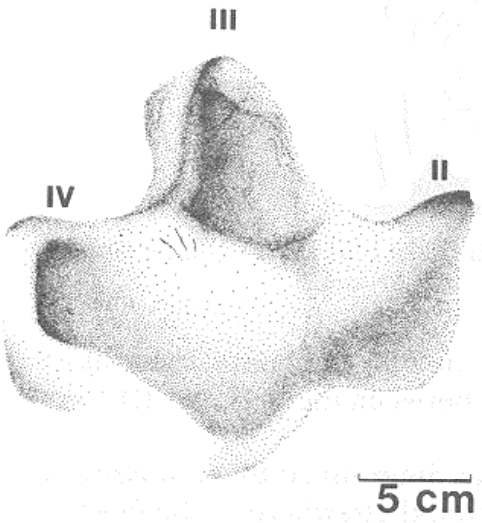

Fig.3. *Amblydactylus kortmeyeri* sp. nov. Paratype I (BC719): interpretative drawing. (The specimen is so deep that satisfactory photographs of it could not be obtained.)

Diagnosis: Tridactyl pedal impressions, broader than long, with large, distinct phalangeal pads. Outline of ichnite is more strongly concave posteromedially than it is posterolaterally. The total divarication of digits II and IV is 70—80°; the anterior outline of digit IV is broad and rounded.
Description: The holotype of *Amblydactylus kortmeyeri* (Fig.2) is a natural cast of a tridactyl pedal impression. The medial margin of digit II is nearly parallel to the longitudinal axis, at an angle of approximately 15°. The divarication of lines drawn from the most posterior point of the ichnite to the tips of digits II and IV is 70°. Computation of the interdigital angles (see Sarjeant, 1971, 1975) is difficult in this ichnospecies because of the presence of fleshy digital pads. The longitudinal axes of digits II and IV, as determined by the orientations of the deepest parts of the depressions made

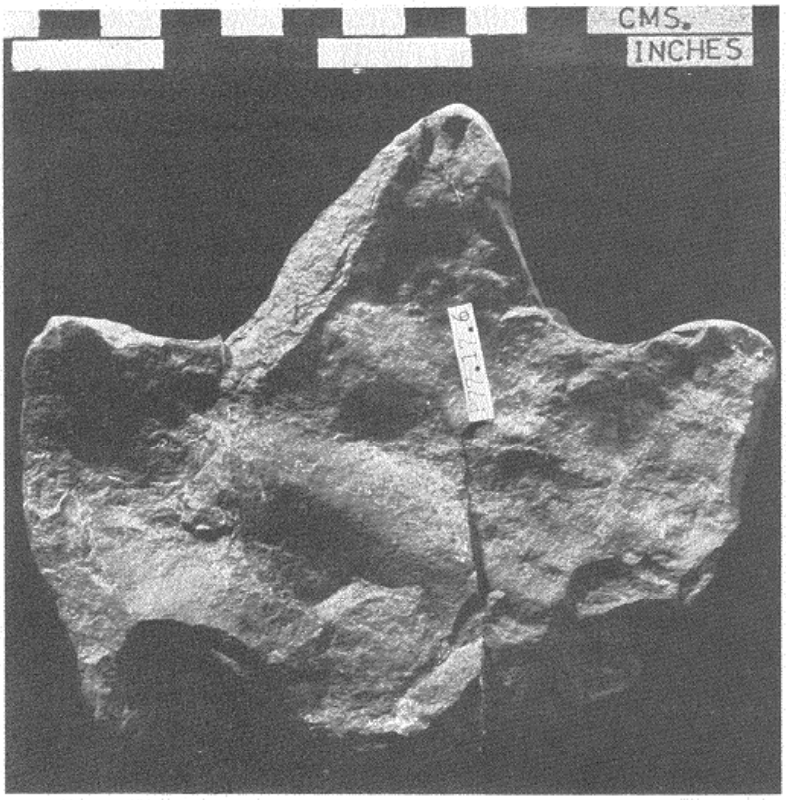

Fig. 4. *Amblydactylus kortmeyeri* sp. nov. Paratype II (PMA P76.17.6a), photographed in the same position as drawn in Fig. 3.

by the digital pads, are roughly parallel to the medial and lateral margins of the ichnite; the interdigital angles are thus 0° between digits II and III, and 15° between digits III and IV.

The ichnite was made by a left pes. This was determined by comparing the outline of the print with those of trackways found elsewhere in the Peace River Canyon.

