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Vertebrate ichnites from the Boulder Creek Formation (Lower Cretaceous: middle to ?upper Albian) of northeastern British Columbia, with a description of a new avian ichnotaxon, *Paxavipes babcockensis* ichnogen. et isp. nov.

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ABSTRACT

This is the first detailed report of vertebrate tracks from alluvial plain deposits of the Boulder Creek Formation (Lower Cretaceous: middle to ?upper Albian) from outcrop exposures in northeastern British Columbia. Several *in situ* dinosaur tracks observed in vertical section are described, as well as the recovery and description of an isolated track slab discovered in the Boulder Gardens recreation area south of Tumbler Ridge, British Columbia. The vertebrate ichnites consist of three small tridactyl theropod dinosaur prints, one tetradactyl ornithopod print, and 72 small tridactyl tracks of avian affinity which are described as a new ichnotaxon herein. The avian prints are small (under 30 mm length) and are characterised by a large divarication between digits II and III and comparatively lesser divarication between digits III and IV. The pace and stride are short and the pace angulation is high. The tracks are similar to those produced by extant shorebirds and the track-maker likely occupied a similar niche. The avian prints are described herein as a new ichnotaxon, *Paxavipes babcockensis* ichnogen. et isp. nov. Two of the theropod footprints are identified as *Irenichnites gracilis*, an ichnotaxon described in 1932 by C.M. Sternberg from the Lower Cretaceous (Aptian) Gething Formation near Hudson's Hope, British Columbia. One of the *Irenichnites gracilis* prints displays skin impressions associated with the digital pads of digit III and the metatarsal pad. This is the first record of skin impressions from prints of *Irenichnites gracilis*. The ornithopod track is partial and unidentifiable to a particular ichnotaxon, but displays skin impressions on the metatarsal pad and at the base of the second digit impression. The skin impressions from the ornithopod track differ from the *Irenichnites gracilis* skin impressions.

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1. Introduction

The first fossil footprints recovered from the Boulder Creek Formation were discovered in August, 2005 by Curtis Lettely (then a Ph.D. student of the Ichnology Research Group at the University of Alberta) during the course of a preliminary geological investigation in the Boulder Gardens recreational area south of Tumbler Ridge, British Columbia (Fig. 1). This area is within the boundaries of the
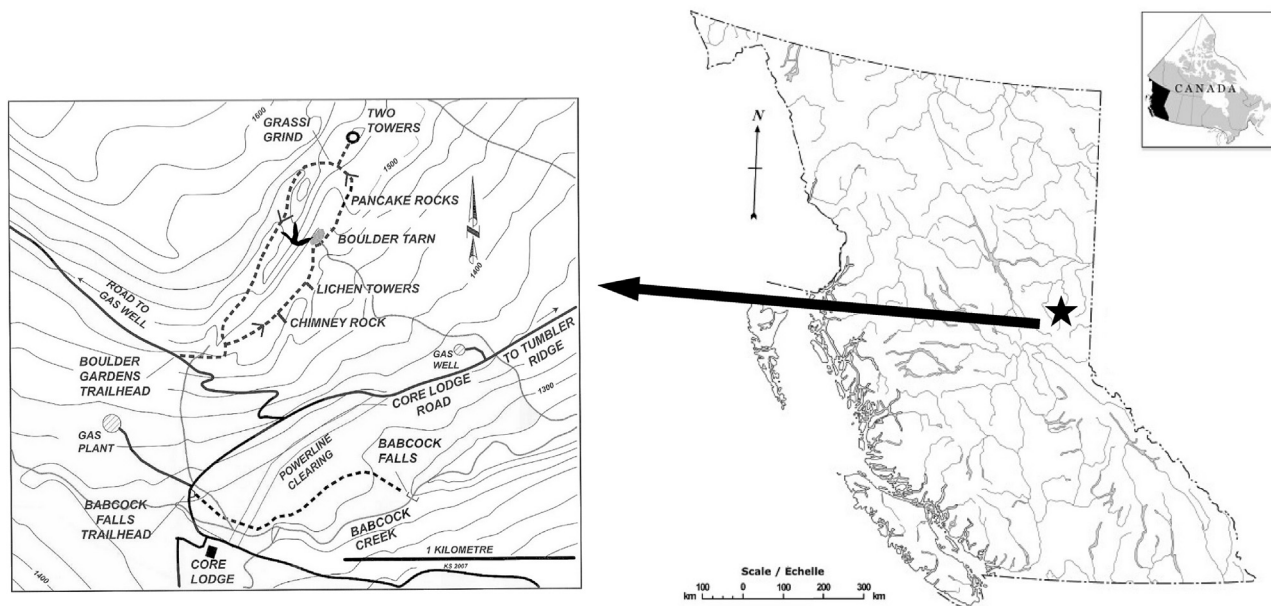
Fig. 1. Map showing the locality (bird track symbol) where the PRPRC 2005.15.001 slab was discovered. Provincial map modified from The Atlas of Canada website (http://atlas.gc.ca/site/html) made freely available via open government licence (http://open.canada.ca/en/open-government-licence-canada). The Boulder Garden trail map was modified from Helm (2008) with written permission of the author.

recently established Tumbler Ridge Global Geopark which is part of the Global Geoparks Network, supported by UNESCO. The slab was discovered embedded vertically and partially buried in the talus and soil at the base of a short, steep cliff. Most of the rocks in the Boulder Gardens recreational area are covered with lichen colonies as was also the case for a portion of the track face of this slab. At the time of discovery only the most distinct avian tracks and two theropod tracks were visible (see Fig. 2 of Buckley and McCrea, 2009).

The track slab was removed to the PRPRC via helicopter on October 4, 2005 and accessioned into the collections (PRPRC 2005.15.001). However, before the tracks could be studied a considerable growth of lichen on the track surface first had to be removed (see 2. Methods below). From observations of the replica cast and the original trackslab (Fig. 2) a trackway map was prepared (Fig. 3). Seventy-two avian prints, three theropod, and one small ornithopod dinosaur prints were mapped. Five avian trackways were discernable with between three to six footprints per trackway (Figs. 3 and 4). The avian prints are unusual in that digit II–III impressions exhibit higher divarications than that observed for digits III–IV, a characteristic that is also found in *Barrosopus slobodai* from Argentina (Coria et al., 2002).

The dinosaur footprints are small and at least two of them (Fig. 5) are identified as *Irenichnites gracilis*, originally described

Fig. 2. A view of a portion of PRPRC 2005.15.001, after cleaning, showing two small, tridactyl theropod tracks (*Irenichnites gracilis* PRPRC 2015.001.073 & 074) and many small tridactyl prints of avian affinity. Scale bar = 10 cm. Numbers correlate to those in the trackway map (Fig. 3).
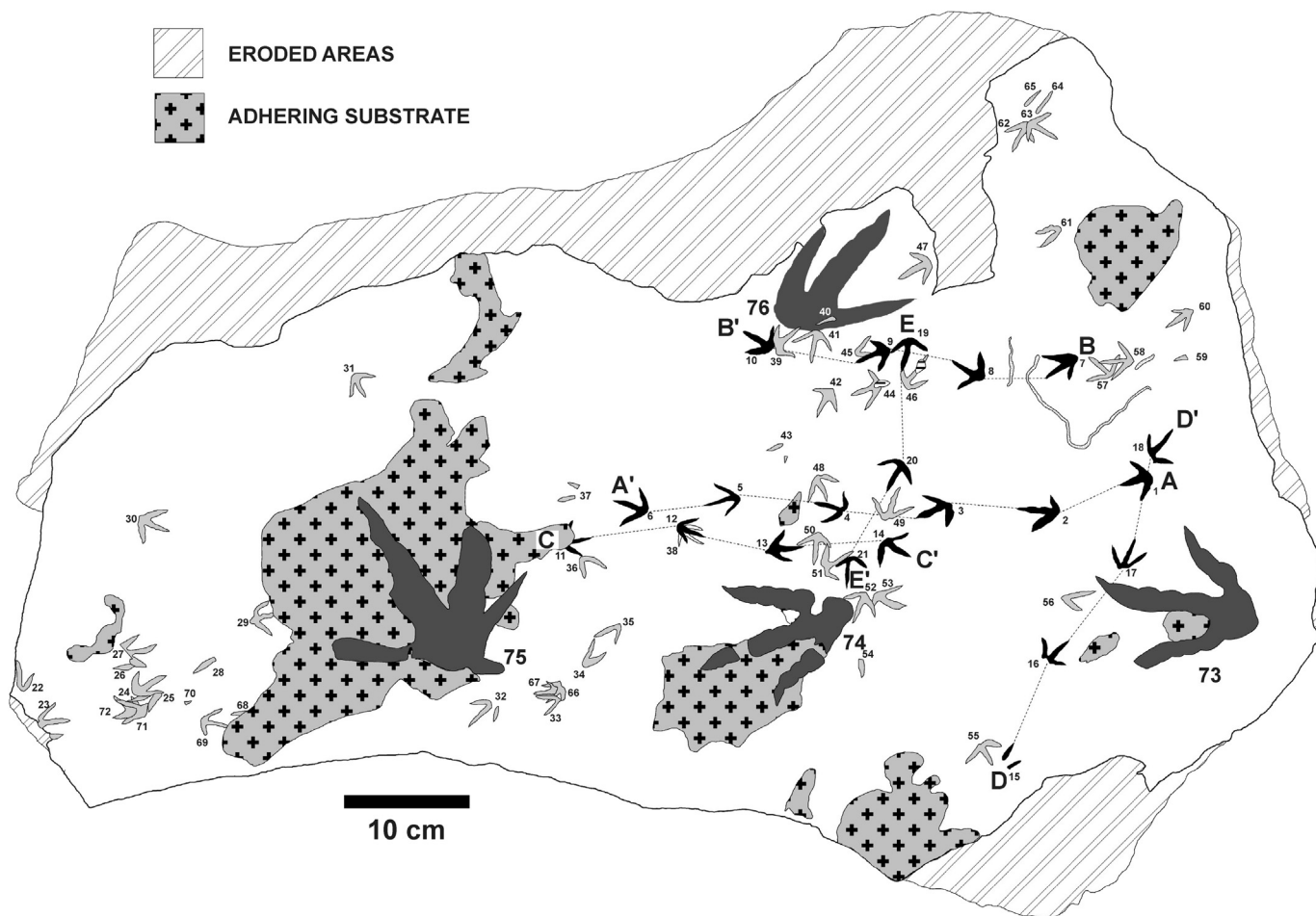
Fig. 3. Trackway Map of PRPRC 2005.15.001. Avian trackways (A–E) are indicated by black shading and connecting lines. The beginning of each trackway is indicated by an uppercase letter (e.g. A). The end of a trackway is indicated with an uppercase letter with an apostrophe (e.g. A′). All footprints are numbered.

by Sternberg (1932). One of the prints of *Irenichnites gracilis* (PRPRC 2005.15.001.074) displays skin impressions on the proximal ends of the digit and the metatarsal pad traces (Fig. 6 A–B). A slightly larger tetradactyl ornithopod print (PRPRC 2005.15.001.075) also has skin impressions with larger skin tubercles.

