

# THE VERTEBRATE ICINOLOGICAL RECORD OF THE MORRISON FORMATION (UPPER JURASSIC, NORTH AMERICA)

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**Abstract**—Tracks in the Upper Jurassic Morrison Formation of the western United States include at least 12 morphotypes, represent more than 250 individual trackways at a total of 50 localities, and occur in every state in which the formation is exposed. The track types include representatives of turtles, crocodilians, pterosaurs, theropods, sauropods, ornithopods, stegosaurs, and possibly lacertilians. Tracksites most commonly preserve tracks as natural impressions (or rarely casts) in sandstone bedding surfaces (SB sites), particularly in the lower half of the formation. Sites with tracks made into red and green floodplain muds and preserved as natural sandstone casts below sandstone ledges are next most common (FP sites); limestone bedding surface sites containing natural impressions are the least abundant (LS sites). LS and FP sites are dominated by sauropod and theropod trackways, whereas the SB sites collectively preserve a greater diversity of track types and are dominated by theropod, ornithopod, and indeterminate tridactyl trackways. Sauropods and theropods demonstrate very different patterns of abundance in the various preservation environments: sauropods are more commonly found in FP environments (77% of localities versus 31% for theropods) but theropods are more commonly found in SB environments (50% of localities versus 25% for sauropods). This suggests different track preservational biases (larger tracks occurring mainly at FP sandstone overhangs and not on smaller SB sandstone pieces, which contain a diversity of small theropod and other track types) or a minor environmental separation for sauropods and theropods within the Morrison basin. If the latter possibility has influenced the pattern, theropods may have been found in fewer FP and LS environments simply because of their lower predator population levels, but why they would be so much more common than sauropods in SB environments is difficult to assess.

## INTRODUCTION

The Upper Jurassic Morrison Formation of the western United States has long been famous for its large collections of fossil vertebrates, especially large dinosaurs. It is now also known to contain a number of vertebrate tracksites, many discovered quite recently. There are now 50 sites documented in the Morrison. These sites contain tracks of a variety of vertebrate taxa; most tracks are of dinosaurs, but several sites include tracks of turtles, crocodilians, and ?lepidosaurs. The vertebrate tracks known from the Morrison Formation were briefly summarized by Lockley et al. (1998a).

Recorded tracksites and trackways give us an opportunity to evaluate the Morrison fauna as represented by the track record at least in a general sense, as the specific identities of most trackmakers are impossible to determine. The aim of this study is to review the known track types, summarize the current state of knowledge of the Morrison ichnofauna, and to discuss what the record indicates of the relative abundances of general types of vertebrates and what these ichnological abundances imply for Morrison Formation vertebrate paleoecology.

Abbreviations: DMNH, Denver Museum of Nature and Science, Denver; MWC, Museum of Western Colorado, Grand Junction; SDSM, South Dakota School of Mines & Technology, Rapid City; YPM, Yale Peabody Museum, New Haven.

## HISTORICAL REVIEW

The first report of vertebrate tracks in the Morrison Formation by Marsh (1899) described tridactyl prints from the southern Black Hills of western South Dakota. He attributed these to large theropods and large ornithopods, and at least one of the tracks does appear to conform to the shape expected for an ornithopod (Farlow and Lockley, 1993). The tracks also appear to have come from near the top of the formation (Foster, 1996).

Hatcher (1903) figured a tetradactyl print found near the Garden Park, Colorado, dinosaur quarries; this track has been identified as a

camptosauroid manus impression (Harris, 1998) and as a crocodilian pes impression (Conrad et al., 1987; Lockley and Prince, 1988; Prince and Lockley, 1989), and has been referred to the new crocodilian ichnogenus *Hatcherichnus* by Foster and Lockley (1997).

Burbank (1930) referred to the “fossilized footprint of a dinosaur” in the Morrison Formation near Ouray in southwestern Colorado, but it appears this site was actually in the Summerville Formation.

In 1935, tracks were recognized in exposures along the Purgatoire River in southeast Colorado and reported in a series of short notes in popular magazines (MacClary, 1936, 1938). R. T. Bird (1939a) only briefly mentioned the site in Colorado, as he soon afterward heard of the Lower Cretaceous sauropod tracks in Texas (Bird, 1939b). Two of the Colorado tracks (DMNH 1471) were collected for the Denver Museum of Nature and Science from the site, and a small segment of trackway (DMNH 1498) was collected from the Morrison downstream from the site, near Higbee, in 1937 (Markman, 1936, 1937). Despite Bird’s familiarity with the Morrison and its dinosaurs, it is not clear that he even knew that the tracks were in this formation, even though the DMNH specimens were correctly identified as coming from lower Morrison beds. Neither Bird nor MacClary commented in detail on the affinity of the tracks. Bird suggested that the large tracks may have been made by sauropods but was confused by the overlap of manus and pes prints (cf. Peabody, 1959) which made the trackmaker appear bipedal. These Colorado tracks were restudied nearly fifty years later, during the recent revival in Morrison vertebrate ichnological research (Lockley et al., 1986; Lockley and Prince, 1988; Prince and Lockley, 1989).

Schoff and Stovall (1943) located a tracksite in the Morrison of the Oklahoma Panhandle north of Boise City during Stovall’s dinosaur excavations in the area in the late 1930’s. No tracks are currently exposed at this site. However, theropod and pterosaur tracks are known to the west near Kenton (Lockley et al., 2001).

Look (1955) reported theropod tracks from a limestone in the Morrison Formation near Grand Junction, Colorado (Lockley and Jennings,

1987). Museum of Western Colorado archives suggest that these tracks were found in the vicinity of East Creek.

In 1957, W. L. Stokes described tracks from the lower Salt Wash Member of the Morrison in Arizona which he attributed to pterosaurs (ichnogenus *Pteraichnus*). The identity of the trackmaker responsible for these prints, and others subsequently found lower in the Jurassic section, has been debated, especially by Padian and Olsen (1984) and Padian (1998), who prefer a crocodilian as the trackmaker. Subsequent work indicates that these tracks probably belong to pterosaurs after all (Lockley et al., 1995; Mazin et al., 1995). Logue (1977) reported pterosaur tracks from the Morrison Formation at Alcova, Wyoming, and West (1978) first reported those from near Kenton, Oklahoma (Lockley et al., 2001).

All other Morrison tracksites have been found in the last fifteen to twenty years; many in the last ten. There are now approximately 50 sites known from the Morrison Formation, and these contain trackways representing several hundred individuals. This census almost doubles the number reported by Lockley and Hunt (1994, 1995).

## METHODS

We compiled a list of the known vertebrate track sites in the Morrison Formation, ranging from sites with multiple trackways to those with single footprints. Data included with the list were the location, approximate stratigraphic level, sedimentological context, track types, numbers of trackways and track-bearing layers. The list is updated frequently as more sites are found.

The tracks at each site were first identified to general category: sauropod, large or small theropod, large or small ornithopod, stegosaur, crocodilian, or possibly lepidosaurian. When possible, tracks were identified to the level of ichnogenus. Named ichnogenera from the Morrison Formation include: the crocodilian track *Hatcherichnus* (Foster and Lockley, 1997); the pterosaur track *Pteraichnus* (Stokes, 1957); the sauropod tracks *Brontopodus* (Farlow et al., 1989) and *Parabrontopodus* (Lockley et al., 1994a); the ornithopod tracks cf. *Anomoepus* and *Dinehichnus* (Lockley et al., 1998b); and the stegosaur track *Stegopodus* (Lockley and Hunt, 1998).

The numbers of trackways of theropods, sauropods, ornithopods, stegosaurs, and others are tallied in Table 1.

Tracks most often occur as one of three preservation types: natural sandstone casts, natural impressions in sandstone, or natural impressions in limestone (Table 2).

## MORRISON TRACK LOCALITIES

### ARIZONA

#### Apache County

##### Stokes Locality

Stokes (1957) found and named *Pteraichnus saltwashensis* at a site in the Morrison in northeastern Arizona. This site has been approximately relocated, but no additional trackways were found in the Salt Wash. More pterosaur tracks were found in the Tidwell Member and in the underlying Wanakah Formation in the area. The type trackway was collected and is at the Utah Museum of Natural History.

##### Tsetah Wash Overlook

This site, located in extreme northeastern Arizona and called Teec Nos Pos by Lockley and Mickelson (1997), contains a single 20 cm-long theropod track preserved as an impression in sandstone 25 cm above the base of the Salt Wash Member. Below this and nearby in the Tidwell Member of the Morrison are well-preserved tracks of a sauropod and of pterosaurs. These tracks occur between the Bluff Sandstone and the Salt Wash Members in a 1 m-thick unit probably equivalent with the Tidwell Member of Peterson (1988). Tracks from this locality, including the Salt Wash theropod, were illustrated by Lockley and Mickelson (1997), who place

the pterosaur and sauropod tracks in the Bluff-Summerville sequence. Regardless of the formation to which these layers are assigned, nothing below the Salt Wash was used in the analysis for this report. The theropod track was photographed but not collected or cast.

##### Tsetah Windmill

Two individual theropod trackways are found at this site in northeastern Arizona, which is probably close to the Stokes Locality (Fig. 1). The tracks are on a bedding plane of ripplemarked sandstone 9m above the base of the Salt Wash Member, and the two trackways, each with two tracks, consist of footprints that are 22 cm and 33 cm long.

