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New interpretations of *Ignotornis*, the first-reported Mesozoic avian footprints: implications for the paleoecology and behavior of an enigmatic Cretaceous bird

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ABSTRACT

The type material of *Ignotornis mcconnelli*, the first reported Mesozoic bird track, consists of a large, monospecific sample of ∼70 footprints comprising at least 15 recognizable trackways. However, the exact type horizon and locality, discovered in 1930 in the Cretaceous Dakota Group near Golden, Colorado, was not indicated in the original 1931 description by Maurice Mehl, and only the single holotype trackway was illustrated. In 1988, the known sample was doubled by the discovery of ∼70 additional tracks representing at least seven trackways, but again the exact type horizon and locality remained uncertain. In 2007, we discovered what we infer to be the original type locality, and identified approximately 150 additional footprints comprising at least 17 additional trackways. During the study we also located three more specimens, in other collections, comprising at least 60 tracks and 10 trackways. Thus, the type (holotype, paratype, and topotype) sample now consists of ∼360 footprints comprising about 50 trackways, of which 41 have been measured. Although most footprints from the 1930, 1988, and 2007 finds all appear to originate from the same "type" horizon associated with a volcanic ash, a few tracks were found in 2007 at two additional levels.

The relatively long, reversed hallux and the incipient semi-palmate webbing in the hypex between digits III and IV make *Ignotornis* distinct from any other Cretaceous bird tracks known from North America. These features, used to infer the extant forms with which *Ignotornis* is most convergent, are reminiscent of small herons, and unlike the typical tracks of most Cretaceous shorebird-like species which resemble those of plovers and sandpipers. Clearly defined parallel and sub parallel trackways indicate gregarious behavior, while some trackways indicate unusual "shuffling" and "stop-start" progression, probably related to some type of "foot-stirring" foraging activity. The concentration of abundant *Ignotornis* tracks at a single locality within the ichnologically-famous "Dinosaur Freeway" (represented by more than 60 dinosaur and crocodile dominated track assemblages) suggests that the *Ignotornis* track maker was a "rare-bird" in the region during the Cretaceous.

1. Introduction

Ignotornis mcconnelli (Mehl, 1931a) is one of the most distinctive and well-preserved of all fossil bird footprints. It is also of historical importance as the first trackway of a Mesozoic bird ever reported. In fact, other well-documented Mesozoic bird tracks were not reported for almost 40 years after Mehl's discovery (in 1930) until Kim (1969) described *Koreanaornis hamanensis* from the Lower Cretaceous Haman Formation of South Korea. The next report came more than a decade thereafter when Currie (1981) named *Aquatilavipes swiboldae* from the Lower Cretaceous (Aptian) Gething Formation of British Columbia. Since this latter discovery, reported exactly 50 years after the publication of Mehl's historic paper, a number of other Mesozoic (Cretaceous) bird tracks have been documented from various localities around the world. However, the number and diversity known from North America remains relatively low.

Ignotornis mcconnelli was discovered by N. H. McConnell, who donated the material to the University of Colorado Museum of Natural History at Boulder (UCM). The tracks occur in the late Albian-early Cenomanian South Platte Formation, which is in the upper part of the Cretaceous Dakota Group (Figs. 1 and 2). In the sequence stratigraphic framework of Weimer (1984, 1989), the track-bearing units occur in Sequence 3. This stratigraphic unit has

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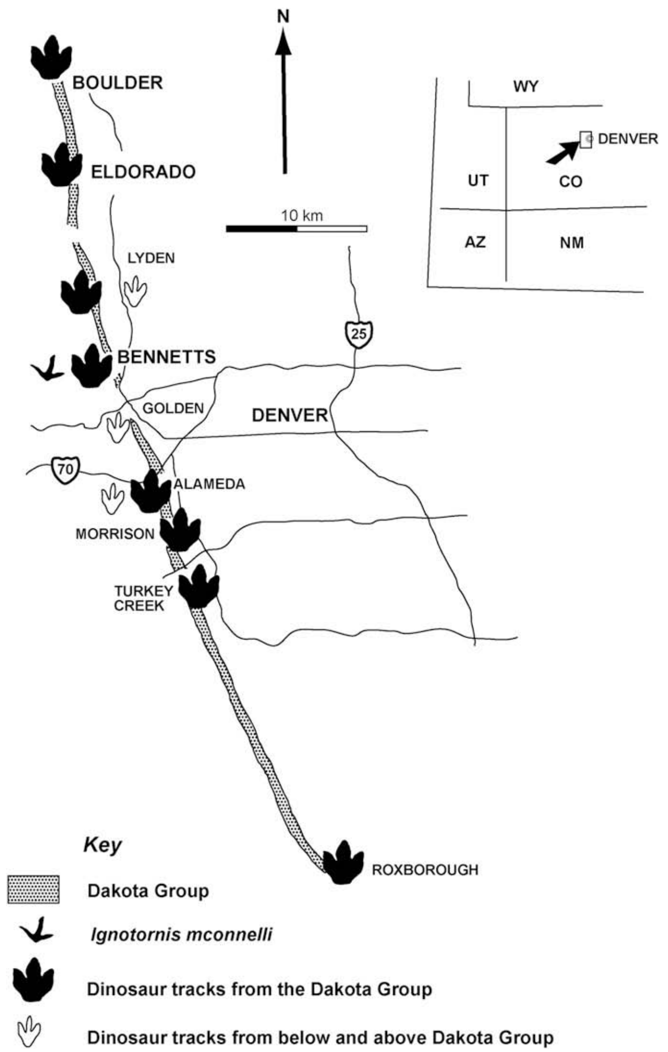

Fig. 1. Locality map for vertebrate tracksites in the Dakota Group between Boulder and Roxborough, Colorado. Modified after Lockley et al. (1989).

since become well-known for the so called Dinosaur Freeway (Lockley et al., 1992a) due to the abundance of dinosaur track localities distributed over a wide area of the high plains region between Boulder, Colorado and northeastern New Mexico. Despite reports of more than 60 dinosaur track localities that all share very similar ichnofaunal assemblages, the Golden locality remains the only one that produces *Ignotornis*. In fact, the ichnogenus is unknown anywhere else in North America and is rare elsewhere in the world. For this reason, the *Ignotornis* type locality and type material retain special significance in Mesozoic avian ichnology. Therefore, the purpose of this paper is to provide more thorough descriptions of the type material (holotype, paratypes and topotypes), most of which has not been studied in detail. We also resolve previous uncertainty about the spatial (geographic) and temporal (stratigraphic) distributions of the tracksites and can now confidently define three, correlated bird track-bearing outcrops (Sites 1–3), two of which have multiple track layers (Figs. 3 and 4). A fourth site, located several hundred meters to the south, produces very poorly-preserved bird tracks which are not described here. Finally we consider the paleobiological and taphonomic implications of the track assemblages and discuss the significance of *Ignotornis* track morphology (Fig. 5) in the context of the rapidly growing ichnological record for Cretaceous birds.

2. Material and historical background

2.1. Specimens discovered before 2007

When Mehl (1931a) named *Ignotornis mcconnelli* he illustrated a single specimen consisting of a single trackway preserved as a natural cast (UCM 17614). This holotype (Figs. 5 and 6) was re-illustrated by Lockley et al. (1992b), Lockley and Hunt (1995) and Kim et al. (2006) but without detailed, accompanying analysis. Mehl (1931b, p. 331) reported that through the "courtesy of Professor Junius Henderson of the University of Colorado" at Boulder, he had "been permitted to study a series of about 70 bird tracks from the base of the upper massive sandstone of the 'Dakota' near Golden Colorado" (Figs. 1 and 2). These tracks are preserved as natural casts, (convex epirelief) on four slabs of gray to buff colored sandstone, all originally incorporated collectively under the catalog number UCM 17614. The protruding track casts have as much as 5–10 mm of relief and, in many cases, are broken off flush with the bedding plane surface, revealing strong color contrasts between the "background" surface and the sharp outlines of the broken casts, which nevertheless preserve the shape of the tracks with great fidelity (e.g., Figs. 6–9). Prior to examination of the specimens by the present authors, small pieces that had separated from some of the track casts were glued back in place. The original description (Mehl, 1931a) gives no indication of the lithology of the underlying layer on which the tracks were originally registered. As noted below, we have ascertained that this was a volcanic ash, which evidently contributed to the excellent preservation of the tracks.

Although four specimens were originally cataloged together as UCM 17614, only one slab with this number, showing a single trackway consisting of six tracks (Fig. 6), was explicitly designated as the "type" by Mehl (1931a, p. 444) who also stated that "in addition there are other similar, but less well-preserved footprints representing one or more other progressions." Here "progression" evidently means a trackway or sequence of footprints made by a single individual. This statement is ambiguous, because the number of specimens is not explicitly mentioned: however it is clear that these "other" footprints are not on the same slab. They are, therefore, distinct from the holotype (trackway 1 in Table 1) and can be formally considered as both paratypes and topotypes (trackways 2–15 in Table 1). We have clarified the cataloguing ambiguity by giving separate specimen numbers to the three unillustrated, non-holotype slabs, previously catalogued under UCM 17614; these are designated as paratypes (UCM 98120–98122), and are all illustrated here for the first time (Figs. 7–9). Replicas of all four slabs in the University of Colorado at Denver (CU) collections also have separate numbers (CU 203.4 for the holotype, and CU 203.5–203.7 for the paratypes). As noted below, we do not know with absolute certainly that the four specimens were found in close proximity on the same surface, because the outcrop extends along strike for ~800 m, as originally noted by Mehl (1931a). However, based on lithological similarity, this is the most parsimonious conclusion.

The UCM collections also contain four "counterpart" plaster molds, dated 1930, made and signed by Mehl himself. This date and the name R. Farmer are imprinted on the undersides of these plaster replicas, and Mehl (1931a) noted that Russell Farmer was a student at the University of Missouri at the time the research was undertaken. Two plaster replicas (Fig. 10A and B) were impressions made directly from the natural casts that comprise the holotype trackway (UCM 17614) and the best preserved paratype (UCM 98120). These counterparts are well-made, and appear to have been fashioned directly from the convex epirelief surfaces, probably using a separator. The resulting impressions (concave epireliefs) show the tracks as they would have originally appeared before being covered by sand.

Fig. 2. Aerial photograph of the *Ignotornis* type locality taken in 2002. Prominent zig-zag white scar represents quarried area of hogback. Exact track location is not shown in order to protect the site.

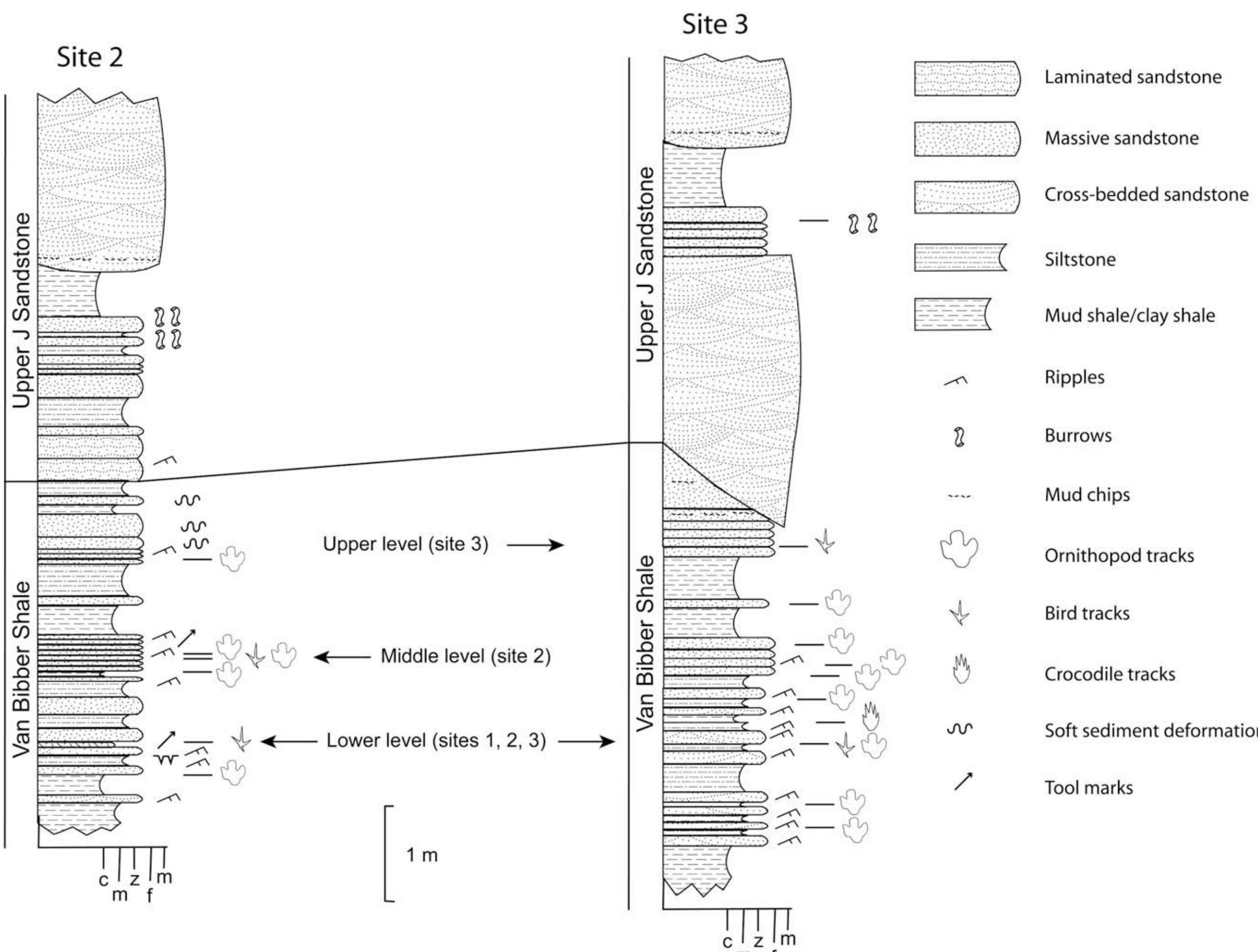

Fig. 3. Detailed stratigraphic column, from Sites 2 and 3 showing lower, middle and upper bird track-bearing layers, and a layer with crocodylian swim tracks from just above the lower bird track layer at Site 3. Note multiple dinosaur track layers.

