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Tetrapod footprints – their use in biostratigraphy and biochronology of the Triassic

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Abstract: Triassic tetrapod footprints have a Pangaea-wide distribution; they are known from North America, South America, Europe, North Africa, China, Australia, Antarctica and South Africa. They often occur in sequences that lack well-preserved body fossils. Therefore, the question arises, how well can tetrapod footprints be used in age determination and correlation of stratigraphic units?

The single largest problem with Triassic footprint biostratigraphy and biochronology is the non-uniform ichnotaxonomy and evaluation of footprints that show extreme variation in shape due to extramorphological (substrate-related) phenomena. Here, we exclude most of the countless ichnospecies of Triassic footprints, and instead we consider ichnogenera and form groups that show distinctive, anatomically-controlled features.

Several characteristic footprint assemblages and ichnotaxa have a restricted stratigraphic range and obviously occur in distinct time intervals. This can be repeatedly observed in the global record. Some reflect distinct stages in the evolutionary development of the locomotor apparatus as indicated by their digit proportions and the trackway patterns. Essential elements are archosaur tracks with *Rotodactylus*, the chirotherian ichnotaxa *Protochirotherium*, *Synaptichnium*, *Isochirotherium*, *Chirotherium* and *Brachychotherium*, and grallatorids that can be partly linked in a functional-evolutionary sequence. Non-archosaur footprints are common, especially the ichnotaxa *Rhynchosauroides*, *Procolophonichnium*, *Capitosauroides* and several dicynodont-related or mammal-like forms. They are dominant in some footprint assemblages.

From the temporal distribution pattern we recognize five distinct tetrapod-footprint-based biochrons likened to the known land-vertebrate faunachrons (LVFs) of the tetrapod body fossil record: 1. Dicynodont tracks (Lootsbergian = Induan age); 2. *Protochirotherium* (*Synaptichnium*), *Rhynchosauroides*, *Procolophonichnium* (Nonesian = Induan–Olenekian age); 3. *Chirotherium barthii*, *C. sickleri*, *Isochirotherium*, *Synaptichnium* ('*Brachychotherium*'), *Rotodactylus*, *Rhynchosauroides*, *Procolophonichnium*, dicynodont tracks, *Capitosauroides* (Nonesian–Perovkan = Olenekian–early Anisian); 4. *Atreipus–Grallator* ('*Coelurosaurichnus*'), *Synaptichnium* ('*Brachychotherium*'), *Isochirotherium*, *Sphingopus*, *Parachirotherium*, *Rhynchosauroides*, *Procolophonichnium* (Perovkan–Berdyanian = Late Anisian–Ladinian); 5. *Brachychotherium*, *Atreipus–Grallator*, *Grallator*, *Eubrontes*, *Apatopus*, *Rhynchosauroides*, dicynodont tracks (Otischalkian–Apachean = Carnian–Rhaetian).

Tetrapod footprints are useful for biostratigraphy and biochronology of the Triassic. However, compared to the tetrapod body fossil record with eight biochrons, the five footprint-based biochrons show less resolution of faunal turnover as ichnogenera and ichnospecies at best reflect biological families or higher biotaxonomic units. Nevertheless, in sequences where body fossils are rare, footprints can coarsely indicate their stratigraphic age.

Tetrapod footprints of Triassic age are known from North America, South America, Europe, North Africa, China, Australia, Antarctica and South Africa (Figs 1 & 2). The Triassic footprint record is archosaur-, lepidosauromorph/ archosaur-omorph- (*Rhynchosauroides*) and synapsid-dominated (Haubold 1971b, 1984; Klein & Haubold 2007), and it includes the oldest dinosaur tracks. Much has been written about Triassic tetrapod footprint biostratigraphy, especially based on the European and North American records (see below).

Our goal here is to present a Pangaea-wide Triassic biostratigraphy and biochronology based on tetrapod footprints. To do so, we briefly discuss some problems of footprint ichnotaxonomy and their bearing on footprint biostratigraphy (see Lucas 2007 for a more extensive review of these issues). We follow with a review of the principal Triassic tetrapod footprint assemblages. We conclude with a synopsis of Triassic tetrapod footprint biochronology that recognizes five biochrons and compare that biochronology to Triassic tetrapod biochronology based on body fossils.

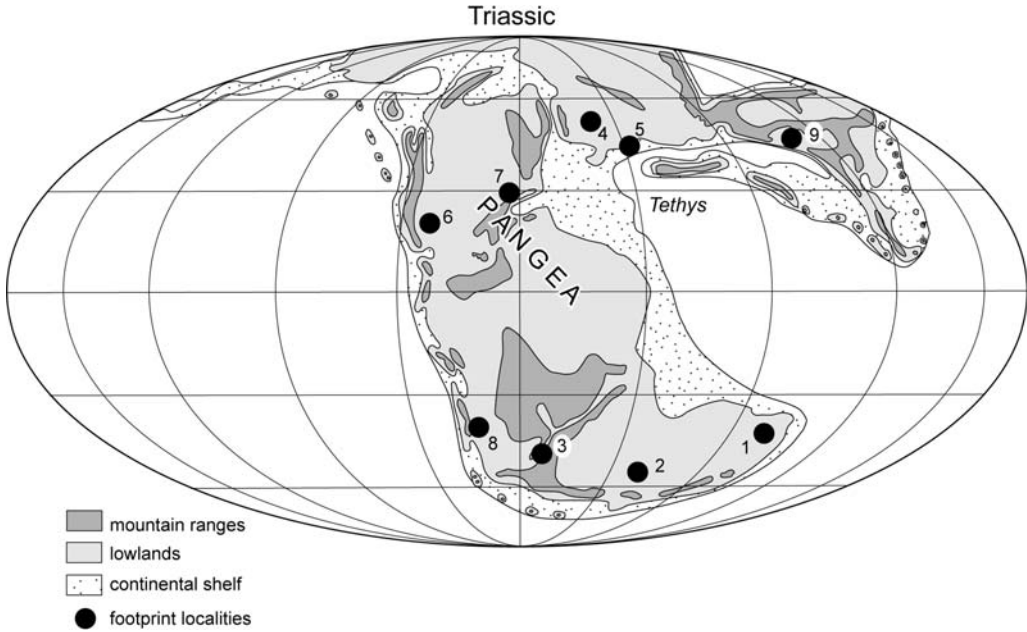


Fig. 1. Distribution of principal Triassic tracksites on Triassic Pangaea. Locations are: 1, Sydney basin, Australia; 2, Karoo basin, South Africa; 3, Antarctica; 4, western Europe, 5, Italy; 6, Chinle basin, western United States; 7, Newark basin, New Jersey; 8, Argentina; and 9, Yangtze basin, China. Base map after Wing & Sues (1992).

Epoch	Age num. age my	Germany	Europe Greenland	North America		Southern Africa	South America, Austr., Antarct., N-Africa, China
				Chinle	Newark		
Upper Triassic	199.6		▼ Höganäs Fm., Schonen, S	?		▼ Santo Domingo ? ARG	
	206		Mercia Mudstone Group, GB; Fleming Fjord Fm., Greenland	▼ Rock Point Bell Spr. Redonda Sheep Pen Sloan Can. Petrified F. Dockum	▼ Passaic Gettysb.	▼ Lower Elliot Fm. ?	▼ Los Colorados Fm.
	226	▼ Burg- / Stubensandstein	▼ Keuper, Anduze, La Grand-Combe, Alès, FR; Diavel Fm., CH; Hauptdolomit, IT Monticello Fm., IT		▼ Cow Br. Lockat. Wolfvillon Pekin	▼ Molteno Fm. ?	▼ Timezgadiouine Fm., Argana Basin MOROCC. Vera Portezuelo
Middle Triassic	237	▼ Benker Sandstein	▼ Payzac, Ardèche, FR; Montemarcello Fm., La Spezia, IT Finhaut, CH			footprint levels A1 - A7	▼ Los Rastros ARG ?
	240.5	▼ marginal siliciclastic facies of the Muschelkalk in Northern Bavaria	▼ Massif Central, FR; Richthofen, Voltago Congl., Dolomites, IT; Winterswijk, NL				▼ Ischichuca
	247	▼ Röt Fm.	▼ Lodève, FR; Tarporley Siltst., Helsby Sst. Fm., Auchenheew Beds, GB; Molina de Aragón, SP	▼ Holbrook Wupatki Member	Moenkopi Fm., Arizona		▼ Cerro de Las Cabras Tarjados Fm., ARG
Lower Triassic	251	▼ Solling Fm., Thüring. Chiroth. Sst. Hardegsen Fm., Hessen Dethfurt Fm., Hessen	▼ Labyrinthodont. Beds, Wióry, PL				▼ Guanling Fm. Prov. Guizhou, China
						▼ Karoo Basin	▼ Southern Sidney Basin, AUS; Antarctica

Fig. 2. Principal Triassic footprint horizons and footprint localities. German section and numerical age according to Menning & German Stratigraphic Commission (2002) and Bachmann & Kozur (2004).

Triassic tetrapod footprint ichnotaxa

The use of tetrapod footprints in biostratigraphy and biochronology depends on the following criteria: (1) a stable and uniform ichnotaxonomy; (2) ichnotaxa with limited stratigraphic (temporal) ranges; and (3) wide geographical distribution of the ichnotaxa used for correlation. Triassic tetrapod ichnotaxonomy began with the binominal naming of *Chirotherium barthii* and *C. sickleri* from the Bunter (Lower–Middle Triassic) of Hildburghausen, Germany, by Kaup (1835*a, b*). At present, a large number of ichnogenera and ichnospecies from the Triassic have been introduced by various authors (see Haubold 1971*b*, 1984; Klein & Haubold 2007 for reviews). Some are considered invalid, whereas others are still under discussion and may be extramorphological (substrate-related) variations. In Triassic ichnotaxonomy (and in tetrapod ichnotaxonomy in general), the influence of the substrate on footprint shape is still not adequately considered, nor fully understood. Work on this topic is in progress (e.g. Laporte & Behrensmeier 1980; Cohen *et al.* 1991; Manning 2004; Diedrich 2005; Milàn & Bromley 2006, 2008; Milàn *et al.* 2004). Indeed, even the differentiation of ichnotaxa based on mathematical, including statistical, approaches (Demathieu 1998) may often reflect substrate rather than anatomical signals. Nevertheless, it can be helpful to quantify and demonstrate different morphologies of footprints by landmark analysis or other methods that are independent of the subjective view of the observer (Karl & Haubold 1998; Klein & Haubold 2003).

Tetrapod ichnotaxa should be based on anatomical rather than substrate- or facies-controlled features. In contrast to invertebrate trace fossils, tetrapod footprints are identified by their relationship to the locomotor anatomy of supposed trackmakers. This focuses attention on the number, shape and proportions of digits, the shape of the sole surface and the trackway pattern. For example, different evolutionary developments are distinct in archosaur footprints and can be likened to the evolution in some lineages of dinosaurs as well as of the crocodylian stem-group and osteological taxa close to the crown-group of Archosauria (Haubold & Klein 2000, 2002; Haubold 2006; Lucas 2003, 2007; Hunt & Lucas 2007*b*; Klein & Haubold 2007). The distinct evolutionary stages reflected in some archosaur footprints in these lineages have a restricted stratigraphic/temporal range within the Triassic, as do some osteological taxa (Lucas 1998, 1999). This makes them useful for biostratigraphy and biochronology.

Nevertheless, ichnospecies cannot be attributed to species based on body fossils (Peabody 1955*a*). They are, instead, equivalent to osteological genera or families that have lower evolutionary

turnover rates (Lucas 2007). Moreover, evolution may have only affected parts of the body other than the limbs. For example, tridactyl theropod footprints of the *Grallator*–*Eubrontes* type are of similar shape from the Late Triassic to the Jurassic. Thus, the foot morphology of theropod trackmakers was obviously consolidated in the Carnian–Norian and subsequently underwent no essential change. Therefore, a zonation based on tetrapod footprints is possible at only a relatively low resolution. Nevertheless, the intercontinental distribution of Triassic ichnotaxa such as *Rotodactylus*, *Chirotherium*, *Grallator* or *Eubrontes* and their abundance (Peabody 1948, 1955*b*; Haubold 1967, 1971*a, b*; Tresise & Sarjeant 1997; Haubold & Klein 2000; Lü *et al.* 2004; King *et al.* 2005; Lucas *et al.* 2006*a*; Klein & Haubold 2007) enables the correlation of sequences with an otherwise poorly known body fossil record.

