THE TRIASSIC TETRAPOD TRACK RECORD: ICHNOFAUNAS, ICHNOFACIES AND BIOCHRONOLOGY

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Abstract—Triassic tetrapod tracks have long been studied, including classic ichnofaunas such as those of the lower Newark Supergroup of eastern North America and the Buntsandstein of central Europe. They are known from all seven continents and encompass five archetypal vertebrate ichnofacies for nonmarine environments (Chelichnus, Grallator, Batrachichnus, Brontopodus, Characichnos), all of which are present in the Triassic: (1) Chelichnus ichnofacies – Brasilichnus ichnocoenosis; (2) Grallator ichnofacies – Grallator ichnocoenosis; (3) Batrachichnus ichnofacies – Chirotherium and Apatopus ichnocoenoses; (4) Brontopodus ichnofacies – Dicynodontipus, Therapsipus, Brachychirotherium and Evazoum ichnocoenoses; and (5) Characichnos ichnofacies – unnamed ichnocoenosis. There are five temporal subdivisions of the Triassic that can be recognized based on tetrapod tracks: (1) earliest Triassic – dicynodont tracks; (2) Early-Middle Triassic (Olenekian-early Anisian) – chirothere-(archosaur-) dominated assemblage; (3) late Middle Triassic (late Anisian-Ladinian) – dinosauromorph assemblage; (4) early Late Triassic (Carnian-early Norian) – tridactyl dinosaur assemblage; and (5) late Norian-Rhaetian – sauropodomorph track assemblage.

INTRODUCTION

Triassic tetrapod tracks are among the longest studied and the best known tetrapod footprints and they include the classic ichnofaunas of the Chine Group of the American Southwest, the lower Newark Supergroup of eastern North America and the Buntsandstein of central Europe (Hunt and Lucas, 2006b; Lucas, 2007). There is thus a very large database of Triassic tetrapod tracks, which are known from six continents (North America, South America, Europe, Asia, Australia, Antarctica: Fig. 1). Lucas (2006) recently provided a synthesis of the biochronology and biostratigraphy of these ichnofaunas, and Hunt and Lucas (2007b) reviewed the tetrapod ichnofacies of the Triassic. The purpose of this paper is to provide an overview of the Triassic track record — its extent, ichnofacies and biochronology.

TRIASSIC TETRAPOD TRACK RECORD

Introduction

The first Triassic tetrapod tracks were described by Sickler (1834, 1835) from the upper part of the Buntsandstein (Olenekian) near Hildburghausen (Thuringia, Germany). Subsequently, Kaup (1835a, b) named these tracks Chirotherium barthii and Chirotherium sickleri, which became the first published binoms of tetrapod tracks.

Triassic tetrapod tracks are now known from North America, South America, Europe, North Africa, Australia, Antarctica and South Africa (Fig. 1). The Triassic track record is archosaur- and synapsid-dominated and includes the oldest dinosaur tracks. The oldest footprints attributed to mammals are also of Late Triassic age, but they are rare (Sarjeant, 2000). The following review is principally based on Lucas (2007) and Hunt and Lucas (2006b).

Earliest Triassic

The oldest Triassic tetrapod tracks are dicynodont footprints from the Karoo basin in South Africa (Watson, 1960), the Fremouw Formation of Antarctica (MacDonald et al., 1991) and the Sydney basin in Australia (Retallack, 1996).

Early Triassic-early Middle Triassic

The best known Triassic footprint assemblage is of late Early to early Middle Triassic (Olenekian-Anisian) age and has a Euramerican distribution. This is a chirothere-(archosaur-) dominated assemblage that also persists during most of the Middle Triassic.

