

ARCHOSAUR FOOTPRINTS – POTENTIAL FOR BIOCHRONOLOGY OF TRIASSIC CONTINENTAL SEQUENCES

HENDRIK KLEIN¹ AND HARTMUT HAUBOLD²

¹ Rübzahlstr. 1, D-92318 Neumarkt, Germany, e-mail: klein.dinotracks@combyphone.de;

² Institute for Geological Sciences, Martin-Luther-University Halle-Wittenberg, Von-Seckendorff-Platz 3, D-06120 Halle, Germany, e-mail: hartmut.haubold@geo.uni-halle.de

Abstract—Historically, footprint-bearing localities in eastern and western North America and southern Thuringia and northern Bavaria have played pivotal roles in Triassic archosaur footprint research. In a nearly complete sequence of formations and footprint-horizons in the Moenkopi Group (U.S.A.), Newark Supergroup (U.S.A. and Canada), and Buntsandstein, Muschelkalk, and Keuper groups (Olenekian to Norian-Rhaetian) of central Europe, the principal morphs of archosaur footprints are represented by *Rotodactylus*, *Synaptichnium*, *Isochirotherium*, *Brachychirotherium*, *Chirotherium*, *Sphingopus*, *Parachirotherium*, *Atreipus*, and *Grallator*. Additionally, the temporal and, in principal, the evolutionary “root” is documented by *Protochirotherium* from the early Olenekian of Hessen. Of utmost significance is the evolutionary succession from *Chirotherium* to *Grallator*. Therein, the development of two key features seen in the origin and early evolution of dinosaurs – tridactyl foot-morphology and the bipedal gait – is documented between the Olenekian and Norian. The stratigraphic distribution of these forms and their potential for biochronology yields a biochronological sequence we sketch out as follows: For the Triassic we discriminate six successive biochrons (I–VI). Each biochron is marked by an index taxon (in bold), a characteristic footprint assemblage, and its stratigraphic distribution. I. *Protochirotherium* (*Synaptichnium*), Late Induan–Olenekian. II. *Chirotherium*, *Rotodactylus*, *Isochirotherium*, *Synaptichnium* (“*Brachychirotherium*”), Late Olenekian–Anisian. III. *Sphingopus*–*Atreipus*–*Grallator*, *Rotodactylus*, *Isochirotherium*, *Synaptichnium* (“*Brachychirotherium*”), Late Anisian–Ladinian. IV. *Parachirotherium*–*Atreipus*–*Grallator*, *Synaptichnium* (“*Brachychirotherium*”), Late Ladinian. V. *Atreipus*–*Grallator*, *Brachychirotherium*, Carnian–Norian. VI. *Grallator*–*Eubrontes*, *Brachychirotherium*, Norian–Rhaetian.

In addition to their biostratigraphic utility, the succession of ichnotaxa and ichno-assemblages also reflects evolutionary developments in foot morphology and in the locomotor apparatus of the Archosauria, a progression thus far incompletely documented by the body fossil record. As a consequence of their limited temporal ranges, and their intercontinental distributions in large quantities, the principal archosaurian ichnotaxa open up additional and innovative possibilities for the biochronology of continental sequences.

INTRODUCTION AND BACKGROUND

The scientific history of Triassic tetrapod tracks begins with the description and binominal naming of the famous footprints and trackways of *Chirotherium barthii* and *C. sickleri* from the Buntsandstein near Hildburghausen in Thuringia, Germany by Sickler (1834) and Kaup (1835). These momentous events were followed, beginning in 1836, by documentation of the extensive discoveries in the “New Red Sandstone” (now the Newark Supergroup) of Connecticut and Massachusetts by E. Hitchcock with the descriptions of important ichnotaxa like *Eubrontes* and *Grallator* (Hitchcock, 1845, 1858). The next phase of significance commenced in the middle of the twentieth century with the study of the Early-Middle Triassic tetrapod ichnofauna of the Moenkopi Formation of Arizona by F.E. Peabody. In his pioneering monograph, Peabody (1948) demonstrated for the first time the intercontinental distribution of *Chirotherium*, with identical ichnospecies (*C. barthii* and *C. sickleri* [= *C. minus*]) present in both the Moenkopi Formation and the Solling Formation of southern Thuringia. *Rotodactylus* constitutes another remarkable tetrapod ichnotaxon from Arizona described by Peabody that was subsequently recognized preserved in association with *C. barthii* and *C. sickleri* in several strata in the Buntsandstein near Hildburghausen, further supporting the correlation between the two units. Building on the results of Peabody (1948, 1955a, 1956), Haubold (1967, 1971a, b), in his studies of the track assemblages in the Buntsandstein, further substantiated the intercontinental distribution of *Rotodactylus*.

In the following decades, the anatomical interpretations of *Chirotherium*, *Rotodactylus*, *Eubrontes*, *Grallator*, and other classical

Triassic ichnotaxa were shown to parallel the evolutionary sequence of Triassic archosaurs documented by an increasing quantity of skeletal evidence. It was J. Walther (1917) who first proposed a dinosaur-like producer based on the footprint morphology and trackway pattern of *Chirotherium*. Soergel (1925) likened the *C. barthii* track maker to *Euparkeria*, a taxon whose phylogenetic position is presently recognized as close to the base of the hypothesized crown-group Archosauria (Gauthier, 1986; Sereno, 1991). This corresponds well with the geological age and the morphology of *C. barthii*. Based on these data, and following the excellent reconstruction of *Euparkeria* presented by Paul (2002), the *Chirotherium* track maker was reconstructed and displayed in a life-size bronze-sculpture in the *Chirotherium* Monument that was inaugurated in 2004 in the market-place of Hildburghausen, close to the type locality of *Chirotherium barthii* (Haubold, 2006).

The most common and popular interpretation of *Chirotherium barthii* and *C. sickleri* as tracks of various members of the Crurotarsi is not followed here. To the contrary, the Olenekian to early Anisian age of *Chirotherium*: (1) supports a more general interpretation in the sense stated above, and (2) the morphology of the pes imprints of both *C. barthii* and *C. sickleri* include and presage the tridactyl pattern of the later dinosaurs, and of theropods in particular. Support for this interpretation is further substantiated by the development of the two key-features in the evolution of dinosaurs: tridactyly and bipedality, both of which are reflected in a stratigraphic succession of footprint morphs and trackways from *Chirotherium*, *Sphingopus*, *Parachirotherium* and *Atreipus* through *Grallator* and *Eubrontes* (Haubold and Klein, 2000, 2002). For *Synaptichnium* and “*Brachychirotherium*,” as well as

Isochirotherium in the Middle Triassic and *Brachychirotherium* (*sensu stricto*) in the Upper Triassic, a general affinity with the Crurotarsi appears to be realistic. However, this cannot be demonstrated convincingly as is usually supposed, and there is no evidence for any synapomorphies of the group in these footprints. The correlation of footprint morphs, beginning in the Lower Triassic with *Protochirotherium*, with the archosaurian evolutionary “grades” seems to be well substantiated, in particular by the extraordinarily fine preservation of the latter described by Fichter and Kunz (2004) from the Detfurth Formation of the Middle Buntsandstein of Hessen.

The *Rotodactylus* track maker has been interpreted as a member of the *Lagosuchia* resp. *Dinosauromorpha* (Haubold, 1967, 1999; Haubold and Klein, 2002), a conclusion supported by correspondence of the tracks with skeletal anatomy. Of importance is the geological age of the tracks compared to their proposed skeletal correlates: *Rotodactylus* and *Chirotherium*, as well as *Isochirotherium* and *Synaptichnium* (“*Brachychirotherium*”), occur as early as the Olenekian-Anisian transition, and prove a diversity that has to be younger than the hypothetical stage of Archosauria, i.e., the beginning of the differentiation of this crown-group.

Early-Late Triassic archosaur tracks come from sequences with multiple horizons in localities as far removed today as southern Thuringia and northern Bavaria on one side and Arizona, Connecticut and Massachusetts on the other. In tandem, they play key roles in the biochronological documentation of the evolution of archosaurian foot morphology and locomotion by fossil imprints and tracks. On both

continents, sequences with known track horizons range from the Olenekian to the Norian-Rhaetian (Fig. 1). Through intensive research, important correlative locations have been discovered in other regions of Germany, Switzerland, France, Great Britain, Italy and Poland. In North America, the number of occurrences in the Triassic of the Newark Supergroup, for example in Pennsylvania, and in the Chinle Group of Colorado, New Mexico, Utah, Arizona and Texas have increased. Triassic archosaur tracks are known from Lesotho in southern Africa (Molteno and Lower Elliot formations), South America (Argentina), and southern China (Guanling Formation of the Guizhou Province [Lü et al., 2004]).

The large number of ichnogenera with archosaurian affinities that have been described so far – roughly 50, even excluding *Chirotherium*, *Rotodactylus*, *Eubrontes* and *Grallator* – is a further indication that the record is truly extensive. Besides *Chirotherium* itself, the following ichnogenera are considered chirotherian: *Brachychirotherium* Beurlen, 1950, *Isochirotherium* Haubold, 1971, *Parachirotherium* Kuhn, 1958, *Protochirotherium* Fichter and Kunz, 2004, *Parasynaptichnium* Mietto, 1987, *Sphingopus* Demathieu, 1966, and *Synaptichnium* Nopcsa, 1923. Furthermore we consider as archosaur tracks forms that have been described under the following names: *Aetosauripus* Weiss, 1934, *Agialopopus* Branson and Mehl, 1932, *Agrestipus* Weems, 1987, *Anchisauripus* Lull, 1904, *Atreipus* Olsen and Baird, 1986, *Banisterobates* Fraser and Olsen, 1996, *Batrachopus* Hitchcock, 1845, *Brontozoum* Hitchcock, 1847, *Coelurosaurichnus* v. Huene, 1941, *Dahutherium* Montenat, 1968, *Dinosaurichnium* Rehnelt, 1950, *Eubrontes* Hitchcock, 1845, *Evazoum* Nicosia and Loi, 2003, *Gigandipus* Hitchcock, 1856, *Grallator* Hitchcock,

		Archosaur- track- bearing units in North America and Germany - Correlation					
		North America		SouthernThuringia/ Northern Bavaria/ North. Hessen		Ichnotaxa	
Epoch	Age	NM, AZ, CO, UT, WY, TX	NJ, PA, VA, NC, CAN				
		Formations	Formations	Formations	Track Levels		
Late Triassic	Norian-Rhaet.	Chinle Group Rock Point Bell Springs Sheep Pen Sloan Canyon Redonda Bull Canyon Petrified Forest Bluewater Creek Garita Creek Dockum	Newark Supergroup Passaic Gettysburg Cow Branch Lockatong Wolfville Stockton Pekin	Keuper	Löwenstein	Burgsandstein	Grallator - Eubrontes Atreipus - Grallator Brachychirotherium Apatopus, C. lulli *
	Carnian				Hassberge Stuttgart	Coburger Sandstein Blasensandstein Ansbacher Sandstein	Brachychirotherium Atreipus - Grallator C. wondrai #
Middle Triassic	Ladinian	Moenkopi Group Holbrook and Anton Chico Wupatki	?	Muschelkalk	Benk	Benker Sandstein	Parachirotherium-Atr.-Grall. # Synaptichnium/ "Brachy." #
	Anisian				Grafenwöhr Eschenbach	mu, marginal facies Fränk. Chiroth.Sst. Grenzquarzit Plattensandstein Thüring. Chiroth. Sst.	Sphingopus-Atr.-Grall. # Synap/ "Brachy .", Iso., Roto. C. moquinense, rex *
Early Triassic	Olenekian			Buntsandstein	Röt		Chirotherium barthii Chirotherium sickleri C. moquinense *
	Induan				Solling		Isochirotherium Synap., Roto. Rotodactylus Protochirotherium #
					Detfurth ←		

FIGURE 1. Archosaur footprint horizons and track-bearing formations in North America and southern Thuringia/northern Bavaria (Germany). In nearly complete sequences, the intercontinental distributions of characteristic ichnotaxa are used for correlation. Notice conformity of the assemblages at the corresponding levels and differences due to the gap in the North American record between the late Anisian and late Ladinian.

