

TETRAPOD ICHNOFACIES OF THE UPPER JURASSIC MORRISON FORMATION, WESTERN UNITED STATES

ADRIAN P. HUNT AND SPENCER G. LUCAS

New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, NM 87104-1375

Abstract—Three fundamental terms in ichnology are: (1) assemblage, which is equivalent to an assemblage of body fossils; (2) ichnocoenosis, which is a trace fossil assemblage produced by a biological community that can be characterized by morphological criteria; and (3) ichnofacies, which refer to recurrent ichnocoenoses that represent a significant portion of Phanerozoic time. There are five archetypal vertebrate ichnofacies for nonmarine environments (*Chelichnus*, *Grallator*, *Brontopodus*, *Batrachichnus*, *Characichnos*), of which four are present in the Morrison: (1) *Grallator* ichnofacies – unnamed ichnocoenosis; (2) *Batrachichnus* ichnofacies – *Pteraichnus* ichnocoenosis; (3) *Brontopodus* ichnofacies – *Brontopodus*, *Parabrontopodus* and *Dinehichnus* ichnocoenosis; and (4) *Characichnos* ichnofacies – *Hatcherichnus* and *Chelonichnus* ichnocoenosis. The newly defined Late Jurassic *Megalosauripus* ichnocoenosis is not present in the Morrison Formation but is of global significance.

INTRODUCTION

The vertebrate fauna of the Upper Jurassic Morrison Formation of western North America embodies the global view of a dinosaur community with its long history of study, its large and emblematic taxa (*Apatosaurus*, *Diplodocus*, *Stegosaurus*, *Allosaurus*), its massive quarries (e.g., Dinosaur National Monument, Cleveland-Lloyd quarries) and its beautifully preserved skeletons (e.g., Foster, 2003). However, the tetrapod ichnology of the Morrison was poorly studied until the 1980s. This coincided with a renaissance in tetrapod ichnology that was catalyzed by the “First International Symposium of Dinosaur Tracks and Traces” held at the New Mexico Museum of Natural History in 1986 (Gillette and Lockley, 1989).

Hasiotis (2004) recently provided an overview of the ichnology of the Morrison Formation (but see Bromley et al., in review), which did not utilize the ichnofacies concept. The purpose of this paper is to provide an overview of the Morrison vertebrate ichnofauna in the context of archetypal ichnofacies (Hunt and Lucas, 2006b).

TETRAPOD ICHNOCOENOSIS AND ICHNOFACIES

Hunt and Lucas (2006b) provided a discussion of terminology relevant to the study of tetrapod ichnofacies:

1. The basic collective term for trace fossils is “ichnoassemblage,” which is equivalent to an assemblage of body fossils (Bromley, 1996). This term implies nothing about the timing of the emplacement of the biogenic structures.

2. An ichnocoenosis can be defined as a trace fossil assemblage produced by a biological community that can be characterized by morphological criteria (independent of depositional environment or biological affinities) (e.g., Bromley, 1996; McIlroy, 2004).

3. Seilacher (1964, p. 303) introduced the term ichnofacies for “general trace associations, or types of ichnocoenosis, representing certain facies with a long geologic range.” These high-level ichnofacies have been referred to as archetypal (Frey and Pemberton, 1987), and there is consensus that ichnofacies should refer to recurrent ichnocoenoses that represent a significant portion of Phanerozoic time.

Seilacher (1964) recognized that there are recurrent associations of invertebrate ichnofossils, which he referred to as ichnofacies. Subsequently, he named six archetypal ichnofacies after typical ichnofossils, two of which occur in nonmarine environments – *Scoyenia* and *Skolithos* (Seilacher, 1964, 1967; Buatois and Mángano, 2004). Seilacher’s work stimulated numerous studies of invertebrate ichnofacies. Subsequently several additional archetypal invertebrate ichnofacies have been named in nonmarine

environments including *Mermia* (Buatois and Mángano, 1995, 2004), *Coprinsphaera* (Genise et al., 2000), *Psilonichnus* (Frey and Pemberton, 1987) and *Octopodichnus* (Hunt and Lucas, 2006b).

Baird (1965) was apparently the first to raise the issue of ichnofacies with regard to tetrapod traces when he noted that the differences between the Permian tetrapod ichnofaunas of redbeds and eolianites in the American West might be the result of facies differences. However, it was 30 years before Lockley et al. (1994c) provided a cogent synthesis and discussion of tetrapod ichnofacies. Subsequently, Hunt and Lucas (2006b) defined five archetypal tetrapod ichnofacies for nonmarine environments: *Chelichnus*, *Grallator*, *Brontopodus*, *Batrachichnus* and *Characichnos* ichnofacies (Table 1). Hunt and Lucas (2006b) argued that all previously defined tetrapod ichnofacies lacked the stratigraphic and geographic range that would warrant their consideration as archetypal ichnofacies and they considered them to be more properly termed ichnocoenoses.

MORRISON TETRAPOD TRACK RECORD

Introduction

Marsh (1899) first described tetrapod tracks from the Morrison Formation. He interpreted some of these tridactyl tracks as ornithomimid, but they are now considered theropod tracks (Lockley et al., 1998). The first large Morrison Formation tracksite to be described was the Purgatoire site in southeastern Colorado (MacClary, 1938; Lockley et al., 1986).

