Chapter 10
The Mesozoic Vertebrate Radiation in Terrestrial Settings

Massimo Bernardi, Fabio Massimo Petti, Laura Piñuela, José Carlos García-Ramos, Marco Avanzini, and Martin G. Lockley

10.1 Introduction

Given their worldwide abundance, it is not surprising that the study of Mesozoic vertebrate tracks is the most ancient branch of vertebrate ichnology. Dinosaur tracks were first observed and figured by Native Americans by, if not before, the seventeenth century (Lockley et al. 2006a), and the first document dates back to the earliest nineteenth century when Pliny Moody reported the discovery of large tracks in the eastern U.S. With Edward Hitchcock (who would eventually coin the world "ichnology"), tracks began to be approached scientifically (e.g., Hitchcock 1858) and subsequent papers by Wolfgang Soergel (Soergel 1925), Othenio Abel (Abel 1935)

M. Bernardi (✉)
Department of Geology and Palaeontology, MUSE - Museo delle Scienze,
Corso del Lavoro e della Scienza 3, 38122 Trento, Italy

School of Earth Sciences, University of Bristol, Queen's Road, Bristol BS8 1RJ, UK
e-mail: massimo.bernardi@muse.it

F.M. Petti
Department of Geology and Palaeontology, MUSE - Museo delle Scienze,
Corso del Lavoro e della Scienza 3, 38122 Trento, Italy

PaleoFactory, Dipartimento di Scienze della Terra, Sapienza Università di Roma,
Piazzale Aldo Moro, 5, 00185 Rome, Italy

L. Piñuela • J.C. García-Ramos
Museo del Jurásico de Asturias [MUJA], Colunga, Asturias, España

M. Avanzini
Department of Geology and Palaeontology, MUSE - Museo delle Scienze,
Corso del Lavoro e della Scienza 3, 38122 Trento, Italy

M.G. Lockley
Dinosaur Tracks Research Group, University of Colorado Denver,
PO Box 173364, Denver, CO 80217-3364, USA

and Roland Bird (Bird 1939, 1944) brought consciousness and the first scientific methods into the discipline. Haubold (1971a, b) published two seminal papers which constituted the base of the first reliable track-trackmakers associations.

In the late twentieth century, the discovery of numerous and vast dinosaur tracksites contributed to the so-called "renaissance" in vertebrate ichnology (Lockley and Gillette 1987) and brought the first solid attempts to standardize study procedures (Leonardi 1987). With this new impetus the first ideas were put forward for using track data for palebiologic (mainly behavioral and physiologic) studies (Lockley and Gillette 1987). This continued in the last two decades with the publication of several seminal volumes, especially on dinosaur tracks (Leonardi 1987, 1994; Gillette and Lockley 1989; Thulborn 1990; Lockley 1991; Lockley and Hunt 1995a; Lockley and Meyer 2000). In order to fully contribute to the paleobiology of dinosaurs, however, the long-standing debate of the relation between tracks and trackmakers needed to be addressed. No paleobiologic inference can in fact be drawn except by interpreting tracks as the result of the activity of a trackmaker, identified as belonging to a particular taxon. It is commonly assumed that tracks can rarely be accurately associated with their producers at the species or genus level (Farlow and Pianka 2000; Carrano and Wilson 2001). During its two centuries of history, however, vertebrate ichnology built a broad consensus on the assignment of some footprint morphogroups to broad taxonomic categories, based on clear analysis of the morphologies of digits, hands, and feet, and comparisons of tracks with hand and foot skeletons (e.g., Haubold 1971a, b; Demathieu and Demathieu 2004; Padian et al. 2010; Heckert et al. 2010) or, rarely, on the direct association of track and fossil material (e.g., Voigt et al. 2012). Most authors agree that a trackmaker attribution at a high taxonomic level is often possible (e.g., Baird 1980; Sarjeant 1990; Olsen et al. 2002; Carrano and Wilson 2001; Thulborn 2006), and in fact morphofamilies or ichnofamilies have been referred to in the literature since the early twentieth century (Lull 1904). In the 1980s, Demathieu and colleagues began to elaborate on the possibility of implementing tracks in phylogenetic studies (Demathieu 1981; Demathieu and Haubold 1978). Demathieu also pioneered the use of vertebrate tracks in many other areas of paleobiologic studies (Demathieu 1986); since then, a synapomorphy-based approach has been employed in a number of studies (Olsen 1995; Olsen and Baird 1986; Olsen et al. 1998; Wilson and Carrano 1999; Haubold and Klein 2000, 2002; Padian 2003; Wilson 2005; Wright 2005; Brusatte et al. 2010b; Kubo and Kubo 2012; Bernardi et al. 2015). This perspective has considerably constrained potential trackmakers finally allowing full hypothesis testing and a better integration of vertebrate ichnology in paleobiologic analysis.

10.2   Trends and Events During the Mesozoic

10.2.1   Tetrapods Across the PT Boundary

A track is the result of the activity of a producer, or trackmaker, namely a track is the imprint of an autopodium (a limb) registered during locomotion. The vertebrate track record can be thought as an archive of the evolution of foot morphology and

posture of extinct and extant vertebrates. Here we must also remember that tracks also record many details of soft tissue morphology, not revealed by body fossils, which in many cases may lack foot skeletons, even when other key diagnostic elements are present. When consecutive steps are impressed as an animal moves, in fact, a trackway is formed and its parameters (i.e., width, distance between single tracks, angle between tracks, distance of the tracks from midline, etc.) can be used to accurately define the walking posture of its producer. Assessing posture from a skeleton involves observing limb articular surfaces and manipulating (physically or virtually) bones at the hip, knee, and ankle in the hindlimb, and shoulder, elbow, and wrist in the forelimb. This procedure is time-consuming and necessitates good preservation of the joints, which is not often the case. On the contrary, basic trackway parameters, such as those listed here, can be easily measured in all kinds of trackways and are less dependent on substrate consistency and taphonomic deformation with respect to single-track descriptive measurements (i.e., interdigital angles). Furthermore, the track record is often much more abundant than the skeletal one, thus giving opportunities to statistically analyze the data.

Limb postures of tetrapods vary from sprawling to erect. An erect limb can be found within birds and cursorial mammals, where the limbs are held under the body and move in a parasagittal plane. On the other hand, a sprawling limb posture is seen in limbed squamates and all limbed amphibians, where the proximal limb segments are highly abducted and swing largely in a horizontal plane (Blob 2000). Posture can change during locomotion, a classic example being crocodiles which show a sprawling posture at low speeds and a semi-erect one when running (Zug 1974; Carpenter 2009). An erect limb posture is energetically advantageous over a sprawling limb posture, especially for large animals. Stresses over the knee and elbow joints are reduced and respiration is facilitated when the limbs are held vertical (Carrier 1987).

From skeletal studies, it is known that Late Permian tetrapods such as temnospondyl amphibians, pelycosaurs, and pareiasaurs were largely sprawlers (Carroll 1988; Benton 2005). Late Triassic faunas were instead dominated by erect forms such as dinosaurs and crurotarsan archosaurs (Nesbitt 2011). The postural transition from sprawling to erect between those times can be described by looking at skeletal remains, but these are scanty in the Early and Middle Triassic. Vertebrate ichnology has allowed a better understanding of this event, especially regarding the exact pattern, timing, and possible correlation with other events by studying fossil trackways.

A key study in this respect was developed by Kubo and Benton (2009). The authors used a classic, simple measure to distinguish sprawlers from erect walkers: the ratio of stride length to trackway width, indicated by the pace angulation (Peabody 1959). This is defined as the angle formed by three continuous front or hind footprints (Peabody 1959) (Fig. 10.1). Pace angulation is dependent on body size and speed, but limb posture is the key factor in determining pace angulation. As exemplified by neoichnologic studies, values lower than 107°, in fact, indicate the producer performed a sprawled locomotion while values greater than 138° indicate erect locomotion (Kubo and Benton 2009).

By analyzing a large dataset of Late Paleozoic to Early Mesozoic tetrapod trackways, the authors found a clear distinction between Permian and Triassic samples
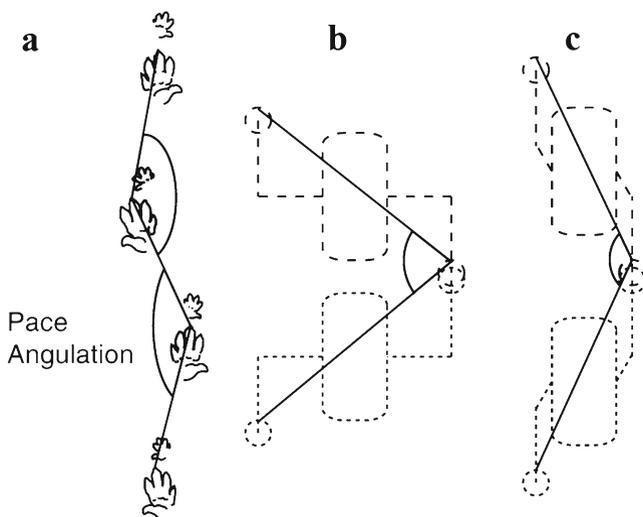
Fig. 10.1 Pace angulation, the angle formed by three consecutive footprints, can be used as a proxy for trackmaker's posture. Using the measuring method shown in (**a**), Kubo and Benton (2009) discovered that the shift from a sprowler posture (**b**) to a more erect one (**c**) occurred across the Permian-Triassic boundary, and may thus be related with the profound impact of the devastating mass extinction event. Modified from Kubo and Benton (2009)

when median values rise from 87.5° (Late Permian) to 139.5° (Early Triassic), whereas within those epochs no significative change in the distributions of pace angulation could be found. All tetrapods, whether synapsids or archosaurs, show the same postural shift across the Permo-Triassic boundary and once the posture had changed, there was no significant change in mean pace angulation through the Triassic. This shift was mostly caused by the increase in the number of chirotheriid trackways from the Early Triassic. The ichnofamily Chirotheriidae (Abel 1935) is a form family comprising the ichnogenera *Chirotherium* Kaup, 1835; *Brachychirotherium* Beurlen, 1950; *Isochirotherium* Haubold, 1971b; *Synaptichnium* Nopcsa, 1923; *Parasynaptichnium* Mietto, 1987, and *Protochirotherium* Fichter and Kunz, 2004. These have been consistently attributed to archosaurs, usually to crurotarsans (pseudosuchians) and basal archosauriforms (Krebs 1965; Haubold 1967, 1971a, 1971b, 1984, 1986, 1999, 2006; Lockley and Meyer 2000; Demathieu and Demathieu 2004; Gand et al. 2010; Bowden et al. 2010; Heckert et al. 2010; Lucas and Heckert 2011; Desojo et al. 2013; Bernardi et al. 2015) and show *manus* (fore foot) and *pes* (hind foot) imprints with a compact anterior digit group I–IV and a postero-laterally positioned, strongly reduced digit V, which are apomorphies of Archosauromorpha (Nesbitt 2011). Thus it is clear that archosaurs (and to a lesser extent, therapsids) were responsible for the high pace angulation of Triassic trackways. Footprints made by amphibians, procolophonids, and small basal diapsids indicate retained sprawling limb posture (Haubold 1971a, b). The abundance of trackways from the Permian up to the Triassic provides resolution that the rare skeletal fossil tetrapods of this age do

not. In addition to providing a description of the pattern of this event, dating indicates that the shift was accomplished already 6 myr after the profound Permo-Triassic mass extinction; this is considerably earlier than the 15–20 myr suggested by the study of locomotory evolution based on skeletal fossils (Charig 1972; Kemp 1982; Bonaparte 1984; Parrish 1987; Kubo and Benton 2009). The ichnologic record also supports a late Permian-Early Triassic radiation of archosauriforms not well documented by skeletal material. By analizing several chirotheriid footprints from the upper Permian of the Southern Alps (Italy), Bernardi et al. (2015) showed that archosauriforms had already undergone substantial taxonomic diversification by the late Permian, widening the geographical distribution of this clade before and after the P-T boundary (Bernardi et al. 2015). Furthermore, analysis of body size, as deduced from track length, allowed formulating a new hypothesis on the response of archosauriforms to the end-Permian events, proposing that their body size did not change significantly from the late Permian to the Early Triassic (Bernardi et al. 2015).

10.2.2   The Origin of Dinosauromorphs

In vertebrate ichnology synapomorphy-based studies are still rare. However, it now appears possible to integrate this discipline into paleobiologic studies if rigorous descriptions are coupled by thoughtful character-based evaluation of potential trackmakers. When synapomorphic characters are found, potential trackmakers can be constrained considerably, allowing full hypothesis testing. More simply, each find that reveals new morphotypes of trackways or skeletal remains of limbs/feet showing apomorphic characters, helps constrain possible track-trackmaker correlations more accurately. Using this approach, tracks and trackways become "biologically informative" and can thus be of interest for paleobiologic analysis. The synapomorphy-based technique focuses on the identification of osteologic-derived character states in the tracks that result from the impression of corresponding (synapomorphic) characters in the autopodia of the trackmaker. These characters allow the recognition of a particular clade independent from the defined body-fossil distributions (see Olsen et al. 1998; Carrano and Wilson 2001; Wilson 2005). This approach has been applied only recently (e.g., Olsen 1995; Olsen and Baird 1986; Olsen et al. 1998; Wilson and Carrano 1999; Carrano and Wilson 2001; Haubold and Klein 2000, 2002; Padian 2003; Wilson 2005; Wright 2005; Brusatte et al. 2010b; Kubo and Kubo 2013; Bernardi et al. 2015).

The most recent advances in the understanding of the origin of dinosaur lineages are a good example of the potential for integrating ichnologic studies with cladistic approaches. The resulting contribution is that, conceived in this way, vertebrate ichnology can give to a deeper understanding of patterns and processes in the evolution of life. Dinosauromorpha is a clade including all taxa closer to dinosaurs than to the other main archosaur clades (i.e., pterosaurs and crocodylomorphs). Dinosauromorphs originated, and radiated in the Triassic, and several taxa are now known that vary in size, feeding, and locomotory features, and that were spread over

most of western Pangea (Langer et al. 2013). However, both the timing and pattern of the early radiation of this lineage are poorly understood (see Marsicano et al. 2015 for a recent update). The oldest known body fossils of dinosauromorphs are silesaurids, which are Anisian in age (Nesbitt et al. 2010; Peecook et al. 2011; Barrett et al. 2015). Silesaurids occupy a derived position within Dinosauromorpha (Ezcurra 2006; Nesbitt et al. 2010; Nesbitt 2011), and therefore imply the presence of other dinosauromorph groups such as lagerpetids, and non-silesaurid dinosauri-formes before that time. No such Early Triassic groups are documented in the body fossil record. However, the Early Triassic archosaur track record is rich (see Klein and Haubold 2007 and references therein), raising the intriguing possibility that dinosauromorph tracks can be recognized among the diverse ichnoassociations. *Rotodactylus*, a common ichnogenus in the latest Olenekian–Ladinian worldwide (Peabody 1948; Gand and Demathieu 2005; Gand et al. 2005; Klein and Haubold 2007), has been long attributed to basal dinosauromorphs (Haubold 1999; Haubold and Klein 2002); however, a strict synapomorphy-based assessment was lacking. Recently, Brusatte et al. (2010a) presented a formal analysis corroborating this identification. *Rotodactylus*, in fact, possesses unequivocal features of dinosauro-morphs, such as reduction of digits I and V and digitigrade posture. Moreover Brusatte et al. (2010a, see also; Niedźwiedzki et al. 2013), described a new ichno-genus named *Prorotodactylus*, discovered in the Early Triassic of Koszary and Stryczowice, Poland. *Prorotodactylus* can be assigned to Dinosauromorpha thanks to the presence of unequivocal synapomorphies such as the bunched metatarsus, reduction of digits I and V, the posterior deflection of digit V, and the manifest digi-tigrady. Brusatte et al. (2010a) suggested *Lagerpeton* as possible trackmaker, and although this is (Niedźwiedzki et al. 2013) or might be (Langer et al. 2013) the case, an attribution of *Prorotodactylus* to dinosauromorphs appears quite solid (Niedźwiedzki et al. 2013; but see Klein and Niedźwiedzki 2012). The nearly com-plete absence of autopodia in the skeletal record (with the notable exception of *Lagerpeton*, Sereno and Arcucci 1994) prevents an evaluation of digit ratios across other dinosauromorph taxa (see Langer et al. 2013 for a discussion) and enhance the importance of the above cited ichnotaxa in exploring the early history of this group. The synapomorphy-based identifications of *Rotodactylus* and *Prorotodactylus* shed new light on the debate over the posture of the earliest dinosauromorphs; both show that these early forms were much more digitigrade than any other closely related archosaurs and that they walked on all fours (Fig. 10.2b). The ichnogenus *Sphingopus*, which is found in numerous Olenekian to Middle Triassic sites all over the world (Klein and Haubold 2007), shares the apomorphic characters described in *Prorotodactylus*; however, the lack of associated manus imprints and high pace angulation indicates that the trackmaker was walking bipedally. Furthermore, *Sphingopus* is much larger than the other dinosauromorph tracks. The tendency toward a full tridactyl morphology, with digit III being the longest, suggest that *Sphingopus* isp. was produced by a dinosauromorph more derived than the *Proroto dactylus*/*Rotodactylus* trackmaker, and therefore suggests that bipedality was acquired and the trackmaker was closer to the origin of dinosaurs (Fig. 10.2c).
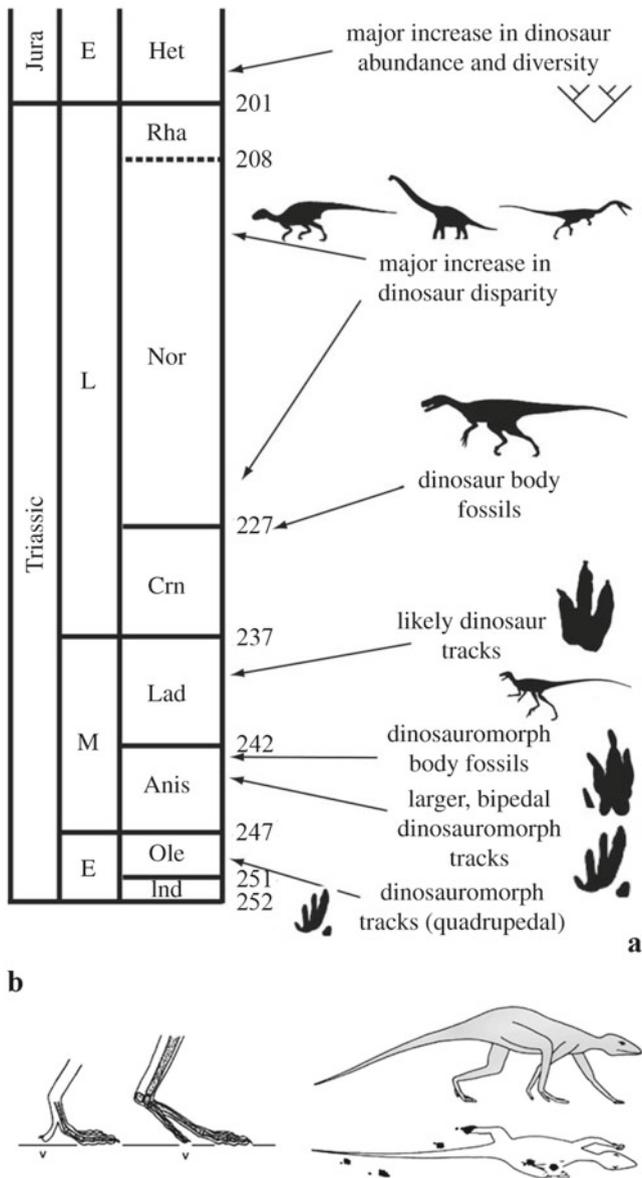
Fig. 10.2 Footprints attributed to dinosauromorphs and early dinosaurs can be integrated with skeletal data to build a general timeline of early dinosaur history. Footprints, as those described by Brusatte et al. (2010b), document the earliest phase of this radiation and predate timing of emergence of the various groups (**a**). (**b**) Shows a likely reconstruction of an early dinosauromoph as reconstructed on the base of *Rotodactylus* trackways. (**a**) Modified from Brusatte et al. (2010b), (**b**) modified from Haubold (1999) and Niedźwiedzki et al. (2013)

The stratigraphically successive records of *Prorotodactylus* and *Rotodactylus* documented by Brusatte et al. (2010a) show that changes in foot anatomy were occurring in dinosauromorphs during the Olenekian; the appearance of *Sphingopus* documents the evolutionary shift from quadrupedality to bipedality, and from small to large size, in the dinosaur lineage. Tracks, identified using synapomorphies, can thus provide new data on the timing and pattern of character acquisition during early dinosauromorph radiation (Fig. 10.2a). Such data are currently not visible in the body fossil record. Furthermore, being older than indicated by the skeletal record, tracks might indicate that the appearance of the dinosauromorph lineage can be linked with the Permian—Triassic mass extinction event (Brusatte et al. 2010a; Niedźwiedzki et al. 2013).