The first described tracks of this assemblage were from the upper part of the Buntsandstein (Solling Formation: Olenekian) (Sickler, 1834, 1835: Kaup, 1835a, b), but elsewhere in Germany, similar track assemblages occur in the uppermost Buntsandstein (Röt Formation: e.g., Willruth, 1917; Soergel, 1925; Rühle v. Lilienstern 1939; Schreiber, 1956; Krebs, 1966; Haubold 1971b; Demathieu and Leitz, 1982; Haderer et al., 1995; Ebel et al., 1998). The Röt yields a diversity of archosaur ichnogenea, including Chirotherium, Isochirotherium, Synaptichnium, Brachychirotherium and Rotodactylus. Equivalent ichnofaunas outside of Germany come from France (Provence, Massif Central, Alpes Maritimes) and the Vosges of the French-German-Belgian borderland (e.g., Charles, 1949; Demathieu and Durand, 1975; Demathieu and Leitz, 1982; Orzag-Sperber, 1966; Demathieu, 1977, 1984). The Buntsandstein ichnofaunas have a demonstrated age range of late Olenekian through early Anisian (Noneiskien-Perovkan: Lucas, 1998, 2007; Lucas and Schoch, 2002).

The Moenkopi Formation in Arizona and New Mexico has a very similar ichnofauna of early Anisian age. Most tracks can be assigned to Chirotherium, Isochirotherium and Rotodactylus, as well as the synapsid track Therapsipus (Peabody, 1948; Hunt et al., 1993b; Nesbitt and Angielczyk, 2002; Lucas et al., 2003). In Italy, there are Rynchosauroides tracks in the Olenekian Werfen Formation (Mietto, 1986). Early Anisian rocks in Italy yield archosaur tracks referred to a variety of ichnogenea, including Rynchosauroides, Chirotherium, Brachychirotherium, Synaptichnium, Parasynaptichnium and Isochirotherium (e.g., Abel, 1926; Mietto, 1987; Sirna et al., 1994; Avanzini et al., 2001; Avanzini and Lockley, 2002).

Late Middle Triassic

The Anisian interval of the Muschelkalk in Germany and the Netherlands yields tetrapod ichnofaunas in carbonate tidal flat facies that are dominated by the ichnogenea Rynchosauroides and Procolophonichnium; chirothere tracks are much rarer (Demathieu and Oosterink, 1983, 1988; Diedrich, 1998, 2000, 2002a, b).

Marginal siliciclastic equivalents of the Muschelkalk in Germany and from the French Middle Triassic yield chirothere-dominated ichnofaunas into rocks as young as Ladinian, including the ichnogenea Isochirotherium, Synaptichnium, Sphingopus, Brachychirotherium and Rotodactylus (e.g., Demathieu, 1966, 1970, 1971; Demathieu and Gand, 1972, 1973; Courel and Demathieu, 1973, 1976; Gand, 1976, 1977;
Middle Triassic red beds in Italy (Avanzini and Neri, 1998; Avanzini, 1999, 2002; Avanzini et al., 2001; Avanzini and Leonardi, 2002), Great Britain (Sarjeant, 1967, 1970, 1996; King and Benton, 1996) and Spain (Demathieu et al., 1978) also have a similar ichnofauna. In Argentina, chirothere tracks dominate the Lower and Middle Triassic records in San Juan, Mendoza and La Rioja provinces (e.g., Huene, 1931b; Rusconi, 1951, 1967).

Huene (1931a) named *Rigalites ischigualastianus* for tracks from the Middle Triassic (Berdyankian = Ladinian?) Los Rastros Formation in San Juan Province of Argentina. Melchor and De Valais (2006) also listed records of *Rigalites* from the Berdyankian Cerros de las Cabras and Ischichuca formations in Mendoza and La Rioja provinces. *Rigalites* is the trackway of a quadruped in which the pes is much larger than the manus, the pes nearly oversteps the manus and both manus and pes are pentadactyl (we regard the supposed tetradactyl pes of *Rigalites* as a result of extramorphological variation). The tracks are obviously chirothere, and the neotype illustrated by Melchor and De Valais (2006, text-fig. 7) is strikingly similar to some of the *Brachychirotherium* tracks illustrated by Klein et al. (2006). Therefore, we regard *Rigalites* as a junior synonym of *Brachychirotherium*.