2. Methods

2.1. Preparation and replication

Extant lichen colonies encrusting the original track specimen were removed using a chemical technique reported by Buckley

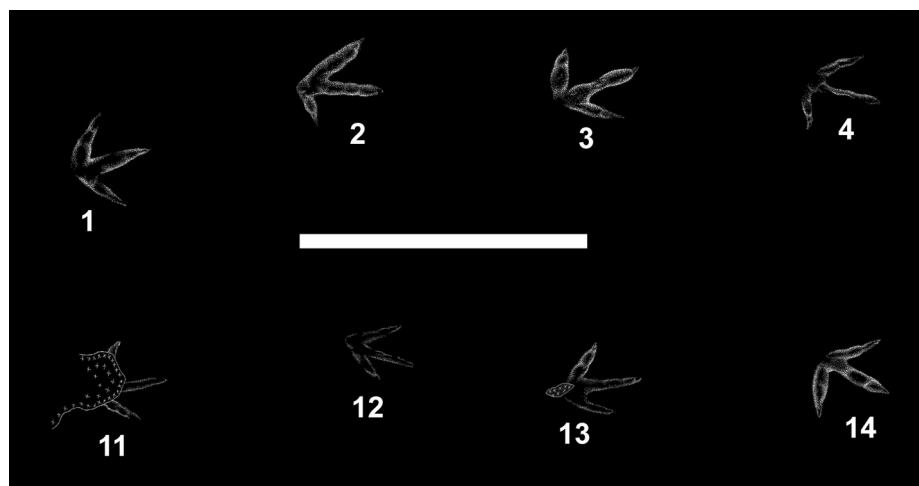**Fig. 4.** Illustration of footprints within two avian trackways from PRPRC 2005.15.001. Top: Footprints from trackway A (Fig. 3). Bottom: Footprints from trackway C (Fig. 3). Scale = 10 cm. Numbers correspond to those in Fig. 3.
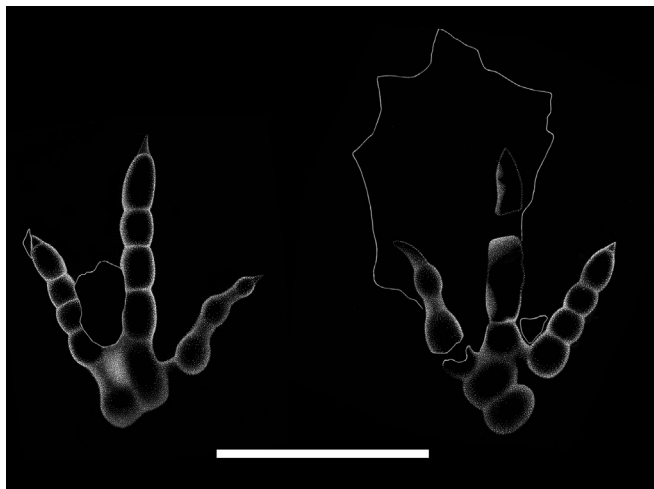
Fig. 5. Illustration of PRPRC 2005.15.001.073 (left image), and PRPRC 2005.15.001.074 (right image). Scale = 10 cm.

and McCrea (2007, 2009). Once the lichen had been removed, a latex 'master' mould of the track surface was made (PRPRC 2005.15.001M), and from this a master cast composed of FGR (fibre-glass reinforced) plaster was prepared (PRPRC.2005.15.001MC).

2.2. Measurements

Measurements (Tables 1 and 2) were taken following the methods of Leonardi (1987) with measurements of footprint length/footprint width (FL/FW) after McCrea and Sarjeant (2001) (Fig. 7). Preparation of the specimen to remove extant lichen colonies was described in Buckley and McCrea (2009).

2.3. Ichnology specimens and data

Multivariate analyses were conducted on track and trackway data collected by the authors for *Paxavipes babcockensis* nov. ichnogen. nov. isp. (PRPRC 2005.15.001), and on data collected by the authors and Coria et al. (2002) for *Barrosopus slobodai* (MCF-PVPH-SB 415-17c). Data presented in Azuma et al. (2002) for *Aquatilavipes izumiensis*, and by McCrea and Sarjeant (2001) for *Aquatilavipes swiboldae* (holotype TMP 1979.023.0037, and specimens TMP 1998.089.0021, TMP 1998.089.0020, and TMP 1990.030.0001) were used as representatives of ichnofamily Avipedidae to compare with the proposed new ichnofamily Paxavipedidae.

2.4. Multivariate analysis materials and methods

Univariate and multivariate (discriminant and canonical variate analyses) were conducted using PAleontological STatistics (PAST) software, version 2.19 (Hammer et al., 2001). Footprint length to footprint width ratio (FL:FW) and total divarication (DIVTOTAL) were not included in analyses so as not to exaggerate the variation contributed to the dataset by FL, FW, and divarication, respectively.

Discriminant analysis projects a multivariate dataset to maximize the separation of two *a priori* determined groups in one dimension (Hammer and Harper, 2006), and is a useful tool for testing hypotheses of morphologic similarity. Using the available data, the analysis attempts to separate individual specimens: in this case, individual footprints from both *Paxavipes babcockensis* and *Barrosopus slobodai*, into the *a priori* determined groups. A 90% or greater correct identification of the individual prints into the two *a priori* categories is sufficient support for the presence of two morphologically distinct groups (Hammer and Harper, 2006). Discriminant analysis was conducted on both isolated tracks and tracks from trackways separated into the ichnotaxonomic groups, *Paxavipes* and *Barrosopus*, respectively. Canonical variate analysis (CVA) performs the same analysis as that of discriminant analysis,

Fig. 6. Left: PRPRC 2005.15.001.074, *Irenichnites gracilis* (10 cm scale with mm divisions). Dark arrows indicate areas with skin impressions. Avian print PRPRC 2005.15.001.052 indicated by a white arrow, is visible adjacent to the posterior portion of the metatarsal pad impression. Right: Magnified view of proximal digit III and metatarsal pad area with skin impressions of PRPRC 2005.15.001.074. Arrows indicate areas with skin impressions. Avian footprint partially visible on the bottom of photograph. Scale in cm and mm.

Table 1
Measurements of avian trackways A-E PRPRC 2005.15.001 (see Fig. 3).

	Print#	FL (mm)	FW (mm)	FR	FL/FW	DL (mm)			DW (mm)			DIV			PL (mm)	SL (mm)	PA (mm)
						II	III	IV	II	III	IV	II—III	III—IV	Total			
Trackway A	1 R	27.6	35.2	17	0.78	24.0	27.6	20.6	5.4	6.1	4.8	51	54	105	–	–	–
	2	32.9	38.6	8	0.85	18.9	32.9	29.3	4.2	5.2	7.1	61	42	103	82.6	–	161
	3	28.8	32.6	24	0.88	20.2	28.8	23.0	5.5	7.1	5.3	58	38	96	89.3	169.0	169
	4	29.5	32.0	17	0.92	18.2	29.5	23.9	4.0	3.3	4.0	63	37	100	83.2	173.0	173
	5	28.3	27.6	14	1.03	19.7	28.3	20.3	3.1	2.2	2.8	42	43	85	88.9	172.0	162
	6	27.9	33.4	19	0.84	20.2	27.9	24.6	3.3	3.9	4.4	55	46	101	74.2	161.0	–
Trackway B	7 R	31.9	28.0	40	1.14	20.1	31.9	24.6	3.1	4.2	7.9	43	33	76	–	–	–
	8	33.6	36.7	25	0.92	22.6	33.6	25.1	4.8	4.4	3.1	61	50	101	75.9	–	157
	9	27.4	–	26	–	17.2	27.4	–	5.3	4.0	–	55	–	–	82.2	154.0	165
	10	28.4	33.2	26	0.87	16.8	28.9	24.1	4.2	4.2	4.7	75	31	106	90.0	172.0	–
Trackway C	11 R	–	29.8	13	–	–	–	–	–	2.8	4.2	55	41	96	–	–	–
	12	23.7	21.0	19	1.13	17.2	23.7	18.2	3.3	4.2	3.3	33	38	71	93.9	–	158
	13	26.8	24.5	11	1.09	19.8	26.8	19.5	4.3	3.8	3.3	47	34	81	77.9	168.0	158
	14	27.3	36.5	30	0.75	21.7	27.3	20.9	5.9	4.9	3.3	67	48	115	93.6	169.0	–
Trackway D	15 R	–	–	0	–	–	–	–	–	3.2	2.4	–	44	–	–	–	–
	16	20.5	27.8	17	0.74	15.1	20.5	18.6	3.4	4.1	2.5	62	56	118	99.1	–	165
	17	27.0	27.1	6	1.0	17.4	27.0	21.5	4.4	3.7	3.6	52	40	92	100.1	197.0	157
	18	27.9	31.6	16	0.88	19.4	27.9	18.0	4.2	3.2	3.1	67	44	111	94.1	190.0	–
Trackway E	19 R	26.6	31.0	0	0.86	18.2	26.6	20.1	3.8	3.4	3.8	71	48	119	–	–	–
	20	27.0	30.3	14	0.89	19.4	27.0	19.2	2.9	3.7	3.8	53	46	99	99.8	–	153
	21	24.4	–	11	–	19.4	24.4	–	4.2	3.7	–	66	–	–	89.6	183.0	–
	Avg.	**27.8**	**30.9**	**17**	**0.92**	**19.2**	**27.8**	**21.8**	**4.2**	**4.1**	**4.1**	**57**	**43**	**99**	**88.0**	**173.0**	**162**

but on three or more *a priori* separated groups. Hotelling's t² results (the multivariate version of a t-test) were provided to show the level of significance of the separations. Significance for both analyses is measured at $p \geq 0.05$.

2.5. Osteology specimens and data

Angles for intertrochlear and plantar displacement were measured from digital photographs taken with a Sony α350 SLR 12.1 megapixel digital camera. Images were edited and angles were measured using Adobe Photoshop 7.0. Intertrochlear angles were measured from the long axes of the intertrochlear grooves of distal metatarsals II and IV, each measured from the intertrochlear groove of metatarsal III, as viewed from the distal end of the tarsometatarsus. Plantar angles were measured from the extensor end of the intertrochlear grooves of distal metatarsals II and IV as viewed from the distal end of the tarsometatarsus, and each angle for metatarsals II and IV were measured from the extensor end of the intertrochlear groove of metatarsal III. Tarsometatarsi were measured for *Charadrius vociferus* (BCPM 00978, BCPM 10760; UAMZ 4931, UAMZ 5663, UAMZ 5751, UAMZ 5752, UAMZ 6787) and *Charadrius semipalmatus* (BCPM 17454, BCPM 23807; CVM 14485) for Charadriidae, and *Actitis macularia* (BCPM 23257; UAMZ 5335, UAMZ 6879), *Calidris alba* (BCPM 18305; UAMZ 6770), and *Calidris melanotos* (CVM 14484, CVM 14556) for Scolopaciidae.

2.6. Interspecific vs. ontogenetic variation in foot size

Discriminant and canonical variate analyses were run with unadjusted linear data. This was done for two reasons. First, there are no visible size classes among the trackways for each ichnotaxon, so

Table 2
Measurements of (isolated?) prints PRPRC 2005.15.001 (see Fig. 3).