Attempts to outline a tetrapod ichnostratigraphy of Triassic sequences were made by Haubold (1969, 1971*b*, 1984, 1986), Demathieu & Haubold (1972, 1974), Olsen (1980, 1983), Lockley & Hunt (1995), Hunt & Lucas (2007*a, b*), Lucas (2003, 2007) and Klein & Haubold (2007). Further contributions can be found in Ellenberger (1970, 1972, 1974), Demathieu (1984), Olsen & Galton (1984), Olsen & Baird (1986), Silvestri & Olsen (1989), Silvestri & Szajna (1993), Lockley *et al.* (1996), Szajna & Silvestri (1996), Avanzini *et al.* (2001), Lucas & Hancox (2001), Olsen *et al.* (2002), Szajna & Hartline (2003), Lucas & Huber (2003), Lucas & Tanner (2004), Gand *et al.* (2005), Lucas & Sullivan (2006) and Lucas *et al.* (2006*a, b, c*). Presently, the non-uniform ichnotaxonomy of Triassic tetrapod ichnotaxa hinders a generally accepted and conclusive concept. Many of the described ichnospecies are dubious, except some well-substantiated ichnotaxa such as *Chirotherium barthii* and *C. sickleri*, among others. Therefore, ichnogenera are considered by us to be the operational taxonomic units of a Triassic footprint biostratigraphy and biochronology.

Triassic tetrapod footprint assemblages

Lowest Triassic

Tetrapod footprints from this interval have been described from the Karoo basin (South Africa), the southern Sydney basin of Australia, and from Antarctica (Watson 1960; MacDonald *et al.* 1991; Retallack 1996). At these localities, the sequences largely straddle the Permian–Triassic boundary, and the footprints are in strata that in South Africa and Antarctica can be assigned to the Lootsbergian land–vertebrate faunachron (LVF) of latest Changshingian–Induan age (Lucas 1998, 2007;

Hunt and Lucas 2007b). The poorly-preserved footprints from Australia were assigned to *Dicynodontipus* and attributed to dicynodont trackmakers, in particular *Lystrosaurus* (Retallack 1996); however, this relationship cannot be demonstrated conclusively.

From the Bunter of Poland (Wióry, Holy Cross Mountains), extensive surfaces with footprints are known (Fig. 3). They occur within a fluvial sequence, the 'Labyrinthodontidae beds', which can be considered to be of late Induan to Olenekian age (Ptaszynski 2000; Niedzwiedzki & Ptaszynski 2007). Archosaur tracks of the chirothere morphological group dominate these assemblages. Indeed, Fuglewicz *et al.* (1990), Ptaszynski (2000) and Niedzwiedzki & Ptaszynski (2007) identified *Synaptichnium*, *Brachychirotherium* and *Isochirotherium* (Fig. 3b–d). The presence of the two latter forms, however, is dubious because the preserved footprint morphology does not match the diagnoses of these ichnotaxa (Beurlen 1950; Haubold 1971b; Karl & Haubold 1998, 2000). Instead, all these imprints from Poland reflect conservative foot structures because of their long pedal digits IV and V. In their overall shape, they resemble *Protochirotherium wolfhagense*, a chirotherian ichnotaxon described by Fichter & Kunz (2004) from the Detfurth Formation (Middle Bunter, Olenekian) of northern Hessen, Germany (Figs 3a & 4). The material from Poland was therefore referred to *Protochirotherium* by Klein & Haubold (2007). Possible trackmakers are archosauriforms close to the base of the crown-group Archosauria (Sereno 1991).

Further characteristic footprints described from the Polish Bunter are *Rhynchosauroides* (lepidosauromorph and/or archosauromorph), *Procolophonichnium* (primitive amniote), *Capitosaurioides* (amphibian) and a purported new ichnogenus, *Prorotodactylus* (Fuglewicz *et al.* 1990; Ptaszynski 2000; Fig. 3e–f). Footprint surfaces in the Hardegen Formation (Middle Bunter, Olenekian) of Northern Hessen, Germany, record *Synaptichnium*, '*Isochirotherium*' and *Rhynchosauroides* (Demathieu & Haubold 1982).

Upper Lower Triassic to Lower Middle Triassic

In this stratigraphic interval, the diversity of imprint forms increases. A large number of archosaur footprint taxa can be discriminated by different digit proportions and trackway pattern. Thus, chirotheres are represented by four ichnogenera: *Synaptichnium*, *Brachychirotherium*, *Isochirotherium* and *Chirotherium* (Haubold 1971b).

Synaptichnium (Fig. 5a, b) reflects primitive foot morphology in its long pedal digits IV and V. It continues from the Induan and Olenekian into

the Anisian. It is part of the assemblages in the Moenkopi Formation of Arizona (Peabody 1948), and the Middle Triassic of Great Britain (Tresise & Sarjeant 1997; King *et al.* 2005).

The presence of *Brachychirotherium* in the Lower and Middle Triassic is dubious. Forms that have been described under this name from the Bunter (Olenekian–Anisian) of Germany and the Middle Triassic (Anisian–Ladinian) of France and Argentina (Haubold 1971b; Demathieu & Gand 1973; Courel & Demathieu 1976; Demathieu & Demathieu 2004; Melchor & De Valais 2006) are mostly extramorphological variants of *Synaptichnium* (Fig. 5c–d). The substrate-controlled transition to *Synaptichnium* has been demonstrated by material from the German Middle Triassic (Anisian) by Klein & Haubold (2004). Furthermore, the analysis and revision of the type material of *Brachychirotherium* from the Upper Triassic (Carnian) of Germany by Karl & Haubold (1998, 2000) revealed that the inclusion of these Lower to Middle Triassic forms in the ichnogenus is problematic. The forms from the Lower and Middle Triassic are thus referred to here as '*Brachychirotherium*' (Klein & Haubold 2007).

Isochirotherium (Fig. 5e–g) is a characteristic ichnotaxon of the Middle Triassic. Characteristic features are the dominance of digits II and III in the pes and the comparatively small manus (Haubold 1971b). This ichnogenus is present in footprint assemblages of the German Bunter ('Thüringischer Chirotheriensandstein'), the Middle Triassic of Great Britain (Tresise & Sarjeant 1997, King *et al.* 2005) and the Moenkopi Formation of Arizona (Peabody 1948). Possible trackmakers are crurotarsans.

In *Chirotherium* (Figs 5h–j & 6), more advanced foot structures are visible in the reduction and posterior shift of pedal digit I, and in the dominance of the digit group II–IV. Other characteristic features are the reduction of manual digits IV and V and the narrow trackway pattern (Walther 1917; Soergel 1925; Haubold 1971a, 2006). In particular, *Chirotherium barthii* (Figs 5h, j & 6a, c–e) displays an initial trend toward the tridactyl pattern later seen, for example, in the autopodia of dinosaurs. *Chirotherium sickleri* (Figs 5i & 6b) shows a more conservative pattern, with long pedal and manual digits IV.

The taxonomic status of some large chirotherians from the Moenkopi Formation is questionable, such as *Chirotherium moquiense* and *C. rex* (Peabody 1948, 1956). The Moenkopi material is presently under revision by the authors. Assemblages with *Chirotherium* are known from the Bunter of Germany ('Thüringischer Chirotheriensandstein', Haubold 1971a, 2006), Great Britain (Tresise & Sarjeant 1997; Clark *et al.* 2002; King *et al.* 2005), France (Demathieu 1984), Spain

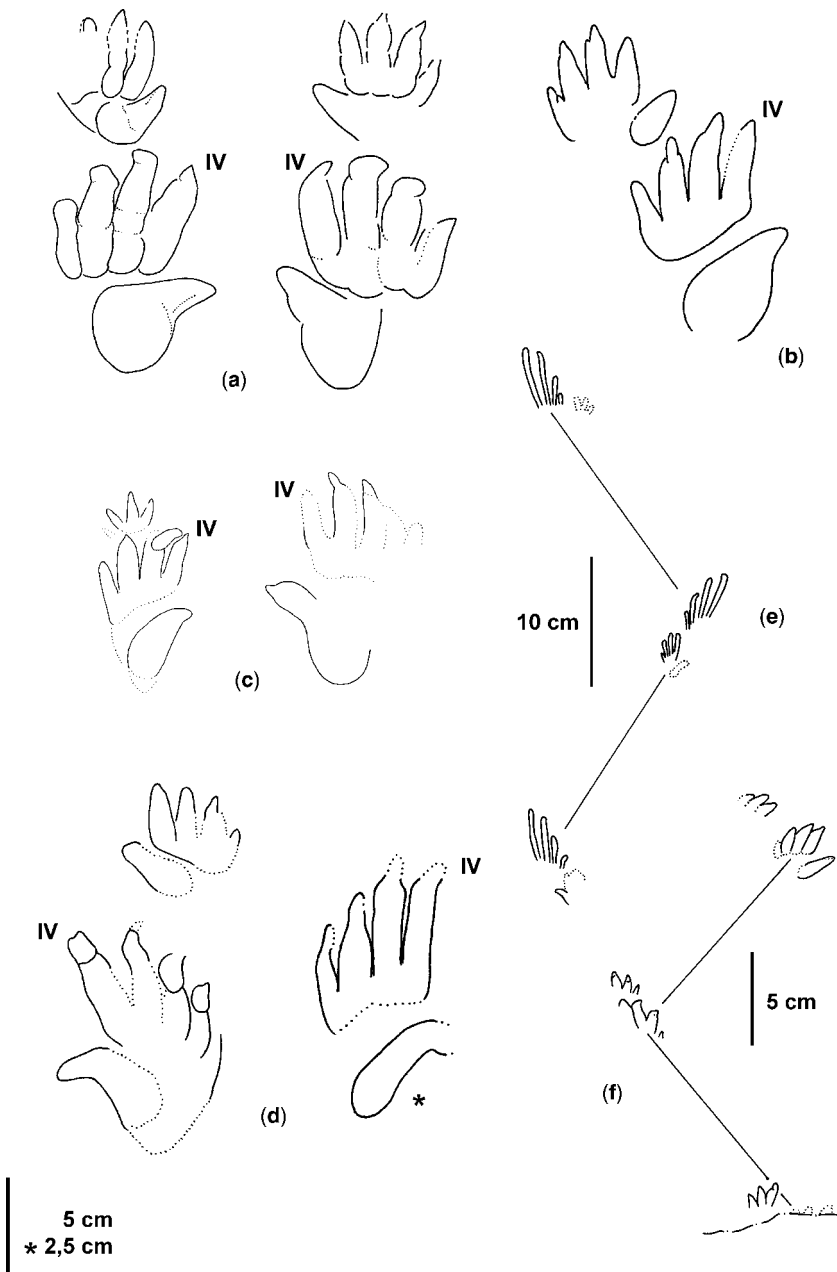


Fig. 3. Characteristic footprints from the lowest Triassic. **(a)** *Protochirotherium wolfhagense*. **(b, c)** *Protochirotherium* (*Brachychotherium*, *Isochirotherium* after Fuglewicz *et al.* 1990; Ptaszynski 2000). **(d)** *Synaptichnium*. **(e)** *Rhynchosauroides*. **(f)** *Procolophonichnium*. **(a)** Detfurth Formation (Olenekian), northern Hessen, Germany. **(b–f)** Labyrinthodontidae beds (Induan), Wióry, Poland. After Fuglewicz *et al.* (1990), Klein & Haubold (2007), Ptaszynski (2000).

(Calderon 1897), Arizona (Moenkopi Formation: Peabody 1948), Argentina (Rusconi 1951; Peabody 1955*b*; Melchor & De Valais 2006), and China (Lü *et al.* 2004).