## COLORADO

### Eagle County

#### Rancho Del Rio

This site is located near the Colorado River in the Park Range of central Colorado (Lockley et al., 1986; Lockley and Hunt, 1995). Steeply dipping beds of the lower Morrison Formation here contain a trackway of shallow, narrow-gauge, sauropod manus-pes sets of the ichnogenus *Parabrontopodus*. Several other levels of the Morrison in the area contain highly trampled surfaces, and a small manus-pes natural cast set was found by Gerard Gierlinski in the area. Two of the levels contain tridactyl tracks, and below the level of the main sauropod trackway are two impressions in sandstone that may be pterosaur manus tracks. The sauropod trackway occurs in deposits that appear to represent a lacustrine shoreline, and the trackway consists of fairly shallow impressions. The footprint lengths of the pes tracks are about 65 cm.

#### State Bridge

This site is near the Colorado River in the Park Range of central Colorado, and contains tracks of nine small tridactyl dinosaurs, a theropod, and possibly a sauropod (Fig. 2). The footprints of the theropod have particularly wide digit divarication (Lockley et al., 1998a). The tracks are in a friable silty sandstone just below a mudstone relatively low in the formation, but the site has mostly eroded away in recent years.

### Fremont County

#### Garden Park 1

Hatcher (1903) illustrated a single, tetradactyl, natural cast track from a sandstone at Garden Park. Harris (1998) identified the track as being made by a camptosaurid manus, whereas Foster and Lockley (1997) identified it as a crocodilian pes and referred it to the new genus *Hatcherichnus*, which is based on a specimen from the Salt Wash Member of the Morrison Formation in Utah.

#### Garden Park 2

Harris (1998) illustrated four tracks from the Garden Park region. These are preserved as natural sandstone casts and are 13 cm–42 cm in length. Two of these are identified as ornithopods and two are theropods.

### Jefferson County

#### Dinosaur Ridge

This site is along the Alameda Parkway roadcut west of Denver and very near Arthur Lakes's old quarries in the Morrison. At the locality, several sauropod tracks are preserved as natural sandstone casts, some of which project downward into the underlying mudstone bed, and at least one set of several tracks from one trackway is preserved as cross-sectional views of sandstone infillings of impressed sandstone layers. These tracks had traditionally been identified as load structures.

TABLE 1. Trackway counts for each track locality in the Morrison Formation.

| Locality Name        | Theropods | Sauropods | Ornithopods | Stegosaurs | Misc. | Notes                                               |
|----------------------|-----------|-----------|-------------|------------|-------|-----------------------------------------------------|
| Stokes Locality      | 0         | 0         | 0           | 0          | 1     | <i>Pteraichnus</i>                                  |
| Tsetah Wash Overlook | 1         | 0         | 0           | 0          | 0     |                                                     |
| Tsetah Windmill      | 2         | 0         | 0           | 0          | 0     |                                                     |
| Rancho Del Rio       | 0         | 2         | 0           | 0          | 0     | <i>Parabrontopodus</i>                              |
| State Bridge         | 11        | 0         | 1           | 0          | 0     |                                                     |
| Garden Park I        | 0         | 0         | 0           | 0          | 1     | <i>Hatcherichnus</i> (Foster and Lockley, 1997)     |
| Garden Park II       | 4         | 0         | 0           | 0          | 0     |                                                     |
| Dinosaur Ridge       | 0         | 3         | 0           | 0          | 0     |                                                     |
| Interstate 70        | 0         | 1         | 0           | 0          | 0     |                                                     |
| Fort Collins         | 0         | 1         | 0           | 0          | 0     |                                                     |
| Purgatoire River     | 41        | 40        | 2           | 0          | 0     | <i>Brontopodus</i> (1); <i>Parabrontopodus</i> (15) |
| Black Ridge Trail I  | 0         | 1         | 0           | 0          | 0     |                                                     |
| Black Ridge Trail II | 0         | 0         | 2           | 0          | 0     | <i>Anomoepus</i> ?                                  |
| Cactus Park          | 1         | 0         | 0           | 0          | 0     |                                                     |
| Colbert Canyon       | 0         | 1         | 0           | 0          | 0     |                                                     |
| East Creek           | 6         | 0         | 0           | 0          | 0     |                                                     |
| Fruita Paleo Area    | 1         | 0         | 0           | 0          | 1     | lacertilia?                                         |
| Grand Junction       | 1         | 0         | 0           | 0          | 0     |                                                     |
| West Monument Mesa   | 0         | 1         | 0           | 0          | 0     |                                                     |
| Pollock Canyon       | 0         | 0         | 2           | 0          | 0     | <i>Dinehichnus</i>                                  |
| Upper Ute Canyon     | 1         | 1         | 2           | 0          | 2     | Sauropoda; <i>Chelonipus</i> ; <i>Dinehichnus</i>   |
| Black Dinah Mine     | 3         | 0         | 5           | 0          | 0     | <i>Anomoepus</i> ? (4)                              |
| Higbee               | 1         | 0         | 0           | 0          | 0     |                                                     |
| Ninaview             | 1         | 0         | 0           | 0          | 0     |                                                     |
| Livingston           | 1         | 1         | 0           | 0          | 0     |                                                     |
| Romeroville          | 1         | 0         | 0           | 0          | 0     |                                                     |
| Cimarron Valley      | 0         | 1         | 0           | 0          | 0     |                                                     |

**Interstate 70**

This site is in the roadcut west of Denver and contains a single sauropod manus-pes track set cast in sandstone high in the Morrison (Lockley, 2001; Houck, 2001). The underlying rock is mudstone.

**Larimer County****Fort Collins**

This locality is west of the city of Fort Collins and consists of eight tracks that are part of one trackway of a narrow-gauge sauropod with pes impression lengths of approximately 50 cm. The tracks are in sandstone that appears to represent a lacustrine delta (Lockley et al., 1986).

**Las Animas County****Purgatoire River**

This site, discovered in the 1930's but studied in detail by Lockley et al. (1986), is the largest currently known in the Morrison Formation, with more than 1300 tracks from 100 trackways of theropods and sauropods, and with some possible ornithopod trackways. The sauropods represent the type trackways of the ichnospecies *Parabrontopodus mcintoshii* (Lockley et al., 1994a), the narrow-gauge type of sauropod trackway that occurs at several sites in the Morrison. There are approximately 41 theropod trackways and 40 sauropod trackways (Lockley et al., 1997). Most tracks occur as impressions in the top of an oolitic limestone bed (number 2) that was probably at or near the shoreline of a lake (Lockley and Prince, 1988; Prince and Lockley, 1989). Three other track-bearing beds have been iden-

tified (numbers 1, 3, and 4). Bed 1 is heavily trampled with a few recognizable sauropod and small theropod tracks as well as trampled unionid bivalves and plant remains.

**Mesa County****Black Ridge Trail I**

This site is in Colorado National Monument near the top of the Salt Wash Member and off the southern part of the Black Ridge Trail. A single natural sandstone cast of a sauropod pes is preserved at the base of a 4 m-thick, medium grained, trough and planar bedded sandstone bed. The claystone into which the track was made is light green in the upper 10-15 cm and bright reddish brown below with mottling between the two. The track is about 60 cm in length and the base of the sandstone unit contains casts of mudcracks, indicating drying of the originally wet mud surface into which the track was made prior to deposition of the sandstone.

**Black Ridge Trail II**

A recently found slab containing two short trackways probably of ornithopod dinosaurs, was located north of the previous site and just off the Black Ridge Trail (Fig. 3). The specimen is in the collections of Colorado National Monument under accession number COLM 00203. The two trackways are roughly parallel, although on the loose slab it is impossible to determine what the original direction of travel was. The tracks are preserved as natural sandstone casts and may have come from the Salt Wash Member. The pes tracks are about 9 cm long and some are associated with indistinct possible manus casts just behind some of the pes tracks.