Tracksites

The majority of Morrison tracksites are small and do not preserve many tracks (e.g., Lockley, 1986, 1988, 1990; Lockley and Hunt, 1998). Such sites include the Black Hills of South Dakota (Marsh, 1899; Foster, 1996), Carrizo Mountains in Arizona (Stokes, 1957; Lockley and Mickelson, 1997), Arches area (Engelmann and Hasiotis, 1999), Moab *Stegopodus* site (Lockley and Hunt, 1998), Cleveland-Lloyd quarry area (Lockley et al., 1998b), Copper Canyon (Foster et al., 1999) and Bullfrog in Utah (Meyer et al., 1994), Garden Park (Harris, 1998), Colorado National Monument (Lockley and Foster, 2006; Engelmann and Hasiotis, 1999), State Bridge (Lockley and Hunt, 1995) and Black Dinah Mine near Uravan (Lockley et al., 1998b) in Colorado, Howe quarry area (Lockley et al., 1998e; Kvale et al., 2004) and Little Houston quarry (Foster and Lockley, 1995) in Wyoming (Fig. 1).

Larger Morrison tracksites include Hidden Canyon (Barnes and Lockley, 1994), Boundary Butte (Lockley et al., 1998a), Valley City (Lockley, 1991; Lockley and Hunt, 1995) in Utah, and Rancho del Rio near State Bridge in Colorado (Lockley and Hunt, 1995) and Como Bluff

in Wyoming (Southwell et al., 1996) (Fig. 1). The only really large tracksite in the Morrison Formation is in the Purgatoire Valley of Colorado (e. g., Lockley et al., 1986, 1994a). Three track levels are preserved close to river level in an arcuate area with a length of about 400 m (Lockley and Hunt, 1995, figs. 4.48–4.49).

Track Types

The Morrison ichnofauna includes the tracks of sauropod, theropod, ornithopod and stegosaur dinosaurs and crocodiles, turtles and pterosaurs. The majority of Morrison sauropod tracks derive from the Purgatoire tracksite and are referred to the narrow-gauge ichnogenus *Parabrontopodus* (Lockley et al., 1994a). *Parabrontopodus* also occurs at other tracksites such as Rancho del Rio (Lockley and Hunt, 1995; Lockley et al., 1998b). The wide-gauged ichnogenus cf. *Brontopodus* occurs at the Valley City and Hidden Canyon tracksites in central Utah (Barnes and Lockley, 1994; Lockley and Hunt, 1995).

Theropod tracks are numerous in the Morrison Formation (e. g., Lockley et al., 1998b; Foster and Lockley, 2006;). Theropod tracks represent several morphologies varying in size and morphology (Lockley et al., 1998b, fig. 2), but the Morrison theropod tracks lack an adequate ichnotaxonomy.

Ornithopod tracks are uncommon in the Morrison Formation. Lockley et al. (1998a) named *Dinehichnus* for 45 tracks representing 18 trackways from Boundary Butte near the Arizona/Utah border. Lockley and Foster (2006) describe additional specimens from near Colorado National Monument in Colorado. Lockley et al. (1998b) described a second type of ornithopod Morrison track type from Black Dinah Mine near Uravan that resembles the Early Jurassic *Anomoepus*. Hasiotis (2004, fig. 27f) identified a “well-preserved ornithopod track,” but we are unable to confirm this attribution.

Lockley and Hunt (1998) named a stegosaur track from the Morrison as *Stegopodus*. Gierlinski et al. (2005) suggested that in addition to the holotype, other Morrison stegosaur tracks might include specimens from near the Cleveland Lloyd quarry and one from near Yale quarry 10 (Como Bluff). Stegosaur tracks are obviously rare in the Morrison Formation.

The majority of pterosaur tracks from the Jurassic of western North America derive from pre-Morrison (Summerville) strata, including probably the holotype of *Pteraichnus* (Lockley et al., 1995). However, *Pteraichnus* does occur in the Morrison (e. g., Lockley et al., 1998b; Mickleson et al., 2004; Hasiotis, 2004).

The Morrison Formation track record encompasses swimming traces of several kinds. These include the crocodilian trace *Hatcherichnus* and turtle traces (Lockley et al., 1998b; Foster et al., 1999; Avanzini et al., 2005). Lockley and Foster (2006) describe *Chelonichnus* from western Colorado. Note that Hasiotis (2004) described small reptile swimming traces from the Tidwell Member, which we consider part of the Summerville Formation, not the Morrison Formation (Lucas and Anderson, 1997). These tracks may be undertracks rather than swimming traces.

The scope of this paper does not include all tetrapod trace fossils. However, we concur with Bromley et al. (in review) that many of the structures in the Morrison Formation that Hasiotis (2004) interpreted as tetrapod burrows strongly resemble concretionary bodies found in some paleosols. We have similar concerns about specimens described in Hasiotis et al. (2004).

MORRISON TETRAPOD ICHNOFACIES AND ICHNOCOENOSSES

History of Study

Lockley et al. (1994c) named a *Brontopodus* “ichnofacies” (ichnocoenosis of current usage) to include ichnoassemblages of the Jurassic and Cretaceous age dominated by sauropod tracks. This “ichnofacies” explicitly included Morrison ichnofaunas. Hunt and Lucas (2006b) defined

an archetypal *Brontopodus* ichnofacies to include all ichnocoenoses that are dominated by the tracks of terrestrial herbivores.