10.2.3 The Origin and Early History of Dinosaurs

The vertebrate track record can be used to make inferences about the spatial and temporal distribution of tetrapod taxa and can give reliable clues, although at a coarse taxonomic level, into tetrapod diversity. If parsimoniously interpreted, it can complement the skeletal record offering a "total evidence" approach to the study of evolutionary patterns and timing of events.

The study of early Mesozoic vertebrate terrestrial ecosystems is a lively field in both vertebrate paleontology and paleoichnology, mostly powered by the debates on dinosaur origins and their early history. The appearance of dinosaurs during the Triassic marked the onset of a faunal diversification that has dominated terrestrial ecosystems for almost 230 Myr (Brusatte et al. 2008a). As discussed, the possible contribution of track data to this and other taxon-based debates, depends on reliable identification of dinosaur trackmakers.

Triassic tridactyl prints are traditionally assigned to Dinosauria (see Lucas et al. 2006 and reference therein). Supposed dinosaur tracks are recognized on the base of few synapomorphies: (1) the prevalence of the digit II–IV group, (2) mesaxonic pattern of foot structure, (3) digit I reduced and shifted backwards (and thus often not preserved in tracks), and (4) tendency towards digitigrady (see also Thulborn 1990; Haubold 1999; Brusatte et al. 2010b). However, this morphotype cannot be unambiguously assigned to Dinosauria using apomorphy-based identifications; a functionally tridactyl pes is found also in some non-dinosaurian dinosauriforms (Gauthier 1986; Brinkman and Sues 1987; King and Benton 1996; Novas 1992; Carrano and Wilson 2001; Fraser et al. 2002; Dzik 2003; Marsicano et al. 2007; Nesbitt et al. 2007; Brusatte et al. 2010b). Furthermore, no synapomorphies of three-toed footprints can discriminate among theropods, basal saurischian, and basal ornithischian groups (Olsen et al. 1998). "Theropod-like" tracks can, however, be identified on the basis of the following characters: (1) asymmetry of the track with angle between digit III and II lower than III-IV, (2) digit III longer than IV > II, (3) sharp claw traces on all digits, and (4) tip of digit II turned inwards (Bernardi et al. 2013). Lockley (2001, 2007a, 2009) has also argued that narrowness and strong mesaxony distinguishes theropod tracks from those of tridactyl ornithischians. Nevertheless, no clear

synapomorphy can be described in tridactyl tracks to clearly distinguish between dinosaurian- and non-dinosaurian-dinosauriforms. All Triassic functionally tridactyl tracks with digitigrade pes produced by bipedal parasagittal posture should be loosely attributed to an archosaur on the dinosaur line. Some derived characters, such as those listed by Bernardi et al. (2013), can be used in support of an attribution to Dinosauria, but a "gray zone" will always exist.

Debates on dinosaur origin thus focus around three main topics: (1) timing of appearance, (2) pattern and pace of early diversification (body size and biogeography), and (3) dynamics of replacement of crurotarsan archosaurs by dinosaurs. If the first relies on new discoveries of older specimens and reliable dating of the dinosaur-bearing formations, the second refers to dinosaurs having experienced a rapid diversification or having a deeper origin ("slow fuse") not documented (with the possible notable exception of Nesbitt et al. 2013) by current knowledge of the fossil record. The last needs data from mixed assemblages to test for habitat preferences and niche competition, and the in situ nature of footprints can be of great value in this respect.

10.2.3.1 Timing of Appearance

The exact timing of dinosaur origins remains unclear (Benton 1983; Brusatte et al. 2008a). The oldest record of dinosaurs based on skeletal remains is from the Carnian of Argentina (Benton 1983; Sereno and Arcucci 1994; Sereno 1999; Irmis et al. 2007; Brusatte et al. 2010b; Langer et al. 2010; Ezcurra 2010; Martinez et al. 2011), although Nesbitt et al. (2013) reported a possible earlier dinosaur from the Anisian of Tanzania. By the Carnian-Norian transition, all three major dinosaur lineages (Ornithischia, Sauropodomorpha, Theropoda) are documented (Brusatte et al. 2010b; Irmis et al. 2007; Langer et al. 2010). This forces researchers to focus mostly on the still poorly known Middle Triassic record. Furthermore, ghost lineages inferred from phylogenetic analyses predict that Dinosauria and its immediate stem lineage should be as old the early Middle Triassic (Sereno and Arcucci 1994; Nesbitt et al. 2010).

Early Triassic tracks previously attributed to dinosaurs have been reconsidered as partially or badly preserved "chirotheroids" (King and Benton 1996; see also Cavin et al. 2012). Although track-bearing formations cannot be always confidently dated, functionally tridactyl footprints are documented in the Middle Triassic of France (Demathieu 1989; Lockley and Meyer 2000), Germany (Haubold and Klein 2000, 2002), Italy (Avanzini 2002), and Argentina (Marsicano et al. 2007 and references therein), and have been generally attributed to dinosauromorphs. Dinosaur tracks have been reported from the Middle Triassic Los Rastros Formation (Argentina) by Marsicano et al. (2004, 2007; see also Marsicano and Barredo 2004; Melchor and Valais 2006) but have been considered ambiguously identified by others (Langer et al. 2010; Irmis 2011). Therefore the ichnologic record, although failing to definitively prove a Middle Triassic origin for dinosaurs, clearly indicates the presence of a diverse fauna of dinosauromorphs with functionally tridactyl digitigrade pedes, and possibly true dinosaurs during the Middle Triassic (Fig. 10.3), a condition that the body-fossil record is only recently beginning to document (Nesbitt et al. 2013).
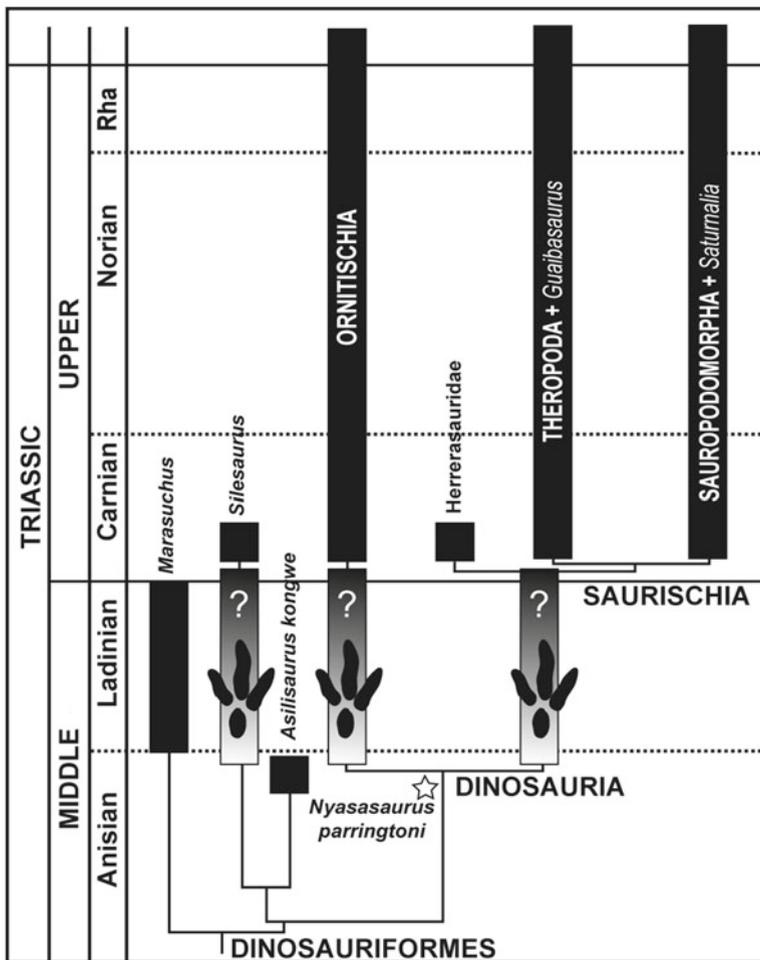
Fig. 10.3 A calibrated phylogeny of early dinosaurs and sister taxa based on both skeletal and ichnological data. The possible presence of dinosaurs in the Middle Triassic as testified by controversial footprints have recently received support from the description of *Nyasasaurus* which is considered either within, or sister-taxon of, Dinosauria. Modified from Marsicano et al. (2007) and Nesbitt et al. (2013)

10.2.3.2 Early Diversification

Although the first unequivocal dinosaur body fossils are known from the Carnian (Brusatte et al. 2010b; Langer et al. 2010; Nesbitt et al. 2013), Brusatte et al. (2008a, 2010b) demonstrated that dinosaurs increased their diversification and their morphologic disparity only from the Norian; dinosaurs experienced a burst of diversification only after the Triassic–Jurassic transition.

At the end of the Triassic the dinosaurs experienced an increase in maximum body size, later expressed as an increase in average body size (Sookias et al. 2012; Turner and Nesbitt 2013). Late Triassic tridactyl footprints are well known from USA, Europe, South America, Australia, and Africa (e.g., Tucker and Burchette 1977; Biron and Dutuit 1981; Mietto 1988; Olsen and Baird 1986; Thulborn 2000; Gatesy 2001; Knoll 2004; Milàn and Gierliński 2004; Weishampel et al. 2004; Lockley and Eisenberg 2006; Silva et al. 2007; Meyer et al. 2013). The Triassic record of large tridactyl tracks (e.g., Thulborn 2003; Bernardi et al. 2013; Meyer et al. 2013) has invalidated the hypothesis of Olsen et al. (2002) of a dramatic increase in size at the Triassic-Jurassic boundary. However, the increasing abundance toward the end of the Triassic of medium- and large-sized theropod tracks (*Eubrontes* and *Grallator* above all) marked a crucial phase in dinosaur history, when the main radiation or diversification of theropods and the evolution of large species got underway during the Late Triassic (Lockley and Hunt 1995a). Furthermore, if the attribution of the largest Late Triassic tracks is correct, the estimated body length, calculated according to Thulborn's (1990) equations ($h = 3.06 \times \text{FL}1.14$ and $L = 4\,h$), would be more than 5 m. Their estimated body mass value, following Weems (2006), would have been about 200 kg (Bernardi et al. 2013). This size is not known from dinosaur skeletal remains of Carnian age (Benton 2006; Brusatte et al. 2010b) and is approximated only by the Norian theropod dinosaur *Liliensternus* (Cuny and Galton 1993; Lucas et al. 2006).

Tracks are also a valuable tool that gives us insight into the geographic distribution of the first dinosaurs. The earliest skeletal remains of dinosaurs are from southern Pangaea and the oldest possible dinosaur tracks are from Argentina. The earliest dinosaur from northern Pangaea has recently been dated as "middle" Norian of western North America (Nesbitt et al. 2009). This has led to the view that the major dinosaurian clades (Ornithischia, Sauropodomorpha, Theropoda) may have originated in southern Pangaea (Brusatte et al. 2010b; Langer et al. 2010). The paleogeographic importance of this distribution, however, is compromised by the absence of well-preserved skeletal remains of Carnian age from northern localities (northern Africa, Europe, North America) (Langer 2005; Nesbitt et al. 2007; Martinez et al. 2011). Tracks, however, indicate that dinosaurs were already present by the Late Carnian in northern Pangea (Bernardi et al. 2013, Fig. 10.4). With the exclusion of the possible earliest dinosaur *Nyasasaurus* (Nesbitt et al. 2013), this would imply a nearly contemporaneous appearance of dinosaurs on all of Pangea (Bernardi et al. 2013).

10.2.3.3 Dynamics of Replacement

In the past, the Late Triassic was described as the period when the faunas dominated by crurotarsan archosaurs were competitively replaced by those dominated by dinosaurs (Bakker 1972; Charig 1984). A growing consensus now suggests that dinosaurs were initially rare components of Triassic terrestrial ecosystems and that their ascent was gradual (Brusatte et al. 2008b). It was only after the Triassic–Jurassic transition that dinosaurs became dominant in terrestrial vertebrate ecosystems

Fig. 10.4 The ichnological record provides valuable data on both temporal and spatial distribution of basal dinosaurs. Tracks, for example, indicate the presence of archosaur faunas, which include dinosaurs, during the early Late Triassic both in Laurasia and Gondwana. This pattern is not (yet) documented by body-fossil data. Modified from Brusatte et al. (2010a, 2011)

worldwide (Benton 1983; Sereno 1999 see also Brusatte et al. 2010b). The body fossil record has shown that in the Late Triassic, during the first 25–30 million years of dinosaur history, crurotarsans had double the variety of body plans, lifestyles, and diets in comparison with contemporary dinosaurs (Brusatte et al. 2008a, 2010b; 2011; see also, Benton 1983; Sereno 1999). In addition to crurotarsans, Triassic dinosaurs lived together with dicynodont synapsids (Dzik et al. 2008) and coexisted with dinosauromorphs for at least 20 million years (Irmis et al. 2007). The scarcity of Early to Middle Triassic terrestrial body fossils, however, leaves open questions on taxonomic abundance, composition, diversity, and regional specificity of such dinosaur communities (Irmis et al. 2007; Dzik et al. 2008; Nesbitt et al. 2009; Ezcurra 2010; Irmis 2011). The track record can be integrated into this picture.

As a general depiction, while the upper Triassic ichnologic record is characterized by dinosaur, dinosauromorph, crurotarsan archosaurs, and nonmammalian therapsid tracks (Marsicano and Barredo 2004; Bernardi et al. 2013; Lockley and Meyer 2000; Klein and Haubold 2007; Lucas and Tanner 2007), the Lower Jurassic record is dominated by saurischian dinosaurs (Lockley and Hunt 1995a; Lockley and Meyer 2000; Olsen et al. 2002; Avanzini et al. 2006; Avanzini and Petti 2008). Well-diversified tetrapod ichnoassemblages are known from the Middle to Late Triassic of both southern and northern Pangaea (see Bernardi et al. 2013). Olsen and Huber (1998) reported the co-occurence of *Apatopus*, cf. *Brachychirotherium*, and

small bipedal and tridactyl forms, possibly produced by "dinosaurian" trackmakers in the Carnian of North Carolina, while Cameron and Wood (2003, 2004) described a rich association composed of *Atreipus*, *Brachychirotherium*, *Grallator,* and *Rhynchosauroides* from the Carnian of Canada. Similar assemblages are ubiquitous in the western USA (Lockley and Hunt 1995a). Marsicano and Barredo (2004) reported the presence of crurotarsal archosaurs, dinosaurs (sauropodomorphs and theropods) and nonmammalian therapsids (small cynodonts and large dicynodonts). Nicosia and Loi (2003) described a rich Carnian ichnoassociation from Italy with crurotarsan and dinosaurian tracks. D'Orazi Porchetti et al. (2008) and Bernardi et al. (2013) document the co-occurrence of large- and middle-sized dinosaurs, dinosauriforms, and crurotarsans in the late Carnian (Tuvalian) of the southern Alps. Therefore, the record of ichnofaunal assemblages composed of large and small dinosaurs, dinosauriforms and non-dinosaurian archosaurs and their co-occurrence with dinosauriforms and crurotarsal archosaurs provides support to the non-abrupt replacement of the more archaic faunas by dinosaur-dominated ones. Furthermore, the co-occurrence of dinosaurs, dinosauriforms, and crurotarsal archosaurs in the Middle to Late Triassic (Ladinian to Late Carnian) documents a prolonged coexistence of different groups of archosaurs, even in the same environment. This provides support to the view of crurotarsan-dominated faunas being neither rapidly outcompeted nor quickly opportunistically replaced by dinosaurs, but rather substituted by a more gradual process of ecologic replacement (Irmis et al. 2007; Nesbitt et al. 2010; Brusatte et al. 2010b; Martinez et al. 2011).

10.2.4   A Look into Sauropod Paleobiology

One key feature of tracks that neatly distinguishes them from body fossils is that they cannot be transported post-mortem, in this case, "post-emplacement". Tracks thus provide a direct indication of environmental and/or habitat preferences of the producer (Thulborn 1982; Lockley 1991; Wilson and Carrano 1999; Carrano and Wilson 2001). To better understand habits, locomotory attitudes or geographic distribution of particular groups, it is therefore useful to integrate body fossil findings with track data. A good example in this respect is provided by the sauropod dinosaur record.