In Middle Triassic assemblages, which are both Anisian and Ladinian (Perovkan-Berdyanian; Lucas, 1998) in age, the only biostratigraphic datum that can be used to distinguish them from the earlier chirothere assemblage is the Ladinian lowest occurrence of dinosaur or dinosaur-like (dinosauromorph) tracks (Lucas, 2007), the upper Keuper in Germany and equivalent strata in Switzerland and Great Britain (e.g., Beurlen, 1950; Heller, 1952; Haubold, 1971b, 1984; Demathieu and Wiedmann, 1982; Olsen and Baird, 1986; Haderer, 1988, 1990, 1991; Lockley et al., 2006; Karl and Haubold, 1998, 2000; Lockley and Meyer, 2000; Gand et al., 2000), the Upper Triassic portion of the Newark Supergroup in eastern North America (e.g., Lull, 1953; Olsen and Baird, 1986; Silvestri and Szajna, 1993; Szajna and Silvestri, 1996; Olsen et al., 1998; Lucas and Sullivan, 2006) and the Chinle Group in the American Southwest (e.g., Baird, 1964; Conrad et al., 1987; Hunt et al., 1993a; Lockley and Hunt, 1995; Lockley et al., 2001; Lucas et al., 2001; Hunt and Lucas, 2006a; 2007a).

In Morocco, the Carnian interval of the Argana Group yields a similar footprint assemblage that includes *Rhynchosauroides, Brachychirotherium, Atreipus* and *Grallator* (Biron and Dutuit, 1981). The South American Late Triassic footprint record is from Argentina (Brazilian records are doubtful: Leonardi, 1994). Prosauropod, small (2000) identify these tracks as “Parachirotherium-Atreipus-Grallator” and conclude that they represent dinosauromorph track makers.

**Late Triassic**

The Late Triassic footprint record is distinct from older Triassic footprint assemblages in its near domination by bona fide dinosaur tracks. These are generally assigned to the ichnogenera *Grallator, Atreipus, Eosauroopus* and *Evazoum* (Lockley et al., 2006). *Brachychirotherium* records begin earlier in the Triassic, but it is the most common and characteristic Late Triassic chirother footprint ichnogenus.

Late Triassic tetrapod footprint assemblages dominated by these ichnogenera are known from the lower Stormberg Group (Molteno and lower Elliott formations and equivalents) of southern Africa (e.g., Ellenberger, 1970; Olsen and Galton, 1984; Raath et al., 1990; Raath, 1996), the upper Keuper in Germany and equivalent strata in Switzerland and Great Britain (e.g., Beurlen, 1950; Heller, 1952; Haubold, 1971b, 1984; Demathieu and Wiedmann, 1982; Olsen and Baird, 1986; Haderer, 1988, 1990, 1991; Lockley et al., 2006; Karl and Haubold, 1998, 2000; Lockley and Meyer, 2000; Gand et al., 2000), the Upper Triassic portion of the Newark Supergroup in eastern North America (e.g., Lull, 1953; Olsen and Baird, 1986; Silvestri and Szajna, 1993; Szajna and Silvestri, 1996; Olsen et al., 1998; Lucas and Sullivan, 2006) and the Chinle Group in the American Southwest (e.g., Baird, 1964; Conrad et al., 1987; Hunt et al., 1993a; Lockley and Hunt, 1995; Lockley et al., 2001; Lucas et al., 2001; Hunt and Lucas, 2006a; 2007a).

