

## Jurassic tetrapod footprint ichnofaunas and ichnofacies of the Western Interior, USA

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**Abstract.** The Jurassic tetrapod track record of the Western Interior, USA, is one of the most diverse, complete and well-studied in the world, spanning a relatively continuous representation of Lower, Middle and Upper Jurassic formations. Although a few of these formations, notably the Morrison Formation, have yielded abundant body fossils, the majority lack abundant skeletal remains and, while track-rich, are in some cases completely barren of body fossils. Thus, the track record assumes great importance as the most complete and representative record of changing tetrapod faunas through time in a region where the body fossil record is often sparse or absent. In the Lower and Middle Jurassic, many distinctive assemblages are associated with eolian units (Wingate, Navajo and Entrada) that are almost devoid of body fossils. However, the former two units are rich in synapsid tracks characterized as the *Brasilichnium* ichnofacies. In the Middle Jurassic, fluctuating sea-levels exerted important controls on the distribution of theropod and pterosaur-dominated ichnofaunas associated with coastal plain and marginal marine settings. The Morrison ichnofauna is a reliable reflection of the body fossil record of that formation. Ongoing efforts to group and classify the various tetrapod ichnofaunas into tetrapod ichnofacies and tetrapod biochron categories have, in some cases, provoked stimulating, if sometimes inconclusive, debate.

### INTRODUCTION

The Jurassic of the Western Interior of the USA is historically famous for its Upper Jurassic dinosaurs and other tetrapods, collected for more than a century from the world famous Morrison Formation, which is widely distributed over several western states (Dodson *et al.*, 1980). However, the region has also become well-known for multiple reports of tetrapod ichnofaunas from at least six other track-rich formations including, in ascending stratigraphic order, the Wingate, Kayenta, Navajo, Carmel, Entrada and Summerville formations and their equivalents (Fig. 1). Unlike the fluvio-lacustrine Morrison Formation these other formations provide

widespread evidence of life in the various eolian and marginal marine paleoenvironments that prevailed throughout much of the Early and Middle Jurassic. The importance of these ichnofaunas in all these pre-Morrison deposits is that they occur in formations in which skeletal remains are rare if not almost completely absent. Thus they are, in conjunction with limited evidence of invertebrates, the main source of information on the tetrapod paleoecology. Here, we present a review of the footprint ichnofaunas known from all these formations, many of which are widely distributed in the western USA, between the Canadian and Mexican borders. Discussion of other vertebrate trace fossils such as burrows and coprolites is outside the scope of this paper.

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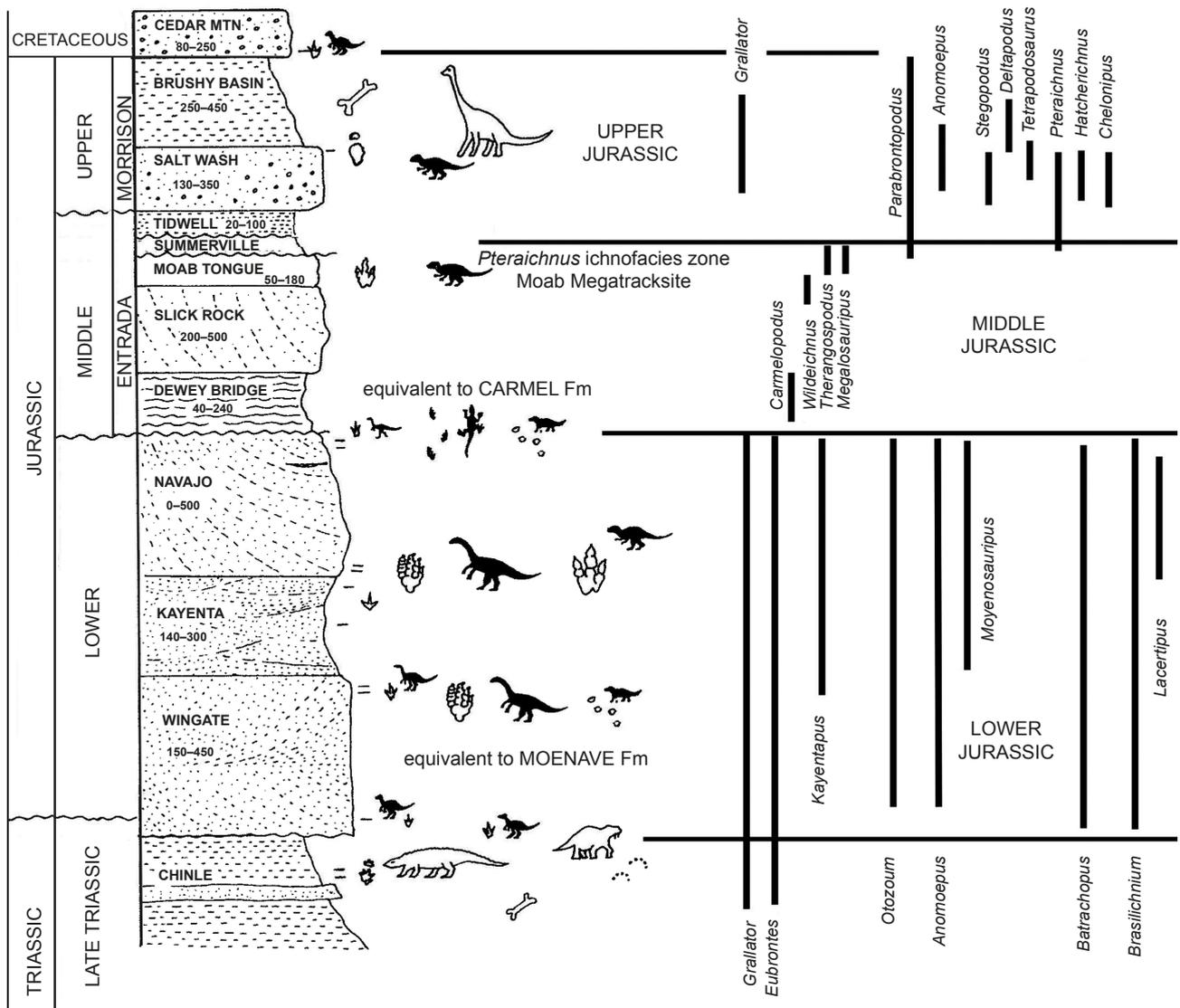


Fig. 1. Schematic representation of important track-rich formations and major ichnotaxa reported from the Jurassic of the Western Interior USA

Stratigraphic column (left) modified after Lockley (1991a, fig 8.2), with approximate stratigraphic ranges of key ichnogenera (right). Note that Lower, Middle and Upper Jurassic assemblages are quite distinct

In addition to describing the representative ichnofaunas known from each formation, we outline the implications they provide for understanding the paleoecology of these units. A synthetic understanding of these ichnofaunas is facilitated by three distinct approaches, recently discussed in the ichnological literature. These are in historical order of origination: the ichnofacies concept, which attempts to place distinct ichnofaunas in their paleoenvironmental context (Lockley *et al.*, 1994; Hunt, Lucas, 2007; Lockley, 2007), the classification of deposits by their relative richness in tet-

rapod body and/or trace fossils (Lockley, Hunt, 1994) and the biochron concept (*sensu* Lucas, 2007).

Lastly, we briefly compare the Jurassic ichnofaunas of the Western Interior USA with those reported from other regions. This exercise highlights two factors: first, the degree to which the Western Interior track record is relatively continuous and complete in comparison with other areas, and second, the global and inter-regional variation in ichnofaunal composition attributable to variation in facies, outcrop availability and preservation potential.