TABLE 1. contd.

| Locality Name          | Theropods | Sauropods | Ornithopods | Stegosaurs | Misc. | Notes                                           |
|------------------------|-----------|-----------|-------------|------------|-------|-------------------------------------------------|
| Southern Black Hills   | 4         | 0         | 1           | 0          | 0     |                                                 |
| Cleveland-Lloyd        | 1         | 2         | 0           | 1          | 0     |                                                 |
| San Rafael River       | 0         | 2         | 0           | 0          | 0     |                                                 |
| Copper Canyon          | 0         | 0         | 0           | 0          | 2     | <i>Chelonipus</i> (Foster et al., 1999)         |
| Henry Basin            | 1         | 0         | 0           | 0          | 0     |                                                 |
| Lost Spring            | 0         | 1         | 0           | 0          | 0     |                                                 |
| Arches West            | 0         | 0         | 0           | 1          | 0     | <i>Stegopodus</i> (Lockley and Hunt, 1998)      |
| East Dalton Wells      | 1         | 3         | 0           | 0          | 0     |                                                 |
| Hidden Canyon Overlook | 1         | 6         | 0           | 0          | 0     | <i>Brontopodus</i> (3)                          |
| Valley City            | 6         | 1         | 0           | 0          | 0     | <i>Brontopodus</i>                              |
| Boundary Butte         | 0         | 2         | 16          | 0          | 0     | <i>Dinehichnus</i>                              |
| East Canyon            | 1         | 1         | 0           | 0          | 0     |                                                 |
| La Sal Loop Road       | 0         | 2         | 0           | 0          | 0     |                                                 |
| Two Mile Creek         | 0         | 1         | 0           | 0          | 1     | <i>Hatcherichnus</i> (Foster and Lockley, 1997) |
| Como Bluff             | 27        | 5         | 1           | 0          | 0     | <i>Anomoepus</i> ?                              |
| Sheep Creek            | 0         | 1         | 0           | 0          | 0     |                                                 |
| Coyote Basin           | 0         | 0         | 0           | 0          | 1     | Tridactyl (poor preservation)                   |
| Howe Quarry            | 3         | 0         | 0           | 0          | 0     |                                                 |
| Little Houston Creek   | 0         | 0         | 0           | 0          | 11    | Tridactyl, small                                |
| Cattle Pond            | 1         | 0         | 0           | 0          | 0     | small                                           |
| Dry Poison Creek       | 0         | 0         | 0           | 0          | 17    | Tridactyl, small                                |
| Alcova Lake            | 1         | 1         | 0           | 0          | 5     | Tridactyl (2); <i>Pteraichnus</i> (3)           |
| Split Rock Waterfall   | 0         | 1         | 0           | 0          | 0     |                                                 |
| Rabbit Ridge West      | 1         | 0         | 0           | 0          | 0     | Large                                           |
| Cedar Ridge            | 0         | 0         | 0           | 0          | 1     | <i>Hatcherichnus</i> ?                          |
| North Copper Ridge     | 0         | 0         | 0           | 0          | 1     | <i>Hatcherichnus</i> ?                          |
| Warm Springs Ranch I   | 1         | 0         | 0           | 0          | 7     | Tridactyl (6); indet. (1)                       |
| Warm Springs Ranch II  | 0         | 0         | 0           | 0          | 2     | Tridactyl; indet.                               |
|                        |           |           |             |            |       | All:                                            |
| Totals                 | 125       | 82        | 32          | 2          | 53    | 294                                             |

### Cactus Park

A single theropod track was found at this locality in March, 1995, but was not collected. The site is in the Uncompahgre Uplift south of Grand Junction, Colorado, and the track is preserved as a natural sandstone cast and is approximately 13 cm in length.

### Colbert Canyon

This locality is located in the lower part of the Morrison and consists of a trampled surface at the top of a limestone bed. No distinctly identifiable tracks are known but the area appears to have had many overlapping tracks.

### East Creek

This site is south of Grand Junction and was found by Al Look. There were approximately six relatively large theropod tracks (up to about 45cm), most of which were natural casts in limestone of tracks that had been made into mudstone. Two photos of the tracks are on file in the MWC photo archive.

### Frost Locality

One small sauropod track and one tridactyl track were found as natu-

ral sandstone casts in the Salt Wash Member near the east entrance of Colorado National Monument. These were photographed but not collected.

### Fruita Paleontological Area

This area has produced several small theropod tracks and what may be a spheodontian or lizard track in sandstone low in the Morrison Formation. The tracks were found by crews working with George Callison, but were not collected.

### Grand Junction

This site was discovered by Robert Young and is outside Grand Junction, near the east entrance of Colorado National Monument. A single small theropod track occurs here.

### West Monument Mesa

This locality is in a Salt Wash Member sandstone cliff above and northwest of the Liberty Cap Trail within Colorado National Monument. The level is near the top of the Salt Wash, about the same level as the Black Ridge Trail site. A single sauropod right pes track occurs here as a natural sandstone cast near the base of an approximately 10 m-thick sandstone unit. The track is at the bottom of a high overhang and is difficult to measure directly but it appears to be about 10 cm deep and 50 cm long. Under-

TABLE 2. Morrison Formation tracksite preservation types and inferred paleoenvironments.

| Abbr. | Name                       | Environment                    | Track preservation                                                 | Number of Tracksites |
|-------|----------------------------|--------------------------------|--------------------------------------------------------------------|----------------------|
| SB    | Sandstone bedding surfaces | Channel sand bars; sand splays | Impressions in sandstone; rare raised tracks caused by compression | 26                   |
| FP    | Floodplain mudstone        | Floodplain mud flats           | Sandstone natural casts above red and green muds                   | 21                   |
| LS    | Limestone bedding surfaces | Lake and pond shoreline        | Impressions in limestone                                           | 8                    |

lying the track is a red and light green-gray laminated and mottled silty claystone unit into which the track was originally made. The track also seems to preserve four indistinct toe impressions.

#### Pollock Canyon

This locality is just to the west of the Fruita Paleontological Area and is in a sandstone bed at the base of the Salt Wash Member of the Morrison. The site contains two short trackways of tridactyl animals consisting of two tracks each. The tracks appear to be those of moderately small ornithopods and may be referable to the ichnogenus *Dinehichnus* (Lockley et al., 1998b). The two trackways contain footprints that are about 18 cm and 21 cm in length.

#### Upper Ute Canyon

At least one sauropod pes track is preserved as a natural sandstone cast in the lower Salt Wash Member in the southern part of Colorado National Monument. The track is about 66 cm long and the original impression was made upon a thin sandy layer. The underlying unit of red and green laminated sandstone and siltstone was deformed underneath by the track as well, as the layer is not folded but is downturned and pinched by compression caused by the foot. Approximately 1.2 m to the west, in the direction the track appears to be trending, there is visible downwarping of the same sandstone layer just in from the surface of the outcrop, and this may be another track from the same trackway.

West of the sauropod track site by one hundred meters or so is another site that has natural casts of tracks of a theropod, the ornithopod ichnogenus *Dinehichnus*, and the type material of a new species of the Morrison turtle tracks *Chelonipus* (Lockley and Foster, 2006).

#### Split Rock Waterfall

Three natural casts of sauropod footprints occur in the upper Brushy Basin Member at this site in Rabbit Valley. The tracks were made into a gray slightly sandy silt between two coarse-grained channel sand units within a thick sequence of red and green mudstone.

#### Montrose County

##### Black Dinah Mine

This locality is on the east side of the Paradox Valley, near the town of Bedrock. The site is in a Salt Wash Member sandstone bed and contains trackways of seven individuals. The tracks range in size from 6 to 20 cm and appear to be of small ornithopods and theropods. The ornithopod tracks are nearly as wide as long and have relatively wide digit divarications and may be referable to the ichnogenus cf. *Anomoepus*. The theropod tracks are noticeably longer than wide, with narrow digit divarications and some

pad and claw impressions. There are four or five ornithopod trackways and three theropod trackways.

#### Otero County

##### Higbee

This locality is in southeastern Colorado, northeast of and downstream from the Purgatoire River site (Lockley et al., 1986). The site contained a single trackway consisting of four tridactyl, possibly theropod tracks, each approximately 15 cm in length. The specimen was collected and is now at the Denver Museum of Nature and Science (DMNH 1498). The site was in the lower part of the Morrison, and the tracks occur as impressions in a limestone bed.

#### Uncertain Location

##### (Bent County or Las Animas County)

##### Ninaview

Somewhere on a private ranch, this site is east of the Purgatoire River locality in southeastern Colorado. It contained at least one track of a small tridactyl animal but little else is known of the locality. Both authors have seen photographs of the site and confirmed its existence by discussion with land managers. However, the owners have not permitted direct access.

#### MONTANA

##### Park County

##### Livingston

This locality is near the Mother's Day Quarry worked by the Museum of the Rockies and contains an impression of a theropod track and a natural cast of a sauropod track (S. Hasiotis and G. Englemann, pers. comm., 1996).

#### NEW MEXICO

##### San Miguel County

##### Romeroville

This locality is along Interstate 25 south of Las Vegas, New Mexico, and contains two tracks of one theropod trackway. The tracks are preserved as impressions in a ripplemarked sandstone low in the Morrison and the one fully preserved track is 27 cm long (Lucas et al., 1990).



FIGURE 1. Theropod dinosaur track in the Salt Wash Member of the Morrison Formation at the Tsetah Windmill tracksite in Arizona.

## OKLAHOMA

### Cimarron County

#### Cimarron Valley

This site is low in the formation north of Boise City and purportedly contains tracks of at least one sauropod (Conrad et al., 1987). The tracks were collected by the University of Oklahoma but were later destroyed by vandals.

## SOUTH DAKOTA

### Fall River County

#### Southern Black Hills

Marsh (1899) described and illustrated several large theropod tracks and one or two supposed ornithopod tracks from west of Hot Springs, South Dakota, in the first report of dinosaur footprints from the Morrison Formation. The stratigraphic origin of these tracks has been debated, it being uncertain whether or not they might have come from the overlying Cretaceous Lakota Formation, but based on the notes of H. F. Wells, who collected the specimens, the tracks do seem to have come from the top of the Morrison Formation (Foster, 1996). The tracks occur as natural sandstone casts and were originally made into an underlying pale green clay bed. The size range of the tracks is from 33 to 49 cm, and at least one slab of the tracks is in the collections of the Yale Peabody Museum (YPM 2140).