In Morocco, the Carnian interval of the Argana Group yields a similar footprint assemblage that includes *Rhynchosauroides, Brachychirotherium, Atreipus* and *Grallator* (Biron and Dutuit, 1981). The South American Late Triassic footprint record is from Argentina (Brazilian records are doubtful: Leonardi, 1994). Prosauropod, small
ichnofacies for nonmarine environments:

Subsequently, Hunt and Lucas (2007) defined five archetypal tetrapod ichnofacies for "general trace associations, or types of ichnotaxa that can be characterized by morphological criteria (independent of depositional environment or biological affinities) (e.g., Bromley, 1996; McIlroy, 1948, Haubold, 1971a; Lucas et al., 2003) (Fig. 2). Other common ichnotaxa are Rotaactylus, Rhynchosauroides, Isochirotherium and Synaptichnium.

Hunt and Lucas (2006b) named the Brontopodus ichnofacies for 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 four ichnocoenoses within the Brontopodus ichnofacies. The oldest ichnocoenosis, the Rotodactylus ichnocoenosis, occurs in the earliest Triassic (possibly restricted to the Induan) and is characterized by dicynodont footprints in southern Africa, Antarctica and Australia (Watson, 1960; MacDonald et al., 1991; Retallack, 1996). Hunt and Lucas (2006b) termed this the Dicynodontipus ichnocoenosis (Fig. 2).

The majority of Early Triassic to early Middle Triassic ichnofaunas represent the Chirotherium ichnocoenosis of the Batrachichnus ichnofacies. However, a small number of localities are dominated by therapsid tracks. Hunt and Lucas (2006b) termed this the Therapsipus ichnocoenosis for the therapsid ichnotaxon from the Moenkopi Formation of Arizona (Hunt et al., 1993b).

Herein, we recognize a new ichnocoenosis in the Anisian carbonate tidal flats of Germany and the Netherlands. This Procolophonichnium ichnocoenosis represents a temporal equivalent of the red-bed Chirotherium ichnocoenosis (Lucas, 2007). This ichnocoenosis is dominated by tracks of Procolophonichnium and Rhynchosauroides with only rare chirothera tracks (Demathieu and Oosterink, 1983, 1988; Diedrich, 1998, 2000, 2002a, b; Lucas, 2007).

**Triassic Tetrapod Ichnofacies and Ichnocoenoses**

**Introduction**

Hunt and Lucas (2007b) provided a discussion of terminology relevant to the study of tetrapod ichnofacies. 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; Hunt and Lucas, 2007). Seilacher (1964, p. 303) introduced the term ichnofacies for “general trace associations, or types of ichnocoenoses, representing certain facies with a long geologic range.” Subsequently, Hunt and Lucas (2007) defined five archetypal tetrapod ichnofacies for nonmarine environments: Chelichnus, Grallator, Brontopodus, Batrachichnus and Characichnos ichnofacies (Table 1). The following review is principally based on Hunt and Lucas (2006b, 2007).

**Brachychirotherium Ichnofacies**

Hunt and Lucas (2007b) 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. Hunt and Lucas (2006b, 2007) recognized two ichnocoenoses of this ichnofacies in the Triassic (Fig. 2; Table 1).

Hunt and Lucas (2007b) named the Chirotherium ichnocoenosis for the well-studied Early-Middle Triassic ichnofaunas of Europe and North America that are dominated by Chirotherium tracks (e.g., Peabody, 1948, Haubold, 1971a; Lucas et al., 2003) (Fig. 2). Other common ichnotaxa are Rotodactylus, Rhynchosauroides, Isochirotherium and Synaptichnium.

**Grallator Ichnofacies**

Hunt and Lucas (2007b) 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 four ichnocoenoses within this ichnofacies in the Triassic and herein we define a fifth (Fig. 2; Table 1).

The oldest ichnocoenosis within the Brontopodus ichnofacies occurs in the earliest Triassic (possibly restricted to the Induan) and is characterized by dicynodont footprints in southern Africa, Antarctica and Australia (Watson, 1960; MacDonald et al., 1991; Retallack, 1996). Hunt and Lucas (2006b) termed this the Dicynodontipus ichnocoenosis (Fig. 2).

