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Distribution and Significance of Mesozoic Vertebrate Trace Fossils in Dinosaur National Monument

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Search for new tracksites has now revealed a total of 25 localities in the older Mesozoic sedimentary rocks of Dinosaur National Monument (DNM). To date, the most productive units have proved to be the Late Triassic Chinle Group and the mainly Early Jurassic Glen Canyon Group in the western part of DNM. In addition several sites, that are an integral part of the overall paleontological picture, have been found just outside the boundaries of DNM. All these sites (and stratigraphic levels) add up to a total of about 45 tracksites in the DNM area.

Chinle sites have now yielded dozens of trackways of theropod dinosaurs, ?prosauropod dinosaurs, mammal-like reptiles, ?phytosaurs, aetosaurs, lepidosaurs and tanystropheids, producing one of the most diverse Late Triassic track assemblages known anywhere. The ?prosauropod tracks are the first Late Triassic examples ever reported from the North American continent. The Lower Jurassic has also yielded theropod and prosauropod dinosaur tracks. These tracks are useful for correlation with other Early Mesozoic tracksites around the world and can be used to help construct a series of track zones (or Palichnostratigraphy) for the western United States.

The discovery of prosauropod tracks (Pseudotetrasauropus) in the Chinle Group and in the lower part of Glen Canyon Group (Otozoum) points to a much wider distribution of prosauropod tracks in the western United States than previously supposed, and the need for a thorough study of these and similar track types. Further examination of the Jurassic Carmel Formation close to the DNM boundaries, reveals several tracksites that require further study.

The purpose of this ongoing study is to locate and document fossil footprint sites in Mesozoic strata at Dinosaur National Monument (DNM) and interpret the track assemblages for the information they provide on behavior, paleoecology and biostratigraphy (palichnostratigraphy). The Mesozoic Era (Triassic, Jurassic and Cretaceous Periods) is commonly referred to as the Age of Dinosaurs, though dinosaurs did not make their first appearance until late in the Triassic. Thus the scope of the project includes analysis of the tracks of predinosaurian (Early and Middle Triassic) vertebrates, as well as study of Late Triassic through Late Cretaceous vertebrate footprints. As outlined in five previous reports (Lockley et al. 1990, 1991a, b, 1992a, b), abundant tracks have been found in and
around DNM in the Chinle and Glen Canyon Groups and in the Carmel Formation. As shown below, these early Mesozoic track-bearing units reveal many track types that can be found in similar aged strata at other sites around the world. Thus a major research objective of this project is to make comparisons with ichnological (footprint) data emerging from other areas.

Not only may tracks be used for interpretations of behavior (locomotion, speed etc.), and paleoecology (census of ancient animal communities), but they also contribute to the applied science of biostratigraphic correlation (palichnostratigraphy) and can help with determining the ages of various sedimentary formations both regionally and globally.

METHODS AND STUDY AREAS

Our study is primarily a field oriented reconnaissance program designed to locate tracksites in space and time (stratigraphic position). To this end most field time is devoted to systematic search of good exposures, especially in situ bedding planes. Once discovered tracksites are mapped, track and trackway outlines are traced with acetate film overlays, and photographed in such a way that all important tracks, trackways, and their orientations, are accurately recorded. Important representative tracks and trackways are also replicated in latex rubber and later cast in plaster and/or fibreglass in the lab. If original specimens are unique, threatened by erosion, or otherwise suitable for collection, they are removed to DNM Quarry for curation. All specimens and replicas are then designated DNM numbers. Each site is also designated a preliminary (or field) locality number and tracksite locations are recorded to the nearest sixteenth section.

There is one further important component to this study, namely synthesis of the data into the large ichnological data base that is accumulating for the western United States.

The net result of these ongoing studies is that discoveries from one area, such as DNM, can not be viewed in isolation. The identification of track types, their attribution to various groups of trackmakers, and the significance of their stratigraphic position must be understood in reference to other areas. As shown, our understanding of the taxonomic, paleoecological and biostratigraphical significance of the track assemblages at DNM, depends to a significant degree on results from other areas. For example, recent discoveries of tracks in several formations in the Glen Canyon National Recreation Area (GCNRA: see Lockley et al. 1992c) have helped establish a workable scheme of track zones (Palichnostratigraphy) for the entire Colorado Plateau Region, and even beyond, allowing for comparisons between North America and other continents.

