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DINOSAUR AND TURTLE TRACKS FROM THE MORRISON FORMATION (UPPER JURASSIC) OF COLORADO NATIONAL MONUMENT, WITH OBSERVATIONS ON THE TAXONOMY OF VERTEBRATE SWIM TRACKS

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Abstract—Two small bedding plane exposures in the Morrison Formation of Colorado National Monument (Mesa County, western Colorado) reveal vertebrate tracks attributable to small ornithopod dinosaurs (ichnogenus *Dinehichnus*) a theropod, and turtles (ichnogenus *Chelonipus*, here identified as a component of the Morrison ichnofauna for the first time). These two ichnogenera are rare in the Morrison Formation, having been, in each case, previously reported only from one other tracksite locality. Both the dinosaur and turtle tracks show parallel orientations towards the north and northwest and indicate distributions influenced by current flow. The interpretation and ichnotaxonomy of turtle and other vertebrate swim tracks is also discussed, with reference to the concept of vertebrate ichnofacies. It is clear that *Chelonipus* is typical of fresh-water fluvial deposits in both North America and Europe throughout the Mesozoic. We therefore name a *Chelonipus* ichnofacies, based on these recurrent associations. This ichnofacies is easily distinguished from the *Chelonichnium* ichnofacies which is based on recurrent associations of marine turtle tracks made in carbonate facies.

INTRODUCTION

In 2005, Marilyn Sokolosky of Fruita, Colorado, reported a new vertebrate fossil footprint site in the Morrison Formation exposed within Colorado National Monument. The outcrops consist of an alternating succession of fluvial sandstones and mudstones provisionally assigned to the Salt Wash Member (Figs. 1 and 2), although this area has been mapped as Tidwell Member by Scott et al. (2001). Preliminary investigations indicate that there are multiple track- and trace-bearing levels attributed to diverse invertebrates and vertebrates. However, many of these levels reveal only undiagnostic dinoturbation, or complex invertebrate bioturbation that is outside the scope of this study to investigate in detail. This paper, therefore, focuses on distinctive vertebrate tracks found at two horizons. The first horizon reveals at least eight tracks of small bipedal dinosaurs and the second reveals several dozen tracks attributed to turtles. We also discuss the context and preservation of these tracks and their implications for interpreting behaviour.

METHODS

Outcrops at the study site consist of road-cut cross sections with few extensive bedding plane exposures (Figs. 1 and 2). The section was measured in order to place the tracks in the context of the local sedimentary geology. Tracks are preserved as natural casts on the underside of small overhangs which are difficult to view. In this preliminary investigation we photographed the tracks and traced them on clear acetate film. Selected tracks were also molded by hand with ‘Sculptey’ clay which produces a ‘mold’ from the natural cast. Plaster casts were then made from these before the clay was baked to produce hard copies. Latex molds were then made from the baked clay so that a second, reverse generation of plaster casts would be made. Thus, we preserved both cast replicas and their counterpart molds, without any damage to the original tracks. This allowed us to again trace selected well-preserved track replicas in the laboratory where more detail could be discerned. Replicas are housed in both the CU Denver Dinosaur Tracks Museum collections (prefix CU) and the Museum of Western Colorado collections (prefix MWC). Some of these specimens are compared with specimens in the joint collections (prefix CU-MWC).

The track-bearing sandstone beds are not suitable for easy collecting or excavation, though small portions have become detached, and other

