

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 – *Brasilichnium* 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 Chinle 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 binomens 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 ichnogenera, 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-Sperberg, 1966; Demathieu, 1977, 1984). The Buntsandstein ichnofaunas have a demonstrated age range of late Olenekian through early Anisian (Nonesian-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 *Rhynchosauroides* tracks in the Olenekian Werfen Formation (Mietto, 1986). Early Anisian rocks in Italy yield archosaur tracks referred to a variety of ichnogenera, including *Rhynchosauroides*, *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 ichnogenera *Rhynchosauroides* 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 ichnogenera *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,

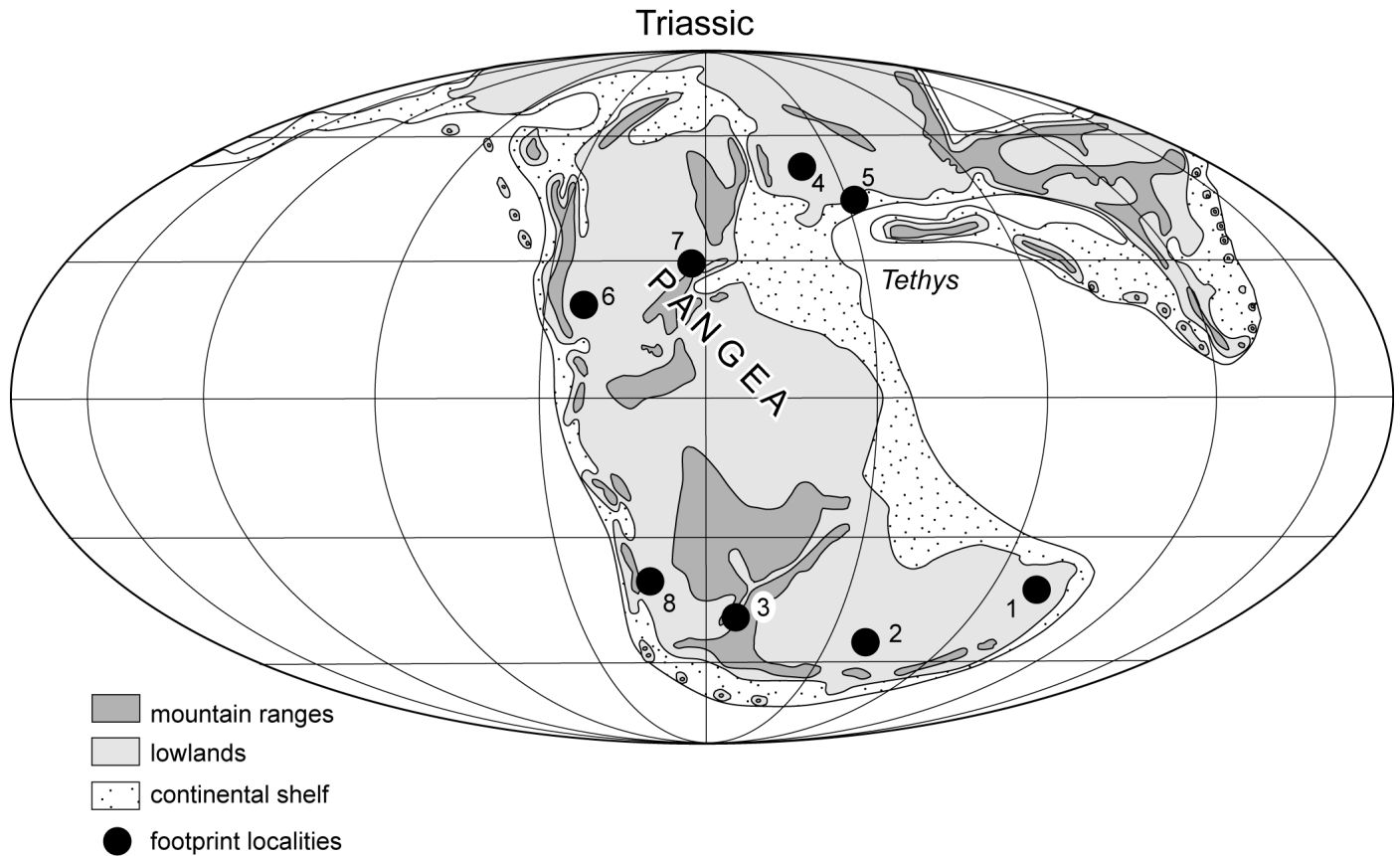


FIGURE 1. Distribution of principal Triassic tracksites on Triassic Pangea (from Lucas, 2007). Locations are: 1, Sydney basin, Australia; 2, Karoo basin, South Africa; 3, Antarctica; 4, western Europe; 5, Italy; 6, Chinle basin, western United States; 7, Newark basin, New Jersey-Pennsylvania; 8, Argentina. Base map after Wing and Sues (1992).