1858, *Gregaripus* Weems, 1987, *Otozoum* Hitchcock, 1847, *Pachysaurichnium* Demathieu and Weidmann, 1982, *Prorotodactylus* Ptaszynski, 2000, *Rigalites* v. Huene, 1931, *Swinertonichnus*, Sarjeant, 1967 and *Thecodontichnus* v. Huene, 1941. These ichnotaxa pertain to specimens from different parts of the Triassic and their alphabetical listing above does not indicate an evaluation of their validity. A special taxonomic situation surrounds the tracks from the Upper Triassic of Lesotho for which Ellenberger (1972) introduced a wide variety of names like *Anatrisauropus*, *Bosiutrisauropus*, *Deuterosauropodopus*, *Deutrotisauropus*, *Paratetrasauropus*, *Paratrisauropus*, *Pentasauropus*, *Prototrisauropus*, *Pseudotetrasauropus*, *Pseudotrisauropus*, *Psilotrisauropus*, *Qemetrisauropus*, *Sauropodopus*, *Seakatrisauropus*, *Tetrasauropus*, and *Trisauropodiscus*. Comparisons of these with ichnotaxa described from elsewhere, and consensus on synonymies, are still in progress; most of his ichnotaxa have not been recognized outside Lesotho and are generally perceived (even in the absence of detailed analyses) as junior synonyms of other, better-known ichnotaxa.

Even larger is the number of ichnospecies that have been established within the aforementioned ichnogenera. For *Chirotherium* alone, the authors counted 50 species names; for all chirotherians, in nearly any combination within the ichnogenera, there are at least 75 ichnospecies. Altogether, about 50 ichnogenera and about 180 ichnospecies have been ascribed to Triassic archosaurs. The status of many ichnotaxa is doubtful; in many cases, they are demonstrably synonyms of well-established taxa. However, this synonymy is evaluated differently, depending on the material and the describing author. Some authors have erected ichnotaxa while ignoring extramorphology, a phenomenon that was recognized as having a misleading influence on tetrapod ichnotaxonomy as long ago as Peabody (1948). For many of the named ichnotaxa, synonymy remains open, and such forms must be considered phantom taxa (*sensu* Haubold, 1996).

Following the very precise guidelines established by Peabody (1955a), ichnospecies and ichnogenera cannot be definitively attributed to a species or genus that is based on body fossils. Body fossil genera are nearly equivalent to ichnospecies. So, the lowest level to which a Triassic archosaur track can be differentiated corresponds with an osteological genus. Consequently, the number of named ichnotaxa cited above would imply a correlative number of osteological ichnogenera. This seems unrealistic – the presently documented ichnological archosaur diversity in the Triassic must be reduced substantially to a smaller number of ichnogenera and ichnospecies.

TRIASSIC ARCHOSAUR FOOTPRINTS – THE EVIDENCE

Early Early Triassic

Tetrapod footprints from this interval come from the Labyrinthodontidae Beds (late Induan) of Wióry (Poland) and from the Dethfurt and Hardegsen formations (early Olenekian) of northern Hessen, Germany (Demathieu and Haubold, 1982; Fuglewicz et al., 1990; Ptaszynski, 2000; Fichter and Kunz, 2004). Essential components of these assemblages are *Synaptichnium* (Fig. 2A-B) and *Protochirotherium*, including the type species of the latter, *P. wolfhagense* Fichter and Kunz, 2004 (Figs. 2C, 3A-B). The status of *Synaptichnium* and the relationship to *Protochirotherium* is uncertain (see also below). From the locality in Poland, *Brachychirotherium* and *Isochirotherium* were described by Fuglewicz et al. (1990) and Ptaszynski (2000). However, the features exhibited by these specimens, particularly the digit proportions (long pedal digit IV), differ from those listed in the diagnoses for these taxa (Beurlen, 1950; Haubold, 1971b; Karl and Haubold, 1998). We therefore refer this material to *Protochirotherium* (Fig. 2D-E). *Synaptichnium* and *Protochirotherium* indicate a primitive archosaur foot morphology typified by long pedal digits IV and V.

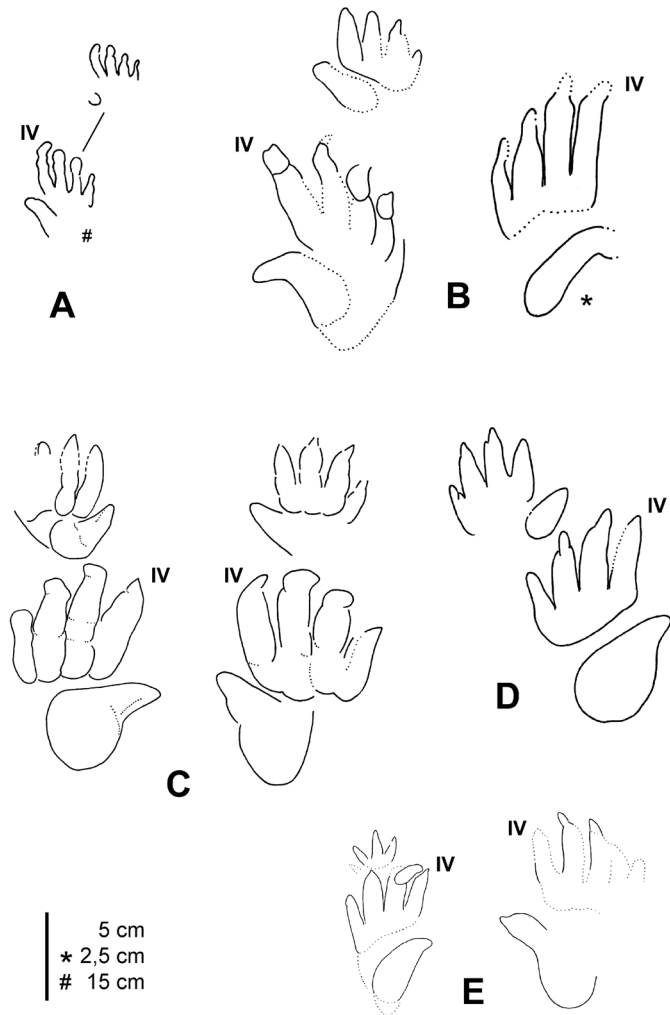


FIGURE 2. Characteristic archosaur footprints from the early Early Triassic. **A, B**, *Synaptichnium*, Hardegsen Fm., Hessen and Labyrinthodontidae beds, Wióry, Poland. **C**, *Protochirotherium wolfhagense* Fichter and Kunz, 2004, Dethfurt Fm., Hessen (holotype at right). **D, E**, *Protochirotherium* (*Brachychirotherium* and *Isochirotherium* after Ptaszynski, 2000 and Fuglewicz et al., 1990), Labyrinthodontidae beds, Wióry. Notice digit proportions and long digits IV and V in the pes. **A** after Demathieu and Haubold (1982); **B, D, E** after Ptaszynski (2000) and Fuglewicz et al. (1990).

Late Early Triassic and Middle Triassic

Beginning in the late Olenekian, there is evidence of a broad spectrum of archosaur tracks in the global record, exemplified by *Rotodactylus*, *Synaptichnium*, *Isochirotherium* and *Chirotherium*, reflecting different evolutionary developments in foot morphology and a biological diversity not thus far documented by the skeletal record. From strata in the “Thüringischer Chirotheriensandstein” (late Olenekian-Anisian) of southern Thuringia, dense concentrations of pentadactyl pes and manus impressions of *Rotodactylus* are known (Fig. 4A-C; Haubold, 1967, 1971a, b, 1999). A characteristic feature of *Rotodactylus* is the dominance of digit group II-IV and the extreme posterior position of a small punctiform mark that constitutes the impression of digit V. The digit proportions are $I < II < III < IV$. Trackways preserve evidence of long strides and a primary, lateral overstep of the manus by the pes, though respective values of overstepping and stride length show high variability. The data indicate cursorial trackmakers that, with our present knowledge, must be attributable to dinosauromorphs comparable in “grade” to lagosuchians

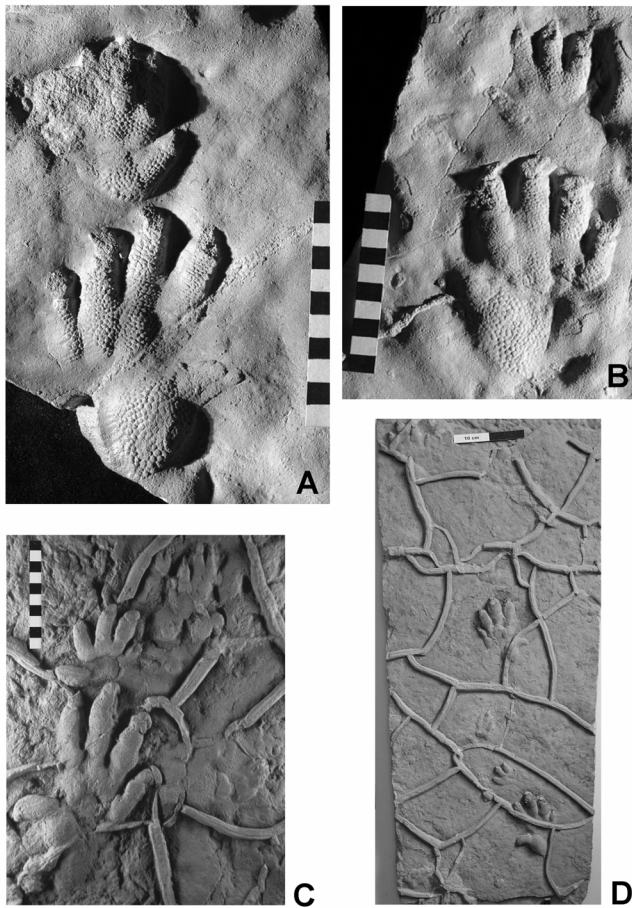


FIGURE 3. **A, B**, *Protochirotherium wolfhagense* Fichter and Kunz, 2004 pes and manus imprints with preserved skin impressions (holotype at right) from the Detfurth Fm. (Olenekian) of Hessen, Germany. **C, D**, *Chirotherium barthii* and *C. sickleri* from the type surface in the Thüringischer Chirotheriensandstein, Olenekian-Anisian of southern Thuringia (Germany). **C**, *C. barthii* (center), *C. sickleri* (upper right) and small “*Brachychirotherium*” (lower right). **D**, Trackways of *C. barthii* and *C. sickleri*. Notice differences in digit proportions, particularly the long pedal digit IV in *C. sickleri* compared with *C. barthii*. **A, B**, from casts in the Institute for Geological Sciences, Martin-Luther-University Halle-Wittenberg (original material in the Provincial Museum Wolfhagen, Hessen); **C, D**, from Haubold (2006).