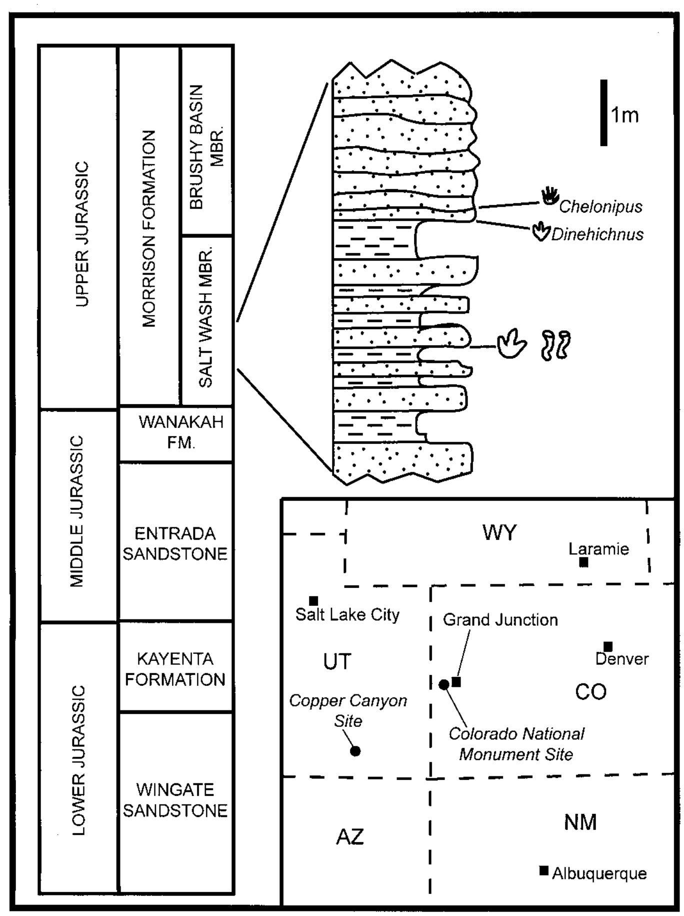

FIGURE 1. Location (inset) of the turtle tracks at Colorado National Monument and from Copper Canyon. Simplified stratigraphic section at the tracksite, in context of the Jurassic section at Colorado National Monument. The stratigraphic section shows the upper track bearing horizons examined in this study.

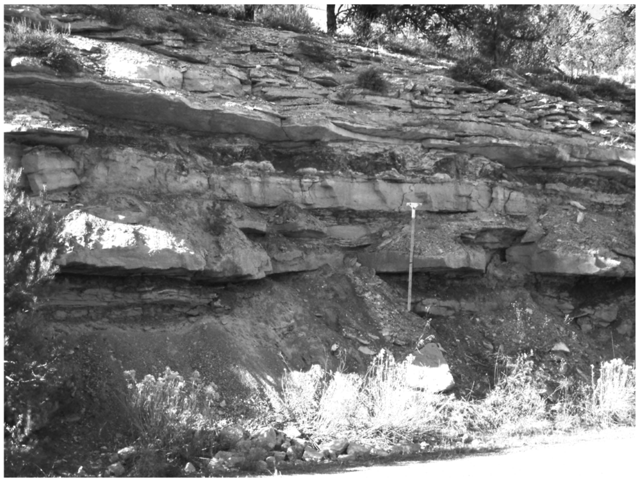

FIGURE 2. Photograph of tracksite. J-staff scale is 1.5 m.