Numerous studies of locomotory dynamics in this group attribute different footprint morphotypes to distinct trackmakers. Many authors (Farlow et al. 1989; Farlow 1992; Lockley et al. 1995a; Moratalla et al. 1995; Wilson and Carrano 1999; Lockley et al. 2002, 2005; Day et al. 2002a; Henderson 2002) have observed that sauropod trackways could be essentially subdivided into two broad categories: "narrow gauge" and "wide gauge" (Fig. 10.5). Sauropod trackways can also show (or lack) claw and phalangeal impressions in the manus (Farlow et al. 1989; Lockley et al. 1995a; Wilson and Carrano 1999; Day et al. 2004). "Wide-gauge" trackways are those in which manus and pes prints are well separated from the midline, and which frequently lack pollex claw impressions (e.g., *Brontopodus* Farlow et al. 1989); "Narrow gauge" trackways have manus and pes prints that approach or intersect the trackway midline, and have pollex claw impressions (e.g., *Parabrontopodus*
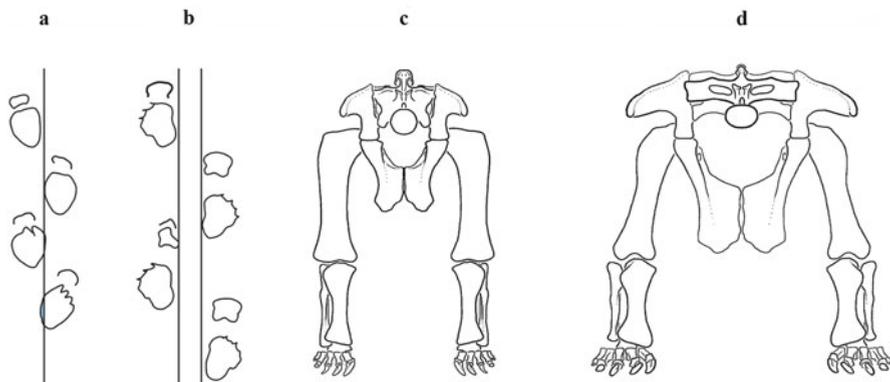
Fig. 10.5 Many authors (see text for discussion) have observed that sauropod trackways could be essentially subdivided into two broad categories: "narrow gauge" (**a**) and "wide gauge" (**b**). These reflect the postural difference between non-titanosaur (**c**, here represented by *Camarasaurs*—pelvic girdles and hindlimbs in anterior view) and titanosaur sauropods (**d**, here *Opisthocoelicaudia*). This inference allowed full integration of ichnogical and skeletal data, which contributed to a better understanding of sauropod paleobiology. Modified from Lockley et al. (1995b), and Wilson and Carrano (1999)

Lockley et al. 1995a). Lockley (1999, 2001, 2007a) also argued that there is a positive correlation between narrow gauge and small manus forms, and between wide-gauge and large manus forms. Furthermore, large and small manus forms have been independently identified among the various chirotherian ichnotaxa (Lockley 2007a). Such differences in turn speak to changes in the position of the center of gravity in various archosaur clades.

Ichnologic investigations suggest that the transition from narrow- to wide-gauge occurred during the Kimmeridgian-Tithonian (Wilson and Carrano 1999). "Wide-gauge" trackways show a trend towards an increase of manus print dimensions through time. This feature and the age of "wide-gauge" trackways closely match the evolutionary trend seen in the sauropod body fossil record. Skeletal remains record a gradual shift of the center of gravity toward the front, with the consequent growth of the forelimbs in response to the greater weight they had to support. This evolutionary change coincides with the appearance of Titanosauriformes Salgado, Coria and Calvo 1997 (including Brachiosauridae Riggs 1904 and Titanosauria Bonaparte and Coria 1993) (Wilson 1995; Upchurch et al. 2004), animals that would have produced tracks with larger manus impressions. The lack of digital impressions in the manus ichnites of the "wide-gauge" trackways could also be referred to the appearance of Titanosauriformes; indeed both Brachiosauridae and Titanosauria are characterized by the progressive reduction and loss of phalanges and claws in the manus (Wilson and Sereno 1998; Upchurch et al. 2004; Apesteguía 2005). In particular, Titanosauria probably walked only on the distal parts of their metacarpal bones (Salgado et al. 1997; Wilson and Sereno 1998). It is thus difficult to envisage digital or claw marks produced by individuals belonging to Titanosauriformes. Wilson and Carrano (1999) argued that hindlimb modifications, such as outwardly angled femora, offset knee

condyles, and a more eccentric femoral midshaft cross-section, could be responsible for wide-gauge tracks. All these features are synapomorphies of titanosaurs, and thus support the hypothesis that they were the producers of wide-gauge trackways. Temporal and geographic distribution of titanosaurs is coherent with this hypothesis; "wide-gauge" trackways predominate during the Cretaceous and are found world-wide. After Wilson and Carrano's (1999) proposals, other studies have cast some doubt on this correlation. D'Emic (2012) suggested that some Late Jurassic non-titanosaurs might have femoral cross-sections similar to those of titanosaurs. Henderson (2006) proposed that all large sauropods (over 12.6 tonnes) would have been constrained to adopt a wide-gauge stance in order to maintain stability during locomotion; trackway gauge could also be influenced by the degree of lateral motion of the trackmaker (Carpenter 2009). Recent discovery of sauropod trackways from Switzerland, Morocco (both of Jurassic age), and Spain (Cretaceous age) show that single sauropod trackmakers were able to adopt both narrow and wide gauge as testi-fied by the occurrence of differently spaced tracks along single trackways (Marty et al. 2010; Castanera et al. 2012a, b). Furthermore, wide-gauge trackways could have appeared more than once in sauropod evolution. Wide-gauge trackways are not exclusive to titanosauriform sauropods and caution must be applied ascribing a track-way to an ichnotaxon on the basis of this character (Castanera et al. 2012a, b).

Sauropod tracks have provided important clues for the understanding of the environmental preferences of this clade. Based on the analysis of a dataset of sauropod trackways, Lockley et al. (1995b) found a good correlation between sauropod tracksites and coastal environments, and noted that they are primarily associated with tropical and subtropical paleolatitudes (mean average Northern Hemisphere = 25°), and semi-arid or seasonal climatic carbonate depositional environments (lacustrine or marine carbonate platform). Butler and Barrett (2008) partially confirmed these results: the percentage of Cretaceous sauropod tracks in coastal environments is remarkable (32 %) if compared with the con-temporaneous sauropod body fossil record (7 %). Nevertheless, statistic analysis of the ichnologic data does not indicate that sauropod trackways are overrepre-sented if compared to those of other herbivorous dinosaurs. In contrast, the body fossil record supports previous hypotheses of a preference for inland settings (e.g., Lehman 1987; Hunt et al. 1995a). However, it should be noted that these results might be hindered by preservational biases that are not yet fully under-stood (Mannion and Upchurch 2010). Using a new large data set of sauropod skeletal remains, Mannion and Upchurch (2010) found a significant positive association between non-titanosaurs and coastal environments, and between titanosaurs and inland environments. Their analysis of track records also high-lighted a positive correlation between narrow-gauge trackways and coastal envi-ronments, and wide-gauge trackways and inland environments; this reinforced the hypothesis of Wilson and Carrano (1999) that wide-gauge trackways were produced by titanosaurs. The hypothesis of Mannion and Upchurch (2010) has been partially put into question by isolated findings of wide-gauge trackways preserved in coastal environments (e.g., Castanera et al. 2011).

10.2.5 Clues About Theropod Paleobiology

Most famously among track features, trackways allow estimation of speed (Alexander 1976, 1989; Thulborn 1981, 1990). In fact, debates about speeds attained by dinosaurs led to a revival of tetrapod ichnology (Alexander 1976; Lockley 1998). Early estimates of rapid progression of large dinosaurs were proposed in support of the idea that dinosaurs were highly active and possibly warm-blooded (Russell and Belland 1976; Czerkas and Olson 1987); however, later studies based on larger samples and updated formulae concluded that most medium- to large-sized theropods walked fairly slowly (Farlow 1981; Thulborn 1990). Estimates of the speeds of theropod dinosaurs are based on the formula of Alexander (as corrected by Thulborn 1990); speed (v, velocity) is calculated on the basis of stride length (SL) where $v \approx 0.25\ g^{0.5}\ SL^{1.67}\ h^{-1.17}$, where hip height ($h$) of a trackmaker can be estimated from footprint length (FL): $h \approx 8.60\ FL^{0.85}$ (Thulborn 1984; Thulborn and Wade 1984). This formula was successively slightly modified by Weems (2006) to estimate basal theropod dinosaur speeds ($v = 0.16\ SL^2\ h^{-1.5}\ g^{0.5}$). The same formula can be used for any bipedal dinosaurs (see Currie 1983, 1995), while no similar, reliable formulae are available for quadrupedal dinosaur taxa. Using musculoskeletal modeling and Computer Aided Engineering, Mallison (2011) questioned the validity of the Alexander formula to assess speed in dinosaurs without knowing the frequency of the stride. He suggested that speeds calculated from tracks should be better considered as the slowest speeds at which the animals moved.

Tracks and trackways have also been long used to establish dynamics of foot movement (Avanzini 1998; Gatesy et al. 1999; Gatesy 2001, 2003; Manning 2004; Milàn et al. 2004, 2006; Avanzini et al. 2012; Ellis and Gatesy 2013), locomotion (Alexander 1976, 1985, 1989; Thulborn 1981, 1990) and contributed in the debate about theropod posture (Lockley 1998). The high pace angulation exhibited by theropod trackways, for example, shows that theropods placed their hind feet close to, or on, the midline (Alexander 1976, 1985). This optimizes the efficiency by reducing the energy lost through lateral displacement of the center of gravity (Thulborn 1981, 1990), and is characteristic of a highly specialized locomotory control system. Lockley (2007a) regarded such narrow trackway configurations as a manifestation of an intrinsic morphodynamic organization in theropods. Furthermore, saurischians in general had narrow bodies, narrow feet, and other laterally compressed skeletal elements, although this contrasts with the wide-gauge trackway configurations and wide bodies and feet seen in derived saurischians such as the titanosaurs. Furthermore, Day et al. (2002b) showed that large theropods were able to change their speed instantaneously, highlighting their high maneuverability and balance control.

Theropod trackways do not typically include hand imprints, which is again an expression of a posterior center of gravity (Lockley 2007a). Only when the trunk was lowered toward a substrate, as in a crouched posture, could the hands potentially produce impressions. Crouching has been demonstrated by a few extraordinary discoveries of impressions of autopodia associated with metatarsals and pelvic girdle imprints. Milner et al. (2009) reported unambiguous theropod manus impressions associated

with a crouching trace that indicate the avian orientation of the manus (with a medially facing palm) evolved early within the history of Theropoda (see Gierliński et al. 2009 and references therein for further examples). The crouching trace was registered when the animal rested on the substrate in a posture similar to that of modern birds; the traces include well-defined impressions made by both hands, the ischial callosity, pedes, and the tail. This trace constitutes evidence that an Early Jurassic theropod expressed two bird-like features: anatomic restriction to a palms-medial manual posture, and symmetric leg positions while resting (Fig. 10.6). Inferences that theropods displayed behavior analogous to modern birds are intriguing but often too speculative. Recently discovered Cretaceous theropod tracks in Colorado provided extensive physical evidence of substrate scraping behavior by large theropods; they were considered as compelling evidence of "display arenas" or leks, and consistent with "nest scrape display" behavior among many extant ground-nesting birds (Lockley et al. 2016).

Another iconic example of the impact that ichnology has had on postural biomechanic reconstructions is the case of the orientations of dinosaur trunks and tails. Analysis of trackways have clearly shown that most dinosaurs walked with their tails carried well off the ground, so tail-drag traces are rare (Irby and Albright 2012; García-Ramos et al. 2004, 2006; Platt and Hasiotis 2008; Kim and Lockley 2013). The presence of tail traces, therefore, implies either a pathologic condition of the
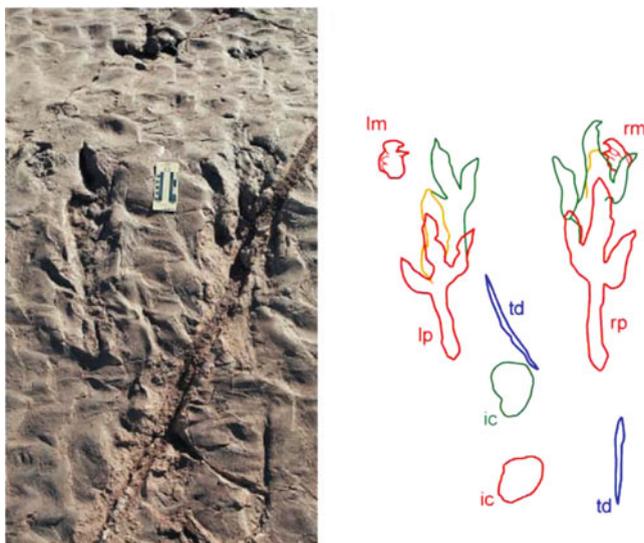
Fig. 10.6 Footprints provide clues to the individual behavior of trackmakers. These crouching traces described by Milner et al. (2009), for example, demonstrate that avian orientation of the manus, with medially facing palms, evolved by the Early Jurassic within Theropoda. Such conclusion would have never been reached on the base of skeletal record alone. Modified from Milner et al. (2009)

trackmaker or an atypical mode of locomotion because dinosaurs used their tails for balance on land (Galton 1970; Farlow et al. 2000; Fujita et al. 2012).

Tracks can also be used to assess the effects of traumas and illness in dinosaur bones and therefore the evolution of phatologic behavior. Tracks and trackways indicative of pathologies (e.g., fractures in pedal phalanxes) are relatively frequent, especially in middle to large-sized theropods (Tanke and Rothschild 1997, 2002; Rothschild et al. 2001; Rothschild and Tanke 2005). Many of the trackways described refer to large carnivorous dinosaurs that show missing or curled digits (Lockley 1991; Tanke and Rothschild 1997). Footprint and trackway evidence of limping theropods (Ishigaki 1986; Dantas et al. 1994; Lockley et al. 1994b) suggests injury or arthritis. Foot pathologies in large bipedal dinosaurs however have also been used to infer more active life-styles or natural fragility of the narrow, protruding digits (Laws 1997; Tanke and Rothschild 1997). For other good examples of pathologic tracks, see Abel (1935), Thulborn (1990) and Avanzini et al. (2005).

Tracks have also helped unveil another aspect of dinosaur behavior: their ability to swim. No skeletal remains can help addressing this question, and tracks attributable to swimming theropods have been reported, among others, by Coombs (1980), Milner et al. (2006), Ezquerra et al. (2007) and Xing et al. (2013a) (similar reports are available also for other dinosaur taxa; e.g., Currie 1983; Fujita et al. 2012). Theropods could float, as demonstrated by clawing traces left in the sediment as they swam (Ezquerra et al. 2007); the trackway shows that this theropod used a pelvic paddle motion, i.e. they were powered by alternating movements of the two hind limbs, like in living aquatic birds, and swam with amplified asymmetric walking movements to maintain its direction while swimming perpendicular to a water current (Ezquerra et al. 2007). The track record, therefore, has shown that dinosaurs (mostly theropods) colonized areas that included aquatic environments and were therefore probably able to swim.

10.2.6   Evidence for Gregariousness

Gregariousness is a form of social interaction between individuals that probably evolved to increase the fitness of single individuals within a group (Alexander 1974). Gregariousness allows greater defense of individuals from predators, increases effective access to food, efficiency of breeding, effective migration, and enhances the probability of safely raising the young (Currie and Eberth 2010). In order to maintain group cohesion, individuals within a group must synchronize their behavior in terms of time spent resting, foraging, and moving (Conradt 1998).

Tracksites, together with nesting sites, provide some of the most reliable proof about the gregariousness in extinct animals, in particular among dinosaurs (Ostrom 1972; Currie 1983; Lockley et al. 1986; Farlow et al. 1989; Horner and Gorman 1990; Carpenter 1999). Fossil trackways made by multiple individual animals can provide important qualitative and quantitative information about their social behavior.

Evidence for gregariousness in dinosaurs is difficult to gain from the body fossil record, and only bone bed assemblages may reflect such group behavior. Bone beds are concentration of bones in a localized area or stratigraphically limited sedimentary unit, in which the bones belong to more than one individual (see Rogers et al. 2007 for more details). Significant work on bone beds assemblages has provided compelling evidence on the gregarious habits of some ornithischian dinosaurs and the coexistence of multispecific individuals in the same habitat (Rogers 1990; Varricchio and Horner 1993; Mathews et al. 2009; Zhao et al. 2007).

In the study of dinosaur tracks, gregariousness may be deduced by the recognition of some peculiar features, primarily by the occurrence of multiple parallel trackways, exhibiting a preferring directionality (Ostrom 1972; Currie 1983; Lockley 1991). However, there is no arbitrary minimum number of adjacent parallel trackways for indicating gregarious behavior (Lockley and Matsukawa 1999). The presence of many parallel trackways does not necessarily constitute proof of a herding behavior, and data should be critically examined: trackways could have been made by animals that have walked alone at different times, and selected the same direction for the presence of a physical constraint, such as narrow river valley, shoreline, or the banks of a river (e.g., Ostrom 1972). Depths of the tracks in each trackway must be taken into consideration; similar-sized dinosaurs, walking contemporaneously on a substrate characterized by similar physical properties, probably produced parallel trackways with comparable depths. By contrast, parallel trackways with different track depths suggest that the animals walked on that substrate at different times, perhaps months, days, or even years later one from the other. A useful parameter to recognize gregariousness from track data is the intertrackway spacing (i.e., an index of regularity of spacing between parallel trackways; Lockley 1989; Lockley et al. 1998). In recent years, several trackways characterized by regular intertrackway spacing have been reported (Lockley et al. 1986, 2006b; Farlow et al. 1989; Lim et al. 1989; Li et al. 2008), suggesting animals that walked shoulder to shoulder, and thereby substantiating the hypothesis of their social behavior. Parallel trackways curving or swerving in unison could also provide evidence of herd habits among the trackmakers (Lockley and Hunt 1995a, b; Lockley and Matsukawa 1999).

Such ichnologic evidence for gregarious behavior in dinosaurs has been reported from Jurassic and Cretaceous sites in North America (Currie 1983, 1995; Lockley et al. 1983, 1986, 1992a, 1998; Farlow 1987; Farlow et al. 1989; Pittman and Gillette 1989; Hawthorne 1990; Carpenter 1992; Barnes and Lockley 1995; Lockley and Hunt 1995a, b; Cotton et al. 1998; Kvale et al. 2001; Schumacher 2003; Myers and Fiorillo 2009), South America (Leonardi 1989; Lockley et al. 2002; Fig. 10.7), East Asia (Lim et al. 1989; Matsukawa et al. 1997, 2001, 2005; Lockley et al. 2002, 2006b, 2012a, b; Hwang et al. 2004; Li et al. 2008; Xing et al. 2013a), Europe (Kaever and Lapparent 1974; Delair 1981; Agirrezabala et al. 1985; Viera and Torres 1992; Lockley et al. 1995c; Moratalla et al. 1997; Day et al. 2002a, 2004; Piñuela et al. 2002; Pérez-Lorente 2003; García-Ramos et al. 2004; Clark et al. 2005; Vila et al. 2008; Castanera et al. 2011, 2013, 2014; García-Ortiz and Pérez-Lorente 2014), Africa (Lingham-Soliar et al. 2003) and Australia (Thulborn and Wade 1979, 1984).