The majority of Early Triassic to early Middle Triassic ichnofaunas represent the Chirotherium ichnocoenosis of the Batrachichnus ichnofacies. However, a small number of localities are dominated by therapsid tracks. Hunt and Lucas (2006b) termed this the Therapsipus ichnocoenosis for the therapsid ichnotaxon from the Moenkopi Formation of Arizona (Hunt et al., 1993b).

Herein, we recognize a new ichnocoenosis in the Anisian carbonate tidal flats of Germany and the Netherlands. This Procolophonichnium ichnocoenosis represents a temporal equivalent of the red-bed Chirotherium ichnocoenosis (Lucas, 2007). This ichnocoenosis is dominated by tracks of Procolophonichnium and Rhynchosauroides with only rare chirothera tracks (Demathieu and Oosterink, 1983, 1988; Diedrich, 1998, 2000, 2002a, b; Lucas, 2007).

Hunt and Lucas (2007b) redefined Lockley’s (2007) Late Triassic Grallator-Brachychirotherium-Rhynchosauroides ichnofacies as the Grallator ichnocoenosis of the Grallator ichnofaunas. Further study of Late Triassic ichnofaunas by Hunt and Lucas (2006b) indicated that four individual ichnocoenoses can be discriminated within this plexus, and two of them can be assigned to the Brontopodus ichnofacies, and one each to the Grallator and Batrachichnus ichnofacies.

Hunt and Lucas (2006b) recognized the Evazoum ichnocoenosis for Late Triassic ichnofaunas that are numerically dominated by tracks of quadrupedal herbivores (e.g., Lockley and Hunt, 1995, fig. 3.25). The Redonda Formation of east-central New Mexico is typical of these ichnofaunas (Klein et al., 2006). The ichnogenus Evazoum also occurs in Wales and Lesotho and often co-occurs with Eosauropus (Lockley et al., 2006), in, for example, western North America, Lesotho and Wales (Lockley and Hunt, 1995; Lockley and Meyer, 2000). In Switzerland and Greenland, Eosauropus occurs without Evazoum (Lockley and Meyer, 2000). Hunt and Lucas (2006b) diagnosed the Evazoum ichnocoenosis as consisting of ichnofaunas in which more than 40% of the specimens represent Evazoum and/or Eosauropus.

Other Late Triassic ichnofaunas, dominated by the tracks of quadrupedal herbivores, are composed of more than 50% Brachychirotherium tracks (e.g., sites in the Chinle Group of western North America, including Shay Canyon in Utah and sites in Sloan Canyon in New Mexico). These tracksites typically have 0-10% Evazoum or Eosauropus. Hunt and Lucas (2006b) assigned these ichnofaunas to the Brachychirotherium ichnocoenosis (Fig. 2).

**Grallator Ichnofacies**

Hunt and Lucas (2007b) proposed the Grallator ichnocoenosis 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. We recognize four ichnocoenoses of the Grallator ichnofacies during the Triassic (Table 1).

As noted above, Hunt and Lucas (2007b) recognized a Grallator ichnocoenosis in the Late Triassic. There are many Late Triassic ichnofaunas in which the most abundant (> 50%) ichnogenus is Grallator. Notable ichnofaunas occur at the very top of the Chinle Group or in the overlying Wingate Sandstone in Colorado (Gaston et al., 2003; Lucas et al., 2006b); other prominent examples are in Wales, France, Germany, Italy, Switzerland and Greenland (Lockley and Meyer, 2000, figs. 4.4, 4.10, 4.14).

Hunt and Lucas (2006b) noted that there is potential to subdivide the Grallator ichnocoenosis, and it clearly includes several sub-ichnocoenoses, e.g., on the Colorado Plateau, the upper and lower Wingate Sandstone have different sub-ichnocoenoses: a lower Eosauropus sub-ichnocoenosis includes Brasiliichnium, Brachychirotherium, and Eosauropus, and an upper Otozoum sub-ichnocoenosis includes Eubrontes, Batrachopus and Otozoum (Lucas et al., 2006b).
Permian to the Early Jurassic.