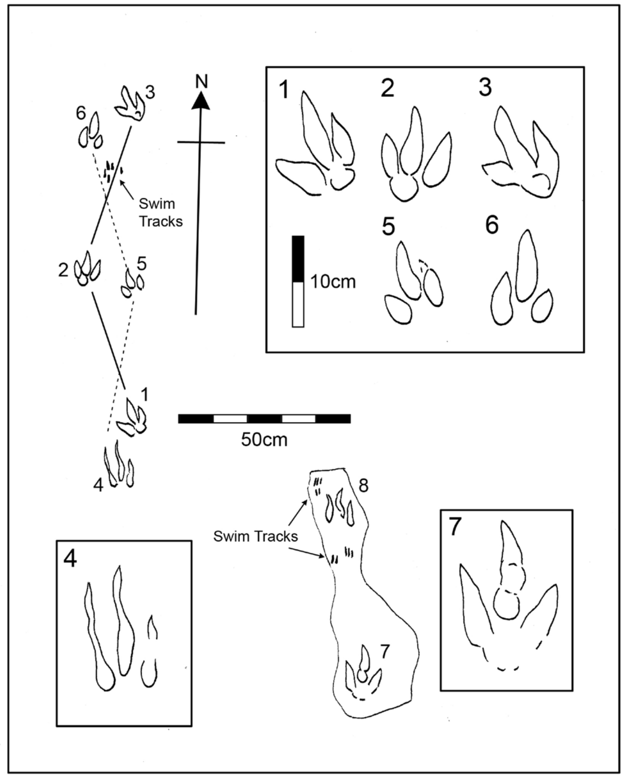

FIGURE 3. Line drawing map of tridactyl tracks based on field tracing, with numbers indicating, trackway segments comprised of tracks 1-3 (solid lines), 4-6 (dotted lines) and 7-8. See text for details. Small turtle swim tracks have similar alignment to tridactyl tracks.

parts may erode out in the near future. We therefore propose to make latex molds of the mapped surfaces at a future date, when decisions about collecting original material will again be considered.

TRIDACTYL TRACKS: EVIDENCE AND INTERPRETATIONS

Eight tridactyl tracks were recorded in partial trackway configurations at the base of a complex channel sandstone sequence about two meters thick. Thus, the tracks were made before the fluvial system was well-established in this immediate area. The tracks are all oriented to the north. The tracks range in size (foot length) from 8.5 to 16.0 cm. However, measurement of other parameters such as step and stride are too ambiguous to determine confidently due to the unusual trackway configurations, which suggest both normal walking and slipping or sliding in a subaqueous setting or as the result of current activity compromising normal terrestrial locomotion.

As shown in Figure 3, the tracks are clustered in two areas. The simpler of the two groupings is a pair of tracks that appear to be in sequence. The larger track (foot length and width 16 and 11 cm respectively), designated number 7, is shallow but appears to represent a normal walking track, possibly of a theropod as indicated by faint pad impressions on the central digit. The second track, designated number 8, is smaller (11.0 by 7.0 cm) and less complete, appears to be a slide mark similar to the swim track morphotype named *Characichnos* by Whyte and Romano (2001).

The second grouping is more complex, consisting of six sub-parallel tracks (Fig. 4) that appear amenable to at least two interpretations. The first interpretation is that there are two trackways with similar orientation, and with successive footprints placed close together, so as to appear as pairs situated more or less side by side. The numbering scheme used here is designed to facilitate this interpretation, which is further supported by the similarity in size of tracks 1, 2 and 3 (mean length and width 10.97 and 7.87 cm) and the similar step lengths of 44.5 and 49.5 cm respectively for steps between footprint 1 and 2 and between 2 and 3 (Table 1). These tracks resemble normal *Dinehichnus* (Lockley et al., 1998) walking tracks and have a well-defined positive (inward) rotation of between 15 and 29^{o} (mean 23.3^{o}).

By contrast tracks 4, 5 and 6 are smaller (mean length and width 9.5 and 6.73 cm), and track 4 is essentially a *Characichnos*–type swim track. Nevertheless tracks 5 and 6 also resemble *Dinehichnus* and show positive inward rotation of about 14^{o} and more or less consistent step lengths of 46.5-51.0 cm (see Table 1). This interpretation is also supported by the consistent position of tracks 1-3 in front of tracks 4-6. As noted below, this configuration is hard to reconcile with alternate interpretations.

The second possible interpretation is that the tracks represent a single animal that progressed in 'hops' or some other form of progression that produced pairs of right and left footprints situated more or less side by side. This latter interpretation perhaps receives some support from the presence of elongate claw scratch marks in both the first two tracks in the sequence. This might suggest that the trackmaker stood in water in which a current pushed the animal in the direction of progression. Many small scratch marks attributed to turtles also provide evidence of current flow in this direction (towards about 20^{o}). This interpretation requires that we infer a type of subaqueous hopping encouraged by current flow in which the trackmaker picked up and put down both feet more or less simultaneously. Alternatively, the trackmaker could have taken normal steps from left to right or right to left, followed by only a 'half stride' in which the next step was short, coming to rest beside the other foot in a 'standing ' position: i.e. with both feet side by side rather than with the leading foot being placed one step length ahead of the trailing foot. The weakness of this interpretation is that it does not explain the difference in size and positioning of the 'side by side' footprints. Similarly, if this interpretation is followed one would also have to explain why the left and right footprints are alternately behind and ahead of each other in successive 'side by side' groupings.

