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RESEARCH PAPER

What do their footprints tell us? Many questions and some answers about the life of non-avian dinosaurs

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Abstract

Dinosaur tracks are considerably common in the fossil record and were described from many areas in the world. They provide a live picture of dinosaur behaviour and offer valuable data about different aspects of the trackmaker paleobiology. The dinosaur ichnological record allows gain information about autopod anatomy, functional adaptations, stance and gaits with which dinosaurs moved. This information, which is often difficult to obtain from the body-fossil record alone, allows making inferences not only concerning the single individuals who produced the footprints, but also within an evolutionary context. Footprints provide also evidences about the abilities that dinosaurs had to swim, run or live with certain pathologies. They also allowed inferring how they move in herds or even made courtship rituals. The study of tracks also enables the reconstruction of paleocommunities including predator–prey interaction. On the other hand, footprints are useful paleoenvironmental indicators, informing about moisture content, bathymetry, paleocurrents, subaqueous substrates, zonations in lacustrine margins, etc. In addition, it has been proposed that dinosaur track assemblages can be related to certain facies (ichnofacies), in order to refine paleoenvironmental reconstructions. Dinosaur tracks can sometimes be in the shadow with respect to the skeletal record. However, the data obtained from the ichnological record complements and completes the knowledge we have about the life of dinosaurs, even showing previously unknown aspects. This work is an overview of the information we can obtain from the study of non-avian dinosaur footprints, trying to answer some questions about their life.

Keywords Dinosaur tracks · Paleoecology · Locomotion · Paleoenvironment · Mesozoic

¿Qué nos dicen sus huellas? Muchas preguntas y algunas respuestas sobre la vida de los dinosaurios no avianos

Resumen

Las huellas de dinosaurios son considerablemente comunes en el registro fósil y se han descrito en muchas zonas del mundo. Proporcionan una imagen dinámica del comportamiento de los dinosaurios y ofrecen datos valiosos sobre diferentes aspectos de su paleobiología. El registro icnológico permite obtener información sobre la anatomía de los autopodios, las adaptaciones funcionales, las posturas, y los modos de andar con los que se desplazaban los dinosaurios. Esta información,

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que a menudo es difícil de obtener solo del registro corpóreo, permite hacer inferencias sobre los individuos que produjeron las huellas tanto de forma aislada, como también dentro de un contexto evolutivo. Las huellas proporcionan evidencias sobre las habilidades que tenían los dinosaurios para nadar, correr o vivir con ciertas patologías. Es posible inferir cómo se movían en manadas o incluso si realizaban rituales de cortejo. También posibilitan la reconstrucción de paleocomunidades incluyendo la interacción depredador-presa. Por otro lado, las huellas son indicadores paleoambientales útiles, informando sobre el contenido de humedad, batimetría, paleocorrientes, sustratos subacuáticos, zonaciones en márgenes lacustres, etc. Además, se ha propuesto que las asociaciones de huellas de dinosaurios pueden relacionarse con ciertas facies (icnofacies), ayudando a refinar las reconstrucciones paleoambientales. Las huellas de dinosaurios a veces pueden estar eclipsadas por el registro óseo. Sin embargo, los datos obtenidos del registro icnológico pueden complementar y completar el conocimiento que tenemos sobre la vida de los dinosaurios, mostrando incluso aspectos previamente desconocidos. Este trabajo es una revisión de la información que podemos obtener del estudio de las huellas de los dinosaurios no avianos, intentando dar respuesta a algunas preguntas sobre su vida.

Palabras Clave Huellas de dinosaurio · Paleoecología · Locomoción · Paleoambiente · Mesozoico

1 Introduction

Footprints are ethologic structures made by autopodia of vertebrates modifying a substrate. Their study provides valuable information about different aspects of the paleobiology of their trackmakers, such as locomotion, autopod anatomy, and intra/inter-specific behavior (e.g. Citton et al., 2018; Farlow, 2018; García-Ortiz & Pérez-Lorente, 2014). The in situ nature of footprints makes tracks reliable indicators of biodiversity in space and time, once confidently achieved producer identification, since each footprint witnesses an animal who lived, at least temporarily, in a particular area and in a determinate time interval. For all these reasons, ichnological studies contribute to the reconstruction of paleocommunities, help to infer paleoecological aspects and provide information about the fauna that inhabited certain paleoenvironments (e.g. Castanera et al., 2014; Díaz-Martínez et al., 2022; Falkingham, 2014; Melchor, 2015).

Dinosauria is a clade of archosaurs that originated in the Late Triassic, about 230 My ago (Langer et al., 2010), and became extinct (except avian dinosaurs) at the end of the Cretaceous period (Brusatte et al., 2015). During their evolutionary history dinosaurs occupied a plethora of environments, reaching a cosmopolitan distribution from low latitudes to the polar circle (Rich et al., 2002; Russell & Paesler, 2003; Woodward et al., 2011). The clade is composed of two major groups: Ornithischia and Saurischia (e.g. Weishampel et al., 2007; Langer et al., 2010; Langer et al., 2017 but also see Baron et al., 2017 for another proposal). Ornithischia includes ankylosaurs (armored herbivorous quadrupeds), stegosaurs (plated herbivorous mainly quadrupeds), ceratopsians (bipedal or quadrupedal herbivores with developed facial horns and frills extending over the neck), pachycephalosaurians (bipedal herbivores with thick skulls), and ornithopods (bipedal or quadrupedal herbivores including "duck-bills"). Saurischia contains theropods (mostly bipedal carnivores and birds), and sauropodomorphs (mostly large herbivorous quadrupeds with long necks). Dinosaur footprints for the mentioned groups (Fig. 1) have been found in diverse terrestrial and transitional environments, such as fluvial, lacustrine, alluvial, volcanic, aeolian, or coastal (e.g. Cónsole-Gonella et al., 2017, 2021; de Souza Carvalho et al., 2013; Díaz-Martínez et al., 2015a, 2017; Houck & Lockley, 2006; Milàn & Loope, 2007; Nadon, 1993; Paik et al., 2010).

Discovering a dinosaur footprint often sparks numerous questions upon first inspection. Some of these inquiries may include: how did the footprints look like? who left these footprints? how was the anatomy of their autopods? was the dinosaur walking bipedally or quadrupedally? how fast were dinosaurs? could dinosaurs swim? did dinosaurs sustain injured? what was their mating behavior like? were dinosaurs social animals? how did the dinosaurs hunt? where did the dinosaurs live? With this manuscript, we would like to show that footprints provide valuable information about the life of dinosaurs that is often unknown from the study of bones and we try to answer some of the raised questions with known examples from the literature and the studied areas where the authors have worked. The aim is to try to answer the question in the title and provide some clues about what the footprints can tell us.