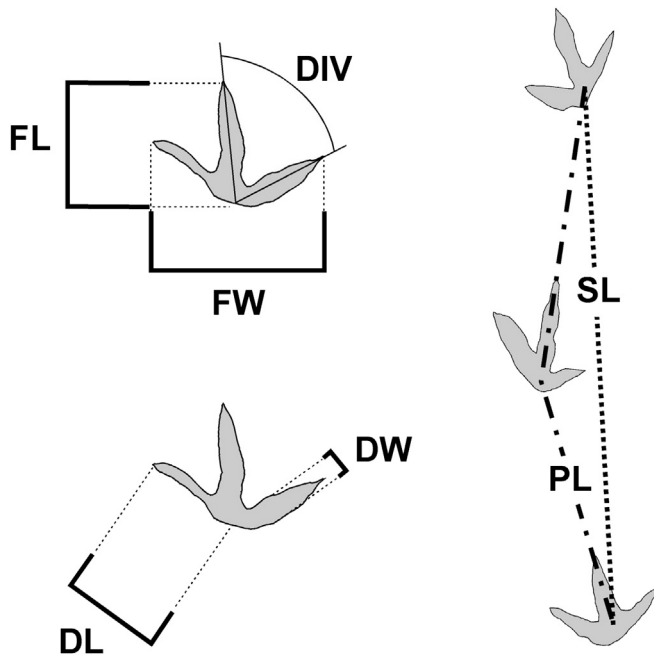| Print#	FL (mm)	FW (mm)	FL/FW	DL (mm)			DW (mm)			DIV		
				II	III	IV	II	III	IV	II—III	III—IV	Total
24 R	30.3	25.5	1.20	19.8	30.3	23.5	5.6	4.4	3.8	47	24	71
30 L	27.2	31.8	0.86	19.7	27.2	23.1	7.2	4.5	4.4	59	36	95
31 R	19.7	24.7	0.80	16.2	19.7	18.1	3.8	2.8	3.2	56	37	93
41 L	25.6	28.2	0.91	18.4	25.6	18.1	2.8	3.3	3.1	53	48	101
42 L	25.2	26.7	0.94	17.7	25.2	18.2	3.9	4.5	3.4	55	41	96
44 L	26.4	30.6	0.86	15.4	26.4	21.7	4.3	3.1	3.3	69	42	111
46 R	31.3	27.5	1.14	18.5	31.3	19.2	3.7	3.1	3.5	51	41	92
47 L	29.7	28.0	1.06	19.0	29.7	21.7	4.5	5.0	4.3	54	37	91
48 R	22.9	29.5	0.78	18.0	22.9	21.7	2.5	3.4	3.7	50	42	92
49 R	28.0	35.7	0.78	24.2	28.0	22.4	3.9	3.8	3.1	57	44	101
50 L	25.3	29.0	0.87	20.2	25.3	18.0	4.4	3.7	3.9	53	46	99
51 L	28.5	30.0	0.95	16.0	28.5	19.3	5.3	4.3	5.3	68	50	118
52 L	28.1	30.5	0.92	19.3	28.1	21.9	3.9	3.8	4.1	52	43	95
55 L	21.9	33.0	0.66	20.1	21.9	18.6	4.6	4.4	4.7	63	51	114
57 L	25.5	37.9	0.67	22.0	25.5	21.1	5.5	4.7	3.3	68	57	125
58 L	24.8	34.4	0.72	21.0	24.8	22.0	4.5	3.4	2.9	67	43	110
60 R	25.7	20.6	1.25	17.7	25.7	16.9	3.3	4.5	3.2	40	35	75
62 R	27.9	26.7	1.04	17.6	27.9	20.7	3.3	3.1	3.2	48	42	90
63 L	27.7	30.5	0.91	15.3	27.7	19.7	3.2	3.0	3.1	64	52	114
Avg.	**26.4**	**29.5**	**0.91**	**18.7**	**26.4**	**20.3**	**4.2**	**3.8**	**3.7**	**57**	**43**	**99**

Fig. 7. Methods of trackway and footprint measurements used in this study. DIV, digit divarication; DL, digit length; FL, footprints length; FW, footprint width; PL, pace length; SL, stride length.

we can assume that all the footprints within each separate ichnotaxon were produced by track-makers that were approximately the same size and/or ontogenetic stage. Therefore, any difference in size between two ichnotaxa is not likely to be ontogenetic. Second, although shorebird young are precocial and their young mature at a slower rate relative to birds with altricial young (Gill, 2007), the young of shorebirds reach maturity quickly: young of *Charadrius vociferus* (Killdeer) leave the nest within 24 h of hatching, and at day 17 the growth curve of chicks asymptotes (Bunni, 1959; Jackson and Jackson, 2000), and the young of *Actitis macularia* (Spotted Sandpiper) reach 82% of their adult wing-tip to wing-tip length at day 15 (Oring et al., 1997). Unless two different size classes of footprints are documented within the sample in question, it is parsimonious to assume that the track-makers of each ichnotaxon are of adult or approaching adult-size. Two avian ichnotaxa that exhibit a significant difference in size may reflect two separate track-making species.

There is a dearth of documentation on postnatal development in digit length, foot length, and allometric growth of pes elements (i.e. phalangeal size) for extant shorebirds. However, postnatal hind limb development (except for pes phalanges) has been documented for both extant (ostrich, emu, rhea, kiwi) and extinct palaeognaths (*Aepyornis* sp., *Dinornis* sp.). *Aepyornis* sp. shows accelerated hind limb growth relative to forelimb development (Balanoff and Rowe, 2007), and Turvey and Holdaway (2005) show that the ossification rates and growth of the hind limbs of *Dinornis* sp. and the growth and ossification of the tarsometatarsii closely follows that of the femorae, which also exhibit accelerated relative hind limb development. Whether extant shorebirds exhibit relatively accelerated pes growth with respect to body size remains to be documented. The rapid attainment of adult body size by many extant shorebirds allows us to assume that, given the equal investment in both cursorial and aerial locomotory modes (Dial, 2003), hind limb and foot length of both extant and extinct shorebirds reached adult body size within several days of leaving the nest.

3. Geological setting, environment and paleontology

There are three terrestrial formations of Albian age in the Peace Region of British Columbia. In ascending order these are the Gates, Boulder Creek and Goodrich Formations. The vertebrate ichnofauna of the middle Albian Gates Formation (western Alberta, and northwestern British Columbia) is well-known (McCrea et al., 2014 and references therein), and although vertebrate tracks have previously been observed in the Boulder Creek and Goodrich Formations (McCrea et al., 2014) they are less well-known. The Gates and Boulder Creek Formations are separated by marine sediments of the Hulcross Formation. The Boulder Creek and Goodrich formations are separated by marine sediments of the Hasler Formation.

3.1. Stratigraphic relationships and age of the Walton Creek Member of the Boulder Creek Formation

In the foothills of British Columbia, the Albian Boulder Creek Formation was defined by Stott (1982) as a sandstone-rich succession that conformably overlay marine mudstone of the Hulcross Formation. Gibson (1992) subsequently divided the Boulder Creek Formation into a lower marine sandstone named the Cadotte Member, and an upper nonmarine unit called the Walton Creek Member. The top of the Cadotte Member is marked by a sharp but commonly pedogenically modified surface, above which lie alluvial and lacustrine deposits of the Walton Creek Member. The Hulcross and Boulder Creek Formations can be traced from the Foothills for >300 km eastward into the subsurface of BC and Alberta, where they are equivalent to the Peace River Formation, the latter being divided into the Harmon, Cadotte and Paddy members in ascending order (Fig. 8).

A recent regional allostratigraphic and sedimentological analysis, incorporating both outcrop and subsurface data (Rylaarsdam, 2006; Roca et al., 2008; Buckley and Plint, 2013), showed that the Cadotte and Paddy members of the Peace River Formation (the Cadotte and Walton Creek members of the Boulder Creek Formation) represent two distinct tectono-stratigraphic episodes (Plint et al., 2012). The Cadotte Member is of broadly tabular geometry and records the northward progradation of an ENE-WSW-trending strandplain during a period when the basin was experiencing a relatively low rate of flexural subsidence. In contrast, the Paddy/Walton Creek member forms a strongly wedge-shaped body that thins from about 125 m thick in the British Columbia Foothills to less than 10 m to the north and east of the town of Peace River, some 300 km to the East.

In subsurface, the Paddy Member was divided into nine allomembers (labelled A–I) on the basis of marine, brackish and lacustrine flooding surfaces (Rylaarsdam, 2006; Roca et al., 2008). Paddy allomembers onlap progressively eastward onto the top of the underlying Cadotte Member. This stratigraphic relationship indicates a temporal break between the top of the Cadotte and the base of the overlying Paddy Member. The magnitude of the stratigraphic hiatus increases eastwards to encompass most of the time represented by the Paddy. Thus, in the vicinity of the town of Peace River, the Cadotte Member is directly overlain by the Paddy allomember G, lower allomembers having lapped out further to the west (Roca et al., 2008).

Roca et al. (2008) concluded, on the basis of subsurface correlations, that the basal transgressive surface of the marine Joli Fou Formation erosively overlay the top of the Paddy Member. However, correlations were not unequivocal, and it is possible that the uppermost few metres of the Paddy Member are laterally intergradational with the basal few metres of the Joli Fou Formation.

The Hulcross Formation is dated as early middle Albian based on the presence of *Pseudopulchellia pattoni* and *Haplophragmoides*
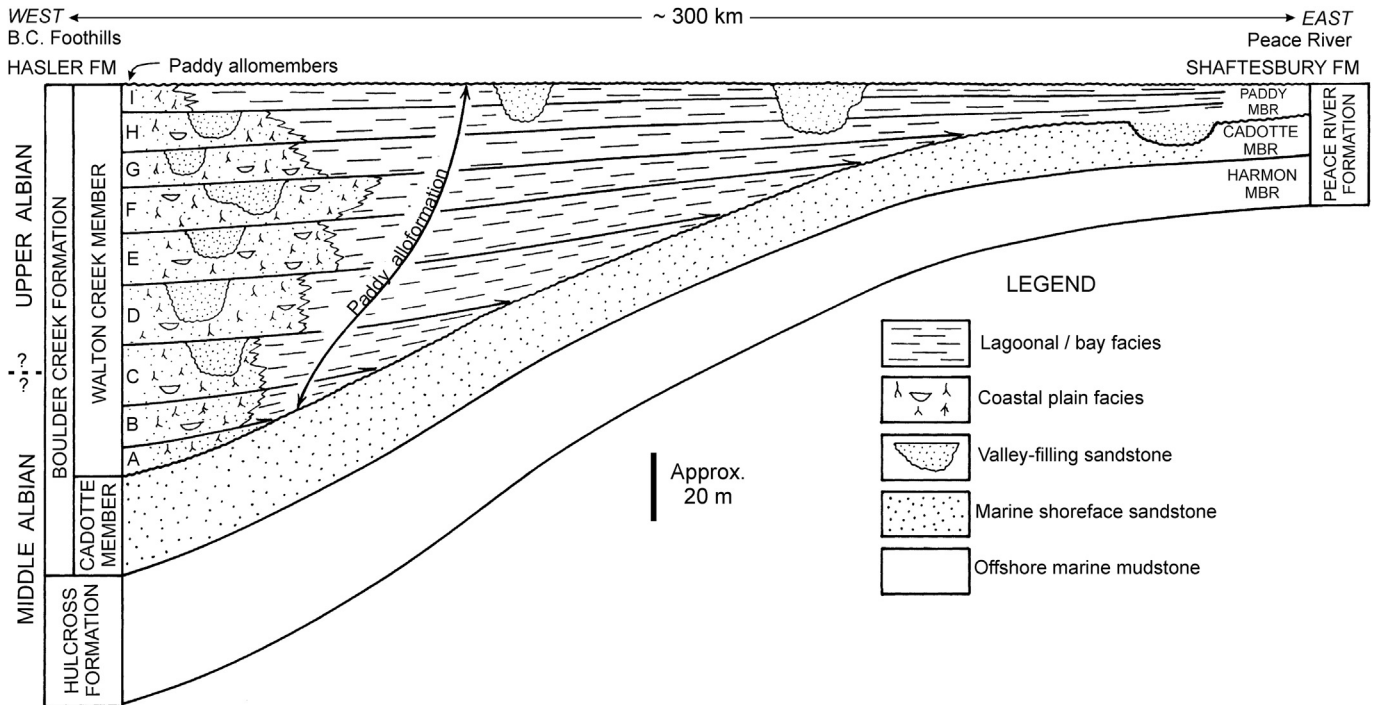
Fig. 8. Summary of stratigraphic relationships between Albian strata in the Rocky Mountain Foothills and the adjacent Plains to the east, Roca et al. (2008).

multiplum, whereas the overlying Cadotte Member contains *Gastroplites kingi*, *Gastroplites allani*, and *Ammobaculites* sp., which are indicative of a late middle Albian age (Caldwell et al., 1993). Because diagnostic marine fossils are largely absent from the Walton Creek and Paddy strata, their age is not well-constrained. Near the town of Peace River, strata high in the Paddy Member (Paddy allomember PH in the allostratigraphic scheme of Roca et al., 2008), contain *Inoceramus comancheanus* (Leckie and Singh, 1991). This bivalve is also common in the Joli Fou Formation, and is indicative of an early late Albian age. By inference therefore, the age of the Walton Creek and Paddy strata therefore ranges from late middle Albian to early late Albian (Fig. 8).