Another characteristic ichnotaxon of this stratigraphic interval is *Rotodactylus* (Fig. 5k–l). These are small pes and manus impressions, often in dense concentrations on track surfaces. The pes

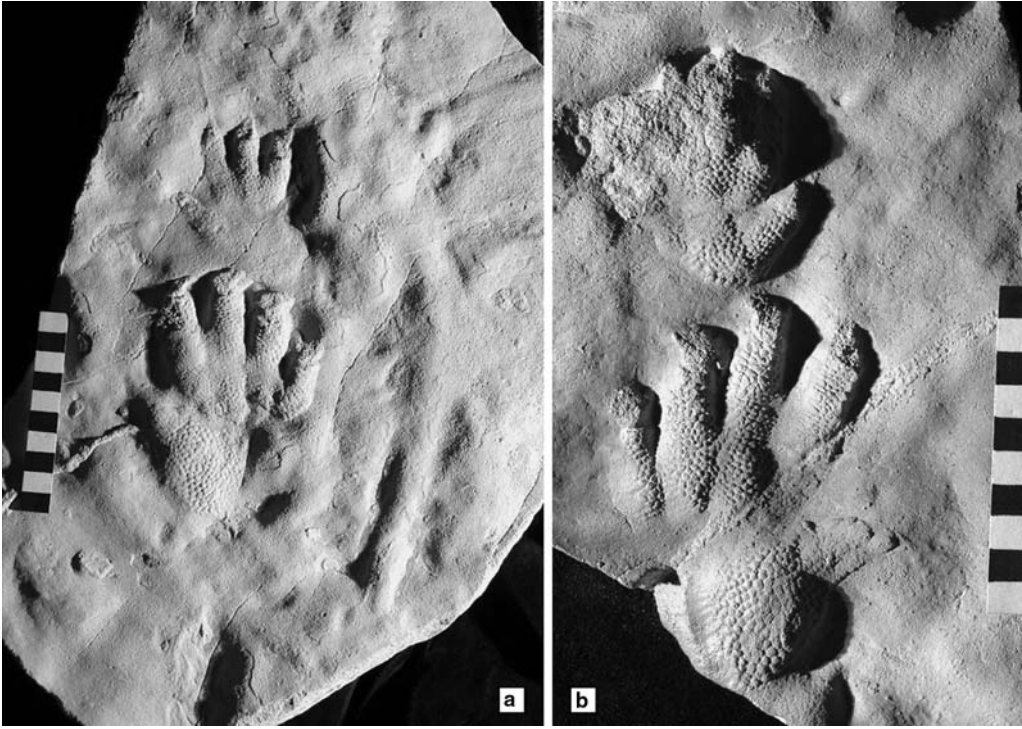


Fig. 4. *Protochirotherium wolfhagense* Fichter & Kunz, 2004 (a) holotype; (b) additional specimen from surface type. Pes and manus imprints with skin structure from the Detfurth Formation (Olenekian) of northern Hessen, Germany. Photos: S. Voigt, Freiberg. Scale bars in cm.

shows a dominance of digits II, III and IV, with IV the longest. Digit V is in an extremely posterior position and only visible as a small circular impression. The manus is of similar shape, and in digit IV it may be shorter. Trackways show wide lateral overstep of the manus by the pes and a long stride length, depending on the velocity of movement. Peabody (1948) was the first to posit a cursorial, dinosaur-like animal (pseudosuchian) as the trackmaker of *Rotodactylus*. Haubold (1967, 1971a, b, 1999) described *Rotodactylus* from surfaces of the German Bunter ('Thüringischer Chirotheriensandstein') and attributed it to a dinosauromorph producer. *Rotodactylus* is known in particular from assemblages of the Moenkopi Formation of Arizona (Peabody 1948), the German Bunter (Haubold 1967, 1971a, b, 1999) and the Middle Triassic of France (Demathieu 1984).

Non-archosaur footprints co-occur with *Rhynchosauroides* (Fig. 7a). *Rhynchosauroides* is a small, pentadactyl and lacertoid imprint form with slender, inwardly curved digits I–IV. Digit IV is longest, and digit V is short and postero-laterally positioned. The pes and manus are of similar shape. Trackways mostly show lateral overstep of the manus by the pes. *Rhynchosauroides* is present in most assemblages of this stratigraphic interval

(e.g. Peabody 1948; Tresise & Sarjeant 1997; Demathieu 1984; Haubold 1971a; Melchor & De Valais 2006).

Therapsid footprints (Fig. 7c, d) are known from the ichnogenera *Dicynodontipus* from the Bunter of Germany (Haubold 1966, 1971a; Demathieu & Fichter 1989) and *Therapsipus* from the Moenkopi Formation (Holbrook Member) of Arizona (Hunt *et al.* 1993). The morphology is characterized by a pentadactyl pes and manus of similar shape and size with short and straight digits. In the smaller *Dicynodontipus* (Fig. 7c), they are of subequal length, and digit V is shifted backward. Some trackways show the manus overstepped by the pes, dependent on the velocity of movement. *Therapsipus* (Fig. 7d) is a large form (25 cm pes length). Following Hunt *et al.* (1993), digit III in the pes and digits III and IV in the manus are longest.

Procolophonichnium (Fig. 7b) encompasses the footprints of small, primitive amniotes. The pes and manus imprints are of similar morphology. They are semi-plantigrade to digitigrade and pentadactyl. Digit length increases from I to III, digits IV and III are subequal in length, and digit V is shorter. Trackways are broad, with the smaller manus

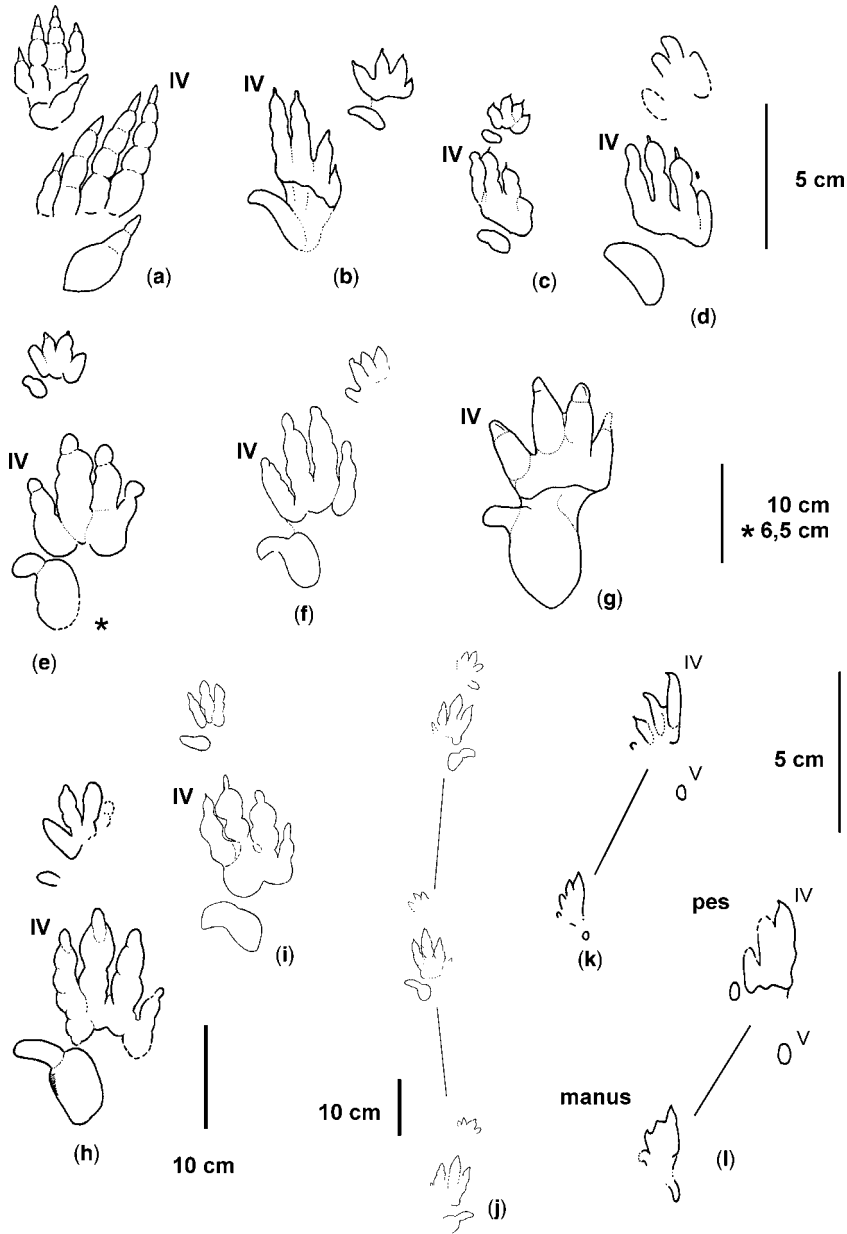


Fig. 5. Archosaur footprints from the Upper Lower Triassic–Lower Middle Triassic. (a, b) *Synaptichnium*; (c, d) '*Brachychirotherium*'; (e–g) *Isochirotherium*; (h, j) *Chirotherium barthii*; (i) *C. sickleri*; (k, l) *Rotodactylus*. (c, e, h, i, k) 'Thüringischer Chirotheriensandstein' (Bunter), southern Thuringia. (d) Röt Formation (Bunter), northern Bavaria. (a, f) Bunter of Great Britain. (b, g, j, l) Moenkopi Formation, Arizona. After Baird (1954), Haubold (1971a, b), Peabody (1948), Soergel (1925).

anterior to the pes. They are known, for example, from the German Bunter (Rühle von Lilienstern 1939; Haubold 1971a).

Capitosauroides (Fig. 7e) refers to semi-plantigrade, pentadactyl pes and manus imprints

with short, blunt and clawless digits that diverge widely. They have been attributed to amphibians (Haubold 1971a). The Bunter of Germany and the Moenkopi Formation of Arizona have provided examples (Haubold 1971a; Peabody 1948).

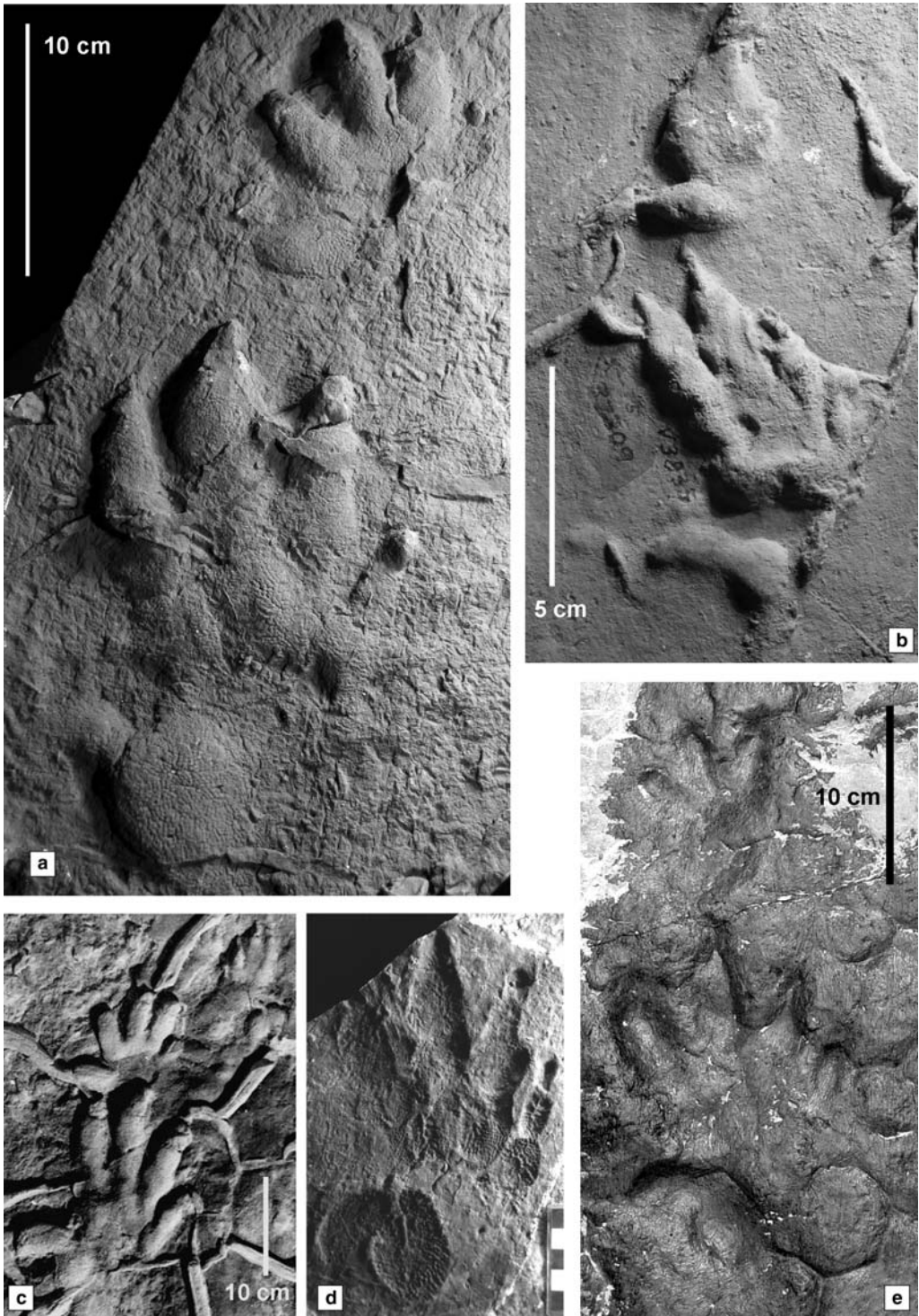


Fig. 6. Archosaur footprints from the Upper Lower Triassic–Lower Middle Triassic. (a, c–e) *Chirotherium barthii*; (b) *Chirotherium sickleri*; (a, b) Moenkopi Formation, Arizona; (c) ‘Thüringischer Chirotheriensandstein’ (Bunter), southern Thuringia; (d) Cerro de Las Cabras Formation, Argentina; (e) Guanling Formation, Guizhou Province, China. Photos: (c) D. Hildebrand; (e) H. Lü; others, H. Klein.