## UTAH

### Emery County

#### Cleveland-Lloyd Area

Four isolated tracks have been found in the vicinity of the Cleveland-Lloyd Quarry in Utah, and these include: ?stegosaur pes track (Bakker, 1996) and theropod track natural casts from high in the Morrison near the visitors center; an adult sauropod pes and juvenile sauropod manus and pes set, preserved as natural casts, from southwest of the quarry (G. Nadon, pers. comm., 1996).

#### San Rafael River

This site is located near the top of the Brushy Basin Member, east of the San Rafael River and just south of Interstate 70. The locality contains two sauropod pes tracks preserved as natural sandstone casts at the base of a thick, pebbly, crossbedded sandstone bed. The tracks are approximately 75 cm and 37 cm in length. The underlying rock into which the tracks

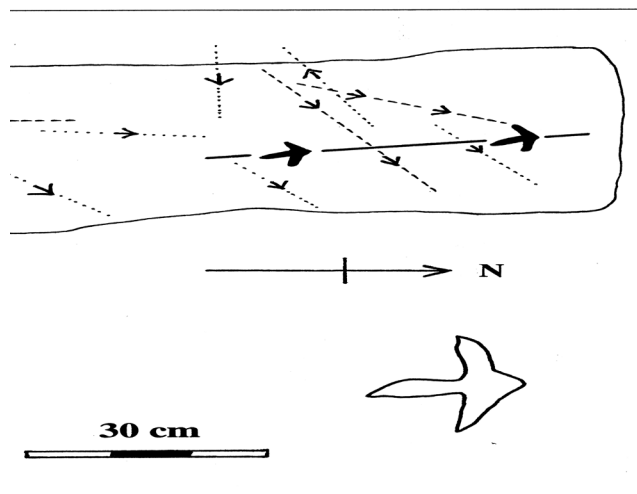


FIGURE 2. Map of some of the tridactyl tracks from the Morrison Formation at State Bridge, Colorado, with enlargement of two wide-splayed theropod tracks.

were made is thinly laminated red mudstone, and there are at least 11 indeterminate track casts in the same outcrop area and at the same level.

### Garfield County

#### Copper Canyon

This locality is several miles north of Lake Powell west of Lost Spring canyon. Twenty-eight tracks are preserved as natural sandstone casts in a channel sandstone unit near the base of the Salt Wash Member. The tracks are relatively small and are mostly three- and four-toed tracks, possibly belonging to turtles (Foster et al., 1999). The tracks and trackway are similar in many respects to *Chelonichnium* from the Kimmeridgian of France, which has been attributed to a turtle (Bernier et al., 1982), though the Morrison tracks are smaller. In any case, these tracks, along with those from Upper Ute Canyon in Colorado National Monument, are unlike any others in the Morrison Formation.

#### Henry Basin

This locality was found by Fred Peterson and contains a single tridactyl track in the Tidwell Member in mudstone interpreted as a subaerially exposed mudflat.

#### Lost Spring

This site is east of Copper Canyon and north of Lake Powell and consists of two, probably consecutive, right pes tracks of a large sauropod preserved as natural sandstone casts at the base of a thick sandstone unit (Meyer et al., 1994). The tracks were made into reddish brown paleosol mud and infilled with sandstone and preserve three fairly distinct claw impressions and two impressions of blunt digits IV and V; both tracks are part of one trackway. The site is at a level near the middle of the Salt Wash Member, and the tracks are among the best-preserved sauropod footprints in the Morrison.

### Grand County

#### Arches West

This site occurs at the base of the Salt Wash Member near Arches National Park east of the Moab airport. A manus track described and named as *Stegopodus czerkasi* was found here as a natural sandstone cast originally made into mudstone (Lockley and Hunt, 1998). It is associated with a deep and deformed cast of a larger tridactyl track, which could conceivably be that of a stegosaur hind foot. The manus track is believed to be that of a stegosaur, although the affinity of the pes track is less certain (Lockley

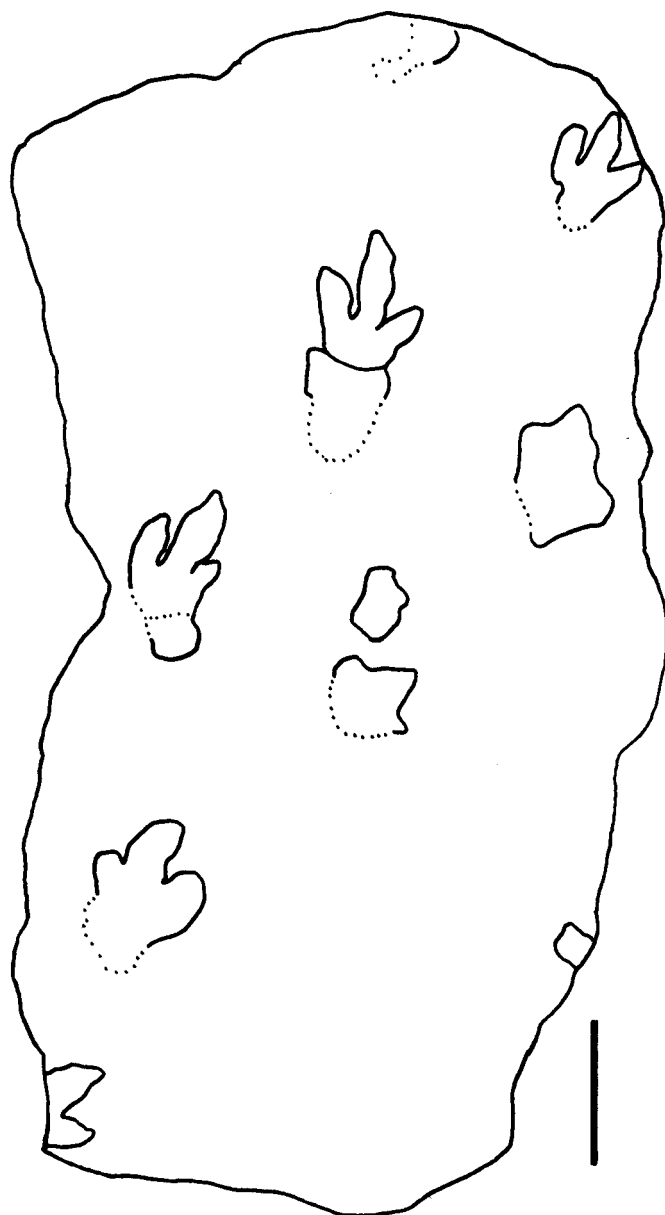


FIGURE 3. Drawing of a slab of ornithomimid tracks from near the Black Ridge Trail in Colorado National Monument. Scale bar = 10cm.

and Hunt, 1998). These tracks and a pes cast from the Cleveland-Lloyd area are the only known tracks from the Morrison that have been attributed to stegosaurs.

#### East Dalton Wells

This site, found by George Engelmann, is north of Moab, and is near the base of the Brushy Basin Member. Three isolated sauropod tracks are preserved as well as a large tridactyl track that probably belongs to a theropod. At least nine other bulbous, but indistinguishable track casts occur here too. Tracks are preserved as natural sandstone casts below a meter-thick channel sandstone overhang and were originally made into mud that is now mottled red and green. In places, sand filled mudcracks in both the mud and the footprints, indicating that the originally wet mud into which the tracks were made dried before being filled in with sand.

#### Hidden Canyon Overlook

This site is located northwest of Moab in eastern Utah. Three parallel trackways of wide-gauge sauropods (*Brontopodus* sp.) are preserved on a ripplemarked, channel sandstone paleosurface in the Salt Wash Member (Barnes and Lockley, 1994). In addition to the three sauropods, a theropod track and three other sauropod tracks are preserved as impressions in the same area. The sauropod pes tracks from the parallel trackways range from 58 to 68 cm in length, and the isolated sauropod pes tracks are 47 cm, 52 cm, and 62 cm. The theropod track is 42 cm in length. Also noted in sandstones at approximately the same stratigraphic level in the area were several dinosaur bone scraps and fossil wood.

The tracks occur at the top of a 5 m-thick, tan to white, medium-grained sandstone bed, 25 m up from the base of the Salt Wash. The sandstone is composed of three bedsets separated by thin clay clast lags and contains 10-60 cm crossbeds. The paleosurfaces on which the tracks occur appear to be tops of sandflats and also preserve several bar fronts and a drainage channel. The surfaces of the apparent sandflats all around the area contain linguoid current ripples indicating eastward flow (contrary to Barnes and Lockley, 1994), and at least one bar front preserves apparent falling water marks. The drainage channel flows eastward off a sandflat surface to an apparent downstream bar edge. There is also an area east of the three sauropod trackways that contains planar crossbeds dipping inward on three sides to a central low area, and this feature may represent an emergent sand nucleus. All of these features from the Hidden Canyon Overlook track site are believed to represent elements of a sandy braided stream environment, possibly similar to the modern South Saskatchewan River (Cant and Walker, 1978; Cant, 1982).

This is one of the few Morrison sites where sandy-facies depositional environments are preserved as exhumed paleosurfaces. The site has potential for further sedimentological study.