1978, 1980; Gand and Pellier, 1976; Gand et al., 1976). 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 DeValais (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-Berdyankian: 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). These tracks are not simply extramorphological variants of chirothere tracks (Haubold, 1999; Haubold and Klein, 2000; Lucas, 2007). In Germany, tridactyl *Atreipus*- and *Grallator*-like tracks have their lowest occurrence in the Ladinian Benker Sandstein (Rehnel, 1950, 1952, 1959, 1983; Weiss, 1976, 1981) and increase in abundance up section. Haubold and Klein

(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*, *Eosauropus* and *Evazoum* (Lockley et al., 2006). *Brachychirotherium* records begin earlier in the Triassic, but it is the most common and characteristic Late Triassic chirothere 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

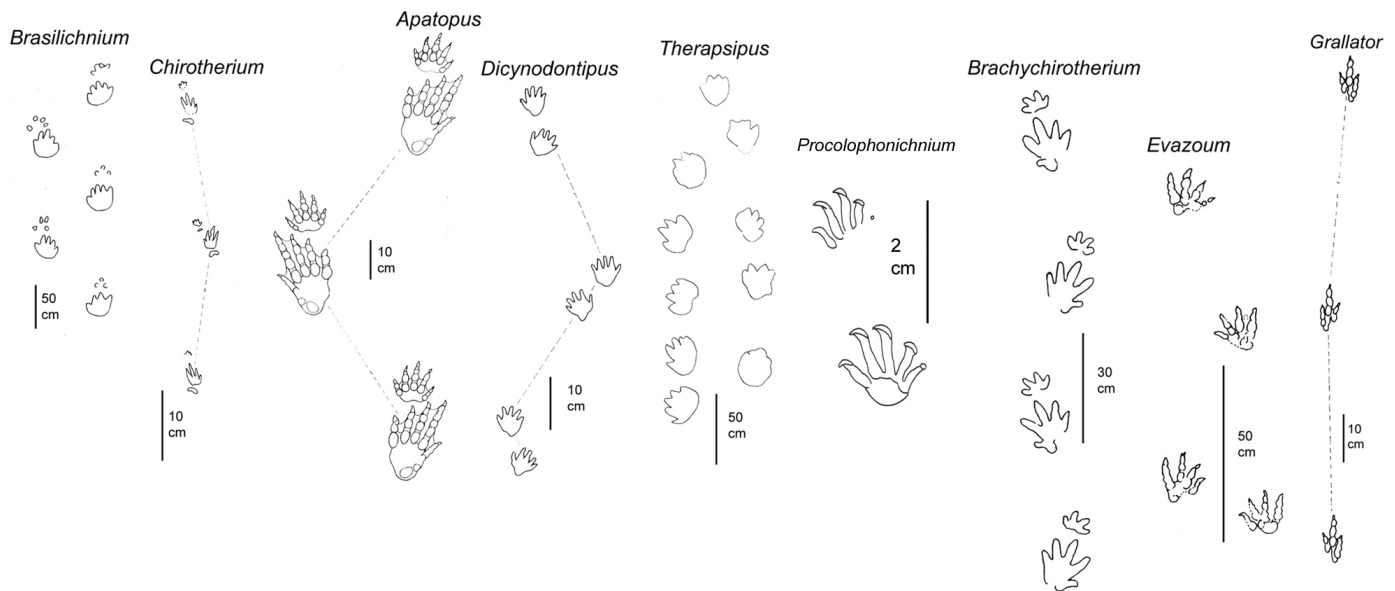


FIGURE 2. Representative tracks of the *Grallator*, *Brontopodus*, *Chelichnus*, *Batrachichnus* and *Characichnos* ichnofacies from the Triassic (after Lockley and Hunt, 1995; Haubold, 1984; Demathieu and Oosterink, 1983). *Brasilichnium* ichnocoenosis of the *Chelichnus* ichnofacies. *Chirotherium* and *Apatopus* ichnocoenoses of the *Batrachichnus* ichnofacies. *Dicynodontipus*, *Therapsipus*, *Procolophonichnium*, *Brachychirotherium* and *Evazoum* ichnocoenoses of the *Brontopodus* ichnofacies, and *Grallator* ichnocoenosis of the *Grallator* ichnofacies.

theropod, synapsid (both small cynodont and large dicynodont) and chirothere (*Brachychirotherium*) tracks are known from Upper Triassic strata in Rio Negro, San Juan and La Rioja provinces (e.g., Casamiquela, 1964; Bonaparte, 1969; Arcucci et al., 1995, 2000; Marsicano and Barredo, 2000). Late Triassic theropod tracks are also known in Australia from the Sydney basin in New South Wales and the Callide basin in southeastern Queensland (e.g., Molnar, 1991; Thulborn, 1998).