2 Material and methods

Institutional Abbreviations

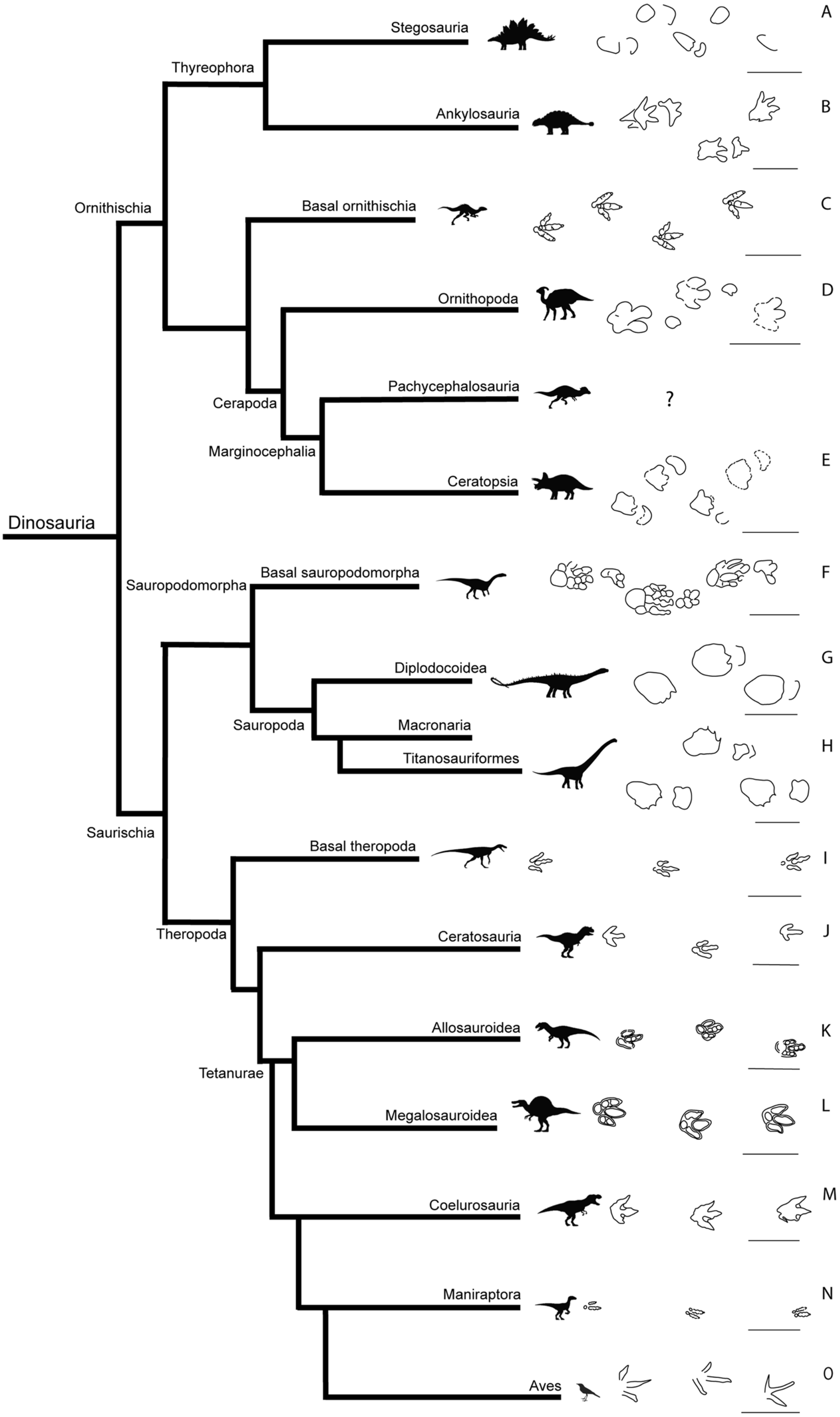
MNS Museo Numantino de Soria

MAP Museo Aragonés de Paleontología

This work is a bibliographical review of dinosaur ichnological data in order to try to answer several questions about the life and behaviour of the different groups of dinosaurs.

Taking into account the field experience of the authors, particular examples in which they are involved are selected

Fig. 1 Simplified cladogram of the Dinosauria (after https://opengeology.org) showing partial trackways of footprints related to the aforementioned clades (attributions are putative in some cases). Trackways are redrawn from: A, *Deltapodus ibericus* (Cobos et al., 2010); B, *Tetrapodosaurus borealis* (McCrea et al., 2001); C, *Anomoepus scambus* (Olsen & Rainforth, 2003); D, *Hadrosauropodus leonardii* (Currie, 1983; classification after Díaz-Martínez et al., 2015c); E, *Ceratopsipes goldenensis* (Lockley and Hunt, 1994); F, *Otozoum* isp. (Masrour and Pérez-Lorente, 2014); G, *Parabrontopodus mcintoshi* (Lockley et al., 1994); H, *Brontopodus birdi* (Farlow et al., 1989); I, *Grallator* isp. (Lockley et al., 2014); J, *aff. Asianopodus* isp. (Heredia et al., 2020); K, *Megalosauripus transjuranicus* (Razzolini et al., 2017); L, *Jurabrontes curtedulensis* (Marty et al., 2018); M, *Bellatoripes fredlundi* (McCrea et al., 2014); N, *Dromaeosauripus hamanensis* (Kim et al., 2008); and O, *Koreanaornis* isp. (Lockley et al., 2010). Scale bar: all the scales are 1 m except: B, F, I and M 50 cm; C and I 25 cm; and N 5 cm



in order to illustrate the review. Thus, representative cases are provided in the figures and are either taken from the literature (redrawn or modified) cited accordingly. Pictures from specific material are also figured. Some dinosaur tracks that will be discussed in subsequent sections are still in the field, or stored in the aforementioned institutions. The tracks shown in the examples come from tracksites (named in the sequence figured in the text) located in the Maestrazgo basin (Teruel Province) and eastern Cameros basin (La Rioja and Soria provinces). These tracksites are: Aliaga-Miravete megatracksite (Camarillas Fm., Barremian, Navarrete et al., 2014); Río Alcalá tracksite (Camarillas Fm., Barremian, Cobos et al., 2016); Las Cuestas I tracksite (Huérteles Fm., Berriasian, Castanera et al., 2012; Pascual-Arribas et al., 2008); Las Villasecas (Huérteles Fm., Berriasian, Barco et al., 2005; Castanera et al., 2015); Valdehijuelos tracksite (Huérteles Fm., Berriasian, Pascual-Arribas and Hernández-Medrano, 2011; Castanera et al., 2015); Barranco de La Canal (Enciso Gr., Barremian-Aptian, Pérez-Lorente, 2003; Razzolini et al., 2016); La Torre 6B tracksite (Enciso Gr., Barremian-Aptian, Navarro-Lorbés et al., 2021); La Virgen del Campo 4 trackiste (Enciso Gr., Barremian-Aptian, Ezquerra et al., 2007); La Laguna tracksite (Urbion Gr., Barremian-Aptian, Navarro-Lorbés et al., 2023); Las Cerradicas tracksite (Villar del Arzobispo Fm/Cedrillas Fm, Tithonian, Castanera et al., 2011, 2013a, 2013b; Aurell et al., 2019; Campos-Soto et al., 2017); Fuentesalvo tracksite (Huérteles Fm., Berriasian, Castanera et al., 2013b); and Soto 2 tracksite (Oncala Gr., Berriasian, Pérez-Lorente, 2015).