#### Copper Ridge (Valley City)

Located north of Moab, not far from US Highway 191, this site contains tracks of a large, turning, wide-gauge sauropod (*Brontopodus*), a limping theropod, and three other theropods, as well as large and small tridactyl tracks that may belong to either theropods or ornithomimids (Lockley and Hunt, 1995). Tracks are preserved as impressions in ripplemarked sandstone bedding surface of the upper Salt Wash Member. The paleoenvironment may have been that of a sandy braided stream.

This site on Bureau of Land Management land has interpretive signs and is open to public visitation.

#### West Rabbit Ridge

This site, found in 2001 just a few hundred meters west of the Utah-Colorado border, contains a single track of a large theropod. The track is an impression about 45 cm long and is preserved in a meter-thick sandstone unit in the middle of the Salt Wash Member.

#### San Juan County

##### Boundary Butte

This locality is in far southeastern Utah and preserves tracks of small ornithomimid dinosaurs as impressions in white sandstone near the base of the Salt Wash Member. The 16 ornithomimid trackways at this site include the type specimen of *Dinehichnus socialis* (Lockley et al., 1998b). The trackways are in two groups, the smaller of which appears to have been travelling slightly faster than the other, and most tracks are 10-15 cm in length, though one is 28 cm. Members of each group were travelling in roughly the same direction. Two shallow impression tracks of sauropod hind feet occur at this site as well.

## East Canyon I and II

These sites are close to each other in the lower Salt Wash Member south of the La Sal Mountains. One natural sandstone cast of a sauropod track made into red mud and a theropod track impression made into sand are located within several meters above the Tidwell Member.

### La Sal Loop Road

This locality is at the base of the Salt Wash Member. Several natural sandstone casts of sauropod pes and manus tracks occur immediately above a red mudstone unit, just above the Tidwell Member (Fig. 4). The sauropod pes tracks are only moderately well preserved and most are about 50 cm in length.

### Two Mile Creek

This site is in a uranium mine east of the La Sal Mountains close to the Utah-Colorado border. The tracks of a crocodilian occur as natural casts in sandstone on the roof of the mine near the top of the Salt Wash Member and occur at a surface between bedsets in a crossbedded sandstone. The crocodilian tracks are the type of the ichnospecies *Hatcherichnus sanjuanensis*, and just above the mine there is a single sauropod pes natural sandstone cast of a track made into what is now red and green mudstone (Foster and Lockley, 1997). The sauropod pes track is 59 cm long and preserves three toe impressions.

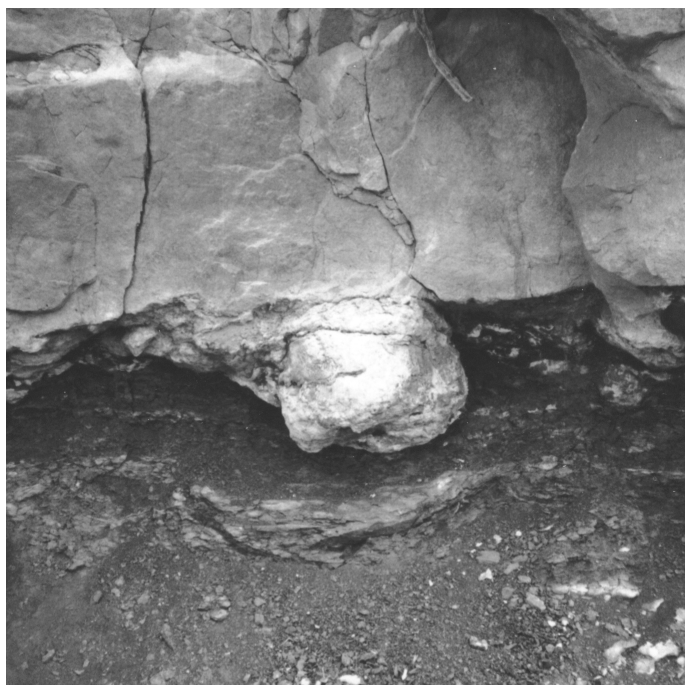
## WYOMING

### Albany County

#### Como Bluff (Jane Austen)

This site is very low in the Morrison near Rock Creek, west of Reed's Quarry 13 in the eastern Como Bluff region. Tracks of several theropods and sauropods as well as possibly ornithopods occur as impressions in a thin limestone unit (Southwell and Lockley, 1996; Southwell et al., 1996). The site (named "Jane Austen" by its discoverer, Pat Redman, when Bob Bakker put him on the spot and asked for the name of the first woman writer that came to mind) contains at least 28 tridactyl (probably theropod) trackways, at least one ornithopod (?*Anomoepus*), and perhaps six sauro-

FIGURE 4. Natural sandstone cast of a sauropod manus track from the lower Salt Wash Member at the La Sal Loop Road tracksite near Moab, Utah.



pods. Most of the theropod tracks are relatively long and narrow and range in size between 15 and 20 cm, though some are considerably larger. Some of the theropod tracks preserve pad and claw impressions, and the ornithopod track is 11.6 cm long.

### Sheep Creek

Bakker (1986) mentioned several sauropod track impressions in a limestone bed low in the Morrison near the Sheep Creek quarries in Wyoming, north of Como Bluff.

## Big Horn County

### Coyote Basin

This locality is near Shell and contains a short trackway of an apparently tridactyl animal on a current ripplemarked sandstone bedding plane relatively low in the Morrison (Kvale and Vondra, 1985). The tracks are very poorly preserved.

### Howe Quarry

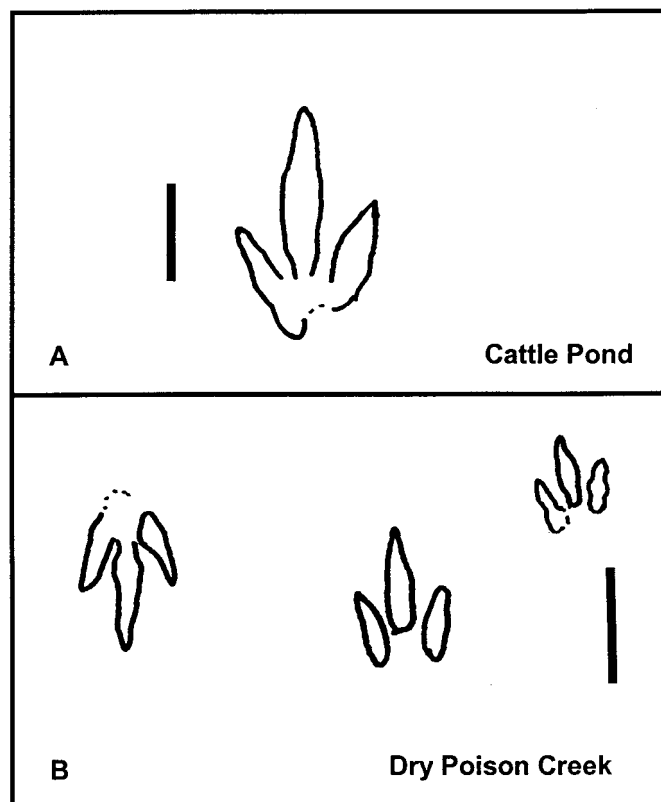
Several theropod tracks were described from among sauropod bones within the new part of the Howe Quarry in northern Wyoming, near Shell (Lockley et al., 1998c). These represent two medium- to large-sized theropods (47 cm and 43 cm footprint lengths) and a small theropod (12 cm). The larger tracks may represent *Allosaurus* (Lockley et al., 1998c).

## Crook County

### Cattle Pond

This locality is near a stock pond on a ranch in the Black Hills of northeastern Wyoming and contained a single natural sandstone cast of a theropod track found in 1998 (Fig. 5a). The track is 12 cm long and is in a

FIGURE 5. Small theropod tracks ("grallatorid") from the Morrison Formation of Wyoming. A) Track from the Cattle Pond site in the northwestern Black Hills. B) Several tracks from the Dry Poison Creek site near Buffalo. Scale bars = 5 cm.



thin, ripplemarked sandstone that may represent a splay deposit. The track is in the collections of the South Dakota School of Mines and Technology.

#### Little Houston Creek

This site contains small, tridactyl tracks, possibly belonging to theropods, preserved as impressions in a sandstone slab from just below a quarry in the middle part of the Morrison of northeastern Wyoming, south of Devils Tower National Monument (Foster and Lockley, 1995). There are 12 tracks and at least 10 trackways represented. Some pad and claw impressions are preserved in some tracks, but the possibility that some of these tracks represent small ornithopods cannot be ruled out. At 6.3 cm to 16 cm in length, these are among the smallest dinosaur tracks currently known from the Morrison Formation. The slab was collected in 1992 and is stored but not yet cataloged at the SDSM.

#### Fremont County

#### Cedar Ridge

This site in the Morrison southeast of Lander and along the edge of the Wind River Mountains has several natural sandstone casts of crocodilian (*Hatcherichnus*?) tracks. The uncollected tracks are on large, loose blocks of sandstone, and their precise original stratigraphic level has not been determined.

#### Hot Springs County

#### Warm Springs Ranch

Jennings et al. (this volume) report on several sites containing small tridactyl tracks and small enigmatic tracks from near Thermopolis.