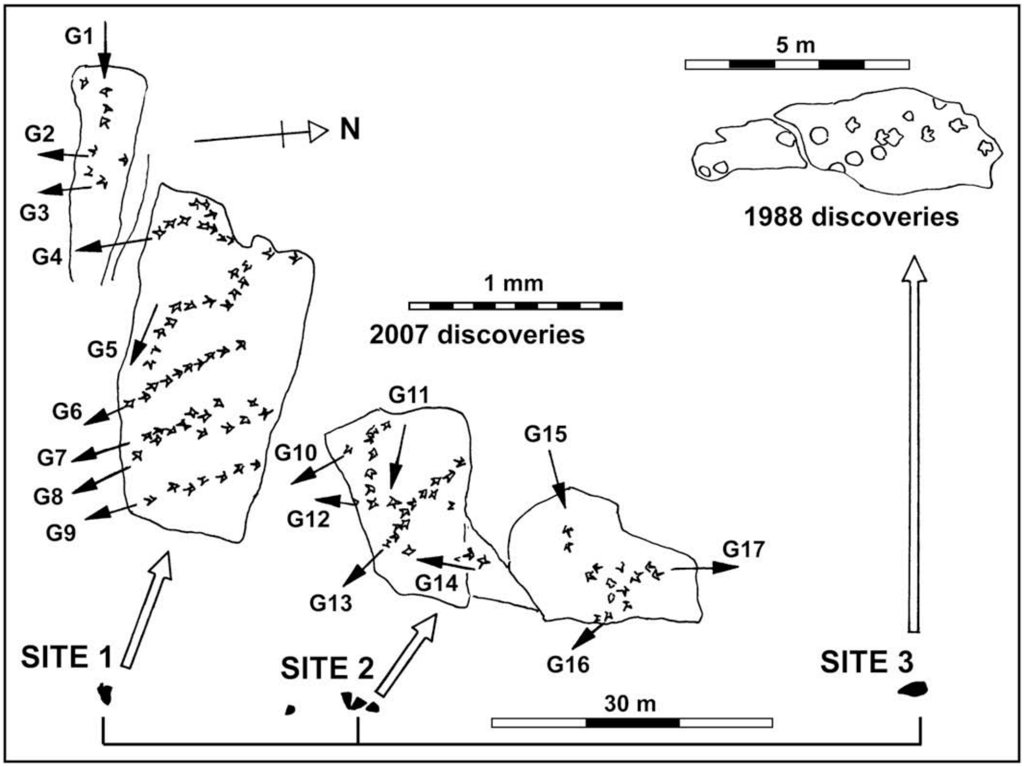

Fig. 4. Line drawing showing outcrop of type *Ignotornis* horizon, with three locations from which *in situ* tracks have been recovered. Site 1 is inferred to be the original discovery site yielding specimens shown in Figs. 6–9, and corresponding replicas (Fig. 10) as well as *in situ* trackways shown in Fig. 15 and specimen shown in Fig. 12. Site 2 shows *in situ* track bearing beds ∼25–30 m north of site 1, and Site 3 shows a slab discovered ∼60 m to the north from the same horizon (Lockley et al., 1989). See Figs. 13 and 14.

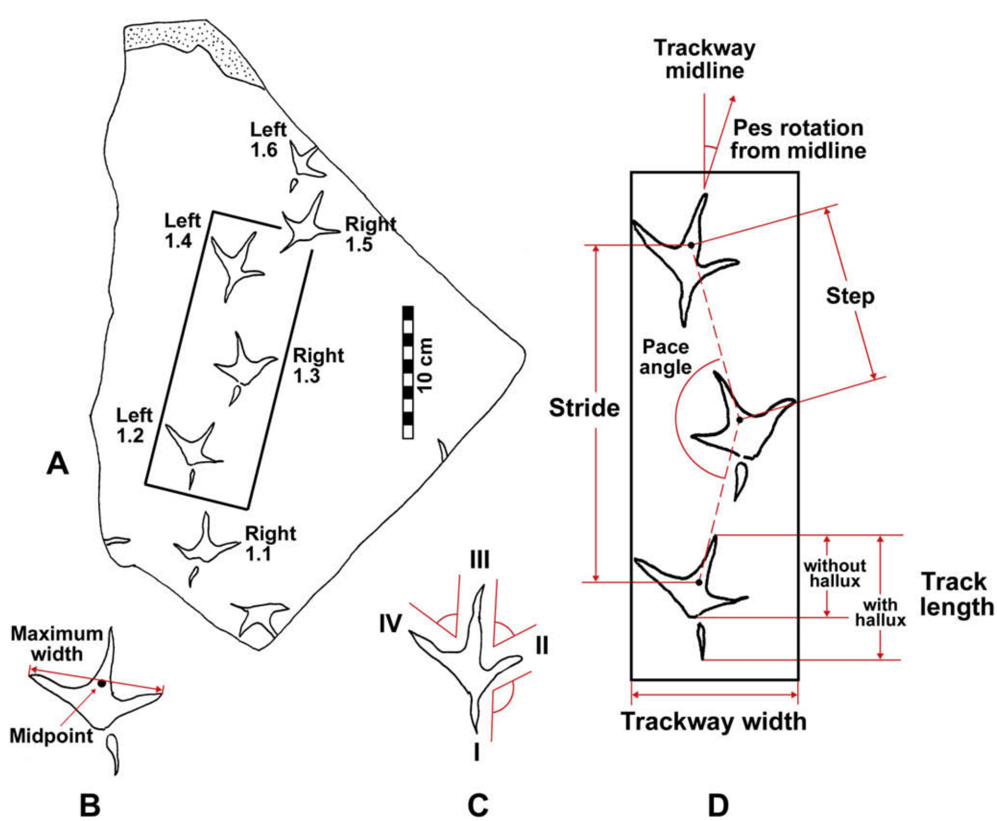

Fig. 5. Parameters of *Ignotornis* tracks measured. A: holotype (cf. Fig. 6) with natural cast orientation reversed to show left and right tracks in correct aspect. B: determination of track midpoint, C: divarication angles, D: other standard morphometric parameters: see text for details.

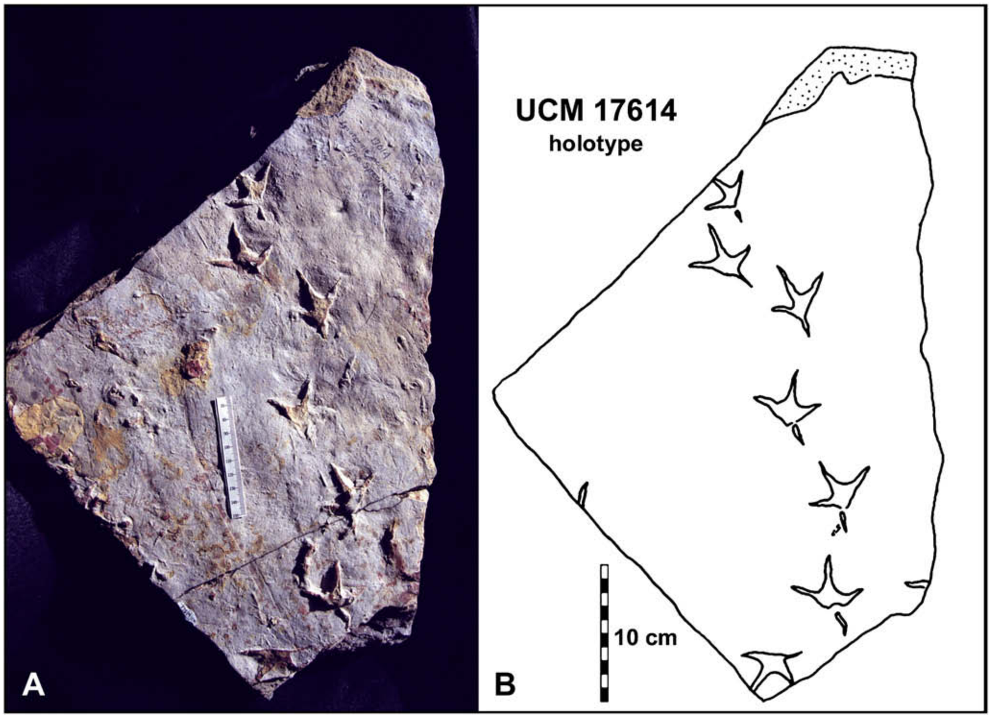

Fig. 6. A, Photograph and B, line drawing of the *Ignotornis mcconnelli* holotype (UCM 17614) also preserved as replica CU 203.4 in the CU Denver Dinosaur Tracks Museum collections. This trackway is designated as trackway 1: see Figs. 7–9 and Table 1 for trackways 2–15.

Two other plaster casts of non-avian tracks in the UCM collection evidently were collected in the early 1930s by Mehl or his associates from the same general area. They represent convex epireliefs of large indistinct impressions labeled, in the UCM collections, as "dinosaur tracks." They reveal no associated bird tracks, and bear little or no resemblance to typical dinosaur tracks from the area. Based on size and shape, they may be poorly preserved examples of the enigmatic traces that Mehl (1931a, p 445) described as tracks of "a new quadruped with webbed feet" and named *Walteria jeffersonensis* (Mehl, 1931a). Because the name *Walteria* was preoccupied, this track type was renamed as *Mehliella jeffersonensis* by Strand (1932). The nomenclatural history of this ichnogenus is complex and will be described elsewhere, but its co-occurrence with bird and dinosaur tracks is relevant to our interpretation of the paleoecology of the *Ignotornis* site. Although *Mehliella* has been attributed to a turtle (Kuhn, 1963) and tentatively attributed to an ankylosaur, by other authors (Haubold, 1971, 1984; Thulborn, 1990) not familiar with the field locality, Lockley

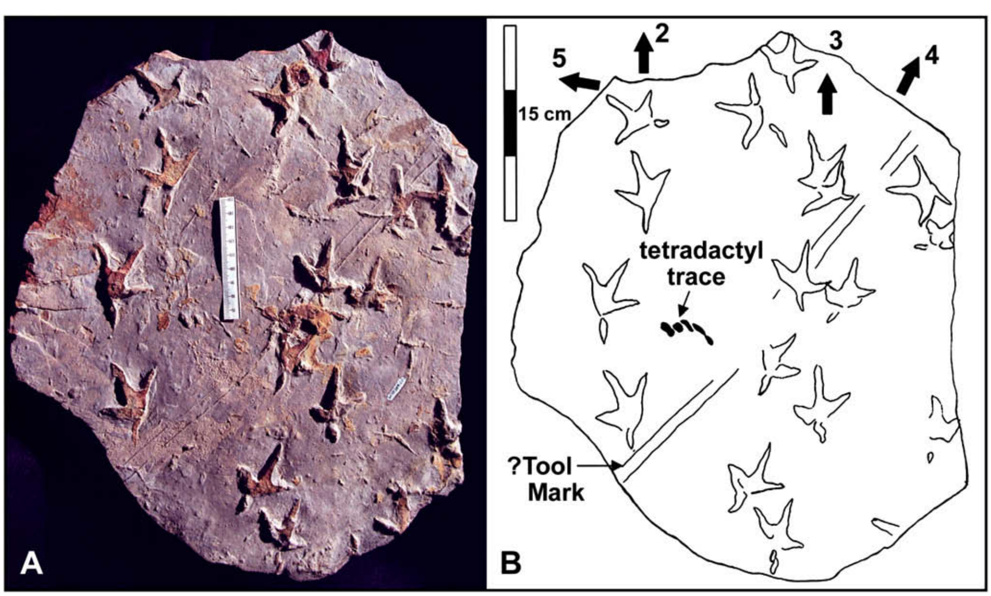

Fig. 7. A, Photograph and B, line drawing of the *Ignotornis mcconnelli* paratype (UCM 98120) also preserved as replica CU 203.5 in the CU Denver Dinosaur Tracks Museum collections.

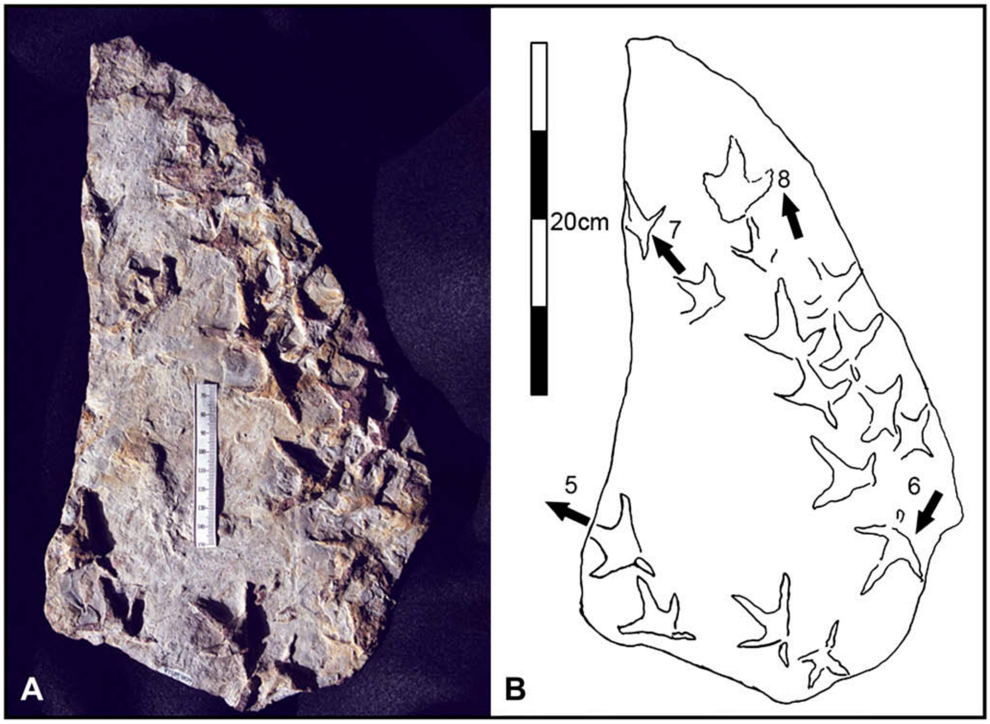

Fig. 8. A, Photograph and B, line drawing of the *Ignotornis mcconnelli* paratype (UCM 98121) also preserved as replica CU 203.6 in the CU Denver Dinosaur Tracks Museum collections.