These considerations lead us to conclude that the six tracks number 1-6 (ichnogenus *Dinehichnus*) were made by two trackmakers proceeding in the same direction. The gait of both animals may have been slightly disturbed by progression over a soft slippery substrate and current flow in the direction of travel. Following the interpretations of Lockley et al. (1998) of type *Dinehichnus*, the trackmakers were probably ornithopod dinosaurs, possibly *Dryosaurus*. A third animal, probably a theropod, progressed in the same direction about 60 cm to the east of the *Dinehichnus* trackmakers. It is not possible to determine the time interval required for the passage of the three individuals, or the order of their progression through this area. However, the two *Dinehichnus* trackways are very similar in depth and mode of preservation, so were probably made at the same time.

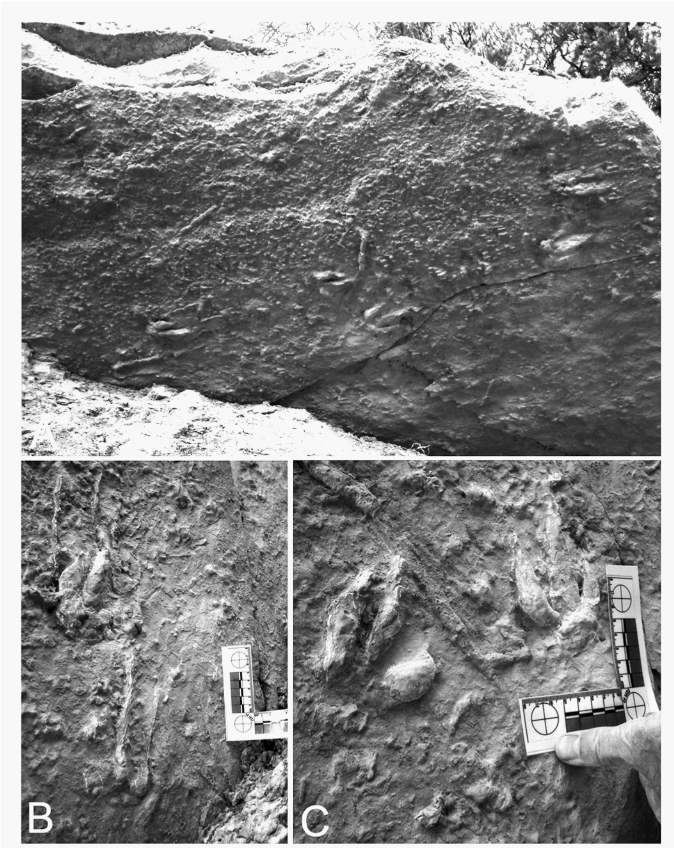

FIGURE 4. Photos of tridactyl tracks. **A:** shows tracks 1-6 representing two trackways (1-3 and 4-6) oriented towards the north. Compare with Fig 3. **B:** shows tracks 1 and 4 side by side, **C:** shows tracks 2 and 5 side by side.

Table 1. Measurements (in cm) for tridactyl tracks: (brackets indicate uncertain measurements or tracks distorted by preservation or 'slide' traces). Mean measurements for trackways 1-3 and 4-6 given in **bold**.

Track number	Footprint length	Footprint width	Step	Stride
1	11.3	8.3	1-2 44.5	-
2	10.6	7.3	2-3 49.5	1-3 91.5
3	11.0	8.0	-	-
Mean 1-3	**10.97**	**7.87**	**47.0**	**91.5**
4	(13.5)	6.5	4-5 51.0	4-6 97.0
5	8.5	6.6	5-6 46.5	-
6	10.5	7.1	-	-
Mean 4-6	**9.5**	**6.73**	**48.75**	**97.0**
7	16.0	11.0	7-8 47.0	-
8	(11.0)	(7.0)		