Fig. 10.7 Footprints provide clues on the social behavior of dinosaurs. Here spectacular parallel trackways at the Humaca dinosaur tracksite (Chuquisaca, Bolivia) interpreted as evidence of gregarious behavior by Lockley et al. (2002). Direction of progression is towards the *right* of picture. From Lockley et al. (2002)

Evidence suggests that large herbivorous dinosaurs, especially sauropods and ornithopods often traveled in herds, and that both groups acquired gregarious tendencies early in their histories (see Lockley and Matsukawa 1999 and Myers and Fiorillo 2009 and references therein). Sauropod trackways indicate groups of 40 or more individuals (Day et al. 2002a, 2004) and show either mixed-age or are age-segregated ichnologic assemblages (Lockley et al. 1986, 1995c, 2002; Castanera et al. 2011). The co-occurrence of adult and juvenile trackways may suggest protracted parental care far beyond the hatchling stage of development; groups of small-sized trackways may be interpreted as herds of juveniles or (as in the case of archipelago paleoenvironments) as the presence of dwarfed populations (Benton et al. 2010). Few tracksites exhibit parallel trackways of different species or groups (e.g., Day et al. 2002a, 2004).

Much evidence of possible social behavior in other groups of herbivorous dinosaurs, such as ankylosaurs (McCrea and Currie 1998; McCrea 2000) and ceratopsians (Lockley and Hunt 1995b) has now also accumulated. Evidence of gregariousness in carnivorous dinosaur trackways, particularly non-avian theropods, is less common than in other groups of dinosaurs, and the interpretations of such evidence remain more controversial. Some researchers support this hypothesis (Lockley and Matsukawa 1999; Carvalho and Pedrão 2000; Smith et al. 2002; Lingham-Soliar et al. 2003; Clark et al. 2005; Barco et al. 2006; Li et al. 2008; Currie and Eberth 2010; McCrea et al. 2014) while others prefer to consider track-

way data as coincidental instances of normally solitary individuals converging on a common point (e.g., food source, Roach and Brinkman 2007).

10.2.7 On the Tracks of Birds

Birds are among the most diversified and thoroughly analyzed vertebrate groups, but both their origin and evolution remain controversial. The skeletal record of birds is strongly biased by the nature of bones that, in this group, are mostly small and delicate so that limbs are commonly lost in taphonomic decay processes (Davis and Briggs 1998; Brand et al. 2003). This makes the bird fossil record highly incomplete, and only a multidisciplinary approach, including paleornithology, paleoichnology, and molecular studies, can help in the understanding avian origins and radiation.

The skeletal record indicates an initial avian radiation around the Jurassic-Cretaceous boundary (about 145 million years ago) and an early Paleogene diversification for modern birds (Neornithes) (e.g., Clarke et al. 2005; Dyke and Kaiser 2011; Brocklehurst et al. 2012; Ksepka and Boyd 2012). Molecular studies and recent combined molecular and morphologic analyses, instead, indicate that modern birds began radiating in the Early Cretaceous (Cooper and Penny 1997; Haddrath and Baker 2012; Jetz et al. 2012; Lee et al. 2014).

Tracks similar to those of modern birds (i.e., shorebirds, small ducks, small herons, roadrunners) are only 15-20 million younger than the oldest avian skeletal remains, which is in agreement with molecular data (Brown et al. 2008). In contrast, the oldest body-fossil records of anseriforms and possibly charadriiforms date to the latest Cretaceous (ca. 70 million years ago), and are even younger for ciconiiforms and cuculiforms (Lockley and Harris 2010; Fig. 10.8). This could be explained through the following two hypotheses: (1) pre-latest Cretaceous occurrence of neornithians, implying that the body fossil record is strongly biased toward the preservation of non-neornithian birds, or (2) neornithians converged in foot morphology with their non-neornithian, Cretaceous ancestors. The latter appears more parsimonious suggesting that convergent evolutionary programs, in similar niches and at different periods, produced not only similar pedal morphologies but also similar size (Lockley and Harris 2010).

Feeding behavior has been also inferred from different fossil bird tracks by comparing them with traces characteristic of modern birds. For example several *Ignotornis* trackways exhibit reduced pace length, interpreted as a type of "foot stirring" behavior characteristic of modern herons "stirring" up the substrate for feeding (Lockley et al. 2008, 2009). The most noticeable example of feeding behavior was reported from the Cretaceous of Korea (Lockley and Harris 2010; Lockley et al. 2012a; Kim et al. 2012). Traces consist of sets of fine, zigzag, arcuate to semicircular grooves that "sweep" back and forth across the trackway, indistinguishable from those of modern spoonbills (Swennen and Yu 2005). But spoonbills are not recorded in the Cretaceous fossil record, and no spoonbill morphology is known in any Cretaceous bird. The ichnologic record thus adds new data to the Cretaceous avian diversity.
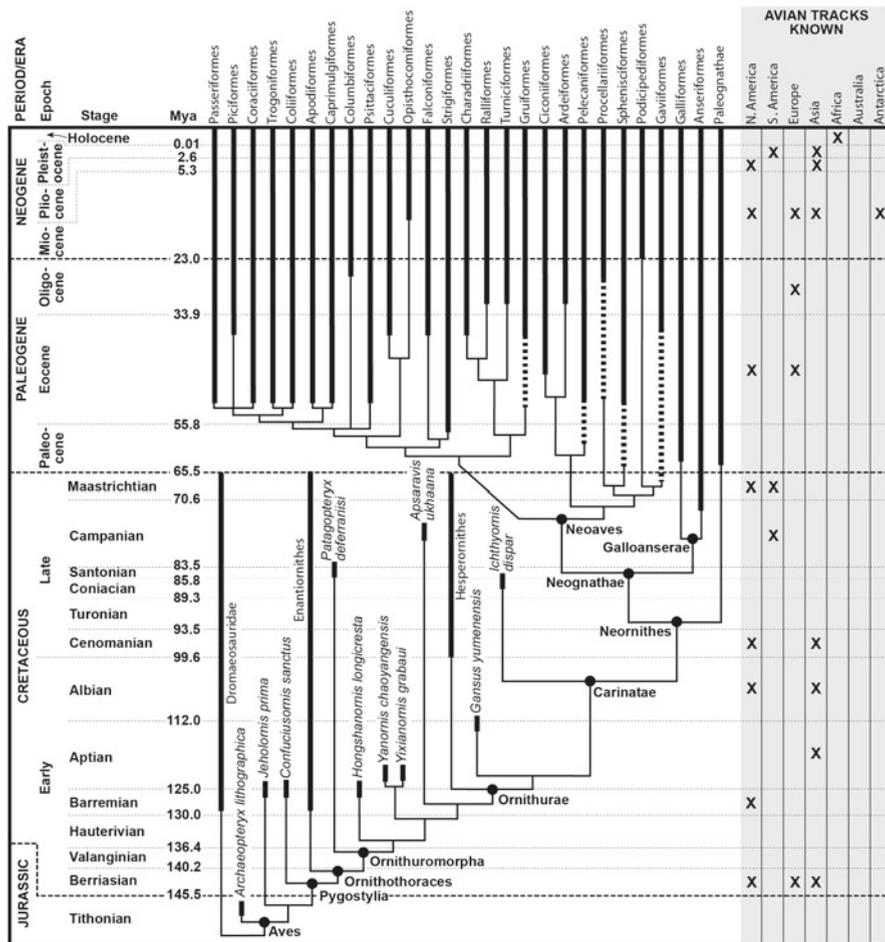
Fig. 10.8 Paleornithology and avian paleoichnology provide complementary data on the evolution of birds. This cladogram superimoposed on geologic time scale shows both taxon ranges based on skeletal data and associated footprint occurrences. See text for discussion. Modified from Lockley and Harris (2010)

The primary Mesozoic bird tracksites were recently reviewed by Lockley and Harris (2010) but there are new findings reported every year (Falk et al. 2010, 2014; Falk 2011; Fiorillo et al. 2011; Xing et al. 2011, 2013b; Contessi and Fanti 2012; Huh et al. 2012; Kim et al. 2012; Lockley et al. 2012c, d; Azuma et al. 2013; Martin et al. 2014). Most fossil bird tracks exhibit sizes and morphologies similar to those of extant shorebirds and water-birds (Greben and Lockley 1992), and are generally associated with lake basin, fluvial floodplain, coastal plain, and marine shoreline deposits (Lockley and Harris 2010). This bias is strictly related to the physical properties of these environments that apparently facilitate the registration and preservation of tracks, and the creation of

what has been called the shorebird ichnofacies (Lockley et al. 1994a; Lockley 2007b). Tracks of birds with feet adapted for perching, such as songbirds or raptors, have much less chance to be produced and preserved; the same happens with birds that live in environments where the burial and preservation of tracks is less frequent or improbable (mountain, forest, open marine, etc.). Even though there are many avian skeletal and track fossils, the two records do not match each other and few footprints were probably produced by the feet represented by the skeletal remains (Lockley and Harris 2010). This mismatch and all the previously mentioned data strongly indicate that morphologies and behaviors of many modern birds actually evolved convergently with many of their extinct, Mesozoic relatives. A striking example is provided by the discovery of an Early Cretaceous (Aptian-Albian 120–110 Ma) trackway: *Shandongornipes muxiai* (Li et al. 2005). This discovery shows the evolution of a terrestrial, zygodactylous bird that is unknown in the body fossil record; it probably occupied a roadrunner-like niche indicating evolutionary convergence of an early Cretaceous bird with the locomotory habits and possible ecology of modern birds (see Lockley et al. 2007).

The majority of the fossil bird tracksites discovered to date are in East Asia, primarily in China and South Korea (Azuma et al. 2002, 2013; Li et al. 2002; Kim et al. 2006, 2012; Lockley et al. 2006b, 2007, 2009, 2012c, d; Xing et al. 2011, 2013b; Contessi and Fanti 2012; Huh et al. 2012; He et al. 2013; Falk et al. 2014). The high frequency could be related to the abundance of lake deposits in these regions, but the contemporaneous Chinese and North Korean skeletal records are also very rich in birds. The complementary evidence thus indicates that the distribution pattern may reflect a true center of avian radiation (Lockley and Harris 2010).

10.2.8 Pterosaur Locomotion

Pterosaurs are the earliest known vertebrates to have evolved powered flight. These winged reptiles first appeared in the Late Triassic and went extinct at the end of the Cretaceous period (Buffetaut and Mazin 2003). Since their first discovery, there has been considerable debate over their terrestrial locomotor capabilities, in particular whether they walked bipedally (Cuvier 1809) or quadrupedally with their hindlimbs splayed (Soemmerring 1812, 1817). Some eminent paleontologists considered that pterosaurs were unable to walk (Abel 1925) or were bad walkers with their hindlimbs unsuitable for a quadrupedal gait (Wellnhofer 1978). The hypothesis that pterosaurs were digitigrade bipeds with an erect stance was supported and argued with phylogenetic and osteologic analysis by Padian (1983, 1984, 1985, 1987, 1988, 1991), Padian and Rayner (1993), Paul (1987) and Bennett (1990). In contrast, several researchers, on the basis of osteologic arguments, claim that pterosaurs were quadrupedal plantigrades, with semi-erect or possibly even sprawling stances (Pennycuick 1986; Unwin 1987, 1989; Wellnhofer and Vahldiek 1986; Wellnhofer 1988, 1991a, b).

As was the case for other extinct track-making animals, ichnology provided unequivocal evidence in resolving this long-standing dispute. Already in 1957 Stokes described a short trackway composed of tridactyl manus and tetradactyl pes prints

(Stokes 1957). He instituted the new ichnotaxon *Pteraichnus saltwashensis* that he identified as produced by a quadrupedal pterodactyloid pterosaur. This attribution was endorsed by subsequent findings (Stokes 1978; Wellnhofer 1978; Stokes and Madsen 1979), but was strongly opposed by Padian and Olsen (1984) who proposed they were made by a crocodilian trackmaker. *Pteraichnus* was no longer considered a pterosaur ichnotaxon (Unwin 1986, 1989; Prince and Lockley 1989; Lockley 1991; Wellnhofer 1991a; Bennett 1992). New discoveries provided new information (Logue 1994; Hunt et al. 1995b; Lockley and Hunt 1995a) and Mazin et al. (1995) and Lockley et al. (1995d) independently demonstrated that *Pteraichnus* could be attributed to pterosaurs (Fig. 10.9). To date, this interpretation is accepted by most pterosaur researchers (Lockley et al. 1996, 1997; Bennett 1997; Mazin et al. 1997, 2001; Unwin 1997a, b, 2006; Wright et al. 1997; Kubo 2008; Witton 2013). Ichnology therefore provided definitive evidence that pterosaurs walked on all fours.

These studies also demonstrated that at low-velocity walking, the body was held upright, with the forelimbs held more vertically and the *mani* brought close to the axis of the trackway, so they could not be starched much foreword. Conversely, at

Fig. 10.9 Fossil trackways attributed to pterosaurs provided exceptional insight into the functional morphology and behavior of these flying reptiles. Furthermore, they solved the long-standing debate over pterosaur terrestrial locomotion. The tracks called *Pteraichnus* show that pterosaurs employed a plantigrade, quadrupedal stance and gait with the hind limb partially—to fully—abducted. From Unwin (1996)
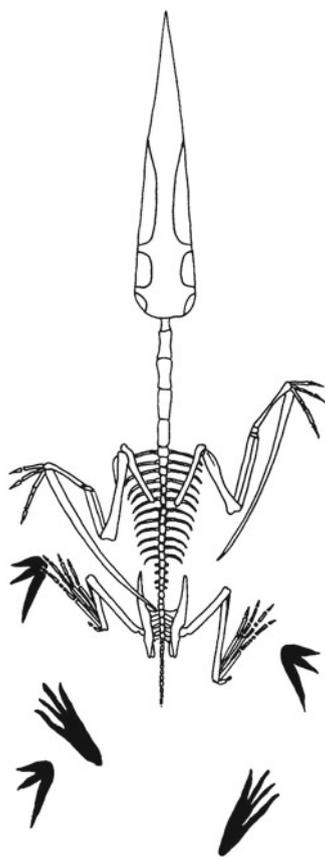
higher velocities, the body was held less erect (possibly subhorizontally) allowing the long forelimbs to reach a more distant anterior point (Mazin et al. 2001). Trackways were also useful to infer the landing behavior of pterosaurs, which like modern birds used their wings to stall before landing (Mazin et al. 2009).

Pterosaur tracks are abundant in the Upper Jurassic rocks of Arizona, Colorado, Oklahoma, Utah and Wyoming (Stokes 1957; Lockley et al. 1995d, 1996; Lockley and Wright 2003; Lockley et al. 2008), France (Mazin et al. 1997, 2003, 2009; Billon-Bruyat and Mazin 2003), Poland (Pienkowski and Niedzwiedzki 2005), and Spain (García-Ramos et al. 2000, 2002, 2006; Meijide Calvo and Fuentes Vidarte 2001; Fuentes Vidarte et al. 2004a, b; Sánchez-Hernández et al. 2009). Tracks of Cretaceous age are much larger than those of the Late Jurassic, which agrees with body size trends of skeletal remains (Buffetaut and Mazin 2003). Large body size in this group can have evolved as early as Late Jurassic as testified by abundant footprints from Spain (García-Ramos et al. 2000, 2002, 2006) and few skeletal remains from Switzerland (Meyer and Hunt 1999). Pterosaur tracks have been reported from the Lower Cretaceous of China (Li et al. 2002; Zhang et al. 2006; Xing et al. 2013b, c), England (Delair 1963, reinterpreted by Wright et al. 1997), Germany (Hornung and Reich 2013), Japan (Lee et al. 2010), South Korea (Kim et al. 2006; Lee et al. 2008), Spain (Pascual Arribas and Sanz Pérez 2000; Meijide Calvo 2001; Fuentes Vidarte 2001; Hernández Medrano et al. 2006; Moratalla and Hernán 2009; Sánchez-Hernández et al. 2009), and USA (Maryland; Lockley and Rainforth 2002). In the Upper Cretaceous, they are known from Argentina (Calvo and Lockley 2001), Mexico (Rodríguez de la Rosa 2003), South Korea (Lockley et al. 1997; Hwang et al. 2002) and USA (Colorado, Lockley and Rainforth 2002; Utah, Lockley et al. 1995d). Upper Cretaceous Korean tracks, known as *Haenamichnus*, are the largest pterodactyloid tracks (up to 33 cm) and were made by a trackmaker not yet known from the body fossil record.

Pterosaur tracks have been also used as an indicator of body mass. Kubo (2011) tried to correlate the foot area with weight. He used seven ichnospecies of pterosaur tracks and estimated body weights of pterosaurs as ranging from 110 to 145 kg. This result indicates that large pterosaurs were ten times heavier than the heaviest modern birds.

The pterosaur track record provides evidence about the preferred environments and behaviors of these flying reptiles. Most Upper Jurassic pterosaur tracks are found in marginal marine, carbonate, and clastic-evaporitic lagoonal deposits whereas Cretaceous tracksites are associated with fluvial and freshwater deposits (Lockley and Rainforth 2002). The Late Jurassic record is consistent with the hypothesis, inferred also through the body fossil record, that pterosaurs inhabited marine shoreline habitats. This view is further corroborated by the discoveries of "swimming" and "feeding traces" (García-Ramos et al. 2000, 2002, 2006; Lockley and Wright 2003; Witton 2013; Lockley et al. 2014). They consist of scrape marks that are interpreted as traces produced by

paddling limbs, a random distribution of tracks without evidence of trackways, and small circular paired depressions left in the substrate by beak prods of pterosaurs in search of food. This evidence reveals that pterosaurs could probably swim, or at least float on the surface of the water, like modern seabirds (Witton 2013; Hone and Henderson 2014; Li et al. 2015).

10.3 Conclusions

By applying rigorous analytic methods, which allow full hypothesis testing, vertebrate ichnology can provide reliable information about paleobiology (documenting evolutionary patterns, tempo of evolution, locomotion, posture, size, speed, social and individual behavior), paleobiodiversity (indicating the presence of taxa undocumented by the skeletal record), paleoecology (giving hints on environmental/habitat preferences and faunal composition) and paleobiogeography (providing presence/absence data on geographic distribution) of trackmakers, vertebrate ichnology is finally sitting at the "high table" of paleobiology.