(Haubold, 1999). *Rotodactylus* was first described from material from the Moenkopi Group of Arizona by Peabody, 1948 (see above). Additional important evidence comes from the Middle Triassic of France (Demathieu and Gand, 1973).

Synaptichnium continues from the Early into the Middle Triassic.

This ichnogenus retains an overall conservative foot structure and long digits IV and V. (Fig. 5A-E). Such footprints are recorded on surfaces in the Moenkopi Group of Arizona (Peabody, 1948) and the Middle Triassic of England, France, Italy and Germany (Demathieu, 1970; Tresise and Sarjeant, 1997; Avanzini, 2000; Klein and Haubold, 2004). The ichnotaxonomic situation in *Synaptichnium* is complicated by the following circumstances: (1) no type has been fixed thus far (see Nopsca 1923, Haubold, 1971b), (2) *Synaptichnium* in the early Early Triassic can possibly be synonymized with *Protochirotherium* (see above), and (3) footprints described under *Synaptichnium* from the late Early – Middle Triassic show a transition to “*Brachychirotherium*” in different extramorphological variations, (Klein and Haubold, 2004; see below). The ichnotaxon is presently under revision by the authors. A primary component of the assemblages in Germany and France are footprint morphs that have been referred to *Brachychirotherium* (Haubold, 1971b). However, in the revision of the type material from the Keuper (Karl and

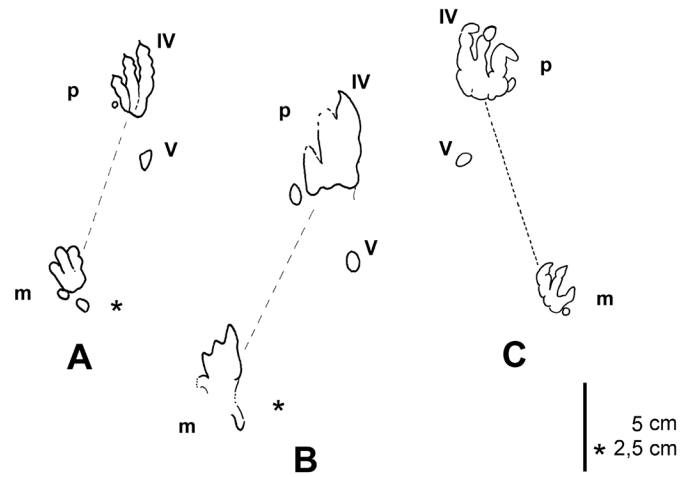


FIGURE 4. Tracks of *Rotodactylus* from late Early and Middle Triassic. **A**, *Rotodactylus matthesi*, Thüringischer Chirotheriensandstein, southern Thuringia. **B**, *Rotodactylus cursorius*, Moenkopi Group, Arizona. **C**, *Rotodactylus lucasi*, Anisian-Ladinian, Massif Central, France. Notice posterior position of digit V and overstepped manus. After Peabody (1948), Haubold (1967), and Gand (1976).

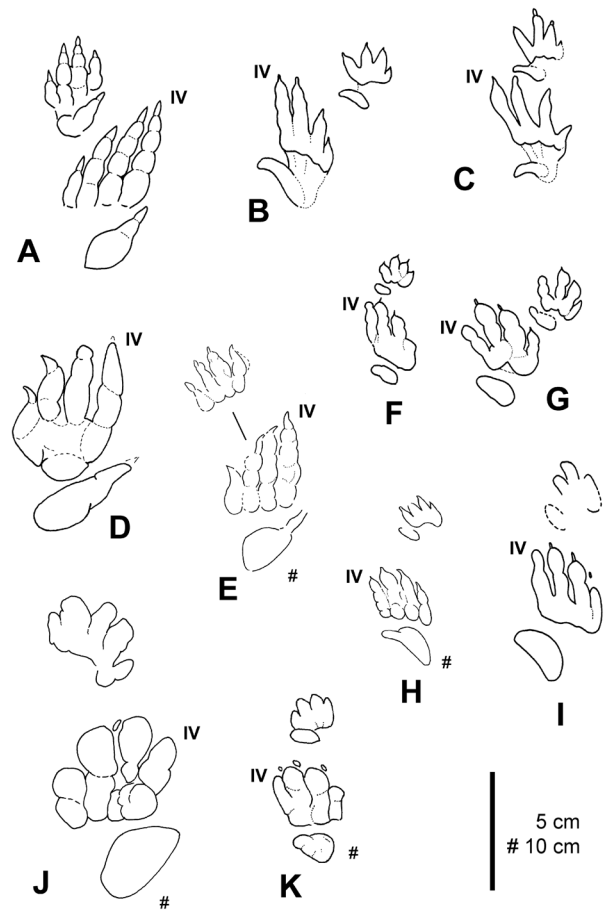


FIGURE 5. **A-E**, *Synaptichnium* and **H-K**, “*Brachychirotherium*” from the late Early and Middle Triassic, from **A**, Great Britain; **B, C**, Moenkopi Group, Arizona; **D, J, K**, Anisian-Ladinian, Massif Central, France; **E**, Eschenbach Fm., northern Bavaria; **F, G**, Thüringischer Chirotheriensandstein, southern Thuringia; and **H, I**, Röt Fm., northern Bavaria. Notice conservative pes morphology with long digits IV and V. After Peabody (1948), Haubold (1971b, 1984), and Klein and Haubold (2004).

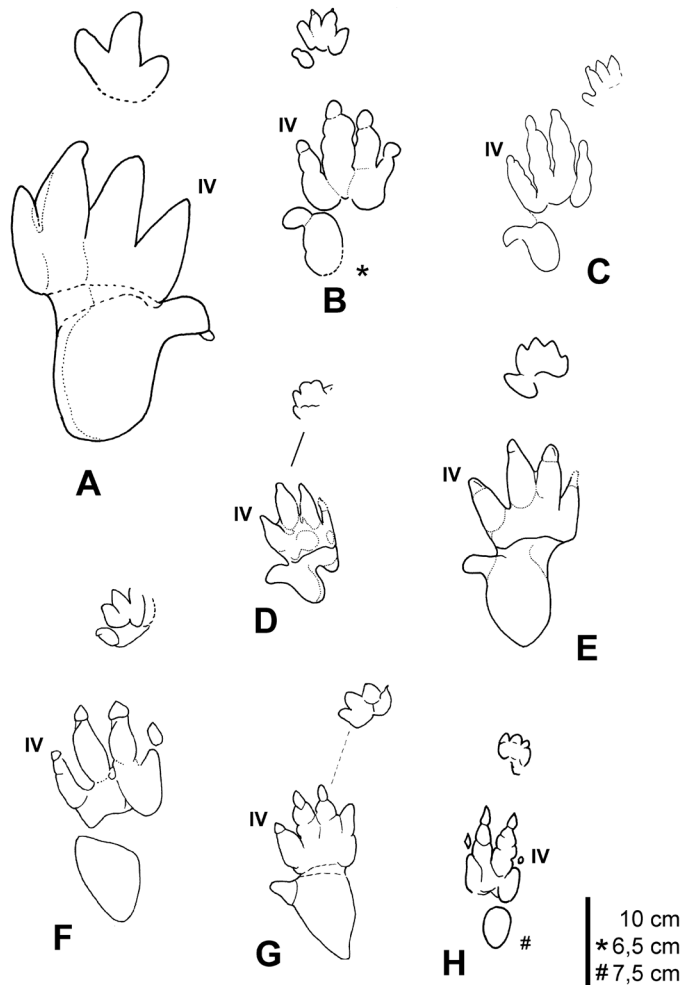


FIGURE 6. *Isochirotherium* from the late Early and Middle Triassic, from **A, B**, Thüringischer Chirotheriensandstein, southern Thuringia; **C**, Cheshire, Great Britain; **D, E**, Moenkopi Group, Arizona; and **F-H**, Anisian-Ladinian, Massif Central, France. Important are the digit proportions in the pes, with digits II and III longest, in some cases II>III. The manus is extremely small compared to the pes. After Peabody (1948), Demathieu (1970), Haubold (1971b) and Courel and Demathieu (1976).

Haubold, 1998, 2000), their relationship to Late Triassic *Brachychirotherium* turned out to be problematic. Consequently, the so-called “brachychirotherians” of the Middle Triassic are referred to here as “*Brachychirotherium*” (Fig. 5F-K). They are demonstrably extramorphological variants of *Synaptichnium* (Klein and Haubold, 2004), though they form a characteristic and striking group of track morphs particularly in the late Middle Triassic (Demathieu, 1970; Demathieu and Gand, 1973; Courel and Demathieu, 1976; Demathieu and Demathieu, 2004).

Isochirotherium (Fig. 6A-H), the type species of which is *Isochirotherium soergeli* from surfaces of the “Thüringischer Chirotheriensandstein” (Fig. 6B), exhibits a striking dominance of II and III in the digit proportions of the pes (II > III in part) and an extremely small manus impression compared to that of the foot (Haubold, 1971b). This track type can be interpreted as an evolutionary trend toward a tridactyl foot pattern comprised of digits I, II, III rather than the II, III, IV pattern displayed by *Grallator*, for example. The tracks are also present in the Moenkopi Group of Arizona and the Middle Triassic of Great Britain, France and Italy (Peabody, 1948; Courel and Demathieu, 1976; Gand, 1979; Tresise and Sarjeant, 1997; Avanzini and Lockley, 2002).