TURTLE TRACKS AND THEIR INTERPRETATION

At least fifty distinctive turtle tracks of *Chelonipus* type were recorded as natural casts on a single bedding plane about 10 centimeters above, and a few meters west of the dinosaur track-bearing level (Figs. 1 and 5-7). This shows that the tracks were made *within* a fluvial channel system rather than in floodplain or overbank mud that was subsequently filled in by channel sand. Almost all the tracks show consistent orientations towards the north-northeast (Fig. 5). Individual tracks vary in size and shape, in part due to variation in preservation (Fig. 6). Most are wider than long with only toe impressions and no heel traces. These toe traces are tapered anteriorly but terminate posteriorly in a transverse wall, which sometimes marks the front of a small sediment mound behind the track. Such track morphology indicates that the trackmakers dug in the toes of their feet without making heel impressions. Smaller tracks show only three digit impressions (digits II-IV) and measure only 1.2 by 2.7 cm (footprint length and width respectively). Larger tracks show five digit impressions (digits I-V) and measure up to 2.8 cm by 5.1 cm (footprint length and width respectively). Some tracks show four digit impressions.

The length of digit traces is variable, and may be due to differences in the angle of penetration of the foot, or dragging of toes as the foot left the substrate. However, in all cases the longest digit traces are II, III and IV. Where preserved digit traces I and V are short. Foot traces with all toe impressions are quite symmetrical and conform well to the morphology of turtle feet (Foster et al., 1999). Some tracks occur in pairs and may represent manus-pes pairs, but may also represent a double trace made by the same foot. Although some tracks occur in parallel lines and therefore represent trackways, it is hard to discern alternating left and right tracks that would be expected in a well-preserved walking trackway. Thus, given the emphasis of toe impressions we infer that the tracks are 'swim tracks' made by partially buoyant animals.

These turtle tracks are very similar to those found in Utah in Copper Canyon and reported by Foster et al. (1999). Four types of turtles are currently known from the Morrison Formation: *Glyptops*, *Dinochelys*, *Uluops*, and *Dorsetochelys*. Both *Uluops* and *Dorsetochelys* are known only from high in the formation at Como Bluff, Wyoming. *Dinochelys* is found somewhat lower in the Morrison, but only *Glyptops* has been found well down into the levels equivalent to the lower Salt Wash Member (Foster, 1998). There is no way to necessarily determine what known genus, if any, made the turtle tracks described here, but it is worth noting what forms were around at the time.

SOME OBSERVATIONS ON SWIM TRACKS

As indicated in Table 2, there are at least four names that have been introduced to describe three and four toed swim tracks attributed to turtles, crocodilians and dinosaurs. Although some of these names suggest an attribution to known trackmaker groups, we can not use purported trackmaker affinities as criteria for naming tracks. The distinctions must be made on the basis of track morphology parameters such as number and relative length and width of digit impressions.

We infer that six of the dinosaur tracks are similar to *Dinehichnus socialis* (Lockley et al., 1998) and herein infer that they can be assigned to this ichnospecies. However, as noted above, one track appears distorted into three elongate, parallel scratch marks of the type assigned to the ichnogenus *Characichnos* by Whyte and Romano (2001) which they interpreted as 'swim track' traces produced by theropod dinosaurs. It is inherently problematic to use two ichnogenera to label different tracks in the same trackway, and we infer that *Characichnos* is an extramorphological label, that may potentially be produced by any trackmaker that used three toes to create parallel traces. Thus, tridactyl track 4 in the inferred ornithopod track assemblage 1-6 appears to have created the *Characichnos* track type in association with otherwise diagnostic walking *Dinehichnus* tracks.

Track number 7 is probably a theropod track, but can not be assigned to an ichnogenus due to lack of visible morphological detail. Track number 8 appears to be of the *Characichnos* type.