(2003) suggested that it is more likely a crocodylian trackway, of the type identified at several sites in the area.

Additional specimens from the site in the University of Colorado at Denver (CU) collections, include two donated specimens. A small slab (CU 203.2; Fig. 11) with a single track figured by Lockley and Rainforth (2002) – was donated to CU Denver by the Colorado School of Mines Geological Museum, and is presumed to have originated from the *Ignotornis* type locality. We therefore consider it to be another topotype. Likewise, late in the course of the present study another large slab was donated to CU Denver, by J. Sawdo,

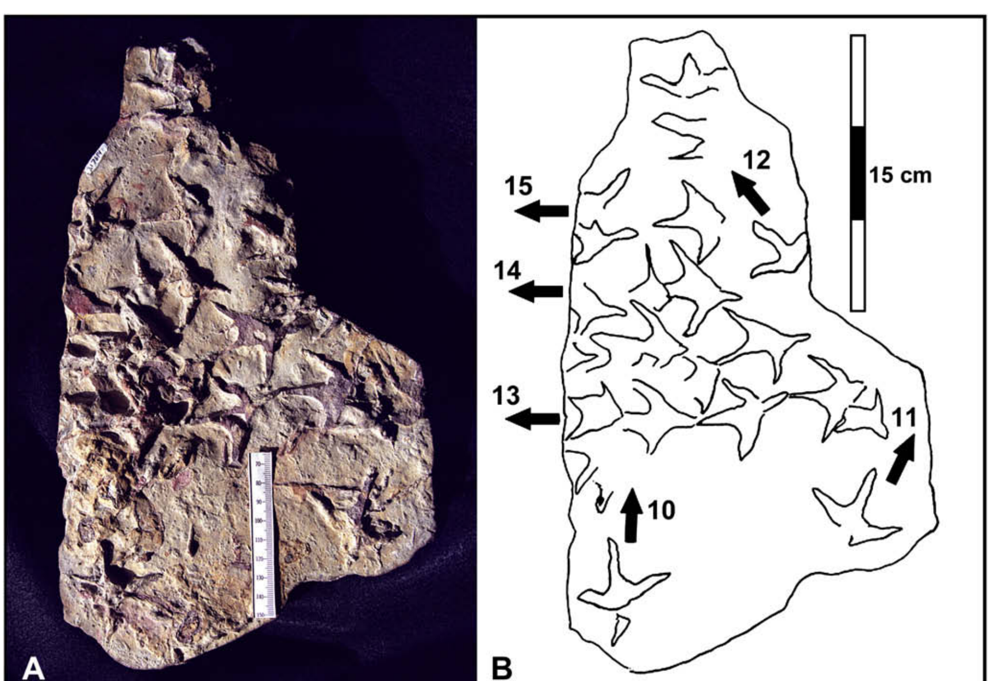

Fig. 9. A, Photograph and B, line drawing of the *Ignotornis mcconnelli* paratype (UCM 98122) also preserved as replica CU 203.7 in the CU Denver Dinosaur Tracks Museum collections.

Table 1
Measurements for *Ignotornis* trackways from the type locality (Site 1). Trackways 1–15 represent the 1930s sample in the UCM collection. Trackways G1–G9 represent well-preserved specimens from what we infer to be the same (type) locality

Track #	Track length w/hallux	Track length w/o hallux	Track width	Step	Stride	Pace angle	Track-way width	I–II angle	II–III angle	III–IV angle	II–IV angle	Inward rotation	Right or Left
Holotype; UCM 17614:													
1.1	5.9	3.9	5.1	–	–	–	–	85	62	63	125	18	R
1.2	5.7	4.0	5.0	7.2	–	143	7.0	115	60	65	125	18	L
1.3	5.1	3.7	5.2	7.3	14.0	150	7.0	95	60	63	123	21	R
1.4	5.6	4.0	4.7	8.0	14.7	118	8.4	120	50	55	105	17	L
1.5	5.3	4.0	4.9	6.0	12.1	120	7.6	90	60	65	125	5	R
1.6	–	–	4.6	4.9	9.4	–	–	100	57	50	107	15	L
mean	**5.5**	**3.9**	**4.9**	**6.7**	**12.6**	**132.8**	**7.5**	**100.8**	**58.2**	**60.2**	**118.3**	**15.7**	
Paratype 1; UCM 98120:													
2.1	6.3	4.5	5.2	–	–	–	–	90	60	46	106	40	L
2.1	6.6	4.5	5.2	8.7	–	160	5.6	95	57	50	107	25	R
2.3	6.4	4.4	5.2	8.4	16.8	–	–	90	60	50	110	25	L
mean	**6.4**	**4.5**	**5.2**	**8.6**	**16.8**	**160**	**5.6**	**91.7**	**59**	**48.7**	**107.7**	**30**	
3.1	5.4	4.1	4.6	–	–	–		95	80	60	140	15	R
3.2	5.9	4.4	4.3	10.3	–	152		115	80	60	140	5	L
3.3	*5.3*	4.2	4.6	10.0	19.7	160	6.0	90	80	55	135	8	R
3.4	5.6	4.4	4.4	8.5	18.3	158	6.0	105	82	52	134	8	L
3.5	–	–	4.4	8.7	16.9	–	6.0	110	67	53	120	10	R
mean	**5.6**	**4.3**	**4.5**	**9.4**	**18.3**	**156.7**	**6.0**	**103**	**77.8**	**56**	**133.8**	**9.2**	
4.1	6.1	4.4	4.6	–	–	–	–	120	60	60	120	18	L
4.2	6.1	4.2	*4.2*	9.8	–	140	6.7	100	52	68	120	0	R
4.3	5.6	4.1	4.1	7.0	15.8	–	–	100	70	65	135	15	L
mean	**5.9**	**4.2**	**4.3**	**8.4**	**15.8**	**140**	**6.7**	**106.7**	**60.7**	**64.3**	**125**	**11**	
5.1	*5.2*	3.4	5.7	–	–	–	–	65	90	72	162	18	L
5.2	–	–	5.1	7.4	–	135	8.0	80	–	–	130		R
5.3	5.3	3.7	5.5	8.6	14.6	133	8.5	80	80	65	145	11	R
5.4	5.3	3.7	5.1	8.6	15.5	–	–	90	72	63	135	11	R
mean	**5.3**	**3.6**	**5.4**	**8.2**	**15.1**	**134**	**8.3**	**78.8**	**80.7**	**66.7**	**143**	**13.3**	
Paratype 2; UCM 98121:													
6.1	5.3	3.9	5.0	–	–	–	–	95	60	50	110	−16	L
6.2	4.9	3.9	5.0	6.2	–	128	7.5	70	50	75	125	38	R
6.3	–	–	5.2	4.8	9.7	–	–	110	75	55	130	–	L
mean	**5.1**	**3.9**	**5.1**	**5.5**	**9.7**	**128**	**7.5**	**91.7**	**61.7**	**60.0**	**121.7**	**11**	
7	**5.4**	**4.2**	**5**	–	–	–	–	**85**	**60**	**65**	**125**	–	R
8	**5.1**	**4**	**4.6**	**3.6**	**4.3**	**64**	**7.5**	**90**	**80**	**75**	**155**	**11**	R + L
9	–	–	–	–	–	–	–	–	–	–	–	–	?
Paratype 3: UCM 98122:													
10	5.4		5.1	–	–	–	–	92	73	73	146		L
11	5.2	4	5.2	–	–	–	–	–	80	60	140	–	R
12	–	3.5	–	–	–	–	–	–	75	55	130		
13.1	–	3.5	4.5	–	–			–	37	68	105	16	R
13.2	5.3	3.9	5.0	4.9	–	65	8.1	90	64	51	115	10	L
13.3	5.1	3.5	4.5	4.2	4.9			122	65	47	112	6	R
mean	**5.2**	**3.6**	**4.7**	**4.6**	**4.9**	**65.0**	**8.1**	**106.0**	**55.3**	**55.3**	**110.7**	**10.7**	
14	–	–	**5.2**	–	–	–	–	**105**	**70**	**55**	**125**	–	L
15	–	**3.8**	**4.5**	–	–	–	–	–	**65**	**55**	**120**	–	L
Inferred *in situ* topotype: CU 203.28 (New Golden Slab)													
G1.1	–	3.5	4.4	–	–	–	–	–	65	105	160	10	R
G1.2	–	4.3	4.0	8.5	–	150	5.9	–	–	87	–	28	L
G1.3	–	4.0	4.9	7.3	15.2	–	–	–	57	60	117	30	R
mean		**3.9**	**4.4**	**7.9**	**15.2**	**150**	**5.9**		**61.0**	**84.0**	**138.5**	**22.7**	
G2.1	–	–	–	–	–	–	–	–	–	–	–	–	
G3.1	–	**4.0**	**5.0**	–	–	–	–	–	**48**	**62**	**110**	–	L
G4.1	–	4.5	5.0	–	–	–	–	–	–	–	–	–	L
G4.2	5.5	4.4	5.0	7.2	–	138	7.0	107	63	65	128	25	R
G4.3	6.0	5.0	4.9	6.0	12.3	–	–	80	75	75	150	22	L
mean	**5.8**	**4.5**	**5.0**	**6.6**	**12.3**	**138**	**7.0**	**93.5**	**62.0**	**67.3**	**129.3**	**23.5**	
G5.1	6.0	4.4	5.1	–	–	–	–	95	80	53	133	10	R
G5.2	5.3	4.4	5.3	7.5	–	148	6.8	–	50	77	127	30	L
G5.3	5.0	4.2	5.3	7.0	13.8	–	–	100	62	58	120	24	R
mean	**5.4**	**4.3**	**5.2**	**7.3**	**13.8**	**148**	**6.8**	**97.5**	**64.0**	**62.7**	**126.7**	**21.3**	
G6.1	5.4	4.0	4.0	–	–	–	–	112	68	57	125	42	L
G6.2	5.0	4.1	3.9	6.5	–	155	5.0	112	43	62	105	34	R
G6.3	5.0	3.8	3.9	6.0	12.0	155	4.9	128	35	60	95	23	L
G6.4	4.9	4.1	3.7	5.7	11.6	167	4.1	92	57	47	104	33	R
G6.5	5.1	4.0	4.0	6.2	11.4	50	7.5	130	45	70	115	20	L
G6.6	4.9	3.9	4.0	3.2	5.3[a]	–	7.0	100	62	58	120	10	R
G6.7	–	4.0	4.0	6.3	6.5	70	5.5	–	–	–	–	34	L
G6.8	5.5	4.7	–	7.8	14.2	–	–	–	–	–	–	5	R

(*continued on next page*)

Table 1 (*continued*)

Track #	Track length w/hallux	Track length w/o hallux	Track width	Step	Stride	Pace angle	Track-way width	I–II angle	II–III angle	III–IV angle	II–IV angle	Inward rotation	Right or Left
mean	**5.1**	**4.1**	**3.9**	**6.0**	**11.1**	**119.4**	**5.7**	**112.3**	**51.7**	**59.0**	**110.7**	**25.1**	
G7.1	–	–	–	–	–	–	–	–	–	50	–	18	R
G7.2	5.7	4.3	4.5	9.0	–	120	7.6	63	77	55	132	19	L
G7.3	5.8	4.2	4.5	7.0	14.2	–	–	93	62	56	118	−11	R
mean	**5.8**	**4.3**	**4.5**	**8.0**	**14.2**	**120.0**	**7.6**	**78.0**	**69.5**	**53.7**	**125.0**	**8.7**	
G8.1	–	4.0	4.7	–	–	–	–	–	71	71	142	12	L
G8.2	–	4.0	–	9.5	–	170	5.2	–	–	57	–	30	R
G8.3	–	4.3	4.5	8.2	17.0	–	–	–	45	70	115	37	L
mean		**4.1**	**4.6**	**8.9**	**17.0**	**170.0**	**5.2**		**58.0**	**66.0**	**128.5**	**26.3**	
G9.1	–	4.2	4.5	–	–	–	–	–	50	63	113	12	R
G9.2	–	3.9	–	9.0	–	158	5.9	–	–	60	–	20	L
G9.3	–	3.9	–	8.5	17.0	161	5.6	–	–	57	–	25	R
G9.4	5.1	4.1	4.6	7.8	16.2	144	6.6	133	65	45	110	10	L
G9.5	5.9	4.8	4.7	7.4	14.7	–	–	92	58	42	100	14	R
G9.6	5.2	4.0	4.8	–	–	–	–	95	80	45	125	12	L
mean	**5.4**	**4.2**	**4.7**	**8.2**	**16.0**	**154.3**	**6.0**	**106.7**	**63.3**	**52.0**	**112.0**	**15.5**	

[a] Measurement affected by minor fault displacement.

who recollects (*pers. comm.*) that the specimen was found in the early 1980s, as a loose slab, located very near what we now consider to be the type locality (Site 1). This specimen (CU 203.35) reveals a well-preserved trackway of 10 footprints (Fig. 12) associated with a surface that is lithologically identical to the holotype and paratype specimens. We therefore consider it to be another topotype. Mr. Sawdo also fortuitously discovered a photograph in a collection of old scientific papers of unknown provenance which shows another bird track specimen (Fig. 10C) with the following text written by Mr. McConnell on the reverse:

> "*(raised) casts of bird tracks made in clay and covered with sand. From "Dakota" Hogback one mile North of Golden, Colorado. Geology maps at this point show at least 1 3⁄4 miles of sedimentary deposits covered this strata. No remains of animals have been found.*
> "*ignotornis mcconnelli*"
> *H.N. McConnell*
> *Specimen show [sic] is about 28 inches long. Now at Univ. of Missouri. Shows optical illusion when held at certain angles to light.*
> *Described in American Journal of Science, May 1931 (#125)*"

Mr. H.N. McConnell, after whom Mehl (1931a) named the tracks, may have written this text on the back of the photo. The first section ends with what appears to be his signature, indented below the formal track name, and the remaining text follows as a footnote. The reference to an "optical illusion" almost certainly refers to the fact that at certain angles the photo of natural casts (convex hyporelief) may appear as natural impressions (concave epirelief). The specimen (Fig. 10C) shows at least 35 individual tracks comprising at least 6 trackways. However, we have been unable to locate this University of Missouri (UM) specimen even though another much smaller UM specimen with a dozen tracks has been found in the UM collections.