Hasiotis (2004) provided an overview of Morrison ichnology and ichnofacies. However, this review poses many problems, including its discussion of ichnofacies (Bromley et al., in review). Bromley et al. (in review) stressed several issues regarding Hasiotis’ (2004) discussion of ichnofacies, including: (1) confusion of ichnocoenoses with archetypal ichnofacies; (2) acknowledgment that ichnocoenoses could be recognized in the Morrison (Hasiotis, 2004, p. 248) but failure to define them; (3) failure in recognizing that archetypal ichnofacies are defined based on ichnotaxa, not on their paleoenvironmental significance (interpretative); and (4) confusion of paleosols, environments, and ichnofacies. In addition, Hasiotis (2004) failed to acknowledge the widespread acceptance of the concept of ichnofacies in nonmarine environments (e. g., Buatois and Mángano, 1995; Genise et al., 2000; Metz, 2000; Uchman and Álvaro, 2000; Melchor et al., 2003; Melchor, 2004; McIlroy, 2004; Hunt and Lucas, 2005, 2006a, b). Hasiotis (2004) also failed to accurately apply previously defined ichnofacies and even questioned the overall utility of the concept itself (Bromley et al., in review). Thus, Hasiotis (2004) indicated that Morrison lacustrine trace fossils do not fit the *Mermia* ichnofacies. This is not surprising given that he includes trace fossils that “reflect relatively firm substrates and shallow water with intermittent subaerial exposure” (Hasiotis, 2004, p. 242) in the category of lacustrine trace fossils, though the *Mermia* ichnofacies is characterized by permanent subaqueous conditions (e. g., Buatois and Mángano, 1995).

Hasiotis (2004, p. 182) disputed the utility of vertebrates in general and vertebrate traces in particular as specific palaeoecological and palaeoenvironmental indicators. This echoes the opinions of Bromley (1996) and McIlroy (2004), who suggested that vertebrate ichnocoenoses have no sedimentological connotation because the environmental specificity of tetrapod ichnofacies is in doubt. Hunt and Lucas (2006b), however, noted that all named vertebrate ichnocoenoses are restricted to a particular kind of environment, such as the duneface setting of the *Chelichnus* ichnofacies. Tetrapods are not only vagrant but also potentially wide ranging (compared to invertebrates), so invertebrate ichnologists tend to under-appreciate the environmental restrictions of tetrapods, which have been empirically demonstrated (Cohen et al., 1993; Hunt and Lucas, 2006b).

Ichnofacies and Ichnocoenoses of the Morrison Formation

Brontopodus ichnofacies

Hunt and Lucas (2006b) proposed the *Brontopodus* ichnofacies for medium diversity ichnofaunas in which the majority of tracks are of terrestrial herbivores with a small quantity (generally > 10%) of terrestrial carnivore tracks. This ichnofacies includes coastal plain-marine shoreline environments and some lacustrine shorelines, and it ranges from Late Permian to Recent in age. Hunt and Lucas (2006b) recognized several constituent ichnocoenoses of the *Brontopodus* ichnofacies.

The *Brontopodus* ichnocoenosis was first defined as an ichnofacies (Lockley et al., 1994c; Hunt and Lucas, 2006b). This ichnocoenosis was originally defined to include ichnofaunas dominated by sauropod tracks (Lockley et al., 1994c). Hunt and Lucas (2006b) restricted the ichnocoenosis to Early Cretaceous ichnofaunas dominated by wide-gauge *Brontopodus*. We recognize herein that the *Brontopodus* ichnocoenosis extends into the Late Jurassic and temporally overlaps the *Parabrontopodus* ichnocoenosis of Hunt and Lucas (2006b), which encompasses ichnofaunas dominated by the narrow-gauge *Parabrontopodus* (Fig. 2). Both the *Parabrontopodus* and *Brontopodus* ichnocoenoses occur in the Upper Jurassic of Europe—both ichnocoenoses are common in the Kimmeridgian, but in the Portlandian the *Brontopodus* ichnocoenosis dominates (Lockley and Meyer, 2000). The most important localities are in the Iberian Peninsula, Switzerland and Germany (Lockley and Meyer, 2000). Narrow gauge trackways from Niger may also represent the *Parabrontopodus* ichnocoenosis (Lockley et al., 1994b).

Ornithopod tracks are uncommon in the Morrison Formation, but we recognize a *Dinehichnus* ichnocoenosis for ichnoassemblages dominated by that ichnogenus (Fig. 2). The *Dinehichnus* ichnocoenosis also occurs at the Late Jurassic San Martinho do Porto tracksite in Portugal (Meyer et al., 1998; Lockley and Meyer, 2000).

***Grallator* ichnofacies**

Hunt and Lucas (2006b) proposed the *Grallator* ichnofacies for medium to high diversity ichnofaunas (five to eight ichnogenera) dominated by tracks of tridactyl avian and non-avian theropods (usually dominant) or of other habitual bipeds. Tracks of bipedal and quadrupedal ornithischians, sauropods and herbivorous mammals are also locally common in this ichnofacies. This ichnofacies extends from the Late Triassic to the Recent and often characterizes lacustrine margin environments. There are some tracksites in the Morrison that are dominated by the tridactyl tracks of non-avian theropods. These include Como Bluff (Southwell et al., 1996), Statebridge (Lockley et al., 1998b) and Howe quarry (Lockley et al., 1998e), and possibly other sites such as Garden Park (Harris, 1998). Unfortunately, there is no usable ichnotaxonomy for the Morrison theropod tracks, so this ichnocoenosis cannot be named (Fig. 3). There are other theropod-dominated tracksites from the Late Jurassic, but further ichnofacies analysis depends on the creation of a robust ichnotaxonomy.