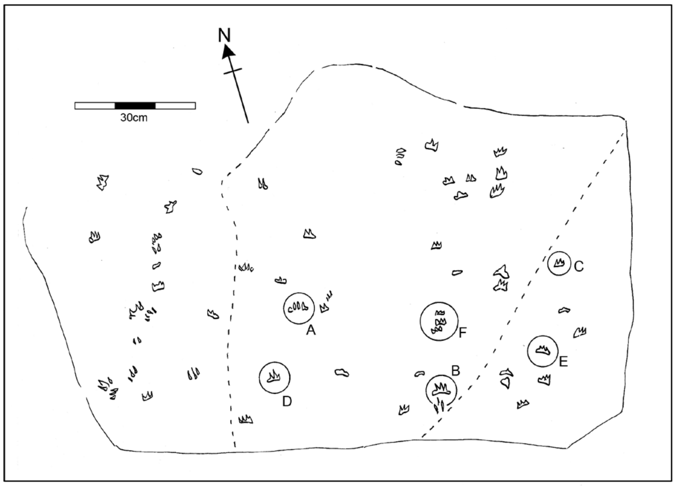

FIGURE 5. Line drawing map of turtle tracks based on field tracing. Dashed line represent fractures in track-bearing surface. Replicated tracks **A-F** were reposited in the CU Denver Dinosaur Tracks Museum collection (CU- 197.4- 197.9 respectively) and in the Museum of Western Colorado collections. See Fig. 6 for details of morphology for **A-E**.

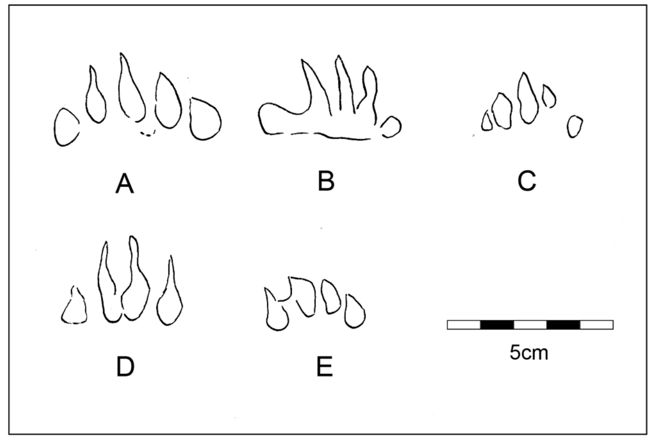

FIGURE 6. Detailed line drawing of selected turtle tracks A-E respectively correspond to tracks CU- 197.4- 197.8 in the University of Colorado at Denver Museum collections (see Fig. 5 for location on map)

We infer that the turtle tracks are similar to those named as *Chelonipus torquatus* by Ruhle von Lilienstern (1939) and *C. plieninergi* by Haubold (1971), both of which come from the Upper Triassic of Germany. Even though likely made by turtles of a different type, these tracks should not be confused with *Chelonichnium* described by Bernier et al. (1982) from the Late Jurassic lithographic limestones of Cerin, France. These French tracks are larger than the German ichnites. Moreover, they occur in marine deposits and they consistently exhibit at least four elongate digit impressions. As noted by Lockley and Meyer (2000), these tracks occur in association with pairs of large, widely spaced tridactyl tracks named *Saltosauropus latus*. This ichnospecies was originally attributed to hopping dinosaurs (Bernier et al., 1984) as the name implies, but later attributed to large swimming turtles (Thulborn, 1989, 1990). We agree with the swimming turtle trackmaker interpretation (e.g. Lockley, 1991; Lockley and Meyer, 2000), which has now been proven beyond reasonable doubt by new discoveries (Gaillard et al., 2003). These latter authors have essentially proven that the *Saltosauropus* manus impression may have five digits (see Table 2), although this is not explicitly stated as a formal revision of *Saltosauropus*. Thus, *Saltosauropus* can be considered a behavioral variation of the ichnotaxon *Chelonichnium*: i.e., the former is a swim track and the latter a walking trace, probably made by the same type of trackmaker. The name *Saltosauropus* is clearly misleading as it was not made by a hopping dinosaur. It is possible to make the case that it is a junior synonym, and behavioral variant of *Chelonichnium*, which, as the name implies, is correctly attributed to a turtle trackmaker. However, *Saltosauropus* is also similar morphologically to *Chelonipus*. Thus, a case could be made for abandoning the ichnogenus *Saltosauropus* and either referring *S. latus* to *Chelonichnium latus*, or to *Chelonipus latus* (Ruhle von Lilienstern, 1939). The latter name would be the most appropriate and parsimonious given its historical priority and morphological similarity. The taxonomic status of these ichnogenera was discussed recently by Avanzini et al. (2005) who reported *Chelonipus* tracks from the Upper Jurassic of Spain that are very similar to those described herein from the Morrison Formation.