#### Johnson County

#### Dry Poison Creek

This locality is in a sandstone unit on the east slope of the Bighorn Mountains near the Sheridan College quarries and the old Poison Creek Quarry (Flynn et al., 1997). At least 25 tracks representing perhaps 17 trackways of small, tridactyl dinosaurs, possibly theropods, were found in 1997 by Brian Flynn (Fig. 5b). The tracks are in a fine-grained sandstone, are fairly shallow, and many seem to trend north-south.

#### Natrona County

#### Alcova Lake

This site has been found recently and contains natural sandstone casts and impressions of a small ornithopod track (11 cm), many pterosaur tracks, a sauropod track, three tridactyl tracks (10 cm, 22 cm, and 30 cm), and a possible crocodilian (Southwell and Connely, 1997; Connely, this volume). The paleoenvironment appears to be lower deltaic plain and/or channel splays.

#### TRACK TYPES

##### CHELONIA

##### *CHELONIPUS* SP.

Turtle tracks have been identified from the Salt Wash Member in Utah and in Colorado (Foster et al., 1999; Lockley and Foster, this volume). These tracks are comparable to *Chelonipus*. They are approximately 1.7–2.5 cm across and consist of three to five roughly parallel digit scrape marks, and the tracks themselves are closely spaced (Fig. 6). Some have short, rounded heel impressions.

##### LACERTILIA INDET.

The record of possible lacertilian tracks consists of a single track in a sandstone at the Fruita Paleontological Area in western Colorado. The site has not yet been relocated.

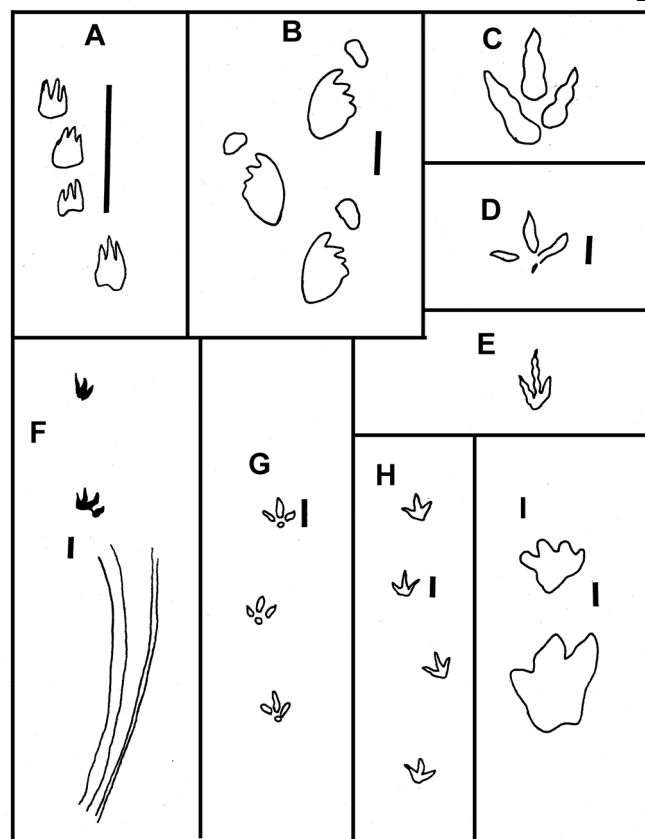


FIGURE 6. Vertebrate track types in the Morrison Formation. A) *Chelonipus*, turtle tracks. B) cf. *Brontopodus*, sauropod dinosaur tracks. C) Allosaurid theropod dinosaur track. D) "Wide-splay" theropod dinosaur track. E) "Grallatorid" theropod dinosaur track. F) *Hatcherichnus*, crocodilian tracks and probable tail trace. G) *Dinehichnus*, ornithopod dinosaur tracks. H) cf. *Anomoepus*, ornithopod dinosaur tracks. I) *Stegopodus*, stegosaurian dinosaur tracks. Scale bars = 10cm, except B which is 30cm. C–E scale bar in D.

#### CROCODYLIA

##### *HATCHERICHNUS SANJUANENSIS*

Crocodilian tracks are known from four localities in the Morrison Formation, the type locality of *Hatcherichnus* southeast of the La Sal Mountains in San Juan County, Utah (Fig. 6), the Garden Park area of Colorado (a track originally illustrated by Hatcher, 1903), and new sites at Cedar Ridge near Lander, Wyoming, and north of Moab, Utah. The tracks include a four toed pes and a manus with only three digits impressed, although crocodilians had five digits on the manus (Foster and Lockley, 1997). The type tracks include associated possible tail drag marks as well. Most of the tracks indicate a moderately large crocodilian with a pes width over 10cm. The presence of only three manus digit impressions, the lack of a pes heel impression, the presence of tracks of only the left side limbs, and the tail swish and drag marks all suggest that the type of *Hatcherichnus* represents an animal pushing off in very shallow water, or otherwise not walking.

#### PTEROSAURIA

##### *PTERAICHNUS SALTWASHENSIS*

*Pteraichnus* was named by Stokes (1957) based on a well preserved trackway from a sandstone in the Salt Wash Member of the Morrison in northeastern Arizona. This is in an area in which theropod tracks have been found subsequently. The identification of this track type as belonging to pterosaurs has been debated, and for some time the track type was thought to belong to crocodilians (Padian and Olsen, 1984). It has since been reassigned to pterosaurs, however (Lockley et

al., 1995; Mazin et al., 1995). *Pteraichnus* tracks have since been found in the lower Morrison Formation in Wyoming and Oklahoma.

## DINOSAURIA

### THEROPODA

#### LARGE (“ALLOSAURID”)

Large theropod tracks of a size and shape consistent with having been made by allosaurids are found at sites such as Purgatoire River, West Rabbit Ridge, and Copper Ridge (Valley City). These tracks are generally 30–45 cm in length (Fig. 6), and it is possible that they were made by other non-allosaurid theropods such as megalosaurs or ceratosaurs.

#### SMALL (“GRALLATORID”)

These tracks are small (~10–20 cm) and of a shape similar to the Early Jurassic form ichnogenus *Grallator* (Fig. 6). The tracks have narrow divarication angles, narrow clawed digits, and appear to have been made by small theropods.

#### “WIDE SPLAY”

The “wide splayed” theropod tracks are about 20 cm wide and have narrow digits and very wide divarication. This track type is known only from the State Bridge site in Colorado (Figs. 2 and 6) and is very unusual for the Morrison Formation. The narrow, clawed digits suggest theropod affinities, but it is possible that they were made by ornithopods.

#### INDET. TRIDACTYL

These footprints are small (6–10 cm) and are consistent with theropod tracks in generally having three narrow, distally-tapering digits with low divarication angles. The digits are not widely splayed as in some ornithopods, but the skeletal foot structure of small ornithopods is quite similar to that of theropods and so it is difficult to be certain of the affinities of these particular Morrison tracks. They may well represent tracks of very small ornithopods. The indeterminate tridactyl tracks are known from several sites, including Little Houston Creek, which has the smallest tridactyl tracks known from the Morrison Formation (Foster and Lockley, 1995).

### SAUROPODA

#### CF. *BRONTOPODUS*

These wide-gauge sauropod tracks are found at several sites in the Morrison Formation, including Hidden Canyon Overlook in Utah, where there are three parallel trackways preserved on what was a sandy braided stream bar. The pes tracks are generally 50–60 cm in length and their medial edges often separated along the mid-line by about 10 cm (Fig. 6). The trackways from the Morrison are referred to this ichnogenus originally named by Farlow et al. (1989) based on the well preserved Lower Cretaceous tracks from Texas. The Morrison tracks may have been made by camarasaurids or brachiosaurids.

#### *PARABRONTOPODUS MACINTOSHI*

This ichnospecies was named by Lockley et al. (1994a) based on the narrow-gauge trackways at the Purgatoire River site in the lower Morrison in southeastern Colorado. The pes tracks are about the same length as those referred to *Brontopodus* but are closer together and often overlap the midline of the trackway. The manus tracks are also generally smaller relative to the pes than in *Brontopodus*, and *Parabrontopodus* may represent tracks of diplodocids. Wright (2005) noted similarities of *Parabrontopodus* to *Breviparopus* from the Middle Jurassic of Morocco (Dutuit and Ouazzou, 1980) and suggested that the two may be synonymous.

### ORNITHISCHIA

#### *STEGOPODUS CZERKASI*

*Stegopodus* was named by Lockley and Hunt (1998) for a manus and pes from near Arches National Park in Utah (Fig. 6). The tracks are similar to the foot structure of stegosaurs and to predicted stegosaur

tracks illustrated by Thulborn (1990). The manus is tetradactyl and the pes tridactyl. Unnamed stegosaur pes tracks have also been reported from near the Cleveland-Lloyd Quarry (Bakker, 1996).

#### CF. *ANOMOEPUS*

These small ornithopod tracks are known from western Colorado and have widely splayed digits but lack the manus impressions seen in some Early Jurassic *Anomoepus* trackways from New England (Fig. 6). The trackways also demonstrate a slight inward rotation of the tracks toward the trackway midline, which may be characteristic of ornithopod trackways.