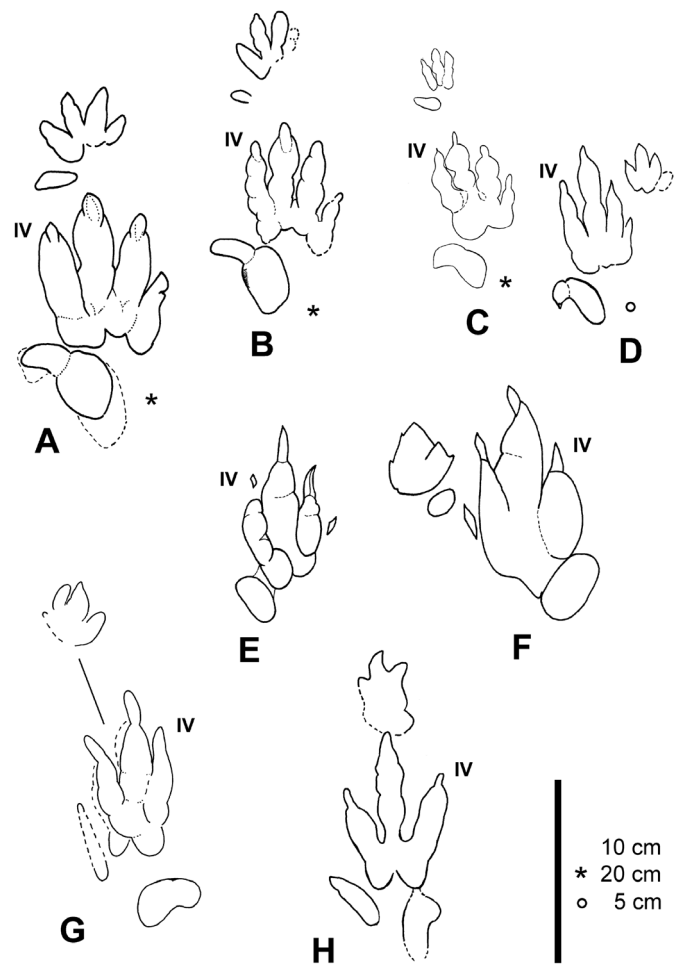


FIGURE 7. Pentadactyl tracks from the late Early and Middle Triassic showing the initial stages of a trend toward tridactyly via reduction of digit V and a posterior shift of digit I. **A, B**, *Chirotherium barthii*, type surface of the Thüringischer Chirotheriensandstein, Hildburghausen. **C, D**, *C. sickleri*, Thüringischer Chirotheriensandstein. **E, F**, *Sphingopus ferox*, Anisian/Ladinian, Massif Central, France. **G, H**, *Sphingopus* isp. and *Parachirotherium postchirotherioides*, Eschenbach–Benk fms., northern Bavaria. After Demathieu (1966, 1970), Haubold (1971a, b), and Haubold and Klein (2000).

In *Chirotherium*, particularly in the type species *C. barthii*, the initial stages of the development of the tridactyl dinosaurian foot are indicated by the posteriorly shifted pedal digit I and the dominance of digits II-IV (Figs. 3C-D, 7A-B; Haubold and Klein, 2002). *Chirotherium* manus impressions display a distinctive (dinosaurian) reduction of digits IV and V. Compared to *C. barthii*, the smaller *C. sickleri* appears to be more conservative in its retention of a long pedal digit IV (Figs. 3C-D, 7C-D). *C. barthii* footprints are one of the best documented Triassic archosaur tracks, including specimens from the classic Buntsandstein locality (Olenekian-Anisian) of Hildburghausen (Haubold 1971a, 2006) and abundant material from corresponding stratigraphic levels in England (Tresise and Sarjeant, 1997), Arizona (Peabody, 1948), France (Demathieu, 1984), Spain (Calderon, 1897), Scotland (Clark et al., 2002), Argentina (Peabody, 1955b) and China (Lü et al., 2004).

Between the late Anisian and late Ladinian, additional tracks with a principally pentadactyl imprint morphology similar to *C. barthii* can be recognized in *Sphingopus* and *Parachirotherium*. (Fig. 7E-H). The dominance of the main digit-group II-IV, with III being longest, is a striking feature, as is the posteriorly-shifted digit I, following the trend established by *C. barthii*. The type species, *S. ferox* (Fig. 7E-F), was first described by Demathieu (1966) from the Middle Triassic of the

eastern margin of the Massif Central (France). Subsequently, *Spingopus* has been documented in strata of similar age from the western margin of the Bohemian Massif in northern Bavaria (Haubold and Klein, 2002; Fig. 7G). *Parachirotherium postchirotherioides* is known from the Benker Sandstein (Middle Keuper, Late Ladinian) of northern Bavaria (Rehnelt, 1950; Kuhn, 1958; Haubold and Klein 2000; Fig. 7H). *Spingopus* and *Parachirotherium* possess small manus imprints.

The oldest truly tridactyl pes imprints are late Anisian in age. They occur alongside pentadactyl *Spingopus* and *Parachirotherium* tracks, often in trackways demonstrating that the track maker was capable of adopting a facultatively bipedal gait. They have been described under the names *Coelurosaurichnus* and *Anchisauripus* (Rehnelt, 1950; Weiss 1976; Demathieu, 1989; Gand and Demathieu, 2005; Gand et al., 2005), and they can be referred to *Atreipus-Grallator* (Figs. 8A-D). Especially in *Parachirotherium*, the transition from a pentadactyl quadruped to a tridactyl biped is documented in single trackways (Haubold and Klein, 2000).

Late Triassic

In this time interval, assemblages with archosaur tracks are characterized by the following taxa and imprint forms:

Brachychirotherium (Fig. 9A-E), beginning in the Carnian, with

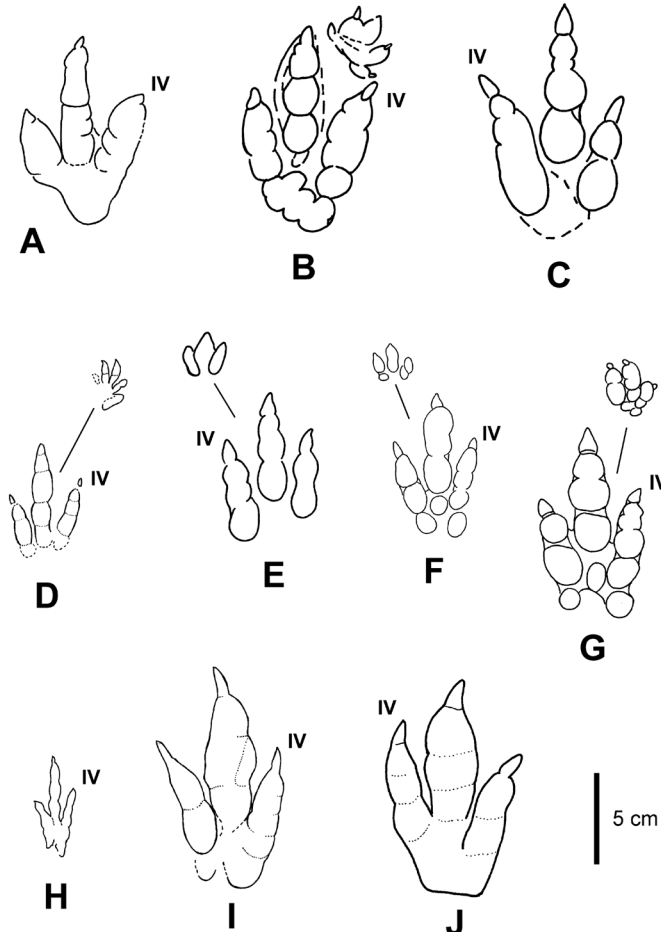


FIGURE 8. Tridactyl tracks *Atreipus-Grallator* (“*Coelurosaurichnus*,” “*Anchisauripus*”) from the Middle and Late Triassic with occasional impressions of the manus, reflecting a tendency toward bipedalism, from A-C, Anisian-Ladinian, Massif Central, France; D, Upper Ladinian, Benker Sandstein, northern Bavaria; E, Carnian, Massif Central, France; F, Carnian, Ansbacher Sandstein, northern Bavaria; G, Norian, Newark Supergroup; and H-J, Upper Carnian, Coburger Sandstein, northern Bavaria. After Haubold (1971b), Olsen and Baird (1986), Courel and Demathieu (2000), Haubold and Klein (2000), and Gand and Demathieu (2005).

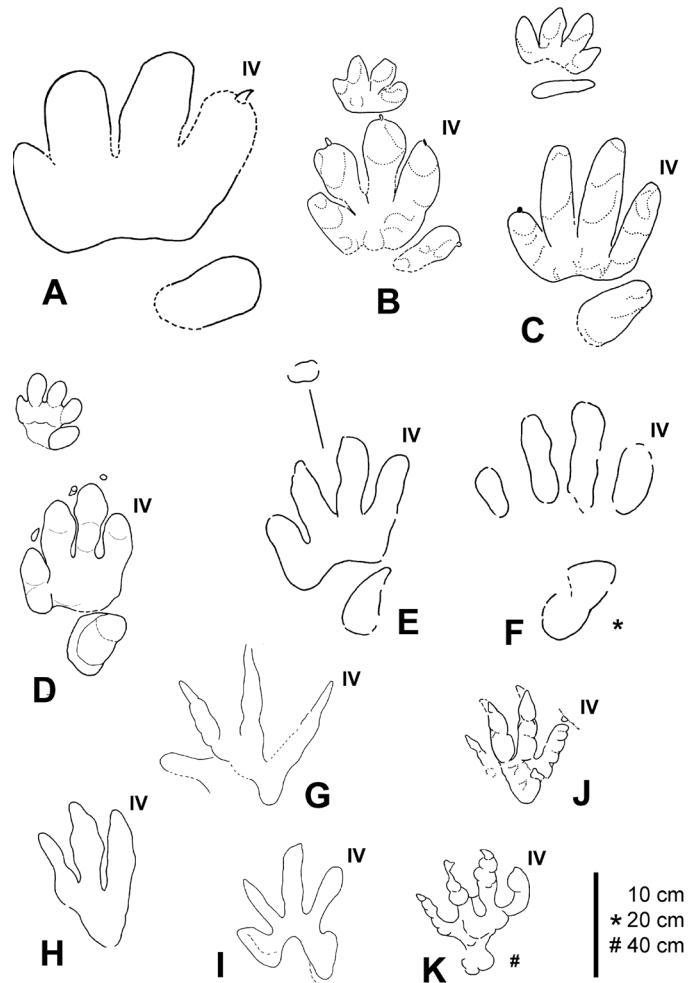


FIGURE 9. *Brachychirotherium*. A, *Brachychirotherium hassfurtense* (type species), Late Carnian, Coburger Sandstein. B, C, *B. thuringiacum*, Late Carnian, Coburger Sandstein and Blasensandstein, northern Bavaria. D, *B. parvum*, Passaic Fm., New Jersey. E, *B. sp.*, Passaic Fm., Pennsylvania. F-K, Extramorphological variations of *Brachychirotherium* (“*Pseudotetrasauropus*,” “*Evazoum*,” “*Otozoum*”), from F, Norian, Lower Elliot Fm., South Africa; G-I, Norian, Redonda Fm. New Mexico; J, Carnian, Italy; and K, Norian, France. After Baird (1957), Karl and Haubold (1998), Gand et al. (2000), Nicosia and Loi (2003), and Klein et al. (2006).

the type species *Brachychirotherium hassfurtense* (Fig. 9A) plus *B. thuringiacum* (Fig. 9B-C) from surfaces of the Coburger- and Blasensandstein of northern Bavaria and southern Thuringia (Beurlen, 1950, Karl and Haubold, 1998, 2000), this ichnogenus occurs in North America up to the Triassic-Jurassic boundary (Baird, 1957, Silvestri and Szajna, 1993; Silvestri and Olsen, 1989; Szajna and Silvestri, 1996; Szajna and Hartline, 2003; Olsen et al., 2002; Fig. 9D-E). *Brachychirotherium* is characterized by a broad, pentadactyl pes imprint with short, blunt digits and tiny claws. The fifth digit, represented only by an oval basal pad, occupies a posterolateral position. The manus exhibits a similar morphology.