***Batrachichnus* ichnofacies**

Hunt and Lucas (2006b) proposed the *Batrachichnus* ichnofacies for ichnofaunas in which the majority of tracks are of quadrupedal carnivores with a moderate-high diversity (four to eight ichnogenera). This ichnofacies represents tidal flat-fluvial plain environments from the Devonian to the Cretaceous.

We place the *Pteraichnus* ichnocoenosis of Hunt and Lucas (2006b) (= *Pteraichnus* ichnofacies of Lockley and Meyer, 2000) within the *Batrachichnus* ichnofacies because it is dominated by the tracks of quadrupedal carnivores (Fig. 3). This ichnocoenosis is much more common in strata subjacent to the Morrison, but it is present within this unit. The *Pteraichnus* ichnocoenosis is widespread in the Summerville Formation (including the Tidwell Member, which some workers consider a member of the Morrison (e. g., Lockley et al., 1995, 1996; Lockley and Mickelson, 1997; Mickelson et al., 2004). The *Pteraichnus* ichnocoenosis is also present in the Upper Jurassic of Europe, particularly in the Craysac lithographic limestone (Lockley and Meyer, 2000).

***Characichnos* ichnofacies**

Hunt and Lucas (2006b) proposed the *Characichnos* ichnofacies for medium diversity ichnofaunas in which the majority of tracks are swimming traces (parallel scratch marks) and fish swimming trails (*Undichna*). This ichnofacies represents shallow lacustrine (and estuarine) environments. They recognized several constituent ichnocoenoses, including the *Hatcherichnus* ichnocoenosis from the Morrison Formation, which is characterized by crocodile swimming traces (Foster and Lockley, 1997; Hunt and Lucas, 2006b) and which is now known from additional localities near Moab, Utah and near Lander, Wyoming (Foster, pers. commun., 2006) (Fig. 3). Lockley and Meyer (2000) recognized a *Chelonichnium* ichnocoenosis (ichnofacies in their definition) characterized by ichnoassemblages dominated by turtle swimming tracks of the ichnogenus *Chelichnus*. We recognize this ichnocoenosis in the Morrison based on the turtle tracks described by Foster et al. (1999) and Lockley and Foster (2006) (Fig. 3). The *Chelonichnium* ichnocoenosis occurs in the Upper Jurassic of Europe, notably the Cerin lithographic limestone of France and the Lastres Formation of Spain (represented by the ichnogenus *Emydhipus*) (Lockley and Meyer, 2000; Avanzini et al., 2005).

***Chelichnus* ichnofacies**

Hunt and Lucas (2006b) proposed the *Chelichnus* ichnofacies for

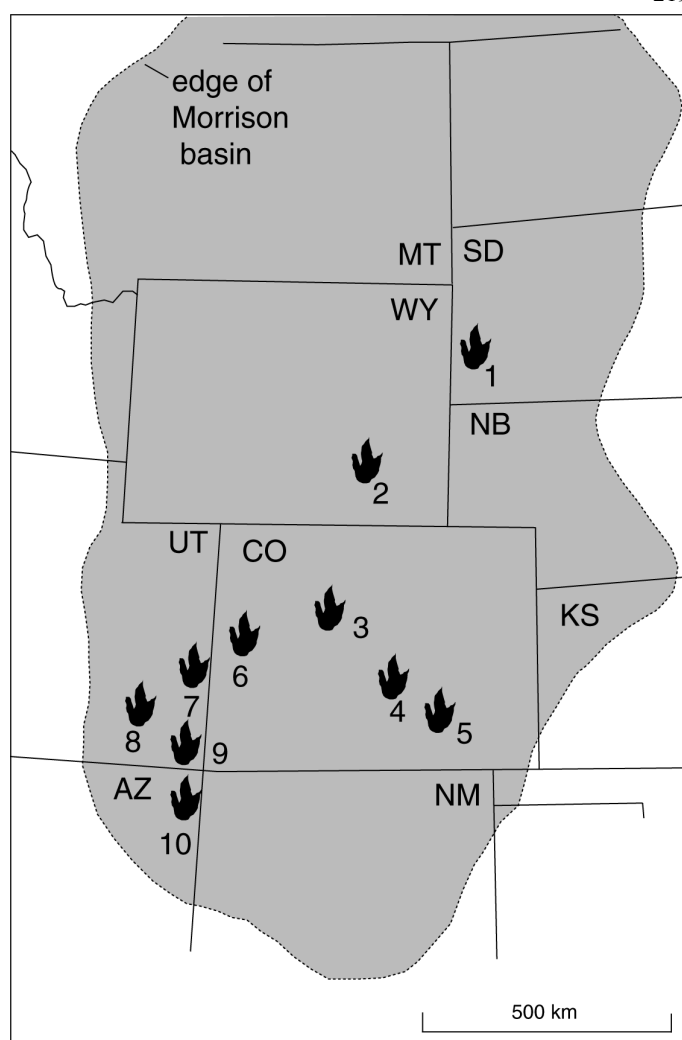


FIGURE 1. Distribution of some principal tracksites and tracksite-rich areas in the Upper Jurassic Morrison Formation of the western United States. 1. Black Hills. 2. Como Bluff. 3. Statebridge. 4. Garden Park. 5. Purgatoire valley. 6. Colorado National Monument. 7. Moab. 8. Bullfrog. 9. Boundary Butte. 10. Carizozo Mountains.

ichnofaunas that have a low diversity (less than five ichnogenera) of tetrapod tracks in which manus and pes tracks are equant in shape of subequal size and have short digit impressions. This ichnofacies is recurrent in dune faces of eolian environments (Fig. 1), and it extends from the Early Permian to the Early Jurassic. The *Chelichnus* ichnofacies is not present in the Morrison Formation or any other Upper Jurassic stratigraphic unit. This is due to a paucity of the appropriate aeolian facies.