RESULTS TO DATE

During the first two years of investigations, detailed study was focused in the western part of DNM, in the area of the Red Wash drainage (so called "racetrack" area) and the south side of Split Mountain. Because many tracksites were recognized in Late Triassic and Early Jurassic deposits in these areas, search for tracksites was extended to these beds in the eastern part of DNM resulting in the discovery of a few additional sites. However it has become clear that the western part of DNM is particularly rich in sites, and since the end of the 1991 field season (Lockley et al. 1991b, 1992b), we have discovered nine more sites (UCD 92-17 to 92-25) in western DNM, and another important locality on BLM land, herein referred to as the Cub Creek site, just outside DNM. This latter site is a good example of a locality that has proved crucial to our understanding of the spatial and temporal distribution significance of certain track types.

THE CHINLE GROUP

As discussed in Lockley et al. (1990, 1991a,b, 1992a,b), the term Chinle Formation, is used by Rowley et al. (1979) for Late Triassic deposits of the DNM area, while the term Popo Agie Formation is used by students of these beds in northwestern Colorado and southern Wyoming. Recently Lucas (1991, and in press) has proposed the
term Chinle Group to include a total of 27 named formations, including the lower Gartra and Popo Agie Formations which are separated from the upper Bell Springs Formation by an unconformity. This latter unit is equivalent to the Red Siltstone Member (Pipirigos and O'Sullivan 1978), and the Rock Point Sequence (Lucas 1991, and in press). As the Lucas classification is new, will simply use the term Chinle Group, as equivalent to the term Chinle/Popo Agie of previous reports (see Lockley et al. 1991a, 1992a, b). We note however that Hunt and Lucas (1992) have made an interesting observation about the distribution of tracks in the Chinle Group. They suggest, that the vast majority of tracksite occur in the upper or Rock Point sequence. As reported in Lockley et al. (1990-1992), all the tracksites discovered to date are in the upper unit of the Chinle Group.

The Chinle tracks discovered, in DNM, in 1990 and 1991 included Brachychotherium, Grallator/Agialopous, Gwyneddichnium, Rhynchosauroides, and unnamed tracks attributable to synapsids and problematic tracks attributed to phytosaurs (cf. Chirotherium sensu Conrad et al. 1987). Further work in 1992 led to the documentation and discovery of eight new Chinle Group sites, in DNM, (UCD 92-18a-c, UCD 92-19-20 and 92-23-25) and the Cub Creek site.

As reported by Lockley et al. (1992b) localities UCD 92-18a-c have yielded tridactyl dinosaur tracks (cf. Grallator specimens Dino 15654-57) and a single Brachychotherium manus track. All subsequent localities are reported here for the first time. UCD-92-19, a locality very near UCD 91-11, has yielded two Gwyneddichnium tracks. UCD 92-20 and 92-23 have each revealed two small tridactyl tracks (cf. Grallator) from the Chinle Group-Glen Canyon Group contact zone at localities in tributaries of Cub Creek west and south of Josie's Cabin respectively (Figure 1). UCD 92 24-25 represent new localities in the vicinity of UCD 91-16 (Red Wash northeast of Ruple Ranch: Lockley et al. 1991a,b) that have yielded new specimens of tetradactyl and pentaadactyl tracks attributable to Gwyneddichnium and Rhynchosauroides.

THE CUB CREEK SITE

The Cub Creek site is important for its size, for the quality and diversity of tracks, and for the insights it provides into the distribution of Late Triassic trackmakers. The tracksite site was discovered by Clay Johnson, in 1992, on BLM land just south of the DNM boundary. The locality reveals a series of five track-bearing layers exposed near the top of the Chinle Group (i.e., at the same levels as UCD 92-20 and 92-23). To date several hundred tracks have been identified comprising at least 54 individual trackways. Thus the site has yielded about as many tracks as the combined total from all other Chinle Group sites in the DNM area, therefore making a significant contribution to the overall Chinle Group census for this area (cf. Lockley et al. 1992b).

The lowest track bed has yielded a left foot impression (CU-MWC 163.10) from a single Grallator trackway (Figure 1). The second through fifth track beds are all stratigraphically close to the top of the Chinle Group (Figure 1), and consist of track bearing surfaces exposed on the underside of overhangs at the base of a cliff formed by the overlying Glen Canyon Sandstone. The second track bearing bed yields five trackways assignable to the ichnogenus Pseudotetrasauropus and eight to what we have, until now, called the phytosaur morphotype (Chirotherium sp., Conrad et al. 1987, Lockley et al. 1992a,b). The Pseudotetrasauropus trackways (Figure 2) represent the first ever reported from North America, and have helped us to recognize at least one other Pseudotetrasauropus trackway specimen derived from the Chinle Group (formerly Dockum Group) of eastern New Mexico (= University of Michigan specimen shown in Figure 2). This track type (Pseudotetrasauropus), attributed to a prosauropod trackmaker, was previously known only from the Late Triassic of southern Africa (Ellenberger 1970, 1972, 1974), and we herein report it in North America for the first time. The third track-bearing layer exposes four trackways (3 = Chirotherium sp., 1 = Brachychotherium). The 15 cm thick sandstone bed between track surface two and three provides an excellent example of vertebrate bioturbation, mainly attributed to the large Chirotherium sp. trackmaker.