All digits and the metatarsal—phalangeal pad were impressed deeply into the sediments when the footprint was formed, the deepest impression being made by the third digit. There was a large, bulbous fleshy pad associated with the bones of each digit; no interphalangeal constrictions were developed on the digital pads. The ventral surfaces of the digital pads of digits III and IV were convex in transverse and longitudinal sections. In longitudinal vertical section, the ventral surface of the pad of digit II was convex proximally and distally, but shallowly concave between these regions.

The metatarsal—phalangeal pad made a depression that is shallower than those made by the digits and is separated from them by low ridges. The surface of this region of the ichnite is irregular, suggesting that the ventral surface of the metatarsal—phalangeal pad was not smoothly convex.

The outline of the ichnite is more deeply excavated between the medial edge of the impression of digit II and the "heel" of the metatarsal—phalangeal pad imprint than it is between the lateral edge of the depressions

made by digit IV and the "heel". The outlines of digits II and III taper distally to points that lie on the longitudinal axes of these digits. The broad, rounded anterior outline of digit IV meets the nearly straight lateral outline in a distinct junction lateral to the longitudinal axis of the digit. In shape, the impression of digit IV is similar to that of a digital pad of a hadrosaur ichnite, as described by Langston (1960).

The footprint includes a clear impression made by the web that joined digits III and IV, and an indistinct impression made by the interdigital web between digits II and III. The interdigital webs were attached to the lateral and medial surfaces of the toes. The unguals of digits II and IV did not leave distinct impressions. However, the ichnite indicates that there was a large, distally blunt ungual on the third digit.

Paratype I (Fig.3) is a poorly preserved footprint formed in ripple-marked silts with dessication cracks. Partial sediment infilling obscures many of the details; nevertheless, it has the same diagnostic details as the holotype. The ichnite is approximately 10% wider than it is long; however, the blunt anterior outline of digit III suggests that the entire length of this digit was not preserved. The larger width to length ratio of Paratype I, when compared with the holotype, can be accounted for partially by the wider divarication of the digits. The divarication of digits II and IV is 80°, 10° greater than that of the holotype. (Differences of this magnitude can be expected to be produced by variations in the nature and hardness of the substrate on which the animals were walking or by variations in the manner and speed of locomotion). There were large, fleshy digital pads. The lateral and medial digits diverge from the longitudinal axis of the footprint at relatively low angles. A distinct, rounded posterior margin was left by the metatarsal–phalangeal pad. In transverse section, the outline of the foot is more deeply excavated posteromedially than it is posterolaterally. The impression made by digit III is deep and is separated from the impressions of digits II and IV and of the metatarsal–phalangeal pad by a pronounced ridge. This ridge is most conspicuous between the third and fourth digital imprints. (The holotype does not exhibit such a marked ridge.) One of the most interesting features of Paratype I is its size, approximately half the linear dimensions of the holotype.

Paratypes II–V are natural casts of seven footprints on three overturned siltstone blocks found in close proximity on a talus slope. The three blocks probably originally formed parts of a single mass that broke apart on falling from the cliff face; the outlines of the three blocks are not compatible, indicating that there must have been an indeterminable amount of rock separating the sections when they were *in situ*. Each of the smaller two blocks exhibited a single ichnite and was collected. The largest block was too massive for removal from the site; consequently, a latex mould was made of the whole surface and three ichnites were collected.

The footprints on all three blocks are the same type and size; they were unquestionably made by animals of the same type at the same time. The

natural casts (Figs. 5A, D) probably include subtraces (Sarjeant, 1975). When the ichnites were removed from the blocks, it was found that the newly exposed surfaces on the undersides of the natural casts (Fig. 3B) gave a better impression of what the footprints would have looked like when they were made.