This ichnofacies is recurrent on dune faces in eolian environments, and it extends from the Early Permian to the Early Jurassic.

Hunt and Lucas (2007b) redefined the *Brasilichnium* ichnofacies of Lockley et al. (1994) as an ichnocoenosis of this ichnofacies (Table 1; Fig. 2). *Brasilichnium* is abundant in the Early Jurassic Navajo Sandstone and coeval Aztec Sandstone in western North America (Utah, California, Colorado). The *Brasilichnium* ichnocoenosis is also locally present in the lower Wingate Sandstone in western Colorado (Schultz-Pittman et al., 1996; Hunt and Lucas, 2006b).

**Characichnos Ichnofacies**

Hunt and Lucas (2007b) proposed the *Characichnos* ichnofacies for medium diversity ichnofaunas in which the majority of tracks are tetrapod swimming traces (parallel scratch marks) and fish swimming trails (*Undichna*). This ichnofacies represents shallow lacustrine (and tidal) environments. Swimming traces are notably abundant in various Triassic units in the western United States, including the Moenkopi Formation (Lower-Middle Triassic) and equivalent strata in Arizona, Utah, Wyoming and New Mexico (e.g., Peabody, 1948; Boyd and Loope, 1984; McAllister and Kirby, 1998; Schultz et al., 1994; Lucas et al., 2003; Mickelson et al., 2006a, b) and the Chinle Group (Upper Triassic) in Arizona and New Mexico (e.g., Hunt et al., 1993a; Hunt and Lucas, 2006b). There is no named ichnocoenosis of this ichnofacies in the Triassic.

**Late Triassic Ichnocoenoses**

There are thus five ichnofaunas present in the Late Triassic: *Evazoum*, *Brachychirotherium* (*Brontopodus* ichnofaunas), *Grallator* (*Grallator* ichnofacies), *Apatopus* (*Batrachichnus* ichnofaunas) and *Brasilichnium* (*Characichnos* ichnofacies). The *Apatopus* ichnocoenosis is geographically restricted to eastern North America (although *Apatopus* occurs at one locality in Utah: Foster et al., 2003) and probably environmentally controlled by the distribution of large rift lakes. The *Evazoum* ichnocoenosis is principally restricted to western North America, where it is replaced in the uppermost Chinle, Wingate and Sheep Pen formations (latest Triassic) by the *Grallator* ichnocoenosis. The Shay Canyon tracksite in Utah pertains to the *Brachychirotherium* ichnocoenosis and is stratigraphically lower in the upper Chinle. It may represent a lateral equivalent of the *Evazoum* ichnocoenosis or it may be stratigraphically lower, which would suggest a temporal progression of ichnocoenoses from *Brachychirotherium* to *Evazoum* to *Grallator* (Hunt and Lucas, 2006b).

The ichnofaunas of the lower Chinle are poorly known but include *Brachychirotherium*, lack *Evazoum*, and several include *Barrancapus* (Hunt and Lucas, 2006a). These ichnofaunas may represent the *Brachychirotherium* ichnocoenosis (possibly a *Barrancapus* sub-ichnocoenosis). *Barrancapus* appears to be a potential ichnogenus based on ichnotaxon of the Barrancan sub-lvf (land-vertebrate faunachron) of the Revueltaan lvf. *Eosauros* and *Evazoum* are index ichnotaxa of the Apachean lvf (Hunt and Lucas, 2006b).