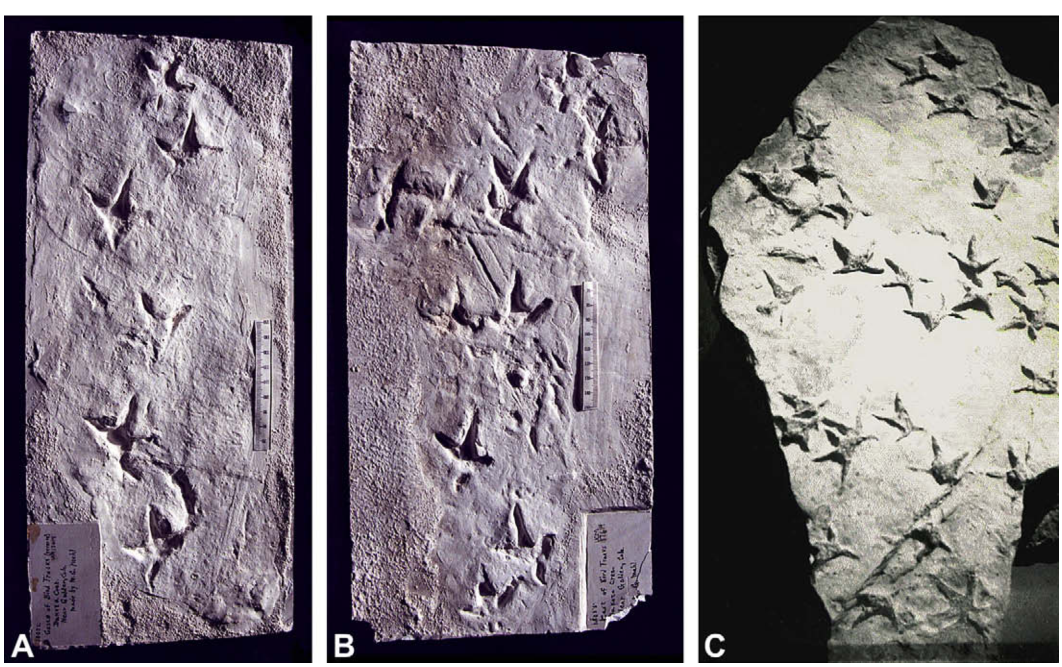

Fig. 10. A and B, Photographs of two plaster 'cast' counterparts labeled and signed by Mehl of the two best preserved *Ignotornis* trackways. These counterparts restore the natural casts (convex epireliefs) into replicas of the original impressions, as they would have appeared in the muddy substrate. C: photo of specimen purported to have been sent to the University of Missouri. Photograph was evidently signed by H. F. McConnell (see text for details).

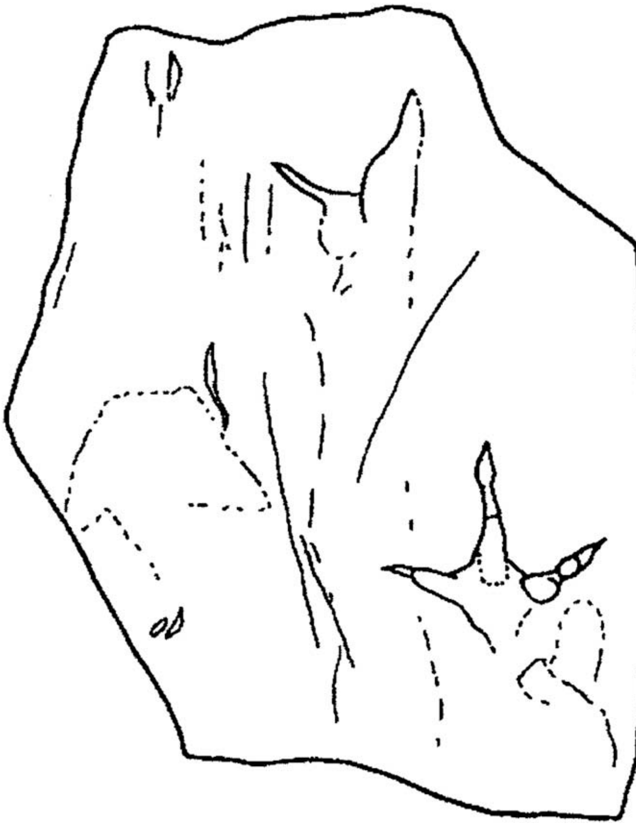

Fig. 11. Line drawing of small CU 203.2 slab with *Ignotornis mcconnelli* topotype (after Lockley and Rainforth, 2002). Well-preserved track (lower right) is 4.9 cm wide.

To the best of our knowledge, except for finding specimen CU 203.35, there was no systematic attempt to relocate or restudy the *Ignotonis* type locality between 1931 and the late 1980s. Reconnaissance of the area in 1988 resulted in the discovery of a large ($\sim 6 \times 2$ m) slab (Figs. 13 and 14), at the locality now designated as Site 3 (Fig. 4). This slab includes many *Ignotornis* track casts on the same surface as dinosaur undertracks. The block (CU 203.1; catalogued in the CU Denver collection but now on long term loan to the Nakasato Dinosaur Center, Japan) reveals at least 70 birds tracks preserved as natural casts (Fig. 13). These were briefly noted by Lockley et al. (1989) as the first co-occurrence of bird and dinosaur undertracks on the same surface. They were again illustrated by Lockley (1991) and Lockley and Hunt (1995) without detailed description.

2.2. Rediscovery of the Ignotornis locality

The *Ignotornis* type locality was originally described by Mehl (1931a, p. 444) as "about one and a half miles northwest of Golden Colorado." This places the type locality at the south end of a NNW-SSE trending ridge along which the Dakota Group outcrops for at least 800 m (Fig. 2). We infer that prior to 2007 a total of $\sim$200 *Ignotornis* tracks (Figs. 6–14) from the three Golden localities had been excavated and distributed to four different museums between the 1930s and the 1980s. During the course of ongoing studies of Cretaceous bird tracks, it became evident that the combined collections represent a substantial sample of a historically important ichnotaxon that has never been described in detail. This prompted us to revisit the locality. We not only located many additional specimens but found what we now infer to be the original discovery site (probably Site 1, which in turn is very close to Site 2: Fig. 4) Most of these tracks occur at the same stratigraphic level as that inferred for the type section. The lithology and style of preservation is similar not only for the holotype and paratypes (UCM specimens shown in Figs. 6–9) but also for many of the topotype specimens described herein (Figs. 11 and 12) as well as for specimens from nearby Site 3 (Figs. 14 and 15). This type horizon, the lowest with bird tracks, is exposed discontinuously for about 80 m at the southern end of the aforementioned $\sim$800 m outcrop (Figs. 3 and 4). The outcrop was artificially created by quarrying operations to remove clay for brick making (Waage, 1961). These operations continue today on state land north of the track-bearing exposures. However, clay excavation was abandoned long ago at the southern end of the outcrop, which is on City of Golden land. Thus, the track beds are safe from damage by quarrying, and cannot be collected without a state permit. These southern exposures reveal long fault planes associated with the Golden Fault complex. They also reveal additional poorly preserved bird tracks, dinosaur tracks, and crocodylian swim tracks that will be described in a separate paper.

2.3. The local distribution of Ignotornis tracksites in space and time

The trackways from the lower 'holotype' horizon have been recognized at three exposures herein designated as Sites 1–3 (Fig. 4). Site 1 is inferred to be original discovery site which reveals multiple newly-discovered and well-preserved trackways (Figs. 15

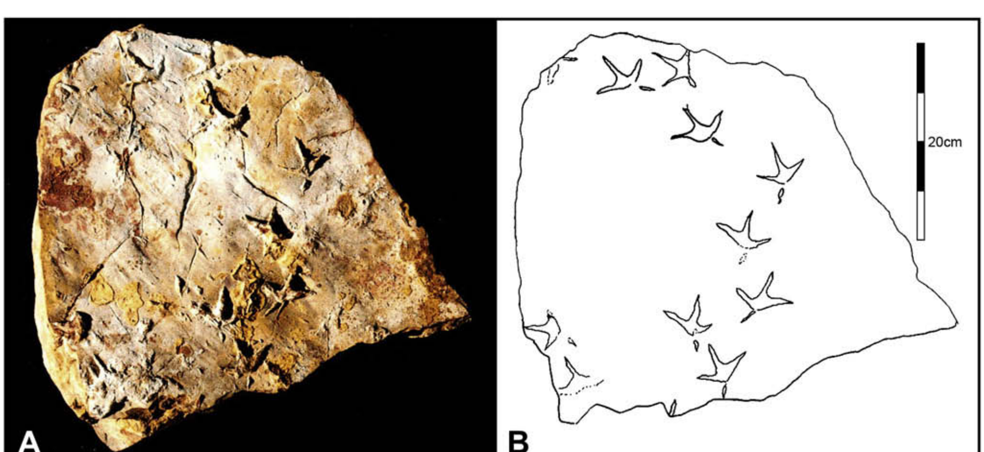

Fig. 12. A: Photograph and B: line drawing of the *Ignotornis mcconnelli* specimen CU 203.35 in the CU Denver Dinosaur Tracks Museum collections.

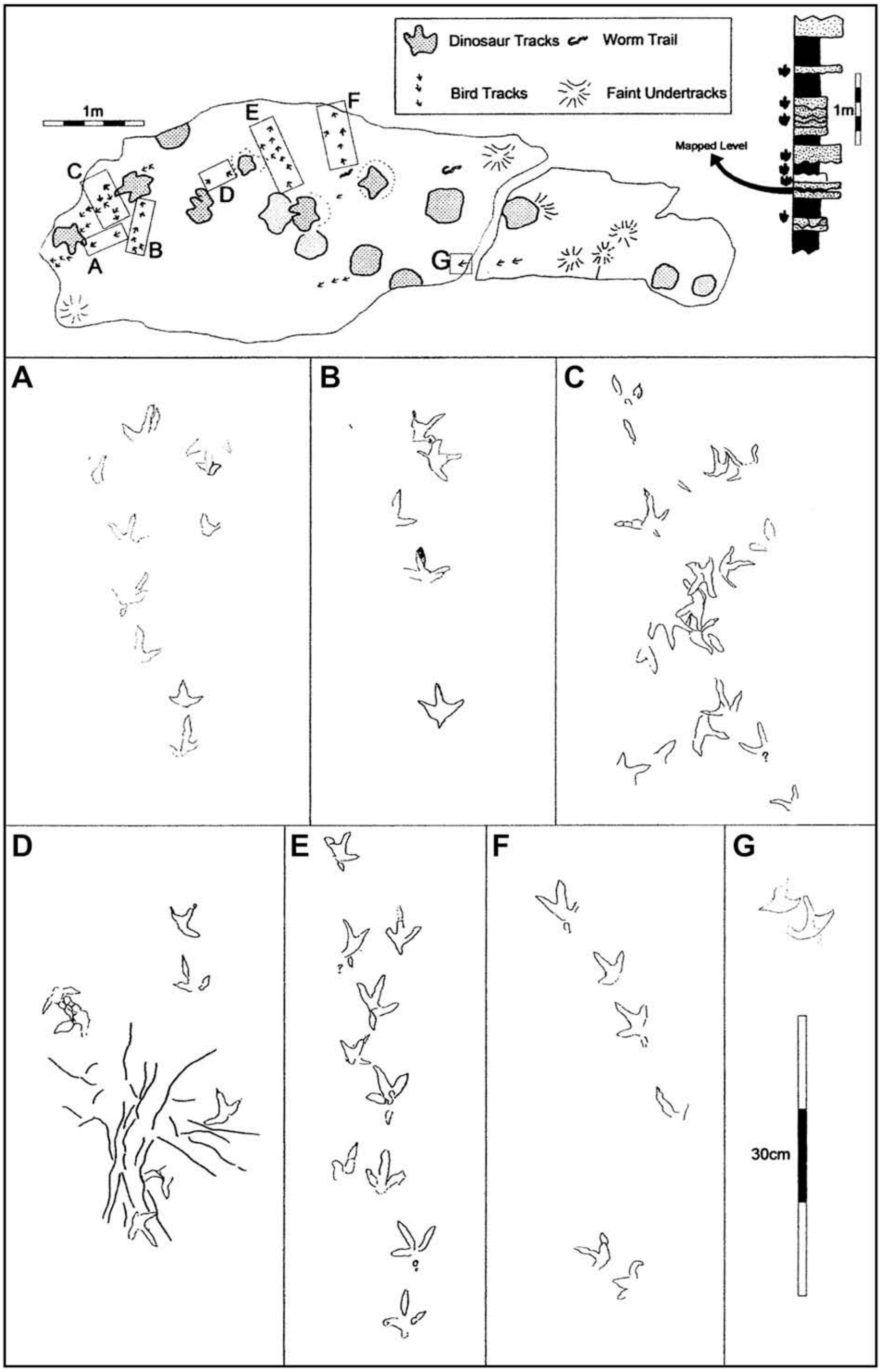

Fig. 13. Line drawing (top) of large slab CU 203.1 with *Ignotornis mcconnelli* topotypes and dinosaur tracks (modified after Lockley, 1991, figure 9.8), with details of seven track clusters (A–G) which show partial trackway segments and other isolated tracks. D: shows cast of a dinosaur undertrack with radial cracks. Compare with Fig. 14.

and 16). Site 2 is only 20 m to the north of Site 1 (Fig. 4) and represents the same stratigraphic horizon. Site 2 reveals additional, new and variably preserved trackways, and is important because the thin, 2–3 cm layer of cream-colored volcanic ash in which the *Ignotornis* tracks were made is preserved in situ, whereas it is mostly eroded away at sites 1 and 3 where underlying beds have been removed by quarrying. For this reason the most complete stratigraphic section occurs at Site 2 (Fig. 3), and represents a proxy "type section" in the immediate vicinity of Site 1. Site 3, 60 m north of Site 2, was discovered in 1988 and is the source of the large slab excavated at that time (Lockley et al., 1989).