## LOWER JURASSIC TETRAPOD ICHNOFAUNAS OF THE WESTERN INTERIOR, USA

There are many reports of Lower Jurassic ichnofaunas from the western USA. These deal with literally hundreds of sites, especially in the Glen Canyon Group of Utah, Colorado and Arizona represented by the Wingate, Moenave, Kayenta and Navajo formations (Lockley, Hunt, 1995; Lockley *et al.*, 1998a, 2004, 2014a; Milner *et al.*, 2006a, b); see Lucas *et al.* (2006a, b) for a summary of relationship (equivalency) between the Wingate and Moenave formations with special reference to tetrapod ichnofaunas. These formations are represented by extensive eolian deposits, especially the Wingate and Navajo formations, but also pertain, more locally, to “silty” fluvio-lacustrine floodplain deposits. It is important to note that while the Glen Canyon Group is well differentiated into formations in some areas, in others it is undifferentiated. Body fossils are scarce, especially in the eolian facies, but tracksites are common in most facies.

### TETRAPOD ICHNOFAUNAS FROM THE WINGATE SANDSTONE

The Wingate Sandstone is well exposed in parts of western Colorado and eastern Utah, where it often forms sheer cliffs defining deep canyons. While such topography facilitates rock falls, which have exposed a number of relatively large track-bearing surfaces, the number of known *in situ* sites remains relatively small in comparison with those reported from other formations. Moreover, it has recently been established that in some regions the basal units of the Wingate Sandstone contain diagnostic Late Triassic tracks such as *Brachychirotherium* (Lockley *et al.*, 1992, 2004; Lucas *et al.*, 2006b), *Evazoum* (Lockley *et al.*, 2006a; Lockley, Lucas, 2013) and *Eosauropus* (Lockley *et al.*, 2006b, 2011a). Such information is only pertinent to the present discussion insofar as it helps define the ichnological base of the Jurassic. Moreover, these basal Wingate, or basal Glen Canyon occurrences not only represent Late Triassic trackmakers (Gaston *et al.*, 2003), but they also occur in localized non-eolian units within the Wingate.

Other than these examples, the main body of the Wingate Sandstone represents eolian paleoenvironments, with local intercalations of water-lain sediment representing only local flooding. The dominant ichnotaxa represent small theropods (cf. *Grallator*), small crocodylomorphs (*Batrachopus*) and small mammaliform trackmakers (cf. *Brasilichnium*). Some of the more abundant and better documented ichnofaunas come from the Gateway region of western Colorado close to the northeastern limit of well-exposed outcrops. Other simi-

lar ichnofaunas occur near Moab and the Circle Cliffs in Utah. Also from the Wingate of the Gateway area, Lockley *et al.* (2004) reported the earliest occurrence of ichnogenus *Otozoum*, which is usually attributed to a prosauropod. Thus, the ichnofauna from the Jurassic portion of the Wingate indicates the presence of theropod and prosauropod dinosaurs, crocodylomorphs and mammaliform trackmakers. With the exception of *Otozoum*, all represent relatively small trackmakers.

### TETRAPOD ICHNOFAUNAS FROM THE MOENAVE FORMATION

Generally speaking, the Moenave Formation is equivalent to the Wingate Formation (Lucas *et al.*, 2006a, 2011) where it represents a heterolithic, non-eolian facies representing fluvio-lacustrine sequence of mudstones, siltstones and sandstone, rich in tetrapod tracks, invertebrate traces and body fossils of vertebrates, invertebrates and plants. Like the aforementioned Wingate Sandstone, the Moenave Formation also spans the Jurassic-Triassic boundary. In recent years the St. George Dinosaur Tracksite in Washington County, Utah, has been the focus of much attention in the tetrapod ichnology community for its abundant fauna of dinosaur and other tetrapod tracks (Lockley *et al.*, 2004; Milner *et al.*, 2006a, b). These tracks include abundant examples of *Grallator*, *Eubrontes*, *Batrachopus* and hitherto undescribed *Sillimanius*- and *Stenonyx*-like forms. Of particular interest are abundant examples of well-preserved swim tracks attributed to the trackmakers of both *Grallator* and *Eubrontes* (Milner *et al.*, 2006b), but ichnologically referable to the “swim tracks” ichnogenus *Charaichnos* (Whyte, Romano, 2001). Despite the importance of the St. George tracksite for the size of the sample, quality of preservation and first report of *Charaichnos* and *Selenichnus* (Lockley *et al.*, 2004) from the southwestern USA, the more common ichnogenera (*Grallator*, *Eubrontes* and *Batrachopus*) had previously been reported from the region; see Olsen and Padian (1986) for first reports of *Batrachopus* from the Moenave in the southwestern USA.

Clearly the Moenave tetrapod ichnofauna is quite different from that of the Wingate Sandstone, which is representative of the *Brasilichnium* ichnofacies (cf., Lockley *et al.*, 1994) or *Chelichnus* ichnofacies (*sensu* Hunt, Lucas, 2007). In general terms the St. George ichnofaunas are very similar to the famous Connecticut valley ichnofaunas described by Hitchcock (1858) and Lull (1953) both in terms of quality of preservation and ichnotaxonomic composition. The main differences are that *Anomopus*, which is common in Connecticut, is rare in the Moenave of the St. George area. Conversely, swim tracks have only been reported comparatively rarely from Connecticut (Coombs, 1980). The now famous

St George Dinosaur Tracksite at Johnson Farm is in the Whitmore Point Member of the Moenave Formation, where multiple track-bearing levels have been recorded (Milner *et al.*, 2006a, b; Lucas *et al.*, 2011a). According to Lucas *et al.* (2011a) at least some of the lower levels may be latest Triassic in age.

### TETRAPOD ICHNOFAUNAS FROM THE KAYENTA FORMATION

The Kayenta Formation first became ichnologically “well known” when Welles (1971) named a large tridactyl theropod trackway as *Kayentapus* (see Lockley *et al.*, 2011a for review). Although similar to *Eubrontes* in general morphology, this relatively gracile track has been analyzed morphometrically by Weems (1992) who regarded the ichnogenus as valid and distinct from *Eubrontes*. This conclusion was further supported by Piubelli *et al.* (2005) who also recognized the validity of the ichnogenus and, in addition, identified it as globally widespread; *i.e.*, occurring in Europe and southern Africa as well as North America. It has also been reported from China (Xing *et al.*, 2013a, b).

A number of Kayenta Formation sites are known from which multiple trackways of large theropods are known. Many of these have been assigned to *Eubrontes*, which frequently co-occurs with *Grallator*. Such *Eubrontes*-dominated sites include the so called Desert Tortoise Sites from southwestern Utah (Lockley *et al.*, 2006c), and a number of sites from the Lake Powell area in south central Utah (Lockley *et al.*, 2014a). In the case of the Lake Powell tracksites, the majority occur in what Lockley *et al.* (2014a) refer to as the Kayenta-Navajo transition zone, which, according to Kirkland *et al.* (2011) occurs in the lower part of the Navajo Sandstone. Sites also occur in this transition zone in the Vermillion Cliffs area (Lockley *et al.*, 2006d). Regardless of the stratigraphic interpretation this zone is track rich throughout much of southern Utah, yielding *Eubrontes*, *Kayentapus*, *Grallator*, *Otozoum*, *Anomoepus*, *Moyenisauripus* and *Batrachopus*. For example, an *Otozoum*-dominated assemblage was recently reported from the Moab area (Lockley, Gierlinski, 2014). *Anomoepus* and *Moyenisauripus* have also been reported from both the Wingate-Kayenta transition and the Kayenta-Navajo transition (Lockley, Hunt, 1995; Lockley, Gierlinski, 2006; Lockley *et al.*, 2014a).