Imprint forms that have been described under *Pseudotetrasauropus*, *Evazoum* or *Otozoum* from the Carnian-Norian of South Africa, North America, Italy and France (Ellenberger, 1970, 1972; Gand et al., 2000; Lockley et al., 2000, 2006; Lucas et al., 2001; Nicosia and Loi, 2003; Fig. 9F-K) are, in most cases, extramorphological variants of *Brachychirotherium* that appear different because their manufacture was controlled by differing conditions of the substrate and, possibly, variable gaits (see Klein et al., 2006 for details).

Atreipus, *Grallator*, and *Eubrontes* (type species *Atreipus*

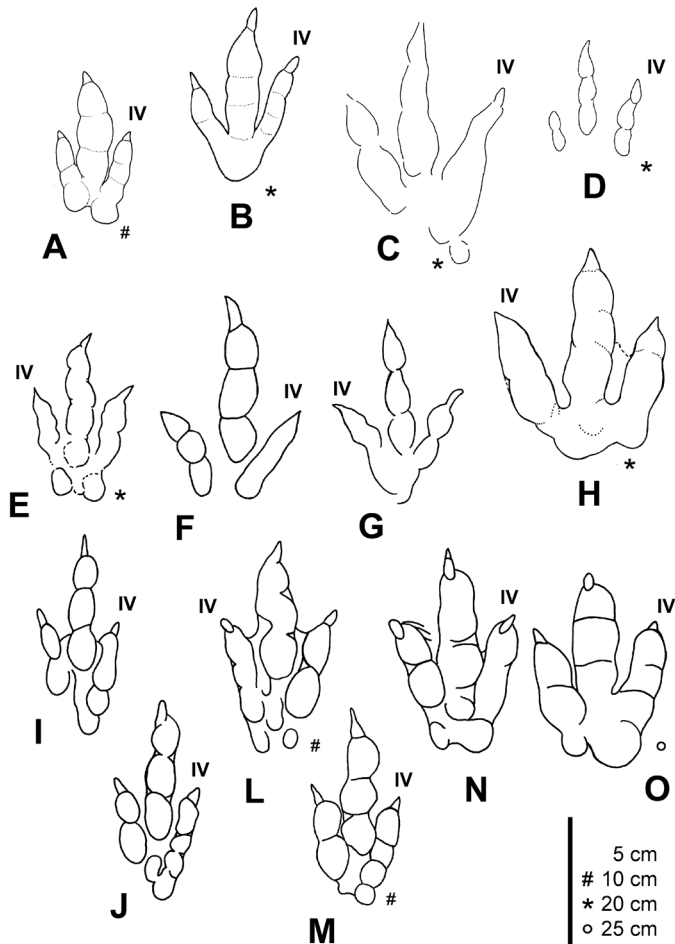


FIGURE 10. *Grallator*–*Eubrontes*. Tridactyl bipedal tracks from the Norian to Early Jurassic; from **A**, Norian, Wales, Great Britain; **B**, ?Rhaetian–Early Jurassic, northern Bavaria; **C**, Lower Elliot Fm., South Africa; **D**, Norian, southern France; **E–G**, Norian, Chinle Group, Utah, New Mexico, Colorado; **H**, Rhaetian, Sweden; and **I–O**, Lower Jurassic Newark Supergroup, (**I, J**, *Grallator*; **L, M**, *Anchisauripus*; and **N, O**, *Eubrontes*). After Haubold (1971b), Gierlinski and Ahlberg (1994), Lockley and Hunt (1995), Olsen et al., (1998), Hunt et al. (2000), Gaston et al. (2003), and Gand and Demathieu (2005).

milfordensis from the Passaic Formation, and *Grallator parallelus* and *Eubrontes giganteus* from the Lower Jurassic part of the Newark Supergroup [Hitchcock, 1836, 1845, 1947, 1858; Bock, 1952; Olsen and Baird, 1986; Silvestri and Olsen, 1989; Silvestri and Szajna, 1993; Szajna and Silvestri, 1996; Olsen et al., 2002; Szajna and Hartline, 2003]) are tridactyl, mesaxononic pes imprints of different sizes (Figs. 8E–J, 10) that are widely distributed between the Carnian and Early Jurassic, with occurrences in Germany, Great Britain, Switzerland, France, Sweden, Greenland, and the Lower Elliot Formation of South Africa (Ellenberger, 1970, 1972, 1974; Furrer, 1993; Gierlinski and Ahlberg, 1994; Jenkins et al., 1994; Lockley et al., 1996; Gatesy et al., 1999; Haubold and Klein, 2000, 2002; Gand et al., 2000, 2003; Milàn et al., 2004). Occasionally manus imprints are associated with older trackways (e.g., *Atreipus*). From the late Norian, for example in the Redonda Formation of New Mexico, only bipedal *Grallator* and *Eubrontes* are present, though in the Newark Supergroup *Atreipus* still occurs in the Rhaetian.

INTERPRETATION – THE BIOCHRONOLOGICAL POTENTIAL

From the preceding overview, it is obvious that the vertical (stratigraphic) distribution of some archosaurian ichnotaxa and form groups in

the global record demarcate distinct biostratigraphic units that themselves occur in distinct, limited chronostratigraphic intervals. Hence, an attempt is made to establish the following archosaur footprint-based biochronological concept for the Triassic.

Protochirotherium (*Synaptichnium*) is characteristic of the Induan-late Olenekian interval. *Protochirotherium*, temporally as well as morphologically, matches the hypothetical morphology of a basal archosaur and is the basis for later evolutionary developments and form groups. Its position marks the beginning of the biochronological succession. Between the late Olenekian (at which time *Protochirotherium* disappears) and the late Ladinian, further biochronological potential is offered by *Rotodactylus*, *Isochirotherium*, *Synaptichnium* and “*Brachychirotherium*”. Their stratigraphic distributions essentially span the Middle Triassic. The stratigraphic upper limits of *Rotodactylus* and *Isochirotherium* are early Ladinian. *Brachychirotherium* (*sensu stricto*) spans the Upper Triassic, from the Carnian to the Triassic–Jurassic boundary.

The greatest biochronological potential lies in coupling the stratigraphic succession of the tracks with the functional evolutionary stages in the development of the tridactyl foot morphology and bipedal gait of dinosaurs that they delineate. They can be followed in an evolutionary succession between the late Olenekian and Early Jurassic, documenting morphological and behavioral changes, including trackways made by individuals shifting from quadrupedal to facultative bipedal locomotion. This transition is ichnotaxonomically delineated via the following sequence: *Chirotherium* – *Sphingopus* – *Parachirotherium* – *Atreipus* – *Grallator*. The stratigraphic ranges of these five ichnotaxa correspond with the Olenekian–Anisian, Anisian–Ladinian, Ladinian, Carnian–Norian and Norian–Rhaetian, respectively. The range of the pentadactyl forms in this succession is limited to pre-Carnian strata; after that time, the tracks are tridactyl.

An alternative, as well as a supplement and clarification of earlier biochronological concepts, is offered here. Attempts to tie ichnostratigraphy and correlation of sequences have been made by Haubold (1969, 1971b, 1984, 1986), Demathieu and Haubold (1972, 1974), Olsen (1980, 1983), Lockley and Hunt (1993, 1995), and Lucas (2003). Further contributions to this topic can be found in Ellenberger (1970, 1972, 1974), Demathieu (1984), Olsen and Galton (1984), Olsen and Baird (1986), Silvestri and Olsen (1989), Silvestri and Szajna (1993), Lockley et al. (1996), Szajna and Silvestri (1996), Avanzini et al. (2001), Lucas and Hancox (2001), Olsen et al. (2002), Szajna and Hartline (2003), Lucas and Huber (2003), Lucas and Tanner (2004), Gand et al. (2003), Lucas and Sullivan (2006), and Lucas et al. (2006a, b). Evident in all of these studies are different approaches of the respective authors to the fundamental problem of the non-uniform assignment and naming of tracks, particularly the differing methods of evaluating and dealing with extramorphological phenomena, specifically substrate-controlled features in track morphology (see above). As a consequence, different stratigraphic ranges of taxa have been stated and conclusions reached by the different authors. The concept presented here is based on principal form groups and the evolutionary developments they represent. By this reduction to the documentation of essential “lines,” the temporal distribution pattern becomes apparent and offers possibilities for biochronological classification of the Triassic by archosaur footprints.

RESULTS

After analysis of the global record of archosaur tracks from the Triassic, a biochronological succession of six biochronological units (biochrons) is derived from the stratigraphic distribution of several characteristic forms and assemblages. Each unit represents a certain time span, the beginning of which is marked by the first appearance datum (FAD) of an index taxon. In the following, the principal index ichnotaxon is marked in bold. The units are:

I. *Protochirotherium* (*Synaptichnium*): FAD: Late Induan. Distribution: Late Induan–Olenekian.

II. *Chirotherium*, *Rotodactylus*, *Isochirotherium*, *Synaptichnium*

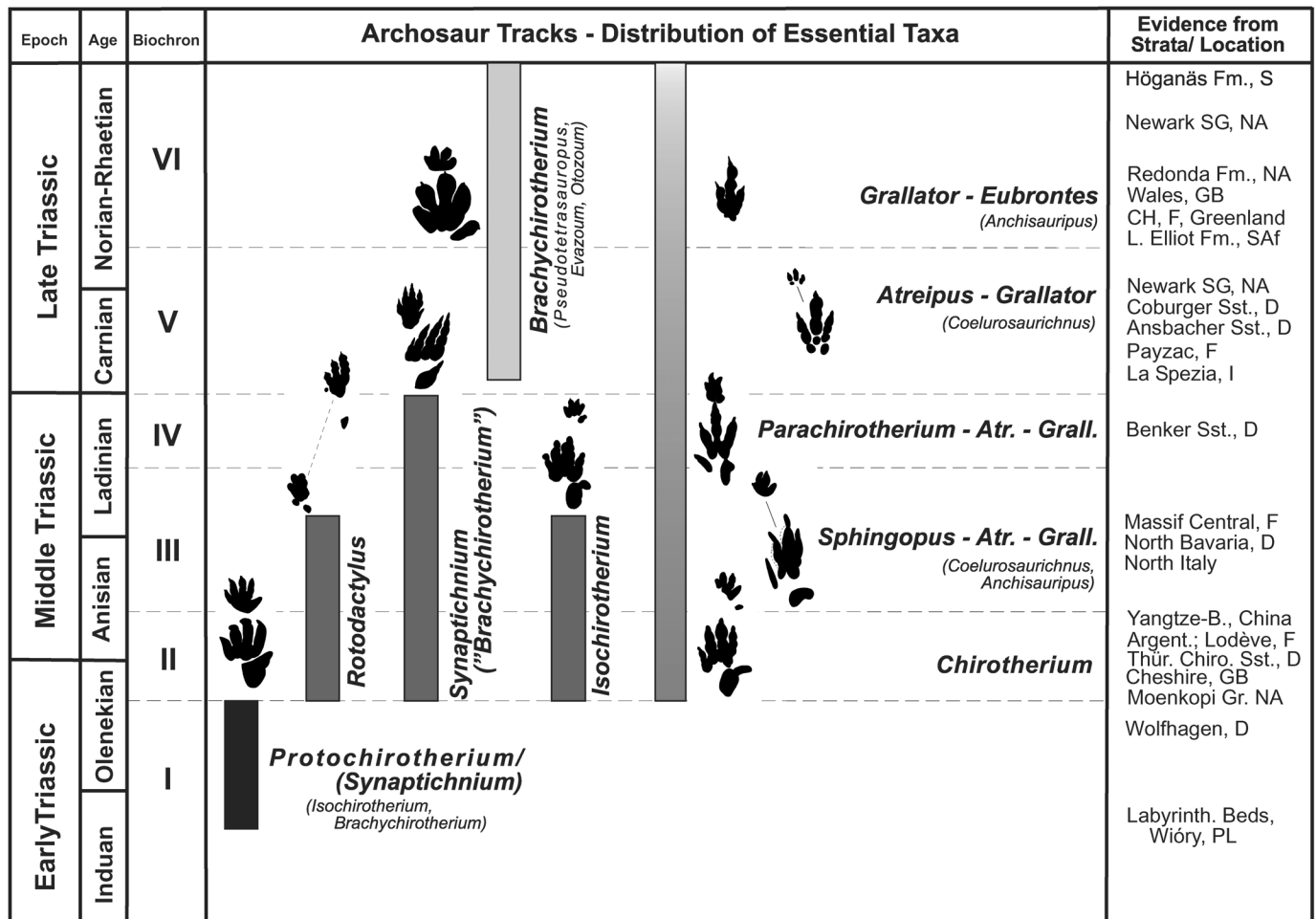


FIGURE 11. Stratigraphic distribution of characteristic archosaur tracks in the Triassic in biochrons I-VI and source track-bearing units and locations. Common synonyms and extramorphological variants that have been treated as distinct ichnotaxa to date are indicated in brackets. The track-bearing strata and locations are listed according to their stratigraphic positions. Notice evolutionary sequence and different stages in the development from pentadactyl to tridactyl pes morphology and of bipedality in *Chirotherium* through *Eubrontes* between the late Olenekian and Norian-Rhaetian. After Haubold (1971b), Olsen and Baird (1986), Karl and Haubold (1998), and Haubold and Klein (2000).

("Brachychirotherium"): FAD: late Olenekian. Distribution: Late Olenekian-Anisian.

III. *Sphingopus* – *Atreipus* – *Grallator*, *Rotodactylus*, *Isochirotherium*, *Synaptichnium* ("Brachychirotherium"): FAD: Late Anisian. Distribution: Late Anisian-Ladinian.

IV. *Parachirotherium* – *Atreipus* – *Grallator*, *Synaptichnium* ("Brachychirotherium"): FAD: Late Ladinian. Distribution: Late Ladinian.

V. *Atreipus*-*Grallator*, *Brachychirotherium*: FAD: Carnian. Distribution: Carnian-Norian.

VI. *Grallator*-*Eubrontes*, *Brachychirotherium*: FAD: Norian. Distribution: Norian-Rhaetian.

Most of the taxa that have been described and named can now be referred to one of these biochrons. In Figure 11, the different evolutionary sequences and biochrons are plotted. The composition of the ichnotaxonomic groupings and track sequences is based on the following ichnotaxa:

1. *Protochirotherium*. Late Induan-late Olenekian. Type species: *P. wolfhagensis* Fichter and. Kunz, 2004.

2. *Rotodactylus*. Late Olenekian-early Ladinian. Type species: *R. cursorius* Peabody, 1948.

3. *Synaptichnium*. Late Induan-late Ladinian. Type species: *S. pseudosuchoides* Nopcsa, 1923.

4. "Brachychirotherium." Late Olenekian-Late Ladinian. Tracks described under *Brachychirotherium* but with a doubtful relation to Upper

Triassic forms (see Karl and Haubold, 1998; Klein and Haubold, 2004).

5. *Brachychirotherium*. Carnian-Rhaetian. Type species: *B. hassfurtense* (Beurlen 1950); see also Karl and Haubold, 1998, 2000).

6. *Isochirotherium*. Late Olenekian-early Ladinian. Type species: *I. soergeli* (Haubold 1967); see also Haubold, 1971b.

7. *Chirotherium*. Late Olenekian-early Anisian. Type species: *C. barthii* Kaup, 1835.

8. *Sphingopus*. Late Anisian-early Ladinian. Type species: *Sphingopus ferox* Demathieu, 1966.

9. *Parachirotherium*. Late Ladinian. Type species: *P. postchirotherioides* (Rehnelt 1950); see also Kuhn, 1958.

10. *Atreipus*. Carnian-Norian. Type species: *A. milfordensis* (Bock 1952); see also Olsen and Baird, 1986.

11. *Grallator*. Norian-Early Jurassic. Type species: *Grallator parallelus* (Hitchcock 1847); see also Hitchcock, 1858.

12. *Eubrontes*. Norian-Early Jurassic. Type species: *E. giganteus* (Hitchcock 1836); see also Hitchcock, 1845.

CONCLUSIONS

The stratigraphic distribution of the principal morphs of archosaur tracks reflects different phylogenetic trajectories of the locomotor apparatus and foot morphology of archosaurs through the Triassic. Several functional evolutionary track sequences can be differentiated, each composed of characteristic taxa and form groups that characterize a certain

time span. Beginning with early forms like *Protochirotherium* and *Synaptichnium* and through *Isochirotherium*, *Rotodactylus*, and *Brachychirotherium*, the evolution of the plesiomorphic tridactyl dinosaurian foot morphology and bipedality is documented in tracks from *Chirotherium* to *Eubrontes*. The sequence offers a biochronological potential that has not been considered so far. The stratigraphic distribution pattern is summarized in six units (biochrons I-VI). Although the quantity and quality of anatomical signals preserved in footprints is limited, some archosaur tracks give insight in the evolutionary context of their producers. This information, in tandem with their distinct stratigraphic distributions, makes Triassic archosaur footprints valuable for

biochronology, especially in continental sequences where skeletal evidence is rare or missing. Furthermore, they often appear in dense concentrations and are geographically widespread. This potential can be used and augmented in the future through global prospecting of regions and sequences that have not been examined so far. The recent discovery of *Chirotherium barthii* in the Middle Triassic of the Yangtze basin of southern China (Lü et al., 2004) is just such a positive indication of the potential to utilize the track record of Triassic archosaurs.

ACKNOWLEDGMENTS

The authors thank A.B. Heckert and J.D. Harris who reviewed the manuscript and helped to improve it by their comments.