#### *DINEHICHNUS SOCIALIS*

*Dinehichnus* was named by Lockley et al. (1998b) based on a number of parallel trackways at one site in the Salt Wash Member in southern Utah and may represent the tracks of dryosaurids (Fig. 6). A site found recently in Colorado has two short trackways of *Dinehichnus* (Lockley and Foster, this volume). This ichnogenus also has widely splayed digits and inward rotation of the pes but also has distinct heel pad impressions in each track.

## RESULTS AND GENERAL DISCUSSION

A count of the minimum number of trackways preserved at each of the 50 Morrison Formation tracksites indicates a total sample or proxy census of individuals of more than 260 trackways. Of these, most are theropod, sauropod, and ornithopod dinosaurs (Table 1). Of the track localities for which there are data on the preservational lithology, 45% are sandstone bedding surfaces (SB), 40% are floodplain mudstones (FP), and 14% are limestone bedding surfaces (LS) (Fig. 7). These percentages approximately reflect the amount of each lithology in outcrop, limestones being least common, and sandstones and mudstones more common. In the lower Morrison Formation of the Colorado Plateau sandstone and mudstone units are nearly equally abundant. In the Brushy Basin Member and upper equivalents, mudstones predominate but sandstones are needed in order preserve FP sites.

The overall relative abundances of different vertebrate track types (Fig. 8), shows the domination of the sample by theropod and sauropod dinosaurs, followed by indeterminate tridactyl tracks and ornithopod dinosaurs. All other track types are quite rare. This does not likely reflect the true abundances of the animals in the original standing populations; although theropods were probably more common numerically than sauropods, by far the most abundant dinosaurs in the environment were likely small ornithopod dinosaurs. These trackway counts were converted to

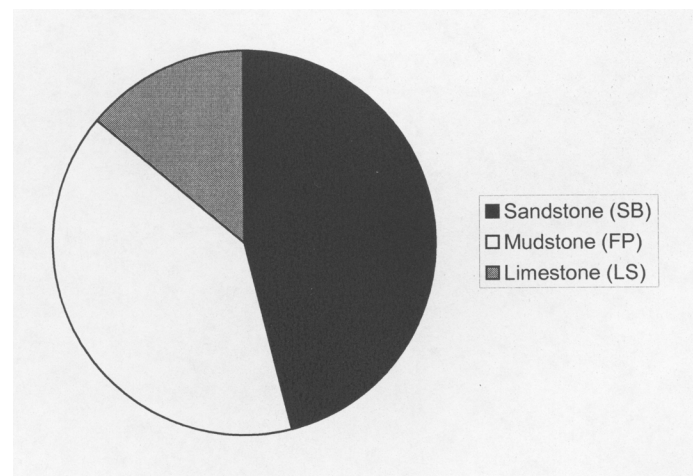


FIGURE 7. Lithologic and paleoenvironmental context summary of the tracksite sample in the Morrison Formation. Total number of tracksites = 55. Abbreviations as in Table 2.

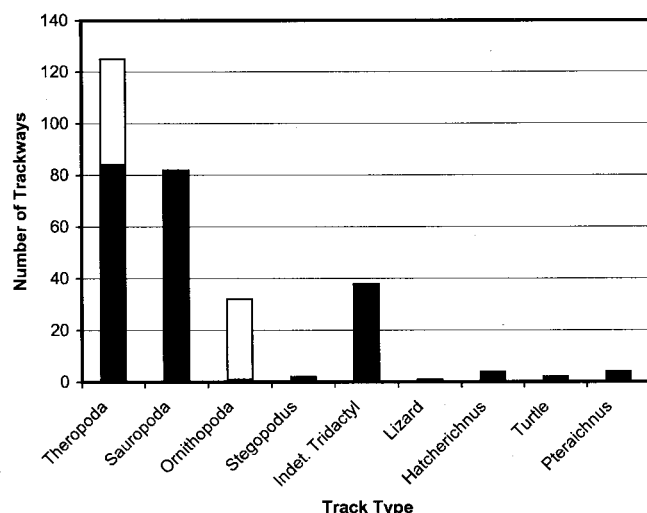


FIGURE 8. Minimum number of trackways of each vertebrate track type in the Morrison Formation. For theropods and ornithopods, white indicates numbers of trackways of small individuals or taxa.

biomass relative abundances by multiplying the trackway numbers by approximate adult masses for each type of animal and normalizing to 100% (Foster, 1998). This was done relative to overall foot and body size, compared to a similar-sized body fossil; thus, although a small theropod track, for example, may represent an adult small theropod or a juvenile *Allosaurus*, the approximate adult mass used was that of a small adult theropod. The biomass relative abundances based on trackway data (Fig. 9a) approximately parallel those based on skeletal data (Foster, 1998, 2003) in that sauropod dinosaurs appear to dominate the vertebrate biomass and in that carnivorous dinosaurs (predators) account for roughly 6% of the biomass. It is important to stress, however, that the population percentages based on raw skeletal or trackway data are drastically different (Fig. 9b), and that the similarities in biomass comparisons may well be accounted for mostly by the massive size of the sauropod species.

Of the general track types, only sauropods, theropods, and ornithopods occur in all three paleoenvironments (FP, LS, and SB) (Fig. 10). Pterosaur, crocodilian, and turtle tracks are only found in SB sites. Sauropod trackways are most commonly found at FP sites, whereas those of theropods are most often associated with SB localities (a distribution for theropods similar to that seen in the Lower Cretaceous of Alberta, as found by McCrea, 2000). The more common occurrence of sauropods at FP sites might be a result of the preservational context of these localities. Most FP sites are sandstone overhangs at which footprints originally made into underlying floodplain muds are preserved as natural sandstone casts; some of these sites are only recognizable as a result of the preservation of deep sauropod pes tracks, and theropod tracks might simply be less often preserved and noted in outcrop in this context. Contrary to a pattern noted previously for sauropod tracks in general, Morrison sauropod tracks more commonly are at FP sites than LS sites.

A similar pattern is found in the number of trackways of each type of animal preserved in different environments (Fig. 11); sauropods and theropods dominate the FP and LS localities, but the greatest diversity is again preserved as SB sites. The one difference in this case is that there are far more sauropod and theropod trackways in LS sites compared to other environments, but this is likely a result of the large trackway sample from the Purgatoire River site in southeastern Colorado, which is in a limestone unit low in the formation (Lockley et al., 1986). This bias might appear to suggest that, as in the sauropod track sample world-wide, sauropods commonly occurred in limestone environments, but looking at the more balanced localities counts (Fig. 10, not dominated by the 1300 tracks at the

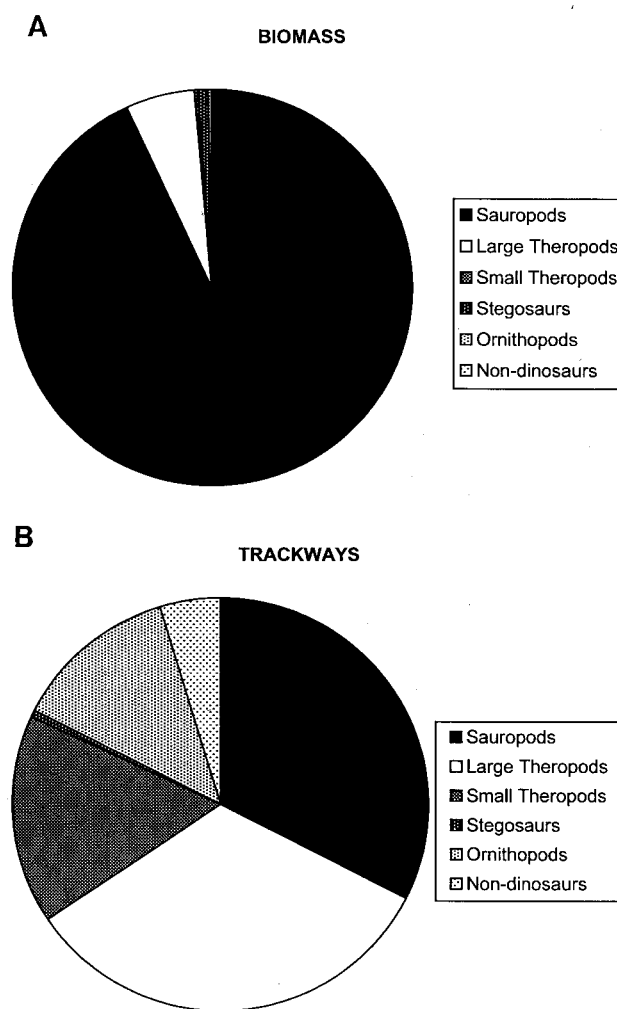


FIGURE 9. A) Biomass distribution of Morrison Formation vertebrates based on adjusted trackway data showing domination by sauropod dinosaurs. Numbers of trackways of each vertebrate type multiplied by approximate average weights and normalized to 100%. Weights: Sauropoda, 15,000kg; Theropoda, 900kg; Stegosaurs, 5000kg; Ornithopoda, 100kg; non-dinosaurs, turtles 5kg, crocodilians 50kg, *Pteraichnus* 5kg. B) Relative abundances of straight trackway counts for the same categories. N = 253.

Purgatoire River), we see that in fact Morrison sauropods are more likely to be found at sites representing floodplain muds than lacustrine limestones.

