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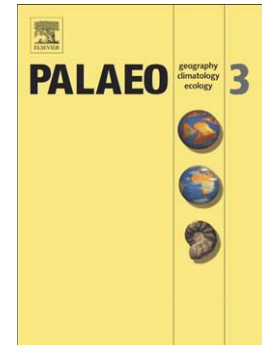
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First report of bird tracks (*Aquatilavipes*) from the Cedar Mountain Formation (Lower Cretaceous), eastern Utah

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Abstract

More than 130 footprints representing ~43 trackways of birds (avian theropods) and two non-avian theropods occur as seven separate assemblages on loose blocks recovered from the Poison Strip Member of the Cedar Mountain Formation, near the Stikes Quarry locality in eastern Utah. Six of assemblages, four with bird tracks and two with small non avian theropod tracks, are inferred to originate from the same stratigraphic horizon, and can therefore be considered part of the same ichnofauna. The seventh assemblages comes from a different horizon a few meters above that yielding the other six assemblages. The bird tracks are all attributed to the ichnogenus *Aquatilavipes*, a track type morphologically similar to those of modern shorebirds. The ichnogenus is also known from broadly coeval ichnofaunas from South Dakota and Canada, and

the identification is confirmed by detailed comparative analysis of available *Aquatilavipes* samples using bivariate and multivariate analyses. This is the first definitive report of bird tracks from the Cedar Mountain Formation and the first evidence of birds from this otherwise richly fossiliferous unit. The ichnofauna is therefore quite unique in comparison with others from this same formation.

1. Introduction

Avian dinosaurs (birds) evolved during the Late Jurassic and have a diverse fossil record by the Early Cretaceous, particularly in China and other parts of Asia, but also in Spain and Australia (Padian, 2004). Bird tracks are known from a number of deposits world-wide but are particularly abundant in Asia, and the oldest known unequivocal bird tracks are currently from the basal part of the Early Cretaceous (e.g., Lockley et al 2006; Lockley and Harris 2010). As with other geologic ages, abundant tracks and diverse bone assemblages of associated faunas do not always occur in the same formations (Lockley 1991), but tracks may indicate the presence of otherwise unknown elements of a fauna. Such is the case with the Cedar Mountain Formation in the western United States.

The Cedar Mountain Formation, exposed in the Rocky Mountain west, especially in eastern and central Utah, is particularly well-known as a major source of vertebrate remains spanning as much as the last 30 Ma of the Early Cretaceous. It is best known for dinosaurs, such as the giant dromaeosaur *Utahraptor*, the primitive therizinosaur *Falcarius*, the ankylosaurs *Gastonia*, *Animantarx*, *Peloroplites*, and *Cedarpelta*, the iguanodonts *Iguanacolossus*, *Planicoxa*, and *Hippodraco*, and the sauropods *Venenosaurus* and *Cedarosaurus*, from such major excavations such as Dalton Wells, Crystal Geyser, Don's Ridge, Tony's Bonebed, and the

Gaston Quarry (Kirkland et al., 1997,1999, 2005; Carpenter et al., 1999, 2008; Tidwell et al., 1999; Eberth et al., 2006; Suarez et al., 2007; Britt et al. 2009; McDonald et al., 2010).

However, until recently relatively few important tracksites have been reported. Most of the recently documented tracksites are quite small (Lockley et al., 1999; Lockley et al., 2004; Cowan et al, 2010) and have yielded mostly dinosaur tracks attributed to theropods, sauropods and ornithischians, that collectively indicate a relatively diverse fauna comparable to that known from the body fossil record. Thus the Cedar Mountain Formation a type 4a deposit as defined by Lockley and Hunt (1994) as one in which body fossil sites are more abundant than tracksites, while both indicate generally similar, rather than significantly different, faunas. This general consistency between body and trace fossils has been underscored by the discovery of the large Mill Canyon Dinosaur Tracksite (MCDT) which has, at one site, yielded well-preserved examples of most of the main dinosaurian trackmaking groups reported from all the other sites (Lockley et al., 2014a,b). The MCDT site however has yielded only two very poorly preserved and somewhat dubious examples of bird tracks, discovered after the ichnofaunas described here, which were originally briefly noted by Wright et al. (2006).

Thus, the discovery in 2005 of avian theropod (bird) footprints, near the bone-rich Stikes Quarry north of Arches National Park in Grand County, Utah, by Rob Gaston and one of us (JF), adds a new dimension to the tetrapod ichnology of the Cedar Mountain Formation and is significant for several reasons: 1) it represents the first report of bird tracks from the Cedar Mountain Formation; 2) no bird remains are known from the body fossil record in the Cedar Mountain Formation; 3) bird tracks are rare in the Early Cretaceous of the entire region; 4) the occurrence reported here is arguably the oldest known for the region, though not globally as reported by Wright et al. (2006); and 5) the tracks are abundant, well-preserved and clearly

different from those reported from the overlying Dakota Group, thus indicating some measure of avian diversity, and differential stratigraphic and facies distribution at this time.

2.Geological setting

In the study area north of Arches National Park, sedimentary rocks dip gently northeast off the Salt Valley Anticline, and the Cedar Mountain Formation is exposed along several kilometers of this outcrop area north and east of the Park. (To south and east of the Colorado River, the Cedar Mountain Formation is sometimes referred to as the otherwise equivalent Burro Canyon Formation.) The stratigraphy of the Cedar Mountain Formation is well known and has been extensively studied in eastern Utah, between the San Rafael Swell and the Colorado-Utah border (Stokes, 1952; Young, 1960; Carter and Gualtieri, 1965; Kirkland and Madsen, 2007; Currie et al., 2008; Sprinkel et al., 2012). The Cedar Mountain Formation overlies the Upper Jurassic Morrison Formation and is under the upper Lower Cretaceous Dakota Formation; in the present study area, the Cedar Mountain Formation consists of three members from bottom to top: the Yellowcat, Poison Strip Sandstone, and Ruby Ranch members. The blocks containing the bird tracks were lying loose on the Upper Jurassic Morrison Formation and lower Cedar Mountain Formation on the slope below and lateral to the Stikes Quarry, which is in the upper Yellowcat Member, about 18 km southeast of Crescent Junction, Utah (Fig. 1). During the present study, a detailed stratigraphic section was compiled, indicating that the bird track-bearing units originated from the Poison Strip Sandstone Member (Figs. 2-3), exposed in a steep cliff section above the Stikes Quarry. However, the lacustrine shoreline facies preserving the tracks is genetically part of the largely lacustrine upper Yellow Cat Member rather than the coarse gravelly fluvial facies of

the main portion of the Poison Strip Member overlying the sandstone unit preserving the tracks (Kirkland and Madsen, 2007). Measurement of this portion of the section required ropes and harnesses. The upper Yellow Cat Member has been dated at basal Aptian (~ 124 Ma) based on detrital zircons (Greenhalgh et al. 2006; Britt et al., 2009), whereas the Poison Strip Sandstone Member is younger Aptian in age (~119–122 Ma). These rocks have been dated as lower to medial Aptian by laser ablation of detrital zircons and by U/Pb dating early diagenetic carbonate (Ludvigson et al., 2010). The Upper Yellow Cat Member has yielded numerous dinosaurs from which only a few have been described such as the small, basal coelurosaur *Nedcolbertia*, the giant dromaeosaur *Utahraptor*, polacanthids ankylosaur *Gastonia*, iguanodontan grade ornithopod, *Hippodraco*, and the brachiosaurid sauropod *Cedarosaurus*, with nondinosaurian taxa including a sphenodontid cf. *Toxolophosaurus*, a basal mesoeucrocodylian, a mammal, and numerous aquatic crocodilian fragments, turtles, and a variety of fishes (Kirkland et al., 1999; Kirkland and Madsen, 2007; Britt et al., 2009). The overlying Poison Strip Sandstone Member has produced several dinosaurs, including the large new genus of plocanthid ankylosaur, cf. *Hoplitosaurus* (Bodily, 1969) that was incorrectly referred to as *Sauropelta* (Carpenter et al., 1969) the iguanodont *Planicoxa* (= iguanodont *Cedroestes*) (DiCroce and Carpenter, 2001; Gilpen et al., 2006) and the titanosauiromorph sauropod *Venenosaurus* (Tidwell et al., 2001). The layer producing the bird tracks is planar bedded, tan, brown-weathering medium-grained sandstone and represents a lacustrine shoreline setting that will be referred to in the basal Poison Strip Sandstone as it is mapped (Doelling and Kuehne, 2013), although genetically part of the Yellow Cat “systems tract.”

3. Material and methods

During the course of the present study, eight loose track-bearing blocks were discovered, each revealing multiple tracks. Together they represent seven assemblages. Six blocks reveal tracks preserved as natural impressions (concave epireliefs) from a single horizon, and two blocks, representing part and counterpart of the same specimen reveals tracks preserved as natural impressions and natural casts (concave epireliefs and convex hyporeliefs). As noted in the previous section, when the stratigraphic section was measured, the horizon from which the six blocks originated was determined to be the lower Poison Strip Sandstone. The seventh and eighth specimens (part and counterpart blocks) also came from close to this horizon, probably stratigraphically from within one or two meters. However, as the blocks have fallen a considerable distance down slope it is impossible to determine their original orientation, or their former geographical relationship to one another. Each block is therefore treated as a separate sub-assemblage or sample that forms part of the total assemblage (composite sample). As shown in Table 1, the number of tracks and associated trace fossils recorded from each block varies, and ranges from at least 67 vertebrate tracks and many invertebrate traces on Block 1, to only one vertebrate track on Block 6.

Table 1. Summary inventory of the five track-bearing blocks and the number of tracks and trackways identified in each sample. Blocks 1, 7 and 8 were collected, blocks 2 and 5 molded and replicated, and blocks 3,4 and 6 left in the field.

| Block/specimen number | Number of tracks | Minimum # of trackways |
|--|-------------------------|-------------------------------|
| Block 1: bird tracks and invertebrate traces | 67 | ~18 |
| Block 2: bird tracks only | 20 | 8 |
| Block 3: bird tracks only | 20 | ?8 |

| | | |
|---|------|-----|
| Block 4: bird tracks only | 4 | 2 |
| Block 5: theropod tracks only | 2 | 1 |
| Block 6: theropod track | 1 | 1 |
| Block 7: with counterpart shows bird tracks only | 19 | ~5 |
| TOTALS | ~133 | ~43 |

All blocks were documented using a combination of the following methods: photography, tracing of the track-bearing surface using clear acetate film, molding of the track-bearing surface with latex in order to make fiberglass and plaster replicas and, in some cases, collecting that portion of the block that contains the track-bearing surface. In cases where the whole track-bearing surface, or the portion of the surface with recognizable tracks, was replicated or collected, the specimen number corresponds to the entire track-bearing surface as described here. Each track-bearing surface (sub-assembly, or sub-sample) is described separately in the following section. All original specimens and first molds and replicas were repositied in the Utah Museum of Natural History (UMNH) Vertebrate Paleontology collections, with additional replicas made for comparative study for the Museum of Western Colorado and the University of Colorado Museum. All specimen numbers are cited in the following section.