The fourth track-bearing layer exposes over 130 individual footprints comprising at least 35 distinct trackway segments (Figure 3). Of these about 26 are attributable to cf. Grallator and represent very small bipedal dinosaurs (footprint length less than 10 cms). Seven trackways are assignable to Brachychotherium and two to Pseudotetrasauropus.
Figure 1. Typical grallatorid tracks from the uppermost part of the Chinle Group in the Cub Creek Area.
Figure 2. *Pseudotetrasauropus* trackways from the "Dockum" Group of New Mexico and the Chinle Group of the DNM area are the first occurrences reported in North America.
As shown in Figure 3 there appears to be a bimodal orientation of trackways towards the north northwest and towards the south. This is more or less parallel to the NNW-SSE ripple crest trend, possibly thus indicating a tendency for trackmakers to move shore parallel. The fifth track-bearing layer has yielded only a single Pseudotetrasauropus trackway.

THE PROSAUROPOD TRACK DILEMMA

The discovery of Pseudotetrasauropus tracks is significant, because it represents the first report of this track type in North America, and, if Ellenberger's interpretation of prosauropod affinity is correct, the first evidence of prosauropods in the Chinle Group. Although a detailed analysis of these tracks is outside the scope of this report, some preliminary observations are warranted, because of the far reaching implications.

Ellenberger (1970, 1972, 1974) named Tetrasauropus and Pseudotetrasauropus to describe various trackways from the Late Triassic of South Africa. The majority of the trackways he described consisted of large footprints (pes tracks about 50 cms or more in length), and most of the examples of the latter ichnogenus were attributed to bipedal animals. However he also described smaller Pseudotetrasauropus tracks comparable in size to the examples illustrated here. These smaller track types show some superficial resemblance to Brachychirotherium pes tracks, but, unlike Brachychirotherium, occur in trackways indicative of bipedal animals (cf. Olsen and Galton 1984). When we examined the Cub Creek specimens, not only did we conclude that the previously undescribed New Mexico specimen was of the same type, but we also recognized that the tracks resemble so called bipedal Brachychirotherium from the Newark Supergroup of North Carolina (Olsen and Galton 1984).

Since Pseudotetrasauropus and Tetrasauropus occur in abundance together in South Africa, this caused us to consider if the large, so called New Mexico chirothere tracks (Chirotherium sp. of Conrad et al. 1987; Lockley et al. 1991b, 1992a, b) might not be related to Tetrasauropus. When this track type was first discovered and described by two of us (Conrad et al. 1987), we suggested that the "trackways resemble those of small sauropods" and considered "prosauropods as possible trackmakers". However the significant differences, including outward-, not inward-curved toe impressions as in Tetrasauropus from Africa, caused us to dismiss an affinity to that ichnogenus. We also doubted, and still do, that these Chirotherium sp. tracks are similar to the only known prosauropod tracks (Navahopus Baird 1980) reported from North America at that time. This caused us to eliminate prosauropods from consideration. Instead we inferred that the tracks were attributable to phytosaurs, another large animal known to have been abundant at that time. It now appears that our dismissal of the prosauropod interpretation may have been premature, and that we must seriously consider that the tracks may be allied to Tetrasauropus. If this interpretation is correct then this is also the first report for this ichnogenus in North America.