Sauropods are known from more than 70% of mudstone (FP) sites and theropods from just 30% of these; theropods are known from 50% of sandstone (SB) localities and sauropods just 25% of the same (Fig. 12). These percentages may reflect a minor paleoenvironmental segregation of theropods and sauropods (along and further away from rivers, respectively) but it more likely suggests a preservational bias in favor of preservation and recognition of different tracks in different types of outcrop.

Most track sites in the Morrison Formation occur low in the unit (Fig. 13). The Colorado Plateau region contains most of the sites in the formation, and most of these are in the Salt Wash Member or equivalent levels. Because sandstone units are key to preserving tracks at the SB and FP locality types, the frequency of sites in the Salt Wash Member may be a result of the abundance of sandstone bedsets in that unit. Sandstone beds are somewhat more evenly distributed stratigraphically in the formation outside the Colorado Plateau in areas further east and north; in these areas, tracksites are not concentrated in the lower part of the formation.

Few studies have been conducted that attempt to view the Morrison fauna as a whole. Dodson et al. (1980) considered dinosaur distribu-

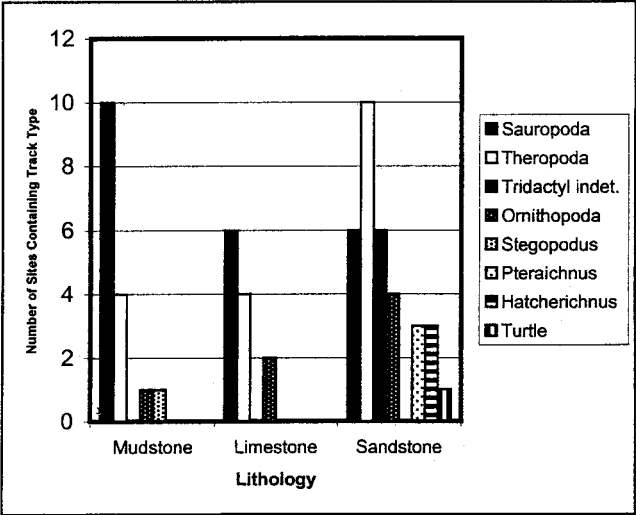


FIGURE 10. Number of sites in different lithologies at which vertebrate track types occur in the Morrison Formation.

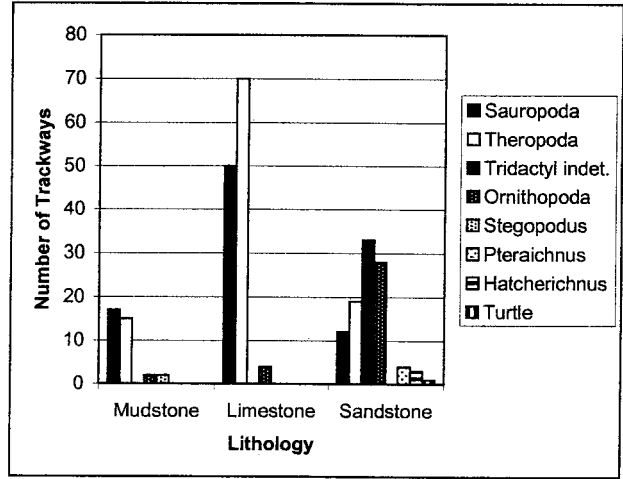


FIGURE 11. Number of trackways in different lithologies at which vertebrate track types occur in the Morrison Formation.

tions in relation to facies somewhat as attempted here, and Russell (1989; in Coe et al., 1987) compiled a chart showing the relative abundance of dinosaurs without giving raw data; these three were based on skeletal data. Schult and Farlow (1992) also presented relative abundance data for Morrison dinosaurs, but based on tracks. Foster (1998, 2003) compiled similar data for skeletal and track material also. Bakker (1997) also speculated about habitat zonation in Morrison dinosaurs. Lockley and Hunt (1994, 1995) were the first to present data based on a specific number of tracksites, citing “at least 30 dinosaur tracksites...(and)...a total of about 200 trackways” (Lockley and Hunt, 1994, p. 102). In that paper, they also classified the Morrison as a type 3b deposit in which track and bone sites are about equally common (type 3) but where there are significant inconsistencies in the track and bone records (subcategory b). The present study, based on track data compiled by Foster (1998), Lockley and Hunt (1995), and Lockley et al. (1998a), provides a more complete ichnological census that can potentially be compared with skeletal data (Coe et al., 1987; Russell, 1989; Schult and Farlow, 1992; Foster, 2003) to assess differences in the trace and body fossil record. Leaving aside the obvious bias against preservation of small non-dinosaurian vertebrate tracks that is evident in the current ichnological database, some general observations can be made regarding the data on dino-

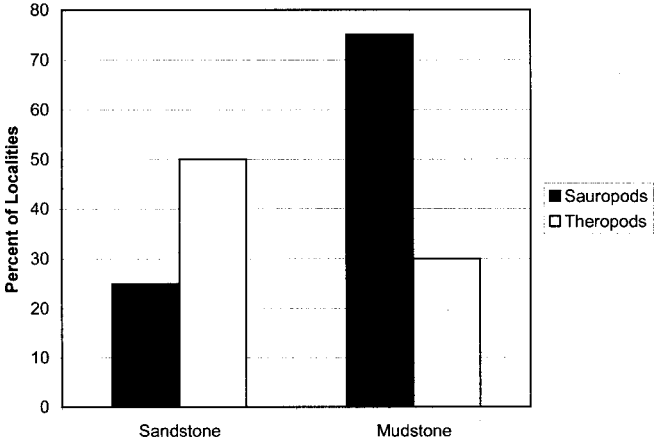


FIGURE 12. Percent of Morrison Formation track localities in sandstone and mudstone at which sauropod and theropod dinosaur tracks have been identified.

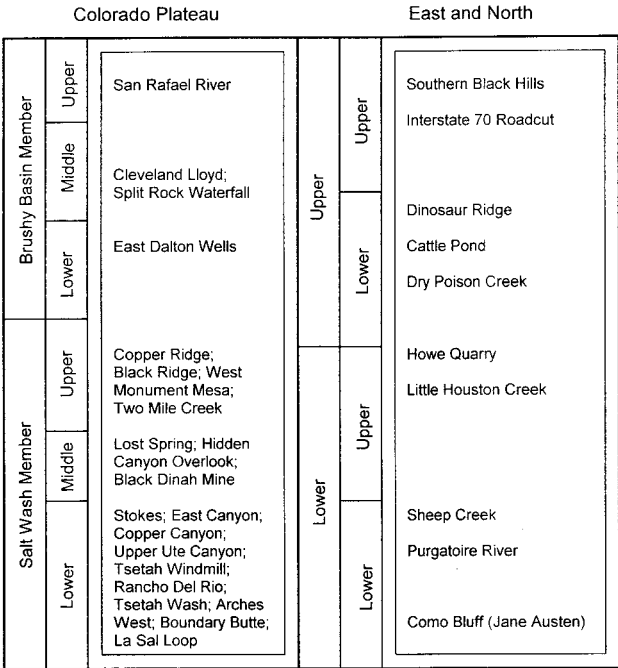


FIGURE 13. Stratigraphic distribution of vertebrate tracksites in the Morrison Formation on the Colorado Plateau and other areas. Tracksites shown in approximate stratigraphic position.

saurian ichnofaunas. The raw data are heavily biased towards saurischians (theropods and sauropods). This is probably in part a true reflection of the dominance of saurischians in Jurassic dinosaur faunas, in comparison with Cretaceous faunas, although as noted, a higher proportion of ornithopods may be inferred (Lockley et al., 1998b) partly on the basis of skeletal data and other theoretical/ecological considerations designed to adjust bias in sampling (Coe et al., 1987; Foster, 2003). However, the saurischian domination pattern may also reflect aspects of paleogeographical and paleoenvironmental reality. The region of Morrison Formation deposition was generally situated at relatively low, subtropical latitudes. In these regions sauropods seem to dominate the ichnofaunas (Lockley, 1991; Lockley et al., 1994a, 1994b), although more data are needed to test this apparent pattern (see also Farlow, 1992; Wright, 2005). By contrast, large ornithischians, which do not dominate until the Cretaceous, appear to be more abundant at higher latitudes, often in coastal

regions (see Lockley and Wright, 2001 for ornithopod tracks and McCrea et al., 2001 for ankylosaur footprints). This raises the question of whether there was a similar tendency towards latitudinal segregation between saurischians and ornithischians during Morrison times. The skeletal record would seem to suggest this is not the case (Foster, 2000). However, the track record is less clear and suggests a distinct paucity of ichnological evidence for stegosaurs and large ornithopods (e.g. *Camptosaurus*). Such discrepancies which gave rise to the designation of the Morrison as a type 3b deposit (Lockley and Hunt, 1994) suggest the possibility of a preservational bias against ornithischian tracks in known track bearing facies (FP, LS, SB). The rarity of stegosaur and camptosaur tracks may relate also to an environmental bias; Dodson et al. (1980) noted an association of *Stegosaurus* with channel deposits

and suggested that the genus may have been a more upland taxon only preserved when washed in, and the near total lack of stegosaur tracks in the Morrison Formation does not contradict this hypothesis. Further study is needed of both track and skeletal distributions to assess the validity of such inferences.

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