Using the actual track-bearing surfaces, replicas, and tracings, the standard track and trackway parameters were measured including track length (L), width (W), divarication angle between digits II and IV (D), rotation of the track axis relative to the trackway midline (R), step (S) stride (s) and trackway width (TW): see Table 2. In cases where trackways are unequivocally identified, average morphometric values for the above listed parameters were calculated.

Although partial tracks are counted in the census of tracks associated with each block (sample), measurements for incomplete, dubious or ambiguous tracks were not recorded.

As noted below, individual tracks can in many cases be unambiguously assigned to trackways. These trackways, indicated by arrows and prefixes (e.g. B1T1t1 = Block 1, Trackway 1, track 1) are identified wherever possible so as to measure trackway parameters, such as mean values for L, W, D, R, TW, S and s (Table 2). In describing trackways consisting of two or more footprints, the label t1 (track 1) is used to designate the most proximal track. Based on the trackway configuration, especially inward rotation, we determine whether tracks are right (r) or left (l). However, where it is not possible to identify unambiguous trackways, individual tracks maybe be inferred to represent remnants of additional trackways based on size, orientation, or other features.

Bivariate and multivariate statistical analyses were performed using PAleontologicalSTatistics (PAST) version 2.17c (Hammer et al. 2001). Analyses were performed using non log₁₀-adjusted data to retain the ichnomorphologic character of size. The Cedar Mountain Formation tracks were analyzed in comparison with a database of Mesozoic avian ichnites (Buckley et al. 2012; Buckley et al. in review), specifically those that are semipalmate anisodactyl tracks (*Koreanaornis hamanensis*, *K. dodsoni*, *Morguiornipes*, *Pullornipes*, *Tatarornipes*, *Aquatilavipes swiboldae*, *A. izumiensis*, *Barrosopus*). Analyzed variables were limited to those collected for (or calculated from) the Cedar Mountain Formation tracks (L, W, D, R, TW, S, and s) to remove as much missing data from the analyses as possible.

The multivariate statistical analyses performed were discriminant and canonical variate analyses. Discriminant analysis projects a multivariate data set down to one dimension in a way

that maximizes separation between two *a priori* separated groups: in this case, the *a priori* groups are known ichnospecies of Mesozoic avian ichnites and the Cedar Mountain Formation avian tracks. This is a useful tool for testing hypotheses of morphologic similarity or difference between two groups. A 90 % or greater separation between two groups is considered sufficient support for the presence of two taxonomically distinct morphotypes (Hammer and Harper 2006): however, 100% is the ideal level of separation. Canonical variate analysis compares specimens *a priori* categorized in three or more groups using the same principles as discriminant analysis. The p_{same} between two *a priori* groups was determined using Hotelling's t^2 test (the multivariate version of the t-test, Hammer and Harper 2006) to determine significance at $p_{\text{same}} \geq 0.05$.

Abbreviations: UMNH, Natural History Museum of Utah, University of Utah; MWC, Museum of Western Colorado; UCM, University of Colorado Natural History Museum.

4. Track and trackway descriptions

Each individual track-bearing surface is described below in order to determine how many measurable tracks and trackways can be identified. Reliable measurements are tabulated in Table 2, following the track and trackway numbering scheme outlined above .

4.1 Block 1 (Figures 4 and 5)

Block 1 is the largest block (95 x 134 cm) with at least 67 partial or complete tracks. The track-bearing surface was molded in latex prior to being collected. The original material from Block 1 is designated as UMNH.VP.24811, with replicas in the Museum of Western Colorado and the University of Colorado Museum (both under UCM 199.66). Within this sample, 48 tracks show complete tridactyl morphology, and have been designated numbers for identification purposes (Figs. 4-5). Although the density of tracks on the surface is relatively high and many different track and trackway orientations have been observed, there are several clear trackway segments (Figs. 4-5) characterized by more or less regular step lengths and alternating left and right tracks that show characteristic inward rotation. We estimate that at least 18 discrete trackways are present. Among the longest trackway segments the following are illustrated separately: B1T1, consisting of individual tracks 14-19, B1T2 (tracks 24-29), B1T3 (tracks 32-36, from the sequence 30-36), B1T4 (tracks 37-39 + 47), and B1T5 (tracks 5-7). Other less clear trackway segments with fewer tracks (2-3) may also be identified. For example, B1T6 probably includes tracks 1, 2 and 3, B1T7 probably includes tracks 8, 12 and 13, B1T13 probably includes tracks 40, 41 and 42. Tracks 20 and 22 may belong in the same trackway, but tracks 43-46 and 48 are treated as isolated footprints.

Table 2. Track and trackway measurements for footprints from Block 1. 48 tracks with clear tridactyl morphology have been designated numbers, and used to calculate mean values. The entire sample represents 67 footprints. Step measurements given in row which corresponds to end of step. Stride measurements given in row between the rows for tracks that make up the stride. Linear measurement averages are calculated to two decimal places, mean angles to only one decimal place.

| Tway/Track r/l | Length L | Width W | Divaric D | Rotation R | Twidh TW | Step | Stride |
|------------------|-------------|-------------|--------------|-------------|-------------|--------------|--------------|
| B1T1t1 = 14 r | 3.30 | 4.20 | 76 | 0 | | | |
| B1T1t2 = 15 l | 4.10 | 5.60 | 72 | 10 | | 14.50 | 29.00 |
| B1T1t1 = 16 r | 4.10 | 4.60 | 94 | 0 | 6.70 | 14.50 | 27.00 |
| B1T1t1 = 17 l | 3.60 | 3.90 | 85 | 11 | 7.20 | 13.30 | 27.70 |
| B1T1t1 = 18 r | 3.90 | 4.40 | 53 | 5 * | 8.00 | 15.00 | |
| B1T1t1 = 19 l | 4.20 | 3.60 | 50 | 0 | | 14.50 | |
| B1T1 mean | 3.87 | 4.38 | 71.7 | 2.7 | 7.30 | 14.36 | 27.90 |
| B1T2t1 = 24 l | 3.60 | 5.00 | 127 | 7 | | | |
| B1T2t2 = 25 r | 4.00 | 4.40 | 120 | 20 | 6.50 | 15.60 | |
| B1T2t3 = 26 l | 4.40 | 4.70 | 102 | 15 | 5.50 | 15.00 | 30.00 |
| B1T2t4 = 27 r | 4.32 | 5.30 | 100 | 14 | 6.00 | 17.00 | 31.00 |
| B1T2t5 = 28 l | 4.30 | 5.80 | 125 | 23 | 5.90 | 15.20 | 32.50 |
| B1T2t6 = 29 r | 3.80 | 5.00 | 105 | 9 | | 15.60 | 32.00 |
| B1T2 mean | 4.07 | 5.03 | 113.2 | 14.7 | 5.98 | 15.68 | 31.38 |
| B1T3t1 = 30 l | 4.10 | 4.40 | 108 | | | | |
| B1T3t2 = 31 r | 4.50 | 5.40 | 110 | | 10.70 | 12.00 | |
| B1T3t3 = 32 l | 4.40 | 5.60 | 100 | 0 | 8.20 | 11.20 | 20.20 |
| B1T3t4 = 33 r | 4.50 | 5.00 | 97 | 4* | 8.00 | 11.30 | 21.50 |
| B1T3t5 = 34 l | 4.70 | 6.50 | 107 | 0 | 7.60 | 10.60 | 20.60 |
| B1T3t6 = 35 r | 4.10 | 5.80 | 99 | 9 | 9.30 | 10.20 | 19.00 |
| B1T3t7 = 36 l | 4.40 | 6.00 | 107 | 16* | | 10.00 | |
| B1T3 mean | 4.38 | 5.53 | 104 | 2.2* | 8.76 | 10.88 | 20.33 |
| B1T4t1 = 37 r | 4.00 | 6.00 | 110 | 16 | | | |
| B1T4t2 = 38 l | 4.50 | 5.60 | 104 | 20 | 6.00 | 15.00 | |
| B1T4t3 = 39 r | 4.00 | 5.30 | 106 | 20 | | 12.20 | 27.00 |
| B1T4t4 = 47 | | | | | | 9.50 | |
| B1T4 mean | 4.17 | 5.63 | 106.7 | 18.7 | 6.00 | 12.23 | 27.00 |

| | | | | | | | |
|--------------------|-------------|-------------|--------------|-------------|-------------|--------------|--------------|
| B1T5t1 = 5 r | 4.70 | 4.20 | 100 | 24 | | | |
| B1T5t2 = 6l | 5.00 | 5.00 | 76 | 0 | | 8.50 | 15.5 |
| B1T5t3 = 7 r | 4.40 | 3.80 | 74 | 8 | | 9.20 | |
| B1T5 mean | 4.70 | 4.33 | 83.3 | 16 | 8.60 | 8.85 | 15.5 |
| B1T6t1 = 1 | 3.60 | 4.70 | 93 | | | | |
| B1T6t3 = 2 | 4.40 | 5.20 | 86 | | | | |
| B1T6t4 = 3 | 4.20 | 4.70 | 98 | | | 13.4 | |
| B1T6 mean | 4.07 | 4.87 | 92.3 | | | 13.4 | |
| B1T7t1 = 8 | 4.30 | 5.90 | 122 | | | | |
| B1T7t3? = 12 | 4.70 | 5.70 | 105 | | | | |
| B1T7t4? = 13 | 4.00 | 6.20 | 116 | | | 13.00 | |
| B1T7 mean | 4.33 | 5.93 | 114.3 | | | 13.00 | |
| B1T8 = 10 | 3.60 | 4.70 | 72 | | | | |
| B1T9 = 11 | 4.30 | 4.70 | 82 | | | | |
| B1T10t1 = 20 | 4.50 | 7.00 | 120 | | | | |
| B1T10tn? = 22 | 4.50 | 5.30 | 105 | | | | |
| B1T10 | 4.50 | 6.15 | 112.5 | | | | |
| B1T11 = 21 | 4.50 | 5.90 | 120 | | | | |
| B1T12 = 23 | 3.90 | 5.30 | 110 | | | | |
| B1T13t1 = 40 | 4.00 | 3.80 | 80 | | | | |
| B1T13t1 = 41 | (3.80) | (3.30) | (65) | | | | |
| B1T13t1 = 42 | 3.60 | 5.20 | 103 | | | | |
| B1T13 mean | 3.80 | 4.50 | 91.5 | | | | |
| B1T14 = 43 | 3.60 | 5.00 | 94 | | | | |
| B1T15 = 44 | 3.90 | 5.20 | 100 | | | | |
| B1T16 = 45 | 4.00 | 5.00 | 117 | | | | |
| B1T17 = 46 | 4.00 | 4.90 | 100 | | | | |
| B1T18 = 48 | 3.50 | 5.70 | 145 | | | | |
| Grand means | 4.07 | 5.15 | 101.7 | 10.0 | 7.33 | 12.63 | 24.42 |

4.2 Block 2 (Figure 6)

Block 2 reveals 20 tridactyl avian theropod (bird) tracks of which 19 are complete enough to show all three digit traces (Fig. 6). Only one is represented by a single toe trace. A mold and replica of this specimen is designated as UMNH.VP.C.220, with duplicate replicas in the MWC and UCM collections as MWC 8235 and UCM 199.80, respectively. Most of these 19 tracks form recognizable trackways including trackway B2T1 which consists of five consecutive tracks and B2T4 consisting of four tracks. B2T2, B2T3, B2T5 and B2T7 each consist only of two consecutive tracks, with B2T6 and B2T8 being the only isolated tracks. Trackways B2T3, B2T4, B2T5, B2T6 and B2T7 are parallel to subparallel, with B2T2, oriented opposite this trend. The general morphology, size range, divarication and rotation patterns are consistent with the samples recorded from blocks 1, 3 and 4 (Tables 1 and 2).