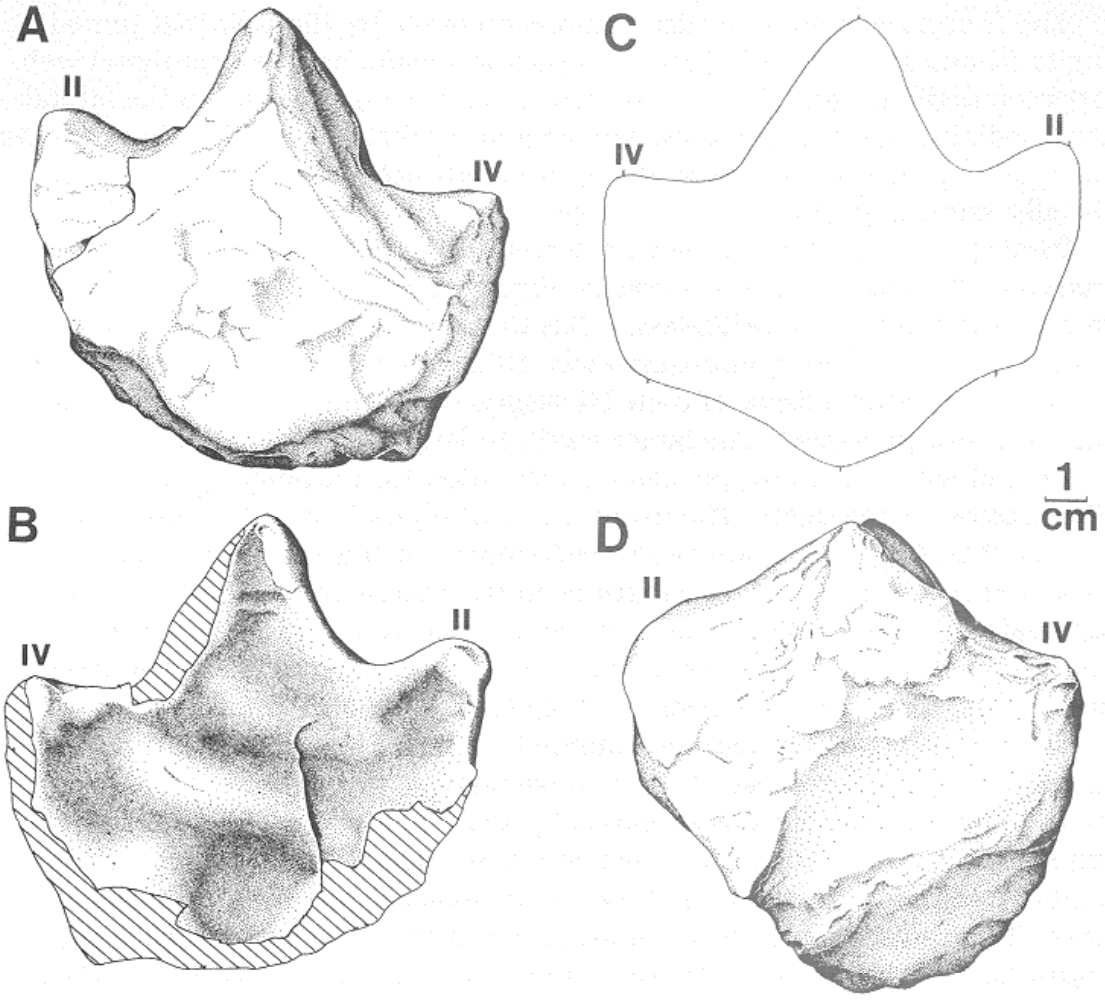

Fig. 5. *Amblydactylus kortmeyeri* sp. nov. Paratypes. A. Natural cast of subtrace of ichnite (Paratype III, PMA P77.17.6a). B. Opposite view of Paratype III. Pedal impression. C. Outline of ichnite of *A. kortmeyeri*, based mainly on the specimen seen in Figs. 4, 5A and 5B. Points marked on outline are those through which lines were drawn to calculate interdigital angles. D. Natural cast of subtrace of Paratype II (BC720).

Each of these ichnites is as broad as, or broader than, it is long. Digit II diverges from the longitudinal margin of Paratype III at an angle of about 8°, and digit IV at 12° (Fig. 5C). The total interdigital divarication varies in Paratypes III—V from 73° to 78°. There were fleshy phalangeal pads associated with each digit. The metatarsal—phalangeal pad left an impression with a well-defined posterior margin. As in Paratype I, there is a prominent

ridge separating the impressions of the phalangeal pads of digits III and IV (Fig.5B). The anterior outlines of the interdigital webs are clearly preserved. The outline of PMA P77.17.6a is very similar to that of the holotype (see Fig.7A). On the basis of the possession of the same diagnostic characteristics as those found in the holotype, the seven ichnites are considered to belong to the ichnospecies *A. kortmeyeri*; their dimensions, however, are only approximately one quarter the size of those of the holotype.