3.2. Facies and depositional environments of the Paddy/Walton Creek Member

As this paper is concerned solely with outcrop material, we refer the track-bearing rocks from the Boulder Gardens to the Walton Creek Member, although Roca et al. (2008) used the term "Paddy Member" to encompass both outcrop and subsurface rocks. Space permits only a very brief summary of the main facies and depositional environments, based on results in Rylaarsdam et al. (2006).

In broad terms, the Walton Creek Member is primarily of non-marine aspect in the British Columbia Foothills, with only minor evidence of brackish and tidal conditions. Towards the east, in subsurface, the Walton Creek/Paddy rocks show progressively more evidence of deposition in shallow, brackish-water bays and low-energy deltaic environments. This lagoonal/deltaic association grades northward into sandstones suggestive of a marine shoreface environment, which in turn passes further northward into offshore mudstones and sandstones with abundant hummocky cross-stratification indicative of significant storm wave influence (Buckley, 2011; Buckley and Plint, 2013).

In the British Columbia foothills, dark grey to black, laminated, non-bioturbated mudstone, in places interbedded with thin beds of fine-grained siltstone or sandstone, forms upward-coarsening units up to 5 m thick. Plant debris, logs of wood and centimetre-scale bands of siderite concretions are common. This facies probably represents shallow vegetated floodplain lakes in which upward-coarsening reflects gradual shallowing. Diffuse punch-down structures are present in this facies, usually near the top of the succession and can be attributed to dinosaurs walking in very soft, non-cohesive sediment (Fig. 9).

Lacustrine mudstones are commonly interstratified with units of dark grey silty clay to siltstone that may be well-laminated, poorly-laminated or massive, the latter having a fine, blocky-weathering appearance. Units are typically 1–3 m thick and can extend hundreds of metres laterally. Upper and lower contacts are usually gradational. Carbonaceous roots are sparse to abundant, but few well-developed paleosols are present. Nodular and spherulitic siderite is also very common. Coals, typically <50 cm thick, are associated with this facies but are not common. This facies represents poorly-drained, vegetated, rapidly-aggrading floodplains (McCarthy and Plint, 1999; McCarthy et al., 1999). Abundant spherulitic siderite indicates bacterially-mediated reducing conditions within the sediment, and a high ground-water table. Rare, sandstone-filled cracks attest to periods of lowered water table and desiccation.

Sheet-like units of very fine-to medium-grained sandstone, typically 10–50 cm thick and 50 to >100 m in lateral extent are interstratified with floodplain mudstone. Sandstone sheets typically have an abruptly gradational or sharp basal contact, and are commonly current-rippled or, rarely, cross-stratified. Roots are ubiquitous, and plant debris, including well-preserved leaves of both angiosperms (magnolia/tulip tree) and gymnosperms (ginkgo) is locally abundant. In some instances these sheet sandstones can be traced to the margins of lenticular, channel-filling sandstones and hence can readily be interpreted as crevasse splay deposits. Splay sandstones are commonly organized in groups of 3–15, separated by centimetre to decimetre thick mudstone beds.

Fig. 9. Dinosaur punch-down structure in thinly-bedded, unconsolidated lacustrine mudstone. Bedded units highlighted. Quintette mine access road, scale bar = 20 cm.

Dinosaur tracks impressed into floodplain mudstone are commonly preserved as natural casts on the basal surfaces of crevasse sandstones (Fig. 10). In other instances, crevasse sandstone beds are punched downward into coaly floodplain mudstone (Fig. 11).

Lenticular, erosive-based bodies of fine-to coarse-grained, current rippled and cross-bedded sandstone are typically 2—5 m thick and <20 m wide. The basal surface is scoured and overlain by a lag of mudstone intraclasts, pebbles and logs. These units are readily interpreted as channel-fills. The channel-fills show little evidence of lateral migration, in the form of lateral-accretion surfaces, and are interpreted as the fills of non-migrating, possibly anastomosed rivers. Anastomosed rivers typify alluvial plains of extremely low gradient (Makaske, 2001; Lumsdon-West and Plint, 2005). Rarely, channel-fills show well-developed lateral-accretion surfaces and are interpreted as meandering river deposits, suggestive of somewhat steeper alluvial gradients.

The background suite of alluvial facies described above is locally replaced by bodies of medium-grained sandstone to fine-grained conglomerate that are up to 25 m thick, a few hundred to a few kilometres wide, that have a strongly erosive base and are recognizable both in outcrop and in well-log cross-sections. These sandstone bodies are typified by decimetre to metre-scale cross-bedding, numerous internal erosion surfaces and large-scale accretion surfaces. These large sandstone bodies are interpreted to have been deposited by braided rivers confined to paleo-valleys.

The preponderance of sideritic and carbonaceous floodplain deposits, shallow lakes and immature paleosols provide evidence that the Walton Creek/Paddy rocks were deposited primarily under conditions of rapid tectonic subsidence that favoured development of a low-gradient alluvial plain characterized by shallow lakes,

poorly-drained floodplain soils and rapid aggradation resulting from frequent overbank flooding. Abundant roots and detrital plant material indicate that the alluvial plain was heavily vegetated, providing food and habitat for dinosaurs, birds, and other vertebrates (turtles, crocodilians, etc.). The pronounced south-westerly thickening wedge shape of the Walton Creek/Paddy rocks provides clear supporting evidence of strongly asymmetrical subsidence adjacent to the Cordilleran fold and thrust belt. In contrast to the fine-grained floodplain deposits, sandstones and conglomerates filling paleo-valleys suggest phases of alluvial incision, possibly related to tectonic uplift, increased fluvial discharge, and/or sealevel fall.

3.3. Context and characteristics of the track-bearing block (PRPRC 2005.15.001)

Specimen PRPRC 2005.15.001 was recovered from the Boulder Gardens recreational area at the base of a cliff on the southeastern slope of Mount Babcock, 24 km south of the town of Tumbler Ridge, British Columbia. The original track slab (PRPRC 2005.15.001) is a natural cast (counter slab) and only small portions of the original, track-bearing surface still adhere to this specimen (Fig. 3). From observations based on the surviving counter slab, the original surface on which the tracks were registered was evidently fine-grained, organic-rich sand covered with a fine organic-rich mud drape. The surface was not uniform in topography at the time the tracks and trackways were registered. There are distinct undulations observable on the surface, which indicate that the sedimentary surface had original topography, as opposed to being the result of post-depositional effects. Original areas of high

Fig. 10. Large tridactyl track impressed into floodplain mudstone and preserved as a natural cast at the base of a crevasse splay sandstone. Bedded units highlighted. Mount Spieker, scale bar = 20 cm.

topography were drier and mud-cracked, and the surface sediments were relatively hard. In contrast, the sediment surface areas of original low topography were damper, softer, and the footprints are more deeply impressed, (Fig. 12).

These undulations are unlikely to be due to post-depositional processes as evidenced by observations of the sediments themselves and by the distribution and preservation of the footprints. The regions of the track slab that preserve evidence of relatively low topography (preserved as high-topography on the counter slab) are where the most deeply-impressed and best-preserved avian prints are found. Conversely, the topographically higher areas (preserved as topographically low areas on the counter slab) possess avian footprints that are only faintly impressed and are less well-preserved. This difference in depth of impression between the topographically high (shallow prints) and low (deep prints) areas of the track slab has been observed within single avian trackways (A, C & E). Topographically low regions also show evidence of sinusoidal invertebrate traces (repichnia, *Cochlichnus* isp.), probably made by nematode worms (Figs. 3 and 13), whereas topographically high areas do not. Additionally, the sedimentary surface in the topographically high areas show small, but distinct desiccation cracks, features that are absent in the topographic lows. From these observations it is evident that, prior to burial, the original track surface possessed topography, possibly ripple-marks. The sediments in the original topographically high areas were dewatered to the point that mud cracks formed and the surface became more resistant to registering avian footprint impressions. The sediments in the topographic lows were either partially saturated with water or even sub-aqueous, possibly forming small pools. The sediments in the

topographic low areas were not resistant to registering avian footprint impressions or even very small worm traces referable to *Cochlichnus* isp. (Hitchcock, 1858).

The track slab was discovered out of context at the base of a cliff face many tens of metres high and could have originated from any point on that face. Most of the sediments in the immediate area are massive, medium-grained sandstones with little organic content. They differ considerably from the sediments that form the track slab. However, exploration along the accessible areas of the cliff face showed small lenses of fine-grained organic-rich sediments within the predominantly coarse-grained sediments. It is possible that the track slab may be a remnant of such a lens.

4. Ichnotaxonomy

Class Aves

Subclass uncertain

Ichnofamily Paxavipedidae ichnofam. nov.

Description. Small tridactyl avian footprints with digit traces united proximally with the metatarsal pad and lacking webbing and hallux. Divarication between digit II and digit III traces greater than that between digit III and digit IV. Trackway characters consistent with a small, short-legged track-maker.

Type Ichnogenus. Paxavipes McCrea et al., herein

Referred specimens. Barrosopus slobodai, Coria et al., 2002.

Ichnogenus *Paxavipes* ichnogen. nov.

Fig. 11. An intensely deformed crevasse splay sandstone that has been punched downward into an underlying coaly mudstone. The deformed bed is erosively overlain by an undeformed, current-rippled crevasse-splay sandstone. Bedded units highlighted. Whatley Creek, scale bar = 20 cm.

Derivation of name. Pax = peace [region], for the Peace Region of British Columbia where the specimen was discovered; avi-, bird, -pes, suffix identifying this as a trace.

Holotype. PRPRC 2005.15.001.014 and PRPRC 2005.15.001.014MC, single natural cast print and trackway C (PRPRC.15.001.011-014 inclusive), *Paxavipes babcockensis* McCrea et al., herein. Lower Cretaceous (middle Albian) of northeastern British Columbia, Canada.

Paratypes. Trackway A PRPRC 2005.15.001.001-006 inclusive, Trackway B PRPRC 2005.15.001.007-010 inclusive, Trackway D PRPRC 2005.15.001.016-018 inclusive.

Included ichnospecies. The ichnogenus is only known from the type ichnospecies.

Type Locality. Boulder Creek Formation: The Walton Creek Member (Lower Cretaceous: middle to ?late Albian), Mount Babcock, south of Tumbler Ridge. Precise locality on file at the Peace Region Palaeontology Research Centre.

Diagnosis. Trackway of a biped consisting of small tridactyl prints, without webbing and hallux. Individual footprints are generally wider than long (FL ~ 27 mm; FW ~ 30 mm); FL/FW ratio approximately 0.91. Divarication between digit traces II—III consistently greater than that between digits III—IV. Inward rotation of pes pronounced.

Description. Trackway of a small biped lacking hallux or web traces, and with divarication angles between traces of digits II

and III averaging 57° and greater than the divarication angles between digits III and IV which average 43°. Tracks averaging 2.7 cm long and 3.0 cm wide (range 2.0 cm—3.4 cm and 2.1 cm — 3.9 cm, respectively). All digit traces are narrow (around 4 mm thick) approximately 22% of the length of digit II, 15% of length of digit III and 19% of digit IV length. Digital pads are evident on some tracks, but are not consistently preserved. There is pronounced inward rotation of prints towards the midline of the trackway. The trackway is narrow with short pace and stride.