There are a few poorly preserved tracks at Site 2 at a second horizon about 90 cm stratigraphically above the lower 'holotype' horizon. This is designated the second or "middle" level (Figs. 3 and 16). In 2007 more tracks were found *in situ* at Site 3, indicating a third level about 2.00 meters stratigraphically above the lower 'holotype level' (Figs. 3 and 17); we refer to this as the "upper" level to distinguish it from the middle and lower levels just described

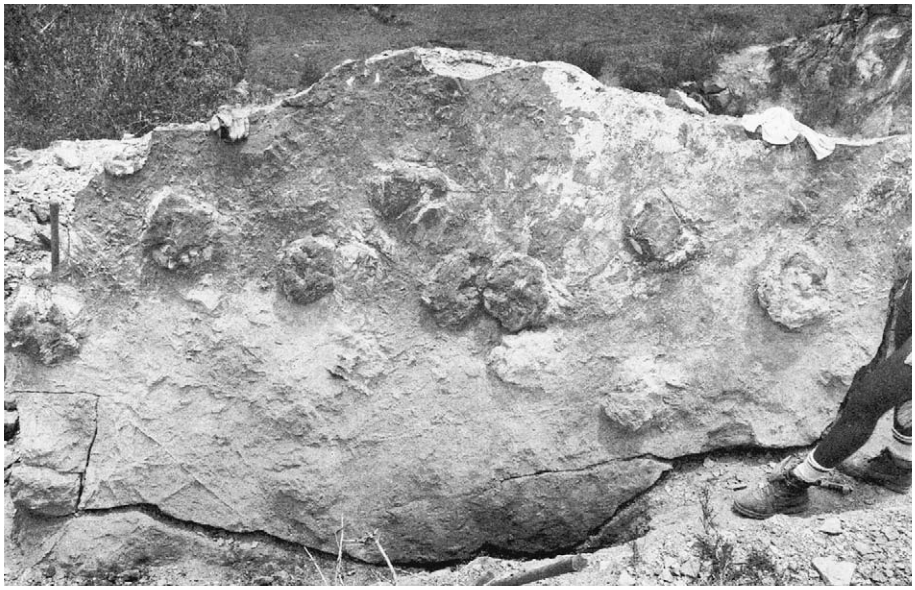

Fig. 14. Photograph of large slab CU 203.1 with *Ignotornis mcconnelli* topotypes and dinosaur tracks (after Lockley, 1991, figs. 4.6). Compare with Fig. 13.

(Figs. 3 and 4). Therefore, the stratigraphic occurrence of bird track levels at Sites 1–3 reveals that the middle level occurs only at site 2 and the upper level only at site 3, as follows:

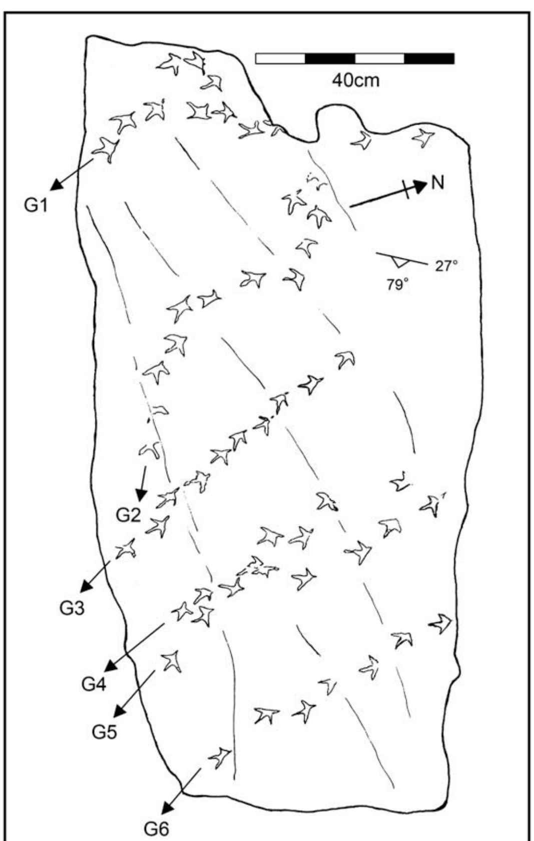

Fig. 15. Line drawing of *in situ* surface with multiple parallel trackways from site 1 (see Fig. 3). We infer that these tracks occur at the locality from which the UCM holotype and paratypes originated. The main trackways from this site have been replicated as specimen CU 203.28. Note sub-parallel orientations of trackways G4–G9.

Site 3: upper level and lower 'holotype' level.
Site 2: middle level, and lower 'holotype' level.
Site 1: lower 'holotype' level only.

Collectively these bird track levels increase the sample size to ~360 tracks, and demonstrate that identifiable *Ignotornis* tracks are distributed for a distance of ~80 meters laterally (northward) from the inferred type locality. They occur at three horizons spanning a stratigraphic interval of about 2 meters. However, the middle and upper layers reveal few well-preserved footprints and no identifiable trackway segments.

This study documents the entire, known *Ignotornis* track sample, including lower level specimens formally designated as the holotype and paratypes from the inferred 1930s discovery site (Site 1), inferred *in situ* topotypes discovered in 2007 from Site 1 and specimens more loosely designated as topotypes from the same general locality (Sites 2 and 3, discovered in 1988 and 2007). We also identify specimens from the middle and upper stratigraphic levels at sites 2 and 3 respectively (Fig. 3) and distinguish between original specimens in museum collections and specimens still in the field that are preserved only as replicas in the CU Denver collections.

3. Methods

We located and mapped *Ignotornis* tracksites (Sites 1–3) in the field and located them in measured stratigraphic sections (Figs. 3 and 4). We examined all the *Ignotornis* material and identified well-preserved tracks and trackways that could be measured. Specimens were photographed and traced on transparent acetate film in order to make black and white line drawings. In this process faint and indistinct tracks that could not be interpreted unambiguously were omitted in order to maximize clear illustration of recognizable tracks. All acetate tracings are original size and are archived in the CU Denver collections. Because the vast majority of the specimens consists of natural casts, the acetate tracings provide a convenient means of 'reversing' the drawings so as to present left and right footprints in their proper orientations; this is demonstrated by comparing the original, negative aspect of the holotype (Fig. 6) with the corrected, positive aspect (e.g., Fig. 10).

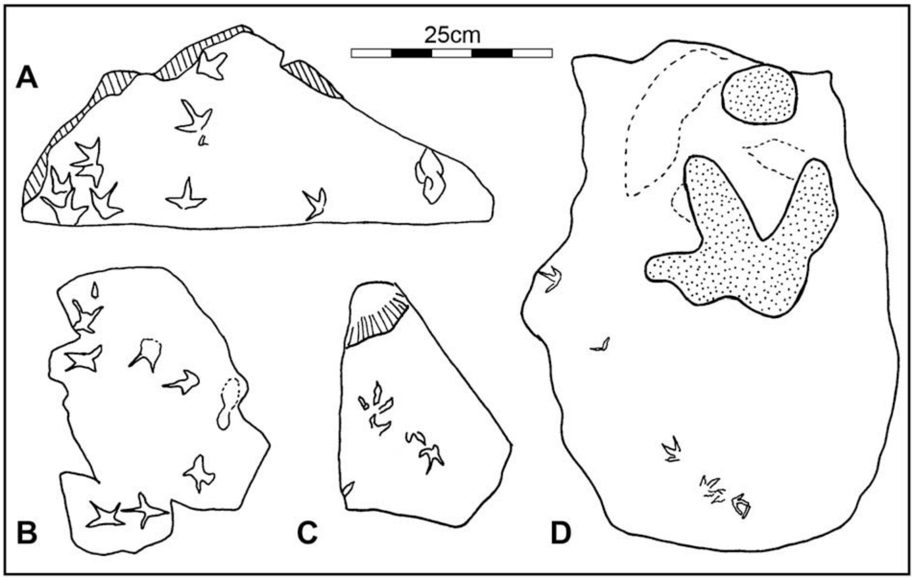

Fig. 16. A and B, Loose specimens (203. 25 and 203.24 respectively) from type horizon found at Site 1. C and D specimens (203. 26 and 203.27 respectively) found at site 2 from middle track horizon.

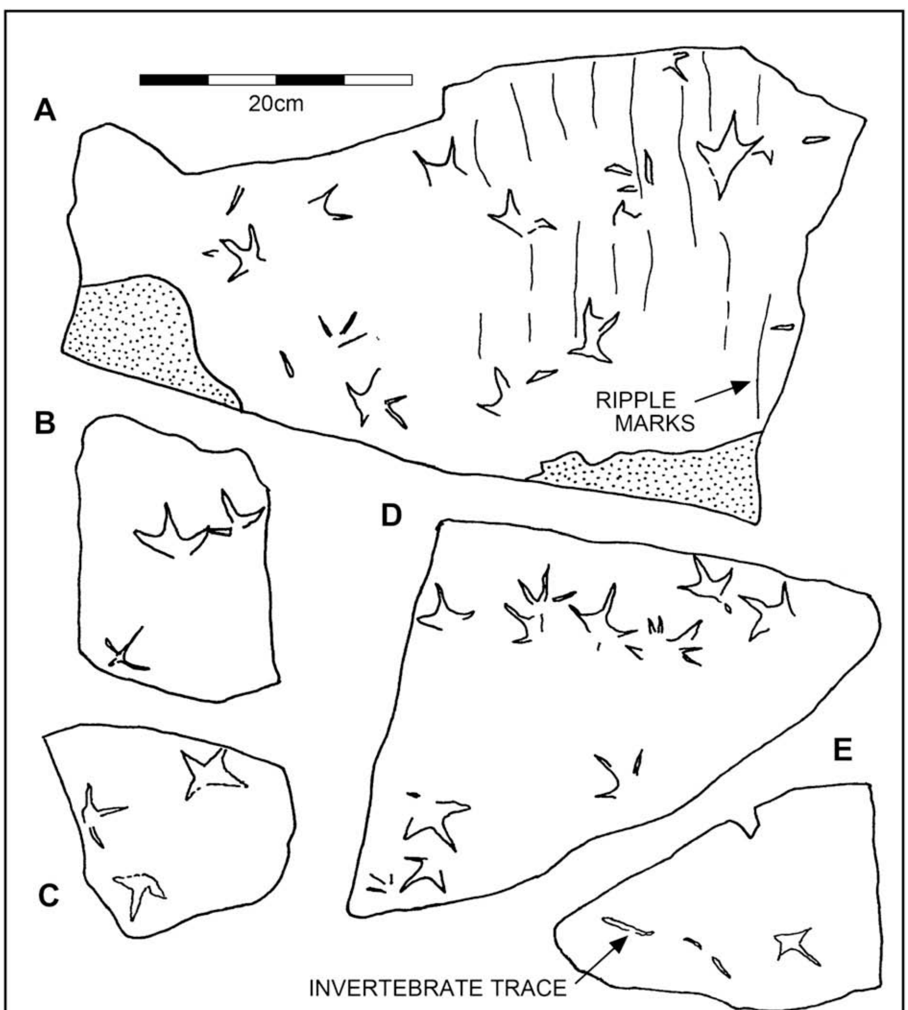

Fig. 17. Loose and *in situ* specimens found at Site 3 from upper horizon. A–E respectively are CU 203.11, CU 203.12, CU 203.13, CU 203.10, and CU 203.14.

Standard trackway parameters (Fig. 5) were measured directly from the original specimens (in the case of the holotype and paratypes), except for *in situ* specimens that were awkward to access. In such cases, measurements were made from tracings or molds (Tables 1–3). For consistency, the same individual (M.G.L.) made the measurements. Also, wherever possible we selected at least three consecutive footprints to measure in order to obtain mean values for trackways with three or more well-preserved footprints. The parameters recorded include track length (with and without hallux) track width, step, stride, pace angulation, trackway width, rotation of the pes relative to the trackway mid-line, and the divarication between digits I–II, II–III, III–IV and II–IV. We selected the mid-point of the track for step, stride and angulation measurements by drawing a transverse line, corresponding to maximum track width, between the distal extremities of digits II and IV, and marking the point at which this line intersects the mid-line of digit III. This mid-point consistently corresponds to the proximal end of digit III, which approximately corresponds to the functional midpoint of the foot where the proximal phalanx of digit III registered on the substrate.

4. Results

4.1. Description of geological setting

Based on our field observations we confirm that approximately 10 m of section in the Van Bibber Shale and 'Upper J' or "First" Sandstone (sensu Waage, 1961) are exposed at the Golden locality. Lithologies include gray and tan fine- and medium-grained sandstone, and gray shale and siltstone (Fig. 3). The lower part of the section (in the upper part of the Van Bibber Shale) is heterolithic, consisting of thinly-interbedded, fine sandstone, siltstone, and clay shale. Beds are 1 to 15 cm thick. Ripple cross-laminations and clay shale partings are common in the sandstone beds. Wave ripples and combined flow ripples are common on the tops of the sandstone beds.

The upper part of the section in the Upper J Sandstone (the 'First Sandstone' sensu Waage, 1961) is coarser, and includes two channel-fill deposits of trough cross-bedded tan medium sandstone (Fig. 3). The basal surfaces are scoured into the underlying sediment, and the upper channel deposit has a mud chip lag. Cross-bed sets are 10–15 cm thick. The two channel deposits are separated from each other by approximately 1.3 m of gray mud shale and laminated tan fine sandstone with gray siltstone partings. Some of the sandstone beds have invertebrate traces on top, but no tracks were discovered. Ripple marks and ripple cross-laminations are lacking, as are clay drapes. Thus, the exposed portion of the 'Upper J Sandstone' or 'First Sandstone' at the Golden locality is lithologically different from the Van Bibber Shale, and probably represents a different depositional environment that was less influenced by fluctuating energy conditions.