Other Late Jurassic Ichnocoenoses

There is one notable Late Jurassic ichnocoenosis that this not present in the Morrison Formation. Lockley and others (e. g., Lockley et al., 1998c-d) have demonstrated the pervasive nature of ichnoassemblages characterized by the theropod ichnotaxa *Megalosauripus* and *Therangospodus*, which occur in Asia (Uzbekistan, Turkmenistan), Europe (Portugal, Germany) and western North America (Arizona, Utah, New Mexico, Oklahoma). We name this the *Megalosauripus* ichnocoenosis after its most characteristic ichnogenus. This ichnocoenosis has potential utility in biostratigraphy as, at least in North America, it is close in age to the Oxfordian-

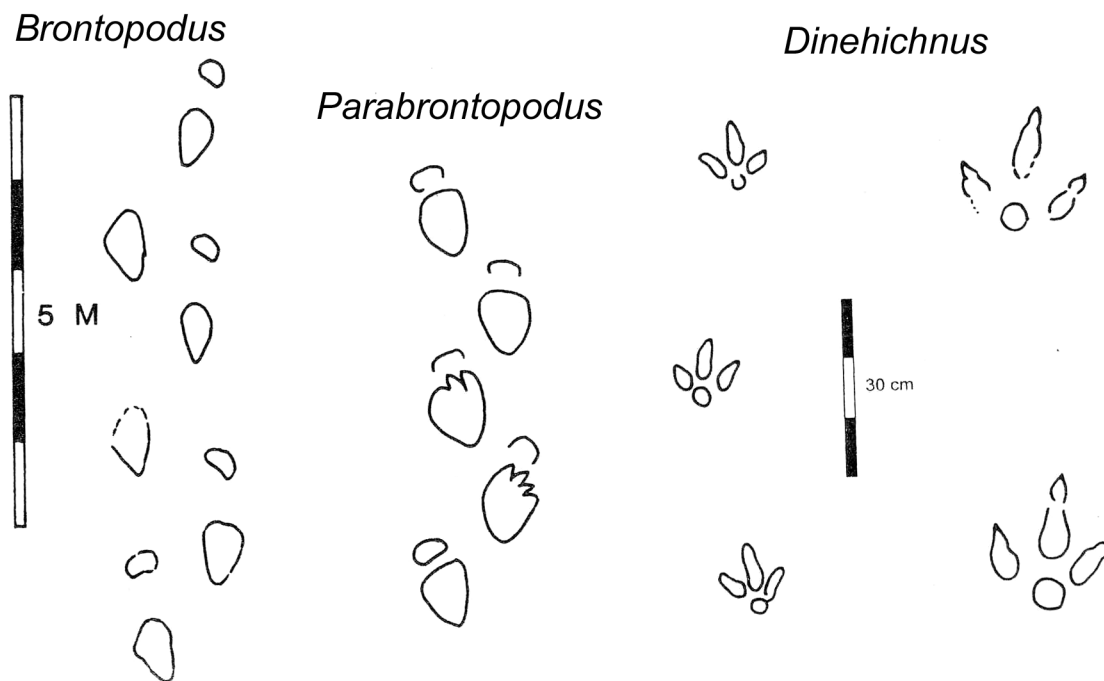


FIGURE 2. Representative tracks of the *Brontopodus*, *Parabrontopodus* and *Dinehichnus* ichnocoenoses of the *Brontopodus* ichnofacies in the Upper Jurassic Morrison Formation of western North America (after Lockley et al., 1998b).