Ichnospecies *Paxavipes babcockensis* isp. nov.

Derivation of name. The specific name refers to Mount Babcock where the type specimen was discovered.

Holotype. The fourth footprint of trackway C (PRPRC 2005.15.001.014) of the original block and PRPRC 2005.15.001.014MC, the fibreglass reinforced (FGR) plaster replica. Lodged at the Peace Region Palaeontology Research Centre, Tumbler Ridge, British Columbia.

Paratypes. Trackway A PRPRC 2005.15.001.001-006 inclusive, Trackway B PRPRC 2005.15.001.007-010 inclusive, Trackway D PRPRC 2005.15.001.016-018 inclusive. Prints in trackways A, B C as above located on PRPRC 2005.15.001MC, the fibreglass reinforced (FGR) plaster replica.

Type Locality. as for ichnogenus

Diagnosis. as for ichnogenus

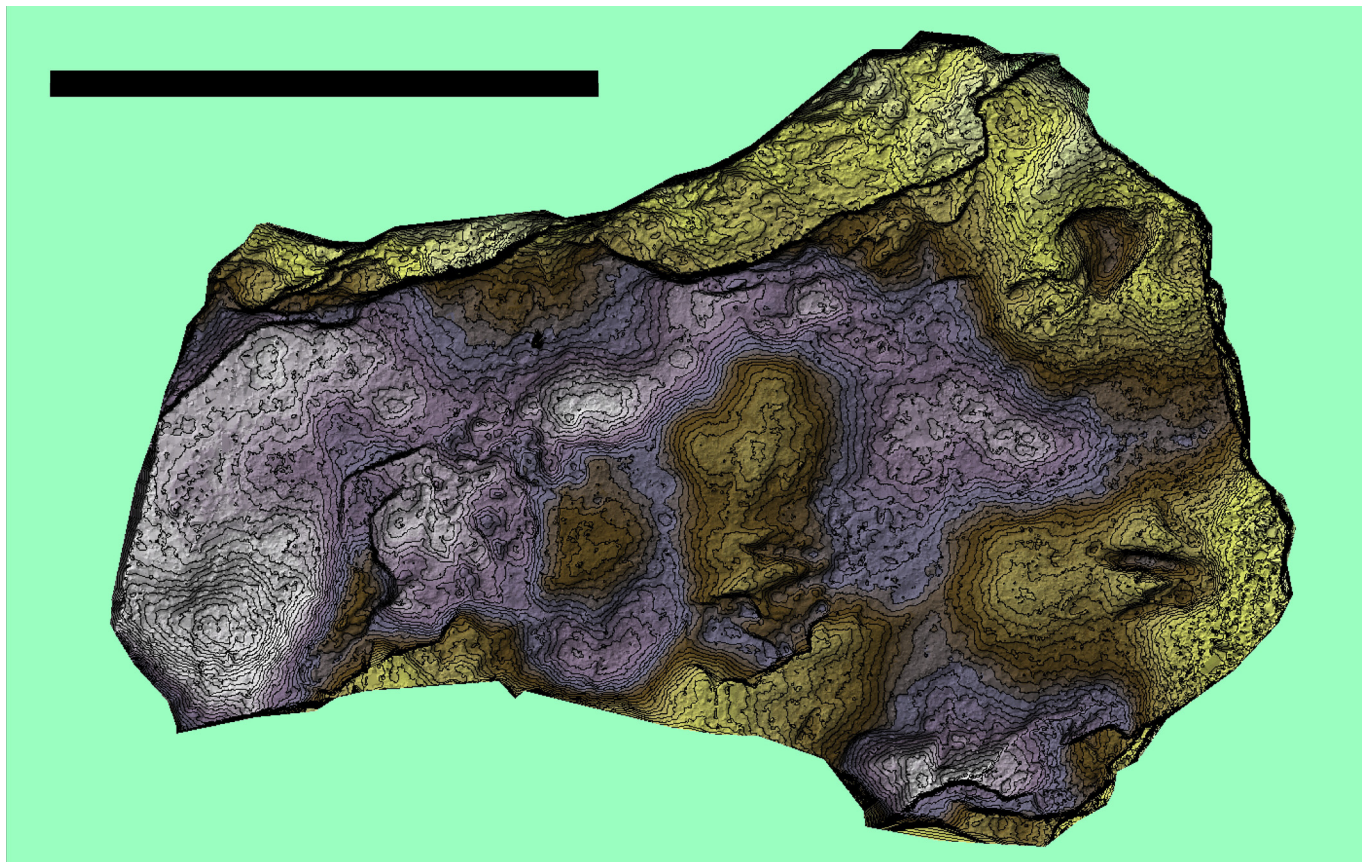*Description. as for ichnogenus*

Fig. 12. Photogrammetric image of the PRPRC 2005.15.001 track block showing variation in topography of the track-bearing surface. Note that this image is of a natural cast and so the types of relief (low to high) were reversed on the original track surface. Scale = 50 cm. Contour interval is 1 mm.
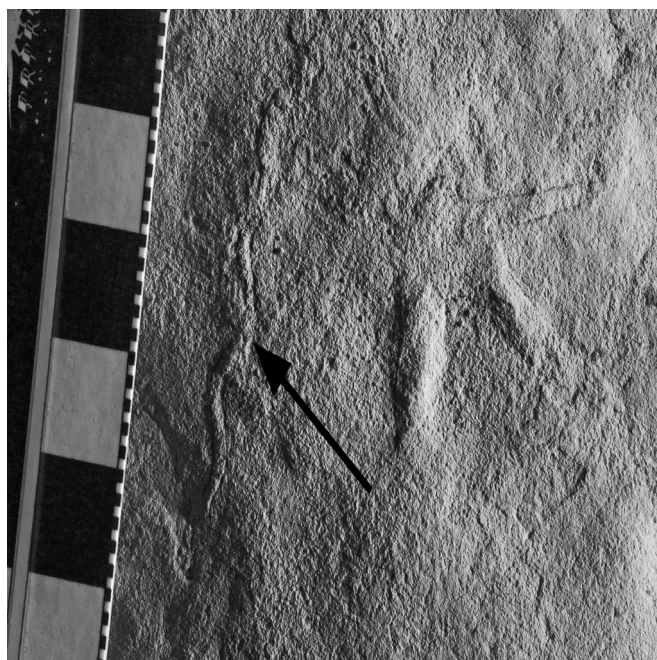

Fig. 13. Possible nematode worm trace (*Cochlichnus* isp.) to the left of a faint avian (*Paxavipes babcockensis* nov. ichnogen. nov. isp.) print (PRPRC 2005.15.001.008). Scale in cm and mm.

Remarks. Paxavipes babcockensis nov. ichnogen. nov. isp. trackways were evidently produced by small short-legged birds. *Paxavipes babcockensis* prints are produced by birds with only three pedal digits with no webbing evident and greater divarication between digits II and III than that between digits III and IV (characters shared with *Barrosopus slobodai*).

Paxavipes babcockensis is similar to *Barrosopus slobodai* (Coria et al., 2002) in many respects, including general size and especially in the high divarication between digits II and III as compared with III and IV. However, *Paxavipes babcockensis* digits are joined proximally via a metatarsal pad which is absent in specimens of *Barrosopus slobodai*, although this may be due to circumstances of preservation.

Barrosopus slobodai footprints show a significantly higher total divarication and trackways have slightly greater pace and stride lengths than those of *Paxavipes babcockensis*. Digit widths of *Paxavipes babcockensis* are more uniform (all close to 4 mm) than those of *Barrosopus slobodai* prints. The outer digits of *Barrosopus slobodai* and *Paxavipes babcockensis* are both shorter than the middle digits, however, the outer digits of *Paxavipes babcockensis* have a greater equality in length than those of *Barrosopus slobodai* where digit IV is longer than digit II and almost as long as digit III.

Barrosopus slobodai and *Paxavipes babcockensis* are similar enough to both be included within the same ichnofamily, but are distinct enough to merit discrimination at the ichnogeneric level. They are

among the smallest avian tracks known from the Mesozoic, although in the size range of *Koreanaornis* (Kim, 1969). However, *Koreanaornis* sometimes registers a small hallux trace, and different divarication morphology (Lockley et al., 1992, 2012).

Barrosopus slobodai and *Paxavipes babcockensis* prints can be distinguished from all other described avian ichnotaxa based on the trait they share in having consistently higher divarication between digits II and III than is found between digits III and IV while lacking visible webbing and hallux impression. There are avian ichnotaxa that do display a consistently higher divarication between digits II and III than digits III and IV; however, these ichnotaxa also display a prominent digit I (*Ignotornis yangi* Kim et al., 2006; *Ignotornis gajiensis* Kim et al., 2012) or display prominent webbing and are larger than *Paxavipes* and *Barrosopus* (*Gyeongsangornipes lockleyi* Kim et al., 2013).

The record of fossil avian tracks and the number of avian ichnotaxa has increased considerably in the past few years, particularly in Asia (Matsukawa et al., 2006; Lockley and Harris, 2010: Lockley et al., 2012). There are now several described avian ichnotaxa from Mesozoic and Cenozoic deposits worldwide. Where trackways exist these can be generally divided in to morphotypes indicating long-legged and short-legged ichnotaxa, each of which can be further sub-divided into categories based on numbers of digits, divarication between digit traces and the presence or absence of webbing. However presence or absence of webbing may be influenced by substrate: for example, traces of extant *Branta canadensis* (Canada Goose, replicas PRPRC NI2009.009, PRPRC NI2014.004) display webbing traces in those prints made in soft, water saturated substrate, while on firm or drier sediment webbing traces are not preserved. As the presence of webbing is highly variable due to substrate conditions we do not consider this a reliable character; however, there are some exceptions. In the case of a few distinctive ichnotaxa such as *Uhangrichnus* isp., and *Presbyornithiformipes* isp., clear web traces have been consistently documented (see Lockley and Harris, 2010 for summary). Likewise, the webbing preserved in some ichnotaxa, such as *Sarjeantopodus* (Lockley et al., 2004) is diagnostic (contra Falkingham et al., 2009) and cannot be dismissed as unusual extramorphological preservation. In short, webbing is a useful character when present, but given its tendency to be inconsistently preserved it should not be the sole character used to differentiate among avian ichnotaxa.

The diagnoses of new ichnotaxa are sufficiently detailed to enable researchers to discriminate between two morphologically similar ichnotaxa. However, some of the earliest diagnoses of avian ichnotaxa are too general (i.e. *Avipeda* isp.) and are in need of future emendation, a task which is beyond the scope of this study. (Buckley et al., 2012; Buckley et al., in press; Lockley and Harris, 2010; McCrea et al., 2014).

Nearly all tridactyl semipalmate avian ichnotaxa described to date either possess nearly equal divarications between digits II—III and III—IV, or have higher divarications between digits III—IV and lower divarications between digits II and III (Buckley et al., 2012; Buckley et al., in press). The proportionally higher divarications between digits II—III consistently found in *Barrosopus* and *Paxavipes* prints make it obvious to distinguish these avian ichnotaxa from others that have been described to date. The high divarication between digits II—III observed in *Barrosopus* and *Paxavipes* may be due to the presence of a distinct osteological feature that is unique to the track-maker of these ichnogenera. Observationally, prints of *Paxavipes* are remarkably similar to those produced by extant members of Charadriiformes, particularly those of the modern Killdeer

(*Charadrius vociferous*) (Elbroch and Marks, 2001; see 5. Ichnomorphology and osteology).