The stratigraphy of the Dakota Group is laterally and vertically variable. As a result various workers have used different terms to describe units in different parts of Eastern Colorado. We here interpret the track-bearing sequence with reference to the stratigraphic terminology that best describes the local sequence at the *Ignotornis* locality and in the immediate vicinity. All of the tracks were found within 80 m along strike at the same general locality, in the refractory clay quarries in the Dakota Group northwest of Golden, Colorado. These tracks occur within a 2-m-thick portion of

Table 2
Measurements for *Ignotornis* trackways (G 10- G17) from Site 2, ~20 m north of the inferred type locality

Track #	Track length w/hallux	Track length w/o hallux	Track width	Step	Stride	Pace angle	Track-way width	I–II angle	II–III angle	III–IV angle	II–IV angle	Inward rotation	Right or Left
Site 2													
G10.1	4.6	3.1	3.7	–	–	–	–	100	52	64	116	35	R
G10.2	–	3.5	3	10.5	–	162	5.0	–	–	–	–	10	L
G10.3	–	–	–	12.0	22.5	–	–	–	–	–	–	28	R
mean	**4.6**	**3.3**	**3.4**	**11.3**	**22.5**	**162.0**	**5.0**	**100.0**	**52.0**	**64.0**	**116.0**	**24.3**	
G11.1	6.2	4.5	5.0	–	–	–	–	–	–	–	–	32	L
G11.2	–	4.5	5.0	9.5	–	–	–	–	–	–	–	–	R
G11.3	–	3.5	4.5	8.0	17.0	–	–	–	–	–	–	24	L
mean	**6.2**	**4.2**	**4.8**	**8.8**	**17.0**	–	–	–	–	–	–	**28.0**	
G12.1	7.0	4.0	5.1	–	–	–	–	–	–	–	–	–	L
G12.2	–	4.5	5.0	9.7	–	172	5.2	103	60	75	135	–	R
G12.3	5.0	4.0	4.9	9.9	19.5	–	–	–	–	–	–	–	L
mean	**6.0**	**4.2**	**5.0**	**9.8**	**19.5**	**172.0**	**5.2**	**103.0**	**60.0**	**75.0**	**135.0**	–	
G13.1	6	4.5	4.1	7.1		116	7.2	110	46	50	96	–	R
G13.2	4.6	3.0	4.0	6.5	12.0	101	7.0	–	–	–	–	–	L
G13.3	4.5	–	3.6	5.2	9.0	–	–	–	–	–	–	–	R
mean	**5.0**	**3.75**	**3.9**	**6.3**	**10.5**	**108.5**	**7.1**	**110.0**	**46.0**	**50.0**	**96.0**		
G14	6.1	4.4	4.9	–	–	–	–	110	55	67	122	–	L
G15.1	5.3	–	–	–	–	–	–	–	–	–	–	–	L
G15.2	5.7	4.2	–	–	–	–	–	–	–	–	–	–	R
mean	**5.5**	**4.2**	**4.9**	–	–	–	–	**110**	**55**	**67**	**122**	–	
G16	–	4.5	–	–	–	–	–	–	–	–	–	–	L
G17.1	–	4.0	4.8	–	–	–	–	–	60	70	130	9	R
G17.2	–	4.0	5.2	8.5	–	90	9.6	–	–	–	–	23	L
G17.3	–	4.6	5.3	5.2	9.7	–	–	–	55	55	110	20	R
mean		**4.3**	**5.1**	**6.9**	**9.7**	**90.0**	**9.6**		**57.5**	**62.5**	**120.0**	**17.3**	
G 18.1	5.2	3.9	5.8	–	–	–	–	78	70	70	140	35	L
G 18.2	5.9	4.4	5.4	5.7	–	80	9.0	78	70	58	128	0	R
G 18.3	6.7	4.3	5.7	7.2	8.5	92	10.3	85	68	56	124	−15	L
G 18.4	5.2	4.4	5.5	6.5	9.8	135	8.2	–	65	61	126	0	R
G 18.5	5.8	4.4	5.4	8	13.1	89	10.7	94	60	58	118	0	L
G 18.6	5.8	4.5	5.6	9.4	12	139	7.5	90	85	61	146	15	R
G 18.7	5.3	3.8	5.1	6.6	15	97	8.7	95	58	67	125	12	L
G 18.8	6.1	4.2	5.2	5.6	9.3	–	–	90	68	56	124	13	R
mean	**5.75**	**4.23**	**5.46**	**7.0**	**11.3**	**105.3**	**9.1**	**87.1**	**68**	**59.6**	**128.9**	**7.5**	

Table 3
Measurements for *Ignotornis* trackways (A–G) from Site 3, ~80 m north of the inferred type locality

Track #	Track length w/hallux	Track length w/o hallux	Track width	Step	Stride	Pace angle	Track-way width	I–II angle	II–III angle	III–IV angle	II–IV angle	Inward rotation	Right or Left
Site 3													
A	–	**4.2**	**5.0**	–	–	–	–	–	**84**	**54**	**138**	–	R
B1	–	**4.2**	**5.2**	–	–	–	–	–	–	–	–	–	R
B2	**5.7**	**4.5**	**5**	–	–	–	–	–	**60**	**60**	**120**	–	R
C	**5.0**	**4.0**	**4.8**	–	–	–	–	**82**	**64**	**46**	**110**	–	?
D		**3.2**	**4.7**										L
E.1	–	4.0	5.2	–	–	–	–	–	65	62	127	22	R
E.2	–	4.2	–	7.2	16.6	157	6.0	–	–	–	–	14	L
E.3	6.0	4.5	4.9	9.2	18.7	170	4.8	93	52	52	104	20	R
E.4	5.5	4.0	5.0	9.5	–	–	–	107	62	46	108	16	L
mean	**5.8**	**4.2**	**5.0**	**8.6**	**17.7**	**164**	**5.4**	**100**	**60**	**53**	**113**	**18**	
F.1	–	4.0	–	–	–	–	–	–	–	–	–	–	?
F.2	5.6	4.2	4.0	–	–	–	–	102	66	60	126	–	R
F.3	–	4.0	4.5	–	–	–	–	–	–	–	–	–	
F.4	6.0	3.2	5.2	–	–	–	–	92	84	50	134	–	L
mean	**5.8**	**3.9**	**4.6**					**97**	**75**	**55**	**130**		
G	–	**4.7**	**5.2**	–	–	–	–	–	**64**	**54**	**118**	–	R

a studied stratigraphic interval approximately 10 m thick (Fig. 3). This section of alternating mudstones (shales) and thin sandstones is in the uppermost units of the Dakota Group known as Sequence 3 (*sensu* Weimer, 1984, 1989). This includes the Kassler Sandstone overlying Sequence Boundary 3 (SB 3) and the overlying Van Bibber Shale Member of the Muddy or J Sandstone (Lockley et al., 1989, 1992a, fig. 14). The track horizons at Sites 1–3 occur, therefore, in the Van Bibber Shale Member of the J sandstone. The terms J Sandstone and D Sandstone are widely used in subsurface descriptions of the Dakota Group by the oil and gas exploration industry (Land and Weimer, 1978). The Sequence 3 deposits, which are essentially co-extensive with the J Sandstone, were originally interpreted rather generally as a deltaic facies (Waage and Eicher, 1960). This interval has also been dubbed the Dinosaur Freeway (Lockley et al., 1992a) and in the broadest sense represents a complex mosaic of facies associated with the coastal plain deposits of the Cretaceous Western Interior Seaway during the Late Albian and Early Cenomanian. At this time sea level was rising and heralding the global Cenomanian transgression (T 6, *sensu* Kauffman, 1977). This caused aggradation of coastal plain sediments, especially in valley systems separated by intervening topographic interfluve highs that were probably fault controlled (e.g., Weimer, 1984, 1989).

The sequence stratigraphy and facies architecture of the Dakota Group is complex and has been studied in detail in southeastern Colorado (Holbrook, 1996, 2001; Holbrook and Wright Dunbar, 1992; Holbrook et al., 2006; Scott et al., 2004) allowing dinosaur tracks in that region to be placed in sequence stratigraphic context (Lockley et al., 2006a). Detailed geochronological studies in southeastern Colorado (Holbrook et al., 2005, 2006; Scott et al., 2004) have also provided a well-calibrated series of dates ranging from about 100–98.47 Ma for the lowermost of these small sequences (Sequence boundary SB 3.1) to between about 97.85–97.17 Ma for the uppermost of these three sequences (Sequence boundary SB 4). These studies helped show that Weimer's Sequence 3 can be subdivided into three smaller sequences, at least in SE Colorado. This conclusion was anticipated by Waage (1961, p. 93) when he described "as many as three transgressive-regressive cycles" in the South Platte Formation as a whole. The oldest of these three cycles consists of the Plainview Sandstone and overlying marine-influenced sand and shale, which can be broken down into two sub-cycles (Waage, 1961, fig. 13). According to Weimer (1984, 1989), this older cycle belongs in Sequence 2, with the base of Sequence 3 (SB 3) located at the base of the overlying Kassler Sandstone.

The stratigraphic setting thus indicates that the *Ignotornis* tracks occur in basal cycle of overlying Sequence 3, i.e., in the upper part of the regressive-transgressive cycle represented by the Kassler Sandstone and the overlying Van Bibber Shale respectively. This sequence is in turn overlain by another sequence referred to by Waage (1961) as the 'First Sandstone' equivalent to the 'Upper J Sandstone' (Fig. 3). This younger unit is easily identified in the study area, where it cuts downward into the Van Bibber Shale. However, in the Golden area it does not contain tracks even though they occur in this unit at Dinosaur Ridge.

4.2. Track descriptions

Our measurements show considerable variation in the configuration of trackways on the various slabs, although some parameters are fairly consistent. For this reason it is best to describe distinctive trackways separately before pooling the data. The trackways are numbered 1–15 (Figs. 6–9) in the UCM sample and A–N in the CU Denver sample (Tables 1–3).

4.2.1. Holotype trackway UCM 17614

The holotype trackway (UCM 17614: Figs. 6 and 10) consists of six consecutive footprints, illustrated by Mehl (1931a, fig. 1), and herein designated as trackway 1, with individual tracks 1.1–1.6. Although Mehl's measurements are useful and interesting for comparative purposes, he did not specify exactly how they were taken. Therefore, for consistency we follow our method (see Fig. 5) and refer to Mehl (1931a) only for the purposes of comparison. Mehl described the length of digits I–IV respectively as 17, 22, 29 and 25 mm, but did not indicate whether these were measurements from one selected footprint or averages. We infer the former case. In conventional ichnological notation digit III is longest > IV, > II > I. It is notable that digit II is consistently short and wide compared to digits III and IV. Other consistent features of all tracks are what Mehl (1931a, p. 444) called "a short web (?) connecting the base of second, third, and fourth digits and possibly a very rudimentary web connection between the base of the first and second digits." We interpret the pattern somewhat differently, and note that the 'web' is more pronounced, and more anteriorly situated in the hypex between digits III and IV than in the hypex between digits II and III, and see no evidence for 'rudimentary' webbing between digits I and II. This condition (hypex web III–IV > hypex web II–III) is typical of the semi-palmate condition seen in many modern birds, as noted by Lockley et al. (2007). Hypex III–IV is typically anterior to hypex II–III in most birds (and most non-avian theropod dinosaurs). Given that this web trace occurs consistently throughout the *Ignotornis* sample of ∼360 footprints, we are very skeptical of recent claims that such web traces are preservational artifacts (Falkingham et al., 2009).

Our measurements for all six footprints (1.1–1.6) in the holotype trackway provide an average track length (with hallux) of 5.5 cm and width of 4.9 cm. Mean step and stride are 6.7 and 12.6 cm respectively (Table 1). This is at variance with Mehl's reference to a stride of "about 7.8 cm" which evidently referred to step (see Fig. 10). The step and stride of the holotype indicate a shortening (deceleration) between tracks 1.4 and 1.6 (Table 1), which may be related to a turn to the left (Fig. 10).

4.2.2. Paratype specimen UCM 98120

This specimen reveals four trackways, here numbered 2–5 (Figs. 7 and 10). In most morphological features these four trackways are similar to the holotype. Average track length in trackway 2 is longer (6.4 cm compared with 5.5 cm for the holotype, and a range of 5.1–5.9 cm for all other measured paratypes: see Table 1). All the trackways on this slab have longer steps and correspondingly greater pace angulations than the holotype, and trackway 5 shows the highest digit II–IV divarication angles in the whole sample. However, in all other respects the track morphologies are similar to the holotype.

4.2.3. Paratype specimen UCM 98121

This specimen (Fig. 8) has four trackways, here numbered 6–9. Trackway 6 shows three footprints with short steps, and trackways 7 and 9 are based on isolated footprints. Trackway 8 is the most interesting and unusual. It consists of at least nine closely spaced, partially-overlapping footprints indicative of a "shuffling" gait. At first sight this assemblage of parallel tracks resembles two overlapping trackways, but on closer inspection it is clear that there are two rows of footprints, one showing all right footprints, the other all lefts. The trackway width is 7.5 cm which is typical of most of the other trackways (mean 7.1 cm: range 5.6–8.3), but the steps are extremely short, creating a very low pace angulation (64°).

4.2.4. Paratype specimen UCM 98122

This specimen (Fig. 9) includes at least six trackways, here numbered 10–15. With the exception of trackway 13, all others are represented by only a single footprint. Trackway 13, like trackway 8 described above, also appears to represent an individual moving with a "shuffling" gait.

4.2.5. Inferred in situ topotype specimen CU 203.28

These *in situ* tracks (Fig. 15) discovered in 2007, occur on an *in situ* bedding plane surface with multiple parallel *Ignotornis* trackways (Figs. 4 and 15) on a hanging wall at the south end of the of the quarry, herein designated as Site 1. The specimen number used here, CU 203.28, refers to a latex mold and replica of the track surface; these were used to facilitate detailed study and measurement in the laboratory (Figs. 4 and 15; Table 1). On the basis of the lithology of the track-bearing unit, similarities in the preservation of the tracks as well- preserved natural casts, and the distribution (spacing) of trackways, we infer this *in situ* outcrop to be the best candidate for the original type locality. For this reason we associate this track-bearing surface with the original holotype specimens and those designated as paratypes and topotypes herein. Indeed, it is possible that the trackways on this surface are continuations of the holotype and paratype trackways. This, at a minimum, allows us to confer topotype status on the new trackways.

The main Site 1 surface is about 85 cm wide (N-S orientation) and 160 cm long (E-W) orientation, with an additional smaller area with several trackways exposed near the southwest corner of this surface (Fig. 4). These two adjacent exposures have been disturbed by multiple small faults with displacements of a few centimeters (shown as E-W lines in Figs. 4 and 14) but both represent the same main surface. Because the tracks are *in situ* it is possible to determine that they are oriented predominantly towards the south (between S and SSW). At least 10 trackways are identifiable. To distinguish these from the 1930s sample we have numbered them with the prefix G, indicating Golden, as G1–G10. Trackways G1–G3, exposed in the small SW sector (Fig. 4) are poorly preserved, but trackways G4–G9 are well preserved, each with between 7 and 10 consecutive footprints. Altogether, the exposures of this surface at Site 1 (Fig. 4) contain a total of at least 67 recognizable footprints.