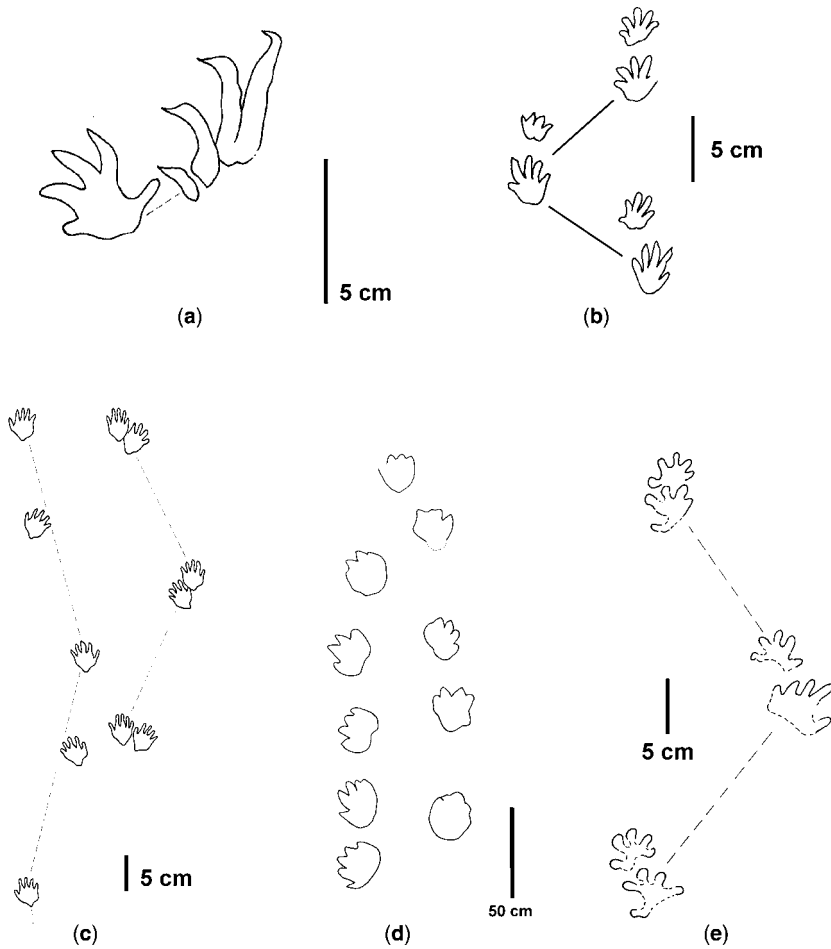


Fig. 7. Non-archosaur footprints from the Upper Lower–Lower Middle Triassic. (a) *Rhynchosaurooides*; (b) *Procolophonichnium*; (c) *Dicynodontipus*; (d) *Therapsipus*; (e) *Capitosauroides*; (a–c, e) Bunter Germany. (d) upper Moenkopi Formation, Arizona (after Haubold 1966, 1971a, b, 1984; Hunt *et al.* 1993).

Upper Middle Triassic

Anisian–Ladinian footprint assemblages are well known from the eastern border of the Massif Central in France (Demathieu 1970; Courel & Demathieu 1976; Gand 1976, 1979a, b), Germany (Haubold & Klein 2002; Klein & Haubold 2004) and Italy (Avanzini 1999, 2000; Avanzini & Lockley 2002; Avanzini & Neri 1998; Mietto 1987). Characteristic ichnogenes are *Isochirotherium*, *Synaptichnium* and ‘*Brachychirotherium*’ (Figs 8a–f & 9a–d), continuing from the lower Middle Triassic.

Sphingopus and *Parachirotherium* (Figs 8g–i & 9e–g) are characteristic upper Middle Triassic ichnogenes. They refer to pentadactyl footprints that follow the trend seen in *Chirotherium*

barthii: (1) reduction and posterior shift of pedal digit I and development of the mesaxonic tridactyl pattern II, III, IV, with digit III longest; and (2) decrease of the palmar surface, indicating a tendency toward bipedality (Haubold & Klein 2000, 2002). *Sphingopus ferox* was named and described by Demathieu (1966) from the Massif Central (France). The ichnogenes was also documented in strata of similar age in Northern Bavaria, Germany (Haubold & Klein 2002). *Parachirotherium postchirotherioides* is known from surfaces of the Benker Sandstein (upper Ladinian) of Northern Bavaria (Rehnel 1950; Kuhn 1958; Haubold & Klein 2000).

Significant is the appearance of the first truly tridactyl pes imprints [*Atreipus–Grallator* (‘*Coelurosaurichnus*’)] in trackways showing the transition

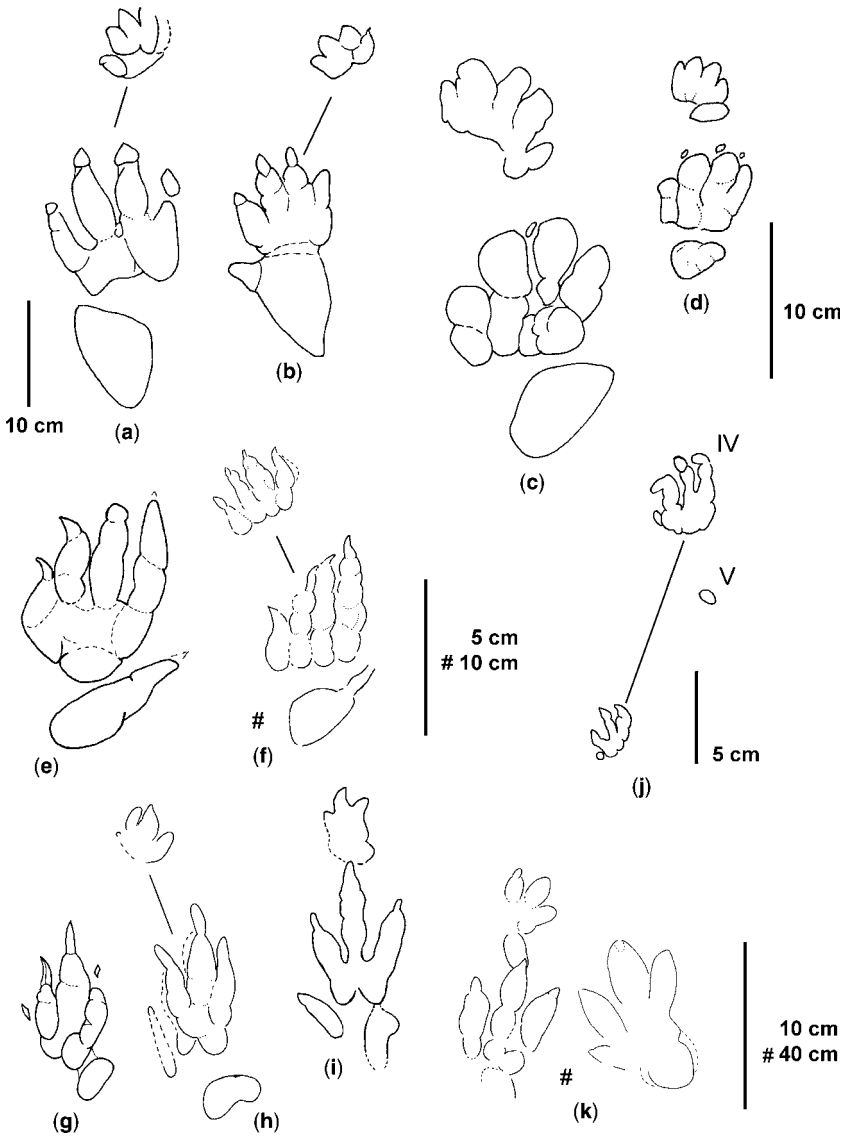


Fig. 8. Upper Middle Triassic archosaur footprints. (a, b) *Isochirotherium*; (c, d) '*Brachychirotherium*'; (e, f) *Synaptichnium*; (g, h) *Sphingopus*; (i) *Parachirotherium*; (j) *Rotodactylus*; (k) *Rigalites*. (a–e, g, j) Anisian–Ladinian, Massif Central, France. (f, h, i) marginal facies of the Muschelkalk and Benker Sandstein (Anisian–Ladinian), northern Bavaria. K, Los Rastros Formation (Ladinian), Argentina. After Courel & Demathieu (1976); Demathieu (1966, 1970); Demathieu & Gand (1973); Gand (1976, 1979a); Haubold (1971b, 1984); Haubold & Klein (2000); Klein & Haubold (2004, 2007).

from quadrupedal to bipedal gait, thus indicating facultative bipedality of probable dinosauriform trackmakers in the Benker Sandstein (upper Ladinian) of Northern Bavaria, Germany (Weiss 1976; Haubold & Klein 2000). Similar trackways appear in the Anisian–Ladinian of France (Gand 1976, 1979a; Gand & Demathieu 2005; Demathieu 1989; Figs 10 & 11a–c).

Rotodactylus occurs in dense concentrations on surfaces of the upper Middle Triassic of France (Demathieu & Gand 1973; Gand 1976, 1979a; Fig. 8j).

Rigalites (Fig. 8k) is a problematic ichnotaxon of archosaur affinity from the Los Rastros Formation (?Ladinian) of San Juan Province, Argentina (Huene 1931; Marsicano *et al.* 2004; Melchor &

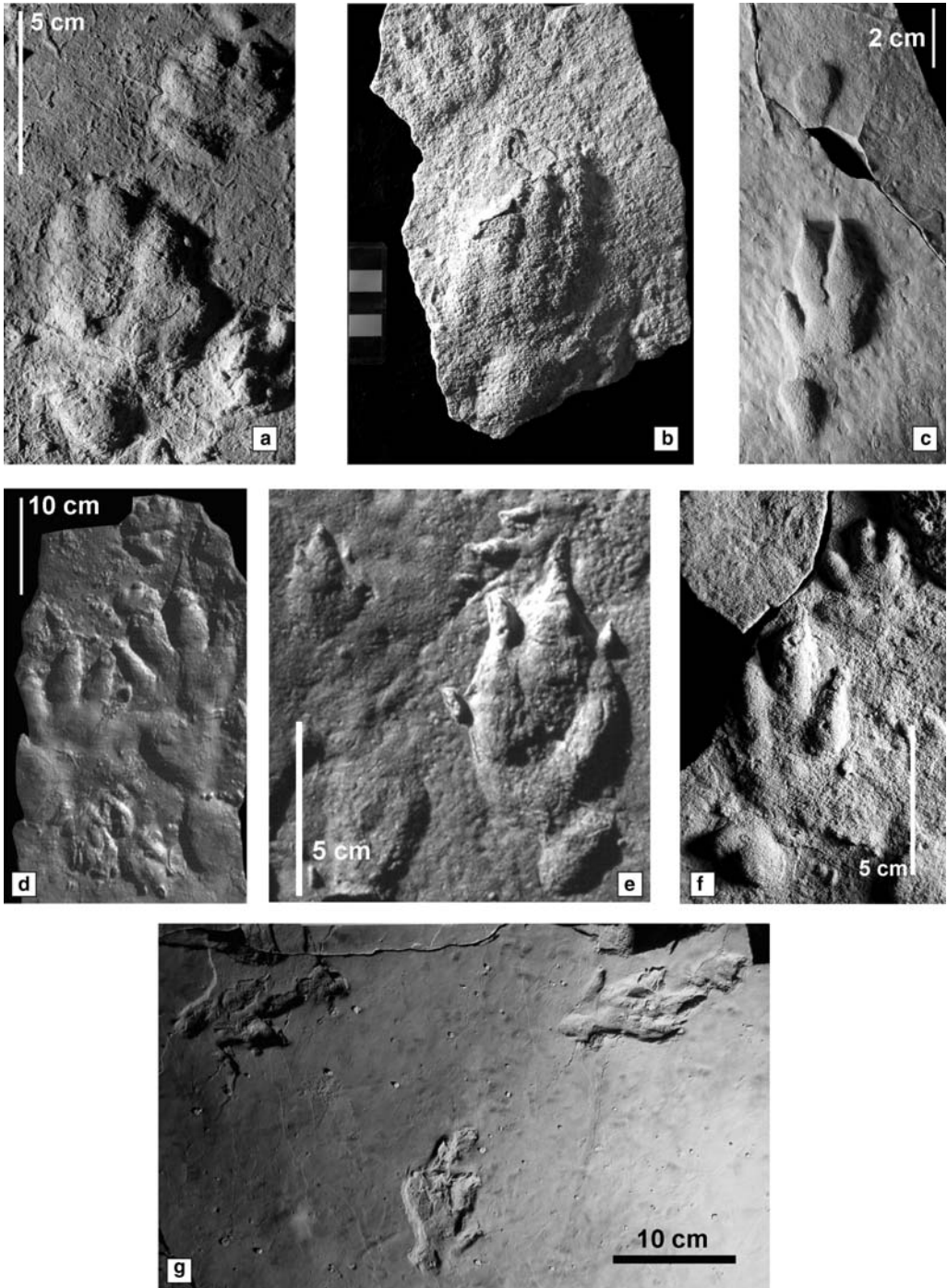


Fig. 9. Upper Middle Triassic archosaur footprints. (a) '*Brachychirotherium*'; (b) *Synaptichnium*; (c, d) *Isochirotherium*; (e, f) *Sphingopus*; (g) *Parachirotherium*. (a, d, e) Anisian–Ladinian, Massif Central, France. (c) Anisian, northern Italy. (b, f, g) Anisian–Ladinian, northern Bavaria. Photos: (c) Marco Avanzini; (d, e) Georges Gand; others, H. Klein.