4.1. Comparing Paxavipes to Barrosopus

A reported ichnotaxon with similar divarication to that of *Paxavipes babcockensis* nov. ichnogen. nov. isp. is *Barrosopus slobodai* from the Cretaceous (Campanian) Argentina (Coria et al., 2002). *Paxavipes babcockensis* possesses a significantly larger divarication between digits II—III than between digits III—IV ($p < 0.0001$). This divarication condition is similar to that of *Barrosopus slobodai* of Argentina (the sample of which is too small to test for a significant difference between digit divarications), although it is not temporally equivalent to *Paxavipes babcockensis* (Early Cretaceous: Albian). It is necessary to determine whether there is a significant quantitative morphologic difference between the *Paxavipes babcockensis* and *Barrosopus slobodai* tracks, as well as establishing the ichnofamily Paxavipedidae as distinct from ichnofamily Avipedidae. Multivariate analyses were used to test the qualitative separation between tracks of *Paxavipes babcockensis* and *Barrosopus slobodai*, and to demonstrate quantitative support for the novel ichnofamily Paxavipedidae as distinct from Avipedidae.

4.2. Discriminant analysis

Discriminant analyses on linear (footprint length and width, digits II—IV lengths and widths, pace and stride lengths) and angle data (digit divarication II—III and III—IV, pace angulation, footprint rotation) demonstrates that footprint groups formed by *Paxavipes babcockensis* and *Barrosopus slobodai* are significantly different ($p_{same} = 1.72 \times 10^{-03}$) with a 91.9% correct placement of individual footprints into the *a priori* groups of "*Paxavipes*" and "*Barrosopus*" (Fig. 14). Separate discriminant analyses on linear footprint and trackway data ($p_{same} = 6.14 \times 10^{-05}$; 91.8% separation) reveals a similar significant separation, while analysis on divarication and footprint angle data alone ($p_{same} = 0.618$; 56.3% separation) do not show significant separation between the prints of *Paxavipes babcockensis* and *Barrosopus slobodai*.

4.3. Separating Paxavipedidae and Avipedidae

The establishment of the ichnofamily Paxavipedidae is supported with both discriminant (Paxavipedidae vs. Avipedidae) and canonical variate (all ichnospecies separate) analyses. Discriminant analyses comparing Paxavipedidae (*Paxavipes babcockensis* and *Barrosopus slobodai*) to Avipedidae (*Aquatilavipes swiboldae*, *Aquatilavipes izumiensis*) show that 91.7% of all footprints were correctly identified to their assigned ichnofamilies and are significantly different ($p_{same} = 1.98 \times 10^{-26}$, Fig. 15).

Canonical variate analyses (CVA) on data from the four ichnotaxa (excluding pace and stride measurements due to a large amount of missing data) shows that all four ichnotaxa are significantly different (Table 3, Fig. 16). Interestingly, *Aquatilavipes izumiensis* is almost isolated in morphospace from *Aquatilavipes swiboldae*, *Barrosopus slobodai*, and *Paxavipes babcockensis*. Examination of the data reveals that *Aquatilavipes izumiensis* has a much larger mean DIVIII—IV relative to DIVII—III when compared to *Aquatilavipes swiboldae*, *Barrosopus slobodai*, and *Paxavipes babcockensis* (Table 4).

5. Ichnomorphology and osteology

5.1. Digit divarication and osteology

One of the diagnostic characters of both *Paxavipes babcockensis* and *Barrosopus slobodai* (Paxavipedidae) is the possession of a
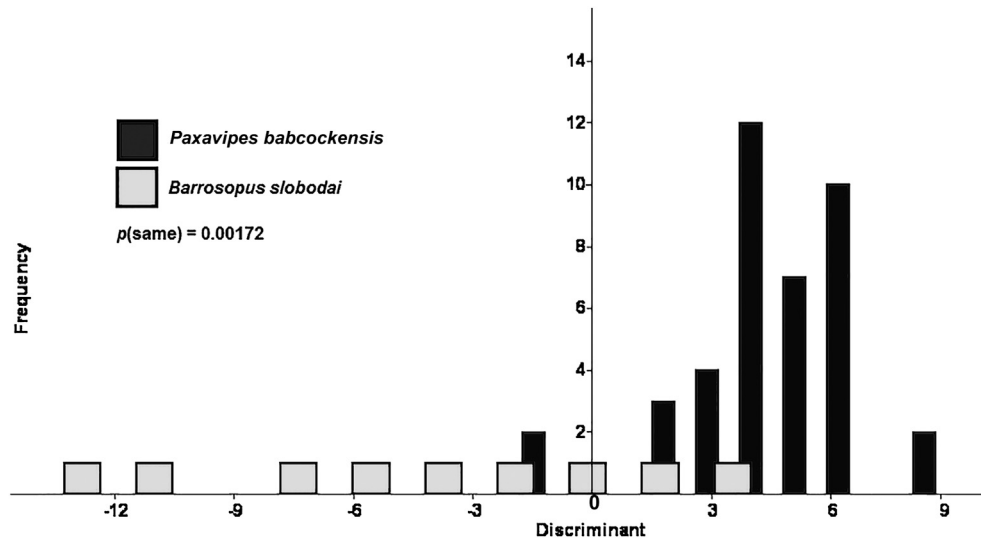
Fig. 14. Discriminant analysis comparing *Paxavipes babcockensis* (black) with *Barrosopus slobodai* (grey) using data from footprint length, footprint width, digit lengths, digit widths (D-II, D-III, D-IV), divarication (DIV II–III, DIV III–IV), pace length, stride length, pace angulation, and footprint rotation. The percentage of individual footprints correctly assigned to *Paxavipes babcockensis* and *Barrosopus slobodai* is 91.8%, indicating that the two track morphologies are distinct.

much larger digit divarication II–III than that of III–IV. Because this feature is consistent among all footprints of *Paxavipes babcockensis*, this particular divarication condition is probably due to the morphology and relative position of distal metatarsals II, III, and IV, rather than an artifact of sediment-digit interaction. The medio-lateral width of the intertrochlear notches between the distal ends of metatarsals II–III and III–IV (incisurae intertrochlearis medialis et lateralis, Baumel and Witmer, 1993), and the degree of plantar displacement of the distal ends of metatarsals II and IV from the saggital plane of the tarsometatarsus, should influence digit divarication.

Extant shorebirds provide modern analogs to investigate a possible osteological explanation for digit divarication in fossil avian footprints. However, unless there are observable differences between the tracks of extant shorebirds, it is fruitless to hypothesize on osteological causes of digit divarication conditions for extant shorebirds. Elbroch and Marks (2001) field guide to modern bird tracks and traces includes line drawings of the tracks of several species of modern shorebird. Using the same techniques to measure digit divarication as were used to document the tracks of *Paxavipes babcockensis* nov. ichnogen. nov. isp., digit divarications were measured from the line images of tracks of plovers
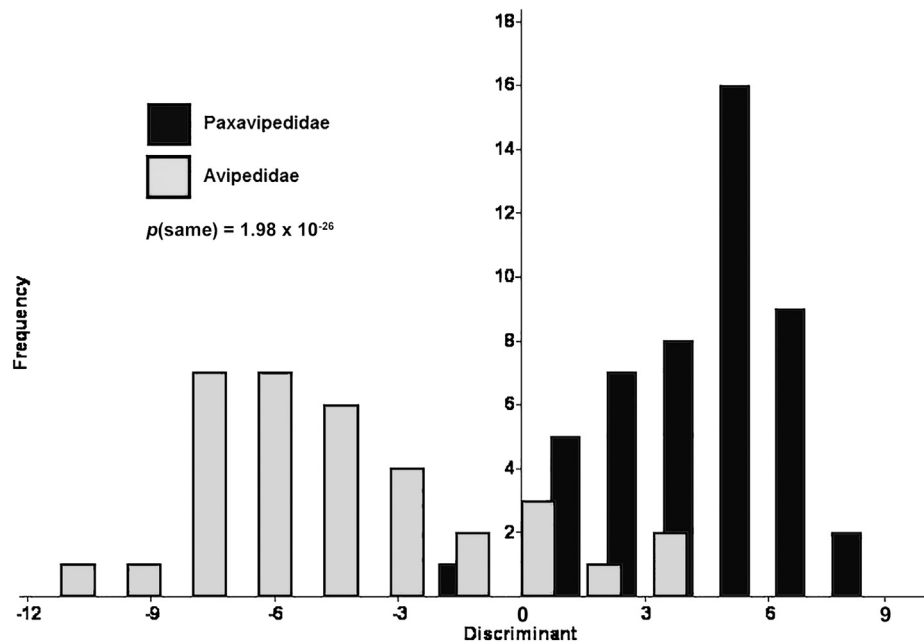

Fig. 15. Discriminant analysis on Avipedidae (*Aquatilavipes swiboldae*, *Aquatilavipes izumiensis*, grey) and the proposed Paxavipedidae (*Paxavipes babcockensis*, *Barrosopus slobodai*, black), using footprint length, footprint width, digit lengths (D-II, D-III, D-IV), and digit divarication (DIV II–III, DIV III–IV). Trackway measurements were excluded given the large amount of missing or unreported data. The two groups are significantly different ($p_{same} = 1.98 \times 10^{-26}$), and 91.6% of individual footprints were correctly assigned to either Paxavipedidae or Avipedidae, respectively.

Table 3

Canonical variate analysis p_{same} results for footprint length (FL), footprint width (FW), digit lengths (DLII, DLIII, DLIV) and divarications (DIVII–III, DIVIII–IV) of *Paxavipes babcockensis*, *Barrosopus slobodai*, *Aquatilavipes swiboldae*, and *Aquatilavipes izumiensis*. All ichnospecies are significantly different from one another, although visually *Aquatilavipes swiboldae* groups more closely in morphospace with *Barrosopus slobodai* and *Paxavipes babcockensis* (Fig. 16): this is due to the much larger DIVIII–IV than DIVII–III in *Aquatilavipes izumiensis* (Table 4).

	Paxavipes	Barrosopus	A. swiboldae	A. izumiensis
Paxavipes	–	1.49×10^{-03}	1.01×10^{-11}	8.45×10^{-22}
Barrosopus	1.49×10^{-03}	–	0.0211	2.31×10^{-06}
A. swiboldae	1.01×10^{-11}	0.0211	–	4.38×10^{-11}
A. izumiensis	8.45×10^{-22}	2.31×10^{-06}	4.38×10^{-11}	–

Table 4

Comparison of the mean divarications DIV II–III and DIV III–IV of *Aquatilavipes* (*Aquatilavipes izumiensis*, Azuma et al., 2002; *Aquatilavipes swiboldae*, McCrea and Sarjeant, 2001) to *Barrosopus slobodai* (Coria et al., 2002) and *Paxavipes babcockensis* nov. ichnogen. nov. isp. The mean divarication values show the main difference between the prints of Avipedidae and Paxavipedidae: that DIV II–III in Paxavipedidae is larger than DIV III–IV, while the opposite is seen in ichnospecies of the ichnogenus *Aquatilavipes*.

Ichnotaxon	Mean DIVII–III	Mean DIVIII–IV
Aquatilavipes izumiensis	52.8	67.3
Aquatilavipes swiboldae	58.1	58.6
Barrosopus slobodai	65.7	49.3
Paxavipes babcockensis	56.7	42.7

(Charadriidae) and sandpipers (Scolopaciidae) (Elbroch and Marks, 2001; Table 5), and show that there is a significant difference in digit divarications II–III for the tracks of plovers, but not for sandpipers (Table 5). Although a small sample, it is sufficient to justify examining a hypothesized osteological cause for differences in digit divarication.