4.2.6. Additional in situ topotype specimens

Additional *in situ* tracks are located at Site 2, about 20 m north of Site 1 (Fig. 4). These exposures reveal surfaces with about 40 additional tracks that we tentatively resolve into eight trackways (G10–G17: see Fig. 4 and Table 2). The style of preservation, and the color of the bedding plane surface (yellow at Site 2 rather than grey at Site 1) differs slightly from that of the UCM holotype and paratypes, including the *in situ* topotypes (CU 203.28) described above. Given that topotypes represent any material of the same taxonomic affinity as a type specimen, that originates from the type locality, the Site 2 specimens must also be considered topotypes. We make this assertion for two reasons: 1) the precise type locality was never designated, although we consider it most likely at or very near to Site 1 (Fig. 4). 2). There is sufficient ambiguity surrounding the exact point of origin of the holotype to allow the possibility that it originated at or near Site 2, 20 m to the north of Site 1. It could even have come from somewhere near site 3, another 60 meters further north, although we consider this unlikely based on color and preservation of the specimens. Regardless of these ambiguities, Sites 1–3 are all so close together (Fig. 4) as to allow all specimens from the lower level (Fig. 3) to be considered part of a single ichnofauna more or less closely associated with the holotype and the presumed type locality.

4.2.7. Inferred topotype specimen CU 203.35

Specimen 203.35 consists of a slab with a well-preserved *Ignotornis* trackway, here designated as G 18 (Fig. 12; Table 2), and two other incomplete tracks, preserved as natural casts. The specimen is very similar in preservation to the original holotype and those designated here as paratypes. Only eight of the ten tracks are complete. Average size of the tracks (length with hallux 5.75 cm, and width 5.46 cm) is slightly larger than in the holotype specimen, with a more irregular gait and slightly greater average digit divarication (compare Tables 1 and 2). The trackway segment indicates a trackmaker that alternated between lengthening and shortening its steps while making a slight right turn.

4.2.8. Topotype slab CU 203.1

This large slab, found at Site 3 in 1998 (Figs. 13 and 14), reveals between 60 and 70 complete and partial *Ignotornis* footprints, associated with at least 20 poorly-preserved dinosaur tracks and undertracks. Some of the bird tracks are obscured by the dinosaur tracks that would have been registered at a later time—they are stratigraphically above the *Ignotornis* tracks but penetrate as undertracks to the *Ignotornis*-bearing surface. Nevertheless, it is possible to recognize at least seven partial bird trackways. In order to distinguish these from the holotype and paratype samples these are referred to as trackways A-G (Fig. 12, Table 3). Many of these trackways are difficult to discern, and in some cases they are obscured by overprinting by other *Ignotornis* footprints or dinosaur tracks. However at least one trackway (E) shows six consecutive footprints with typical *Ignotornis* features, including size (average pes length 5.8 cm), hallux, and inward rotation of the pes (Fig. 13). Trackways A, B and F also show these features to some degree, trackways C, D and G are incomplete and ambiguous. Nevertheless, the trackways and isolated tracks all indicate that the ichnogenus is *Ignotornis* and that the trackmakers were in the same size range as the birds that produced the tracks in the holotype and paratype samples.

4.2.9. Tracks from above the type horizon: the middle level

A few poorly preserved natural casts of bird tracks, provisionally assigned to *Ignotornis*, occur at a horizon ~90 cm above the lower 'holotype' track layer at Site 2 (Fig. 3). At least 10 tracks are identifiable on specimens CU 203.26 and 203.27 (Fig. 15C, D), and other tracks are identifiable in the field. Tiny (trail diameter ~1 mm) zigzagging *Cochlichnus* traces are evident near the footprints on CU 203.27.

4.2.10. Tracks from above the type horizon: the upper level

The upper bird track level 2 m immediately above the Site 3 locality from which CU 203.1 was located (Fig. 3) yielded approximately 30 moderately well- to poorly-preserved *Ignotornis* tracks (Fig. 16). These specimens were preserved as impressions, rather than casts.

5. Synthesis

The discovery of abundant *Ignotornis* tracks (~70 in 1930, another 60 between 1930 and 1983, ~70 in 1988 and at least 163 additional mapped and collected tracks in 2007 and 2008) indicates that the Golden locality yields far more material (~360 footprints) than was indicated by Mehl's 1931 report. Our re-study of the site and specimens in two phases (1988–1989 and 2007–2008) indicates that tracks in fact occur at three stratigraphic levels, although the middle and upper levels (~90 and ~200 cm above the main layer), yield limited material that is not as well-preserved as those from the lower level. The number of known tracks (about 360) and trackways (about 50) discovered by various investigators since 1930 is summarized in Table 4.

Altogether, 41 measurable trackways have been studied in detail. Not all tracks and trackways reveal consistently impressed hallux impressions characteristic of well preserved *Ignotornis mcconnelli,* although there is a strong tendency for the hallux to be well-preserved in specimens we know or infer to originate from Site 1. The lack of hallux impressions in some footprints is probably a preservational, extramorphological artifact and not an indication of a different track morphotype. With such a large sample (Tables 1–4) it is possible to describe the variation in size and gait of the *Ignotornis* trackmakers. Moreover, the readily accessible samples should provide future researchers with abundant material to study variation in track morphometrics and preservation.

Because multiple tracks in each trackway all were produced by one bird, the data was examined by comparing track and trackway parameters of trackway averages or isolated tracks (Table 5). The size consistency among the dimensions of all measurable tracks (Figs. 6–9, 12 and 15) is striking. For example, track lengths (with hallux) and widths in trackway 1 (the holotype) have mean values of 5.5 and 4.9 cm respectively which are almost identical to the overall track length and width means of 5.5 and 4.8 cm for all trackways. The standard deviations of these dimensions are very low (0.42 and 0.43 cm respectively) indicating remarkably little variation. Although tracks are not as well-preserved at Sites 2 and 3 as at Site 1, based on measured track parameters, no evidence was found to differentiate the track samples as morphologically distinct. Because of the size and morphological similarities, we infer that, like the holotype, the paratype and topotype samples all belong to the ichnogenus *Ignotornis*. Thus, we interpret this as a monospecific assemblage of bird tracks, with dinosaur and crocodilian tracks in the vicinity.

Table 4
Summary of *Ignotornis* tracks and trackways discovered and reported since 1930

Date(s) of discovery and collection	Number of tracks	Number of trackways	Source of information
1930	~70	~15	Mehl (1931a)
1830–early 1980s	~60	~11	J. Sawdo pers. comm. Univ. of Missouri
1988	~70	~7	Lockley et al. (1989)
2007–2008	~160	~17	Present study

The digit divarication angles for all trackways are fairly comparable, with standard deviations for the angles between digits ranging from 8–12°. These tracks all possess the typical avian characteristic of having divarication angles between digits II and IV greater than 90°: the overall mean for this angle is 124°. The strong posterior rotation of the hallux (digit I), typically subtends a slightly obtuse angle with digit II, and is also a diagnostic avian feature, associated with various extant and extinct groups, and the overall mean of 98° is consistent with this character.

Analyses of step and stride patterns in the trackways reveal much greater variation than the track dimensions. This is to be expected because all trackmakers can vary their gait depending on speed and substrate conditions. However, in the case of the *Ignotornis* trackmakers there appear to be two quite distinct gaits which we herein refer to as "walking" and "shuffling." The walking gait is the most common and regular, especially with respect to trackway width and rotation of the pes axis (Tables 1 and 2). Trackway width, which tends to narrow slightly as the step length increases, averages 6.8 cm, with a standard deviation of 1.3 cm. The walking gait is apparent in all specimens except for trackways 8 and 13 (UCM 98121 and UCM 98122), which include "shuffling" patterns. The mean "walking" step length (without trackways 8 and 13) is 7.9 cm. Thus, the space between footprints is only a little more than 2 cm longer than the average track length. In almost all cases, where there are no obvious changes of direction, there is an inward rotation of digit III relative to the trackway midline (mean = 18°).

In some normal walking trackways there is an alternation of strong and weak inward rotation of digit III in consecutive left and right footprints. For example, in the case of trackway 4 (paratype UCM 98120) consecutive rotation measurements are 18°, 0° and 15° (for the L-R-L sequence:Table 1). A similar alternating pattern (22°, 14°, 20°, 16° for a R-L-R-L sequence) was recorded for trackway E from Site 3. Such alternating patterns create what may be called "regularly asymmetric" trackways that are distinct from "regularly symmetric" trackways in which rotation patterns are similar in both left and right footprints. Interpretations of such trackways are suggested below. Other trackways may be more variable or irregular with respect to digit III rotation depending on such factors as changing step length (acceleration, deceleration) and changes in direction or even substrate consistency.

The shuffling gaits recorded for trackways 8 and 13 are of particular interest for the insight they offer into the behavior of the trackmakers. It is clear from these two samples that they were made by birds with foot sizes and trackway widths very similar to those recorded for the remainder of the sample; track widths are 4.6 and 4.7 cm respectively for trackways 8 and 13 (Figs. 8 and 9). However, the steps are very short relative to the average footprint length. Thus, in trackway 13 the foot length is 5.2 cm but the step is 4.6 cm. This causes overlap of consecutive tracks that in turn leads to a very distinctive pattern indicating shuffling behavior.

6. Paleoecological inferences

Although *Ignotornis* was the first bird track ever named from the Mesozoic, the holotype, paratype and additional topotype

Table 5
Means of track and trackway parameters from each trackway; each trackway includes one to eight tracks. The overall means, standard deviation, and sample sizes (N) are shown at the bottom of the table

Trackway designation	No. of tracks in trackway	Length with hallux	Length without hallux	Width	Step	Stride	Pace angle	Track-way width	I–II digit angle	II–III digit angle	III–VI digit angle	II–VI digit angle	Inward Rotation
1	6	5.5	3.9	4.9	6.7	12.6	133	7.5	101	58	60	118	16
2	3	6.4	4.5	5.2	8.6	16.8	160	5.6	92	59	49	108	30
3	5	5.6	4.3	4.5	9.4	18.3	157	6.0	103	78	56	134	9
4	3	5.9	4.2	4.3	8.4	15.8	140	6.7	107	61	64	125	11
5	4	5.3	3.6	5.4	8.2	15.1	134	8.3	79	81	67	143	13
6	3	5.1	3.9	5.1	5.5	9.7	128	7.5	92	62	60	122	11
7	1	5.4	4.2	5.0					85	60	65	125	
8	1	5.1	4.0	4.6	3.6	4.3	64	7.5	90	80	75	155	11
9													
10	1	5.4		5.1					92	73	73	146	
11	1	5.2	4.0	5.2						80	60	140	
12	1		3.5							75	55	130	
13	3	5.2	3.6	4.7	4.6	4.9	65	8.1	106	55	55	111	11
14	1			5.2					105	70	55	125	
15	1		3.8	4.5						65	55	120	
G1	3		3.9	4.4	7.9	15.2	150	5.9		61	84	139	23
G2													
G3	1		4.0	5.0						48	62	110	
G4	3	5.8	4.5	5.0	6.6	12.3	138	7.0	94	62	67	129	24
G5	3	5.4	4.3	5.2	7.3	13.8	148	6.8	98	64	63	127	21
G6	8	5.1	4.1	3.9	6.0	11.1	119	5.7	112	52	59	111	25
G7	3	5.8	4.3	4.5	8.0	14.2	120	7.6	78	70	54	125	9
G8	3		4.1	4.6	8.9	17.0	170	5.2		58	66	129	26
G9	6	5.4	4.2	4.7	8.2	16.0	154	6.0	107	63	52	112	16
G10	3	4.6	3.3	3.4	11.3	22.5	162	5.0	100	52	64	116	24
G11	3	6.2	4.2	4.8	8.8	17.0							28
G12	3	6.0	4.2	5.0	9.8	19.5	172	5.2	103	60	75	135	
G13	3	5.0	3.8	3.9	6.3	10.5	109	7.1	110	46	50	96	
G14	1	6.1	4.4	4.9					110	55	67	122	
G15	2	5.5	4.2	4.9					110	55	67	122	
G16	1		4.5										
G17	3		4.3	5.1	6.9	9.7	90	9.6		58	63	120	17
G18	8	5.8	4.2	5.5	7.0	11.3	105	9.1	87	68	61	129	8
A	1		4.2	5.0						84	54	138	
B1	1		4.2	5.2									
B2	1	5.7	4.5	5.0						60	60	120	
C	1	5.0	4.0	4.8					82	64	46	110	
D	1		3.2	4.7									
E	4	5.8	4.2	5.0	8.6	17.7	164	5.4	100	60	53	113	18
F	4	5.8	3.9	4.6					97	75	55	130	
G	1		4.7	5.2						64	54	118	
Mean		**5.5**	**4.1**	**4.8**	**7.6**	**13.9**	**132**	**6.8**	**98**	**64**	**61**	**124**	**18**
Std. Dev.		**0.42**	**0.34**	**0.43**	**1.8**	**4.5**	**32**	**1.3**	**10.2**	**9.6**	**8.2**	**12.2**	**7.1**
N		**27**	**37**	**37**	**22**	**22**	**20**	**21**	**25**	**35**	**35**	**35**	**20**

specimens have not been subjected to any systematic study since Mehl (1931a) published his initial brief description of the single holotype trackway (Fig. 6). This study presents a much richer picture of the track-producing locality, based on a much larger sample of tracks whose morphology has been recorded in detail. Thus, the study allows various paleobiological inferences including:

(1) contribution of footprint morphology to constrain track maker identification;
(2) behavioral inferences of individual behavior based on distinctive trackway gaits;
(3) behavioral inferences of group behavior based on multiple trackway patterns;
(4) paleoenvironmental interpretation of track beds based on sedimentology.

6.1. Track maker identification

It is well-known that the majority of Cretaceous bird tracks indicate shorebirds (Lockley et al., 1992b), many of which left tracks reminiscent of Charadriiformes, comparable to modern sandpipers and plovers (e.g. Murie, 1975; Elbroch and Marks, 2001). Most of these have very short medially-directed hallux traces or no hallux traces at all. Well-developed posterior hallux traces are typical of members of the herons (Ciconiiformes). This family also shows incipient semi-palmate webbing in the hypices between digits III and IV, exactly as seen in *Ignotornis*. While we can not infer that the *Ignotornis* track maker was a heron, egret or other member of the extant Ciconiiformes clade, we can confidently infer that its foot morphology was highly convergent with this group.