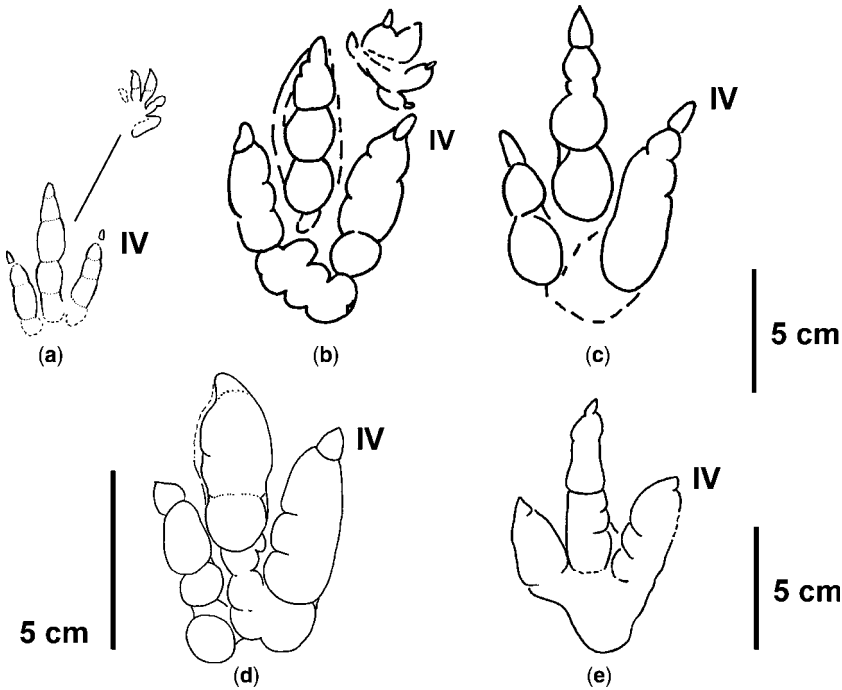


Fig. 10. Tridactyl pes and partly associated manus imprints of dinosauriform archosaurs from the upper Middle Triassic, *Atreipus-Grallator* ('*Coelurosaurichnus*'). (a) Benker Sandstein (upper Ladinian), northern Bavaria. (b–e) Anisian–Ladinian, Massif Central, France. After Gand & Demathieu (2005), Haubold (1984), Haubold & Klein (2000).

De Valais 2006). It encompasses large tetradactyl to pentadactyl pes imprints (more than 35 cm long) associated with a smaller, pentadactyl manus imprint. It shows similarities to large *Parachirotherium* or other chirotherians. Other bipedal to quadrupedal trackways of possible dinosauriform affinity are described from this unit by Marsicano *et al.* (2007).

From Alpine regions in Switzerland, Demathieu & Weidmann (1982) describe an extensive surface from the Ladinian–Carnian boundary. It shows chirotherians and hundreds of undeterminable archosaur footprints and trackways.

Also present in upper Middle Triassic strata are *Rhynchosauroides* and *Procolophonichnium* (Figs 11d & 12a–d). They are dominant in carbonate tidal flat deposits along the margin of the Bohemian and Rhenish massifs in Germany and The Netherlands (Demathieu & Oosterink 1983, 1988; Diedrich 2007), where archosaur footprints are rare.

Upper Triassic

Upper Triassic tetrapod footprint assemblages are archosaur dominated. Most common are tracks of *Brachychirotherium* (*sensu stricto*) and tridactyl imprints of the *Grallator-Eubrontes* type.

Brachychirotherium (*sensu stricto*; Figs 13 & 16a–c) was first named and described by Beurlen (1950) from the Middle Keuper ('Coburger Sandstein', upper Carnian) of northern Bavaria, Germany. Diagnostic features are the broad, pentadactyl pes impression with short, thick digits and tiny claws. Digit V is represented only by an oval basal pad in a position postero-lateral to the rest of the foot. The smaller manus has a similar shape. Karl & Haubold (1998, 2000) analysed the type material and designated a lectotype of the type species *Brachychirotherium hassfurtense* and also confirmed the validity of a second ichnospecies in the Keuper, *B. thuringiacum*.

Brachychirotherium is widespread in the Newark Supergroup of New Jersey and Pennsylvania (Baird 1957; Silvestri & Olsen 1989; Silvestri & Szajna 1993; Szajna & Hartline 2003; Szajna & Silvestri 1996; Olsen *et al.* 2002; Lucas & Sullivan 2006) and in the Chinle Group of the North American Southwest (Lockley & Hunt 1993, 1995; Lucas *et al.* 2001, 2006b, c; Klein *et al.* 2006; Hunt & Lucas 2007a). It is also known from the Los Colorados Formation (Norian) of Argentina (Arcucci *et al.* 2004; Melchor & De Valais 2006), and the Lower Elliot Formation (Norian) of South Africa (Ellenberger 1970, 1972, 1974; Olsen & Galton

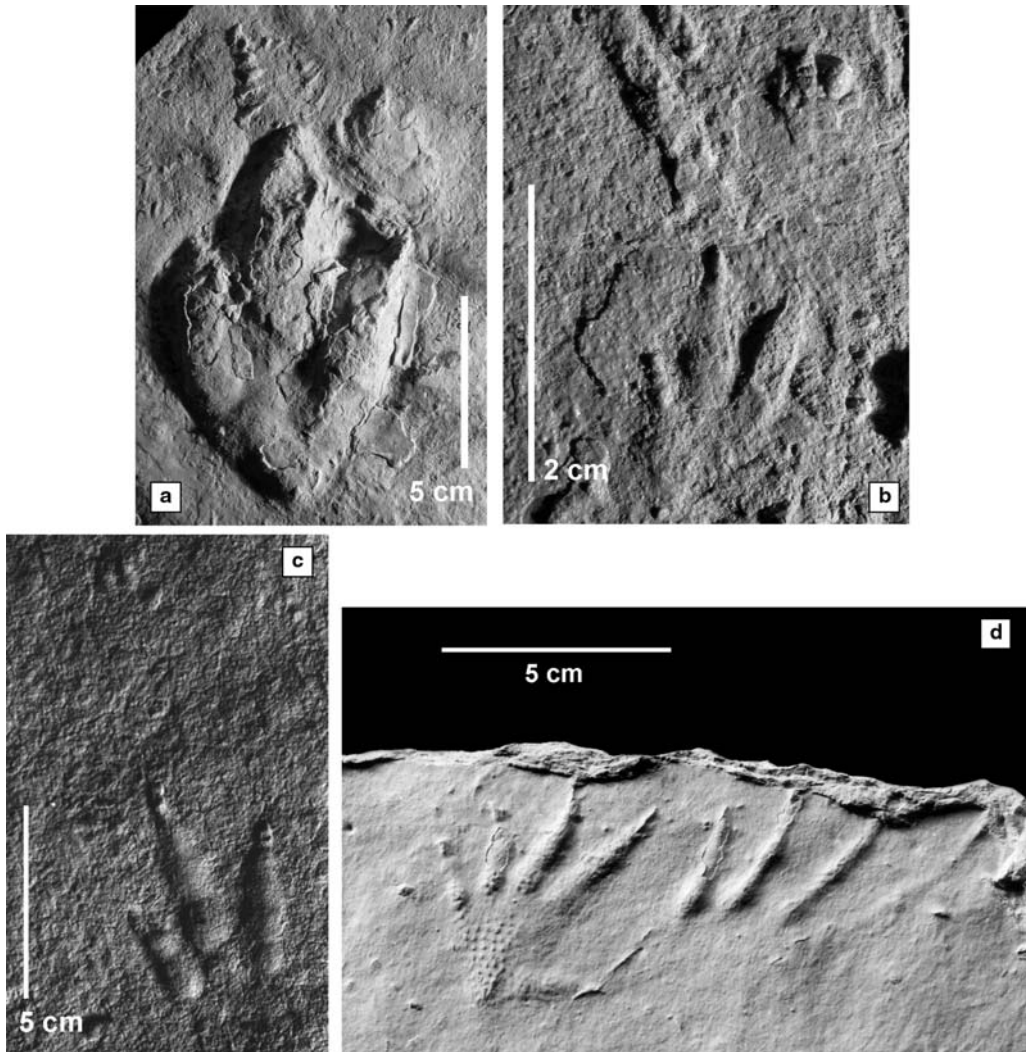


Fig. 11. Footprints from the upper Middle Triassic. (a–c) *Atreipus–Grallator* ('*Coelurosaurichnus*'). (a, b) Anisian–Ladinian of the Massif Central (France). (c) Benker Sandstein (upper Ladinian), northern Bavaria. (d) *Rhynchosauroides*, Anisian of Winterswijk (The Netherlands). Photos (d) Henk W. Oosterink; others, H. Klein.

1984; D'Orazi Porchetti & Nicosia 2007). Probable trackmakers are crurotarsans.

There is some controversy among tetrapod ichnologists concerning the presence and validity of other ichnogenera used for Upper Triassic tracks, especially *Pseudotetrasauropus*, *Tetrasauropus*, *Evazoum*, *Eosauropus*, and *Otozoum* (Fig. 14). The names *Pseudotetrasauropus* and *Tetrasauropus* were originally given to material from the Lower Elliot Formation of Lesotho, southern Africa that was attributed to sauropodomorphs (Ellenberger 1970, 1972, 1974; D'Orazi Porchetti & Nicosia 2007; Fig. 14a–b). Later, footprints

from the Chinle Group of the American Southwest, from Great Britain and from Poland were also assigned to these ichnotaxa (Lockley & Hunt 1993, 1995; Lockley & Meyer 1999; Lockley *et al.* 1993, 1996, 2000, 2001; Lucas *et al.* 2001; Fig. 14f–h; Gierlinski 2007). Some were finally re-assigned to *Evazoum*, an ichnotaxon named from the Carnian of Italy (Nicosia & Loi 2003; Lockley *et al.* 2006b; Fig. 14e) and to *Eosauropus*, another ichnotaxon based on specimens from the American Southwest (Lockley *et al.* 2006a; Fig. 14c). From footprint surfaces of the Norian of France, Gand *et al.* (2000) described *Otozoum*, a