3 Tracks and trackmakers

3.1 Track morphologies. What did the footprints look like?

The majority of bipedal dinosaurs (mainly theropods and some groups of ornithischians) impressed tridactyl footprints. Theropod pes morphology (Farlow et al., 2013) first appears in the ichnological record in the Middle Triassic (Brusatte et al., 2011), some Mya before the earliest theropods. Nevertheless, according to Thulborn (2006), the basal theropods (*Herrerasaurus*) present a particular feet configuration (mesaxonic or weakly ectaxonic, and the hallux might have had a minor supportive role alongside digit II) that allows imprinting both dinosauroid (tridactyl, mesaxonic) and chiroteroiid (tetradactyl, entaxonic) footprints. We have not found in the literature tracks assigned to basal theropods, although almost all the Late Triassic-Early Jurassic theropod tracks have been related with the same ichnotaxa (e.g. *Grallator-Eubrontes* plexus) and traditionally assigned to ceratosaurs, basal tetanurines and carnosaurs (Lockley, 2009; Lucas et al., 2006). Tracks from the *Grallator-Eubrontes* plexus have been also reported from Upper Jurassic and Cretaceous units from different areas (e.g. Castanera et al., 2015, 2016a, 2018; Xing et al., 2021), suggesting that main morphological features in pes anatomy persisted in the geological record among different theropod clades. Within the main theropod track shape, some footprints have been potentially related to ceratosaurs, megalosauroids, allosauroids, coelurosaurs and maniraptorans (Belvedere et al., 2019; Cobos et al., 2014; Fiorillo et al., 2018; Heredia et al., 2020; Kim et al., 2008, 2012; Lockley et al., 2016; Marty et al., 2018; McCrea et al., 2015; Rauhut et al., 2018; Razzolini et al., 2017) based on phenetic and coincidence correlations (see below). Some of the ichnological features used to distinguish among these ichnotypes are footprint and digit proportions, mesaxony and metatarso-phalangeal pad impressions.

Theropod tracks and mainly small and medium-sized ornithischian/ornithopod tracks show morphological similarities, that hinder in some cases a reliable discrimination between theropod and ornithopod tracks, and the subsequent trackmaker identification (Lockley et al., 2009; Castanera et al., 2013a; Lallensack et al., 2020, 2022; see the "ornithotheropod" or "theroornithopod" concept in Díaz-Martínez, 2011). Lockley (2009) stated that a possible cause of such similarities, assuming convergent evolution of foot anatomy in both clades, is due to the use of the same type of locomotion. For instance, small ornithischians tracks (basal ornithischian dinosaurs) are tridactyl to tetradactyl, have elongated digit impressions with several pad imprints, quite blunt claw traces, and a centered metatarso-phalangeal pad impression, and they are sometimes associated with manus tracks (Gierliński, 1991; Avanzini et al., 2001; Díaz-Martínez et al., 2017).

Small to medium-sized ornithopod tracks (possibly produced by dryosaurids or basal ankylopollexian ornithopods) show similarities to basal ornithischian footprints (e.g. *Anomoepus*, Fig. 1C). The pes tracks are tridactyl, quite gracile and apparently have only one digital pad impression in each digit being a few examples of those that show constrictions of individual pads in each digit (an exception is *Wintonopus*, which is small-sized and have broad digit impressions, see Romilio et al., 2013). Manus tracks, when impressed, result in small and rounded/oval morphologies (e.g. Alcalá et al., 2012; Castanera et al., 2013a, 2013b, 2020; Lockley et al., 1998). It is interesting to highlight that the conservative anatomy of some autopodia enhances problems with the identification between several theropod and small to medium-sized basal ornithischian/ornithopod tracks since almost the beginning of the dinosaur record through the Mesozoic.

On the contrary, large ornithopod tracks (ankylopollexian ornithopods) are often much easier to identify (Fig. 1D). The tracks are tridactyl with a large and broad pad impression in each digit, a centered rounded to bilobed metatarsophalangeal pad impression and blunt claw traces (Castanera et al., 2022; Díaz-Martínez et al., 2015b; Lockley et al., 2014). Sometimes, manus tracks are also preserved (Moratalla et al., 1992; Castanera et al., 2013b; García-Cobeña et al., 2023). Other groups of ornithischian dinosaurs such as pachycephalosaurs were bipedal as well (Maidment & Barrett, 2012) and would impress a footprint similar to theropod—small ornithischian/ornithopod, but up to today, no pachycephalosaur footprints have been identified (Díaz-Martínez et al., 2009).

Quadrupedal dinosaurs (stegosaurs, ankylosaurs, ceratopsians and sauropods; Fig. 1) left tridactyl, tetradactyl to pentadactyl pes tracks (depending on the group but also on the manus or pes impressions). The identification of these groups can be problematic when digit impressions are not preserved and the tracks result just a large oval impression, so the trackmaker can be confused (e.g. Cobos et al., 2010). This is even more problematic for the manus prints since some groups (e.g. sauropods and stegosaurs) may show a similar kidney-shaped morphology (see Cobos et al., 2010; Castanera et al., 2016b; Torcida Fernández-Baldor et al., 2021). Thyreophorans (stegosaurs and ankylosaurs, Fig. 1A, B) present tridactyl or tetradactyl pes and manus tracks that vary from kidney-shaped in stegosaurs to star-shaped in ankylosaurs (Cobos et al., 2010; McCrea et al., 2001; Xing et al., 2013). Ceratopsian tracks, which are very scarce in the ichnological record, are characterized by tetradactyl pes and manus imprints (Lockley & Hunt, 1994). Finally, sauropod tracks present a variability of shapes in both manus and pes. Even some researchers distinguish tracks and trackways of different sauropod trackmakers (see Farlow et al., 1989; Farlow, 1992; Lockley et al., 1994; Wright, 2005). The Iberian Peninsula is an excellent example (Castanera et al., 2016b; Torcida Fernández-Baldor et al., 2021) to see how sauropod track morphologies evolved from the Middle Jurassic to the Late Cretaceous showing manus tracks that vary from speech-bubble shape (Middle Jurassic) to kidney-shaped with/without pollex impressions (Jurassic-Cretaceous transition) and horseshoe-shaped (Early Cretaceous onwards), and pes tracks that generally are sub-triangular showing substantial differences in the number (three to four) and orientation of the claw impressions (anterior to antero-laterally directed).

3.2 Trackmaker identity. Who left these footprints?

As seen in the previous section, generally when talking about dinosaur track types it is inherent to investigate their possible trackmakers (Fig. 1). Commonly, the attribution of a track to a putative producer reaches different level of resolution. In many contributions dealing with dinosaur ichnology, it is common to find a section where the systematic affinity of the trackmaker is discussed. This approach has been developed since the beginnings of vertebrate paleoichnology (e.g. Beckles, 1862; Hitchcock, 1836) and continues to be the focus of research today (see Farlow et al., 2013; McCrea et al., 2014; Razzolini et al., 2016), representing one of the more complex questions to be answered. According to Carrano and Wilson (2001), three types of footprint-trackmaker correlations can be carried out: phenetic, coincidence, and synapomorphy-based. The phenetic correlation is based on a direct comparison of the footprints with the shape of known dinosaur autopods. This technique was the first to be used, and is still in use today. In the figures of many works the autopod bones are superimposed to the footprints to show their apparent match (e.g. Beckles, 1862; Hitchcock, 1836; Lull, 1915, 1953; Niedźwiedzki et al., 2012). Currently, this type of correlation is also used based on statistical methods. Several works have been published in which an attempt is made to identify possible trackmakers by searching for homologous points between feet and footprints (Antonelli et al., 2023; Farlow, 2001; Farlow & Chapman, 1997; Farlow & Lockley, 1993; Farlow et al., 2013; Romano & Citton, 2017).