The Kayenta Formation lithofacies has traditionally been divided into a northern sandy facies and a southern silty facies (Harshbarger *et al.*, 1957; Sues *et al.*, 1994). As was the case in comparing the Wingate Sandstone and the age-equivalent, heterolithic silt- and mud-rich Moenave Formation, we find that the faunas and ichnofaunas are significantly dif-

ferent. All the aforementioned reports of sites revealing *Eubrontes*, *Kayentapus*, *Grallator*, *Otozoum*, *Anomoepus* and *Batrachopus* are associated with the northern sandy facies. In contrast the southern silty facies is not known for its track assemblages and instead is important for its vertebrate body fossils including diverse amphibian, turtle, sphenodontid, crocodylomorph, pterosaurian, dinosaurian and mammalian remains (Colbert, 1986). Among the dinosaurs, the theropod *Dilophosaurus* is well-known and often cited as a potential trackmaker of *Eubrontes* (Farlow, Galton, 2003). The ornithischian *Scutellosaurus* is a potential trackmaker for *Anomoepus*. The silty facies of the Kayenta Formation has also yielded important therapsid body fossils such as *Kayentatherium*, *Oligokyphus* and *Dinnetherium* (Jenkins *et al.*, 1983) that may be considered a potential trackmakers for a number of presumed mammaliform tracks found elsewhere in the Glen Canyon Group.

### TETRAPOD ICHNOFAUNAS FROM THE NAVAJO SANDSTONE

The Navajo Sandstone is the best known of the Glen Canyon Group formations, deriving its name from the geographical region surrounding Navajo Mountain, and the eponymous Native American lands known as the Navajo Nation situated in northeastern Arizona and adjacent parts of southeastern Utah and northwestern New Mexico. However, the Navajo Sandstone and its equivalents, known as the Nugget, or Navajo-Nugget Sandstone to the north, can be traced into northern Utah, southern Idaho, northwestern Colorado and southeastern Wyoming. To the west its equivalents, known as the Aztec Sandstone, can be traced into parts of southern Nevada and California. The Navajo Sandstone owes its global, geological fame to its status as one of the best examples of an eolian sand sea or erg deposit, preserving large scale fossil dunes that contribute to the spectacular landscapes in half a dozen national parks and monuments in the American Southwest. Despite the extensiveness of this deposit it has yielded very few body fossils other than the theropod *Segisaurus* (Camp, 1936), recently reported drepanosaurs (Chure *et al.*, 2013), tritylodontids (Winkler *et al.*, 1991), the crocodylian *Protosuchus* (Colbert, Mook, 1951), and the prosauropods *Ammosaurus* (Galton, 1971) and *Seitaaad* (Sertich, Lowen, 2010).

Tetrapod ichnofaunas from the Navajo Sandstone are well-known, diverse and in some cases have proved controversial. Stokes (1978) reported 12 tetrapod tracksites from the Navajo-Nugget that indicated that footprint sites were geographically widespread and indicative of significant tetrapod faunas, sometimes associated with fossil wood. He

implied that this was somewhat surprising, given that the deposit represents a desert erg system, presumed to be hostile to vertebrate life. He also noted that many of the tracksites known at the time represented mammalian or mammaliform trackmakers. However, in reference to one of the sites, near Moab, Utah, he and Jim Madsen reported that certain enigmatic tracks represented pterosaurs (Stokes, Madsen, 1979). As reviewed by Lockley and Hunt (1995) and Lockley (2011a) these tracks were subsequently referred to the crocodylomorph ichnogenus *Batrachopus* (Leonardi, 1987), and later to the mammalian ichnogenus *Brasilichnium* (Lockley, Hunt, 1995; Lockley, 2011a, b). In our opinion there is no evidence for pterosaur tracks from the Navajo Sandstone. Likewise, we are not convinced by reports of pterosaur tracks (cf. *Pteraichnus*) from the Aztec Sandstone of California (Reynolds, 2006a, b), which appear, like those from Moab, to be extramorphological variants of small mammaliform tracks (i.e., *Brasilichnium*), which show considerable extramorphological variation due to having been registered on sloping substrates, mainly dune foresets (McKee, 1944, 1947; Lockley, 2011a).

In addition to abundant reports of *Brasilichnium* from dune facies (Lockley, 2011a), and the aforementioned examples of its misidentification as *Batrachopus* or pterosaur tracks, *Batrachopus* does occur at a number of sites including some in the Lake Powell area of south central Utah (Lockley *et al.*, 2014a). However, it appears that *Batrachopus* is confined to horizontally bedded interdune beds, rather than dune facies. Likewise, *Eubrontes*, *Grallator* and *Anomoepus* tracks also occur abundantly in the interdune facies (Lockley, 2005; Lockley *et al.*, 2014a). Small theropod tracks are occasional found on sloping foreset surfaces (Rainforth, Lockley, 1996a, b). Very small grallatorid (about 5 cm long) tracks regarded by Lockley (2011b) as small *Grallator* were also alternatively labeled as *Stenonyx* by Gierliński and Niedźwiedzki (2002).

In general, the assignment of tracks such as *Eubrontes*, *Grallator* and *Anomoepus* from the interdune facies to appropriate trackmakers is easy because they are generally well-preserved. However, almost all tracks registered on the sloping surface of sand dunes show sub-optimal preservation (McKee, 1944, 1947). This accounts for the uncertainty surrounding the correct ichnotaxonomic assignment of small tracks, noted above; see Lockley (2011a) for likely synonymy of *Brasilichnium* and the oddly-named mammaliform tracks *Bipedopus* and *Semibipedopus* (Faul, Roberts, 1951; Haubold, 1971) and the aforementioned confusion between such mammaloid forms and *Batrachopus*. According to Haubold (1971) some of these small tetrapod tracks, which he named *Lacertipus*, are attributable to lacertoid trackmak-

ers. This conclusion was only tentatively accepted by Lockley and Hunt (1995), who considered that *Lacertipus* might be a preservational and/or behavioral variant of *Brasilichnium*. Recently Chure *et al.* (2014) have confirmed the earlier work of Albers (1975), who recognized a distinctive lacertoid form in the Nugget Sandstone of northeastern Utah, here regarded as equivalent to the Navajo Sandstone. Even though this form may be morphologically different from type *Lacertipus*, and imply a different trackmaker, it appears certain that lacertoid forms registered tracks in the Lower Jurassic dune facies.

Such uncertainty also affects the ichnotaxonomic labeling and inferred identity of the purported prosauropod track *Navahopus* (Baird, 1980). Lockley and Hunt (1995) considered *Navahopus* similar to, or not easily distinguishable from, a large mammaliform track. However, Rainforth (2003) and Hunt and Lucas (2006) considered it a prosauropod track, as originally proposed by Baird (1980). Ostensibly the prosauropod inference is supported by Milàn *et al.* (2008), who named another ichnospecies of *Navahopus* and attributed it to a prosauropod.

The most significant Navajo ichnogenus attributable to a prosauropod is *Otozoum*, first reported by Hitchcock (1847) from the Lower Jurassic of the Connecticut Valley region, and first identified in the western USA, in the Navajo Sandstone of eastern Utah (Lockley, 1990); see Lockley and Hunt (1995) for details. In contrast to *Navahopus*, which is relatively small, poorly preserved and associated with the dune facies, *Otozoum* is often large, well-preserved, with clear impressions of multiple digital pads, and almost invariably associated with the interdune ichnofacies. Assuming that both *Navahopus* and *Otozoum* are of prosauropod affinity, although Baird (1980), considered *Otozoum* crocodylian and Gierliński and Sabath (2008), inferred a basal ankylosaurian origin, it is notable that the smaller form represents a quadruped and the larger form is bipedal except in very rare instances (Rainforth, 2003; Lockley *et al.*, 2006a). This seems to be counterintuitive given that among sauropodomorphs larger forms are typically quadrupedal. Given the uncertainty surrounding *Navahopus*, and the small size of the available sample, it is not clear whether these differences in locomotion reflect significant differences in the identity of the trackmakers, differences in substrate slope and consistency or a combination of both factors.