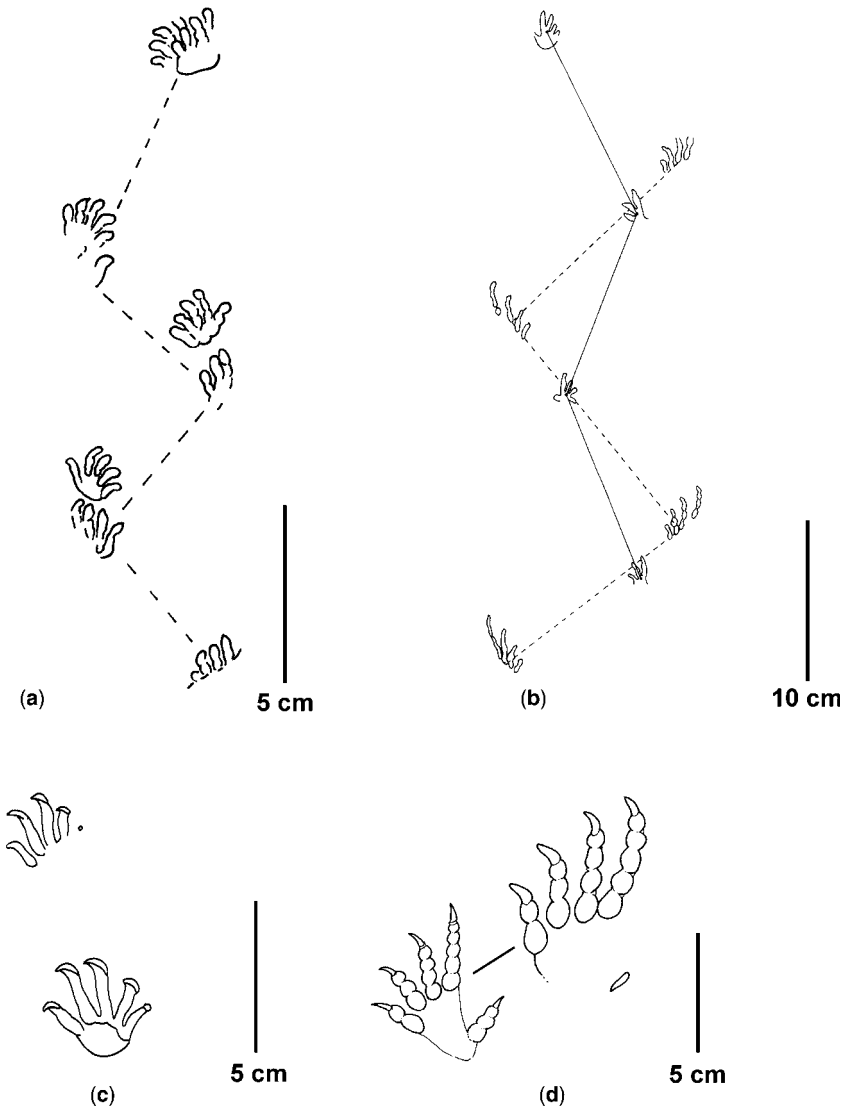


Fig. 12. Non-archosaur footprints from the upper Middle Triassic. (a) *Procolophonichnium* ('*Circapalmichnus*'). (b, d) *Rhynchosaurooides*. (c) *Procolophonichnium*. (a) Anisian–Ladinian of Massif Central (France); (b) Anisian of northern Italy. (c, d) Anisian of Winterswijk (The Netherlands). After Avanzini & Renesto (2002), Demathieu & Oosterink (1983), Gand (1977), Haubold (1984).

taxon known from the Lower Jurassic (Fig. 14d). Rainforth (2003) referred the trackways from France to *Pseudotetrasauropus*. Klein *et al.* (2006), however, considered all these forms to be extramorphological variants of *Brachychirotherium*. They demonstrated the substrate-controlled transition between these forms on track surfaces of the Upper Triassic Redonda Formation (Chinle Group) of New Mexico. Thus, because of disagreements over the ichnotaxonomy of these forms, as

well as their sporadic (though geographically widespread) record, they are not of significance to Triassic footprint biostratigraphy at present.

Grallator and *Eubrontes* (Figs 15d–i & 16d, f) are tridactyl, mesaxononic footprints of different sizes (pes length of *Eubrontes* > 25 cm). They were first described from the Lower Jurassic of the Newark Supergroup by Hitchcock (1836, 1845, 1847, 1858) and can be assigned to theropod trackmakers [Weems (2003) arguments for a prosauropod

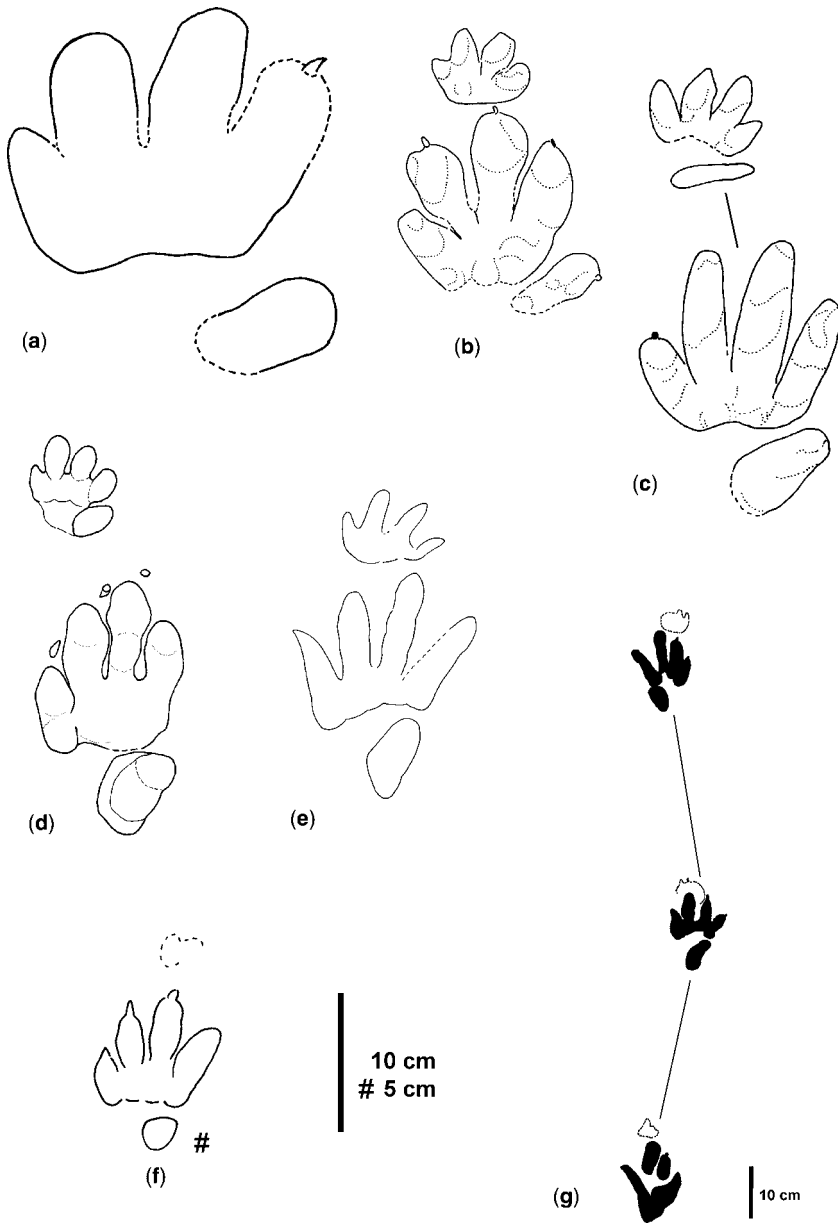


Fig. 13. Pes and manus imprints of *Brachychirotherium*. (a) *B. hassfurtense* (type species); (b, c) *B. thuringiacum* from the upper Carnian of Germany. (d) *B. parvum*, Newark Supergroup (Passaic Formation, Norian), North America. (e, g) Chinle Group (Redonda Formation, Norian), North America. (f) Los Colorados Formation (Norian), Argentina. After Baird (1957), Haubold (1971b), Karl & Haubold (1998), Klein *et al.* (2006).

trackmaker of *Eubrontes* have not been accepted by other ichnologists]. The type material has been re-located and re-examined by Olsen *et al.* (1998).

These theropod footprint ichnogenera are widespread in the Upper Triassic of Pangaea. There is evidence of *Grallator* and/or *Eubrontes* from

countless surfaces in North America (Chinle Group, Newark Supergroup), Greenland (Fleming Fjord Formation), Great Britain (Mercia Mudstone Group), Sweden (Höganäs Formation), France (Carnian–Norian of Ardèche and Alès), Germany (Keuper, Carnian–Norian of Bavaria), Switzerland

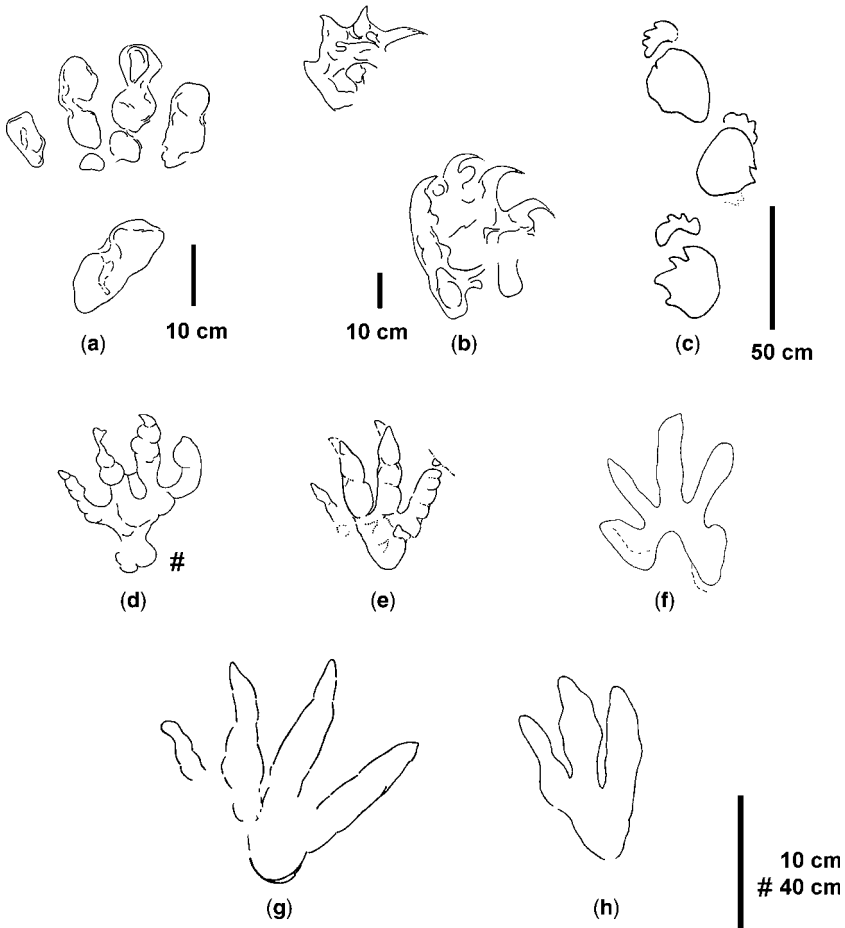


Fig. 14. Imprint forms evaluated differently by various authors either as distinct ichnotaxa or extramorphological (substrate-related) variations of *Brachychirotherium*. (a) *Pseudotetrasauropus*. (b) *Tetrasauropus*. (c) *Eosauropus*. (d) *Otozoum*. (e–h) *Evazoum*. (a, b) Lower Elliot Formation (Norian), southern Africa. (c, f–h) Chinle Group (Norian), North America. (d) Norian, France. (e) Carnian, Italy. After D’Orazi Porchetti & Nicosia (2007), Gand *et al.* (2000), Klein *et al.* (2006), Lockley *et al.* (2006a), Nicosia & Loi (2003).

(Diavel Formation, Norian), Southern Africa (Lower Elliot Formation) and Argentina (Carnian) (e.g. Weiss 1934; Ellenberger 1970, 1972; Furrer 1993; Gierlinski & Ahlberg 1994; Jenkins *et al.* 1994; Lockley & Hunt 1995; Lockley *et al.* 1996; Gatesy *et al.* 1999; Haubold & Klein 2000, 2002; Courel & Demathieu 2000; Gand *et al.* 2000, 2005; Olsen *et al.* 2002; Gaston *et al.* 2003; Szajna & Hartline 2003; Marsicano & Barredo 2004; Milàn *et al.* 2004; Gand & Demathieu 2005; Klein *et al.* 2006; Lucas *et al.* 2006a).

Occasionally, a manus imprint is observed in association with footprints of the *Grallator* morphology (Olsen & Baird 1986; Courel & Demathieu 2000; Gand & Demathieu 2005; Figs 15a, b, c & 16e). For these tracks, Olsen & Baird (1986) introduced a

distinct ichnogenus and named it *Atreipus*. Haubold & Klein (2000) combined grallatorid imprints of facultative bipedal trackways in the plexus *Atreipus–Grallator*. Some authors still use the name ‘*Coelurosaurichnus*’ for these forms (Courel & Demathieu 2000; Gand & Demathieu 2005; Gand *et al.* 2005), and it can be found in the older literature (e.g. Huene 1941; Beurlen 1950; Heller 1952; Kuhn 1958).