Recently Kim et al. (2006) identified the ichnogenus *Ignotornis* in the Lower Cretaceous of Korea, but this is currently the only other report of the ichnogenus outside the type locality. In comparison with *Ignotornis*, the ichnogenus *Hwangsanipes* (Yang et al., 1995) from the Upper Cretaceous of Korea is quite similar, though significantly larger and with a slightly greater web development between digits III and IV.

6.2. Inferences based on trackway gaits

The shuffling behavior inferred from the short-stepping trackways 8 and 13 suggests heron-like behavior that is well documented among extant species. Meyerriecks (1959, 1962) and

Willard (1977) reported 'foot-stirring' in shallow water by herons and other waders, gulls and shorebirds as a means to bring invertebrates to the surface of the substrate. Meyerriecks (1962, p. 51) also classified other heron feeding behaviors that involved standing and foot motion as "stand and wait", "wade and walk slowly", and "disturb and chase."

If the shuffling pattern observed in trackways 8 and 13 do indeed reflect a form of foot-stirring behavior, it suggests that the tracks were made in shallow water. This inference is supported by the relatively deep and clear tracks that indicate a soft substrate that had not dried out prior to track making. However, the lack of evidence for dissolution of the tracks by prolonged submergence suggests that they were likely buried by the overlying sand soon after they were registered. As noted below, the composition and properties of the substrate, whether submerged or emergent, are also important factors in determining preservation.

At the very least, the birds may have simply slowed their gait during foraging as in the "wade and walk slowly" strategy employed by extant herons. Similarly, a "stand and wait" mode may be recorded by trackway G6 in which the regular pattern of left and right footprints in the sequence G 6.1–G 6.5 is interrupted when the next footprints (G6.6 and G6.7) appear side by side immediately in front of G6.5. This strongly suggests that the trackmaker slowed, between G6.5 and G6.6, and then made a temporary stop.

Meyerriecks (1962, p. 50) stated that he would "speculate briefly on the origin and evolution of heron feeding behavior – speculative because behavior does not fossilize and the foraging techniques of many species are not (or poorly) known." The claim that behavior does not fossilize ignores the evidence of trace fossils, and so is overstated. (cf., Seilacher, 1967). However, although there is little direct trace fossil evidence of avian feeding behavior, a few examples are known. One of the best examples is the "dabble trails" made by the beaks of *Presbyornis*-like birds in association with a well preserved trackway (ichnogenus *Presbyornithiformipes*) from the Eocene, Green River Formation (Erickson, 1967; Yang et al., 1995). The shuffling *Ignotornis* trackways represent a different type of feeding trail (Fodichnia) since they were made by the trackmaker's feet rather than their beaks. As such, they appear to be the first reported "foot-generated" avian feeding traces reported from the fossil record.

Excluding the two shuffling trackways, step lengths varied from 5.5 cm in trackway 6, which is a "near-shuffling" gait, to 11.3 cm in trackway G10, which represents the longest step recorded. It is interesting to note that in the *Ignotornis* sample from Korea (Kim et al., 2006) step (or pace) also varies from a 5.5 to 13.0 cm ($n = 10$ trackways), although in both the Colorado and Korea samples, step length variation ranges considerably in individual trackways. It is outside the scope of this paper to analyze and compare inter- and intra-trackway variation in the Colorado and Korean samples. However, we suggest that the alternation of strong and week pes rotation referred to in the aforementioned trackways 4 and E as "regularly asymmetric" (Tables 1 and 3) could be interpreted simply as walking with the trackmaker's head and or body turned to one side (Brown, 1999; Lockley, 2001). Such "regularly asymmetric" patterns include long-short-long-short sequences referred to as "limping" trackways (Lockley et al., 1994). However, it should be noted that "limping" does not imply that we are free to infer a pronounced injury or other obvious abnormality except in cases were additional evidence such as a foot deformity is recorded (Lockley et al., 1994). Slight but repeated irregularities or asymmetries in trackways may simply reflect subtle changes in gait as animals shift their weight to one side or another to accommodate slope, wind, turning of the upper body or other nuances of behavior (Brown, 1999)

6.3. Inferences of group behavior based on multiple trackways

Clear parallel and consistently spaced trackways, such as the G4–G9 cluster (Fig. 15) from Site 1 have rarely been reported for Cretaceous or Cenozoic birds. In this small area (about 1.2 m wide), there are at least six trackways with the same or similar orientations (towards the SE). These generally show a somewhat consistent inter-trackway spacing (*sensu* Lockley, 1989), which, in turn, can be a strong indicator of gregarious behavior.

Variation in track size on the Site 1 track-bearing surface, although not pronounced (Table 1), is enough to suggest multiple individuals rather than repeat activity by the same individual. However, close inspection of these trackways shows that several indicate individual activities that could not have occurred simultaneously if a flock of six individuals passed as a gregarious group moving together in tight formation at a steady walking pace: i.e. shoulder to shoulder on a broad front (*sensu* Lockley, 1989). The evidence that supports this inference is threefold. First, as noted above, one trackway (G6) indicates an individual that stopped (while the other five evidently did not). Second, trackways G7 and G8 cross, which means that one passed later, behind the other. Third, trackways G4 and G5 indicate that the trackmakers were changing direction; in fact, G5 eventually crosses G 6.

Modern herons and egrets sometime congregate in small mono- or multi-specific groups, and may forage in more or less the same direction, while maintaining a preference for certain physical settings and water depths (Meyerriecks, 1962). Thus, the parallel trackways may represent a 'loosely-knit' group of similar-sized, probably monospecific foragers (based on track size and morphology) moving slowly in the same direction. This would have allowed individuals to change direction, slow, stop, and follow in line at a slow walking pace without staying close together in tight formation.

Fuentes Vidarte (1996) reported one example of parallel trackways attributed to birds from the Berriasian of Spain. However, this morphotype, named *Archaeornithipus meijidei* by these authors is not unequivocally avian. The tracks bear little close resemblance to other named avian ichnogenera from the Mesozoic or Cenozoic. Skeptics might interpret these large and variably sized ($\sim$7.5–16.5 cm long) tracks as those of various non-avian dinosaur track makers (Lockley and Meyer, 2000).

Finally, we consider track density which has been used as a possible criterion for paleoecological inference. Although herons are not shorebirds in a strict sense, many shorebirds and other wading birds congregate in abundance, and may be very active in narrow zones, leaving abundant tracks in small areas. High density, often reaching thousands of overlapping tracks per m^2, is quite typical of many shorebird track assemblages (Lockley et al., 1992b). Such high densities create trampled surfaces (e.g., Lucas et al., 2007) where it may become impossible to measure track density accurately. Gregarious behavior in shorebirds may reflect high prey densities, strategies to defend against predation, or behavior that improves foraging success (Puttick, 1984).

The density of *Ignotornis* tracks in the combined holotype and paratype sample is about 70 tracks in an area of approximately 0.35 m^2 (= $\sim$200 tracks m^2) presumed to be from Site 1. The density of the inferred paratype sample ($\sim$60 tracks in an area of approximately 1.10 m^2) is about 55 tracks per m^2. The density of tracks on the small loose slabs from site 1 is $\sim$100 tracks per m^2 and the density from the *in situ* small surfaces at site 2 is about 50 tracks per m ^{2}. Track density is much lower at site 3 ($\sim$4 tracks per m^2), and may indicate less intensive activity by the *Ignotornis* trackmaker towards the north. However, track density at the upper levels from site 3 is quite high, $\sim$160 tracks per m^2. Such data indicates that track densities were variable in a relatively small area. Although this is typical of many modern shoreline environments, it is worth noting that the Dakota reveals neither the abundance of bird track sites nor the high density of footprints reported from some of the Asian tracksites (Lockley et al., 1992b, 2006b). In fact, there is only one other bird tracksite known from the Dakota Group (Anfinson et al., 2004, 2009).

6.4. Paleoenvironmental interpretation of track beds

Flow ripples and the large number of clay drapes in the heterolithic strata, together suggest a tidally influenced shoreline, but no invertebrate trace or body fossils were found to confirm or disprove this hypothesis. All three of the bird track levels are in a ~2 meter section of these heterolithic strata, as are numerous ornithopod tracks and some crocodile swim tracks in the Site 1 to Site 3 sections (Fig. 3) and in laterally correlative beds to both the north and south. In most cases, tracks were impressed on mud and silt or, in the case of bird track level 1, in volcanic ash. They were later filled and covered with fine sand, and are thus preserved as natural casts on the undersides of sandstone beds. Waage (1961) identified kaolinitic volcanic ash units in the upper part of the Van Bibber Shale and suggested that these may be locally useful for correlation, but he makes no mention of bird or other vertebrate tracks.

The same fluctuating energy conditions that formed these heterolithic strata also contributed to the formation, preservation, and exposure of the tracks. Low-energy conditions led to deposition of silt, mud, clay and volcanic ash, providing a substrate for forming tracks. Higher energy led to deposition of sand, which covered and filled the tracks. Fine clay and silt deposition from still water also provided splitting planes between sandstone beds, which allowed the various track levels to be naturally exposed by weathering.

Examination of the lower track-bearing layer at Sites 1–3 reveals that the tracks were made in volcanic ash (still exposed at Site 2) and were subsequently covered by a deposit of sand (Lockley et al., 1989). Identification of the track-bearing unit as a thin (~3 cm) layer of whitish-cream-colored volcanic ash is only possible at Site 2 where the ash is sandwiched between two sandstones (Fig. 3). At sites 1 and 3 the ash has weathered away leaving only the natural casts of the tracks in convex hyporelief. The thickness of this sand overlying the ash is remarkably consistent (between 10 and 15 cm) between Sites 1 and 3. Although the Dakota Group yields relatively few body fossils, the *Ignotornis* trackways and other traces from Sites 1–3 provide a glimpse of an active Cretaceous ecosystem in Van Bibber times. Although few obvious, ichnologically-diagnostic burrow traces co-occur with the *Ignotornis* tracks at Sites 1–3, numerous and diverse fossil burrow traces higher in the 'Upper J Sandstone' (Weimer and Land, 1972; Chamberlain, 1985) indicate significant marginal marine invertebrate activity in the wider area between Boulder and Roxborough (Fig. 1). This also suggests that variation in the paleoenvironments in space and time lead to subtle differences in the degree of marine and non-marine influence in a complex mosaic of coastal plain/wetland facies. Crocodilian and ornithopod tracks from multiple horizons in Sequence 3 deposits even in the small Site 1–Site 3 study area indicate that both aquatic and terrestrial vertebrates shared various shoreline and shallow water habitats with the *Ignotornis* trackmaker.

The fine-grained sediment substrates in which the tracks are emplaced indicate low energy, low gradient settings such as floodplain mudflats and delta plain environments. Mixed current and wave activity may also suggest estuarine conditions. Such muds tend to have high organic content, with low oxygen levels below the surface (Tait and Dipper, 1998). Many extant shorebirds feed on mollusks, crustaceans, worms, and other invertebrates that inhabit these environments. In intertidal areas, feeding is particularly pronounced during falling tides, just before invertebrates retreat from subaerial exposure of the sediment (e.g. Recher, 1966; Puttick, 1984). As noted above, herons and egrets typically feed in such settings. Thus, the interpretation of the *Ignotornis* bearing Upper J Sandstone near Denver as an ancient shallow water delta complex that was influenced by tides (Weimer and Land, 1972), and longer term eustatic sea-level fluctuations (Waage, 1961; Holbrook et al., 2006) suggests a productive feeding area. Periodic light ash falls blanketed the area without accumulating great thicknesses.

The fact that the *Ignotornis* footprints and trackways are concentrated within one small area of the Dakota Group (at Sites 1–3), and occur within at least three different stratigraphic horizons in the same area indicates recurring ecological and taphonomic conditions that attracted the Cretaceous birds and allowed the registration of their footprints. Food resources likely provided the attraction. Unlike non-avian dinosaurs, the primary means of locomotion by most birds is flight. Thus, tracks made by volant birds often reflect searches for food or water. The *Ignotornis* trackmakers returned to the area at least intermittently during the time it took for the three track horizons to be deposited in a sequence about 2 m thick, but it is intriguing that there are no other reports of *Ignotornis* tracks from the Dakota Group, despite the fact that more than 60 other track sites are known. Thus, we conclude that the rarity of *Ignotornis* track reports is not the result of failure to recognize their tracks. This suggests at least three possible alternate explanations. The first is biological, and suggests that the trackmakers had specific habitat preferences and so did not frequent many of the paleoenvironments available in the greater Dakota Group paleoenvironmental complex. Such habitat use may have included migration stopover sites. The second explanation is that the trackmakers did not normally frequent environments where bird tracks were typically preserved. The third is that the volcanic ash provided a temporary substrate on which well preserved tracks could be preserved (Houck et al., 2009). It is possible that combinations of these three factors combined to influence the distributions we see.

7. Conclusions

(1) The present study reports the rediscovery of the *Ignotornis* type locality as one of three sites exposed in the area of Golden, Colorado with *Ignotornis* tracks.
(2) The study also demonstrates that the *Ignotornis* "type sample" (holotype and associated paratypes and topotypes) consists of at least 360 tracks comprising about 50 trackway segments, 41 of which have provided useful measurements. This sample is far larger than previously supposed, and reveals reasonable consistency in track and trackway parameters. Thus we infer a monospecific assemblage of avian track-makers.
(3) The *Ignotornis* sample provides multiple lines of evidence that the track-maker was a small heron-like bird in both pes morphology and behavior.
(4) Trackway patterns indicate that the *Ignotornis* trackmaker sometimes engaged in shuffling locomotion, which may have been a "foot-stirring" foraging strategy. This is the first report of such behavior from the track record.
(5) Trackway patterns indicate that the *Ignotornis* trackmaker also sometimes engaged in gregarious behavior. However, it is likely that the trackmakers foraged in small loosely-knit groups rather than large flocks.
(6) Volcanic ash appears to have been an important factor creating a cohesive substrate and superior preservation at the lower bird track level in which tracks are quite deep. In conjunction with the evidence of foot-stirring this suggests that most tracks were made in shallow water, but not degraded after they were registered.

(7) The *Ignotornis* track maker appears to have been foraging in a coastal delta plain paleoenvironment.
(8) The restriction of evidence for *Ignotornis* to a single tracksite area (among more than 60 known in the Dakota Group) suggests that the trackmaker was somewhat uncommon and either restricted to specific habitats or commonly frequented environments in which track preservation potential was normally low.

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