Dune and interdune facies in the Navajo Sandstone are frequently characterized by quite different ichnotaxa: *Brasilichnium* and arthropod traces dominate the dune forests whereas the other ichnotaxa dominate the interdune facies, which in some cases have developed localized lenticular limestone deposits with algal laminae.

## MIDDLE JURASSIC TETRAPOD ICHNOFAUNAS OF THE WESTERN INTERIOR USA

The more important Middle Jurassic formations of the Western Interior are conveniently grouped into the San Rafael Group composed, in ascending order, of the Carmel, Entrada and Summerville formations and their equivalents (Fig. 1). In their basinal expressions most of these formations are marine, but all have marginal marine and onshore facies that have yielded important tetrapod ichnofaunas.

Two theropod track assemblages were reported from the Carmel Formation in northeastern Utah near Vernal (Lockley *et al.*, 1998b). In this region the Carmel Formation thins and onlaps eastwards from the basin and is probably Bathonian to Callovian in age (Kocurek, Dott, 1983; Peterson, 1994). Both track assemblages are essentially mono-ichnospecific, yielding small- to medium-sized tridactyl tracks that were named *Carmelopodus* (Lockley *et al.*, 1998b). These tracks differ from *Grallator* in lacking the trace of the posterior part of metatarsal IV, and having a wider digit divarication. A similar mono-ichnospecific *Carmelopodus* assemblage was reported from the Red Gulch assemblage from the Middle Jurassic (Bathonian), Canyon Springs Member of the lower Sundance Formation dated at approximately 167 Ma (Schmude, 2000; Kvale *et al.*, 2001; Breithaupt *et al.*, 2004). This discovery was surprising because previous paleogeographic maps indicated that the Red Gulch area was marine at this time. The latter authors claimed that track-bearing surfaces in this region constitute a megatracksite; however, the geographical extent of these track-bearing beds is relatively limited.

### TETRAPOD ICHNOFAUNAS FROM THE ENTRADA SANDSTONE

Until comparatively recently no vertebrate trace or body fossils were known from the Entrada Sandstone, and still only a single crocodylomorph body fossil, *Entradasuchus*, is known (Hunt, Lockley, 1995). This situation changed somewhat dramatically when it was recognized that theropod tracks were abundant at the top of the Moab Member, in a track rich zone referred to as the Moab Megatracksite (Lockley, Jennings, 1987; Lockley, 1991a, b, 1997). As reviewed by Lockley *et al.* (2007) the Entrada was traditionally divided, in ascending order, into the Dewey Bridge, Slick Rock and Moab Tongue members (Doelling, 1985). However, the Dewey Bridge is a silty facies equivalent to the Carmel Formation that has not yielded any tracks, and the Moab Tongue, an eolian facies like the Slick Rock Member, is now referred to by some workers as a member of the Curtis Formation (Doelling, 2001; Doelling *et al.*, 2002).

Preliminary reports of tracks were associated exclusively with the very top of the Moab Member (Lockley, Jennings, 1987; Farlow, Lockley, 1989; Lockley, 1991a, b), which yielded medium- and large-sized theropod tracks, respectively, assigned to the ichnogenera *Therangospodus* and *Megalosauripus* (Lockley *et al.*, 2000a, b). More than two dozen assemblages were recognized in association with the upper surface of this unit, which was shown to be track rich over an area of several hundred square kilometers, comprising the Moab Megatracksite. It is important to note that a megatracksite, as originally defined, is a “regionally extensive” track-bearing unit that can be correlated over 100s of km<sup>2</sup> (Lockley, Pittman, 1989). Moreover, from a genetic viewpoint, the megatracksite represents the reworking of the uppermost Moab Member by the transgression of the upper tongue of the Summerville Formation. Thus, although the tracks are “in” the uppermost layers of the Moab Member, they are arguably genetically related to the Summerville transgression, which, as shown below, is associated with its own distinctive tetrapod ichnofauna.

There have been three significant additions to these reports of the Moab Megatracksite assemblage consisting almost exclusively of *Megalosauripus* and *Therangospodus* co-occurrences. Following the discovery of further tracksites, in the topmost Entrada (Moab) Member, at the Twentymile Wash site near Escalante, Utah, far west of the Moab area (Foster *et al.*, 2000) as well as to the east and northeast (M. Lockley, unpublished data) it has been established that the megatracksite area is much larger, (more than several hundred square kms). Notwithstanding a few tracks reported up to 5 m below the Entrada (Moab Tongue)-Summerville contact, this is the best example of a Jurassic, single surface megatracksite in North America, possibly in the world (Lockley *et al.*, 2007). The first additional discovery was a single sauropod trackway found at the Twentymile Wash site to the west (Foster *et al.*, 2000). This report invites comparison with the second report of the only sauropod trackway from this level in the Moab area (M. Lockley, G. Gierliński, unpublished data). Second, and also of significance, is the report of a number of small theropod tracks (cf. *Wildeckhnus*) from the eolian facies of the Moab Member only a few meters vertically below the megatracksite assemblages (Lockley *et al.*, 2007). These small tracks are more typical of the diminutive dune faunas reported from the Navajo Sandstone and provide a facies-related contrast with the *Megalosauripus-Therangospodus* assemblage, which is associated with planar-bedded, ripple-marked, reworked sandstones associated with the transgression of the upper tongue of the Summerville. Thirdly, it is important to note that recent studies by Castenera *et al.* (2013) have made a marked distinction between North American type *Therangospodus*, from the Moab Megatracksite, and European *Therangospodus*,

from the basal Cretaceous of Spain, which has been shown in some cases to be of ornithopod affinity. Such reevaluation of the Spanish ichnites has implications for ichnotaxonomy, comparative analysis and correlation.

Other ichnites of similar morphology to *Carmelopodus*, but smaller, are reported from the upper part of the Moab Tongue, recently assigned to the Curtis Formation, but formerly considered part of the Entrada Formation (Lockley *et al.*, 2007). These footprints resemble the Middle Jurassic ichnogenus *Wildeichnus* originally recognized in Argentina and recently revised by de Valais (2011).

#### TETRAPOD ICHNOFAUNAS FROM THE SUMMERVILLE FORMATION AND EQUIVALENTS

Tetrapod ichnofaunas from the upper part of the Summerville Formation and its equivalents are among the most distinctive known from the Jurassic of the Western Interior. As summarized by Lockley *et al.* (1995, 2008a), these track assemblages are dominated by *Pteraichnus* tracks registered

in shallow marginal marine facies associated with a large marine embayment (Fig. 2). For historical reasons *Pteraichnus* has proved to be a controversial ichnogenus because of debates about the affinity of the trackmaker. Stokes (1957) correctly identified the track maker as pterosaurian despite dissenting views by Padian and Olsen (1984). Currently, however, there seems little doubt that *Pteraichnus* is pterosaurian (Lockley *et al.*, 1995, 2008a; Mazin *et al.*, 1995) and that the ichnogenus occurs widely in Colorado, Utah, Arizona, Wyoming and Oklahoma. Many of the occurrences are associated with the upper tongue of the Summerville Formation or equivalent deposits: *e.g.*, the Bell Ranch (= Summerville) Formation in southeastern Colorado, and the Windy Hill Member of the Sundance Formation in Wyoming (Meyers, Breithaupt, 2014). In Oklahoma, *Pteraichnus* occurs in the basal Morrison Formation (Lockley *et al.*, 2001), as was the case with the report of Stokes (1957) from the Four Corners area. Theropod tracks are associated with *Pteraichnus* in a few assemblages (Mickelson *et al.*, 2004) and include morphotypes placed in the ichnogenera *Therangospodus* and *Megalosauripus*.