Thus there are clearly dilemmas to be resolved in the recognition of prosauropod tracks in North America. This is partly because various archosaurian tracks (thecodontians, crocodilomorphs and prosauropods) sensu Olsen and Galton (1984 p. 95) and Thulborn (1990, p 179) are thought to be so alike. Previously the only reported prosauropod track type from western North America was Navahopus from the late Early Jurassic. Olsen and Galton (1984) compared this form with Tetrasauropus and even put it in the new, but undefined Ichnofamily Navahopodidae. However it is worth noting that these two track types are very different in size and occur in different epochs that are separated by as much as 30 million years. Recently, we have also recorded Otozoum in western North America (Lockley 1990, 1991; Lockley et al. 1992b) and inferred that it too is attributable to a prosauropod, however, this ichnogenus is currently known only from the Navajo Formation and its equivalents and so is tens of millions of years younger than anything in the Chinle Group. Thus we conclude that Pseudotetrasauropus and Tetrasauropus (or at least Tetrasauropus-like tracks = Chirotherium sp. sensu) Conrad et al. (1987) are present in North America in the Chinle Group, and that they are probably best attributed to prosauropods. The former ichnogenus represents a gracile bipedal animal and the latter, a heavier quadrupedal animal, responsible for significant vertebrate bioturbation at one horizon. Although it is probably correct to attribute Navahopus and Otozoum to prosauropods, both track types occur in rocks that postdate the Chinle by at least 10-20 million years. On both morphological and biochronological grounds they are significantly different. We are undertaking a
Figure 3. Map of the Cub Creek site, late Triassic Chinle Group, with rose diagram to show trackway Pseudotetrasauropus and Tetrasauropus (or at least Tetrasauropus-like tracks = Chirotherium sp. sensu orientations (Grallator = white, other = black).
review of all purported prosauropod tracks including *Agrestipus* from the Late Triassic of Virginia, which Weems (1987) currently attributes to a sauropod. Taken together all the evidence suggests that prosauropods were much more diversified, and widely distributed in space and time in North America than could be inferred from the skeletal record alone.

**DISCUSSION OF CHINLE GROUP TRACKS**

The continuing discovery of track sites in the upper part of the Chinle Group has substantially increased our database. We now know of 35 different sites (including distinct stratigraphic levels) in the DNM area (as compared to 22 reported in Lockley et al. 1992a). With the addition of the Cub Creek site and other new DNM localities the total trackway sample (equivalent to a census of individuals) is 111.

Our studies suggest that there is a pattern to the stratigraphic distribution of Chinle tracks. The lower part of the Red Siltstone Member has so far yielded a *Gwyneddichnium*, *Rhynchosauroides* and small theropod tracks (*Agialopous* and cf. *Grallator*) assemblage, with invertebrate traces, at a level about 20 meters below the top of the formation. This is exactly the same assemblage as has been reported from this stratigraphic level in Moffat County Colorado some 35-40 miles to the northeast (Lockley 1986). By contrast the upper 8-9 meters of the formation, both in the DNM and Redfleet area, appear to yield a preponderance of *Brachychirotherium* tracks (with *Chirotherium* sp. and *Pseudotetrasaurus*), from siltstones and sandstones that are notably more purple and grey than the underlying brick red strata. We therefore tentatively conclude that, locally, the upper beds contain a different, facies-controlled, or biostratigraphically controlled ichnofauna. We also note that the uppermost sandstone beds at DNM, a purple and grey unit 1-2 meters below the base of the Glen Canyon Group, contain abundant bone fragments throughout the area. When looked at as a whole the Popo Agie ichnofauna in the DNM area can be summarized as follows:

<table>
<thead>
<tr>
<th>Dinosaur tracks</th>
<th>Agialopous and <em>Grallator</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sphenodontid/lizard tracks</td>
<td><em>Rhynchosauroides</em></td>
</tr>
<tr>
<td>Tetanurophid tracks</td>
<td><em>Gwyneddichnium</em></td>
</tr>
<tr>
<td>Astrosaur tracks</td>
<td><em>Brachychirotherium</em></td>
</tr>
<tr>
<td>?Phytosaur tracks*</td>
<td><em>?Chirotherium</em> sp. or <em>?Tetrasaurus</em></td>
</tr>
</tbody>
</table>

This list indicates that, within the western part of DNM, most of the major groups of Late Triassic trackmakers known from western North America are represented. This allows for the reconstruction of the animal communities of this well-known epoch. As discussed by Lockley (1986, 1987, 1991, Lockley and Conrad 1989) the *Agialopous*, *Rhynchosauroides* *Gwyneddichnium* assemblage probably represented a community of small reptiles that frequented river and lake shore habitats, perhaps feeding on the abundant invertebrate trace-makers. The *Brachychirotherium* assemblage may represent a more terrestrial community with aetosaurs and prosauropods.