In this review of Mesozoic reptile tracks some milestones of paleoichnologic research have been evaluated with the aim of highlighting the potential of these studies in contributing to the knowledge of evolutionary history and coevolution on the changing Earth. We have shown that vertebrate track record can be used to study the evolution of posture. Studies of the Permian to Triassic tetrapod-track record documents the appearance of upright stance in reptiles and shows a previously hidden correlation between this event and the Permo-Triassic mass extinction. Using synapomorphic characters in tracks has been essential in developing the present understanding of the origin of the dinosauromorph clade. Tracks show that the most basal dinosauromorphs were quadrupedal and that bipedalism was acquired phylogenetically closer to the origin of dinosaurs. An earlier origin of dinosauromorphs might imply a possible link with the Permo-Triassic mass extinction. The ichnologic record can be used to make hypotheses about the spatial and temporal distribution of basal dinosaurs. Tracks indicate the presence of a diverse and widespread fauna of dinosaurs during the early Late Triassic both in Laurasia and Gondwana, a distribution not yet documented by the body-fossil record. Track records provide evidence that habitats were shared by dinosaurian and non-dinosaurian archosaurs in the Late Triassic, and support the hypothesis that crurotarsan-dominated faunas were replaced by dinosaurs through a gradual process of ecologic replacement. Combined analyses of body and track fossils provide insights in the understanding of both environmental preferences and evolution of locomotory mechanisms in sauropod dinosaurs. Ichnologic data reveals the inland preference of wide-gauge titanosaurs highlighting the importance of considering track data in ecologic analysis. Trackways are used to estimate the speeds of trackmakers and provide clues to individual behaviors of theropod dinosaurs. Empiric formulae derived from extant animals constitute the basis of these interpretations, and show that theropods primarily used walking gaits, although some were runners, and there are a few records

of individuals using trotting gaits. Crouching traces demonstrate that the avian orientation of the manus, with a medially facing palm, had evolved by the Early Jurassic within Theropoda. Footprints provide clues on social behavior in dinosaurs. Many sites have shown that herbivorous dinosaurs were at times gregarious. Carnivorous non-avian theropods were sometimes gregarious although interpretations are more controversial. A strong link between paleornithology and avian paleoichnology illuminates aspects of avian evolution, particularly with regard to paleoenvironmental preferences. Ichnology is particularly relevant when studying shorebirds evolution, given the completeness of the track record for this group. Footprints are crucial to understand pterosaur terrestrial locomotion and stance, to estimate body mass, and to learn about their physiology and behavior (swimming, feeding, landing).

References

Abel O (1925) Geschichte und Methode der Rekonstruktion Vorzeitlicher Wirbeltiere. Gustav Fischer, Stuttgart

Abel O (1935) Vorzeitliche Lebensspuren. Gustav Fischer, Jena

Agirrezabala LM, Torres JA, Viera LI (1985) El weald de Igea (Cameros, La Rioja). Sedimentología, bioestratigrafía y paleoichnologia de grandes reptiles (dinosaurios). Munibe. Soc Cienc Aranzadi 37:111–138

Alexander RD (1974) The evolution of social behavior. Annu Rev Ecol Evol Syst 5:325–383

Alexander RM (1976) Estimates of speeds of dinosaurs. Nature 261:129–130

Alexander RM (1985) Mechanics of posture and gait of some large dinosaurs. Zool J Linn Soc 83:1–25

Alexander RM (1989) Dinamics of dinosaurs and other extinct giants. Columbia Univ Press, New York

Apesteguía S (2005) Evolution of titanosaur metacarpus. In: Tidwell V, Carpenter K (eds) Thunder-lizards—the sauropodomorph dinosaurs. Indiana Univ Press, Bloomington Univ Press, New York

Avanzini M (1998) Anatomy of a footprint: bioturbation as a key to understanding dinosaur walk dynamics. Ichnos 6:129–139

Avanzini M (2002) Dinosauromorph tracks from the Middle Triassic (Anisian) of the Southern Alps (Valle di Non-Italy). Boll Soc Paleontol Ital 41:37–40

Avanzini M, Petti FM (2008) Updating the dinosau tracksites from the Lower Jurassic Calcari Grigi Group (Southern Alps, Northern Italy). Stud Trent Sci Nat Acta Geol 83:289–301

Avanzini M, Piubelli D, Mietto P, Roghi G, Romano R, Masetti D (2006) Lower Jurassic (Hettangian-Sinemurian) dinosaur track megasites, Southern Alps, northern Italy. In: Harris JD et al (eds) The Triassic-Jurassic terrestrial transition, New Mexico. Mus Nat Hist Sci Bull 37:207–216

Avanzini M, Piñuela L, García-Ramos JC (2005) Paleopathologies deduced from a theropod trackway. Upper Jurassic of Asturias (N Spain). Book-international symposium on dinosaurs and other vertebrates palaeoichnology, 2010. P 59–60

Avanzini M, Piñuela L, García-Ramos JC (2012) Late Jurassic footprints reveal walking kinemtics of theropod dinosaur. Lethaia 45:238–252

Azuma Y, Tomida Y, Currie PJ (2002) Early Cretaceous bird tracks from the Tetori Group, Fukui Prefecture, Japan. Mem Fukui Pref Dinosaur Mus 1:1–6

Azuma Y, Lü J, Jin X, Noda Y, Shibata M, Chen R, Zheng W (2013) A bird footprint assemblage of early Late Cretaceous age, Dongyang City, Zhejiang Province, China. Cretaceous Res 40:3–9

Baird D (1980) A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona. In: Jacobs LL (ed) Aspects of vertebrate history: essays in honor of Edwin Harris Colbert. Mus Northern Arizona Press, Flagstaff

Bakker RT (1972) Anatomical and ecological evidence of endothermy in dinosaurs. Nature 238:81–85

Barco JL, Canudo JI, Ruiz-Omeñaca JI (2006) New data on *Therangospodus oncalensis* from the Berriasian Fuentesalvo tracksite (Villar del Río, Soria, Spain): an example of gregarious behavior in theropod dinosaurs. Ichnos 13:237–248

Barnes FA, Lockley MG (1995) Trackway evidence for social sauropods from the Morrison Formation, Eastern Utah (USA). Gaia 10:37–42

Barrett PM, Nesbitt SJ, Peecook BR (2015) A large-bodied silesaurid from the Lifua Member of the Manda beds (Middle Triassic) of Tanzania and its implications for body-size evolution in Dinosauromorpha. Gondwana Res 27:925–931

Bennett SC (1990) A pterodactyloid pterosaur pelvis from the Santana Formation of Brazil: implications for terrestrial locomotion. J Vertebr Paleontol 10:80–85

Bennett SC (1992) Reinterpretation of problematical tracks at Clayton Lake State Park, New Mexico: not one pterosaur, but several crocodiles. Ichnos 2:37–42

Bennett SC (1997) Terrestrial locomotion of pterosaurs: a reconstruction based on *Pteraichnus* trackways. J Vert Paleontol 17:104–113

Benton MJ (1983) Dinosaur success in the Triassic: a noncompetitive ecological model. Q Rev Biol 58:29–55

Benton MJ (2005) Vertebrate palaeontology, 3rd edn. Blackwell, Oxford, 455 pp

Benton MJ (2006) The origin of the dinosaurs. In: Proceedings of the 3rd international symposium about paleontology of dinosaur and their environment. Salas de Los Infantes, Burgos, 16–18 September 2004

Benton MJ, Csiki Z, Grigorescu D, Redelstorff R, Sander PM, Stein K, Weishampel DB (2010) Dinosaurs and the island rule: the dwarfed dinosaurs from Hateg Island. Palaeogeogr Palaeoclimatol Palaeoecol 293:438–454

Bernardi M, Petti FM, D´Orazi Porchetti S, Avanzini M (2013) Large tridactyl footprint associated with a diverse ichnofauna from the Carnian of the Southern Alps. In: Tanner LH et al (eds) The Triassic system. New Mexico Mus Nat Hist Sci Bull 61:48–54

Bernardi M, Klein H, Petti FM, Ezcurra MD (2015) The origin and early radiation of Archosauriforms: integrating the skeletal and footprint record. PLoS One 10(6):e0128449

Beurlen K (1950) Neue Fährtenfunde aus der fränkischen Trias. Neues Jahrb Geol 10S:308–320

Billon-Bruyat JP, Mazin JM (2003) The systematic problem of tetrapod ichnotaxa: the case study of *Pteraichnus* Stokes, 1957 (Pterosauria, Pterodactyloidea). Geol Soc Spec Publ 217:315–324

Bird RT (1939) Thunder in his footsteps. Nat Hist 43:254–261

Bird RT (1944) Did Brontosaurus ever walk on land? Nat Hist 53:60–67

Biron P-E, Dutuit JM (1981) Figurations sédimentaires et traces d'activité au sol dans le Trias de la Formacion d'Argana et de l'Ourika (Maroc). Bull Mus Nat Hist Nat, 4ème sér, 3 (section C, 4):339–427

Blob RW (2000) Interspecific scaling of the hindlimb skeleton in lizards, crocodilians, felids and canids: does limb bone shape correlate with limb posture? J Zool 250:507–531

Bonaparte JF (1984) Locomotion in rauisuchid thecodonts. J Vert Paleontol 3:210–218

Bonaparte JF, Coria RA (1993) Un nuevo y gigantesco sauropodo titanosaurio de la Formacíon Río Limay (Albiano-Cenomaniano) de la Provincia del Neuquén, Argentina. Ameghiniana 30:271–282

Bowden AJ, Tresise GR, Simkiss W (2010) *Chirotherium*, the Liverpool footprint hunters and their interpretation of the Middle Trias environment. Geol Soc Spec Publ 343:209–228

Brand LR, Hussey M, Taylor J (2003) Decay and disarticulation of small vertebrates in controlled experiments. J Taphonomy 1:69–95

Brinkman DB, Sues H-D (1987) A staurikosaurid dinosaur from the Upper Triassic Ischigualasto Formation of Argentina and the relationships of the Staurikosauridae. Palaeontology 30:493–503

Brocklehurst N, Upchurch P, Mannion PD, O'Connor J (2012) The completeness of the fossil record of Mesozoic birds: implications for early avian evolution. PLoS One 7:e39056

Brown JW, Rest JS, García Moreno J, Sorenson MD, Mindell DP (2008) Strong mithochondrial DNA support for a Cretaceous origin of modern avian lineages. BMC Biol 6:1–18

Brusatte SL, Benton MJ, Ruta M, Lloyd GT (2008a) Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. Science 321:1485–1488

Brusatte SL, Benton MJ, Ruta M, Lloyd GT (2008b) The first 50 Myr of dinosaur evolution: macroevolutionary pattern and morphological disparity. Biol Lett 4:733–736

Brusatte SL, Nesbitt SJ, Irmis RB, Butler RJ, Benton MJ, Norell MA (2010a) The origin and early radiation of dinosaurs. Earth-Sci Rev 101:68–100

Brusatte SL, Niedźwiedzki G, Butler RJ (2010b) Footprints pull origin and diversification of dinosaur stem lineage deep into Early Triassic. Proc R Soc B 278:1107–1113

Brusatte SL, Benton MJ, Lloyd GT, Ruta M, Wang SC (2011) Macroevolutionary patterns in the evolutionary radiation of archosaurs (Tetrapoda: Diapsida). Earth Environ Sci Trans R Soc Edinb 101:357–382

Buffetaut E, Mazin JM (2003) Evolution and palaeobiology of pterosaurs. Geol Soc Spec Publ 217, 349 pp

Butler RJ, Barrett PM (2008) Paleoenvironmental controls on the distribution of Cretaceous herbivorous dinosaurs. Naturwissenschaften 95:1027–1032

Calvo JO, Lockley MG (2001) The first pterosaur tracks from Gondwana. Cretaceous Res 22:585–590

Cameron B, Wood N (2003) A Late Triassic terrestrial vertebrate community, as indicated by reptile footprints preserved in the Upper Wolfville Formation (Fundy Supergroup) at North Medford, Nova Scotia. Min Matters 2003:3

Cameron B, Wood N (2004) A comparison of the Late Triassic dinosaur fotprintss *Atreipus acadicus* and *Grallator* (Grallator) sp. from the Upper Wolfville Formation at North Medford, Nova Scotia. Min Matters 2004:4

Carpenter K (1992) Behavior of hadrosaurs as iinterpreted from footprints in the "Mesaverde" Group (Campanian) of Colorado, Utah, and Wyoming. Contrib Geol Univ Wyoming 29:81–96

Carpenter K (1999) Eggs, nests, and baby dinosaurs: A look at dinosaur reproduction. Indiana Univ Press, Bloomingtong, IN

Carpenter K (2009) Role of lateral body bending in crocodylian track making. Ichnos 16:202–207

Carrano MT, Wilson JA (2001) Taxon distributions and the vertebrate track record. Paleobiology 27:563–581

Carrier DR (1987) The evolution of locomotor stamina in tetrapods—circumventing a mechanical constraint. Paleobiology 13:326–341

Carroll RL (1988) Vertebrate paleontology and evolution. W H Freeman & Co, New York, 698 pp

Carvalho I, Pedrão E (2000) Brazilian theropods from the equatorial atlantic margin: behaviour and environmental setting. In: Pérez-Moreno BP et al (eds) Aspects of theropod paleobiology. Gaia 15:369–378

Castanera D, Barco JL, Díaz-Martínez I, Herrero Gascón J, Pérez-Lorente F, Canudo JI (2011) New evidence of a herd of titanosauriform sauropods from the lower Berriasian of the Iberian range (Spain). Palaeogeogr Palaeoclimatol Palaeoecol 310:227–237

Castanera D, Pascual C, Canudo JI, Hernández N, Barco J (2012a) Gauge variations in sauropod trackways from the Huérteles Formation (Berriasian) of the Cameros Basin (Spain): implications for sauropod ichnotaxonomy. Abstract volume 10th EAVP meeting, 2012. p 35–37

Castanera D, Pascual C, Canudo JI, Hernández N, Barco J (2012b) Ethological variations in gauge in sauropod trackways from the Berriasian of Spain. Lethaia 45:476–489

Castanera D, Pascual C, Razzolini NL, Vila B, Barco JL, Canudo JI (2013) Discriminating between medium-sized tridactyl trackmakers: tracking ornithopod tracks in the base of the Cretaceous (Berriasian, Spain). PLoS One 8(11):e81830

Castanera D, Vila B, Razzolini NL, Santos VF, Pascual C, Canudo JI (2014) Sauropod trackways of the Iberian Peninsula: palaeoetological and palaeoenvironmental implications. J Iber Geol 40:49–59

Cavin L, Avanzini M, Bernardi M, Piuz A, Proz P-A, Meister C, Boissonnas J, Meyer C (2012) New Triassic trackways from the autochthonous of the Triassic of the Aiguilles Rouges Massif, and re-evaluation of the dinosaur record in Valais, SW Switzerland. Swiss J Palaeontol 131:317–324

Charig AJ (1972) The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. In: Joysey KA, Kemp TS (eds) Studies in vertebrate evolution. Oliver and Boyd, Edinburgh

Charig AJ (1984) Competition between therapsids and archosaurs during the Triassic Period: a review and synthesis of current theories. Sym Zool Soc Lond 52:597–628

Clark NDL, Ross DA, Booth P (2005) Dinosaur tracks from the Kilmaluag Formation (Bathonian, Middle Jurassic) of Score Bay, Isle of Skye, Scotland, UK. Ichnos 12:93–104

Clarke JA, Tambussi CP, Noriega JI, Erickson GM, Ketcham RA (2005) Definitive fossil evidence for the extant avian radiation in the Cretaceous. Nature 433:305–308

Conradt L (1998) Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? Proc R Soc B 265:1359–1363

Contessi M, Fanti F (2012) First record of bird tracks in the Late Cretaceous (Cenomanian) of Tunisia. Palaios 27:455–464

Coombs WP (1980) Swimming ability of carnivorous dinosaurs. Science 207:1198–1200

Cooper A, Penny D (1997) Mass survival of birds across the Cretaceous-Tertiary boundary: molecular evidence. Science 275:1109–1113

Cotton WD, Cotton JE, Hunt AP (1998) Evidence for social behavior in ornithopod dinosaurs from the Dakota Group of northeastern New Mexico, U.S.A. Ichnos 6:141–149

Cuny G, Galton PM (1993) Revision of the Airel theropod dinosaur from the Triassic-Jurassic boundary (Normandy, France). Neues Jahrb Geol P A 187:261–288

Currie PJ (1983) Hadrosaur trackways from the Lower Cretaceous of Canada. Acta Paleontol Pol 28:63–73

Currie PJ (1995) Ornithopod trackways from the Lower Cretaceous of Canada. In: Sarjeant WAS (ed) Vertebrate fossils and the evolution of scientific concepts. Gordon and Breach, Newark, NJ

Currie PJ, Eberth DA (2010) On gregarious behavior in *Albertosaurus*. Can J Earth Sci 47:1277–1289

Cuvier G (1809) Memoire sur le squelette fossile d'un reptile volant des environs d'Aichstedt, que quelques naturalistes ont pris pour un oiseau, et dont nous formons un genre de Sauriens, sous le nom de Ptero-Dactyle. Ann Mus Hist Nat Paris 13:424–437

Czerkas S, Olson EC (1987) Dinosaurs past and present. Univ Washington Press, Seattle

Dantas P, Dos Santos VF, Lockley MG, Meyer CA (1994) Footprint evidence for limping dinosaurs form the Upper Jurassic of Portugal. Gaia 10:43–48

Davis PG, Briggs DEG (1998) The impact of decay and disarticulation on the preservation of fossil birds. Palaios 13:3–13

Day JJ, Upchurch P, Norman DB, Gale AS, Powell HP (2002a) Sauropod trackways, evolution, and behavior. Science 296:1659

Day JJ, Norman DB, Upchurch P, Powell HP (2002b) A new trackway locality with implications for theropod dinosaur locomotion. Nature 415:494–495

Day JJ, Norman DB, Gale AS, Upchurch P, Powell HP (2004) A Middle Jurassic dinosaur trackway site from Oxfordshire, UK. Palaeontology 47:319–348

Delair JB (1963) Notes on Purbeck fossil footprints, with descriptions of two hitherto unknown forms from Dorset. Proc Dorset Nat Hist Archaeol Soc 84:92–100

Delair JB (1981) Multiple trackways from the Isle of Purbek. Proc Dorset Nat Hist Archaeol Soc 102:65–68

Demathieu GR (1981) Comparaison des informations fournies par l´ichnologie des vertébrés et par la paléontologie ostéologique dans le domaine de la chrologie. Bull Sci Bourg 34:5–12

Demathieu G (1986) Nouvelles recherches sur la vitesse des vertébrés, auteurs de traces fossiles. Geobios 19:327–333

Demathieu G (1989) Appearance of the first dinosaur tracks in the French Middle Triassic and their probable significance. In: Gillette DD, Lockley MG (eds) Dinosaur tracks and traces. Cambridge Univ Press, Cambridge

Demathieu G, Demathieu P (2004) Chirotheria and other ichnotaxa of the European Triassic. Ichnos 11:79–88

Demathieu G, Haubold H (1978) Du problème de l'origine des dinosauriens d'après les données de l'ichnologie du Trias. Geobios 11:409–412

D'Emic MC (2012) The early evolution of titanosauriform sauropd dinosaurs. Zool J Linnean Soc 166:624–671