The coincidence correlation is mainly based on using the geochronological and geographic data of the footprints, to match them with the dinosaurs found in the same facies and in nearby deposits. For instance, it is common to associate the giant theropod footprints from the Maastrichtian of North America with tyrannosaurid dinosaurs (Lockley & Hunt, 1994; McCrea et al., 2014) because they are the only group of large theropod dinosaurs in that location at that age. Similarly, giant and robust tracks from the Late Jurassic of Europe only fit with megalosaurs as candidate trackmakers (e.g. Belvedere et al., 2019; Cobos et al., 2014; Rauhut et al., 2018). The coincidence correlation is a method that is still widely used today (e.g. Lockley et al., 2011; Fiorillo et al., 2018), and it is especially considered useful in the Triassic because dinosaur clades were less diversified (Lockley & Hunt, 1994).

Finally, the synapomorphy-based correlation uses the derived characters shared between taxa (synapomorphic) observable in the tracks as assignment criteria. It is a rarely used technique due to the difficulty of analyzing feet and footprints together, although it is believed that it may be the most useful in the study of associations between footprints and trackmakers (e.g. Brusatte et al., 2011; Carrano & Wilson, 2001; Díaz-Martínez, 2013; Olsen, 1995; Wright, 2005). Carrano and Wilson (2001) proposed a useful table that relates the osteological feature, the potential ichnological feature and the preservation. For instance, titanosauriforms have “Manual digit I ungual small or absent”, which will be represented in the footprint as "Lack of manual ungual print", and the preservation of this character would be "moderate". This can be seen in several examples of manus sauropod footprints of the Iberian Peninsula that have acquired a horseshoe-shaped without any evidence of this manual claw (Castanera et al., 2016b).

Ideally, to carry out a proper assignment the three types of correlation should work. For instance, sauropod dinosaurs from the end of the Cretaceous are associated with Sauropoda due to their overall shape (phenetic correlation), and to titanosaur dinosaurs since it is the only clade of sauropods present in that age (coincidence correlation) but they also show a synapomorphy-based correlation such as a wide-gauge trackway type and the absence of pollex impression in the manus prints (Castanera et al., 2016b; Vila et al., 2013; Wright, 2005).

Another approach, rooted in the 'reciprocal illumination' discussed by Carrano and Wilson (2001), considers the synapomorphy-based correlation in the light of general track morphology, locomotion and autopod osteology. This approach, which has been proposed based on Permian and Triassic synapsid and therapsid tracks (Citton et al., 2018; Romano et al., 2016; Sacchi et al., 2014) and is potentially unencumbered from the body-fossil record (Citton et al., 2019), founds support in the diachronic conception of the process leading to footprint formation, as repeatedly stated by different authors based on different perspectives (i.e. recognition of different phases during locomotion cycle; e.g. Avanzini, 1998; Baird, 1980; Gatesy, 2003; Gatesy et al., 1999; Thulborn, 2013; Thulborn & Wade, 1989). Diachrony of footprint formation, in this case, concerns the recognition of timing in which different autopodial elements contact the substrate, i.e. the pathway of loading, transfer and unloading of body mass to the ground (i.e. 'axony' sensu Romano et al., 2020). It can indirectly inform, when coupled with resultant three-dimensional morphology, on those ichnological characters mirroring certain osteological traits unambiguously pointing to specific anatomical patterns, as stressed by Romano et al. (2016). Testing such an approach on dinosaur ichnology, in particular for those clades that are characterised by a strong convergence of autopod anatomy (e.g. theropods, Farlow et al., 2013), constitutes an intriguing challenge also considering previous efforts in classifying dinosaur tracks based on a phylogenetic standpoint (Díaz-Martínez, 2013; Sacchi, 2005).

Nevertheless, the only way to be certain that some tracks have been left by a producer is to find a trackway with the trackmaker dead at the end. These types of traces, called *mortichnia* (see Seilacher, 2007), are rare in the fossil record, and have not been described for dinosaur traces. Suggestively, Niedźwiedzki et al. (2012) showed the finding of a *Protoceratops* skeleton that had an associated footprint, which anatomically could belong to a pes of this species. As the authors pointed out "*possibly the first find of a dinosaur track in close association with an articulated skeleton*".

3.3 Autopod soft anatomy. What was the autopod like?

Dinosaurs touch the ground with the soft elements (i.e. skin, corneous sheath) of the autopodial plantar surface. So, footprints can preserve information about the soft tissues of the podotheca, that is, the structure of scales covering the foot in extant birds and also present in some non-avian dinosaurs (Cuesta et al., 2015), such as skin impressions, pad imprints or claw traces. Dinosaur skin impressions have been discovered since the origin of dinosaur research (see Czerkas, 1994). Since then, skin impressions (Fig. 2) have been described in footprints of several groups of dinosaurs including sauropods (Czerkas, 1994; Navarrete et al., 2014; Platt & Hasiotis, 2006; Romano & Whyte, 2012), theropods (e.g. Pascual-Arribas & Hernández-Medrano, 2011; Hendrickx et al., 2022 and references therein), ornithopods (Cobos et al., 2014; Currie et al., 1991; Lockley et al., 2003; McCrea et al., 2014) and ankylosaurs (McCrea et al., 2001, 2014) (no skin trace information has been found for ceratopsids). Generally, these skin impressions are a rounded to polygonal pattern produced by the scaly skin touching the substrate (Kim et al., 2010). It reveals the shape, size, and arrangement of skin papillae. It is common that they are preserved as convex hyporeliefs (natural cast), but there are also some examples as concave epirreliefs (natural impressions) (Currie et al., 1991; Kim et al., 2010, 2019; Paik et al., 2020). In dinosaurs, shape, size and disposition of skin papillae change throughout the body (Hendrickx et al., 2022; Pittman et al., 2022), including the autopods (Cuesta et al., 2015). Nevertheless, despite this heterogeneity in skin papillae impressions, patterns (mainly shape and size) have been identified for the main taxonomic groups (see Kim et al., 2010; Hendrickx et al., 2022). Beautiful examples of skin impressions have been described in stegosaur, ornithopod and sauropod tracks (Fig. 2A, B) in the Iberian Peninsula (García-Ramos et al., 2006; Navarrete et al., 2014; Cobos et al., 2016; Herrero-Gascón & Pérez-Lorente, 2017; Guillaume et al., 2022).