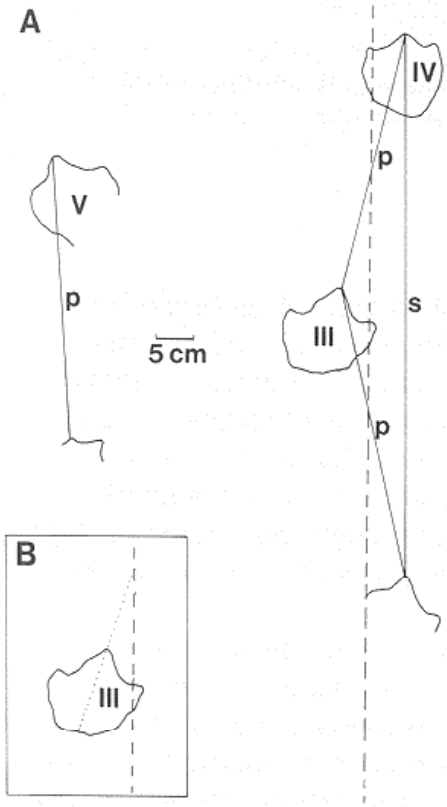

Fig.6. Trackways of *Amblydactylus kortmeyeri* sp. nov. A. III—V = paratype numbers; *p* = pace; *s* = stride. B. Paratype III showing rotation of pes in relation to midline of trackway.

The five ichnites that were preserved on a single block (PMA P77.17.6) are aligned in two diverging trackways (Fig.6). The ichnites of each trackway are of the same type and approximately the same size. The trackway with three ichnites is narrow, with the medial digital impression of each ichnite lying on the longitudinal axis of the trackway. The stride, which can be measured in only one case, is 730 mm. Three measurements of pace were made — 395, 360 and 385 mm. The average pace is 380 mm. The longitudinal axis of Paratype III (Fig.6) is inclined at an angle of about 18° to the longitudinal axis of the trackway. The digits point toward the midline of the trackway; there is no evidence of tail drag.

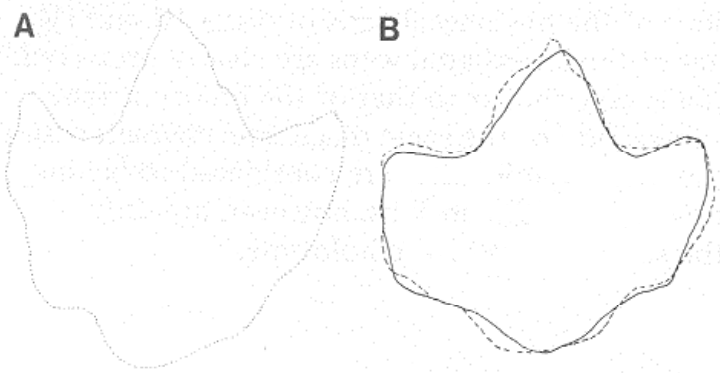

Fig.7. Outline of ichnite of *Amblydactylus gethingi* Sternberg. B. Outlines of the holotype (broken line) and Paratype III (solid line) of *A. kortmeyeri* sp. nov.

DISCUSSION

Amblydactylus kortmeyeri can be distinguished from *A. gethingi* by few characteristics. In the type specimen of *A. gethingi* (N.M.C. 8555), the footprint is almost 10% longer than it is broad, the divarication of digits II and IV is 56°, and there is no evidence of separate phalangeal pads (Sternberg, 1932, p. 73). All of these differences might be accounted for on the basis of differences in the circumstances of formation of the ichnites. However, there is a fundamental difference in the length and shape of digit IV in *A. gethingi* and *A. kortmeyeri* (Fig.7) that justifies a distinction at the specific level.

As noted by Sternberg (1932, p. 72), *Amblydactylus* shows some resemblance to tracks from the Wealden (Lower Cretaceous) of Europe considered to have been made by *Iguanodon*. However, the digital pads appear to have been more swollen in *Amblydactylus* and the digits do not extend as far beyond the webbing as in *Iguanodon* tracks. Moreover, the length to breadth ratio is much lower in *Amblydactylus*.

The shapes of the digital pads of the holotype compare well with those of an isolated hadrosaur ichnite described by Langston (1960). The similarity in the outline of digit IV of our holotype and "digit II" of Langston's hadrosaur ichnite is striking. For convenience, Langston described the ichnite in terms of the right pes, even though he was unable to determine whether the ichnite was made by a right or left pes. The similarities between the contours of his specimen and ours indicate that his hadrosaur ichnite was made by a left pes; the digit described by him as II is thus actually IV. The ratio of width to length of the digital pads is greater in the hadrosaurian ichnite than it is in *Amblydactylus*.

No bones have been found in the Gething Formation to indicate whether *Amblydactylus* was an iguanodontid or a hadrosaurid ornithopod. The footprints are closer in outline to that of a hadrosaur (Langston, 1960) than to those of iguanodonts (Beckles, 1862; Ballerstedt, 1905). The dinosaurs

that made the footprints in the Peace River Canyon of British Columbia lived during Early Cretaceous (Late Neocomian) times. The earliest record of hadrosaurian remains is from the Cenomanian of England (Lydekker, 1888), although the oldest remains known from North America are Santonian in age (Kaye and Russell, 1973).