4.3 Block 3 (no molds made) (Figure 7)

As shown in Figure 7, Block3 reveals about 20 bird tracks, including eight that show complete tridactyl morphology. However, of these eight, five are isolated tracks (B3T2-B3T6) indicating only one three-footprint-sequence that appears to represent a clear trackway(B3T1). Mean L, W, D and R values for B3T1 are 4.3, 5.8, 108.3° and 9.7° (Table 2). The size range of B3T2-B3T6 indicates similar sized trackmakers. Track/trackway orientations appear to be random. None of the tracks on Block 3 shows any pronounced morphometric features that distinguish them from the tracks on blocks 1, 2 or 4. However, the track-bearing surface is undulating, with sinuous ripple crests, which distinguishes the surface from the other bird track-bearing blocks (1, 2 and 4).

4.4 Block 4 (no molds made) (Figure 8)

Block 4 reveals four tracks, three of which occur in a single trackway (B4T1) which consists of three tracks of which the first proximal track is incomplete (Fig. 8). Mean L, W, D and R values for the two other tracks are 3.75, 4.60, 106.5° and 20° (Table 2). It appears that the sequence is r-l-r, with strong inward rotation (30°) on the left side compared with only 10° on the distal track. The single track (B4T2) is 4.1 cm long and 5.5 cm wide with a divarication angle of 110°. Trackways B4T1 and B4T2 are parallel. The proximal and distal steps are 14.5 and 16.1 cm, respectively. None of the tracks on Block 4 shows any pronounced morphometric features that distinguish them from the tracks on blocks 1-3.

4.5 Block 5 (Figure 8)

Tracks from this block, preserved as a mold and replica (cast) UCM.VP.C.221 (and duplicate casts MWC 8236 and UCM 199.81) reveals two relatively small, non-avian theropod tracks averaging 12.65 cm long and 11.70 cm wide, with an average digit divarication angle of 65° (Fig. 8). The l/w ratio = 1.08. The step is 41.5 cm. The surface reveals faint, straight crested, low amplitude ripple marks, with a wavelength of 4-5 cm. This track type is quite distinct from all those reported from blocks 1-4 and is attributed to a relatively small, non-avian theropod. As discussed below, these tracks are not easily attributed to a distinctive or well-defined ichnogenus. Candidate genera that could have made the tridactyl tracks, based on skeletal material from the Cedar Mountain Formation, include *Nedcolbertia* or possibly a small ornithomimid.

4.6 Block 6 (not figured)

A single tridactyl track similar to that found on block 5 (Fig. 8B) has also been identified. It measures 12.2 cm long and 12.6 cm wide with a digit divarication of 60°, which is essentially identical to the two tracks found on block 5.

4.7 Block 7 (Figure 9)

Block 7 (UMNH. VP.24812A, with replica UCM 199.90) consists of a small block with seven complete and about 12 partial tracks preserved as natural casts (concave hyporeliefs). After this specimen was discovered, the counterpart of the same specimen was discovered by one of us (ML) following further search of the area. The counterpart reveals natural impressions matching the first found part and has been designated as UMNH.VP.24812B (with replica UCM 199.91). The counterpart does not add significantly to the count of tracks already given for the first-found specimen (block 7), and for this reason a separate block number is not designated. However about 1 cm stratigraphically below the counterpart surface there is a small area of surface with a faint trace of a single bird track. Technically, unless this could be shown to be an underprint, this single additional track represents another track-bearing layer.

This specimen (Fig. 9) has a slightly different lithology from the six other blocks, and is inferred to have originated from a different layer within the same sandstone unit from which the other track-bearing blocks were derived. It is difficult to infer how many trackways are represented. We infer that five complete tracks oriented close to the long axis of the block may belong to the same trackway (B7T1). The mean trackway width is 8.33 cm and there appears to be an alternation of slightly longer and shorter steps. There are two other complete tracks with different orientations. Other tracks are incomplete and have variable orientations. Track size and morphology is very similar to that of the tracks observed on blocks 1-4: i.e., mean length and width for trackway. B7t1 is 4.10 and 5.60 respectively, with a mean divarication angle of 139°.

4.6 Summary of morphological characteristics of avian theropod tracks

It is clear that the tracks recorded on Blocks 1-4 are all very similar in size and shape. The main differences pertain to slight variation in size, digit divarication, footprint rotation, step, stride and quality of preservation. For example, individual digital pad traces are visible on some of the tracks from Block 1, but are generally not discernible on those from blocks 2-4. The mean size (L and W) for all the tracks from Block 1, representing the largest sample of 18 trackways, is 4.07 cm and 5.15cm respectively, which is in close agreement with the average sizes (4.14 cm and 5.22 cm) for the samples recorded from blocks 2-4 (N= 16: compare Tables 2 and 3). Thus, comparing the largest sample (Block 1) with the pooled sample from Blocks 2-4, the mean size (L and W) differences are only between 1 and 2%. Likewise the respective differences in mean digit divarication (101.7° vs. 105.7°) and step (12.63 vs. 12.48) are very slight: i.e., 4% for divarication, 1% for step, based on larger samples (N = 7-18). Percentage differences in mean stride length (24.42 vs. 20.69) and mean rotation angles (10.0° vs. 12.9°) between the two samples are in part due to smaller sample sizes (N = 4–5).

The close morphological similarity between the 18 measured avian trackways from Block 1 and the 16 from the other three blocks supports the conclusion that the entire sample (except for block 7) is representative of a single ichnotaxon from a single horizon. However, there is some individual variation between trackways. The largest differences in trackway size, based on well-preserved Block 1 trackways with multiple steps, rather than isolated tracks, appear to be between B1T1 (L: 3.87, W: 4.38) and B1T3 (L: 4.38, W: 5.53). The difference in mean length is ~14%, whereas the difference in mean width is 26%. The greater difference in mean width can be accounted for in part by the lower mean digit divarication value in B1T1 which is only 71.7° , compared with an average for the whole sample of 101.7° (divarication difference ~42%).

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Table 3. Track and trackway measurements for the footprint assemblage recorded on blocks 2-4. Note that 30 avian tracks with clear tridactyl morphology have been designated numbers, and used to calculate mean values. With partial, un-measured tracks included, the entire sample for blocks 2-4 represents 46 footprints. Measurements of two non-avian theropod tracks from Block 5 are included. Linear measurement averages are calculated to two decimal places, mean angles to only one decimal place.

| Track/Tway # | Length L | Width W | Divaric D | Rotation R | Twidth TW | Step | Stride |
|-------------------|-------------|-------------|--------------|-------------|-------------|--------------|--------------|
| B2T1t1 | 4.70 | 5.50 | 108 | 5 | | | |
| B2T1t2 | 4.00 | 5.50 | 108 | 26 | 5.80 | 13.50 | 29.50 |
| B2T1t3 | 4.50 | 4.50 | 103 | 22 | 8.20 | 14.10 | 26.20 |
| B2T1t4 | 4.00 | 5.00 | 99 | 18 | 6.00 | 12.80 | 27.00 |
| B2T1t5 | 3.70 | 5.40 | 98 | 12 | | 14.40 | |
| B2T1 mean | 4.18 | 5.18 | 103.2 | 16.6 | 6.67 | 13.75 | 27.57 |
| B2T2t1 | 4.20 | 6.0 | 110 | | | | |
| B2T2t2 | 4.50 | 6.0 | 110 | | | 15.50 | |
| B2T2 mean | 4.30 | 6.05 | 110 | | | 15.50 | |
| B2T3t1 | 4.50 | 5.50 | 110 | | | | |
| B2T3t2 | 4.10 | 4.90 | 105 | | | 13.50 | |
| B2T3 mean | 4.30 | 5.20 | 107.5 | | | 13.50 | |
| B2T4t1 | 3.50 | 3.90 | 120 | 8 | | | |
| B2T4t2 | 3.50 | 4.20 | 110 | 0 | | 10.60 | 21.50 |
| B2T4t3 | 4.50 | 5.50 | 110 | 11* | | 13.20 | 25.70 |
| B2T4t4 | 4.00 | 5.50 | 104 | 24 | | 12.70 | |
| B2T4t mean | 3.88 | 4.78 | 111 | 5.3 | | 12.20 | 23.60 |
| B2T5t1 | 3.00 | 4.70 | 108 | | | | |
| B2T5t2 | 3.60 | 5.70 | 120 | | | 9.00 | |
| B2T5t mean | 3.30 | 5.20 | 114 | | | 9.00 | |
| B2T6 | 3.90 | 4.90 | 87 | | | | |

| | | | | | | | |
|-------------------------------|--------------|--------------|--------------|-------------|-------------|--------------|--------------|
| B2T7t1 | 3.80 | 4.50 | 95 | | | | |
| B2T7t2 | 4.70 | 4.00 | 68 | | | 11.1 | |
| B2T7 mean | 4.25 | 4.25 | 81.5 | | | 11.1 | |
| B2T8 | 4.00 | 4.50 | 80 | | | | |
| B3T1t1 | 4.70 | 6.30 | 100 | 6 | | | |
| B3T1t2 | 4.50 | 5.30 | 110 | 8 | | 10.20 | |
| B3T1t3 | 3.70 | 5.70 | 115 | 15 | | 8.80 | 19.1 |
| B3T1 mean | 4.30 | 5.80 | 108.3 | 9.7 | | 9.50 | 19.1 |
| B3T2 | 4.00 | 5.90 | 135 | | | | |
| B3T3 | 4.80 | 5.30 | 100 | | | | |
| B3T4 | 4.00 | 5.30 | 110 | | | | |
| B3T5 | 4.70 | 5.00 | 98 | | | | |
| B3T6 | 4.50 | 6.10 | 130 | | | | |
| B4T1t2 | 3.90 | 4.70 | 103 | 30 | | 14.50 | |
| B4T1t3 | 3.60 | 4.50 | 110 | 10 | | 16.10 | 30.50 |
| B4T1 mean | 3.75 | 4.60 | 106.5 | 20 | | 15.30 | 30.50 |
| B4T2 | 4.10 | 5.50 | 110 | | | | |
| Grand means blocks 1-4 | 4.14 | 5.22 | 105.8 | 12.9 | 6.67 | 12.48 | 20.69 |
| B5T1t1 | 12.30 | 11.60 | 60 | | | | |
| B5T1t2 | 13.00 | 11.80 | 70 | | | 41.50 | |
| B5T1 mean | 12.65 | 11.7 | 65 | | | 41.5 | |
| B6T1 | 12.20 | 12.60 | 60 | | | | |
| B7T1t1 | 4.20 | 5.80 | 145 | | | | |
| B7T1t2 | 4.00 | 6.10 | 145 | | 7.50 | 8.80 | 14.20 |
| B7T1t3 | 4.10 | 5.20 | 130 | | 8.20 | 6.00 | 12.60 |

| | | | | | | | |
|---------------|-------------|-------------|------------|--|-------------|-------------|--------------|
| B7T1t4 | 4.20 | (5.20) | 135 | | 10.00 | 7.70 | 11.30 |
| B7T1t5 | 4.00 | 5.70 | 140 | | | 6.10 | |
| B7T1t1 | 4.10 | 5.60 | 139 | | 8.33 | 7.15 | 12.70 |
| B7T2 | 4.30 | 6.00 | 125 | | | | |
| B7T3 | 4.30 | 5.70 | 125 | | | | |