**THE GLEN CANYON SANDSTONE**

Previously we reported *Brachychirotherium* from the basal part of the Glen Canyon Group, as the first vertebrate tracks recorded from the Glen Canyon Group in DNM. Later in 1991, Fred Peterson and Dan Chure discovered three toed dinosaur tracks in the upper part of the Glen Canyon Group (=Navajo Formation equivalent) at a locality (UCD 92-17) not far from the DNM Quarry. Our studies show that track-bearing beds can be recognized at seven stratigraphic levels and traced laterally along strike for a distance of about 1 km. For convenience we have subdivided the locality into three sites (UCD 92-17.1, 17.2 and 17.3; see Figure 4). Detailed mapping of five different track-bearing surfaces has revealed a large number of trackways. As reported by Lockley et al. (1992b) we have recorded 96 trackways in the upper two levels of section UCD 92-17.1. Of these, four trackways can be assigned to *Otozoum* with the remainder representing theropods. Herein we also report four trackways (levels) from section 92-17.2 (no mapped surfaces) and a minimum of 29 trackways from the two mapped surfaces in section 92-17.3. The lower of these two surfaces are dominated by *Otozoum* with a minimum of 17 trackways of this ichnogenus and only one tridactyl variety. The upper surface has a tridactyl:*Otozoum* ratio of 8:4. Thus a minimum of 125 trackways are recorded at the entire 92-17 site.
Figure 4. Tracks occur at multiple stratigraphic levels in the upper part of the Glen Canyon Group (=Navajo Formation).
Parallel *Otozoum* trackways at the lower level, in section 92-17.3, suggest that the trackmakers may have been moving in groups. In general however the trackways at all levels suggest quite variable directions of progression. At all levels the tracks are associated with horizontally bedded, sometimes ripple-marked, brown to red stained, often heavily dinoturbated, intervals between eolian cross bedded units. This suggests that the tracks were made in interdune environments subject to periodic wetting or run-off, and that during such wet periods animals were quite active in the area.

**CARMEL FORMATION**

Several Middle Jurassic, Carmel Formation tracksites are situated just outside the DNM boundary south of Daniel’s Ranch, and also in the Redfleet reservoir area. Reconnaissance in the former area has led to the discovery of additional tracks, thus suggesting some potential for discovery of tracks within DNM. Because of the rarity of Middle Jurassic vertebrate remains worldwide, we consider the Carmel tracks very important and we propose to describe available tracks and replicas in a separate report, at a later date. Our preliminary investigations show that the tracks are all those of relatively small tridactylous bipeds, and that the only comparable ichnofauna currently known is one that has been reported from the Middle Jurassic of Yorkshire, England (Whyte and Romano 1981).

**CONCLUSIONS AND PALICHNOSTRATIGRAPHY**

The tracks so far discovered in the DNM area are part of a much larger regional and global picture. For several decades, ichnologists have recognized that Late Paleozoic and early Mesozoic tracks are often quite similar on a global scale. This is because, at that time, the world’s continents were assembled together into the supercontinent Pangaea II, thus allowing free exchange of vertebrates and the establishment of pandemic or cosmopolitan faunas. Because paleontologists recognize this fact it is logical to assume that vertebrates, and their tracks, are potentially useful for biostratigraphic correlation. European ichnologists have also used this same principle to define "track zones" and establish the subdiscipline of "palichnostratigraphy". Some of the pioneers of this field (Haubold and Katsung 1978; Haubold 1984, 1986) have called on North American researchers to adopt a similar approach (see Olsen and Galton 1984).

The discovery of distinctive track assemblages in the Chinle and Glen Canyon Group suggests much promise for dating of rock sequences that are otherwise devoid of fossils. For example the presence of *Brachychirotherium, Anomoepus, Otozoum* and other distinctive zonal ichnotaxa and ichnotaxonomic assemblages provides useful correlations for the upper part of the Chinle Group and various units of the Glen Canyon succession across much of the Colorado Plateau Region, and as far afield as the Newark Supergroup of eastern North America and the Stormberg Series of southern Africa (cf. Haubold 1984, 1986; Olsen and Galton 1984).

The Late Triassic and Early Jurassic palichnostratigraphic zonal scheme that is emerging for the western United States helps underscore the importance of tracks in helping to understand the composition and geologic range of successive animal communities during these epochs. We note specifically that the majority of ichnogenera listed above can be recognized in Late Triassic deposits elsewhere in North America, in Europe and in southern Africa. This distinctive archosaur dominated assemblage includes small tridactyl theropod tracks as a significant component, and attests to the increase in relative abundance of dinosaurs at his time. Successive track zones are heavily dominated by larger tridactyl dinosaurs, without the diverse array of other archosaurian track types. This same pronounced ichnological change at the Triassic-Jurassic boundary is also recognized worldwide (Haubold 1986). Similarly, distinctive tracks like *Batrachopus, Anomoepus, Otozoum* and *Brasilichnium* occur in various track assemblages throughout the Glen Canyon Group on the Colorado Plateau, and correlative strata elsewhere in North America and around the world.

**LITERATURE CITED**