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).

Batrachichnus 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*.

Hunt and Lucas (2006b) recognized a distinctive and pervasive ichnocoenosis throughout much of the Upper Triassic portion of the Newark Supergroup in eastern North America assigned to the *Apatopus* ichnocoenosis. Ichnofaunas of this ichnocoenosis lack *Evazoum* and *Eosauropus*, contain less than 50% *Brachychirotherium* and *Grallator* and are characterized by ichnotaxa that are rare or absent elsewhere, including *Apatopus* and *Gwyneddichnium*.

Brontopodus 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 chirothere tracks (Demathieu and Oosterink, 1983, 1988; Diedrich, 1998, 2000, 2002a, b; Lucas, 2007).

TABLE 1. Archetypal tetrapod ichnofacies (Hunt and Lucas, 2007b) and representative ichnocoenoses of the Triassic.

Archetypal Tetrapod Ichnofacies	Predominant trace fossil types	Constituent Triassic ichnocoenoses	Inferred environment
<i>Chelichmus</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	<i>Brasilichnium</i> (Late Triassic-Early Jurassic: Lockley et al., 1994)	Eolian crossbeds
<i>Batrachichnus</i>	Majority of tracks are of quadrupedal carnivores; medium-high diversity (4-8 ichnogenera)	<i>Chirotherium</i> (Early-Middle Triassic: Hunt and Lucas, 2007); <i>Apatopus</i> (Late Triassic: Hunt and Lucas, 2006b)	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>Dicynodontipus</i> (Early Triassic: Hunt and Lucas, 2006b); <i>Therapsipus</i> (Middle Triassic: Hunt and Lucas, 2006b); <i>Procolophonichnium</i> (Middle Triassic: herein) <i>Brachychirotherium</i> (Late Triassic: Hunt and Lucas, 2006b); <i>Evazoum</i> (Late Triassic: Hunt and Lucas, 2006b)	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	<i>Grallator</i> (Late Triassic: Hunt and Lucas, 2007)	Lacustrine margin
<i>Characichnos</i>	Parallel scratch marks and fish swimming trails (<i>Undichna</i>)	unnamed	Shallow lacustrine/aquatic

Hunt and Lucas (2007b) redefined Lockley's (2007) Late Triassic *Grallator-Brachychirotherium-Rhynchosauroides* ichnofacies as the *Grallator* ichnocoenosis of the *Grallator* ichnofacies. 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* 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. 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 *Brasilichnium*, *Brachychirotherium*, and *Eosauropus*, and an upper *Otozoum* sub-ichnocoenosis includes *Eubrontes*, *Batrachopus* and *Otozoum* (Lucas et al., 2006b).

***Chelichnus* Ichnofacies**

Hunt and Lucas (2007b) proposed the *Chelichnus* ichnofacies for ichnofaunas that have a low diversity (fewer 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 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 notable 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; Mickleson 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 ichnocoenoses present in the Late Triassic: *Evazoum*, *Brachychirotherium* (*Brontopodus* ichnofacies), *Grallator* (*Grallator* ichnofacies), *Apatopus* (*Batrachichnus* ichnofacies) and *Brasilichnium* (*Chelichnus* 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 low 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 index ichnotaxon of the Barrancan sub-lvf (land-vertebrate faunachron) of the Revueltian lvf. *Eosauropus* 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 (palichnostratigraphy): (1) invalid ichnotaxa based on extramorphological variants; (2) slow apparent evo-

lutionary 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 ichnospecies, 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 chirothere assemblage of Olenekian-early Anisian age (early-Middle Triassic), the dinosauromorph 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 chirothere- (archosaur-) dominated assemblage that also persists throughout most of the Middle Triassic. European evidence (especially France) suggests that the chirothere-dominated footprint assemblage continues in red-bed facies into rocks as young as Ladinian (Lucas, 2007). The chirothere-dominated ichnofauna includes the archosaur ichnogenera *Isochirotherium*, *Synaptichnium*, *Sphingopus*, *Chirotherium*, *Rotodactylus*, *Rhynchosauroides* and *Brachychirotherium*, as well as the synapsid track *Therapsipus* (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-Berdyankian: Lucas, 1998) in age. The only biostratigraphic datum to distinguish them from the earlier chirothere 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

more sophisticated analysis of this problem by Haubold (1999; Haubold and Klein, 2000) argues that there was a lengthy and complex evolutionary transition from the dinosauromorph foot/gait to the dinosaur foot/gait well documented in the Triassic of the German section.