Another kind of skin trace is the longitudinal grooves preserved on the sides of the tracks (Fig. 2A, B). Those are pedal/manual integument traces produced when the autopod was moving into the substrate. In this regard, the study of the striations that record the autopod entry and recovery within the substrate can provide information about how the different groups of dinosaurs moved (Apesteguía et al., 2023; Cobos et al., 2016; Gatesy, 2001). Although this kind of structure lacks anatomical information is a valuable tool for

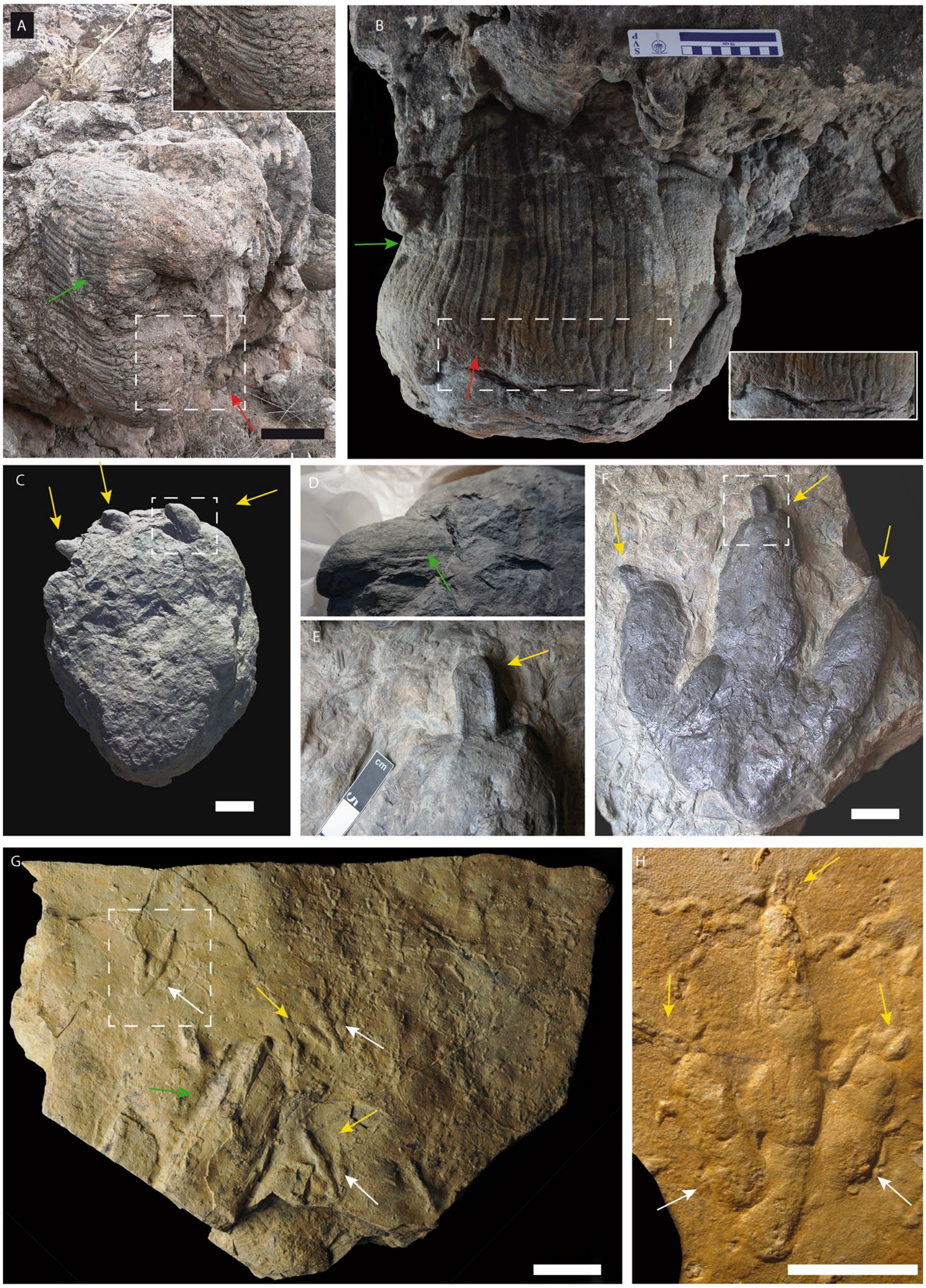


Fig. 2 Examples of dinosaur tracks showing evidence of skin impressions (red arrows), striae (green arrows), claw traces (yellow arrows) and phalangeal pad (white arrows) impressions. **A** Sauropod manus cast (Mi-3.1 m) from the Lower Cretaceous Aliaga-Miravete megatracksite (Teruel province) in lateral view (Navarrete et al., 2014). **B** Ornithopod pes cast (2AS-1-2, MAP-4555) from the Lower Cretaceous Río Alcalá tracksite (Teruel province) in posterior view (Cobos et al., 2016). **C** Sauropod pes track (MNS2006-75-1, corresponding to the track LCU-I-37-12p in Pascual-Arribas et al., 2008; Castanera et al., 2012) from the Lower Cretaceous Las Cuestas I tracksite (Soria province). **D** Detail picture of the claw impression and striations in digit I of the pes track in **C**. **E** Detail picture of the claw mark in digit III of the theropod track in **F**. **F** Giant theropod (*Iberosauripus* isp.) track (MNS96/28) from the Lower Cretaceous of Las Villasecas (Soria Province) (after Barco et al., 2005; Castanera et al., 2015). **G** Theropod tracks (MNS2005-111-4) from the Lower Cretaceous Valdehijuelos tracksite (Soria Province) (after Pascual-Arribas and Hernández-Medrano, 2011; Castanera et al., 2015). **H** Detail picture of one of the tiny theropod footprints (white square) in **G**. Scales: 10 cm (card in **B**); scale bars: 8 cm (**A**), 5 cm (**C**, **F**, **G**), 2 cm (**H**)

the reconstruction of limb movements and walking kinematics of dinosaurs, as has been seen in theropod, ornithopod, sauropod and stegosaurian tracks from the Upper Jurassic-Lower Cretaceous of the Iberian Peninsula (Milàn et al., 2005; García-Ramos et al., 2006; Mateus & Milàn, 2010; Avanzini et al., 2012; Cobos et al., 2016; Herrero-Gascón & Pérez-Lorente, 2017). These kinds of footprints that reveal the trajectory of the trackmaker's foot have allowed to define the concept of four-dimensional (4-D) tracks (Cobos et al., 2016).

Many dinosaur tracks preserve claw traces (Fig. 2) at the end of each digit impression and their morphology depends on each clade (Thulborn, 1990). For instance, theropods (Fig. 2E–H) and basal ornithischians/ornithopods have sharp pes claw traces, sauropods present mainly three to four sharp claw traces (Fig. 2C, D), whereas large ornithopods, thyreophorans and ceratopsians have blunt claw traces. These are produced by the corneous sheath that protects the ungual phalanges. These claw sheaths protrude from the tip of the ungual phalanx by 12–30% in modern birds (Manning et al., 2009; El-Gendy et al., 2012) and extinct avian theropods (Pu et al., 2013). In the unique specimen of the theropod *Concavenator* protrudes 41.27% (digit III) and 31.78% (digit IV) of the total claw length, although it is possible to explain the sheath overcoming based on taphonomic processes (Cuesta et al., 2015).