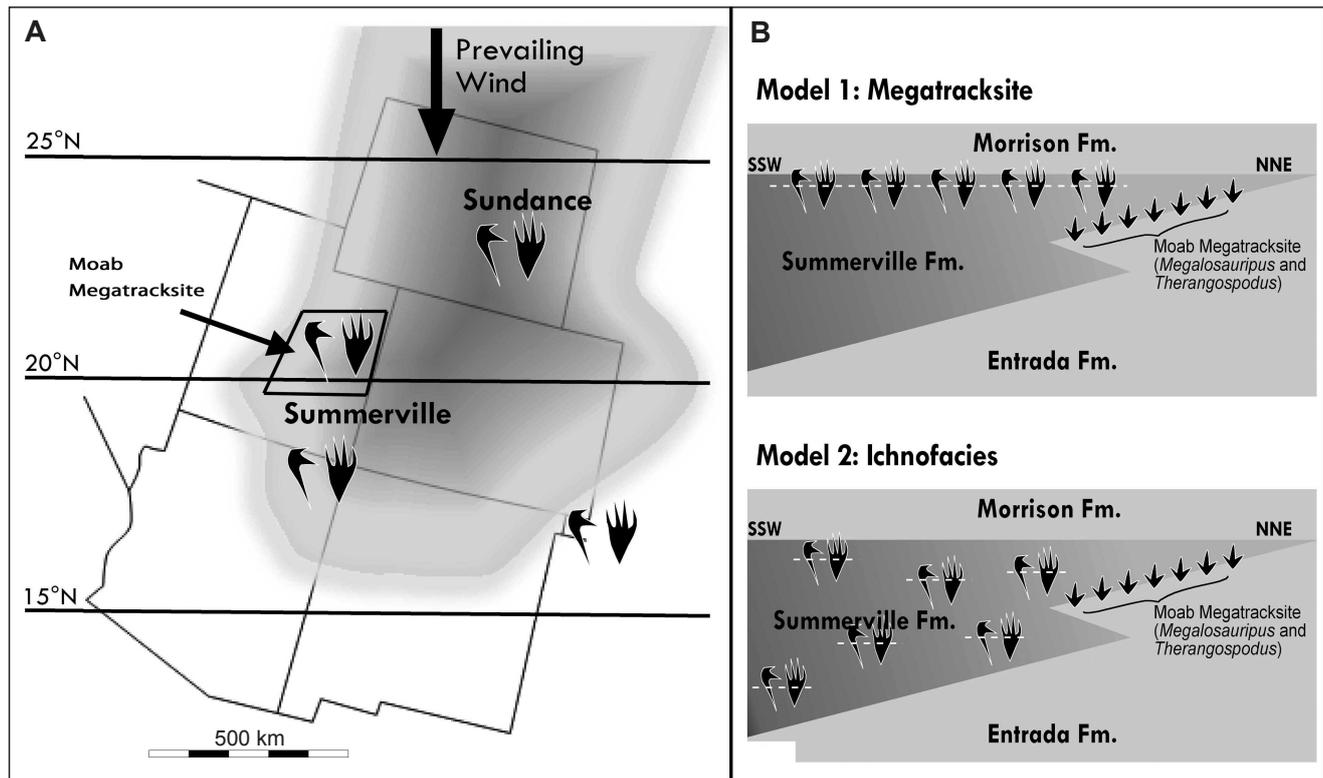


Fig. 2. The distribution of pterosaur tracks in the late Middle to early Upper Jurassic of the Western Interior, after Lockley *et al.* (2008a)

A. Shows the development of a shallow marine embayment associated with deposition of the upper tongue of the Summerville Formation and its equivalents, with the approximate geographical extent of the Moab Megatracksite. B. Shows the contrasting megatracksite and ichnofacies models of pterosaur track distribution discussed by Lockley *et al.* (2008a)

This association of *Pteraichnus* with the *Megalosaurus-Therapsodus* assemblage of the Moab Megatracksite has raised questions about the distribution of pterosaur tracks in relation to the theropod-track-dominated megatracksite. Clearly pterosaur tracks occur in the shallow marine facies that immediately overlie the theropod track assemblages which occur in the reworked sands that form the uppermost units of the Moab Tongue. Clearly, also, as the transgression progressed the distribution of tracks at the Entrada-Summerville interface, as well as in overlying shallow marine sediments were to some degree diachronous, even though, in the case of the interface zone, the track-bearing layers essentially appear to represent a single surface. However, the geographical distribution of pterosaur tracks is reported over a much larger area than the Moab Megatracksite (Fig. 2). Lockley *et al.* (2008) proposed two possible models for the distribution of the pterosaur tracksites. The first envisages the pterosaur tracks confined to a relatively narrow stratigraphic zone, overlying the Moab Megatracksite zone; in effect a *Pteraichnus* megatracksite. The second envisages pterosaur tracks more widely distributed throughout the upper tongue of the Summerville and its equivalents; *i.e.*, an ichnofacies model (*cf.*, Lockley, 2007). The Tidwell Member, formerly considered by some workers as part of the Morrison Formation, is here considered part of the Summerville Formation (McKnight, 1940; Anderson, Lucas, 1992, 1997).

## UPPER JURASSIC TETRAPOD ICHNOFAUNAS OF THE WESTERN INTERIOR, USA

### TETRAPOD ICHNOFAUNAS FROM THE MORRISON FORMATION

Morrison Formation facies and ichnofaunas are quite variable and in some places the transition into basal Morrison units from the underlying Summerville Formation or its equivalents (*e.g.*, Tidwell Member) is not lithologically well-defined. Thus, pterosaur track assemblages occur in the Summerville Formation in southeastern Colorado and in the Morrison Formation at a nearby locality in western Oklahoma (Lockley *et al.*, 2001) and at a site in Arizona (Lockley, Mickelson, 1997). However, generally speaking, the Morrison ichnofaunas are distinct and associated with distinctive fluvio-lacustrine facies. Among the most distinctive ichnofaunal elements reported from the Morrison Formation are crocodylian and turtle tracks (Foster, Lockley, 1997; Foster *et al.*, 1999; Lockley, Foster, 2006), neither of which are found in any of the aforementioned Lower and Middle Jurassic ichnofaunas, though they occur relatively abundantly in the Cretaceous of the Western Interior. The typical

crocodylian ichnogenus is *Hatcherichnus* (Foster, Lockley, 1997), and the typical turtle ichnogenus is *Chelonipus* (Lockley, Foster, 2006).

East of the continental divide the Morrison Formation is generally undifferentiated, whereas to the west it is widely differentiated into two units, a basal sandstone-dominated sequence known as the Salt Wash Member and the overlying mud-dominated Brushy Basin Member. Anderson and Lucas (1992, 1997) include the Tidwell Member of the Morrison Fm. in the Summerville, as originally done by McKnight (1940). Generally speaking, although Morrison Fm. tracksites are quite widely distributed, most are small and have yielded relatively small assemblages consisting of sauropod and theropod tracks (Foster, Lockley, 2006). Moreover, efforts to discern any clear patterns of distribution of ichnotaxa that relate to stratigraphy, paleolatitude or facies within the Morrison Formation have proved largely unsuccessful (Foster, Lockley, 2006). In general, however, the ichnofaunas are saurischian dominated with only relatively few reports of ornithischian ichnites, including *Dineichnus*, an *Anomoepus*-like form (Lockley *et al.*, 1998c), *Stegopodus* (Lockley, Hunt, 1998; Gierliński, Sabath, 2008; Mossbrucker *et al.*, 2008), *Deltapodus* (Milàn, Chiappe, 2009) and a *Tetrapodosaurus*-like form (Lockley *et al.*, 2014b).