Hatcherichnus represents a purported crocodilian track from the Morrison Formation (Foster and Lockley, 1997) and *Albertasuchipes* (McCrea et al., 2004) must also be considered in any discussion of vertebrate swim tracks. The type material of *Hatcherichus* reveals a four-toed pes and three-toed manus impression that shows slight curvature of digit traces and an associated tail trace. However, the type material of *Albertasuchipes* is described as having a three toed manus and pes, though one manus-pes set in the holotype sequence (UALVP 134) specimen shows a four toed manus impression. Moreover this ichnogenus is included in the ichnofamily Batrachopodidae (Lull, 1904), which has a four toed pes and five toed manus.

From a strictly morphological viewpoint these characteristics (a minimum of four manus and pes toes) distinguish *Hatcherichnus, Albertosuchipes* (and *Chelonipus* and *Chelonichnium*) from three-toed tracks such as *Saltosauripus* and *Characichnos*. However, it is clear that aquatic vertebrates such as turtles and crocodilians may leave five, four, or three toed footprints when swimming. Variation in the number of toe impressions depends on many factors including preservation and the extent to which the foot is completely impressed on the substrate. In many cases tracks have not been named. For example, three- and four- toed swim tracks are abundant in the Dakota Group of Colorado, Kansas and New Mexico. These were initially interpreted as ornithischian dinosaur tracks (McAllister 1989a,b) but have since been reinterpreted as crocodilian (Bennett, 1993; Lockley and Hunt, 1995; Kukihara et al., 2005). These tracks are quite large (up to 15 cm long) and the toe impressions are wide and curved. Technically, *Hatcherichnus* is the most suitable name for these Dakota tracks because *Characichnos* digit traces are too narrow and straight and never have an associated fourth digit trace. Likewise, *Saltosauripus* is three toed and not preserved in manus-pes pairs.

Such morphological considerations indicate that the sample described herein consists of small, sometimes five-toed tracks that do not fit the description of the ichnogenera *Hatcherichnus*, *Saltosauripus, Albertasuchipes* or *Characichnos*. This leaves only *Chelonipus* or *Chelonichnium* as suitable labels for the tracks from the Morrison Formation of Colorado National Monument.

SYSTEMATIC OBSERVATIONS

The ichnogenus *Chelonichnium* was adopted by Bernier et al (1982) who argued that this is the best ichnogenus to use for describing turtle tracks. However, they resurrected this ichnogenus usage on the basis of a dubious specimen described by Walther (1904) and did not address the fact that other authors had declared the name a *nomen dubium* (see Avanzini et al., 2005, for review). Likewise, Bernier et al. (1982) did not adequately review the descriptions of *Chelonipus* (Ruhle von Lilienstern, 1939); see Avanzini et al. (2005) for a recent review. We note here for clarification that both *Chelonipus* and *Chelonichnium* are distinct from *Chelichnus*, now considered to be the track of a caseid or dicynodont, that is associated almost exclusively with eolian facies, and which indeed forms the basis for the *Chelichnus* ichnofacies first described by Lockley et al. (1994). *Chelonichnium* has a different morphology and has already been used to identify a *Chelonichnium* ichnofacies associated with sub-aqueous ichnofacies in entirely different lagoonal facies (Lockley and Meyer, 2000).

FIGURE 7. Shows turtle tracks on underside of ledge. Compare with Fig 5.