In Germany, track surfaces of the Benker Sandstein up to the Löwenstein Formation (Gipskeuper) and in the Lower Steinmergelkeuper have quadrupedal, chirotherian-like, pentadactyl pes imprints and trackways assigned to the ichnogenus *Parachirotherium* (Lucas, 2007). Tridactyl *Atreipus*- and *Grallator*- like tracks have their lowest occurrence in the Benker Sandstein (Rehnelt, 1950, 1952, 1959, 1983; Weiss, 1976, 1981) and increase in abundance up section. Haubold and Klein (2000) identify these tracks as “*Parachirotherium-Atreipus-Grallator*” and concluded that they represent dinosauromorph track makers.

Regardless of how these tracks are identified, the lowest occurrence of tridactyl dinosaur or dinosaur-like (dinosauromorph) tracks appears to be Ladinian and may form a valuable biostratigraphic datum. Lucas (2007) recognized the appearance of dinosauromorph tracks in the later Middle Triassic as marking a distinct footprint assemblage of this age.

Late Triassic

There have been attempts to identify two temporally successive Late Triassic footprint assemblages. Thus, Olsen (1980) identified three footprint assemblages in the Newark Supergroup of eastern North America, two of Late Triassic age and one of Early Jurassic age. More detailed stratigraphic data have shown that the two Late Triassic assemblages should be combined into one characterized primarily by *Brachychirotherium*, *Gwyneddichnium*, *Grallator*, *Atreipus* and *Rhynchosauroides* (Silvestri and Szajna, 1993; Szajna and Silvestri, 1996; Lucas and Huber, 2003; Lucas, 2007). Olsen and Huber (1998) raised the possibility that an older, distinctive footprint assemblage may be present near the base of the Newark Supergroup, but when extramorphological variation is considered, this assemblage consists of characteristic Late Triassic ichnotaxa, including *Apatopus*, *Grallator* and *Brachychirotherium*. Haubold (1986) followed Olsen’s (1980) zonation, applying it to the European and South African records. However, current ichnotaxonomy and understanding of stratigraphic distribution makes it clear that only one Late Triassic footprint assemblage can be identified in these regions (Lucas and Hancox, 2001; Lucas and Huber, 2003).

Lockley (1993) and Lockley and Hunt (1994, 1995) also presented a similar zonation for the upper Chinle Group and the Glen

Canyon Group in the western United States. They identified four successive zones, two of which are Late Triassic in age: (1) *Brachychirotherium* and small *grallatorid* zone of the upper Chinle Group (Rock Point sequence of Lucas, 1993); and (2) medium-size *grallatorid* assemblage of the Wingate Sandstone. However, subsequent collecting and stratigraphic data demonstrate that assemblages 1 and 2 are a single assemblage dominated by *Grallator* and *Brachychirotherium*, which Lucas et al. (2006a) termed the *Brachychirotherium* assemblage zone.

However, it is possible to discriminate two successive Late Triassic intervals based on ichnofaunas. The sauropodomorph traces *Evazoum* and *Eosauropus* first appear in the later Norian or Rhaetian. These ichnotaxa occur in the Late Triassic of western North America, Greenland, Switzerland and Lesotho (e.g., Lockley and Hunt, 1995; Lockley and Meyer, 2000; Lockley et al., 2006; Lucas et al., 2006a). Older Late Triassic ichnofaunas lack these ichnotaxa, and their appearance corresponds with the evolution of larger sauropodomorphs in the Norian. The Newark Supergroup is conspicuous among Upper Triassic units that yield significant tracks in lacking these sauropodomorph tracks. It is important to note that the extensive ichnofaunas of the Late Triassic-Early Jurassic Newark Supergroup represent a very narrow range of depositional environments, essentially lacustrine margins of rift basin lakes. These ichnofaunas are distinct from contemporary ichnofaunas in other significant ways, including the presence of *Apatopus* and the prevalence of *Atreipus*.

CONCLUSIONS

There are five 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.

A global Triassic biochronology based on tetrapod body fossils recognizes eight biochronological units (Lucas, 1998). The Triassic tetrapod footprint record resolves to about five time intervals, so it has much less temporal resolution than the body fossil record (Lucas, 2007).

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