The largest dinosaur tracksite in the Morrison Formation is the Purgatoire Valley tracksite of southeastern Colorado, also known as the Picketwire tracksite (Lockley *et al.*, 1986, 1997) where more than 1300 footprints have been reported from four stratigraphic levels, mostly from bed 2, which reveals multiple parallel sauropod trackways, including the narrow gauge morphotype *Parabrontopodus mccintoshi* (Lockley *et al.*, 1994). The site is notable for representing a carbonate lake basin with body fossil evidence of fish, snails, crustaceans, charophytes, horsetails and clams trampled by sauropods. Recently an enlarged area of bed 2 has been exposed and mapped to show additional sauropod and theropod tracks (Schumacher, Lockley, 2014).

## DISCUSSION

There are various precedents for discerning patterns of distribution in the Jurassic ichnofaunas of the Western Interior. These are as follows:

Ichnofaunas may be placed in one of eight categories defined by Lockley (1991a) and Lockley and Hunt (1994), which categorize formations by the relative abundance of tetrapod body and trace fossil assemblages and the degree to which they represent similar or different faunas. This method essentially compares the track record with the body fossil record.

Ichnofaunas may be regarded as a more or less facies-related allowing for the definition of vertebrate or tetrapod

ichnofacies (Lockley *et al.*, 1994; Hunt, Lucas, 2007; Lockley, 2007).

Ichnofaunas may represent temporal biochrons of global significance (*sensu* Lucas, 2007).

Attempts have also been made to compare specific Western Interior ichnofaunas with those from other regions usually on a formation-by-formation or ichnofacies by ichnofacies basis (Lockley *et al.*, 2008a).

Here we briefly review each of these methods of categorization of the Jurassic Western Interior ichnofaunas, in the light of present knowledge.

## TRACKS V. BODY FOSSIL RECORDS

As implied above all the major Jurassic formations from the western USA, including many predominantly marine formations that have marginal marine facies, yield significant tetrapod ichnofaunas (Table 1). Moreover, using the scheme proposed by Lockley (1991a) and Lockley and Hunt (1994) in which formations are categorized according to the relative abundance of tetrapod body and trace fossil assemblages it is clear that the majority of Jurassic formations in this region fall in category 1 (tracks only) or category 2 (tracks far more abundant than bones). In contrast, few formations fall in categories 3, 4 or 5 where tracks are as abundant, or more abundant than bones.

These results are striking because they highlight the importance of tracks in filling in an otherwise very incomplete tetrapod body fossil record. For example, as shown in Table 1, three of the nine terrestrial stratigraphic units discussed (Wingate, Kayenta sandy facies and Carmel) fall into category 1 because they have yielded no tetrapod body fossils. Two others (the Entrada Formation and the Tidwell Member of the Summerville Formation) have yielded only very rare tetrapod body fossils generally inconsistent with the track record, thus technically placing them in category 2b, rather than category 1. Likewise, the Navajo Sandstone is predominantly a category 1 deposit, but due to a small number of body fossils which are consistent with the track record, it is classed as a category 2a deposit. Only the silty facies of the Kayenta Formation, the Moenave Formation and the Morrison Formation, which all share certain fluvio-lacustrine and paleosol facies similarities, can be classed as type 3 or 4 deposits (Table 1). These observations divide the Jurassic successions of the Western Interior into two broad categories of which the first, the track-dominated units (categories 1 and 2) make up the greater portion (6 of 9 units) whereas the second, the body-fossil-dominated units (categories 3 and 4) make up a lesser portion of the successions. There are no category 5 (bones only) deposits. As noted below these differences are facies-related to varying degrees.

## TETRAPOD ICHNOFACIES IN THE JURASSIC OF THE WESTERN INTERIOR

Table 1 serves to demonstrate that there are three important eolian units in the Jurassic successions of the Western Interior. These are the Wingate, Navajo and Entrada sandstones. All have quite similar ichnofaunas dominated by synapsid tracks (*Brasilichnium*) and small theropod tracks in the case of the dune facies of the Wingate and Navajo sandstones, and small theropod tracks in the case of the Entrada Sandstone. The Navajo has a significant number of assemblages associated with inter-dune facies in which large theropod (*Eubrontes*) and large prosauropod (*Otozoum*) tracks occur, often in association with *Grallator*, and sometimes in association with *Anomoepus* or *Moyenisauropus*. Large theropod tracks (*Megalosauripus* and *Therangospodus*) also occur, recurrently, in the uppermost reworked units of the Entrada where they form the Moab Megatracksite complex associated with the onset of the transgressive upper tongue of the Summerville. Because of the recurrence of *Megalosauripus* and *Therangospodus* in similar facies they constitute a distinctive ichnocoenosis or ichnofacies, as discussed below.

The dune facies has been referred to as the *Brasilichnium* ichnofacies (Lockley *et al.*, 1994) and is very similar to Late Paleozoic dune assemblages referred to as the *Chelichnus* ichnofacies (Hunt, Lucas, 2007). No definitive study has yet been undertaken to compare and contrast these two ichnogenes in detail. Both ichnofacies contain almost identical arthropod (spider and scorpionoid) tracks, and as noted by Lockley (2007) the dune ichnofacies, defined on the basis of arthropod traces, is co-extensive with the dune facies defined on the basis of tetrapod tracks. However, Hunt and Lucas (2007) draw a distinction between what they refer to as archetypal or global tetrapod ichnofacies and what they refer to as various component ichnocoenoses. Thus, they regard the *Brasilichnium* ichnofacies as an ichnocoenosis *within* the conceptually larger *Chelichnus* ichnofacies. We regard this distinction as somewhat academic for three reasons. First the concept of archetypal tetrapod ichnofacies (*sensu* Hunt, Lucas, 2007) is based on archetypal, global or Seilacherian invertebrate ichnofacies models, whose relevance to tetrapod ichnofacies models is a matter of debate (Lockley, 2007). Second, various workers (*e.g.*, Bromley, 1996) recognize other ichnofacies categories besides the large-scale global or archetypal variety (see below). Third, subsuming the Mesozoic *Brasilichnium* ichnofacies into the *Brasilichnium* ichnocoenosis within the *Chelichnus* ichnofacies, leads to a rather cumbersome duplication of terminology and the potential for ichnologists to infer that the Paleozoic ichnogenus *Chelichnus* occurs in the Mesozoic or even the Cenozoic, which due to the lack of detailed study has not been demonstrated. As

**Table 1**

**Characterization of major tetrapod track-bearing formations in the Jurassic of the Western Interior in terms of the relative abundance and importance of tetrapod trace and body fossils**

Formation	Track vs. body fossil category	Age	Facies
Morrison	4a-3a	Upper Jurassic	fluvio-lacustrine
Summerville including Tidwell Member	2	Middle to Upper Jurassic	marginal marine (& lagoonal)
Entrada	1-2b	Middle Jurassic	eolian
Carmel	1	Middle Jurassic	marginal marine
Navajo	1-2a	Lower Jurassic	eolian
Kayenta (silty facies)	4a-4b	Lower Jurassic	fluvio-lacustrine
Kayenta (sandy facies)	1	Lower Jurassic	eolian-fluvial
Moenave	3a	Lower Jurassic	fluvio-lacustrine
Wingate	1	Lower Jurassic	eolian

Five point scheme after Lockley (1991a) and Lockley and Hunt (1994) includes formations with only tracks (category 1), with tracks > body fossils (2), tracks = body fossils (3), tracks < body fossils (4) and body fossils only (5). Categories 2–4 includes sub-categories that indicate whether trace and body fossils record similar (a) or different (b) faunas. Note that the silty and sandy facies of the Kayenta Formation are treated separately

noted below, this problem is potentially more confusing and acute with some of the other archetypal ichnofacies labels proposed by Hunt and Lucas (2007).