REFERENCES

- Avanzini, M., 2000, *Synaptichnium* tracks with skin impressions from the Anisian (Middle Triassic) of the Southern Alps (Val di Non – Italy): *Ichnos*, v. 7, p. 243-251.
- Avanzini, M. and Lockley, M., 2002, Middle Triassic archosaur population structure: interpretation based on *Isochirotherium delicatum* fossil footprints (Southern Alps, Italy): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 185, p. 391-402.
- Avanzini, M., Ceoloni, P., Conti, M.A., Leonardi, G., Manni, R., Mariotti, N., Mietto, P., Muraro, C., Nicosia, U., Sacchi, E., Santi, G. and Spezzamonte, M., 2001, Permian and Triassic tetrapod ichnofaunal units of northern Italy: their potential contribution to continental biochronology: *Natura Bresciana (Annali del Museo Civico di Scienze Naturale di Brescia)*, Monografia N. 25, p. 89-107.
- Baird, D., 1957, Triassic reptile footprint faunules from Milford, New Jersey: *Bulletin of the Museum of Comparative Zoology*, v. 117, p. 449-520.
- Beurlen, K., 1950, Neue Fährtenfunde aus der fränkischen Trias: *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, p. 308-320.
- Bock, W., 1952, Triassic reptilian tracks and trends of locomotive evolution: *Journal of Paleontology*, v. 26, p. 395-433.
- Branson, E.B., and Mehl, M.G., 1932, Footprint records from the Paleozoic and Mesozoic of Missouri, Kansas and Wyoming: *Geological Society of America Bulletin*, v. 43, p. 383-398.
- Calderon, S., 1897, Una huella de *Chirotherium* de Molina de Aragon: *Actas de la Sociedad Española de Historia Natural*, v. 26, p. 27-29.
- Clark, N.D.L., Aspen, P. and Corrance, H., 2002, *Chirotherium barthii* Kaup 1835 from the Triassic of the Isle of Arran, Scotland: *Scottish Journal of Geology*, v. 38, p. 83-92.
- Cornet, B. and Traverse, A., 1975, Palynological contributions to the chronology and stratigraphy of the Hartford Basin in Connecticut and Massachusetts: *Geoscience and Man* v. 11, p. 1-33.
- Courel, L. and Demathieu, G., 1976, Une ichnofaune reptilienne remarquable dans les grès Triassique de Largentière (Ardèche, France): *Palaeontographica A*, v. 151, p. 194-216.
- Courel, L. and Demathieu, G., 2000, Une nouvelle ichnoespèce *Coelurosaurichnus grancieri* du Trias supérieur de l'Ardèche, France: *Geodiversitas*, v. 22, p. 35-45.
- Demathieu, G., 1966, *Rhynchosauroides petri* et *Spingopus ferox*, nouvelles empreintes de reptiles de grès triassique de la bordure Nord-Est du Massif Central: *Comptes Rendus de l'Académie des Sciences D*, v. 263, p. 483-486.
- Demathieu, G., 1970, Les empreintes de pas de vertébrés du Trias de la bordure Nord-Est du Massif Central: *Cahiers de Paleontologie*, 211 p.
- Demathieu, G., 1984, Une ichnofaune du Trias moyen du Bassin de Lodève (Hérault, France): *Annales de Paléontologie*, v. 70, p. 247-273.
- Demathieu, G., 1989, Appearance of the first dinosaur tracks in the French Middle Triassic and their probable significance; in Gillette, D.D. and Lockley, M.G., eds., *Dinosaur tracks and traces*: Cambridge, Cambridge University Press, p. 201-207.
- Demathieu, G. and Demathieu, P., 2004, *Chirotheria* and other ichnotaxa of the European Triassic: *Ichnos*, v. 11, p. 79-88.
- Demathieu, G. and Gand, G., 1973, Deux espèces ichnologiques nouvelles des grès à empreintes du Trias du Plateau d'Autun: *Bulletin de la Société d'Histoire Naturelle d'Autun*, v. 67, p. 11-27.
- Demathieu, G. and Haubold, H., 1972, Stratigraphische Aussagen der Tetrapodenfährten aus der terrestrischen Trias Europas: *Geologie*, v. 21, p. 802-836.
- Demathieu, G. and Haubold, H., 1974, Evolution und Lebensgemeinschaft terrestrischer Tetrapoden nach ihren Fährten in der Trias: *Freiberger Forschungshefte C*, v. 298, p. 51-72.
- Demathieu, G. and Haubold, H., 1982, Reptilfährten aus dem Mittleren Buntsandstein von Hessen: *Hallesches Jahrbuch für Geowissenschaften*, v. 7, p. 97-110.
- Demathieu, G. and Weidmann, M., 1982, Les empreintes de pas de reptiles dans le Trias du Vieux Émossion (Finhaut, Valais, Suisse): *Eclogae Geologicae Helveticae*, v. 75, p. 721-757.
- Ellenberger, P., 1970, Les niveaux paléontologiques de première apparition des mammifères primordiaux en Afrique du sud et leur ichnologie. Etablissement de zones stratigraphiques détaillées dans le Stormberg du Lesotho (Afrique du Sud) (Trias supérieur à jurassique); in *Second Gondwana Symposium, Proceedings and Papers*. Council for Scientific and Industrial Research, Pretoria, p. 343-370.
- Ellenberger, P., 1972, Contribution à la classification des Pistes de Vertébrés du Trias: les types du Stormberg d'Afrique du Sud (I): *Palaeovertebrata, Memoire Extraordinaire*, 104 p.
- Ellenberger, P., 1974, Contribution à la classification des Pistes de Vertébrés du Trias: Les types du Stormberg d'Afrique du Sud (II, Les Stormberg Supérieur): *Palaeovertebrata, Memoire Extraordinaire*, 141 p.
- Fichter, J. and Kunz, R., 2004, New genus and species of chirotheroid tracks in the Detfurth-Formation (Middle Bunter, Lower Triassic) of Central Germany: *Ichnos* v. 11, p. 183-193.
- Fraser, N.C. and Olsen, P.E., A new dinosauromorph ichnogenus from the Triassic of Virginia: *Jeffersoniana*, v. 7, p. 1-20.
- Fuglewicz, R., Ptaszynski, T., Rdzanek, K., 1990, Lower Triassic footprints from the Swietokrzyskie (Holy Cross) Mountains, Poland: *Acta Palaeontologica Polonica*, v. 35, p. 109-164.
- Furrer, H., 1993, Entdeckung und Untersuchung der Dinosaurierfährten im Nationalpark: Cratschla Ediziuns Specialas, v. 1, 24 p.
- Gand, G., 1976, Présentation de deux nouveaux assemblages a traces de reptiles des grès triassiques du plateau d'Autun (Autunois, France): *Bulletin de la Société d'Histoire Naturelle d'Autun*, v. 79, p. 15-18.
- Gand, G., 1979, Description de deux nouvelles traces d'*Isochirotherium* observées dans les grès du Trias moyen de Bourgogne: *Bulletin de la Société d'Histoire Naturelle du Creusot*, v. 37, p. 13-25.
- Gand, G. and Demathieu, G., 2005, Les pistes dinosauroïdes du Trias moyen français: interprétation et réévaluation de la nomenclature: *Geobios*, v. 38, p. 725-749.
- Gand, G., Vianey-Liaud, M., Demathieu, G. and Garric, J., 2000, Deux nouvelles traces de pas de dinosaures du Trias supérieur de la bordure Cévenole (La Grand-Combe, Sud-Est de la France): *Geobios*, v. 33, p. 599-624.
- Gand, G., Demathieu, G., Grancier, M. and Sciau, J., 2003, Les traces

- dinosaurioïdes du Trias supérieur français: discrimination, interprétation et comparaison: Bulletin de la Société Géologique de France, 2005, v. 176, p. 69-79.
- Gaston, R., Lockley, M.G., Lucas, S.G. and Hunt, A.P., 2003, *Grallator*-dominated fossil footprint assemblages and associated enigmatic footprints from the Chinle Group (Upper Triassic), Gateway area, Colorado: Ichnos, v. 10, p. 153-163.
- Gatesy, S.M., Middleton, K.M., Jenkins, F.A., Jr., and Shubin, N.H., 1999, Three-dimensional preservation of foot movements in Triassic theropod dinosaurs: Nature, v. 399, p. 141-144.
- Gauthier, J.A., 1986, Saurischian monophyly and the origin of birds; in Padian, K., ed., The origin of birds and the evolution of flight: Memoirs of the California Academy of Science, v. 8, p. 1-55.
- Gierlinski, G. and Ahlberg, A., 1994, Late Triassic and Early Jurassic dinosaur footprints in the Höganäs Formation of southern Sweden: Ichnos, v. 3, p. 99-105.
- Haubold, H., 1967, Eine Pseudosuchia-Fährtenfauna aus dem Buntsandstein Südhörlingens: Hallesches Jahrbuch für Mitteldeutsche Erdgeschichte, v. 8, p. 12-48.
- Haubold, H., 1969, Parallelisierung terrestrischer Ablagerungen der tieferen Trias mit Pseudosuchia-Fährten: Geologie, v. 18, p. 836-843.
- Haubold, H. 1971a, Die Tetrapodenfährten des Buntsandsteins: Paläontologische Abhandlungen A, IV, p. 395-548.
- Haubold, H., 1971b, Ichnia Amphibiorum et Reptiliorum fossilium: Encyclopedia of Paleoherpetology, v. 18, p. 1-124.
- Haubold, H., 1984, Saurierfährten. Wittenberg, Ziemsen, 231 p.
- Haubold, H., 1986, Archosaur footprints at the terrestrial Triassic-Jurassic transition; in Padian, K., ed., The beginning of the Age of Dinosaurs: Cambridge, Cambridge University Press, p. 189-201.
- Haubold, H., 1996, Ichnotaxonomie und Klassifikation von Tetrapodenfährten aus dem Perm: Hallesches Jahrbuch für Geowissenschaften B, v. 18, p. 23-88.
- Haubold, H., 1999, Tracks of the Dinosauromorpha from the Lower Triassic: Zentralblatt für Geologie und Paläontologie I, p. 783-795.
- Haubold, H., 2006, Die Saurierfährten *Chirotherium barthii* Kaup, 1835 – das Typusmaterial aus dem Buntsandstein bei Hildburghausen/Thüringen und das Chirotherium-Monument: Veröffentlichungen Naturhistorisches Museum Schleusingen, v. 21, p. 3-31.
- Haubold, H. and Klein, H., 2000, Die dinosauroiden Fährten *Parachirotherium-atreipus-Grallator* aus dem unteren Mittelkeuper (Obere Trias: Ladin, Karn, ?Nor) in Franken: Hallesches Jahrbuch für Geowissenschaften B, v. 22, p.59-85.
- Haubold, H. and Klein, H., 2002, Chirotherien und Grallatoriden aus der Unteren bis Oberen Trias Mitteleuropas und die Entstehung der Dinosauria: Hallesches Jahrbuch für Geowissenschaften B, v. 24, p. 1-22.
- Hitchcock, E., 1836, Ornithichnology – description of the footmarks of birds (Ornithichnites) on New Red Sandstone in Massachusetts: American Journal of Science, ser. 1, v. 29, p. 307-340.
- Hitchcock, E., 1845, An attempt to name, classify, and describe the animals that made the fossil footmarks of New England: Proceedings of the 6th Annual Meeting of the Association of American Geologists and Naturalists, v. 6, p. 23-25.
- Hitchcock, E., 1847, Description of two new species of fossil footmarks found in Massachusetts and Connecticut, or of the animals that made them: American Journal of Science, ser. 2, v. 4, p. 46-57.
- Hitchcock, E., 1856, Description of a new and remarkable species of fossil footmark, from the sandstone of Turner's falls, in the Connecticut Valley: American Journal of Science, ser. 2, v. 21, p. 97-100.
- Hitchcock, E., 1858, Ichnology of New England. A report on the sandstone of the Connecticut Valley, especially its fossil footmarks: William White, Boston, 220 p.
- Huene, F. von, 1931, Die fossilen Fährten im Rhät von Ischigualasto in Nordwest-Argentinien: Palaeobiologica, v. 4, p. 99-112.
- Huene, F. von, 1941, Die Tetrapoden-Fährten im toskanischen Verrucano und ihre Bedeutung: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie B, v. 86, p. 1-34.
- Hunt, A.P., Lucas, S.G., Lockley, M.G. and Heckert, A.B., 2000, Occurrence of the dinosaurian ichnogenus *Grallator* in the Redonda Formation (Upper Triassic: Norian) of eastern New Mexico; in Lucas, S.G. and Heckert, A.B. (eds.), Dinosaurs of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 39-41.
- Jenkins, F.A., Jr., Shubin, N.H., Amaral, W.W., Gatesy, S.M., Schaff, C.R., Clemmensen, L.B., Downs, W.R., Davidson, A.R., Bonde, N. and Osbaeck, F., 1994, Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, east Greenland: Meddelelser om Grønland Geoscience, v. 32, p. 1-25.
- Karl, C. and Haubold, H., 1998, *Brachychirotherium* aus dem Coburger Sandstein (Mittlerer Keuper, Karn/Nor) in Nordbayern: Hallesches Jahrbuch für Geowissenschaften B, v. 20, p. 33-58.
- Karl, C. and Haubold, H., 2000, Saurierfährten im Keuper (Obere Trias) Frankens, die Typen von *Brachychirotherium*: Berichte der Naturwissenschaftlichen Gesellschaft Bayreuth, v. 24, p. 91-120.
- Kaup, J.J., 1835, Über Thierfährten bei Hildburghausen: Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, v. 1835, p. 227-228.
- Klein, H. and Haubold, H., 2004, Überlieferungsbedingte Variation bei Chirotherien und Hinweise zur Ichnotaxonomie nach Beispielen aus der Mittel- bis Ober-Trias (Anisium–Karnium) von Nordbayern: Hallesches Jahrbuch für Geowissenschaften B, v. 26, p 1-15.
- Klein, H., Lucas, S.G. and Haubold, H., 2006, Tetrapod track assemblage of the Redonda Formation (Upper Triassic, Chinle Group) in east-central New Mexico – re-evaluation of ichnofaunal diversity from studies of new material; in Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C. and Kirkland, J.I., eds., The Triassic-Jurassic terrestrial transition: New Mexico Museum of Natural History and Science, Bulletin 37, p. 241-250.
- Kuhn, O., 1958, Die Fährten der vorzeitlichen Amphibien und Reptilien: Bamberg, Meisenbach, 64 p.
- Lockley, M.G. and Hunt, A.P., 1993, A new Late Triassic tracksite from the Sloan Canyon Formation, type section, Cimarron Valley, New Mexico; in Lucas, S.G. and Morales, M. (eds.), The nonmarine Triassic: New Mexico Museum of Natural History and Science, Bulletin 3, p. 279-283.
- Lockley, M.G. and Hunt, A.P., 1995, Dinosaur tracks and other fossil footprints of the western United States: New York, Columbia University Press, 338 p.
- Lockley, M.G., King, M., Howe, S. and Sharp, T., 1996, Dinosaur tracks and other archosaur footprints from the Triassic of South Wales: Ichnos, v. 5, p. 23-41.
- Lockley, M.G., Lucas, S.G. and Hunt, A.P., 2000, Dinosaur tracksites in New Mexico: a review; in Lucas, S.G. and Heckert, A.B. (eds.), Dinosaurs of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 9-16.
- Lockley, M.G., Lucas, S.G. and Hunt, A.P., 2006, *Evazoum* and the renaming of northern hemisphere "*Pseudotetrasauropus*": implications for tetrapod ichnotaxonomy at the Triassic-Jurassic boundary; in Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C. and Kirkland, J.I., eds., The Triassic-Jurassic terrestrial transition: New Mexico Museum of Natural History and Science, Bulletin 37, p. 199-206.
- Lü, H., Zhang, Y. and Xiao, J., 2004, *Chirotherium*: Fossil footprints of primitive reptiles in the Middle Triassic Guanling Formation, Zhenfeng, Guizhou Province, China: Acta Geologica Sinica, v. 78, p. 468-474.
- Lucas, S.G., 2003, Triassic tetrapod footprint biostratigraphy and biochronology: Albertiana, v. 28, p. 75-84.
- Lucas, S.G. and Hancox, J., 2001, Tetrapod-based correlation of the non-marine Upper Triassic of Southern Africa: Albertiana, v. 25, p. 5-9.
- Lucas, S.G. and Huber, P., 2003, Vertebrate biostratigraphy and biochronology of the nonmarine Late Triassic; in Le Tourneau, P.M. And Olsen, P.E., eds., The great rift valleys of Pangaea in eastern North America, vol. 2: New York, Columbia University Press, p. 143-191.
- Lucas, S.G., and Tanner, L.H., 2004, Late Triassic extinction events: Albertiana, v. 31, p. 31-40.
- Lucas, S.G. and Sullivan, R.M., 2006, Tetrapod footprints from the Upper Triassic Passaic Formation near Graterford, Montgomery County, Pennsylvania; in Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C. and Kirkland, J.I., eds., The Triassic-Jurassic terrestrial