5. Comparative Ichnotaxonomy

All the bird tracks from the Cedar Mountain Formation ichnofauna are characterized by tridactyl morphology with no evidence of a hallux. In North America the best-known and most ubiquitous Cretaceous ichnogenus with the morphological characteristics of these Cedar Mountain Formation tracks is *Aquatilavipes*, originally named by Currie (1981) from the Aptian of British Columbia on the basis of a single assemblage assigned to the ichnospecies *Aquatilavipes swiboldae*, and also known from the purportedly Aptian to possibly Barremian aged Lakota Group of South Dakota (Lockley et al., 2001). This ichnospecies was only the second formally named from the Cretaceous of North America, the first being *Ignotornis mcconnelli*, from the Late Albian to Early Cenomanian Dakota Group of Colorado (Mehl, 1931a,b; Lockley et al., 2009). Despite the abundance of dinosaur tracks in the Dakota Group, now known from more than 120 sites, mostly in Colorado (Lockley et al., 2014c), there are still very few reports of bird tracks from that unit. An additional report from Colorado is somewhat uncertain with regard to ichnotaxonomy, but is provisionally assigned to *Ignotornis* (Lockley et al., 2014d), and the only other report, from Utah, although initially labeled as *Aquatilavipes* (Anfinson et al., 2004), was subsequently re-assigned to ichnogenus *Koreanaornis* (Anfinson et al., 2009). The Dakota

Formation at this site (a few 100 m away) has been dated as Late Albian at 101.4 ± 0.4 Ma (Sprinkle et al., 2012). A single small bird (avian theropod) track, from the Terra Cotta Clay Member of the Dakota Formation in Kansas, has not been assigned an ichnotaxonomic name, but “appears to differ morphologically from the other two named avian ichnotaxa from the Dakota Group” (Falk and Lockley, 2014, p. 339).

As discussed elsewhere (Lockley and Harris, 2010, and references therein) the type material of *Aquatilavipes swiboldae* (Currie 1981) from Canada is not based on an unambiguous trackway. This makes comparison with the Cedar Mountain Formation material difficult, as far as characteristic trackway configurations are concerned. The size of the *A. swiboldae* holotype is given as 3.75 cm long and 4.67 cm wide, which is about 90% of the mean size of the Utah specimens. The divarication of digit traces in the holotype is 118° which is $\sim 10\%$ greater than in the Utah sample. Thus, the Utah sample represents a slight larger track maker with slightly lower divarication angles. However, there are no other morphological features that suggest any significant taxonomic differences.

Lockley et al. (2001, p. 445) reported “quite abundant” bird tracks assigned to ichnogenus *Aquatilavipes* from the Lakota Formation of South Dakota. Two blocks, showing a total of 19 tracks were illustrated using maps and tracings. These tracks were described as occurring in trackways with foot lengths and widths of about 5.00 cm and step lengths between 13.0 and 19.0 cm. An original specimen from the Hermosa site is repositied in University of Colorado Museum collections as UCM 199.65 (Fig. 10.) The specimen shows at least six recognizable tracks of which four appear to form part of a single trackway. Neither the Canadian nor the South Dakota samples differ markedly from the Cedar Mountain assemblages described here.

The aforementioned bird track occurrences from the western USA all pertain to the Lower Cretaceous. However, there are a few noteworthy Upper Cretaceous bird track occurrences noted here for completeness. They include the Lance Formation assemblage from eastern Wyoming which includes at least three distinct morphotypes (Lockley et al., 2004) including the distinctive semi-palmate form *Sarjeantopodus*, and two other un-named morphotypes. Like Xing et al., (2014), we refute the suggestion of Falkingham et al., (2009) that the clearly defined semi-palmate web trace in *Sarjeantopodus* can be interpreted as a preservational artifact. Problems with this interpretation include misinterpretation of the holotype as a left track when it was clearly stated that it is a right track (Lockley et al., 2004). Falkingham et al., (2009) also incorrectly designate the trace of digit II and that of digit IV and vice versa thereby inferring that the web is more developed between II and III, whereas it is more developed between III and IV, which is the typical semipalmate condition, and in fact the only known semipalmate condition in extant birds.

None of these Lance Formation morphotypes have been assigned to *Aquatilavipes*. Another important Upper Cretaceous assemblage was described from the Upper Cretaceous Cantwell Formation of Alaska by Fiorillo et al. (2011) and interpreted as containing at least four, named avian ichnogenera (*Ignotornis*, *Aquatilavipes*, *Gruipeda*, and *Uhangrichnus*) in addition to *Magnoavipes* which these authors also interpret as avian (contra Lockley et al., 2001; Matsukawa et al., 2014). A few bird tracks have also been reported from the Mesaverde Group (Robison, 1991; Lockley 1999).

It is outside the scope of this paper to discuss the ichnotaxonomy of these upper Cretaceous assemblages in any detail, since they are considerably younger (Campanian-Maastrichtian) than the Barremian through early Cenomanian assemblages from South Dakota,

Colorado, and Utah. It is nevertheless worth noting that all the older assemblages appear to be represented by a single ichnotaxon, whereas the better-known Upper Cretaceous assemblages appear to be considerably more diverse.

Multivariate statistical analyses provide more information as to which Mesozoic avian ichnotaxa the Cedar Mountain Formation tracks are most similar. Comparing the Cedar Mountain Formation avian tracks to individual ichnospecies using discriminant analyses reveals informative, if sometimes conflicting, results. The only Mesozoic avian ichnospecies that was shown not to be significantly different from the Cedar Mountain Formation avian tracks was *Morguiornipes robusta* (Fig. 11); however, there are only five individual prints in this group, which renders the resulting comparison inaccurate. *Koreanaornis dodsoni* (Xing et al. 2011) also shows a relatively high p_{same} value and low percentage of correctly classified specimens; however, *K. dodsoni* has more robust digits and fewer, larger digital pads (see Xing et al. 2011, fig. 3) than the avian tracks from the Cedar Mountain Formation. While the rest of the Mesozoic avian ichnotaxa were shown to be significantly different from the Cedar Mountain Formation avian tracks, the comparison with *Aquatilavipes swiboldae* revealed the highest p_{same} value ($p_{\text{same}} = 5.36 \times 10^{-03}$) and only 74.5% of prints were correctly identified to their *a priori* groups.

A further multivariate statistical comparison was done on the Cedar Mountain Formation tracks and those of *A. swiboldae* and *A. izumiensis* (Fig. 12). Canonical variate analysis graphical morphospace grouping reveals a closer morphospace grouping between the Cedar Mountain Formation tracks and *A. swiboldae* ($p_{\text{same}} = 0.028$) than with *A. izumiensis* ($p_{\text{same}} = 3.43 \times 10^{-06}$ overlap of nine footprints).

Other Mesozoic avian ichnotaxa do exhibit a lower percent separation from the Cedar Mountain Formation avian tracks than does *A. swiboldae*; however, the p_{same} values for these comparisons are much smaller (Fig. 11). More important than the statistical results is the comparison of the overall morphology of the Cedar Mountain Formation avian tracks to those tracks of other semipalmate anisodactyl Mesozoic avian prints: the slender anatomy and placement of the digits, the number and small size of the preserved digital pads, and the consistent lack of a preserved digit I shows the greatest similarity with those prints of *Aquatilavipes*, and specifically with those of *A. swiboldae*. The assignment of the Cedar Mountain Formation bird tracks to the ichnogenus *Aquatilavipes* can be done with confidence, and it is likely that the tracks could belong to the ichnospecies *A. swiboldae*. Future work in collecting more data variables and further analyses will likely resolve the ichnospecific identification of the Cedar Mountain Formation *Aquatilavipes* isp. specimens.

6. Discussion

The occurrence of *Aquatilavipes* at the base of the Poison Strip Member of the Cedar Mountain Formation indicates the presence of birds with probable shorebird-equivalent feeding modes and life habits in sandy lacustrine shoreline habitats; these birds were present in what is now the Colorado Plateau region by Aptian time. The timing is in concert with the British Columbian tracks, although the bird tracks from the Lakota Formation in the Black Hills may be slightly older. The Cedar Mountain Formation tracks are generally well preserved and are moderately abundant, and it is conceivable that more can be found at the same site (and at others yet to be located). The occurrence of *Aquatilavipes* in the Cedar Mountain and Lakota formations, as well as in other pre-Albian formations in Canada, contrasts with the late Albian-

Cenomanian occurrences of ichnogenus *Ignotornis* in the coastal plain facies of the Dakota Group: see Carpenter (2014) for recent comments on use of the term Dakota Formation. .

Recent attempts to summarize the avian track record (Lockley and Harris, 2010) have shown that in the Cretaceous, avian track diversity and site density is highest in east Asia, notably in Korea and China, where, in addition to reports of *Ignotornis* and *Aquatilavipes*, the ichnogenera *Koreanaornis*, *Uhangrichnis*, *Hwangsanipes*, *Goseongornipes*, *Gyeongsangornipes*, *Pullornipes*, *Shandongornipes*, *Tatarornipes* and *Moguionripes* also occur (Kim 1969; Yang et al., 1995; Lockley et al., 1992, 2006a,b, 2008, 2012; Xing et al., 2011; Kim et al., 2013). *Pullornipes* comes from the basal Cretaceous, whereas most of the other ichnogenera were, depending on different dating methods, reported from the latter part of the Early Cretaceous, or the early part of the Late Cretaceous. Recent re-dating of a previously-puzzling and anomalously old report of Late Triassic bird tracks (Melchor et al., 2013) as Eocene suggests that *Pullornipes* is likely the oldest reliable report of a bird track. There is some indication that Asian reports of *Aquatilavipes* sometimes represent incorrect identifications of *Koreanaornis*, but in general most of the aforementioned ichnogenera are morphologically distinctive and easily differentiated by rigorous morphometric analyses (Buckley et al., 2012).