The following archosaur-footprint ichnotaxa are also present but generally less widespread and abundant in the Upper Triassic: (1) *Chirotherium lulli* (Fig. 17a), a small chirotherian known from trackways from the Newark Supergroup (Baird 1954); (2) *Apatopus* (Fig. 17b) occurs in the Newark Supergroup and the Chinle Group of North America (Baird

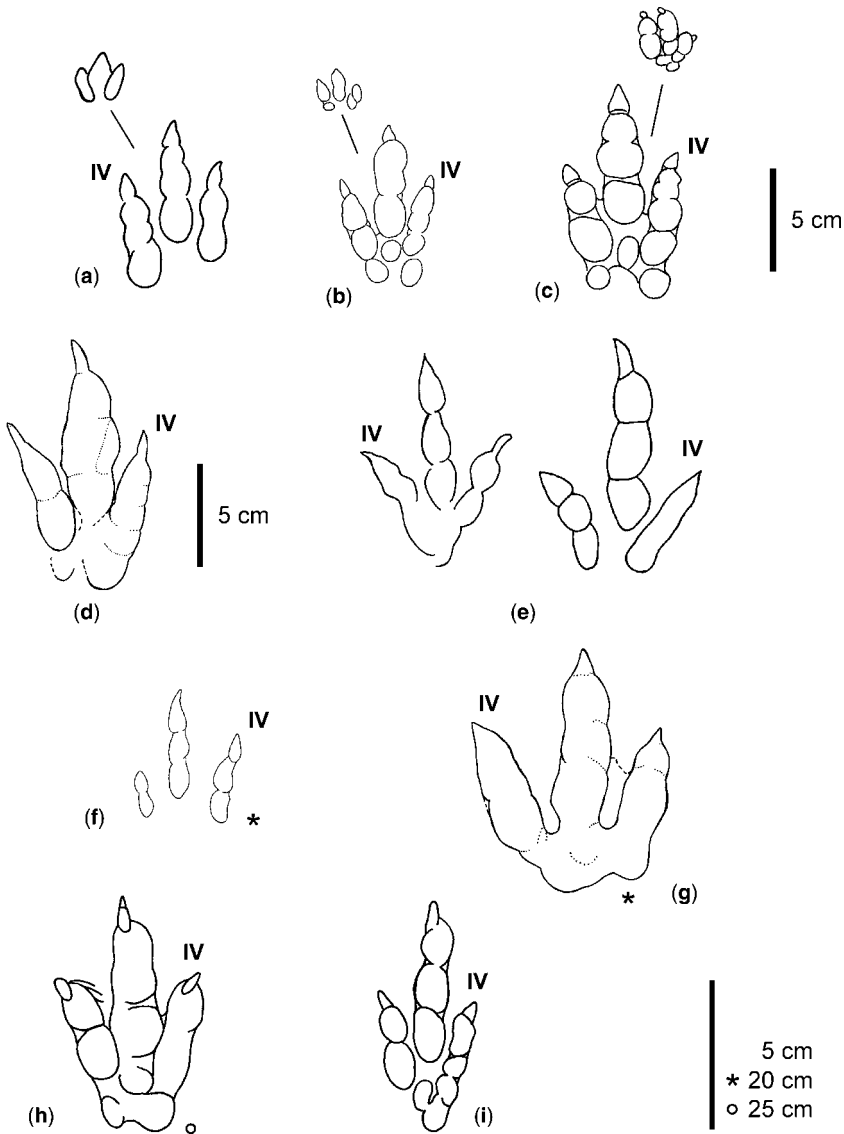


Fig. 15. Tridactyl archosaur tracks from the Carnian through Lower Jurassic. *Atreipus*–*Grallator* with occasionally associated manus and *Grallator*–*Eubrontes* (bipedal theropod footprints). (a) Carnian of southern France. (b) Ansbacher Sandstein (Carnian) of northern Bavaria. (c) Norian of Newark Supergroup, North America. (d) Coburger Sandstein (upper Carnian) of northern Bavaria. (e) Chinle Group (Norian), North America. (f) Norian, France. (g) Rhaetian, Sweden. (h, i) Lower Jurassic of Newark Supergroup, North America (types of *Eubrontes* and *Grallator*). After Courel & Demathieu (2000), Gand & Demathieu (2005), Gaston *et al.* (2003), Gierlinski & Ahlberg (1994), Haubold & Klein (2000), Hunt *et al.* (2000), Olsen & Baird (1986), Olsen *et al.* (1998), Hunt *et al.* (2000).

1957; Foster *et al.* 2003). It shows a conservative morphology of long pedal digits IV and V and a large manus. *Apatopus* has been widely attributed to phytosaurs, however, there is no conclusive evidence supporting this interpretation; (3) *Batrachopus*, an ichnotaxon known from the Jurassic by quadrupedal trackways with tetradactyl to

pentadactyl pes- and manus-imprints, might be also present in the Triassic of the Newark Supergroup. It is attributed to crocodylomorphs. Bird-like footprints have been described from the Santo Domingo Formation (Upper Triassic–Lower Jurassic) of northwestern Argentina and referred to the ichnogenus *Gruipedes* (Melchor *et al.* 2002; De

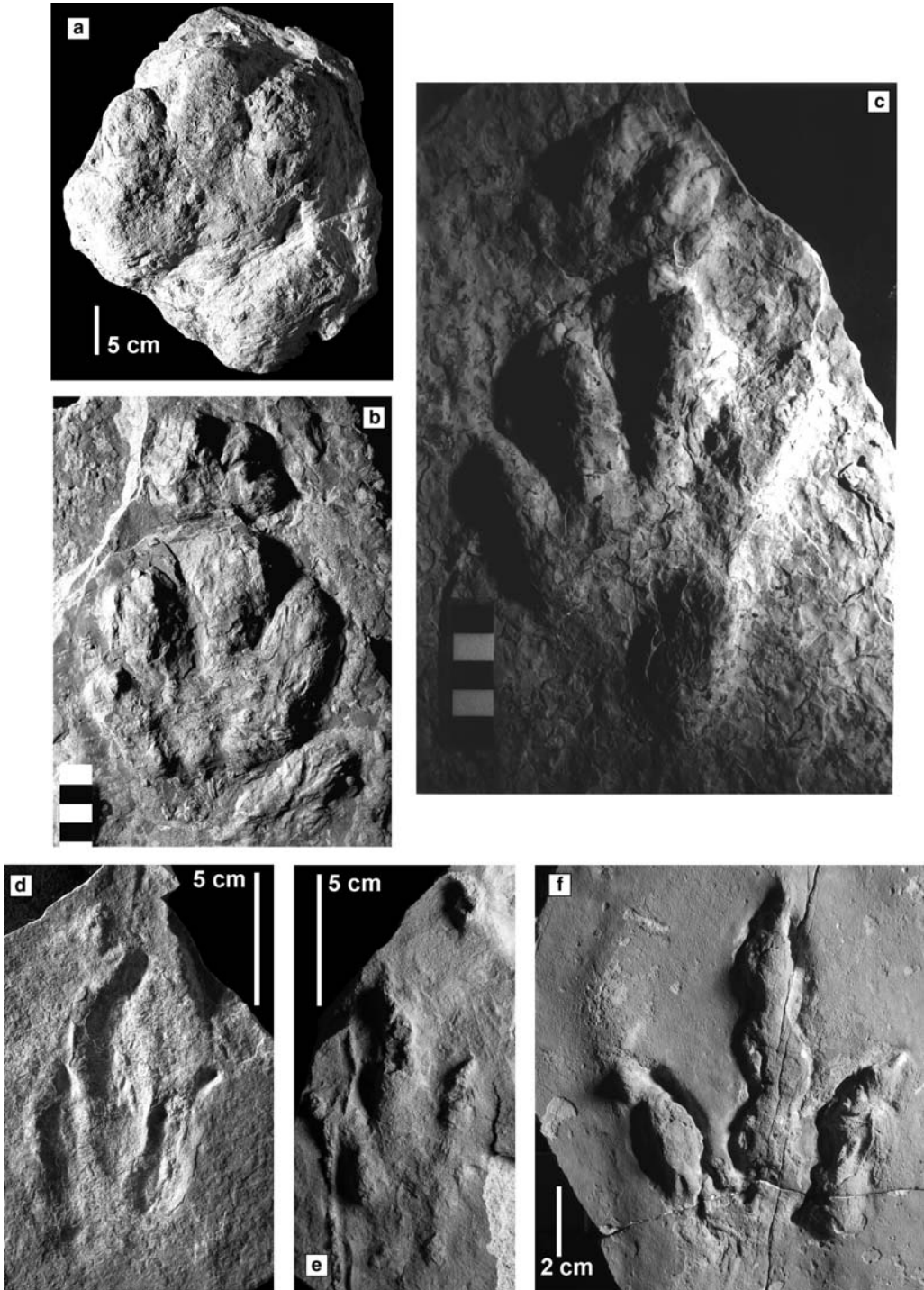


Fig. 16. Characteristic archosaur footprints from the Upper Triassic. (a) pes of *Brachychirotherium hassfurtense* (type species). (b) pes and manus of *B. thuringiacum*. (c) pes and manus of *B. parvum*. (d, e) *Atreipus–Grallator*. (f) *Grallator*. (a, b, d, e) Coburger Sandstein (upper Carnian) of northern Bavaria. (c, f) Chinle Group (Redonda Formation, Norian) of North America.

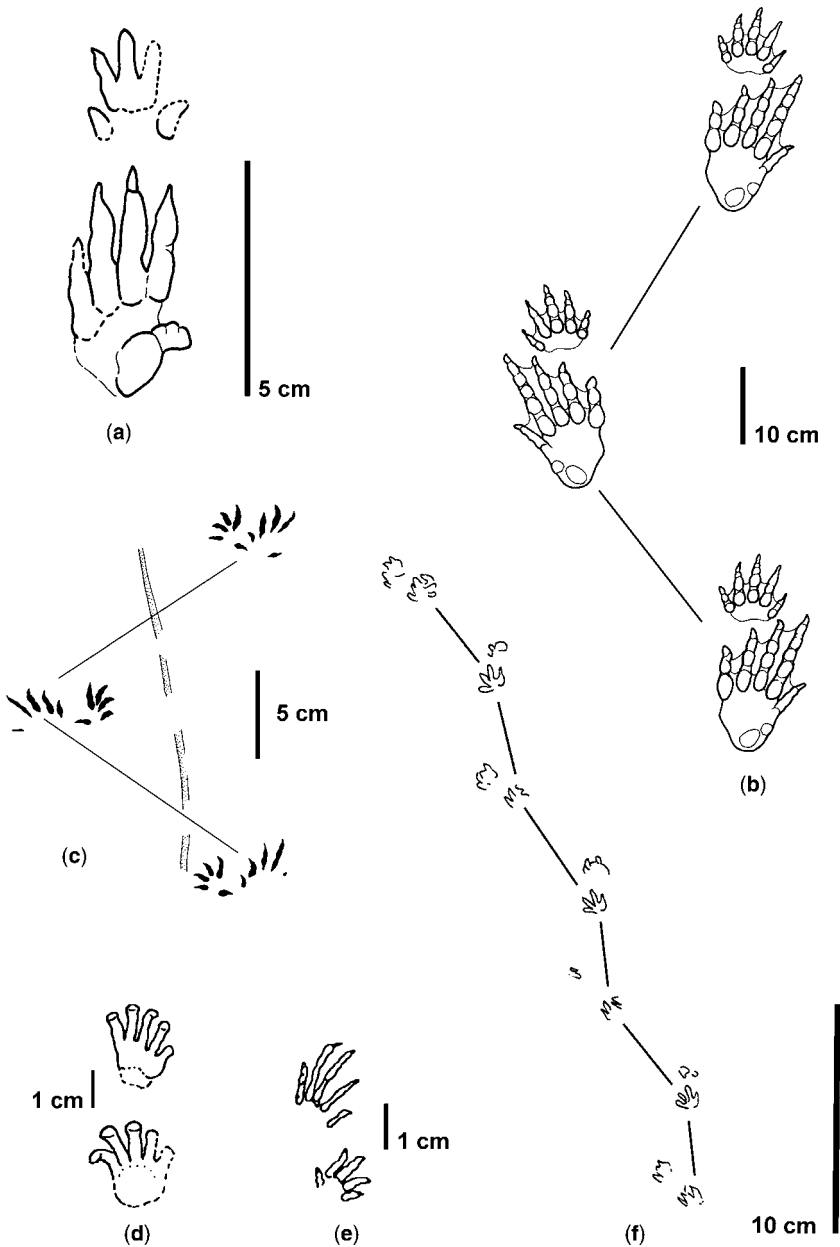


Fig. 17. Imprint forms and trackways from the Upper Triassic. (a) *Chirotherium lulli*. (b) *Apatopus*. (c) *Rhynchosauroides*. (d) *Procolophonichnium*. (e) *Gwyneddichnium*. (f) probable mammal-like (synapsid) trackway. (a, b, d, e) Norian, Newark Supergroup, North America. (c, f) Chinle Group and Wingate Sandstone (Norian–Rhaetian), North America. After Baird (1954, 1957), Haubold (1971b), Lockley *et al.* (2004), Silvestri & Szajna (1993).

Valais & Melchor 2008). Similar forms are known from the Lower Elliot Formation of southern Africa (*Trisauropodiscus*: Ellenberger 1972).