Examination of osteology specimens of the tarsometatarsi of species of extant shorebirds with a semipalmate foot morphology reveals two ways in which the distal ends of metatarsals II and IV are deflected from the midline of the tarsometatarsus (long axis of metatarsal III, Fig. 17, also see Falk et al., 2011), and how this deflection may potentially contribute to digit divarication in avian footprints. One form is the angle difference (herein referred to as the intertrochlear angle) between the trochlear groove of metatarsal II and IV, and the trochlear groove of metatarsal III (Fig. 17A). This angle captures both the medio-lateral length of the intertrochlear notch and the degree of latero- and medioplanter rotation of the distal ends of metatarsals II and IV, respectively. The second

form is the medio- and latero-ventral displacement angle (hereon referred to as the plantar angle) from the distal ends of metatarsal III of the trochlear ends of metatarsals II and IV, respectively (Fig. 17B). Relatively large intertrochlear and plantar angles are hypothesized to result in a large digit divarication for the digits in question.

Examination of the distal metatarsals of extant specimens of both Charadriidae (*Charadrius vociferus*, Killdeer; *Charadrius semipalmatus*, Semipalmated Plover) and the Scolopacidae (*Actitis macularia*, Spotted Sandpiper; *Calidris melanotos*, Pectoral Sandpiper; *Calidris alba*, Sanderling), show there is variation in the arrangement in the distal metatarsals on both specific and familial taxonomic levels (Figs. 18–19). All four study specimens have different intertrochlear and plantar displacement angles II–III, but intertrochlear angle II–III is larger for Charadriidae than Scolopacidae (Fig. 18). Also, there is little variation in intertrochlear angle III–IV among the four study specimens (Fig. 18). Discriminant analysis of Charadriidae and Scolopaciidae shows that they are
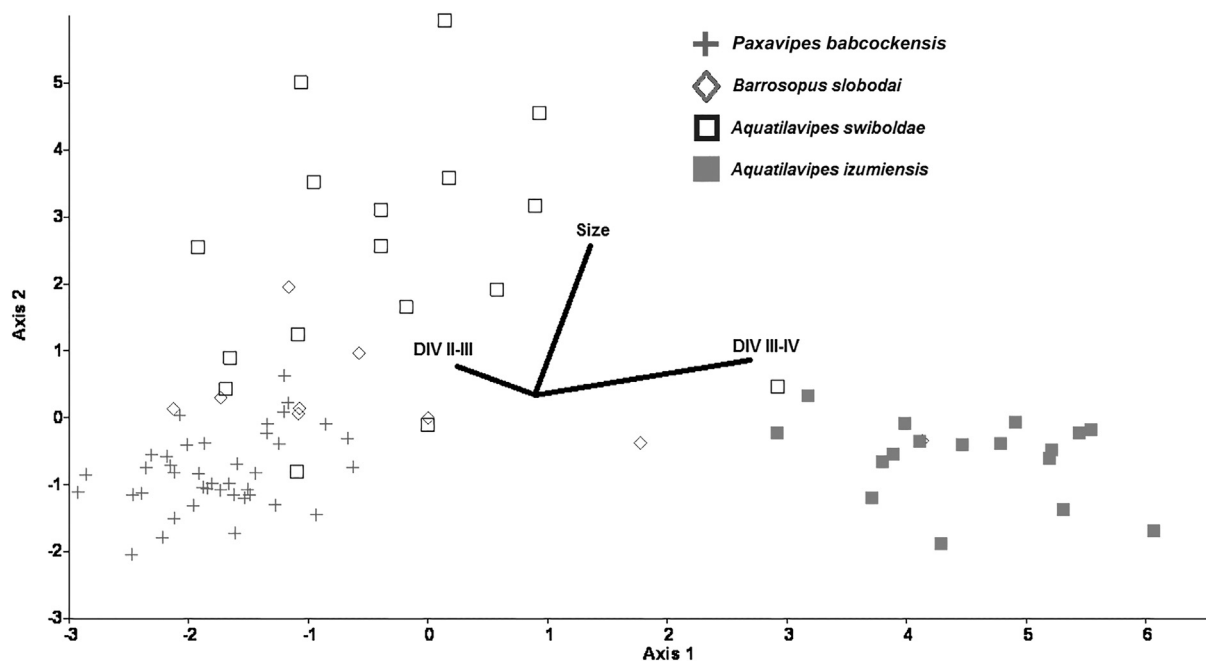

Fig. 16. Canonical variate analysis comparing *Paxavipes babcockensis* nov. ichnogen. nov. isp. (cross), *Barrosopus slobodai* (diamond), *Aquatilavipes swiboldae* (empty square), and *Aquatilavipes izumiensis* (solid square), using footprint length, footprint width, digit lengths (D-II, D-III, D-IV) and digit divarication (DIV II–III, DIV III–IV). In this analysis, axis 1 represents the relationship between the relative sizes of divarication between digits II − II and digits III − IV, and axis 2 represents footprint size. Treating the four ichnospecies separately in the analysis reveals that a) both *Paxavipes* and *Barrosopus* are smaller than *Aquatilavipes swiboldae*, and b) that the large difference between DIV II–III and DIV III–IV in *Aquatilavipes izumiensis* (DIV III–IV is larger) is greater than that seen in *Aquatilavipes swiboldae*: this is represented by the large DIV III–IV vector. This has the effect of "pushing" *Aquatilavipes swiboldae* over into the morphospace occupied by footprints of *Paxavipes* and *Barrosopus* that have a subequal DIV II–III vs. DIV III–IV, as *Aquatilavipes swiboldae* has DIV II–III that is almost equal to DIV III–IV (Table 4). Also, there are some footprints of *Aquatilavipes swiboldae* that display a DIV II–III that is larger than DIV III–IV: this is likely due to natural variation in digit divarication, or possibly a misidentification of "left" versus "right" prints, as no trackways were described by Currie (1981).

Table 5
Digit divarications (in degrees) measured from line drawings of individual tracks figured in Elbroch and Marks (2001) to test the observation that plovers (Charadriidae) have a significantly larger DIV II–III compared to DIV III–IV than do sandpipers (Scolopaciidae). Although the sample size is small, it does show that plover tracks have a significantly larger DIV II–III than DIV III–IV, whereas in sandpipers the DIV II–III and DIV III–IV are not significantly different. "Killdeer trackway 1" refers to the left trackway figured in Elbroch and Marks (2001:p.110), and "Killdeer trackway 2" refers to the right trackway figured in Elbroch and Marks (2001:p.110); "Dunlin#1" refers to the left footprint figured in Elbroch and Marks (2001:p.109), while "Dunlin trackway#2" refers to the right prints figured in Elbroch and Marks (2001:p.109).

Taxon	DIV II–III	DIV III–IV
Piping Plover	71	71
Semipalmated Plover	62	62
Killdeer, trackway 1	72	51
Killdeer trackway 2	76	50
Black-bellied Plover	72	52
$p_{same} = 0.027$		
Least Sandpiper	58	51
Sanderling	65	45
Spotted Sandpiper	59	46
Dunlin#1	43	47
Dunlin trackway#2	57	58
Ruddy Turnstone	49	51
Lesser Yellowlegs	56	63
$p_{same} = 0.361$		

significantly different based on their intertrochlear and plantar displacement angles ($p_{same} = 3.38 \times 10^{-04}$, Fig. 19). The results are comparable with the observations made on the trackways depicted in Elbroch and Marks (2001).

6. Discussion

6.1. Separation of Paxavipes babcockensis and Barrosopus slobodai

Multivariate analyses reveal that, despite the similarity in morphology, *Paxavipes babcockensis* and *Barrosopus slobodai* are discrete morphotaxa, supporting the assignment of *Paxavipes*

babcockensis to a novel ichnogenus and ichnospecies. Although multivariate analyses are useful tools to support or refute the erection of a novel ichnotaxon, they cannot be the sole support for the new ichnotaxon.

6.2. Separation of Avipedidae and Paxavipedidae

Multivariate analyses reveal that there is statistical support for the erection of the novel ichnofamily Paxavipedidae as distinct from the existing ichnofamily Avipedidae based on comparisons with Cretaceous Avipedidae (*Aquatilavipes*).

6.3. Osteology and footprint morphology

Although the sample size in this study is small, there is an indication that some ichnological features, such as digit divarication, are the direct result of osteologic characteristics (see Falk et al., 2011 for ecomorphologic groupings.) Furthermore, the osteologic characters (i.e. intertrochlear angle and intertrochlear notch size) that result in ichnological differences may correlate to systematic differences. In this small study, intertrochlear angle II–III is much larger compared to intertrochlear angle III–IV in the specimens of Charadriidae (plovers) than in Scolopacidae (sandpipers). While the authors are not suggesting the track-makers of *Paxavipes babcockensis* were Early Cretaceous charadriids (Baker et al., 2007 show through multigene Bayesian analysis that Charadriidae diverged during the Late Cretaceous), the results suggest that we can predict that the morphology of the distal tarsometatarsus of the Early Cretaceous shorebird track-maker of *Paxavipes babcockensis* may be similar to that seen in extant plovers. The correlation of pedal osteology, ichnology, and systematics in extant shorebirds is currently being examined by LGB and RTM.

6.4. Dinosaur prints and skin impressions

There are four non-avian prints on PRPRC 2005.15.001, three of which are produced by theropod track-makers, and one by an ornithopod track-maker. Two of the smaller theropod prints
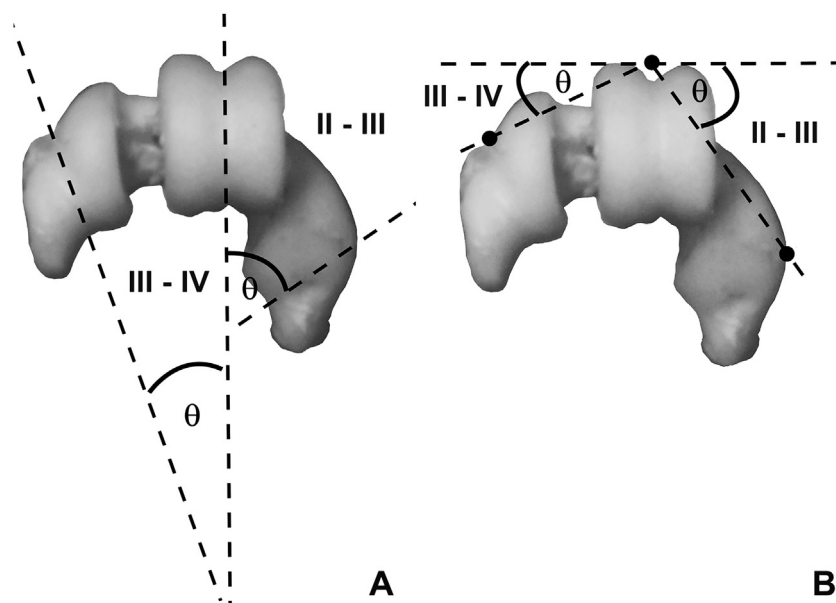