**Triassic Tetrapod Track Biostratigraphy and Biochronology**

**Introduction**

Lucas (2007) reviewed the Phanerozoic record of tetrapod tracks (Devonian-Neogene) and noted that three principal factors limit their use in biostratigraphy and biochronology (palichnnostratigraphy): (1) invalid ichnotaxa based on extramorphological variants; (2) slow apparent evolutionary turnover rates; and (3) facies restrictions. The ichnotaxonomy of tetrapod footprints has generally been oversplit, largely due to a failure to appreciate extramorphological variation. Thus, many tetrapod footprint ichnogenera, and most ichnospacies, are useless “phantom” taxa that confound biostratigraphic correlation and biochronological subdivision. Tracks rarely allow identification of a genus or species known from the body fossil record. Indeed, almost all tetrapod footprint ichnogenera are equivalent to a body fossil-based family or a higher taxon (order, superorder, etc.). This means that ichnogenera necessarily have much longer temporal ranges and therefore slower apparent evolutionary turnover rates than do body fossil genera. Because of this, footprints cannot provide as refined a subdivision of geological time as do body fossils. The tetrapod footprint record is also much more facies controlled than the tetrapod body fossil record. The relatively narrow facies window for track preservation, and the fact that tracks are almost never transported, redeposited or reworked, limits the facies that can be correlated with any track-based biostratigraphy (Lucas, 2007).

**Biostratigraphy and Biochronology**

There is much literature on Triassic tetrapod footprint biostratigraphy, especially based on the European and North American records. The most comprehensive are the publications of Demathieu (e.g., 1977, 1982, 1984, 1994; Demathieu and Haubold, 1972, 1974), who established the presence of three different Triassic footprint assemblages in Europe that Lucas (2007) validated. These are the chirotherian assemblage of Olenekian-early Anisian age (early-Middle Triassic), the dinosaursauromorph assemblage of late Anisian-Ladinian age (late Middle Triassic) and the dinosaur assemblage of Carnian-Rhaetian age (Late Triassic). Lucas (2007) suggested that a fourth footprint assemblage, based on earliest Triassic dicynodont footprints from Gondwana, may also be discernable.

**Earliest Triassic**

The dicynodont tracks from the South Africa, Antarctica and Australia (Watson, 1960; MacDonald et al., 1991; Retallack, 1996) may represent a distinct ichnofauna. Retallack (1996) attributed these tracks to the body-fossil genus *Lystrosaurus*, which defines a classic biochron of earliest Triassic (Induan) age (Lucas, 1998). However, these dicynodont tracks cannot be reasonably be attributed at the generic level so they cannot be used to support the *Lystrosaurus* biochron. There is a need for additional study of the latest Permian and earliest Triassic ichnofaunas. The most significant ichnofaunas of these ages are from South Africa.

**Early-Middle Triassic**

The late Early to early Middle Triassic (Olenekian-Anisian) is characterized by a chirotherian- (archosaurian-) dominated assemblage that also persists throughout most of the Middle Triassic. European evidence (especially France) suggests that the chirotherian-dominated footprint assemblage continues in red-bed facies into rocks as young as Ladinian (Lucas, 2007). The chirotherian-dominated ichnofauna includes the archosaur ichnogenera *Ischichnus*, *Synaptichnium*, *Sphingopus*, *Chirotherium*, *Rotodactylus*, *Rhynchosauroids* and *Brachychirotherium*, as well as the synapsid track *Therapsidus* (e.g., Peabody, 1948; Hunt et al., 1993b; Nesbitt and Angielczyk, 2002; Lucas et al., 2003; Lucas, 2007).

**Late Middle Triassic**

Later Middle Triassic assemblages are both Anisian and Ladinian (Perovkan-Berdyaikian: Lucas, 1998) in age. The only biostratigraphic datum to distinguish them from the earlier chirotherian assemblage is the Ladinian lowest occurrence of dinosaur or dinosaur-like (dinosauromorph) tracks (Lucas, 2007). Apparent tridactyl, bipedal tracks have long been known from Middle Triassic strata in Europe and attributed to dinosaurs by various workers (see review by Demathieu, 1989). More recently, a
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