In contrast, the Cretaceous avian track record in North America is sparser. In addition to the *Aquatilavipes* samples reported here, and from South Dakota and British Columbia, purportedly of Barremian and Aptian age respectively, the only other reports of Lower or “mid” Cretaceous bird tracks from the USA are *Ignotornis* and *Koreanaornis*, respectively from the Dakota Group of Colorado and Utah, and unnamed isolated tracks of probable avian affinity from the Patuxent Formation of the Potomac Group of Maryland (Stanford et al., 2007), which has been dated as upper Aptian (Zarra, 1989). However, in addition there are scattered reports of

bird tracks from the Lower and “mid” Cretaceous of Canada (Lockley et al., 1992; McCrea et al., 2001, 2014; Scott et al., 2001; McCrea and Sarjeant, 2001) and isolated reports of latest Cretaceous (Campanian–Maastrichtian) bird tracks, including the distinctive named semi-palmate ichnogenus *Sarjeantopodus* (Lockley et al., 2004), the ostensibly diverse Alaskan assemblage noted above (Fiorillo et al., 2011) and various unnamed morphotypes (Robison 1991; Lockley et al., 2004). Collectively, all of these bird tracks indicate forms with shorebird-like feet that made tracks essentially indistinguishable from those of modern shorebirds. In this regard, the general appearance of the track assemblages is similar to those reported from East Asia. However, as noted above, thanks in large part to the abundant reports from East Asia, significant ichnotaxonomic differences have been recognized between the Asia and North American ichnofaunas.

The occurrence of *Aquatilavipes* in three locations (British Columbia, South Dakota and Utah) in rocks of purported Barremian to Aptian age suggests that *Aquatilavipes* trackmakers may have been relatively common in the middle of the Early Cretaceous. Although also based on a small sample, the evidence available for the overlying late Albian - early Cenomanian Dakota Group suggests that different birds, the trackmakers of *Ignotornis* and *Koreanaornis*, were present at this time in western North America. The combined trackway evidence suggests the presence of several bird species in the Cedar Mountain Formation and Dakota Group (or Formation) that are as yet unknown from the skeletal record. Although significantly less abundant and diverse than tracks reported from the Lower to ‘mid’ Cretaceous of East Asia, the track record in western North America is nevertheless important given the lack of body fossils, as it represents evidence for a major clade which is typically sparsely represented in the fossil

record at this time, except where special preservation conditions prevailed, as in parts of China (Zhang et al., 2006).

7. Conclusions

- 1) Bird (avian theropod) track assemblages, representing more than 40 trackways, constitute the first report of bird tracks from the Cedar Mountain Formation.
- 2) Based on both standard comparative morphological and detailed statistical analysis the assemblages are interpreted to represent a single ichnogenus, *Aquatilavipes*.
- 3) As no skeletal remains of birds (avian theropods) are known from the Cedar Mountain, the assemblages represent a particularly significant addition to the otherwise abundant and well-known vertebrate faunas of this unit.
- 4) The occurrences are also significant given that reports of bird tracks are quite rare in the Early Cretaceous of the entire region.
- 5) The bird track occurrences reported here are arguably the oldest, or as old as any known for the region.
- 6) *Aquatilavipes* tracks appear locally abundant in lacustrine facies, and are morphologically distinct from those reported from the overlying coastal plain deposits of the Dakota Group. This indicates differences in avian diversity, related to stratigraphy and facies distributions between the Barremian-Aptian and late Albian-early Cenomanian.

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LIST OF FIGURES

Figure 1. Locality map showing location of bird tracks site in relation to the outcrop of the Cedar Mountain Formation in eastern Utah.

Figure 2. Photo of site showing Morrison-Cedar Mountain contact and bird track-bearing unit. Compare with Fig. 3.

Figure 3. Stratigraphic section. Compare with Fig. 2.

Figure 4. Photo (A) and map (B) of block 1 based on replica of UMNH.VP.24811 (UCM 199.66) and tracing T 1423. Note that only trackways B1T1- B1T5 are numbered, compare with Fig. 5 and Table 1.

Figure 5. Trackways B1T1-B1T5 from Block 1 (UMNH.VP.24811).

Figure 6. Map of block 2 based on tracing T 1576 from original specimen and replicas UMNH.VP.C.220 and UCM 199.80.

Figure 7. Map of block 3 based on tracing T 1577 from original specimen, which remains in the field and was not replicated.

Figure 8. Map of blocks 4 and 5 based on tracing T 1576 and T 1577 from original specimen and replica. A replica of theropod tracks from block 5 is cataloged as UMNH.VP.C.221.

Figure 9. Map (left) and photo right of block 7 (UMNH.VP.24812A). Map is based on UCM tracing T 1599 and reversed to show original orientation. Trackway B7T1 is shown in black. This specimen is also represented by the counterpart showing natural casts (UMNH.VP.24812B). See text for details.

Figure 10. Specimen CU 199.65 from the Lakota Group of South Dakota.

Figure 11. Discriminant analyses graphical and significance results in comparing the Cedar Mountain Formation tracks to *Aquatilavipes swiboldae* (top left), *Aquatilavipes izumiensis* (top right), *Barrosopus slobodai* (second row left), *Morguiornipes robusta* (second row right), *Pullornipes aureus* (third row left), *Tatarornipes chabuensis* (third row right), *Koreananornis hamanensis* (bottom left), and *Koreanaornis dodsoni* (bottom right). Morphologic similarity, combined with the multivariate statistical results, shows that the Cedar Mountain Formation tracks are most similar to those of *Aquatilavipes swiboldae*.

Figure 12. Canonical variate analysis graphical morphospace results comparing the Cedar Mountain Formation tracks (rectangle) to those of *Aquatilavipes swiboldae* (oval) and *Aquatilavipes izumiensis* (cross). While all three morphotypes show overlap, the largest amount of morphospace overlap is seen between the Cedar Mountain Formation tracks and *A. swiboldae*. Combined with the morphologic similarity and the results presented in Figure L1, the Cedar Mountain Formation tracks are likely those of *Aquatilavipes* sp.

LIST OF TABLES

Table 1. Summary inventory of the seven track-bearing blocks and the number of tracks and trackways identified in each sample.

Table 2. Track and trackway measurements for the footprint assemblage recorded on block 1. Note that 48 tracks with clear tridactyl morphology have been designated numbers, although with partial tracks included the entire sample represents 67 footprints.

Table 3 Track and trackway measurements for the footprint assemblage recorded on blocks 2-7. Note that 37 avian and three non avian theropod tracks with clear tridactyl morphology, have been designated numbers. With partial, un-measured tracks included the entire sample for blocks 2-7 represents 66 footprints.