Surfaces with grallatorids and other undetermined archosaur footprints have been described

from the Carnian–Norian of Italy (Dalla Vecchia 1996; Dalla Vecchia & Mietto 1998).

Non-archosaur footprints from Upper Triassic strata are *Rhynchosauroides*, *Procolophonichnium*, *Gwyneddichnium*, and mammal-like forms (Bock

1952; Baird 1957, 1964; Kuhn 1958; Haubold 1971b, 1984; Olsen 2002; Silva *et al.* 2008; Fig. 17c–f). Mammal-like imprints similar to *Brasilichnium* occur on some surfaces of the Chinle Group in the American Southwest (Lockley *et al.* 2004; Klein *et al.* 2006). From South America, an assemblage dominated by trackways of small therapsids is known from the Carnian of the Vera Formation in Rio Negro Province of Argentina (Casamiquela 1964; Domnanovich & Marsicano 2006; Melchor & De Valais 2006).

Triassic tetrapod footprint biochronology

The composition and distribution of Triassic tetrapod footprint assemblages reflect ecological/taphonomical peculiarities as well as different directions and stages in the evolutionary development of the locomotor apparatus of some tetrapod groups. In particular, some archosaur footprints show a limited vertical (stratigraphic) range. Their occurrences are restricted to distinct time intervals, thus demarcating distinct biochronological units (Lucas 2003, 2007; Hunt & Lucas 2007b; Klein & Haubold 2007; Fig. 18).

Between the late Olenekian/Anisian and the Norian the development of the tridactyl mesaxonic foot and bipedal gait of dinosaurs is reflected by the footprint record and can be followed in a functional evolutionary succession: *Chirotherium*–*Sphingopus*–*Parachirotherium*–*Atreipus*–*Grallator* (Haubold & Klein 2000, 2002). This has been used for biostratigraphy and biochronology by Klein & Haubold (2007). Thus, *Chirotherium* spans the Olenekian–Anisian, *Sphingopus* the Anisian–Ladinian, *Parachirotherium* the Ladinian, *Atreipus* the Carnian–Norian and *Grallator* the Norian–Rhaetian interval. Klein & Haubold (2007) discriminated six biochrons (I–VI) by the range of archosaur footprint assemblages. The beginning of each is marked by the first appearance datum (FAD) of a characteristic index ichnotaxon (in bold): **I. *Protochirotherium***, 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 and **VI. *Grallator***–*Eubrontes*, *Brachychirotherium*, Norian–Rhaetian.

Lucas (2003, 2007) recognized five Triassic footprint assemblages: 1. Dicynodont tracks, earliest Triassic; 2. Chirothere, Olenekian–Anisian; 3. *Procolophonichnium*–*Rhynchosauroides*, Anisian–Ladinian; 4. Dinosauriform, Ladinian–Carnian;

and 5. Dinosaur, Carnian–Rhaetian. In this scheme, 2 corresponds to II and III, 3 to III, 4 to IV, and 5 to V and VI of Klein & Haubold (2007). Hunt & Lucas (2007b) propose five assemblages: 1. Dicynodont tracks, earliest Triassic; 2. Chirothere, Olenekian–early Anisian; 3. Dinosauriform, late Anisian–Ladinian; 4. Tridactyl dinosaur, Carnian–early Norian; and 5. Sauropodomorph, late Norian–Rhaetian.

In addition to Lucas (2003, 2007), Hunt & Lucas (2007b) recognize a sauropodomorph track assemblage in the Late Norian–Rhaetian based on the taxa *Evazoum* and *Eosauropus* (see above) purportedly first appearing in the late Norian. This is contrary to Klein *et al.* (2006) and Klein & Haubold (2007), who considered the footprints of *Evazoum* to be extramorphological variants of *Brachychirotherium*, a crurotarsan and characteristic of the entire Late Triassic. Furthermore, *Evazoum* was first described from the Carnian of Italy by Nicosia & Loi (2003), thus indicating an earlier appearance.

Independent from further subdivisions proposed by various authors, we can recognize five tetrapod footprint biochrons of Triassic age that can be identified across the Pangaeian footprint record:

1. Earliest Triassic dicynodont footprints. These tracks are from strata of the *Lystrosaurus* assemblage zone and thus are of Lootsbergian (= latest Changshingian–Induan) age (Lucas 1998; Lucas *et al.* 2007). However, there are only a few records of this assemblage and they are restricted to Gondwana, so it needs further documentation before its Pangaeian-wide significance can be established.
2. *Protochirotherium* is characteristic of strata of Nonesian age (= Olenekian). Morphologically, and based on its temporal distribution, it can be considered as the hypothetical 'root' of later locomotory developments in archosaurs. Associated forms are *Rhynchosauroides*, *Procolophonichnium* and footprints of temnospondyls.
3. The appearance of *Chirotherium barthii* and *C. sickleri*, *Rotodactylus*, *Isochirotherium* and *Synaptichnium* ('*Brachychirotherium*') roughly demarcates the Nonesian–Perovkan (late Olenekian–Anisian) transition. *Chirotherium barthii* and *C. sickleri* disappear during the Anisian. The range of the other ichnotaxa spans most of the Middle Triassic (Perovkan–Berdyankian = Anisian–Ladinian) together with *Rhynchosauroides*, *Procolophonichnium*, dicynodont and temnospondyl footprints that continue from the Nonesian. *Rotodactylus* and *Isochirotherium* disappear before the end of the Berdyankian (Ladinian).

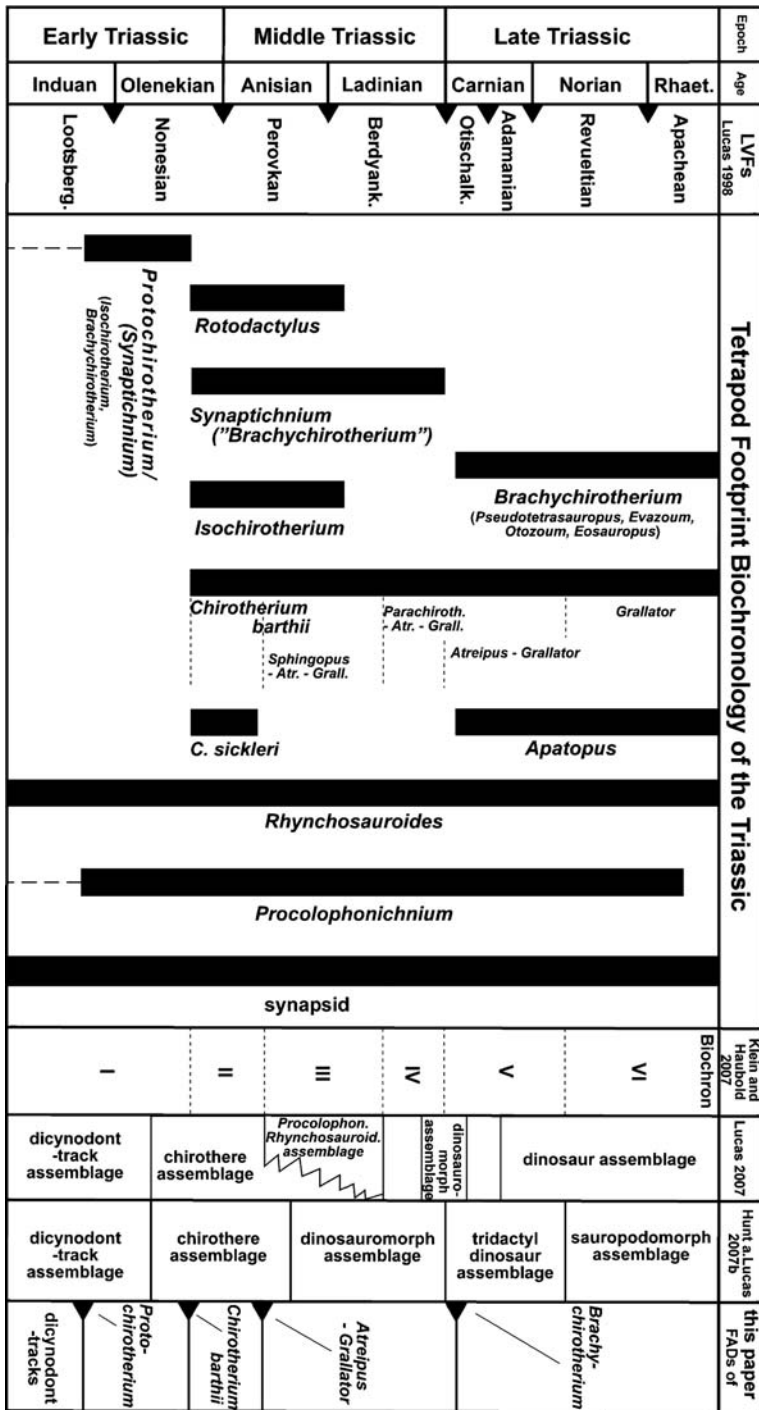


Fig. 18. Stratigraphic distribution of tetrapod footprint taxa and form groups in the Triassic with the biochrons and characteristic assemblages recognized by different authors. Range chart of archosaur footprints after Klein & Haubold (2007).

4. The appearance of tridactyl footprints and quadrupedal to bipedal trackways of the *Atreipus–Grallator* type ('*Coelurosaurichnus*') demarcates the late Perovkian–Berdyanian (= late Anisian–Ladinian) as do pentadactyl footprints of *Sphingopus* and *Parachirotherium*. Other ichnotaxa continue from the Nonesian (see above).
5. *Brachychirotherium (sensu stricto)* appears at the beginning of the Otischalkian (= early Carnian). It is a characteristic ichnotaxon of the Late Triassic, together with *Atreipus–Grallator* (quadrupedal to bipedal trackways), *Grallator* and *Eubrontes* (bipedal trackways). The stratigraphical upper limit of *Brachychirotherium* is the Triassic–Jurassic boundary (end of the Apachean); there is no evidence of *Brachychirotherium* in post-Triassic strata (Lucas & Tanner 2007a, b). The same is true for other chirotheres, and for *Apatopus*, *Procolophonichnium* and *Gwyneddichnium*. The range of *Rhynchosauroides* continues into the Jurassic (Olsen *et al.* 2002), and the same is true of *Batrachopus* and the mammal-like forms, as might be expected.

Rhynchosauroides and *Procolophonichnium*, as well as some dicynodont and temnospondyl footprints, have a long stratigraphic range. They span the complete Triassic Period. Therefore, they are of less utility for biostratigraphy as long as their taxonomy is unclear, as is the case presently. Their dominance in some assemblages (see above) is extremely facies-controlled and biased by ecological and taphonomical effects. *Rhynchosauroides* and *Procolophonichnium* trackmakers obviously frequented some Anisian–Ladinian carbonate tidal flats (assemblage 3 of Lucas 2003, 2007; Demathieu & Oosterink 1983, 1988; Diedrich 2007), an environment that archosaurs (chirothere trackmakers) mostly avoided. However, a few chirotheres are present as well (Demathieu & Oosterink 1988) and, on the other hand, *Rhynchosauroides* is common at least on some fluvial-lacustrine surfaces of the Early through Late Triassic (Demathieu 1966; Haubold 1971a, b).

Evolutionary rather than facies-controlled signals from footprints are suitable to demarcate distinct time intervals in the Triassic and to outline a coarse biostratigraphy and biochronology of the Triassic. This footprint biochronology identifies five intervals of Triassic time, which is less resolution than the eight land-vertebrate faunachrons of Triassic age based on tetrapod body fossils (Fig. 18).

Conclusions

Tetrapod footprints are useful in biostratigraphy and biochronology of the Triassic. However, compared

to body fossils, especially vertebrate bones, they provide lower temporal resolution. Footprints are the result of the interaction between animals and different substrates. Their shape can thus vary immensely, even if left by a single individual. This has produced a complicated and confusing ichnotaxonomy that reflects the subjective ichnotaxonomic evaluation of footprints by different researchers. Many of the purported 'diagnostic' features of tetrapod ichnospecies, but also of some ichnogenera, may be related to extramorphological (substrate-controlled) phenomena. Anatomical signals, such as the number of digits, digit proportions, or the trackway pattern allow discrimination of a number of characteristic form groups and ichnotaxa. In the Triassic, archosaur footprints show a distinct stratigraphic distribution pattern (limited temporal ranges) that can be ascribed to different evolutionary developments of the locomotor apparatus. Several functional-evolutionary sequences and characteristic assemblages can be recognized in the Triassic. They are the basis for the definition of five biochronological units based on tetrapod footprints (Lucas 2003, 2007; Hunt & Lucas 2007b; Klein & Haubold 2007). They can be used to determine the ages of sequences that lack body fossils or can be further used to test and refine Triassic correlations.

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