Desojo JB, Heckert AB, Martz JW, Parker WG, Schoch RR, Small BJ, Sulej T (2013) Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. Geol Soc Special Publ 379

D'Orazi Porchetti S, Nicosia U, Mietto P, Avanzini M (2008) *Atreipus*-like footprints and their co-ocurrence with *Evazoum* from the upper Carnian (Tuvalian) of Trentino-Alto Adige. Stud Trent Sci Nat Acta Geol 83:277–287

Dyke G, Kaiser G (eds) (2011) Living dinosaurs: the evolutionary history of modern birds. Wiley, Oxford

Dzik J (2003) A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. J Vert Paleontol 23:556–574

Dzik J, Sulej T, Niedzwiedzki G (2008) A dicynodont-theropod association in the latest Triassic of Poland. Acta Palaeontol Pol 53:733–738

Ellis RG, Gatesy SM (2013) A biplanar X-ray method for three-dimensional analysis of track formation. Palaeontol Electron 16:1–16

Ezcurra MD (2006) A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* from the Upper Triassic of New Mexico, USA. Geodiversitas 28:649–684

Ezcurra MD (2010) Biogeography of Triassic tetrapods: evidence for provincialism and driven sympatric cladogenesis in the early evolution of modern tetrapod lineages. Proc R Soc Lond B 277:2547–2552

Ezquerra R, Doublet S, Costeur L, Galton PM, Pérez-Lorente F (2007) Were non-avian theropod dinosaurs able to swim? Supportive evidence from an Early Cretaceous trackway, Cameros Basin (La Rioja, Spain). Geology 35:507–510

Falk AR (2011) Tracking Mesozoic birds across the world. J Syst Palaeontol 9:85–90

Falk AR, Hasiotis ST, Martin LD (2010) Feeding traces associated with bird tracks from the Lower Cretaceous Haman Formation, Republic of Korea. Palaios 25:730–741

Falk AR, Lim J-D, Hasiotis ST (2014) A behavioral analysis of fossil bird tracks from the Haman Formation (Republic of Korea) shows a nearly modern avian ecosystem. Vert Palasiatic 52:129–152

Farlow JO (1981) Estimates of dinosaur speeds from a new trackway site in Texas. Nature 294:747–748

Farlow JO (1987) Lower Cretaceous dinosaur tracks, Paluxy River Valley, Texas. South Central Section, Geol Soc Am, Waco, TX

Farlow JO (1992) Sauropod tracks and trackmakers: integrating the ichnological and skeletal records. Zubía 10:89–138

Farlow JO, Pianka ER (2000) Body form and trackway pattern in Australian desert monitors (Squamata: Varanidae): Comparing zoological and ichnological diversity. Palaios 15:235–247

Farlow JO, Pittman JG, Hawthorne JM (1989) Brontopodus birdi, Lower Cretaceous sauropod footprints from the U.S. Gulf Coastal Plain. In: Gillette DD, Lockley MG (eds) Dinosaur tracks and traces. Cambridge Univ Press, Cambridge

Farlow JO, Gatesy SM, Holz T Jr, Hutchinson JR, Robinson JM (2000) Theropod locomotion. Am Zool 40:640–663

Fichter J, Kunz R (2004) New genus and species of Chirotheroid tracks in the Detfurth-Formation (Middle Bunter, Lower Triassic) of Central Germany. Ichnos 11:183–193

Fiorillo AR, Hasiotis ST, Kobayashi Y (2011) Bird tracks from the Upper Cretaceous Cantwell Formation of Denali National Park, Alaska, USA: a new perspective on ancient northern polar vertebrate biodiversity. J Syst Palaeontol 9:33–49

Fraser NC, Padian K, Walkden GM, Davis ALM (2002) Basal Dinosauriform Remains from Britain and the Diagnosis of the Dinosauria. Palaeontology 45:79–95

Fuentes Vidarte C (2001) A new species of *Pteraichnus* of the Spanish Lower Cretaceous. *Pteraichnus cidacoi*. Strata 11:44–46

Fuentes Vidarte C, Meijide Calvo M, Meijide Fuentes F, Meijide Fuentes M (2004a) *Pteraichnus longipodus* nov. ichnosp. en la Sierra de Oncala (Soria, España). Stvdia Geol Salmanticensia 40:103–114

Fuentes Vidarte C, Meijide Calvo M, Meijide Fuentes M, Meijide Fuentes F (2004b) Huellas de pterosaurios en la Sierra de Oncala (Soria, España), nuevas ichnospecies: *Pteraichnus vetustior*, *Pteraichnus parvus*, *Pteraichnus manueli*. Celtiberia 98:471–490

Fujita M, Lee Y-N, Azuma Y, Li D (2012) Unusual tridactyl trackways with tail traces from the Lower Cretaceous Hekou Group, Gansu province, China. Palaios 27:560–570

Galton PM (1970) The posture of hadrosaurian dinosaurs. J Paleontol 44:464–473

Gand G, Demathieu G (2005) Les pistes dinosauroides du Trias moyen francais: interprétation et réévaluation de la nomenclature. Geobios 38:725–749

Gand G, Demathieu G, Grancier M, Sciau J (2005) Les traces dinosauroïdes du Trias supérieur français: discrimination, interprétation et comparaison. Bull Soc Géol Fr 176:69–79

Gand G, De La Horra R, Galán-Abellán B, López-Gómez J, Barrenechea JF, Arche A, Benito MI (2010) New ichnites from the Middle Triassic of the Iberian Ranges (Spain): paleoenvironmental and paleogeographical implications. Hist Biol 22:40–56

García-Ortiz E, Pérez-Lorente F (2014) Palaeoecological inferences about dinosaur gregarious behaviour based on the study of tracksites from La Rioja area in the Cameros Basin (Lower Cretaceous, Spain). J Iber Geol 40:113–127

García-Ramos JC, Piñuela L, Lires J, Fernández LA (2000) Icnitas de reptiles voladores (pterosaurios) con impresiones de la piel en el Jurásico Superior de Asturias (N de España). In: Diez JB, Balbino AC (eds) I Congresso Ibérico de Paleontología, libro de resumos, Évora, Portugal, 12–14 October 2000

García-Ramos JC, Lires J, Piñuela L (2002) Dinosaurios. Rutas por el Jurásico de Asturias. La Voz de Asturias, Lugones, Asturias

García-Ramos JC, Piñuela L, Lires J (2004) Guía del Jurásico de Asturias. Zinco Comunicación, Gijón, Asturias

García-Ramos JC, Piñuela L, Lires J (2006) Atlas del Jurásico de Asturias. Ediciones Nobel, Oviedo

Gatesy SM (2001) Skin impressions of Triassic theropods as records of foot movement. Bull Mus Comp Zool 156:137–149

Gatesy S (2003) Direct and indirect track features: what sediment did a dinosaur touch? Ichnos 10:91–98

Gatesy SM, Middleton KM, Jenkins FA Jr, Shubin NH (1999) Three dimensional preservation of foot movements in Triassic theropod dinosaurs. Nature 399:141–144

Gauthier JA (1986) Saurischian monophyly and the origin of birds. Mem Calif Acad Sci 8:1–55

Gierliński GD, Lockley MG, Niedźwiedzki G (2009) A distinctive crouching theropod trace from the Lower Jurassic of Poland. Geol Quart 53:471–475

Gillette DG, Lockley MG (eds) (1989) Dinosaur tracks and traces. Cambridge University Press, Cambridge

Greben R, Lockley MG (1992) Vertebrate tracks from the Green River Formation, eastern Utah: implications for paleoecology. Geol Soc Am, Rocky Mountain Sect, Abstr Progr 24:16

Haddrath O, Baker AJ (2012) Multiple nuclear genes and retroposons support vicariance and dispersal of the palaeognaths, and an Early Cretaceous origin of modern birds. Proc R Soc Lond Biol 279:4617–4625

Haubold H (1967) Eine Pseudosuchier-Fährtenfauna aus dem Buntsandstein Südthüringens. Hall Jb Mitteldt Erdg 8:12–48

Haubold H (1971a) Die Tetrapodenfährten des Buntsandsteins. Paläontol Abh A 4:395–548

Haubold H (1971b) Ichnia amphibiorum et reptiliorum fossilium. In: Kuhn O (ed) Handbuch der paläoherpetologie, Teil 18. G Fischer, Stuttgart

Haubold H (1984) Saurierfährten. Wittenberg, Ziemsen

Haubold H (1986) Archosaur footprints at the terrestrial Triassic-Jurassic transition. In: Padian K (ed) The beginning of the age of dinosaurs. Cambridge Univ Press, Cambridge

Haubold H (1999) Tracks of the Dinosauromorpha from the Lower Triassic. Zbl Geo Pal 1:783–795

Haubold H (2006) Die Saurierfährten *Chirotherium barthii* Kaup, 1835—das Typusmaterial aus dem Buntsandstein bei Hildburghausen/Thüringen und das Chirotherium-Monument. Ver Nat Mus Schl 21:3–31

Haubold H, Klein H (2000) Die dinosauroiden Fährten *Parachirotherium–Atreipus–Grallator* aus dem unteren Mittelkeuper (Obere Trias: Ladin, Karn? Nor) in Franken. Halles Jahr Geowiss B 22:59–85

Haubold H, Klein H (2002) Chirotherien und rallatoriden aus der Unteren bis Oberen Trias Mitteleuropas und die Entstehung der Dinosauria. Hall Jahr Geowiss B 24:1–22

Hawthorne JM (1990) Dinosaur track-bearing strata of the Lampasas Cut Plain and Edwards Plateau, Texas. Baylor Geol Stud Bull 49:1–47

He Q, Xing LD, Zhang J-P, Lockley MG, Klein H, Persons WS, Qi L-Q, Jia C-K (2013) New Early Cretaceous pterosaur-bird track assemblage from Xinjiang, China: palaeoethology and palaeoenvironment. Acta Geol Sin-Engl 87:1477–1485

Heckert AB, Lucas SG, Rinehart LF, Celeskey MD, Spielmann JA, Hunt AP (2010) Articulated skeletons of the aetosaur *Typothorax coccinarum* Cope (Archosauria: Stagonolepididae) from the Upper Triassic Bull Canyon Formation (Revueltian: Early-Mid Norian), eastern New Mexico, USA. Vert Paleontol 30:619–642

Henderson DM (2002) Wide and narrow-gauge sauropod trackways as a consequence of body-mass distribution and the requirements for stability. Vert Paleontol 22:64A

Henderson DM (2006) Burly gaits: centers of mass, stability, and the trackways of sauropod dinosaurs. Vert Paleontol 26:907–921

Hernández Medrano N, Pacual Arribas C, Latorre Macarrón P, Sanz Pérez E (2006). Huellas de terópodos y pterosaurios en Valdegén 1 (Villar del Río, Soria, España). In: Proceedings of the 3rd international symposium about paleontology of dinosaur and their environment. Salas de Los Infantes, Burgos, 16–18 September 2004

Hitchcock E (1858) Ichnology of New England. A report of the sandstone of the Connecticut Valley especially its footprints. W. White, Boston

Hone DWE, Henderson DM (2014) The posture of floating pterosaurs: ecological implications for inhabiting marine and freshwater habitats. Palaeogeogr Palaeoclimatol Palaeoecol 394:89–98

Horner JR, Gorman J (1990) Digging dinosaurs. Workman Publ, New York

Hornung JJ, Reich M (2013) The First Record of the Pterosaur Ichnogenus *Purbeckopus* in the Late Berriasian (Early Cretaceous) of Northwest Germany. Ichnos 20:164–172

Huh M, Lockley MG, Kim KS, Kim JY, Gwak S-G (2012) First report of *Aquatilavipes* from Korea: new finds from Cretaceous strata in the Yeosu Islands archipelago. Ichnos 19:43–49

Hunt AP, Lockley MG, Lucas SG, Meyer CA (1995a) The global sauropod fossil record. Gaia 10:261–279

Hunt AP, Lockley MG, Hups K, Schultz R (1995b) Jurassic vertebrate paleontology of Cactus Park, west-central Colorado. Geol Soc Am Abstr Prog Rocky Mountains Sec 27:15

Hwang KG, Huh M, Lockley MG, Unwin DM, Wright JL (2002) New pterosaur tracks (Pteraichnidae) from the Late Cretaceous Uhangri Formation, southwestern Korea. Geol Mag 139:421–435

Hwang KG, Huh M, Paik SI (2004) Sauropod trackways from the Cretaceous Jindong Formation at Docheon-ri, Changnyeon-gun, Geongsagnam-do, Korea. J Geol Soc Korea 40:145–159

Irby GV, Albright LB III (2012) Tail drag marks and dinosaur footprints from the Upper Cretaceous Toreva Formation, northeastern Arizona. Palaios 17:516–521

Irmis RB (2011) Evaluating hypotheses for the early diversification of dinosaurs. Earth Environ Sci Trans R Soc Edin 101:397–426

Irmis RB, Nesbitt SJ, Padian K, Smith ND, Turner AH, Woody D, Downs A (2007) A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317:358–361

Ishigaki S (1986) Dinosaur footprints in the Atlas mountains. Nat Study 32:6–9

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. Nature 491:444–448

Kaever M, de Lapparent AF (1974) Les traces de pas de Dinosaures du Jurassique de Barkhausen (Basse Saxe, Allemagne). Bull Soc Geol Fr 16:516–525

Kaup JJ (1835) Über Thierfährten bei Hildburghausen. Neues Jahrb Miner Geogn Geol Petrefakt 1835:227–228

Kemp TS (1982) Mammal-like reptiles and the origin of mammals. Academic, London

Kim JY, Lockley MG (2013) Review of dinosaur tail traces. Ichnos 20:129–141

Kim JY, Kim SH, Kim KS, Lockley MG (2006) The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation, Changseon and Sinsu Islands): More evidence of high avian diversity in East Asia. Cretaceous Res 27:56–69

Kim JY, Lockley MG, Seo SJ, Kim KS, Kim SH, Baek KS (2012) A paradise of mesozoic birds: the world's richest and most diverse Cretaceous bird track assemblage from the Early Cretaceous Haman Formation of the Gajin tracksite, Jinju, Korea. Ichnos 19:28–42

King MI, Benton MJ (1996) Dinosaurs in the Early and Middle Triassic?—The footprint evidence from Britain. Palaeogeogr Palaeoclimatol Palaeoecol 122:213–225

Klein H, Haubold H (2007) Archosaur footprints—potential for biochronology of Triassic continental sequences. New Mexico Mus Nat Hist Sci Bull 4:120–130

Klein H, Niedźwiedzki G (2012) Revision of the Lower Triassic tetrapod ichnofauna from Wióry, Holy Cross Mountains, Poland. Cross Mountains, Poland. New Mexico Mus Nat Hist Sci Bull 56:1–62

Knoll F (2004) Review of the tetrapod fauna of the "Lower Stormberg Group" of the main Karoo Basin (southern Africa): implication for the age of the Lower Elliot Formation. Bull Soc Géol Fr 175:73–83

Krebs B (1965) E. Kuhn-Schnyder und B. Peyer: Die Triasfauna der Tessiner Kalkalpen. XIX. *Ticinosuchus ferox* nov. gen. nov. sp. [E. Kuhn-Schnyder and B. Peyer: The Triassic fauna of the Tessin Limestone Alps. XIX. *Ticinosuchus ferox* nov. gen. nov. sp.]. Schweizerische Paläontologische Abhandlungen. Mem Suisses Paleontol 81:1–140

Ksepka DT, Boyd CA (2012) Quantifying historical trends in the completeness of the fossil record and the contributing factors: an example using Aves. Paleobiology 38:112–125

Kubo T (2008) In quest of the *Pteraichnus* trackmaker: comparisons to modern crocodilians. Acta Palaeontol Pol 53:405–412

Kubo T (2011) Estimating body weight from footprints: application to pterosaurs. Palaeogeogr Palaeoclimatol Palaeoecol 299:197–199

Kubo T, Benton MJ (2009) Tetrapod postural shift estimated from Permian and Triassic trackways. Palaeontology 52:1029–1037

Kubo T, Kubo MO (2012) Associated evolution of bipedality and cursoriality among Triassic archosaurs: a phylogenetically controlled evaluation. Paleobiology 38:474–485

Kubo T, Kubo M (2013) Analysis of Triassic archosauriform trackways: difference in stride/foot-print ratio between dinosauromorphs and other archosauriforms. Palaios 28:259–265

Kvale EP, Johnson GD, Mickelson DL, Keller FLC, Archer AW (2001) Middle Jurassic (Bajocian and Bathonian) dinosaur megatracksites, Bighorn Basin, Wyoming, U.S.A. Palaios 16:233–254

Langer MC (2005) Studies on continental Late Triassic tetrapod biochronology. II The Ischigualastian and a Carnian global correlation. J South Am Earth Sci 19:219–239

Langer MC, Ezcurra MD, Bittencourt JS, Novas FE (2010) The origin and early evolution of dinosaurs. Biol Rev 85:55–110

Langer MC, Nesbitt SJ, Bittencourt JS, Irmis RB (2013) Non-dinosaurian dinosauromorphs. In: Nesbitt SJ, Desojo JB, Irmis RB (eds) Phylogeny and palaeobiology of early archosaurs and their kin. Geol Soc London, Spec Publ 379:157–186

Laws RR (1997) Allosaur traumatism and infection: palaeopathological analysis as a tool for lifestile reconstruction. J Vert Paleontol 17:59–60

Lee MSY, Cau A, Naish D, Dyke GJ (2014) Morphological clocks in palaeontology, and a mid-Cretaceous origin of crown Aves. Syst Biol. doi:10.1093/sybio/syt110, Advanced Onlive Version

Lee Y-N, Azuma Y, Lee H-J, Shibata M, Lü J (2010) The first pterosaur trackways from Japan. Cretaceous Res 31:263–273

Lee Y-N, Lee H-J, Lü J, Kobayashi Y (2008) New pterosaur tracks from the Hasandong Formation (Lower Cretaceous) of Hadong County, South Korea. Cretaceous Res 29:345–353

Lehman TM (1987) Late Maastrichtian paleoenvironments and dinosaur biogeography in the Western Interior of North America. Palaeogeogr Palaeoclimatol Palaeoecol 60:189–217

Leonardi G (ed) (1987) Glossary and manual of tetrapod footprint palaeoichnology. Dept Nac Prod Min, Brazil

Leonardi G (1989) Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation. In: Gillette DD, Lockley MG (eds) Dinosaur tracks and traces. Cambridge Univ Press, Cambridge

Leonardi G (1994) Annotated atlas of South America tetrapod footprints (Devonian to Holocene). Ministry of Mines and Energy, Brasilia

Li D, Azuma Y, Arakawa Y (2002) A new Mesozoic bird track site from Gansu Province, China. Mem Fukui Prefect Dino Mus 1:92–95