Fig. 17. Schematic diagram using *Calidris alba* BCPM 18305 showing measurements taken for intertrochlear angle (A) and plantar angle (B), both of which contribute to the orientation of attached pedal phalanges (digits) during foot registration. The measurements are based on the trochlear grooves of the metatarsals, which will provide not only a consistent and obvious landmark, but also provide the natural "midpoint" of the digit, as there is natural variation in the degree to which pedal phalanges can move medio-laterally.
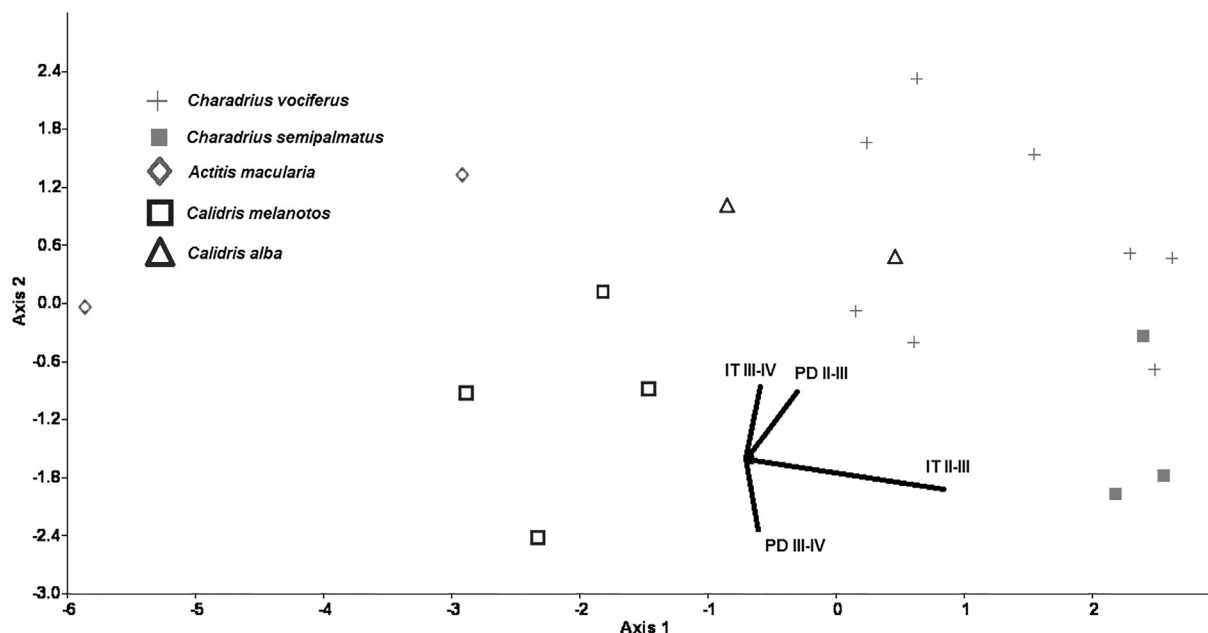
Fig. 18. Canonical variate analysis on extant Charadriidae (*Charadrius vociferus*, cross; *Charadrius semipalmatus*, filled square) and Scolopacidae (*Actitis macularia*, diamond; *Calidris melanotos*, empty square; *Calidris alba*, triangle) on intertrochlear IT(Fig. 17A) and plantar displacement (PD) (Fig. 17B) angles measured from the distal tarsometatarsi of osteology specimens, with axis 1 representing the size of the angle of IT angle between digits II and III, and axis 2 representing the relationship between the relative sizes of the PD angle of digits II − III and IT angle of III − IV with the PD angle of digits III − IV. The specimens separate largely along the metatarsal II–III intertrochlear angle (axis 1), with both *Charadrius vociferus* and *Charadrius semipalmatus* having larger IT II–III than do the sampled scolopaciids. While it is not a large vector, Charadriidae separate from the Scolopacidae along the pedal displacement axis: Charadriidae have a relatively larger pedal displacement angle II–III than Scolopaciidae. Larger IT and PD angles possibly contribute to the larger digit divarication (DIV) II–III relative to DIV III–IV observed in modern Charadriidae, and may also explain the larger DIV II–III seen in the track-maker of *Paxavipes*.

(PRPRC 2005.15.001.073 and 074) are referred to *Irenichnites gracilis*. Sternberg (1932) described *Irenichnites gracilis* as having a consistent separation between digit II and the rest of the print. The second digit impression of PRPRC 2005.15.001.073 is almost separate from the rest of the print. It is likely that all *Irenichnites gracilis* prints would exhibit some degree of digit II separation, depending on the qualities of the track-bearing substrate. The third theropod

track (PRPRC 2005.14.001.076) is not sufficiently preserved to allow assignment to a particular ichnotaxon. The other non-avian track (PRPRC 2005.14.001.075) is a tetradacyl pes, probably of an ornithopod.

There are a small, but growing, number of reports of skin impressions from Cretaceous dinosaur footprints. To date these have been reported for hadrosaurs (Currie et al., 1991; Herrero and Farke,
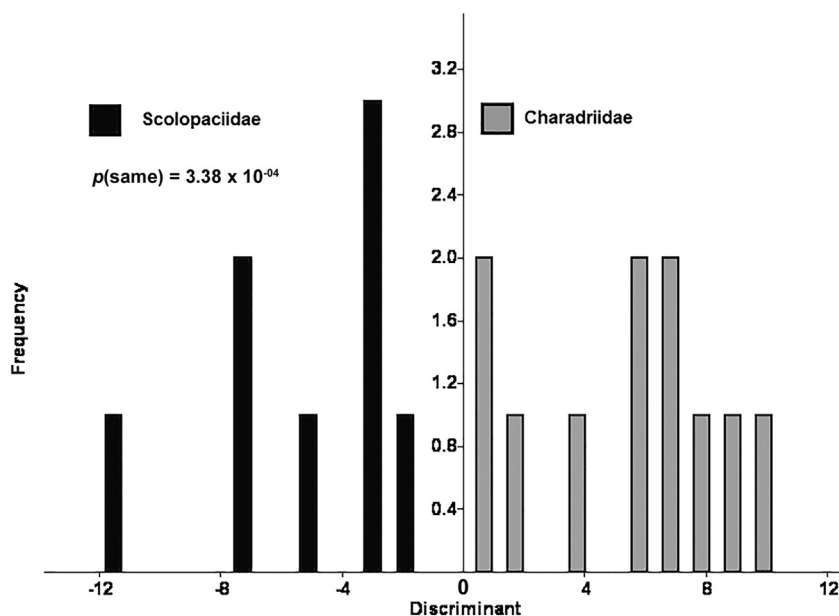

Fig. 19. Discriminant analysis graphical results comparing intertrochlear angle (IT, Fig. 17A) and plantar displacement angle (PD, Fig. 17B) data collected on the distal tarsometatarsii of extant Scolopaciidae (*Actitis macularia*, *Calidris melanotos*, *Calidris alba*), and Charadriidae (*Charadrius vociferus*, *Charadrius semipalmatus*). Charadriidae and Scolopaciidae are significantly different ($p_{same} = 3.38 \times 10^{-04}$), and there was 100% correct identification of each specimen to its *a priori* grouping of either Scolopacidae or Charadriidae. The arrangement of the distal tarsometatarsus appears to correlate the larger digit divarication II–III seen in the measured Charadriidae as compared to the measured Scolopaciidae.

2010; McCrea et al., 2014), ankylosaurs (McCrea et al., 2001, 2014), sauropods (Kim et al., 2010) and medium-sized theropods (Rylaarsdam et al., 2006; Noe et al., 2014). Track specimens PRPRC 2005.15.001.074 and PRPRC 2005.15.001.075 possess skin impressions in the posterior part of the print (metatarsal pads and proximal digital pads). The skin impressions on the *Irenichnites gracilis* print (PRPRC 2005.15.001.074) are the first record of Early Cretaceous skin impressions on small theropod prints of which the authors are aware: see Noe et al. (2014) for a recent report of a 'mid' Cretaceous example from Colorado. The individual tubercles in the Canadian specimen are found on the metatarsal pad, as in the Colorado specimen, and on the proximal digital pads of some digits. The tubercles are small (>1 mm) and are ellipsoidal in shape (approximately 0.7 mm × 0.5 mm) (Fig. 6). The pattern of tubercles is not individual or random; rather, they are sequentially arranged in linear or wavy patterns reminiscent of friction ridge patterns present on the skin surface of other types of vertebrates, including humans.

The skin impressions on PRPRC2005.15.001.075 are on a tetradactyl ornithopod pes print (Fig. 20), similar to *Neoanomoepus*

Fig. 20. Top: Magnified view of skin impressions from the base of digit II of PRPRC 2005.15.001.075. Scale = 10 cm. Bottom: View of the tetradactyl print PRPRC 2005.15.001.075 with digits numbered. A black arrow shows the location of skin impression. Scale = 10 cm.

ichnosp (Lockley et al., 2009). However, PRPRC 2005.15.001.075 is partially covered by adhering sediment that obscures details necessary for precise ichnotaxonomic identification. The ornithopod print is significantly larger than the two *Irenichnites gracilis* prints (PRPRC 2005.15.001.073 and 074). The morphology of the individual tubercles present on PRPRC 2005.15.001.075 is distinct from those of the *Irenichnites gracilis* print (PRPRC 2005.15.001.074) in that the ornithopod tubercles are noticeably larger with an overall sub-round to elliptical shape (approximately 2.0 mm maximum dimension and up to 1.5 mm minimum dimension), and are variably polygonal (hexagonal, pentagonal, etc.) (Fig. 20).

7. Conclusions

The number of fossil vertebrate tracks found in the Boulder Creek Formation is sparse compared to many other track-bearing formations in western Canada (McCrea et al., 2014). Even with such a small sample of specimens which were described in this paper, several significant observations were made, especially in regards to the possibility of identifying osteological characters reflected in avian footprints. The number of avian prints on such a small track slab is great, yet the relative uniformity of these ichnites indicates a rather sparse avian diversity. Because this track slab has a surface area of only about 0.5 m^2 it is unlikely that the record of the vertebrate ichnofauna preserved on it is a complete representation of the vertebrate diversity from this time.

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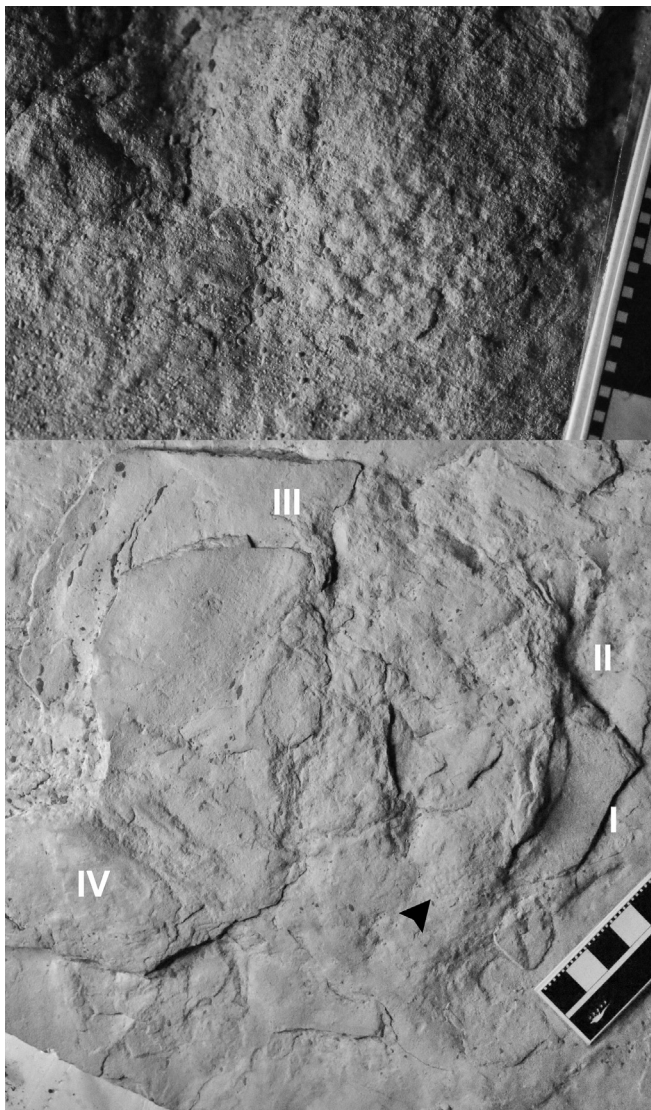
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