In well-preserved tracks of functional tridactyl dinosaurs, one to several pad impressions can be observed in the digit or metatarso-phalangeal areas (Fig. 2G–H). The phalangeal pads presumably help distribute the animal's weight on top of the sole (Ramsay & Henry, 2001). When the animal steps, footpads are compressed dorsoventrally and expanded mediolaterally and proximodistally (Ramsay & Henry, 2001). They deform and absorb mechanical shock, store and return elastic stress energy, and protect from local stress (Taylor et al., 2005). Hitchcock (1858) already indicated that the position of the pad impressions should correspond to the position of the autopod phalanges. The correlation between bones and pads has been made based on two relative positions: arthral, the midpoint of the pad is located at the joint between two phalanges; mesarthral, the midpoint of the pad is located in the middle of the phalanx (Thulborn, 1990). The carcharodontosaurid *Concavenator* (Early Cretaceous, Spain) preserved the impression of soft tissues, and the relationship between pads and phalanges can be seen, suggesting an arthral configuration for that structure (Cuesta et al., 2015). Recent research about the morphology and distribution of scales in non-avialan theropod dinosaurs has identified the same arthral pattern between pads and phalanges (Hendrickx et al., 2022).

Finally, the ichnological record can also preserve other anatomical information about dinosaurs although they are not part of the autopodium, such as traces of metapodium (e.g. Lallensack et al., 2022; Lockley et al., 2003; Romano & Citton, 2017), feathers (e.g. Gierliński 1997) or ischium (Gierliński et al., 2009; Milner et al., 2009; Citton et al., 2015).

3.4 Stance during the locomotion. Was the dinosaur walking bipedally or quadrupedally?

From an anatomical perspective, footprints provide valuable information about the stance during locomotion of the trackmakers. The arrangement of the footprints in trackways confirms some inferences made from osteology, such as sauropods and much of the large ornithischians (e.g. ceratopsians, thyreophorans) were quadrupedal, or that theropods and small ornithischians moved in a bipedal stance (Lockley, 1991; Thulborn, 1984, 1990). The footprint record also testifies facultative quadrupedalism (secondarily quadrupedal stance that evolved from obligately bipedal ancestors, sensu Grinham et al., 2019) as observed in trackways of some groups of dinosaurs (e.g. basal sauropodomorphs, iguanodonts, basal thyreophorans) (Le Loeuff et al., 1999; Avanzini et al., 2003; Castanera et al., 2013a; Díaz-Martínez et al., 2016) and concerning the capability of walking bipedally or quadrupedally.

Theropod dinosaurs seem to have always been bipedal across the different clades (see Fig. 1), although evidence of possible quadrupedal theropod trackways is reported in literature (Li et al., 2019). On the other hand, it is interesting to see how other saurischians like sauropodomorphs had changes in their stance throughout their evolutionary history. For instance, bipedal and quadrupedal sauropodomorph trackways were reported from the Late Triassic and Early Jurassic (Avanzini et al., 2003). The first sauropod trackways were fully quadrupedal and narrow-gauge (Gierliński, 1997; Avanzini et al., 2003; but see also Xing et al., 2016). Just a few million years later in the Middle Jurassic, there are already a co-existence of narrow and wide-gauge sauropod trackways (Day et al., 2002; Santos et al., 2009). Since then both trackway types have been described during the Late Jurassic and the rest of the Cretaceous although the former are considerably scarcer, especially during the last part of the Cretaceous as a consequence of the wide-gauge stance of titanosaurs (Mannion & Upchurch, 2010).

According to their trackways, basal ornithischians moved either bipedally and quadrupedally. Thyreophorans (stegosaurs and ankylosaurs) and ceratopsians would move quadrupedally (Thulborn, 1990). On the other hand, ornithopods would leave bipedal trackways but when they evolve to larger forms (iguanodontians) manus prints are found more frequently (e.g. Castanera et al., 2013a, 2013b; García-Cobeña et al., 2023).

4 Palaeoecology

Tracks and trackways, mainly their arrangement and orientation in the site, are usually used to discuss dinosaur paleoecology. In a broad sense, in this work, we have divided paleoecology (sensu Pianka et al., 2008) into the autoecology (or species ecology), which concerns the study of interactions between an individual, a population, or a species and its total environment; and synecology (or community ecology), which refers to the study of groups of organisms in relation to their environment.

4.1 Autoecology

4.1.1 Speed of displacement. How fast were dinosaurs?

Dinosaurs, as well as the rest of terrestrial vertebrates, could move using different gaits at different velocities. Evidence of running dinosaurs has been reported in several tracksites (e.g. Farlow, 2018; Navarro-Lorbés et al., 2021; Pérez-Lorente, 1996). Alexander (1976) hypothesised that animals run