It is worth noting that the name *Chelonichnium* is not used here in any strict ichnotaxonomic sense. It is merely used to designate the repeat occurrence, in marine sediments, of tracks given this label by Bernier et al. (1982). The use of the name *Chelonipus* to describe the ichnofacies would have required several complicated and inappropriate steps including: the formal rejection of the usage adopted by Bernier et al. (1982), demonstration of close similarity between German, Upper Triassic *Chelonipus* and French, Upper Jurassic *Chelonichnium* (*sensu* Bernier et al., 1982), and the definition of a *Chelonipus* ichnofacies that mixed different turtle track associations from both fresh water and marine facies. These steps could not be justified.

Given the complexities of the ichnotaxonomy of these ichnogenera, we err on the side of caution by simply describing the Morrison forms as *Chelonipus* isp., and offering the following informal description:

Chelonipus isp.

Description: Small symmetric five toed track, wider than long, with digits I and V very short. Digits II, III and IV sub-equal in length, tapering to a short sharp claw impression, with digit III very slightly longer than II and IV. Trackway wide with short step and stride patterns hard to discern. The Colorado National Monument trackway is composed of tracks that in the field are variably preserved and so may appear tri-, tetra- or pentadactyl in character. The impressions of the feet are symmetrical with the central digits II, III and IV longer than the other digits, and digit III the longest by only a very slight margin. It is clear that trackways exist, and that they are wide with short steps and strides, but manus-pes differentiation is difficult. We consider this a diagnostic characteristic of turtle trackways, as would be expected from their locomotor styles (cf., Foster et al.,1999).

DISCUSSION

The Colorado National Monument site provides only the second example of *Dinehichnus* tracks from the Morrison Formation, and only the second example of a well-defined assemblage of turtle tracks of the type that we here assign to *Chelonipus* isp. As noted above, the other, first-reported occurrences of these two ichnogenera occur in deposits in Utah that are stratigraphically correlative (Lockley et al., 1998; Foster et al., 1999). It is possible that both trackmakers (probably dryosaurid ornithopods and turtles) began to appear in the area as the Salt Wash fluvial system developed in this region.

The occurrence of two *Chelonipus* ichnocoenoses in fluvial system deposits is indicative of a more widespread *Chelonipus* ichnofacies. This concept is useful as it shows that this type of track occurs recurrently in many similar freshwater facies: for example, in the Upper Triassic and Upper Jurassic of Europe (Ruhle von Lilienstern, 1939; and Avanzini et al. 2005, respectively) as well as in the Upper Jurassic of the western USA (Foster et al., 1999) and in some Cretaceous deposits (Wright and Lockley, 2001). In so defining a *Chelonipus* ichnofacies as the recurrent association of this ichnogenus in freshwater fluvial deposits, we are able to make a clear distinction between this association and the quite different association characteristic of the *Chelonichnium* ichnofacies as defined in Europe on the basis of multiple occurrences of large marine turtle tracks in carbonate lagoon systems.

To date, at least fifty vertebrate tracksites have been documented in the Morrison Formation (Foster and Lockley, this volume). This report formalizes the use of the ichnotaxon *Chelonipus*, and demonstrates that the ichnogenus is characteristic of a more widely distributed *Chelonipus* ichnofacies. The concept of vertebrate (tetrapod) ichnofacies is currently the subject of lively debate (Hunt and Lucas, in press; Lockley in press).

Table 2. Named swim track ichnogenera with number of digit impressions in type material, with inferred trackmaker according to primary sources. * Refers to our interpretation of the *Saltosauripus* manus as tetra- or pentadactyl, and ** refers to our interpretation of the manus of *Albertasuchipes* as tetra- not tridactyl. *Chelonipus* is not included because, strictly speaking, it was not originally defined as a swim track.

Track name	Number of toe traces in type specimen	Probable trackmaker	References
Chelonichnium	3-5	turtle	Bernier et al. 1982
Saltosauripus	3 (4 or 5) *	dinosaur reinterpreted as turtle	Bernier et al. 1984 Thulborn, 1989
Hatcherichnus	4	crocodilian	Foster and Lockley 1997
Characichnos	3	theropod dinosaur	Whyte and Romano 2001
Albertasuchipes	3 (or 4)**	crocodilian	McCrea et al. 2004

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