Li D, Xing L, Lockley MG, Pinuela L, Zhang J, Dai H, Kim JY, Person WS IV, Kong D (2015) A manus dominated pterosaur track assemblage from Gansu, China: implications for behavior. Sci Bull 60:264–272

Li R, Lockley MG, Liu M (2005) A new ichnotaxon of fossil bird track from the Early Cretaceous Tianjialou Formation (Barremian–Albian), Shandong Province, China. Chin Sci Bull 50:1149–1154

Li R, Lockley MG, Makovicky PJ, Matsukawa M, Norell MA, Harris JD, Liu M (2008) Behavioral and faunal implications of Early Cretaceous deinonychosaur trackways from China. Naturwissenschaften 95:185–191

Lim SY, Yang SY, Lockley MG (1989) Large dinosaur footprint assemblages from the Cretaceous Jindong Formation of southern Korea. In: Gillette D, Lockley MG (eds) Dinosaur tracks and traces. Cambridge Univ Press, Cambridge

Lingham-Soliar T, Broderick T, Ait-Kaci Ahmed A (2003) Closely associated theropod trackways from the Jurassic of Zimbabwe. Naturwissenschaften 90:572–576

Lockley MG (1989) Tracks and traces: new perspectives on dinosaurian behavior, ecology and biogeography. In: Padian K, Chure DJ (eds) The age of dinosaurs short courses in paleontology #2. Paleontological Society, Knoxville, TN

Lockley M (1991) Tracking dinosaurs: a new look at an ancient world. Cambridge Univ Press, Cambridge

Lockley M (1998) The vertebrate tracks record. Nature 396:429–432

Lockley MG (1999) The Eternal Trail: a tracker looks at evolution. Perseus Books, Reading, MA, 334 p

Lockley MG (2001) Trackways-dinosaur locomotion. In: Briggs DEG, Crowther P (eds) Paleobiology: a synthesis. Blackwell, Oxford

Lockley MG (2007a) The morphodynamics of dinosaurs, other archosaurs and their trackways: holistic insights into relationships between feet, limbs and the whole body. In: Bromley RG, Buatois LA, Mángano MG, Genise JF, Melchor RN (eds) Sediment–organism interactions: a multifaceted ichnology. SEPM Spec Pub 88:27–51

Lockley MG (2007b) A tale of two ichnologies: the different goals and missions of vertebrate and invertebrate ichnology and how they relate in ichnofacies analysis. Ichnos 14:39–57

Lockley MG (2009) New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. Geol Quart 53:415–432

Lockley MG, Cart K, Martin J, Prunty R, Houck K, Hups K, Lim J-D, Kim K-S, Houck K, Gierliński G (2014) A bonanza of new tetrapod tracksites from the Cretaceous Dakota Group, western Colorado: implications for paleoecology. New Mexico Mus Nat Hist Sci Bull 62:393–410

Lockley MG, Eisenberg L (2006) A preliminary report on a spectacular dinosaur tracksite in the Chinle Group, Dirty Cevil River Valley, Wayne County, Utah. In: Harris JD et al (eds) The Triassic–Jurassic terrestrial transition. New Mexico Mus Nat Hist Sci Bull 37:263–268

Lockley MG, Gillette DD (1987) Dinosaur tracks symposium signals a renaissance in vertebrate ichnology. Paleobiology 13:246–252

Lockley MG, Harris JD (2010) On the trail of early birds: a review of the fossil footprint record of avian morphological and behavioral evolution. In: Ulrich PK et al (eds) Trends in ornithology research. Nova Science Publ, New York

Lockley MG, Houck K, Yang S-Y, Matsukawa M, Lim S-K (2006a) Dinosaur dominated footprint assemblages from the Cretaceous Jindong Formation, Hallayo Haesang National Park, Goseong County, South Korea: evidence and implications. Cretaceous Res 27:70–101

Lockley MG, Hunt AP (1995a) Dinosaur tracks and other fossil footprints of the Western United States. Columbia Univ Press, New York

Lockley MG, Hunt AP (1995b) Ceratopsid tracks and associated ichnofauna from the Laramie Formation (Upper Cretaceous: Maastrichtian) of Colorado. J Vert Paleontol 15:592–614

Lockley MG, Hunt AP, Meyer C (1994a) Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy. In: Donovan S (ed) The paleobiology of trace fossils. Wiley, Chichester

Lockley MG, Hunt AP, Moratalla J, Matsukawa M (1994b) Limping dinosaurs? Trackway evidence for abnormal gait. Ichnos 3:193–202

Lockley MG, Matsukawa M (1999) Some observations on trackway evidence for gregarious behavior among small bipedal dinosaurs. Palaeogeogr Palaeoclimatol Palaeoecol 150:25–31

Lockley MG, Meyer C (2000) Dinosaur tracks and other fossil footprints of Europe. Columbia Univ Press, New York

Lockley MG, Rainforth EC (2002) The track record of Mesozoic birds and pterosaurs. An ichnological and paleoecological perspective. In: Chiappe LM, Witmer LM (eds) Mesozoic birds: above the head of dinosaurs. Univ California Press, Berkeley

Lockley MG, Wright J (2003) Pterosaur swim tracks and other ichnological evidence of behavior and ecology. In: Buffetaut E (ed) Evolution and paleobiology of pterosaurs. Geolo Soc Spec Publ 217:297–313

Lockley MG, Young BH, Carpenter K (1983) Hadrosaur locomotion and herding behavior: evidence from footprints in the Mesaverde Formation Gran Mesa Coal field, Colorado. Mountain Geol 20:5–14

Lockley MG, Houck KJ, Prince NK (1986) North America's largest dinosaur trackway site: implications for Morrison Formation paleoecology. Geol Soc Am Bull 97:1163–1176

Lockley MG, Holbrook J, Hunt AP, Matsukawa M, Meyer C (1992a) The dinosaur freeway: a preliminary report on the Cretaceous megatracksite, Dakota Group, Rocky Mountain Front Range and Highplains; Colorado, Oklahoma and New Mexico. In: Flores R (ed) Mesozoic of the Western Interior. SEPM, Midyear Mtg, Field Guideb. Tulsa, OKlahoma

Lockley MG, Yang SY, Matsukawa M, Fleming F, Lim SK (1992b) The track record of Mesozoic birds: evidence and implications. Philos Trans R Soc 336:113–134

Lockley MG, Farlow JO, Meyer CA (1995a) *Brontopodus* and *Parabrontopodus* Ichnogen. nov. and the significance of wide and narrow-gauge sauropod trackways. In: Lockley MG et al (eds) Aspects of sauropod biology. Gaia 10:135–146

Lockley MG, Meyer CA, Hunt AP, Lucas S (1995b) The distribution of sauropod tracks and track-makers. In: Lockley MG et al (eds) Aspects of sauropod biology. Gaia 10:233–248

Lockley MG, Meyer C, Santos VF (1995c) Trackway evidence for a herd of juvenile sauropods from the Late Jurassic of Portugal. In: Lockley MG et al (eds) Aspects of sauropod biology. Gaia 10:27–36

Lockley MG, Lim JD, Kim J-Y, Kim K-S, Huh M, Hwang KG (2012a) Tracking Korea's early birds: ichnological insights into avian evolution and behavior. Ichnos 19:17–27

Lockley MG, Logue TJ, Moratalla JJ, Hunt AP, Schultz RJ, Robinson JW (1995a) The fossil track-way *Pteraichnus* is pterosaurian, not crocodilian: implications for the global distribution of pterosaur tracks. Ichnos 4:7–20

Lockley MG, Hunt AP, Lucas SG (1996) Vertebrate track assemblages from the Jurassic Summerville Formation and correlative deposits. In: Morales M (ed) The continental Jurassic. Mus Northern Arizona Bull 60:249–254

Lockley MG, Lim M, Huh S-K, Yang S-Y, Chun SS, Unwin DM (1997) First report of pterosaur tracks from Asia, Chollanam Province, Korea. J Paleontol Soc Korea Spec Publ 2:17–32

Lockley MG, Santos VF, Meyer C, Hunt A (1998) A new dinosaur tracksite in the Morrison Formation, Boundary Butte, Southeastern Utah. Modern Geol 23:317–330

Lockley M, Schulp AS, Meyer CA, Leonardi G, Mamani DK (2002) Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behavior. Cretaceous Res 23:383–400

Lockley MG, Wright JL, Thies D (2005) Some observations on the dinosaur tracks at Müncheagen (Lower Cretaceous), Germany. Ichnos 11:261–274

Lockley M, Matsukawa M, Ohira H, Li J, Wright J, White D, Chen P (2006b) Bird tracks from Liaoning Province, China: new insights into avian evolution during the Jurassic-Cretaceous transition. Cretaceous Res 27:33–43

Lockley MG, Li R, Harris JD, Matsukawa M, Liu M (2007) Earliest zygodactyl bird feet: evidence from Early Cretaceous roadrunner-like track. Naturwissenschaften 94:657–665

Lockley MG, Harris JD, Chin K, Masukawa M (2008) Ichnological evidence for morphological and behavioral convergence between Mesozoic and extant birds: paleobiological implications. In: Uchman A (ed) 2nd Int Congr Ichnol Abstr Book. Polish Geol Inst, Warszawa

Lockley MG, Chin K, Houck M, Matsukawa M, Kukihara R (2009) New interpretations of *Ignotornis* the first reported Mesozoic avian footprints: implications for the ecology and behavior of an enigmatic Cretaceous bird. Cretaceous Res 30:1041–1061

Lockley MG, Huh M, Kim BS (2012b) *Ornithopodichnus* and pes-only sauropod trackways from the Hwasun tracksite Cretaceous of Korea. Ichnos 19:93–100

Lockley MG, Huh M, Gwak S-G, Hwang KG, Paik IS (2012c) Multiple tracksites with parallel trackways from the Cretaceous of the Yeosu City Area Korea: implications for gregarious behavior in Ornithopod and Sauropod dinosaurs. Ichnos 19:105–114

Lockley MG, Li J, Matsukawa M, Li R (2012d) A new avian ichnotaxon from the Cretaceous of Nei Mongol, China. Cretaceous Res 34:84–93

Lockley MG, McCrea RT, Buckley LG, Deock Lim J, Matthews NA, Breithaupt BH, Houck KJ, Gierliński GD, Surmik D, Soo Kim K, Xing L, Yong Kong D, Cart K, Martin J, Hadden G (2016) Theropod courtship: large scale physical evidence of display arenas and avian-like scrape ceremony behaviour by Cretaceous dinosaurs. Sci Rep 6:18952

Logue TJ (1994) Alcova, Wyoming tracks of *Pteraichnus saltwashensis* made by pterosaurs. Geol Soc Am Abstr Prog South Central Region 26:10

Lucas SG, Heckert AB (2011) Late Triassic aetosaurs as the trackmaker of the tetrapod footprint ichnotaxon *Brachychirotherium*. Ichnos 18:197–208

Lucas SG, Tanner LH (2007) The nonmarine Triassic-Jurassic bounday in the Newark Supergroup of eastern North America. Earth-Sci Rev 84:1–20

Lucas SG, Klein H, Lockley MG, Spielmann JA, Gierliński GD, Hunt AP, Tanner LH (2006) Triassic–Jurassic stratigraphic distribution of the theropod footprint ichnogenus Eubrontes. In: Harris JD et al (eds) The Triassic–Jurassic terrestrial transition. New Mexico Mus Nat Hist Sci Bull 37:86–93

Lull RS (1904) Fossil footprints of the Jura-Trias of North America. Mem Boston Soc Nat Hist 5:461–557

Mallison HJ (2011) Fast moving dinosaurs: why our basic tenet is wrong. Vert Paleontol 31:S150

Manning PL (2004) A new approach to the analysis and interpretation of tracks: examples form the dinosaurian. In: McIlroy D (ed) The application of ichnology to palaeoenvironmental and stratigraphic analysis. Geol Soc Spec Publ 228:93–123

Mannion PD, Upchurch P (2010) A quantitative analysis of environmental associations in sauropod dinosaurs. Paleobiology 36:253–282

Marsicano CA, Barredo SP (2004) A Triassic tetrapod footprint assemblage from southern South America: palaeobiogeographical and evolutionary implications. Palaeogeogr Palaeoclimatol Palaeoecol 203:313–335

Marsicano CA, Arcucci AB, Mancuso AC, Caselli AT (2004) Middle Triassic tetrapod footprints of southern South America. Ameghiniana 41:171–184

Marsicano CA, Domnanovich NS, Mancuso AC (2007) Dinosaur origins: evidence from the footprint record. Hist Biol 19:83–91

Marsicano CA, Irmis RB, Mancuso AC, Mundil R, Chemale F (2015) The precise temporal calibration of dinosaur origins. Proc Natl Acad Sci U S A 113:509–513

Martin AJ, Vickers-Rich P, Rich TH, Hall M (2014) Oldest known avian footprints from Australia: Eumeralla Formation (Albian), Dinosaur Cove, Victoria. Palaeontology 57:7–19

Martinez RN, Sereno PC, Alcober OA, Colombi CE, Renne PR, Montañez IP, Currie BS (2011) A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. Science 331:206–210

Marty D, Paratte G, Lovis C, Jacquemet M, Meyer CA (2010) Extraordinary sauropod trackways from the Late Jurassic Béchat Bovais tracksite (Canton Jura, NW Switzerland): implications for sauropod locomotor styles. Abstract volume 8th EAVP meeting, 2010. p 56

Mathews JC, Brusatte SL, Williams SA, Henderson MD (2009) The first *Triceratops* bonebed and its implications for gregarious behavior. J Vert Paleontol 29:286–290

Matsukawa M, Hamuro T, Mizukami T, Fujii S (1997) First trackway evidence of gregarious dinosaurs from the Lower Cretaceous Tetori Group of eastern Toyama prefecture, central Japan. Cretaceous Res 18:603–619

Matsukawa M, Matsui T, Lockley MG (2001) Trackway evidence of herd structure among ornithopod dinosaurs from the Cretaceous Dakota Group of Northeastern New Mexico, USA. Ichnos 8:197–206

Matsukawa M, Shibata K, Kukihara R, Koarai K, Lockley MG (2005) Review of Japanese dinosaur track localities: implications for ichnotaxonomy, paleogeography and stratigraphic correlation. Ichnos 12:201–222

Mazin JM, Hantzpergue P, Lafaurie G, Vignaud P (1995) Des pistes de ptérosaures dans le Tithonien de Crayssac (Quercy, France). C R Acad Sci Paris 321:417–424

Mazin J-M, Hantzpergue P, Bassoullet J-R, Lafaurie G, Vignaud P (1997) Le gisement de Crayssac (Tithonien inferieur, Quercy, Lot, France): decouverte de pistes de dinosaures en place et premier bilan ichnologique. C R Acad Sci Paris 325:733–739

Mazin J-M, Billon-Bruyat J-R, Roller P (2001) If they did it, they were able to do it! A computational reconstruction of pterodactyloid terrestrial locomotion from trackways. Strata Serie 1(11):60–63

Mazin J-M, Billon-Bruyat J-P, Hantzpergue P, Lafaurie G (2003) Ichnological evidence for quadrupedal locomotion in pterodactyloid pterosaurs: trackways from the Late Jurassic of Crayssac (southwestern France). In: Buffetaut E, Mazin J-M (eds) Evolution and palaeobiology of pterosaurs. Geol Soc Spec Publ 217:283–296

Mazin J-M, Billon-Bruyat J-P, Padian K (2009) First record of a pterosaur landing trackway. Proc R Soc B 276:3881–3886

McCrea RT (2000) Dinosaur footprints in the Lower Cretaceous (Albian) Gates Formation of Alberta, Canada: their use in palaeobiology and palaeoenvironmental interpretation. Paleontol Soc Korea Spec Publ 4:169–178

McCrea RT, Currie PJ (1998) A preliminary report on dinosaur tracksites in the Lower Cretaceous (Albian) Gates Formation near Grande Cache, Alberta. New Mexico Mus Nat Hist Sci Bull 14:155–162

McCrea RT, Buckley LG, Farlow JO, Lockley MG, Currie PJ, Matthews NA, Pemberton SG (2014) A "Terror of Tyrannosaurus": the first trackways of tyrannosaurids and evidence of gregariousness and pathology in tyrannosauridae. PLoS One 9:e103613

Meijide Calvo M (2001) Pterosaur trace in Oncala Berriasian (Soria, Spain). New ichnospecies: *Pteraichnus manueli*. Strata 11:72–74

Meijie Calvo M, Fuentes Vidarte C (2001) Huellas de pterosaurios en el Weald de Soria (Espana). Proceedings of the 1st International Symposium about paleontology of dinosaur and their environment. Salas de Los Infantes, Burgos, 21–25 September 1999

Melchor RN, Valais SD (2006) A review of Triassic tetrapod track assemblages from Argentina. Palaeontology 49:355–379

Meyer CA, Hunt AP (1999) The first pterosaur from the Late Jurassic of Switzerland: evidence for the largest Jurassic flying animal. Oryctos 2:111–116

Meyer CA, Marty D, Thüring B, Stecher R, Thüring S (2013) Dinosaurierspuren aus der Trias der Bergüner Stöcke (Parc Ela, Kanton Graubünden, SE-Schweiz). Mitt Nat Ges Basel 14:135–144

Mietto P (1987) *Parasynaptichnium gracilis* nov. ichnogen., nov. sp. (Reptilia: Archosauria Pseudosuchia) nell'Anisico inferiore di Recoaro (Prealpi Vicentine–Italia). Mem Sci Geol 39:37–47

Mietto P (1988) Piste di dinosauri nella Dolomia Principale (Triassico Superiore) del Monte Pelmetto (Cadore). Mem Soc Geol Ital 30(1985):307–310

Milàn J, Gierliński G (2004) A probable thyreophoran (Dinosauria, Ornithischia) footprint from the Upper Triassic of southern Sweden. Bull Geol Soc Denmark 51:71–75

Milàn J, Clemmensen LB, Bonde N (2004) Vertical sections through dinosaur tracks (Late Triassic lake deposits, East Greenland)—undertracks and other subsurface deformation structures revealed. Lethaia 37:285–296

Milàn J, Avanzini M, Clemmensen LB, García-Ramos JC, Piñuela L (2006) Theropod foot movement recorded from Late Triassic, Early Jurassic and Late Jurassic fossil footprints. In: Harris et al (eds) The Triassic-Jurassic Terrestrial Transition. New Mexico Mus Nat Hist Sci Bull 37:352–364

Milner ACR, Lockley MG, Kirkland JI (2006) A large collection of well-preserved theropod dinosaur swim tracks form the Lower Jurassic Moenave Formation, St. George, Utah. In: Harris JD et al (eds) The Triassic-Jurassic Terrestrial Transition. New Mexico Mus Nat Hist Sci Bull 37:315–328

Milner ACR, Harris JD, Lockley MG, Kirkland JI (2009) Bird-like anatomy, posture and behavior revealed by an Early Jurassic theropod dinosaur resting trace. PLoS One 4:e4591