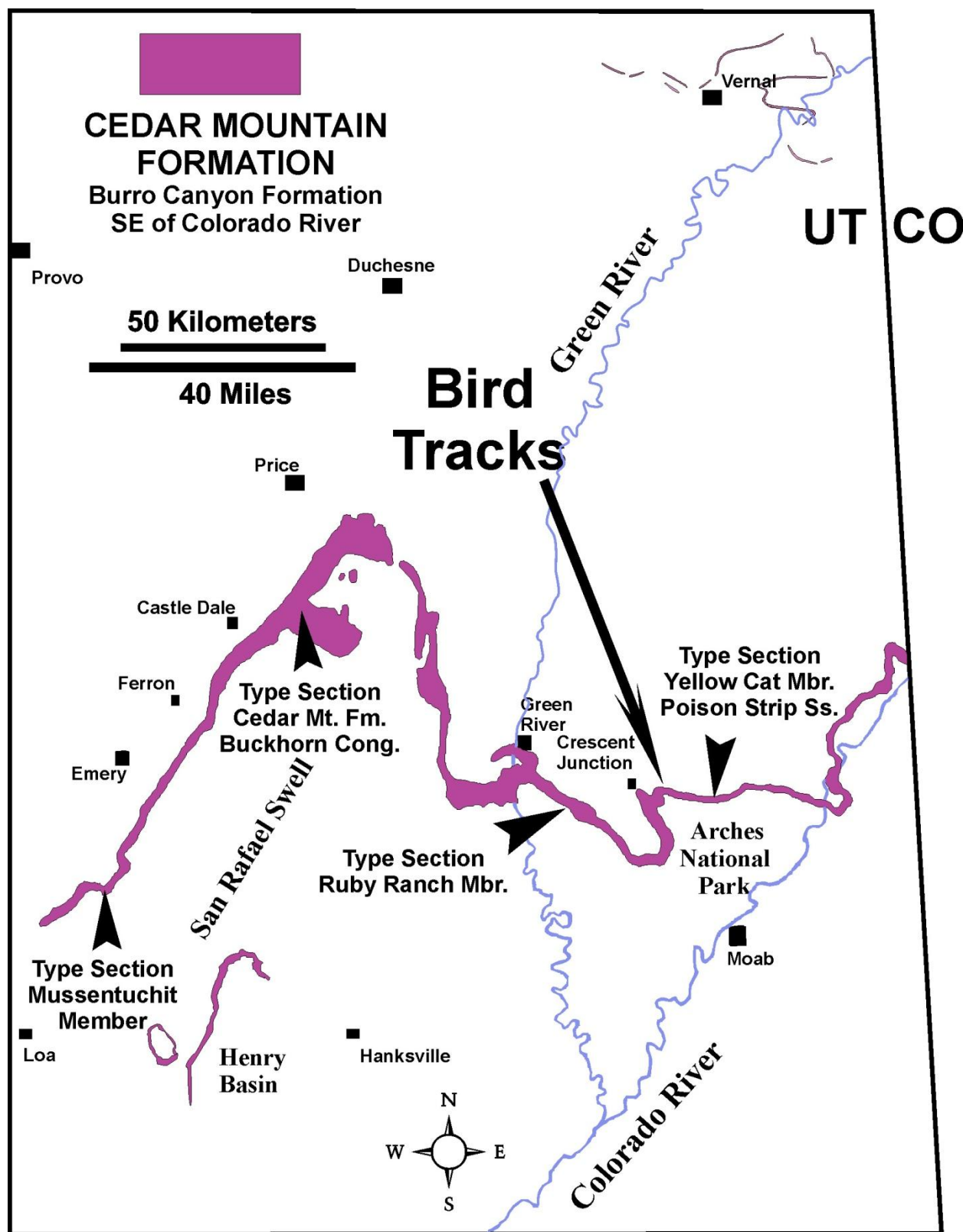


Figure 1

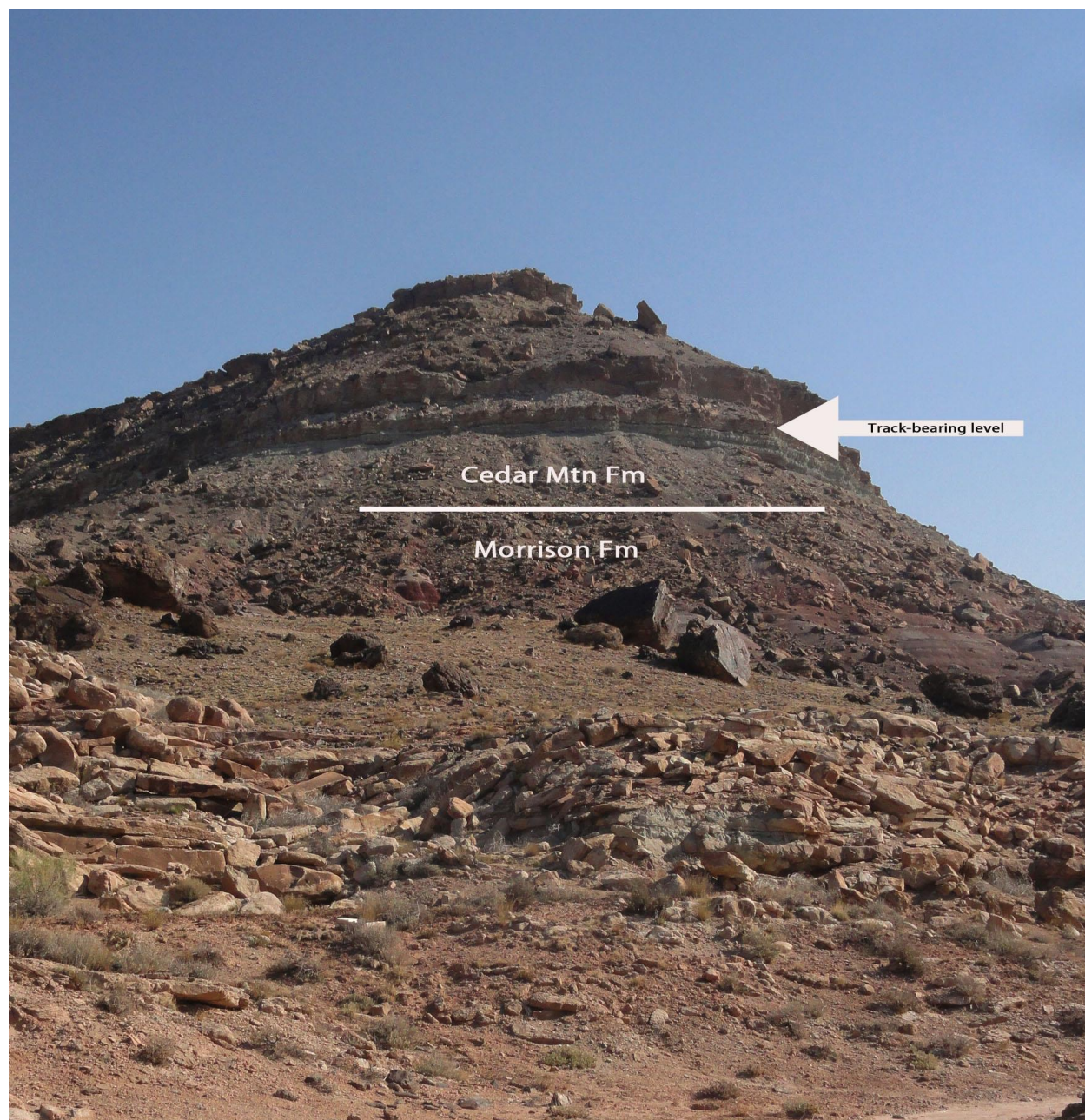


Figure 2

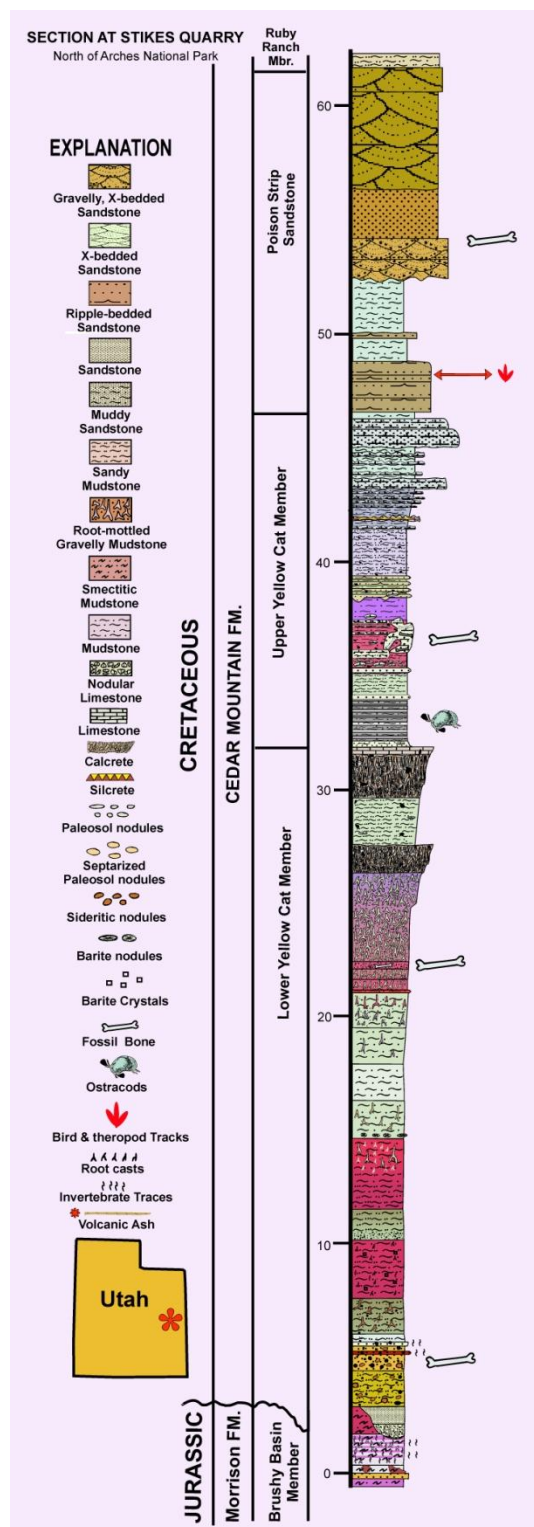


Figure 3

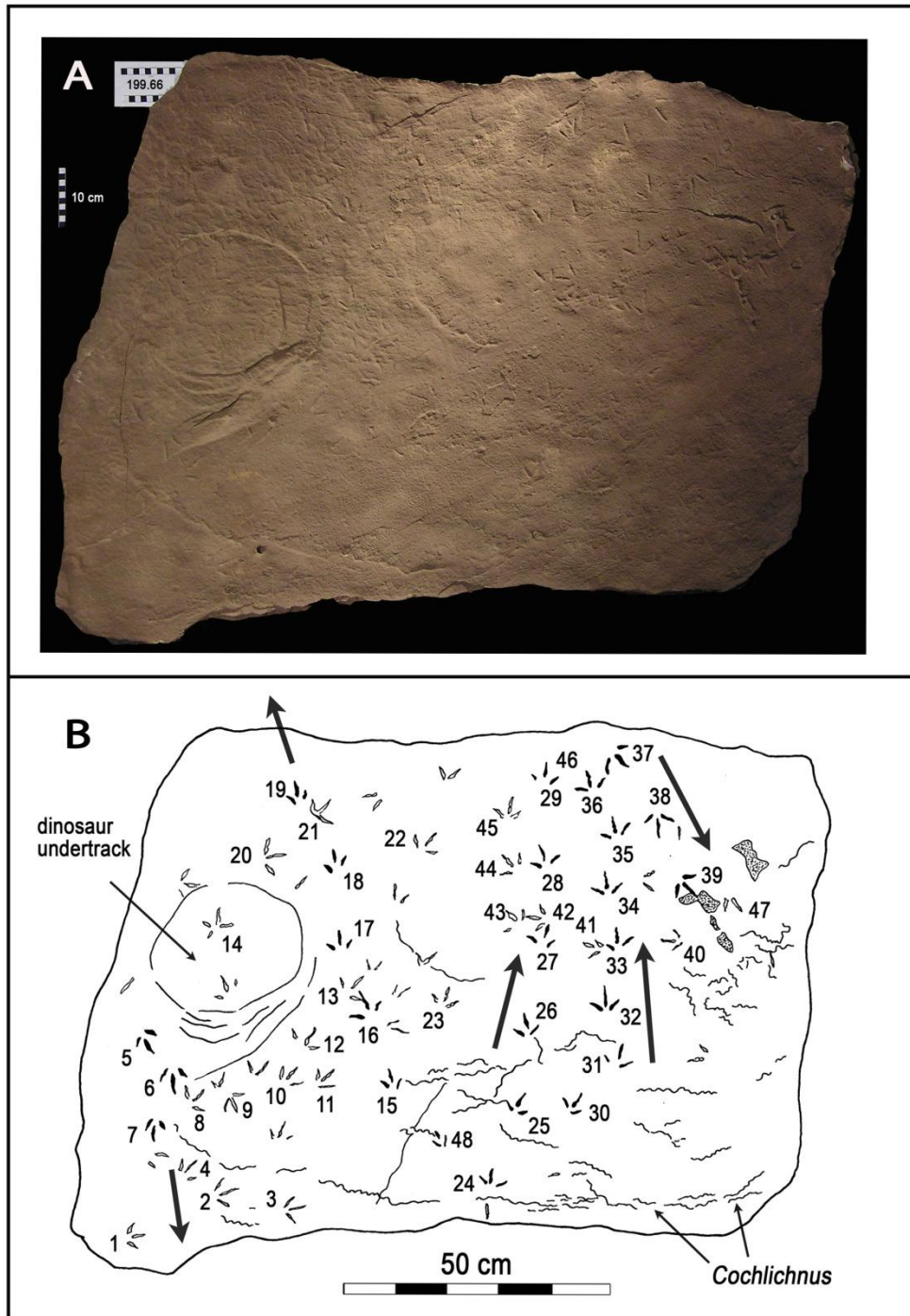


Figure 4

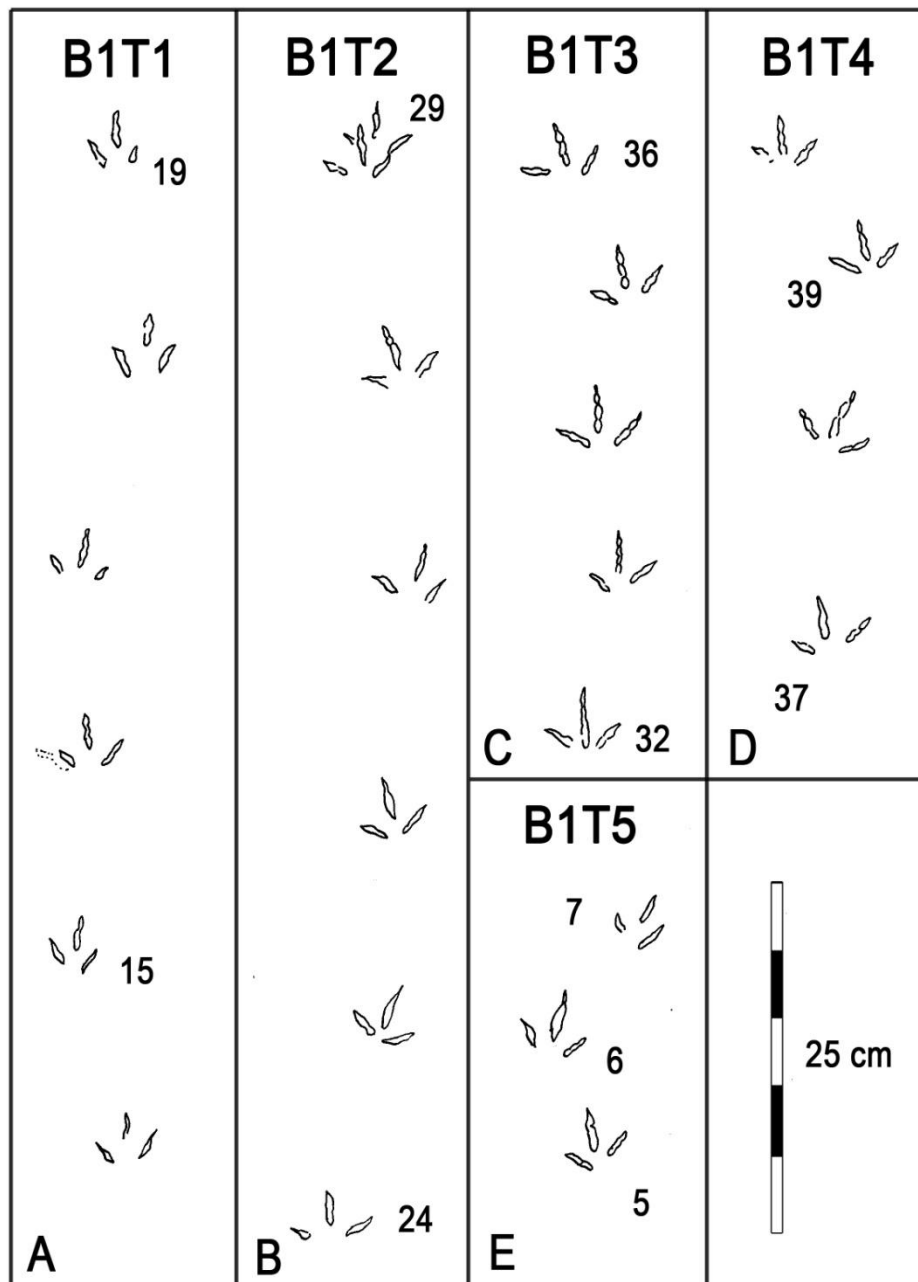


Figure 5

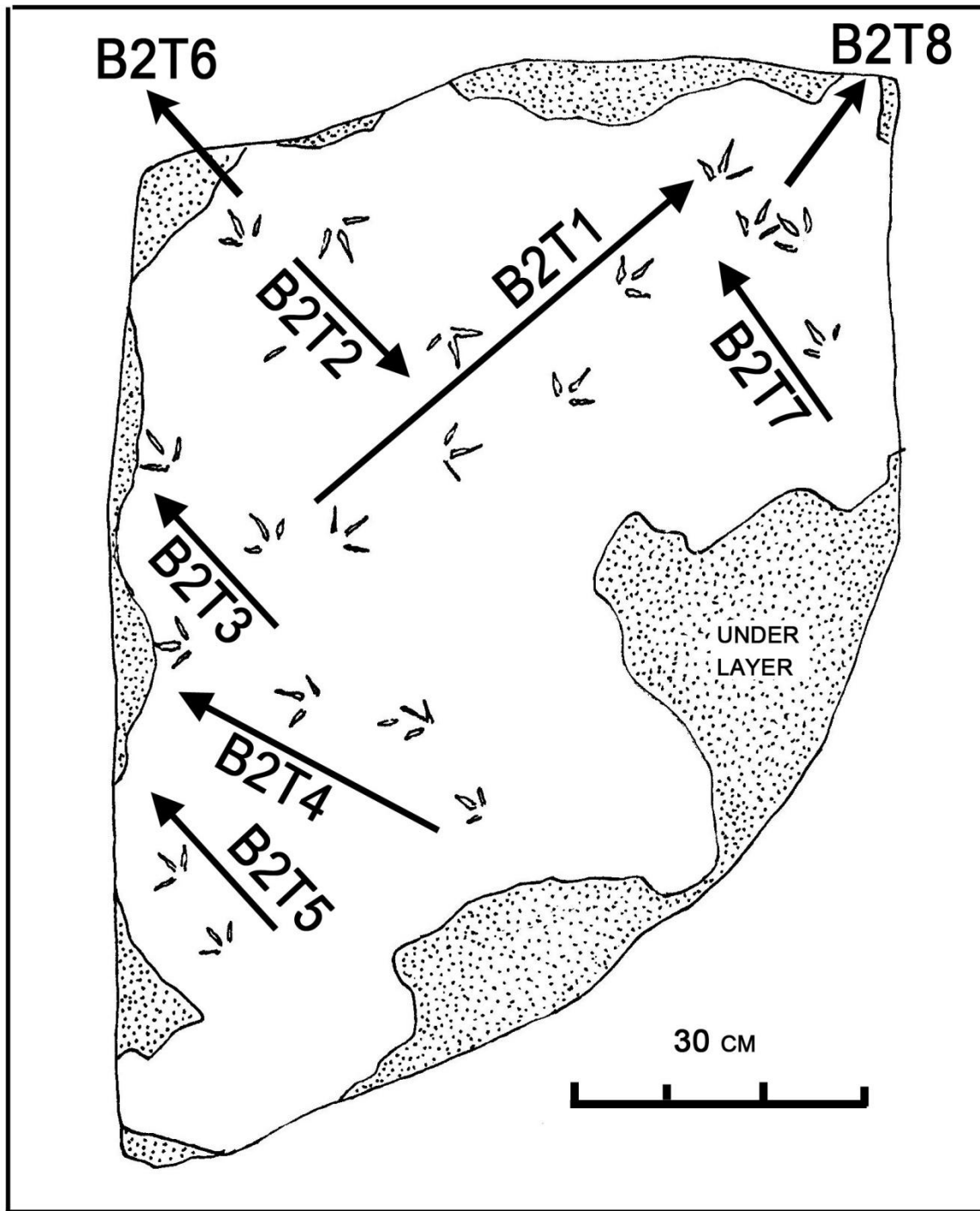