For the purposes of historical consistency we note that in addition to the *Brasilichium* ichnofacies (Lockley *et al.*, 1994; Lockley, 2007) the only other ichnofacies originally identified in Jurassic of the Western Interior was the *Pteraichnus* ichnofacies initially identified in shallow marginal marine clastic facies, but also locally recognized in shallow marine carbonate ichnofacies (Lockley *et al.*, 2001). Hunt and Lucas (2007) regard these as ichnocoenoses (not ichnofacies) and state that they are unsure where these fit in their ichnofacies scheme.

Hunt and Lucas (2007, p. 66) proposed the *Eubrontes* ichnocoenosis as a subcategory of their *Grallator* ichnofacies and identify it as occurring in the Western Interior Jurassic, specifically in the lacustrine portion of the Glen Canyon Group (interdune parts of the Navajo Sandstone) and in the non-lacustrine Entrada Megatracksite. While we can accept, in principle, as noted above, that recurrent interdune and/or lacustrine margin *Grallator-Eubrontes* assemblages rise to the status of an ichnocoenosis or ichnofacies, given the supposed facies relationship between *Grallator* and lacustrine margins (Hunt, Lucas, 2007), it is somewhat inconsistent to include the *Megalosauripus-Therangospodus* assemblages from coastal plain facies in the *Grallator* ichnofacies (or *Eubrontes* ichnocoenosis), either on the basis of arguments per-

taining to facies or ichnotaxonomy. In fact these authors cite “the Middle Jurassic Entrada megatracksite” as a “non-lacustrine” exception. Hunt and Lucas (2007) include shore-bird assemblages from the Cretaceous and Cenozoic in the *Grallator* ichnofacies, because of the morphological similarity between avian and non avian theropods and their affinity to lake margin settings. This would make Holocene hominid tracks from the shores of Lake Managua (Lockley *et al.*, 2009) part of the *Grallator* ichnofacies (*sensu* Hunt, Lucas, 2007), whereas late Pleistocene hominid and bird tracks from marginal marine deposits in Korea (Kim *et al.*, 2009) would be part of their *Brontopodus* ichnofacies. By contrast the sauropod-theropod track assemblages from the Purgatoire Valley lake facies would not be part of the *Brontopodus* ichnofacies (originally defined as an association of sauropod and theropod tracks with carbonate substrates), but instead would be part of the *Grallator* ichnofacies. The reader may wish to refer to the discussion below to evaluate the merits of broadly (globally) or more narrowly (regionally or locally) defined ichnofacies.

Similar problems arise with the *Charaichnos* ichnofacies proposed by Hunt and Lucas (2007), which was created to subsume shallow lacustrine swim trace assemblages. They consider the turtle and crocodylian swim tracks assemblages from fluvial channels, noted above, to represent the *Hatcherichnus* ichnocoenosis within the *Charaichnos* ichnofacies. However, as noted previously *Pteraichnus* swim tracks

assemblages are associated with shallow marine facies, as are marine turtle swim tracks associated with carbonate platforms (Galliard *et al.*, 2003). Thus, swim tracks are associated with many different paleoenvironments (lacustrine, fluvial and marine), and cannot all be placed in the *Charachichos* ichnofacies if, as defined by Hunt and Lucas (2007), it exclusively represents shallow lacustrine settings.

In short, we consider the so-called archetypal or universal tetrapod ichnofacies of Hunt and Lucas (2007) rather too broadly defined on the one hand, and on the other too narrowly associated with a limited number (5) of specific paleoenvironmental categories (*e.g.*, lacustrine margin, shallow lacustrine). Their identification of relatively diverse and widespread tetrapod ichnocoenosis, contrasts with their short list of only five ichnofacies, suggesting that the latter classification is rather too generalized and restricted to reflect the many recurrent facies-related track assemblages found throughout the track record. In short, tetrapod ichnofacies are significantly different from invertebrate ichnofacies, and more diverse, and we suggest these differences should be reflected in a more differentiated concept of tetrapod ichnofacies (Lockley, 2007).

Santi and Nicosia (2008, p. 223) summarized the debate over vertebrate ichnofacies concluding that the previous studies (Lockley *et al.*, 1994; Hunt, Lucas, 2007; Lockley, 2007) were inconsistent due to “different definitions and formalizations” which have led to two opinions which they consider inadequate. But the debate is not simply over two options, nor is there necessarily a need for a single inviolate definition. The problem, as noted by Bromley (1996, p. 209) is “chiefly one of scale.” Bearing in mind that Bromley’s focus was on invertebrate ichnofacies and ichnocoenoses, he pointed out that some authors have suggested the fossil equivalent of an ichnocoenosis (originally defined as an association of traces that can be related to a definite biocoenose, or living community) is an ichnofacies (Dorjes, Hertweck, 1975). This problem of scale was unambiguously addressed by Bromley (1996) in reference to invertebrate ichnofacies when he distinguished between large- or global-scale (archetypal or Seilacherian) ichnofacies, medium-scale ichnofacies which are a subset of global ichnofacies and smaller-scale ichnofacies “useful in defining locally recurring rock facies on the basis of their contained trace fossil assemblages.” Thus, Bromley’s categories are at variance with that of Hunt and Lucas (2007, p. 59), who only recognized one type or scale of ichnofacies (tetrapod ichnofacies) equivalent to the global or archetypal ichnofacies. This boils down to stating that the original definition of vertebrate ichnofacies (Lockley *et al.*, 1994) is consistent with historical precedent inherited from vertebrate ichnology, providing they are not conceptually labelled only as examples of global or archetypal ichnofacies. Likewise, the definition of

ichnofacies by Hunt and Lucas (2007) is consistent with the concept of global and archetypal ichnofacies, but does not encompass ichnofacies identified (named) at smaller, non-global scales (which they label as ichnocoenoses in all non-global instances). Lockley (2007, p. 39) argued that “tetrapod ichnofacies are inherently more diverse and differentiated than invertebrate ichnofacies” being based, as agreed by Hunt and Lucas (2007) on biotaxa (biotaxon ichnofacies) rather than ethology (ethoichnofacies). We argue that a single definition of ichnofacies, synonymous with global or archetypal ichnofacies, is too broad to be applied to the entire ichnological record (invertebrate and vertebrate), without such categories necessarily having to include (or omit) many previously named ichnofacies and ichnocoenoses which are too differentiated and / or facies independent to fit in such broad global categories. Finally as noted by Bromley (1996) and by others (Hunt, Lucas, 2007; Lockley, 2007) the ichnofacies debate is inherently complex. The distribution of traces in relation to facies, and the relationship of such distributions to living communities, is by no means easily discerned from the fossil record. However, it is clear that in some cases vertebrate trace fossil–facies relationship patterns are readily recognizable on various scales. Thus, the use of ichnocoenosis and ichnofacies terminology is justified, even if the definition of such categories is still vigorously debated.