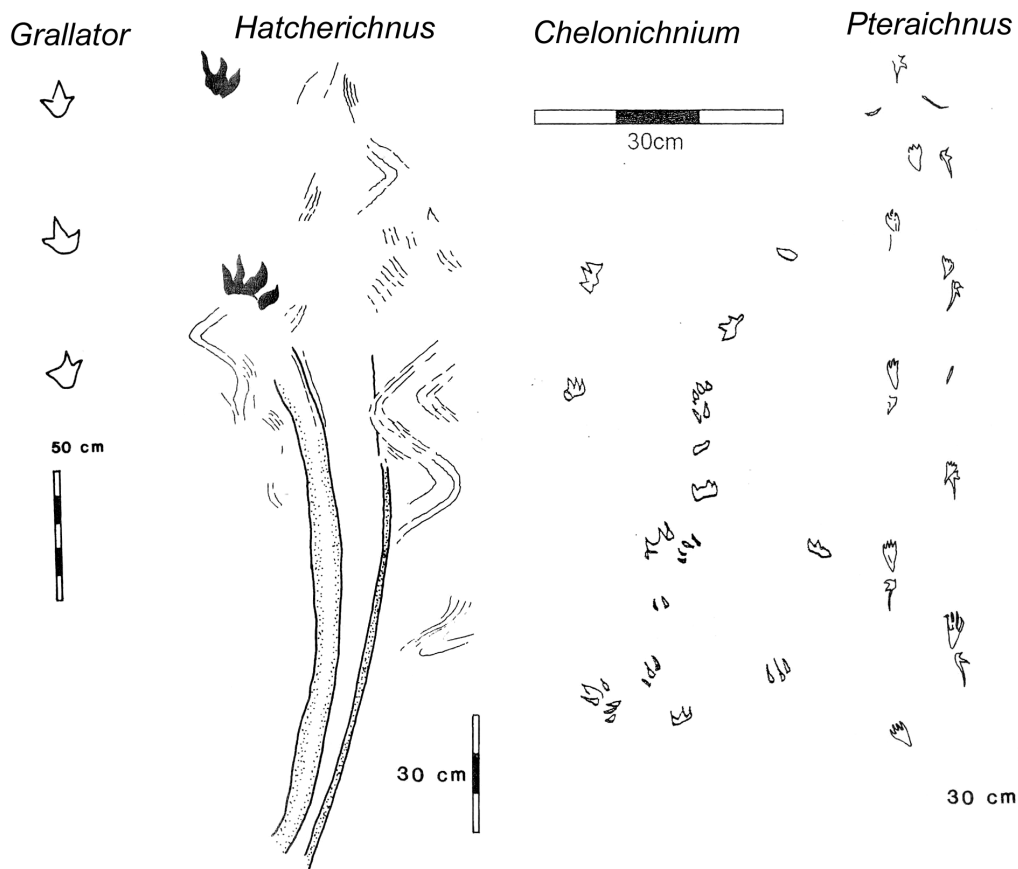


FIGURE 3. Representative tracks of the unnamed theropod ichnocoenosis of the *Grallator* ichnofacies; *Hatcherichnus* and *Chelonichnium* ichnocoenoses of the *Characichichnos* ichnofacies (after Lockley et al., 1998b; Lockley and Foster, 2006), and *Pteraichnus* ichnocoenosis of the *Batrachichnos* ichnofacies and the unnamed theropod ichnocoenosis in the Upper Jurassic Morrison Formation of western North America (after Lockley et al., 1998b).

Kimmeridgian boundary (Lockley et al., 1998c-d). There may also be potential in the future to recognize ichnocoenoses based on Late Jurassic stegosaur and ankylosaur tracks.

ACKNOWLEDGMENTS

We thank Luis Buatois and John Foster for helpful reviews.