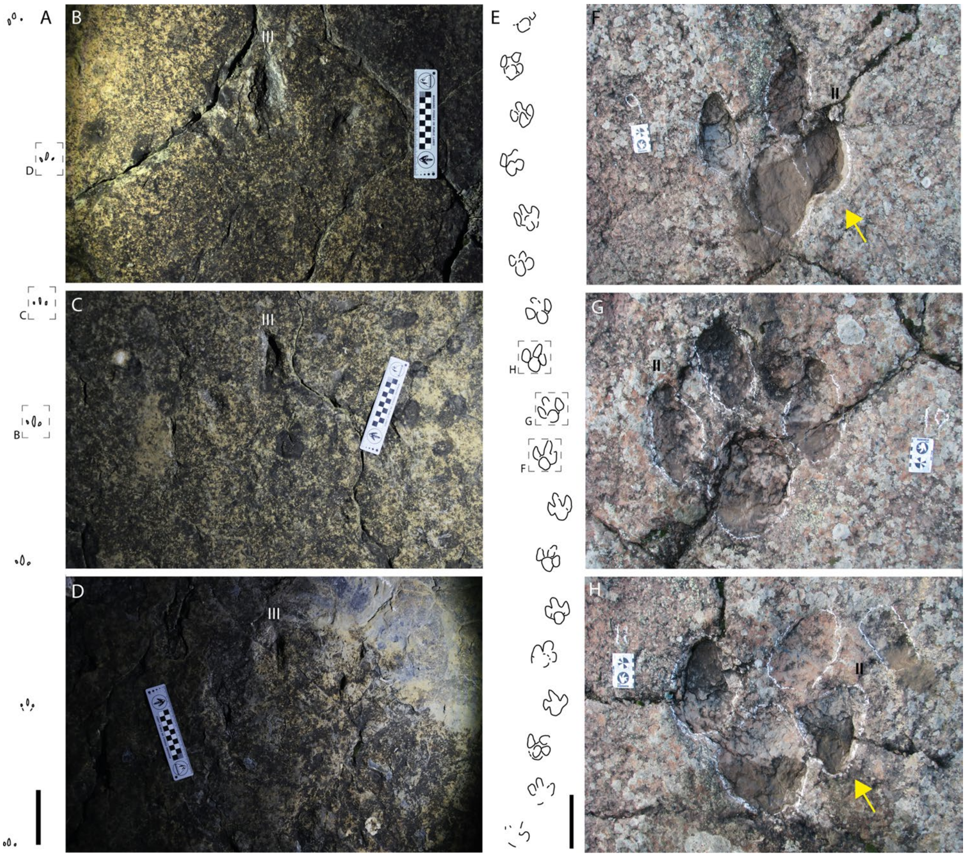


Fig. 3 Examples of running and paleopathological trackways. **A** Sketch of the Lower Cretaceous La Torre 6B trackway (after Navarro-Lorbés et al., 2021) (La Rioja, Spain). **B** Detail of the footprint 4 of the La Torre 6B trackway. **C** Detail of footprint 5 of the La Torre 6B trackway. **D** Detail of footprint 6 of the La Torre 6B trackway. **E** Partial sketch of the Lower Cretaceous Barranco de La Canal ornithopod trackway (after Pérez-Lorente, 2003) (La Rioja, Spain). **F** Detail of footprint 9 (left) of Barranco de La Canal trackway. **G** Detail of footprint 10 (right) of Barranco de La Canal trackway. **H** Detail of footprint 11 (left) of Barranco de La Canal trackway. Yellow arrow indicates the injured digit. Scale bar, 1 m

when the ratio between stride length (Sl) and the acetabular height (h) is greater than 2 ($Sl/h > 2$), and if this ratio is less than 2, the animal walks. Subsequently, Thuborn (1984) proposed the following division: $Sl < 1.9$ walk; $Sl > 2 < 2.9$ trot; and $Sl > 3$ run. In terms of absolute speed, some biomechanical formulas have been proposed, being Alexander's one $v = 0.25\ g^{0.5}\ SL^{1.67} h^{-1.17}$, with a subsequent modification by Ruiz and Torices (2013) $v\ (\pm 12\%) = 0.226\ g^{0.5}\ SL^{1.67} h^{-1.17}$, the most widely used. g, is the acceleration due to gravity, SL is the stride length and h, the hip height (generally h = 4FL, where FL = Footprint lenght, according to Alexander (1976)).

The highest values of running theropod dinosaurs are from the Lower Jurassic of San Juan County (Utah) (Lockley et al., 2021) and the Lower Cretaceous of F6 Ranch (Texas) (Farlow, 1981), with calculated speeds of 10.8–13.8 and 9.4–11.9 ms^{-1}. A recent study identified two running theropod trackways (Fig. 3A, D) among the fastest calculated for dinosaurs in the Lower Cretaceous of La Rioja (Spain) showing a speed between 6.5 and 10.3 ms^{-1} and between 8.8 and 12.4 ms^{-1} (Navarro-Lorbés et al., 2021). It is newsworthy that all of the previously mentioned trackways, which are the fastest in the world to date, have in common a similar size (similar footprint length), showing that the "best runners" were trackmakers with feet between 29 and 39 cm long (Farlow, 2018; Lockley et al., 2021; Navarro-Lorbés et al., 2021). Nevertheless, biomechanical models based on musculoskeletal reconstructions and the application of physical dynamics suggest higher values of maximum speed than those obtained from the ichnological record (see table 3 of Navarro-Lorbés et al., 2021). In this context, there are two scenarios, either the biomechanical calculations are overestimating the maximum speed of these animals, or no trace corresponding to an animal running at the limit of its possibilities has really been found yet.

4.1.2 Paleopathology. Did dinosaurs get injured?

Paleopathology studies ancient diseases and injuries in organisms through the examination of fossils (Rothschild & Tanke, 1992). When the pathologies affect the normal displacement of the organism, the dinosaur in this case can be observed as having abnormal gait or morphology (ichnopathology) (McCrea et al., 2015).

Originally, limping trackways or abnormal dinosaur gaits were generally related to foot injuries (Lockley et al., 1994). McCrea et al. (2015) pointed out that most limping trackways are irregular gaits of healthy animals, rather than pathologically influenced limping behavior, and is important to identify missing, broken or deformed digits

Fig. 4 Examples of swiming trackways. **A**, **B** Buoyancy tracks from the Lower Cretaceous Virgen del Campo 4 trackiste (La Rioja, Spain). **C** Punting track and **D** bouyancy track from the Lower Cretaceous La Laguna tracksite (La Rioja, Spain)

possibly associated with a trackway to propose an ichnopathology. The identification of trackways with ichnopathologies implies that the dinosaur survived the injury for at least some time even being able to be resistant in his recovery from his wounds (McCrea et al., 2015). A good example is the ornithopod trackway from La Canal (Lower Cretaceous, Spain) in which both a small limp and a notable difference in the digit II of the left foot (Fig. 3E–H) compared to the right one have been identified (Razzolini et al., 2016). The authors proposed an antalgic gait due to an injury or pathology on the left digit II.

4.1.3 Aquatic locomotion. Could dinosaurs swim?

Most animals can move through the water even if they do not have an aquatic habit. A true swimming behaviour could lack an ichnological correlate if it implies an animal floating with its entire body weight supported by the water (Thomson & Lovelace, 2014) and there is no interaction with the subaqueous substrate. Thus, the so-called “swim tracks” are produced when the animal is partially or completely submerged in water with the body buoying and generally the pes (sometimes other parts of the body) entered in contact with the subaqueous substrate (Farlow et al., 2018; Lee et al., 2019; Milner & Lockley, 2016). Swim tracks present a series of common features (sensu McAllister, 1989; McAllister & Kirby, 1998; Navarro & Moratalla, 2018), such as (1) reflecture of digits; (2) Z traces; (3) kick-off scours; (4) impressions of only digital tips; and (5) absence of a regular locomotion pattern.

Swim tracks have been related to several groups of Paleozoic, Mesozoic and Cenozoic vertebrates (Thomson & Droser, 2015). If it is considered the position of the trackmaker in the water sheet, the swim tracks can be divided into two groups. 1) Buoyancy tracks, produced when animals are floating on the water surface and touch the subaqueous substrate with their autopod tips (e.g. Milner & Lockley, 2016; Romilio et al., 2013). This kind of tracks has been identified in sauropod, ankylosaurs and stegosaurs (e.g. Farlow et al., 2018; Riguetti et al., 2021; Romano & Whyte, 2015), but are typical of bipedal dinosaurs (both theropod and ornithopod trackmakers) characterized by subparallel long slender grooves and usually classified as *Characichnos* (Ezquerra et al., 2007; Milner et al., 2006; Whyte & Romano, 2001). Good examples were found in the La Laguna and La Virgen del Campo tracksites (Ezquerra et al., 2007; Navarro-Lorbés et al., 2023) in the Lower Cretaceous Urbión and Enciso groups (La Rioja, Spain) (Fig. 4A, B, D). 2) Punting tracks are impressed in subaquatic locomotion (bottom walking) in which the animal pushes off the bed of a water body with its limbs to maintain forward motion (Martinez et al., 1998; Bennett et al., 2014). This kind of behaviour has been recently identified in Early Cretaceous bipedal dinosaurs from the Cameros Basin (Spain) (Navarro-Lorbés et al., 2023) (Fig. 4C), but is present in several extinct and extant tetrapods as crocodilians, turtles, undetermined Permian vertebrates and hippopotami (Gaillard et al., 2003; Avanzini et al., 2005; Bennett et al., 2014; Farlow et al., 2018; Lee et al., 2019; Mustoe, 2019).