The smallest specimens of *A. kortmeyeri* were unquestionably made by juveniles; this is made evident because of the comparably high ratio of breadth to length measurements. Juveniles tend to anticipate the proportions of their adult form in their breadth to length dimensions. For example, the long bones of a juvenile will have a greater absolute shaft diameter than those of a mature animal of comparable size of a different species. A mature, bipedal dinosaur of the same size would have left footprints of considerably more slender proportions, whereas the proportions of the small ichnites are not significantly different from those of the holotype (Fig.5). Despite differences in the preservation, the correlation of characteristics that are considered diagnostic would seem to indicate that both the small and the large ichnites were made by the same species of animal. The linear dimensions of the holotype are approximately four times greater than those of the small ichnites (PMA P77.17.6). Paratype I was made by an animal which had the same pedal characteristics as the animal that made the holotype and PMA P77.17.6 and that which was intermediate in size between them. This is further, strong evidence that the small ichnites represent juveniles of *A. kortmeyeri.* However, since large reptiles potentially undergo a much greater size magnification than this during growth, it may be presumed that the ichnites do not represent a complete range of a growth series.

Both the small (PMA P77.17.6a, Fig.3B) and intermediate (Paratype I, Fig.2) sized footprints have strong ridges posterior to the impression of digit III that are not represented in the large ichnite (PMA P76.11.11). These ridges may either have resulted from the nature of the substrate on which the animals walked or from the mode of locomotion. The small and intermediate sized animals made relatively deeper impressions in the substrate than did the large animal. Considering the much greater proportional weight of the large animal, this strongly suggests that the substrate in which the small and intermediate tracks were made was much softer than that in which the large track was made. This hypothesis is supported by the wider spreading of the digits (higher angle of divarication, greater width to length ratio of the ichnite) in some of the small footprints and in Paratype I and by the clarity of the impressions of the interdigital webs in PMA P77.17.6.

It therefore seems reasonable to assume that the ridges behind the impressions made by digit III are pressure ridges. Their position indicates that once the digital and metatarsal--phalangeal pads had been impressed into the substrate, the weight of the animal shifted to digit III before the foot was lifted again. At the point of time when the weight of the animal

was concentrated on digit III, this digit was exerting greater pressure on the substrate than the rest of the foot, was impressed deeper into it and thereby displaced more substrate posteriorly as the centre of gravity of the animal passed over and anterior to this point of contact. This sequence may well have occurred only when the dinosaur was proceeding at slow to moderate speeds.

The trackways are narrow and the stride is relatively long. There is no tail drag nor any impression of the manus. This would seem to indicate that *Amblydactylus* was a habitual biped and a reasonably efficient walker. The orientation of the footprint in relation to the midline of the trackway suggests either that the longitudinal axis of the foot was orientated antero-medially, or, more likely, that the longitudinal axis of the animal was undergoing a partial rotation as it took a step forward. If the latter was true, the rotation would have originated from the hip and/or knee rather than the foot since there is no evidence of rotational sliding in the ichnites. If the longitudinal axis of the foot was parallel to the longitudinal axis of the body at rest, the trackways suggest that the body was undergoing a rotation of approximately 30° as the dinosaur took a step forward. The degree of rotation would have varied with the mode of locomotion and probably with the type of substrate on which the animal walked.

It is of interest to speculate concerning the presence of two trackways on the same block (Fig.6). The prints of both trackways are of approximately the same size and type, indicating that the two trackways were made either by the same animal or by two juveniles of the same species and age. Since the ichnites have the same depth and quality of preservation, they must have been made within a relatively short span of time. The odds against a single animal walking twice across the same area within a relatively short span of time, both times going in the same general direction, must be extremely high. It also seems unlikely that two juvenile animals of the same species and size would independently walk across the same spot, proceeding in the same direction, with such a short time span. The most likely explanation is that *Amblydactylus* juveniles were gregarious and that two individuals were proceeding in the same direction together.

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Ross Brand, of the British Columbia Provincial Museum, joined the 1977 expedition and was responsible for the production of a large rubber mould of twenty ichnites in three trackways. Palaeobotanical data was gathered by Jeff Doran of the University of Alberta, geological data by Ron Mussieux of the Provincial Museum of Alberta, Dr. C. R. Stelck of the University of Alberta and the second author.

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