## ICHNOFAUNAS AND GLOBAL BIOCHRONS

Lucas (2007) proposed a very simple biochron scheme for the Jurassic based on the ichnotaxonomic composition of global ichnofaunas. He recognized a single Lower Jurassic biochron characterized by the ichnogenera *Grallator*, *Eubrontes*, *Anomoepus*, *Moyenosauripus*, *Otozoum* and *Batrachopus*. As noted above, these six ichnogenera occur in most of the stratigraphic units of the Glen Canyon Group, especially the interdune assemblages. Most elements of this assemblage are widely known from eastern North America, Europe parts of Asia and southern Africa, and so represent a global ichnofauna, albeit with these ichnotaxa only sporadically reported from many southern hemisphere regions. Hence we are in general agreement that the Lower Jurassic biochron is readily recognized as an ichnotaxonomic assemblage, which in the Western Interior is characteristic of much of the Glen Canyon Group. *Brasilichnium* from the dune facies is the only ichnogenus commonly found in this group that is not found elsewhere in other coeval biochron assemblages from North America, Europe and Asia. The same inference applies to *Navahopus*, which is evidently known only from the eolian facies of the Western Interior, where it is rare in comparison with *Brasilichnium*. These examples simply show that there are slight regional differences

in the composition of biochron assemblages due to facies differences and other paleogeographical and paleobiological influences. For example *Otozoum* is rare or unknown as a component of the Lower Jurassic biochron assemblages outside North America.

Lucas (2007) places all Middle and Upper Jurassic ichnofaunas, including those from the Western Interior, in a single Middle and Upper Jurassic biochron. He stated (Lucas, 2007, p. 21) that “The Middle and Late Jurassic footprint record... is a global record dominated by large theropod and sauropod tracks. It may be possible, with a more extensive Middle Jurassic footprint record, to separate the Middle and Late Jurassic into separate assemblages, but for now I combine them into a single global assemblage.” While we accept that the global prevalence of theropod and sauropod tracks may blur the distinction between Middle and Upper Jurassic track assemblages on a global scale, in the Western Interior it is much easier to distinguish Middle from Upper Jurassic assemblages. As noted above the *Carmelopodus*, and *Megalosauripus* plus *Therangospodus* assemblages from marginal marine facies as well as the small theropod (cf. *Wildeichnus*) assemblage from the eolian Moab Tongue Member of the Entrada Fm. (or Curtis of Doelling, 2001; Doelling *et al.*, 2002), and the *Pteraichnus* assemblages from the upper tongue of the Summerville Formation (Fig. 2) represent four distinct Middle to ?basal Upper Jurassic ichnofaunas that are quite distinct from the Morrison ichnofaunas. With two exceptions (in a sample of at least 30 sites), pertaining to the Moab Megatracksite complex, sauropod trackways are absent from these four ichnofaunas. Three of these ichnofaunas represent coastal plain marginal marine environments, and the fourth represents eolian dunes. Since these four ichnofaunas are distinctive ichnotaxonomically and represent four different paleoenvironments, they do not naturally group into a single Middle Jurassic biochron assemblage in this region. Thus, we treat the Middle and Upper Jurassic tetrapod ichnofaunas of the Western Interior as “separate” assemblages recognizing that, for this region, the Middle Jurassic assemblages comprise four discrete assemblages, corresponding to distinct facies, whereas the Upper Jurassic (Morrison) ichnofauna represents a single much more homogeneous facies-related assemblage.

Thus, in contrast to the four Middle Jurassic ichnofaunas from the Carmel, Entrada and Summerville formations the Morrison Fm. ichnofaunas represent a single more or less coherent assemblage associated with a fluvial-floodplain and lacustrine facies complex. The ichnofauna is diverse consisting not only of theropod and sauropod tracks which Lucas (2007) considers typical of his Middle to Late Jurassic biochron, but also containing diverse ornithischian tracks as well as pterosaur, crocodylian and turtle tracks. Again the differences are facies related to various degrees.

## COMPARISON OF WESTERN INTERIOR ICHNOFAUNAS WITH THOSE FROM OTHER REGIONS

As noted above, Lower Jurassic tetrapod ichnofaunas from the Western Interior are very similar to those from the Newark Supergroup of eastern North America where most of the distinctive ichnogenera were first defined (Lucas, 2007 and references therein). Thus global correlations appear relatively convincing and reliable. Recent efforts to eradicate a large number of ill-conceived, “provincial” Lower and Middle Jurassic theropod track ichnotaxa proposed by Chinese workers has also demonstrated that the majority of named Lower Jurassic tracks from Asia belong to the typical *Eubrontes-Grallator* dominated assemblages well-known from North America (Lockley *et al.*, 2013).

However, while attempts have been made to correlate Middle Jurassic tetrapod ichnofaunas from the Western Interior with those reported from other regions, the correlations are somewhat less robust. For example it has been tentatively suggested that *Carmelopodus* occurs in the Middle Jurassic of Europe (Lockley *et al.*, 2000b) and North Africa (Gierliński *et al.*, 2009). However, attempts to correlate the ichnites labeled as *Megalosauripus* and *Therangospodus* between North America and other regions have been compromised by some uncertainty regarding the ichnotaxonomic status of these ichnogenera: *i.e.*, the status of the ichnogenus *Megalosauripus* has been much debated (Lockley *et al.*, 1996; Lockley, Meyer, 2000; Thulborn, 2001) and the validity of European *Therangospodus* has also recently been questioned (Castenera *et al.*, 2013).

As noted above comparisons between the Upper Jurassic ichnofaunas of the Morrison Formation and those from the Upper Jurassic of Europe, especially the Iberian peninsula, have highlighted many similarities in both ichnotaxonomic composition and general diversity (Lockley *et al.*, 2008b; Lockley, 2009). We may conclude therefore that the Jurassic tetrapod ichnofaunas of Western Interior are useful for comparative analysis and important as part of the global picture.

## CONCLUSIONS

The Jurassic tetrapod ichnofaunas of the Western Interior are of considerable importance globally. Most of the classic Lower Jurassic (Liassic) ichnofaunas originally reported from the Newark Supergroup of eastern North America have been identified from the Glen Canyon Group in the western USA. In addition, *Navahopus* was first defined from the eolian facies of this region. Synapsid tracks (*Brasilichnium*) are also common in the Lower Jurassic eolian facies giving insight into the distinctive ecology of the vast sand sea facies of this region (Shibata *et al.*, 2006). The South African

ichnogenus *Moyenosauripus*, also known from Europe, but not reported from the Eastern USA, is also known from the Glen Canyon Group (Lockley, Gierlinski, 2006), and in the silty facies of the Moenave abundant theropod swim tracks (*Charcihnos*) are reported (Milner *et al.*, 2006b).

Many distinctive of Middle to Late Jurassic ichnotaxa including *Carmelopodus*, *Therangospodus* and *Pteriachnus* were first reported from the Western Interior, and have been subsequently identified elsewhere. In the case of all three of these ichnogenera, they occur in marginal marine deposits which have yielded no tetrapod body fossils, and would otherwise be considered barren. However, in all cases the tracks occur in units that have basinal equivalents with datable marine fossils. Thus, they give valuable insight into the terrestrial faunas and ecology of the region (coastal habitats) at this time, and demonstrate that there were significant changes in the tetrapod faunas between the Early and Middle Jurassic. The influx of pterosaurian trackmakers (*Pteraichnus*) in the latest Middle Jurassic to earliest Late Jurassic is particularly striking and relates to the large marine embayment that was established at this time (Fig. 2). Moreover, since 1995 the study of *Pteraichnus* has established beyond doubt that this previously controversial ichnogenus provides multiple insights into the behavior, paleoecology and distribution of pterosaurian trackmakers (Lockley *et al.*, 1995, 2008a and refs therein).

It is arguable that the Upper Jurassic ichnofaunas reported from the Morrison Formation have added relatively little new information to that inferred from the body fossil record obtained from the Western Interior. However, there are indications that the newly obtained record of thyreophoran tracks (*Stegopodus*, *Deltapodus* and *Tetrapodosaurus*) are providing us with new insights into the size and morphology of these trackmakers, which supplement the information obtained from the body fossil record.

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