- transition: New Mexico Museum of Natural History and Science, Bulletin 37, p. 251-256.
- Lucas, S.G., Hunt, A.P. and Lockley, M.G., 2001, Tetrapod footprint ichnofauna of the Upper Triassic Redonda Formation, Chinle Group, Quay County, New Mexico: New Mexico Geological Society, Guidebook 52, p. 177-180.
- Lucas, S.G., Lockley, M.G., Hunt, A.P. and Tanner, L.H., 2006a, Biostratigraphic significance of tetrapod footprints from the Triassic-Jurassic Wingate Sandstone on the Colorado Plateau; in Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C. and Kirkland, J.I., eds., The Triassic-Jurassic terrestrial transition: New Mexico Museum of Natural History and Science, Bulletin 37, p. 109-117.
- Lucas, S.G., Klein, H., Lockley, M.G., Spielmann, J.A., Gierlinski, G.D., Hunt, A.P. and Tanner, L.H., 2006b, Triassic-Jurassic stratigraphic distribution of the theropod footprint ichnogenus *Eubrontes*; in Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C. and Kirkland, J.I., eds., The Triassic-Jurassic terrestrial transition: New Mexico Museum of Natural History and Science, Bulletin 37, p. 86-93.
- Lull, R.S., 1904, Fossil footprints of the Jura-Trias of North America: Memoirs of the Boston Society of Natural History, v. 5, p. 461-557.
- Mietto, P., 1987, *Parasynaptichnium gracilis* nov. ichnogen., nov. isp. (Reptilia: Archosauria Pseudosuchia) nell'Anisico inferiore di Recoaro (Prealpi vicentine – Italia): Memorie Scienze Geologiche, v. 39, p. 37-47.
- Milàn, J., Clemmensen, L.B. and Bonde, N. 2004, Vertical sections through dinosaur tracks (Late Triassic lake deposits, East Greenland) – undertracks and other surface deformation structures revealed: *Lethaia*, v. 37, p. 285-296.
- Montenat, C., 1968, Empreintes de pas de reptiles dans le Trias moyen du plateau du Daüs près d' Aubenas (Ardèche): Bulletin Scientifique de Bourgogne, v. 25, p. 369-389.
- Nicosia, U. And Loi, M., 2003, Triassic footprints from Lericci (La Spezia, northern Italy): *Ichnos*, v. 10, p. 127-140.
- Nopcsa, F. von, 1923, Die Familien der Reptilien: Fortschritte der Geologie und Paläontologie, v. 2, p. 1-210.
- Olsen, P.E., 1980, A comparison of the vertebrate assemblages from the Newark and Hartford Basins (Early Mesozoic, Newark Supergroup) of Eastern North America; in Jacobs, L.L., ed., Aspects of Vertebrate History: Flagstaff, Museum of Northern Arizona, p. 35-53.
- Olsen, P.E., 1983, Relationship between biostratigraphic subdivisions and igneous activity in the Newark Supergroup: Geological Society of America, Abstracts with Programs, v. 15, p. 93.
- Olsen, P.E. and Baird, D., 1986, The ichnogenus *Atreipus* and its significance for Triassic biostratigraphy; in Padian, K., ed., The beginning of the Age of Dinosaurs: Cambridge, Cambridge University Press, p. 61-87.
- Olsen, P.E. and Galton, P.M., 1984, A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg: *Palaeontologia Africana*, v. 25, p. 87-110.
- Olsen, P.E., Smith, J.B., McDonald, N.G., 1998, Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus* and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.): *Journal of Vertebrate Paleontology*, v. 18, p. 586-601.
- Olsen, P.E., Kent, D.V., Sues, H.-D., Koeberl, C., Huber, H., Montanari, A., Rainforth, E.C., Fowell, S.J., Szajna, M.J., and Hartline, W., 2002, Ascent of dinosaurs linked to an iridium anomaly at the Triassic-Jurassic boundary: *Science*, v. 296, p. 1305-1307.
- Paul, G.S., 2002, Dinosaurs of the air: the evolution and loss of flight in dinosaurs and birds: Baltimore, John Hopkins University Press, 460 p.
- Peabody, F.E., 1948, Reptile and amphibian trackways from the Moenkopi Formation of Arizona and Utah: University of California Publications, Bulletin of the Department of Geological Sciences, v. 27, p. 295-468.
- Peabody, F.E., 1955a, Taxonomy and the footprints of tetrapods: *Journal of Paleontology*, v. 29, p. 915-918.
- Peabody, F.E., 1955b, Occurrence of *Chirotherium* in South America: Geological Society of America Bulletin, v. 66, p. 239-240.
- Peabody, F.E., 1956, Ichnites from the Triassic Moenkopi Formation of Arizona and Utah: *Journal of Paleontology*, v. 30, p. 731-740.
- Ptaszynski, T., 2000, Lower Triassic vertebrate footprints from Wióry, Holy Cross Mountains, Poland: *Acta Palaeontologica Polonica* 45, p. 151-194.
- Rehnel, K., 1950, Ein Beitrag über Fährten Spuren im unteren Gipskeuper von Bayreuth: *Berichte der Naturwissenschaftlichen Gesellschaft Bayreuth*, v. 1950, p. 27-36.
- Sarjeant, W.A.S., 1967, Fossil footprints from the Middle Triassic of Nottinghamshire and Derbyshire: *Mercian Geologist*, v. 2, p. 327-341.
- Sereno, P.C., 1991, Basal archosaurs: phylogenetic relationships and functional implications: *Society of Vertebrate Paleontology Memoir*, v. 2, p. 1-65.
- Sickler, F.K.L., 1834, Sendschreiben an Dr. Blumenbach über die höchst merkwürdigen Reliefs der Fährten urweltlicher Tiere in den Hessberger Steinbrüchen bei Hildburghausen: Programm des herzoglichen Gymnasiums zu Hildburghausen. Hildburghausen, Kesselring, 16 p.
- Silvestri, S.M. and Olsen, P.E., 1989, Ichnostratigraphy of the Jacksonwald syncline: the last 7 million years of the Triassic: Geological Society of America, Abstracts with Programs, v. 20, p. 70.
- Silvestri, S.M. and Szajna, M.J., 1993, Biostratigraphy of vertebrate footprints in the Late Triassic section of the Newark Basin, Pennsylvania: reassessment of stratigraphic ranges; in Lucas, S.G. and Morales, M. (eds.), The nonmarine Triassic: New Mexico Museum of Natural History and Science, Bulletin 3, p. 439-444.
- Soergel, W., 1925, Die Fährten der Chirotheria: Gustav Fischer, Jena, 92 p.
- Szajna, M.J. and Hartline, B.W. 2003, A new vertebrate footprint locality from the Late Triassic Passaic Formation near Birdsboro, Pennsylvania; in Le Tourneau, P.M. and Olsen, P.E., eds., The great rift valleys of Pangaea in eastern North America, vol. 2: New York, Columbia University Press, p. 264-272.
- Szajna, M.J. and Silvestri, S.M., 1996, A new occurrence of the ichnogenus *Brachychirotherium*: implications for the Triassic-Jurassic mass extinction event; in Morales, M., ed., The continental Jurassic: Museum of Northern Arizona, Bulletin 60, p. 275-283.
- Tresise, G. and Sarjeant, W.A.S., 1997, The tracks of Triassic vertebrates: fossil evidence from north-west England: London, The Stationery Office, 204 p.
- Walther, J., 1917, Über *Chirotherium*: *Zeitschrift der Deutschen Geologischen Gesellschaft*, v. 69, p. 181-184.
- Weems, R.E., 1987, A Late Triassic footprint fauna from the Culpeper Basin, northern Virginia (U.S.A.): *Transactions of the American Philosophical Society*, v. 77, no. 1, p. 1-79.
- Weiss, W., 1934, Eine Fährten Schicht im Mittelfränkischen Blasensandstein: *Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins*, N.F., v. 23, p. 5-11.
- Weiss, W., 1976, Ein Reptilfährten-Typ aus dem Benker-Sandstein und untersten Blasensandstein des Keupers um Bayreuth: *Geologische Blätter für Nordost-Bayern*, v. 26, p. 1-7.