Moratalla JJ, Hernán J (2009) Turtle and pterosaur tracks from the Los Cayos dinosaur tracksite, Cameros Basin (Cornago, La Rioja, Spain): tracking the Lower Cretaceous bio-diversity. Rev Esp Paleontol 24:59–77

Moratalla JJ, García-Mondejar J, Santos VF, Lockley MG, Sanz JL, Jimenez S (1995) Sauropod trackways from the Lower Cretaceous of Spain. Gaia 10:75–83

Moratalla JJ, Sanz JL, Jiménez S (1997) Información paleobiológica y paleoambiental inferida a partir de las icnitas de dinosaurios: problemas, límites y perspectivas. Rev Esp Paleontol 12:185–196

Myers TS, Fiorillo AR (2009) Evidence for gregarious behavior and age segregation in sauropod dinosaurs. Palaeogeogr Palaeoclimatol Palaeoecol 274:96–104

Nesbitt SJ (2011) The early evolution of Archosauria: relationships and the origin of major clades. Bull Am Mus Nat Hist 352:1–292

Nesbitt SJ, Irmis RB, Parker WG (2007) A critical re-evaluation of the Late Triassic dinosaur taxa of North America. J Syst Palaeontol 5:209–243

Nesbitt SJ, Smith ND, Irmis RB, Turner AH, Downs A, Norell MA (2009) A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. Science 326:1530–1532

Nesbitt SJ, Sidor CA, Irmis RB, Angielczyk KD, Smith RMH, Tsuji LA (2010) Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. Nature 464:95–98

Nesbitt SJ, Barret PM, Werning S, Sidor CA, Charig AJ (2013) The oldest dinosaur? A Middle Triassic dinosauriform from Tanzania. Biol Lett 9:20120949

Nicosia U, Loi M (2003) Triassic footprints from Lerici (La Spezia, Northern Italy). Ichnos 10:127–140

Niedźwiedzki G, Brusatte SL, Butler RJ (2013) Prorotodactylus and Rotodactylus tracks: an ichnological record of dinosauromorphs from the Early-Middle Triassic of Poland. In: Nesbitt SJ, Desojo JB, Irmis RB (eds) Phylogeny and palaeobiology of early archosaurs and their kin. Geol Soc Spec Publ 379:319–351

von Nopcsa F (1923) Die fossilen Reptilien. Fortschritte Geol Paleont 2:1–210

Novas FE (1992) Phylogenetic relationships of the basal dinosaurs, the herrerasauridae. Palaeontology 35:51–62

Olsen PE (1995) A new approach for recognizing track makers. Geol Soc Am Abstr Prog 27:22

Olsen PE, Huber P (1998) The oldest Late Triassic footprint assemblage from North America (Pekin Formation, Deep River basin, North Carolina, USA). Southeastern Geol 38:77–90

Olsen PE, Baird D (1986) The ichnogenus Atreipus and its significance for Triassic biostratigraphy. In: Padian K (ed) The beginning of the age of dinosaurs. Cambridge Univ Press, Cambridge

Olsen PE, Smith JB, McDonald NG (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, USA). J Vert Paleontol 18:586–601

Olsen PE, Kent DV, Sues H-D, Koeberl C, Huber H, Montanari A, Rainforth EC, Fowell SJ, Szajna MJ, Hartline BW (2002) Ascent of dinosaurs linked to an iridium anomaly at the Triassic-Jurassic boundary. Science 296:1305–1307

Ostrom JH (1972) Were some dinosaurs gregarious? Palaeogeogr Palaeoclimatol Palaeoecol 11:287–301

Padian K (1983) A functional analysis of flying and walking in pterosaurs. Paleobiology 9:218–239

Padian K (1984) The origin of pterosaurs. In: Reif W E, Westphal E (eds) Third symposium on Mesozoic terrestrial ecosystems and biota, Tübingen

Padian K (1985) The origin and aerodynamics of flight in extinct vertebrates. Palaeontology 28:413–433

Padian K (1987) The case of the bat-winged pterosaur, In: Czerkas SJ, Olsen EC, (eds) Dinosaurs past and present. Nat Hist Mus Los Angeles and Univ Washington Press 2:64–81

Padian K (1988) The flight of pterosaurs. Nat Hist 97:58–65

Padian K (1991) Pterosaurs: were they functional birds or functional bats? In: Rayner JMV, Wooton RJ (eds) Biomechanics in evolution. Seminar series of the Soc Experim Biol 36, Cambridge Univ Press, Cambridge

Padian K (2003) Pterosaur stance and gait and the interpretation of trackways. Ichnos 10:115–126

Padian K, Olsen PE (1984) The fossil trackway Pteraichnus: not pterosaurian, but crocodilian. J Paleontol 58:178–184

Padian K, Rayner JMV (1993) The wings of pterosaurs. Am J Sci 293A:91–166

Padian K, Li C, Pchelnikova J (2010) The trackmaker of *Apatopus*: early diversification of archosaur stance and gait. Palaeontology 53:175–189

Parrish JM (1987) The origin of crocodilian locomotion. Paleobiology 13:396–414

Pascual Arribas C, Sanz Pérez E (2000) Huellas de pterosaurios en el grupo Oncala (Soria, España). *Pteraichnus palaciei-saenzi*, nov. ichnosp. Estud Geol 56:73–100

Paul GS (1987) Pterodactyl habits—real and ratio controlled. Nature 328:481

Peabody FE (1948) Reptile and amphibian trackways from the Moenkopi Formation of Arizona and Utah. Univ Calif Pub Bull Dept Geol Sci 27:295–468

Peabody FE (1959) Trackways of living and fossil salamanders. Univ Calif Publ Zool 63:1–72

Peecook B, Sidor C, Nesbitt S, Angielczyk K (2011) New data on the archosaur fauna of the Middle Triassic (Anisian) Ntawere Formation of Zambia. J Vert Paleontol 31:1127–1137

Pennycuick CJ (1986) Mechanical constraints on the evolution of flight. In: Padian K (ed) The origin of birds and the evolution of flight. Mem Calif Acad Sci 8:83–98

Pérez-Lorente F (2003) Icnitas de dinosaurios del Cretácico en España. In: Pérez-Lorente F (coord) Dinosaurios y otros reptiles Mesozoicos en España, Cienc Tierra 26:161–214

Pienkowski G, Niedzwiedzki G (2005) Pterosaur tracks from the early Kimmeridgian intertidal deposits of Wierzbica, Poland. Geol Quart 49:339–346

Piñuela L, García-Ramos JC, Lires J (2002) Comportamiento gregario de ornitópodos en el Jurásico Superior de Asturias. In: Pérez-Lorente F (coord) Dinosaurios y otros reptiles mesozoicos de España, Resum, Univ La Rioja, 26–29 November 2002

Pittman JG, Gillette DD (1989) The Briar Site: a new sauropod dinosaur tracksite in Lower Cretaceous beds of Arkansas, USA. In: Lockley MG, Gillette DD (eds) Dinosaur tracks and traces. Cambridge Univ Press, Cambridge

Platt BF, Hasiotis ST (2008) A new system for describing and classifying tetrapod tail traces with implications for interpreting the dinosaur tail trace record. Palaios 23:3–13

Prince NK, Lockley MG (1989) The sedimentology of the Purgatoire tracksite region, Morrison Formation of South-eastern Colorado. In: Gillette DD, Lockley MG (eds) Dinosaur tracks and traces. Cambridge Univ Press, Cambridge

Riggs ES (1904) Structure and relationships of ophistocoelian dinosaurs. Part II. The Brachiosauridae. Field Columbian Mus Publ Geol 2:229–247

Roach BT, Brinkman DL (2007) A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs. Bull Peabody Mus Nat Hist 48:103–138

Rodríguez-de la Rosa R (2003) Pterosaur tracks from the lastest Campanian Cerro del Pueblo Formation of southeastern Coahuila, México. In: Buffetaut E, Mazin JM (eds) Evolution and paleobiology of pterosaurs. Geol Soc Spec Publ 217:275–282

Rogers RR (1990) Taphonomy of three dinosaur bone bed in the upper Cretaceous Two Medicine Formation of northwestern Montana. Palaios 5:394–413

Rogers RR, Eberth DA, Fiorillo AR (2007) Bonebeds. Genesis, analysis, and paleobiological significance. The Univ Chicago Press, Chicago

Rothschild BM, Tanke DH (2005) Theropod paleopathology. State-of-the-art review. In: Carpenter K (ed) The carnivorous dinosaurs. Indiana University Press, Bloomington

Rothschild BM, Tanke DH, Ford T (2001) Theropod stress fractures and tendon avulsions as a clue to activity. In: Tanke DH, Carpenter K (eds) Mesozoic vertebrate life. Indiana University Press, Bloomington

Russell DA, Belland P (1976) Running dinosaurs. Nature 264:486

Salgado L, Coria RA, Calvo JO (1997) Evolution of titanosaurid sauropods. I Phylogenetic analysis based on the postcranial evidence. Ameghiniana 34:3–32

Sánchez-Hernández B, Przewieslik AG, Benton MJ (2009) A reassessment of the *Pteraichnus* ichnospecies from the Early Cretaceous of Soria Province, Spain. J Vert Paleontol 29:487–497

Sarjeant WAS (1990) A name for the trace of an act: approaches to the nomenclature and classification of fossil vertebrate fossils. In: Carpenter K, Currie PJ (eds) Dinosaur systematics: perspectives and approaches. Cambridge Univ Press, Cambridge

Schumacher BA (2003) An addition to the Dinosaur Freeway Megatracksite, Dakota Group (Upper Cretaceous), Bent County, Colorado. Ichnos 10:255–262

Sereno PC (1999) The evolution of dinosaurs. Science 284:2137–2147

Sereno PC, Arcucci AB (1994) Dinosaur precursors from the Middle Triassic of Argentina: Lagerpeton chanarensis. J Vert Paleontol 13:385–399

Silva RC, Carvalho IS, Schwanke C (2007) Vertebrate dinoturbation from the Caturrita Formation (Late Triassic, Paraná Basin), Rio Grande do Sul State, Brazil. Gondwana Res 11:303–310

Smith JA, Sampson S, Loewen M, Santucci V (2002) Trackway evidence of possible gregarious behavior in large theropods from the Lower Jurassic Moenave Formation of Zion National Park. J Vert Paleontol 22(S3):108A–109A

von Soemmerring ST (1812) Über einen Ornithocephalus. Denks Akad Wissens München Math-Phys 3:89–158

von Soemmerring ST (1817) Uber einen Ornithocephalus brevirostris der Vorwelt. Denks Akad Wissens München Math-Phys 6:89–104

Soergel W (1925) Die Fährten der Chirotheria. Eine Paläobiologische Studie, Gustav Fischer, Jena

Sookias RB, Butler RJ, Benson RBJ (2012) Rise of dinosaurs reveals major body-size transitions are driven by passive processes of trait evolution. Proc R Soc B 279:2180–2187

Stokes WL (1957) Pterodactyl tracks from the Morrison formation. J Paleontol 31:952–954

Stokes WL (1978) Animal tracks in the Navajo-Nugget sandstone. Univ Wyoming Contrib Geol 16:103–107

Stokes WL, Madsen JH Jr (1979) Environmental significance of pterosaur tracks in the Navaro Sandstone (Jurassic) Grand County, Utah. Brigham Young Univ Geol Stud 26:21–26

Swennen C, Yu YT (2005) Food and feeding behavior of the black faced spoonbill. Waterbirds 28:19–27

Tanke DH, Rothschild BM (1997) Paleopathology. In: Currie PJ, Padian K (eds) Encyclopedia of dinosaurs. Academic, San Diego, CA

Thulborn RA (1981) Estimated speed of a gait dinosaur. Nature 292:272–252

Thulborn RA (1982) Speeds and gaits of dinosaurs. Palaeogeogr Palaeoclimatol Palaeoecol 38:227–256

Thulborn RA (1984) Preferred gaits of bipedal dinosaurs. Alcheringa 8:243–252

Thulborn T (1990) Dinosaur tracks. Chapman and Hall, London

Thulborn T (2000) Australia´s earliest theropods: footprint evidence in the Ipswich Coal Measures (Upper Triassic) of Queensland. Gaia 15:301–311

Thulborn T (2003) Comment on "Ascent of dinosaurs linked to an iridium anomaly at the Triassic-Jurassic boundary". Science 301:169

Thulborn T (2006) On the tracks of the earliest dinosaurs: implications for the hypothesis of dinosaurian monophyly. Alcheringa 30:273–311

Thulborn RA, Wade M (1979) Dinosaur stampede in the Cretaceous of Queensland. Lethaia 12:275–279

Thulborn RA, Wade M (1984) Dinosaur trackways in the Winton Formation (Mid-Cretaceous) of Queensland. Mem Queensland Mus 21:413–517

Tucker ME, Burchette TP (1977) Triassic dinosaur footprints from south Wales: their context and preservation. Palaeogeogr Palaeoclimatol Palaeoecol 22:195–208

Turner A, Nesbitt SJ (2013) Body size evolution during the Triassic archosauriform radiation. In: Nesbitt SJ, Desojo JB, Irmis RB (eds) Phylogeny and palaeobiology of early archosaurs and their kin. Geol Soc Spec Publ 379:573–597

Unwin DM (1986) Tracking the dinosaurs. Geol Today 2:168–169

Unwin DM (1987) Pterosaur locomotion. Joggers or waddlers? Nature 327:13–14

Unwin DM (1989) A predictive method of the identification of vertebrate ichnites and its application to pterosaur tracks. In: Gillette DD, Lockley MG (eds) Dinosaur tracks and traces. Cambridge Univ Press, Cambridge

Unwin DM (1997a) Locomotory roles of the hind limbs in pterosaurs. J Vert Paleontol 17:82A

Unwin DM (1997b) Pterosaur tracks and the terrestrial ability of pterosaurs. Lethaia 29:373–386

Unwin DM (2006) Pterosaurs from deep time. Pi Press, New York

Upchurch P, Barrett PM, Dodson P (2004) Sauropoda. In: Weishampel DB, Dodson P, Osmólska H (eds) The dinosauria, 2nd edn. Univ California Press, Berkeley

Varricchio DJ, Horner JR (1993) Hadrosaurid and lambeosaurid bone beds from the Upper Cretaceous Two Medicine Formation of Montana: taphonomic and biologic implications. Can J Earth Sci 31:997–1006

Viera LI, Torres JA (1992) Sobre "Dinosaurios coeluridos gregarios en el yacimiento de Valdevajes (La Rioja, España)". Nota de réplica y crítica. Rev Esp Paleontol 7:93–96

Vila B, Oms O, Marmi J, Galobart A (2008) Tracking Fumanya Footprints (Maastrichtian, Pyrenees): historical and ichnological overview. Oryctos 8:115–130

Voigt S, Niedźwiedzki G, Raczyński P, Mastalerz K, Ptaszyński T (2012) Early Permian tetrapod ichnofauna from the Intra-Sudetic Basin, SW Poland. Palaeogeogr Palaeoclimatol Palaeoecol 313–314:173–180

Weems RE (2006) The manus print of Kayentapus minor: its bearing on the biomechanics and ichnotaxonomy of early Mesozoic saurischian dinosaurs. In: Harris JD et al (eds) The Triassic–Jurassic terrestrial transition. Bull New Mexico Mus Nat Hist Sci 37:379–389

Weishampel DB, Dodson P, Olsmólska H (2004) The Dinosauria, 2nd edn. University of California Press, Berkeley and Los Angeles, 861 pp

Wellnhofer P (1978) Pterosauria, handbuch der paläoherpetologie. Gustav Fischer, Stuttgart

Wellnhofer P (1988) Terrestrial locomotion in pterosaurs. Hist Biol 1:3–16

Wellnhofer P (1991a) The illustrated encyclopedia of pterosaurs. Salamander Books, London

Wellnhofer P (1991b) Weitere Pterosaurierfunde aus der Santana-Formation (Apt.) der Chapada do Araripe, Brasilien. Palaeontographica A 215:43–101

Wellnhofer P, Vahldiek BW (1986) Ein Flugsaurier-Rest aus dem Posidonienshiefer (Unter-Toarcian) von Schandelah bei Braunschweig. Paläontol Z 60:329–340

Wilson JA (1995) The evolutionary history of sauropod dinosaurs. Philos Trans R Soc B 349:365–390

Wilson JA (2005) Integrating ichnofossil and body fossil records to estimate locomotor posture and spatiotemporal distribution of early sauropod dinosaurs: a stratocladistic approach. Paleobiology 31:400–423

Wilson JA, Carrano MT (1999) Titanosaurs and the origin of "wide gauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. Paleobiology 25:252–267

Wilson JA, Sereno PC (1998) Early evolution and higher-level phylogeny of sauropod dinosaurs. Soc Vert Paleontol Mem 5:1–68

Witton MP (2013) Pterosaurs. Princeton Univ Press, New Jersey

Wright JL (2005) Steps in understanding sauropod biology: the importance of sauropod tracks. In: Curry Rogers KA, Wilson JA (eds) The sauropods: evolution and paleobiology. Univ California Press, Berkeley

Wright JL, Unwin DM, Lockley MG, Rainforth EC (1997) Pterosaur tracks from the Purbeck Limestone Formation of Dorset, England. Proc Geol Assoc 108:39–48

Xing LD, Harris JD, Jia C-K, Luo Z-J, Wang S-N, Anf J-F (2011) Early Cretaceous bird-dominated and dinosaur footprint assemblages from the northwestern margin of the Junggar Basin, Xinjiang, China. Palaeoworld 20:308–321

Xing LD, Lockley MG, Zhang J-P, Milner ARC, Klein H, Li DQ, Persons WS IV, Ebi JF (2013a) A new Early Cretaceous dinosaur track assemblage and the first definite non-avian theropod swim trackway from China. Chin Sci Bull 58:2370–2378

Xing LD, Lockley MG, Klein H, Zhang J-P, He Q, Divay JD, Qi L-Q, Jia C-K (2013b) Dinosaur, bird and pterosaur footprints from the Lower Cretaceous of Wuerhe asphaltite area, Xinjiang, China, with notes on overlapping track relationships. Palaeoworld 22:42–51

Xing LD, Lockley MG, Piñuela L, Zhang J-P, Klein H, Li D, Wang F (2013c) Pterosaur trackways from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) of Qijiang, Southwest China. Palaeogeogr Palaeoclimatol Palaeoecol 392:177–185

Zhang JP, Li D, Li M, Lockley MG, Bai Z (2006) Diverse dinosaur-pterosaur-bird track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, Northwest China. Cretaceous Res 27:44–55

Zhao Q, Barrett PM, Eberth DA (2007) Social behaviour and mass mortality in the basal ceratopsian dinosaur Psittacosaurus (Early Cretaceous, People's Republic of China). Palaeontology 50:1023–1029

Zug GR (1974) Crocodilian galloping: an unique gait for reptiles. Copeia 2:550–552