Figure 6

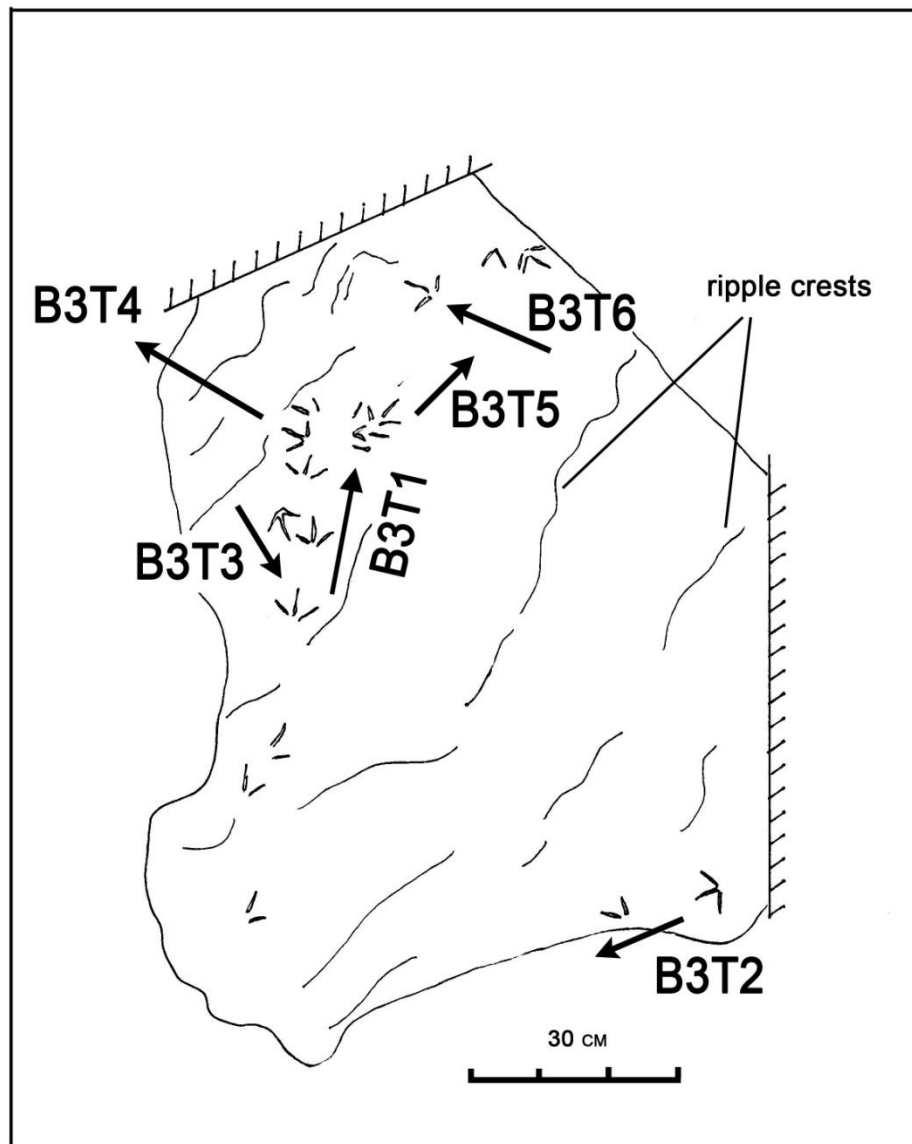


Figure 7

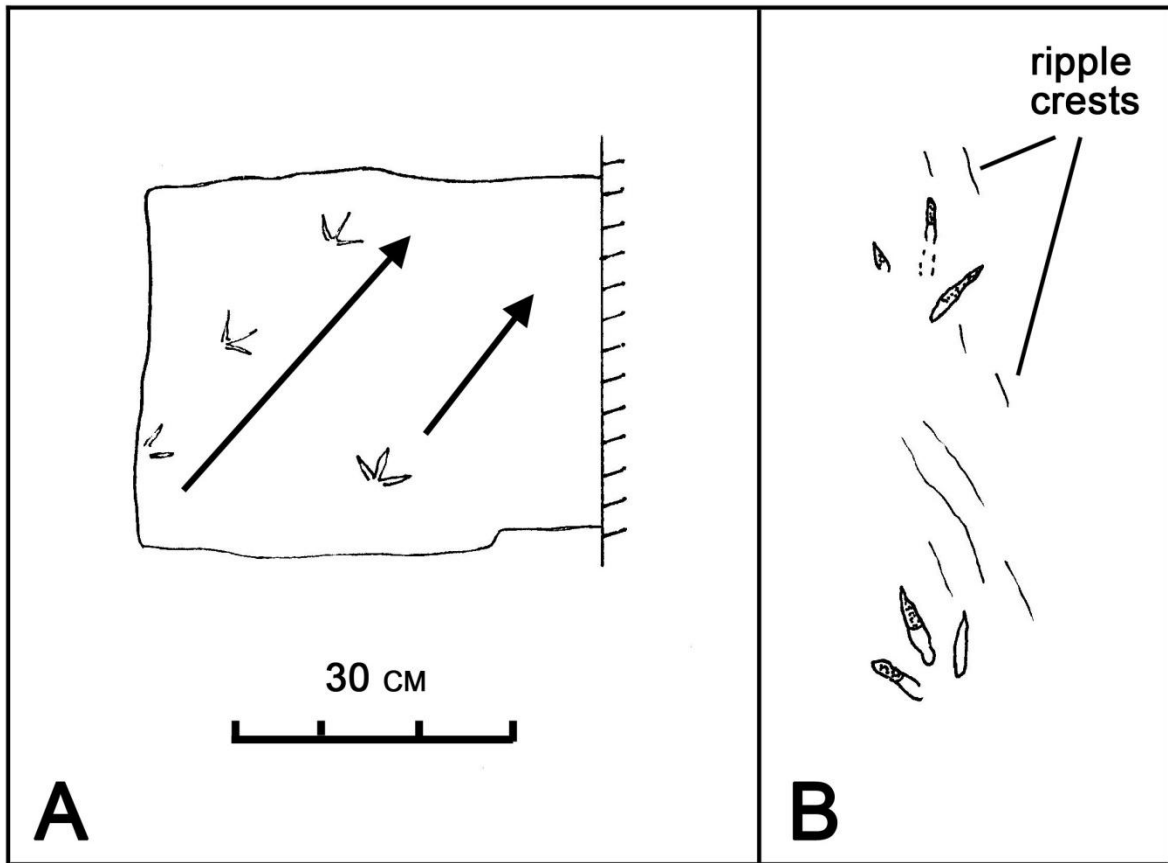


Figure 8

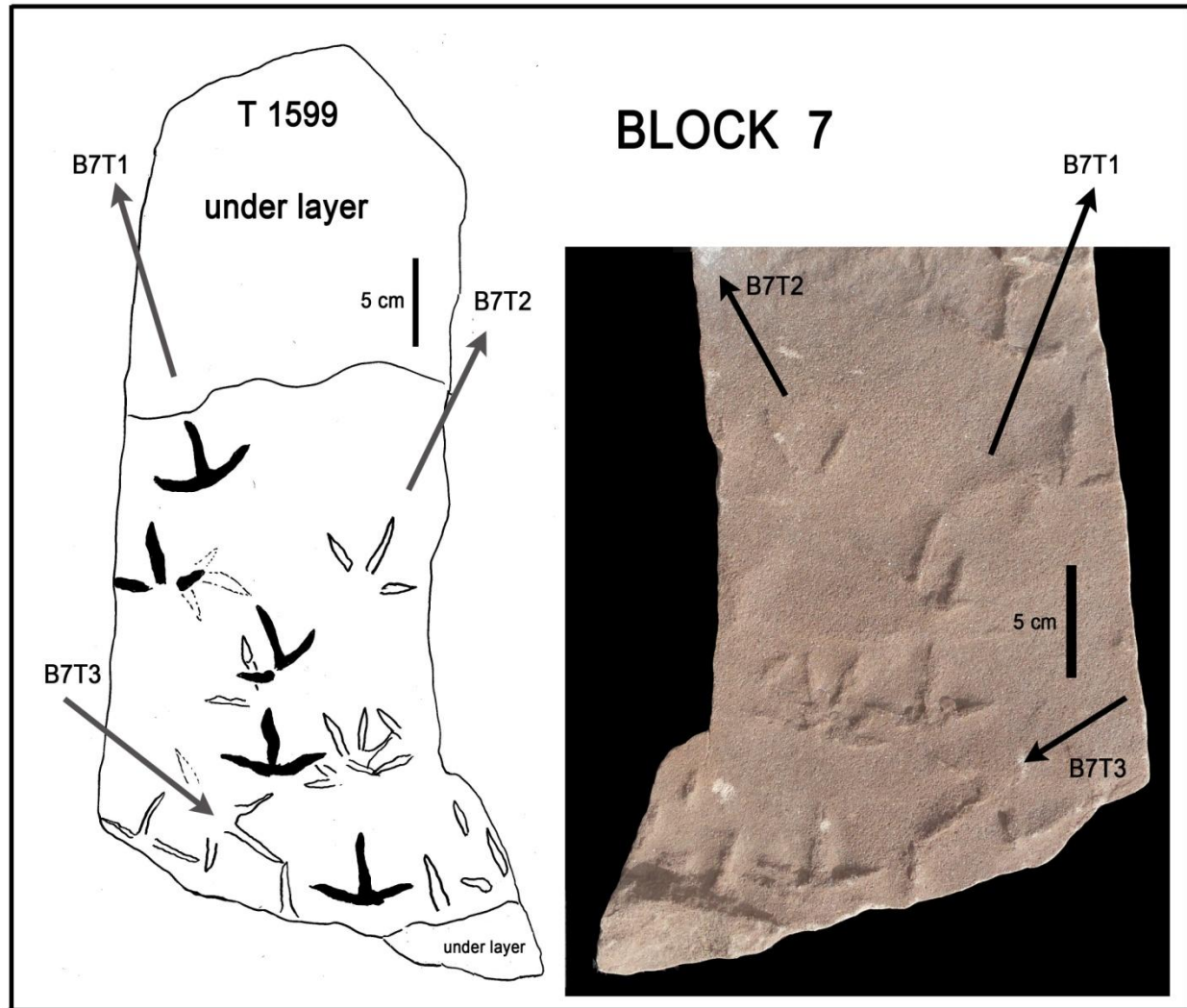


Figure 9



Figure 10

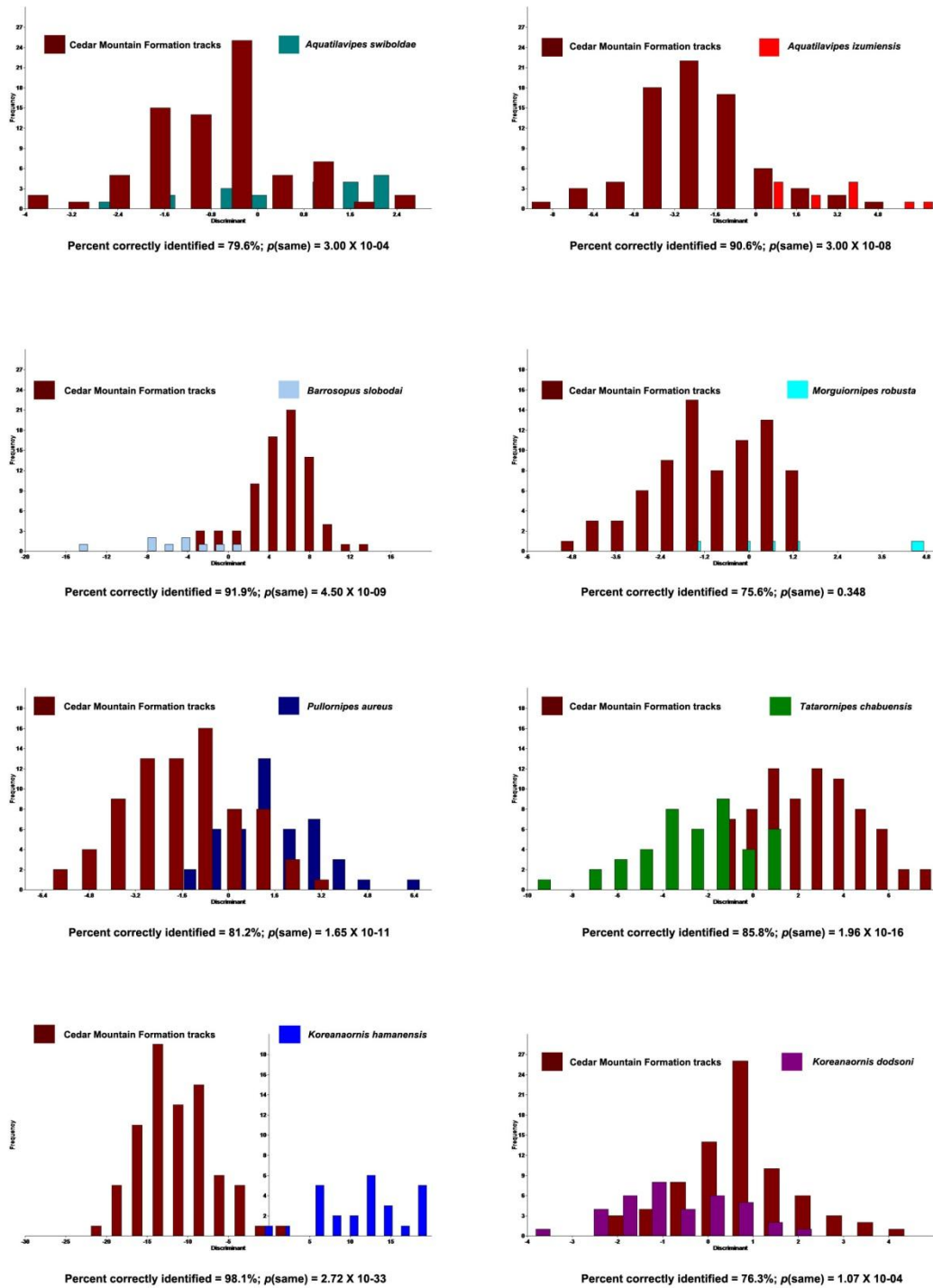


Figure 11

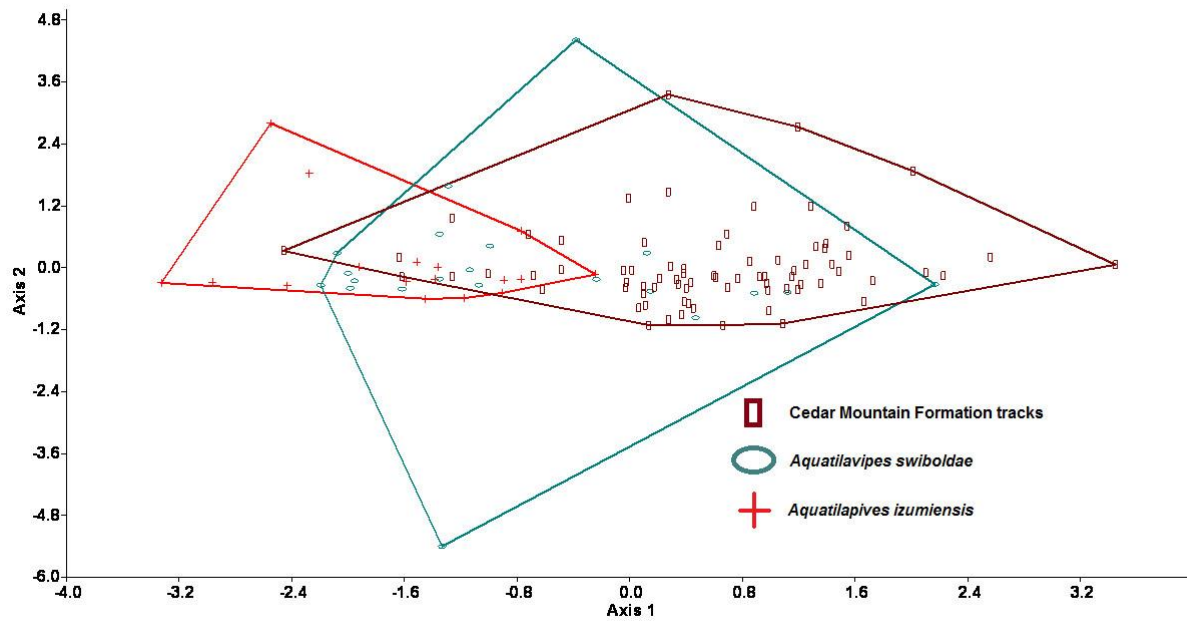


Figure 12

HIGHLIGHTS PALAEO 7946

First report of bird tracks from the Lower Cretaceous Cedar Mountain Formation, Utah.

First bivariate and multivariate analysis of multiple Cretaceous avian ichnotaxa.

Statistical support for validity of most well-known Cretaceous avian ichnotaxa.

Oldest evidence of birds from Cretaceous of USA.