REFERENCES

- Avanzini, M., García-Ramos, J. C., Lires, J., Menegon, M., Piñuela, L. and Fernández, L. A., 2005, Turtle tracks from the Late Jurassic of Asturias, Spain: *Acta Palaeontologica Polonica*, v. 50, p. 743-755.
- Baird, D., 1965, Footprints from the Cutler Formation: U. S. Geological Survey Professional Paper, v. 503C, p. 47-50.
- Barnes, F. A., Lockley, M. G., Trackway evidence for social sauropods from the Morrison Formation, eastern Utah (USA); *Gaia*, v. 10, p. 37-41.
- Bromley, R. G., 1996, Trace fossils: biology and taphonomy (second edition): London, Unwin Hyman, 361 p.
- Bromley, R. G. et al., in review, Discussion of the paper "Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses" by Stephen T. Hasiotis: *Sedimentary Geology*.
- Buatois L.A., Mángano, M. G., 1995, The paleoenvironmental and paleoecological significance of the lacustrine *Mermia* ichnofacies: an archetypical subaqueous nonmarine trace fossil assemblage: *Ichnos*, v. 4, p. 151-161.
- Buatois, L. A. and Mángano, M. G., 2004, Animal-substrate interactions in freshwater environments: applications of ichnology in facies and sequence stratigraphic analysis of fluvio-lacustrine successions; in McIlroy, D., ed., *The application of ichnology to paleoenvironmental and stratigraphic analysis*: Geological Society of London Special Publication, v. 228, p. 311-334.
- Cohen, A., Halpenny, J., Lockley, M. G., and Michel, E. 1993. Modern vertebrate tracks from Lake Manyara, Tanzania and their paleobiological implications. *Paleobiology*, 19: 443-458.
- Engelmann, G. F. and Hasiotis, S. T., 1999, Deep dinosaur tracks in the Morrison Formation: sole marks that are really sole marks: *Utah Geological Survey, Miscellaneous Publication 99-1*, p. 179-184.
- Foster, J. R., 2003, Paleoecological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain region, U.S.A.: *Bulletin of New Mexico Museum of Natural History and Science*, vol. 23, 95 p.
- Foster, J. R., 1996, Fossil vertebrate localities in the Morrison Formation (upper Jurassic) of western South Dakota: *Museum of Northern Arizona, Bulletin*, v. 60, p. 255-263.
- Foster, J. R. and Lockley, M. G., 1995, Tridactyl dinosaur tracks from the Black Hills area of northeastern Wyoming: *Ichnos*, v. 4, p. 35-41.
- Foster, J. R. and Lockley, M. G., 1997, Probable crocodilian tracks and traces from the Morrison Formation (upper Jurassic) of eastern Utah: *Ichnos*, v. 5, p. 121-129.
- Foster, J. R., Lockley, M. G. and Brockett, J., 1999, Possible turtle tracks from the Morrison Formation of southern Utah: *Utah Geological Survey, Miscellaneous Publication 99-1*, p. 3185-192.
- Frey, R. W. and Pemberton, S. G., 1987, The *Psilonichnus* ichnofacies, and its relationship to adjacent marine and nonmarine ichnocoenoses along the Georgia coast: *Bulletin of Canadian Petroleum Geology*, 35: 333-357.
- Genise, J. F., Mángano, M. G., Buatois, L. A., Laza, J. H., Verde, M., 2000, Insect trace fossil associations in paleosols: the *Coprinisphaera* ichnofacies: *Palaios*, v. 15, p. 49-64.
- Gierlinski, G., Mossbrucker, M. T. and Sabath, K., 2005, Stegosaurian footprints from the Morrison Formation of western United States and their implications for other finds: *International symposium on dinosaurs and other vertebrates paleoichnology*, Fumanya, Barcelona, Abstracts Volume, p. 28-29.
- Gillette, D. D. and Lockley, M. G., editors, 1989, *Dinosaur tracks and traces*: Cambridge, Cambridge University Press, 454 p.
- Hasiotis, S. T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: *Sedimentary Geology*, v. 167, p. 177-268.
- Hasiotis, S. T., Wellner, R. W., Martin, A. J. and Demko, T. M., 2004, Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance: *Ichnos*, v. 11, p. 103-124.
- Harris, J. D., 1998, Dinosaur footprints from Garden Park, Colorado: *Modern Geology*, v. 23, p. 291-308.
- Hunt, A. P. and Lucas, S. G., 2005 Tetrapod ichnofacies and their utility in the Paleozoic; in Buta, R. J., Rindsberg, A. K. and Kopaska-Merkel, D. C., eds., *Pennsylvanian footprints in the Black Warrior Basin of Alabama*: Alabama Paleontological Society Monograph, v. 1, p. 113-119.
- Hunt, A. P. and Lucas, S. G., 2006a, Permian tetrapod ichnofacies: *Quarterly Journal of the Geological Society of London*, in press.
- Hunt, A. P. and Lucas, S. G., 2006b, Tetrapod ichnofacies: a new paradigm: *Ichnos*, in press.
- Kvale, E. P., Mickelson, D. L., Hasiotis, S. T. and Johnson, G., 2004, The history of dinosaur footprint discoveries in Wyoming with emphasis on the Bighorn Basin: *Ichnos*, v. 11, p. 3-10.
- Lockley, M. G., 1986, Dinosaur tracksites: fieldguide published in conjunction with the First International Symposium on dinosaur tracks and traces: University of Colorado, Denver, Geology Department Magazine, Special Issue, 56 p.
- Lockley, M. G., 1988, Dinosaur tracks near Denver: *Colorado School of Mines Professional Contributions*, v. 12, p. 288-299.
- Lockley, M. G., 1990, A field guide to Dinosaur Ridge: Denver, Friends of Dinosaur Ridge, 29 p.
- Lockley, M. G., 1991, *Tracking dinosaurs: a new look at an ancient world*: New York, Cambridge University Press, 238 p.
- Lockley, M. G. and Foster, J. R., 2006, Dinosaur and turtle tracks from the Morrison Formation (upper Jurassic) of Colorado National Monument, with observations on the taxonomy of vertebrate swim tracks: *New Mexico Museum of Natural History, Bulletin*, this volume.
- Lockley, M. G. and Hunt, A. P., 1995, Dinosaur tracks and other fossil footprints of the western United States. Columbia University Press, 338 p.
- Lockley, M. G. and Hunt, A. P., 1998, A probable stegosaur track from the Morrison Formation of Utah: *Modern Geology*, v. 23, p. 331-342.
- Lockley, M. G., and Meyer, C. 2000. Dinosaur tracks and other fossil footprints of Europe. Columbia University Press, New York: 323 p.
- Lockley, M. G. and Mickelson, 1997, Dinosaur and pterosaur tracks in the Summerville and Bluff (Jurassic) of eastern Utah and northeastern Arizona: *New Mexico Geological Society, Guidebook 48*, p. 133-138.
- Lockley, M. G., Hunt, A. P. and Meyer, C., 1994c, Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy; in Donovan, S., ed., *The paleobiology of trace fossils*: London, John Wiley, p. 241-268.
- Lockley, M. G., Logue, T. J., Moratalla, J., Hunt, A. P., Schultz, R. J. and Robinson, J. W., 1995, The fossil trackway *Pteraichnus* is pterosaurian, not crocodilian: implications for the global distribution of pterosaur tracks: *Ichnos*, v. 4, p. 1-14.
- Lockley, M. G., Houck, K., Prince, N. K., 1986, North America's largest dinosaur tracksite: implications for Morrison Formation paleoecology: *Geological Society of America, Bulletin*, v. 57, p. 1163-1176.
- Lockley, M. G., Foster, J. R. and Hunt, A. P., 1998b, A short summary of dinosaur tracks and other fossil footprints from the Morrison Formation: *Modern Geology*, v. 23, p. 277-290.
- Lockley, M. G., Farlow, J. O. and Meyer, C. A., 1994a, *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways: *Gaia*, v. 10: 135-146.
- Lockley, M. G., Meyer, C. A., and Dos Santos, 1998c, *Megalosauripus* and the problematic concept of megalosaur footprints: *Gaia*, v. 15, p. 313-337.
- Lockley, M. G., Meyer, C. A., and Moratalla, J. J., 1998d, *Therangopodus*: trackway evidence for the widespread distribution of a Late Jurassic theropod with well-padded feet: *Gaia*, v. 15, p. 339-353.
- Lockley, M. G., Meyer, C. A., Lucas, S. G. and Hunt, A. P., 1994b, The distribution of sauropod tracks and trackmakers. *Gaia* 10: 233-248.
- Lockley, M. G., Dos Santos, V. F., Meyer, C. and Hunt, A. P., 1998a, A new dinosaur tracksite in the Morrison Formation, Boundary Butte, southeastern Utah:

- Modern Geology, v. 23, p. 317-330.
- Lockley, M. G., Meyer, C., Siber, H.-J., and Pabst, B., 1998e, Theropod tracks from the Howe quarry, Morrison Formation, Wyoming: Modern Geology, v. 23, p. 309-316.
- Lockley, M. G., Hunt, A. P. and Lucas, S. G., 1996, Vertebrate track assemblages from the Jurassic Summerville Formation and correlative deposits: Museum of Northern Arizona, Bulletin 60, p. 249-254.
- Lucas, S. G. and Anderson, O., 1997, The Jurassic San Rafael Group, Four Corners region: New Mexico Geological Society, Guidebook 48, p. 115-132.
- Marsh, O. C., 1899, Footprints of Jurassic dinosaurs: American Journal of Science, v. 7 (series 4), p. 227-232.
- MacClary, J. S., 1938, Dinosaur trails in Purgatory: Scientific American, v. 158, p. 72.
- McIlroy, D., 2004, Some ichnological concepts, methodologies, applications and frontiers. In McIlroy, D., ed., The application of ichnology to paleoenvironmental and stratigraphic analysis. Geological Society of London Special Publication, 228: 3-27.
- Melchor, R. N., 2004, Trace fossil distribution in lacustrine deltas: examples from the Triassic rift lakes of the Ischigualasto-Villa Union Basin, Argentina; In: McIlroy D, ed., The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. Geological Society, London, Special Publications, 228, p.335-354.
- Metz R., 200, Triassic trace fossils from lacustrine shoreline deposits of the Passaic Formation, Douglassville, Pennsylvania: Ichnos, v. 7, p. 253-266.
- Meyer, M. G., Lockley, M. G., Robinson, J. W. and Dos Santos, V. F., 1998, A comparison of well-preserved sauropod tracks from the Late Jurassic of Portugal and the western United States: evidence and implications: Gaia, v. 10, p. 57-64.
- Mickelson, D. L., Lockley, M. G., Bishop, J. and Kirkland, J., 2004, A new pterosaur tracksite from the Jurassic Summerville Formation, near Ferron, Utah: Ichnos, v. 11, p. 125-142.
- Stokes W. L., 1957, Pterodactyl tracks from the Morrison Formation: Journal of Paleontology, v. 31, p.952-954.
- Seilacher, A., 1964, Biogenic sedimentary structures; in Imbrie, J. and Newell, N., eds., Approaches to Paleocology: Wiley, New York, p. 296-316.
- Seilacher, A., 1967, Bathymetry of trace fossils: Marine Geology, v. 5, p. 413-428.
- Southwell, B., Lockley, M. G., Bakker, R. T., Connely, M. and Redman, P., 1996, The first report of a dinosaur tracksite from the Morrison Formation at Como Bluff: Museum of Northern Arizona Bulletin, v. 60, p. 133-136.
- Uchman A., and Álvaro, J. J., 2000, Non-marine invertebrate trace fossils from the Tertiary Calatayud-Teruel Basin, NE Spain: Revista Española de Paleontología, v. 15, p. 203-218.

APPENDIX

TABLE 1. Archetypal tetrapod ichnofacies (Hunt and Lucas, 2006) and representative. ichnocoenoses of the Upper Jurassic Morrison Formation of western North America.

Archetypal Tetrapod Ichnofacies	Predominant trace fossil types	Constituent Morrison ichnocoenoses	Inferred environment
<i>Chelichnus</i>	Low diversity ichnofaunas (less than 4 ichnogenera) of tetrapod tracks that have equant shape with subequal manual and pedal impressions and short digit impressions	None	Eolian crossbeds
<i>Batrachichnus</i>	Majority of tracks are of quadrupedal carnivores; medium-high diversity (4-8 ichnogenera)	<i>Pteraichnus</i> (Lockley and Meyer, 2000)	Tidal flat-fluvial plain
<i>Brontopodus</i>	Majority of tracks are terrestrial herbivores with small quantity (generally > 10%) of terrestrial carnivore tracks; medium-high diversity (4-8 ichnogenera)	<i>Brontopodus</i> (Lockley et al., 1994) <i>Parabrontopodus</i> (Hunt and Lucas, 2006) <i>Dinehichnus</i> (herein)	Coastal plain, clastic or carbonate marine shoreline
<i>Grallator</i>	Medium-high diversity ichnofaunas (5-8 ichnogenera) with tracks (usually dominant) of tridactyl avian and non-avian theropods	Unnamed	Lacustrine margin
<i>Characichnos</i>	Parallel scratch marks and fish swimming trails (<i>Undichna</i>)	<i>Hatcherichnus</i> (Hunt and Lucas, 2006) <i>Chelonichnium</i> (Lockley and Meyer, 2000);	Shallow lacustrine/aquatic