4.1.4 Courtship. How was their mating?

Currently, many animals perform courtship ceremonies, usually the male, to find or get a partner with which to reproduce (see Lockley et al., 2016). This type of behavior is very difficult to infer from the fossil record (Senter et al., 2014; Zheng et al., 2017; Zong & Gong, 2018), and unexpected in the ichnological record. In this context, Lockley et al. (2016) evidenced numerous large scrapes, up to 2 m in diameter, at several Cretaceous sites at Colorado (USA). Based on the track morphology, the trackmakers would be large theropods, and most likely the traces would be associated with territorial activity in the breeding season, probably near nesting colonies. The authors concluded that such scrapes indicate stereotypical avian behavior hitherto unknown among Cretaceous theropods. Nonetheless, Moklestad and Lucas (2023) have provided a different interpretation suggesting that such behaviour would be related to digging activities with nesting purposes.

4.1.5 Gregarious behaviour. Were dinosaurs social?

Gregarious behaviour can be inferred in the fossil record in a variety of ways (see Currie & Eberth, 2010) and the footprint record is one of the most common sources of information to infer this kind of behaviour. Since the initial identifications (Bird, 1941, 1944; Ostrom, 1972) it has been described in different groups of dinosaurs such as theropods (e.g. Heredia et al., 2020 and references therein), ornithopods (Castanera et al., 2013a; Lockley & Matsukawa, 1999; Paik et al., 2020; Piñuela, 2016 and references therein), sauropods (e.g. Castanera et al., 2011, 2014; Myers & Fiorillo, 2009 and references therein) and possibly stegosaurids (Alcalá et al., 2014; Mampel et al., 2011). Parallel trackways with the same orientation, of the same morphotype with similar preservation, regular intertrackway spacing and similar speed values are the most significant features to proposed that a group of dinosaurs were walking together as a herd (Castanera et al., 2014; Lockley, 1991). A good example is the Upper Jurassic Las Cerradicas tracksite (Spain), in which parallel ornithopod and sauropod trackways were identified (Fig. 5A) (Castanera et al., 2013a). Several parallel ornithopod trackways were also found in the Lower Cretaceous Fuentesalvo tracksite (Spain) (Fig. 5B) (Barco et al., 2006; Castanera et al., 2013b). Dinosaur footprints accumulations (large amounts of footprints of the same morphotype in a concrete area) can also be interpreted as evidence of gregarious behaviour (García-Ortiz & Pérez-Lorente, 2014). A good example is the Soto 2 tracksite, where several small quadrupedal tracks are located randomly (Fig. 6).

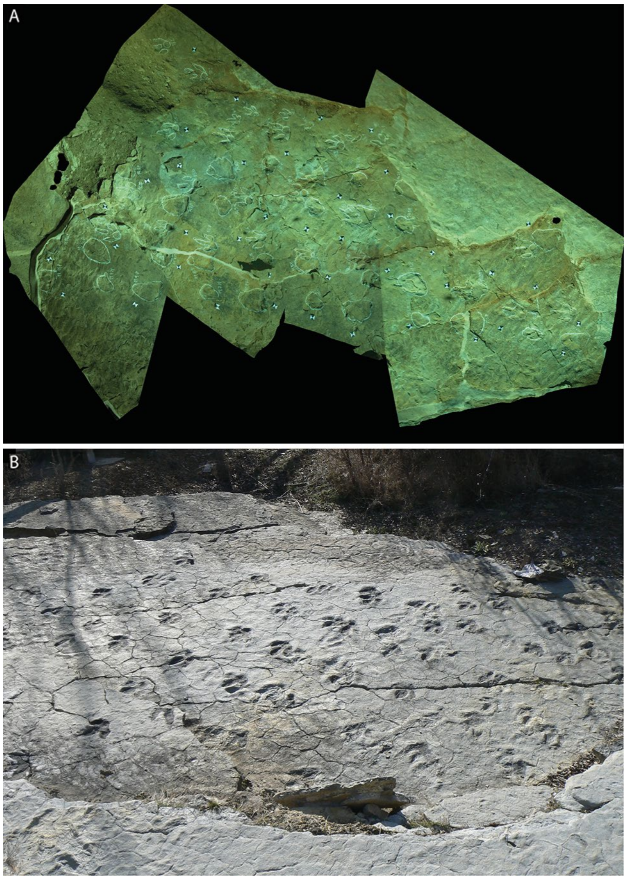


Fig. 5 Two well-known examples of gregarious behaviour among dinosaurs. **A** Upper Jurassic Las Cerradicas tracksite (Teruel province, Spain), sauropod trackways LCR13 and LCR14 and ornithopod trackways LCR15, LCR16 and LCR17 (after Castanera et al., 2011, 2013a). **B** Lower Cretaceous Fuentesalvo tracksite (Soria province, Spain). Picture of the ornithopod trackways in the main surface (after Castanera et al., 2013b)

Fig. 6 An accumulation of quadrupedal dinosaur tracks. **A** Lower Cretaceous Soto 2 tracksite (La Rioja province, Spain). See the hammer into the yellow square for scale

Some samples of dinosaur trackways can also show a preferred orientation showing apparent non-random orientation patterns and multiple parallel trackways whose arrangement is not a consequence of a gregarious behaviour but due to paleoenvironmental and/or paleogeographic constraints (Castanera et al., 2023; Lockley et al., 1986; Ostrom, 1972). There are several examples where this kind of preferred orientation has been related to a physical restriction such as a shoreline so the dinosaurs are walking either parallel or perpendicular to it (e.g. Lockley et al., 1986; Razzolini et al., 2016). Even in larger samples of dinosaur trackways paleogeography can play a significant role in their orientations such as in the case of the dinosaur trackways in the Cameros Basin (Moratalla & Hernán, 2010).

5 Synecology

5.1 Paleocommunities. How did dinosaurs live with each other?

Interspecific inferences are not common in the ichnological fossil record although is relatively common to find footprints of different animals in the same tracksite (e.g. Casanovas et al., 1993; Castanera et al., 2013a, 2023; Torcida Fernández Baldor et al., 2015). It is very difficult to determine whether all the footprints were impressed at the same tracking surface (see below), and thus infer if the trackmakers were at the same time in the same place (trackway synchrony). In this context, the tracksites that were formed in different preservation windows (sensu Díaz-Martínez et al., 2021), that is, the period of time in which a substrate remains mechanically modifiable and capable of being bioturbated (soft substrate) before the lithification, provide different synecological information. Tracksites with short preservational windows (e.g. ponds, flood plains) would show tracks that have been formed in a short period of time (coeval trackways), probably by animals that are related to that environment. However, tracksites with long preservational windows (e.g. lake shores, coastal lagoons) would represent footprints formed over a long time, and may represent the whole community that lives around them. It would be a similar concept to time averaging (sensu Behrensmeyer et al., 2000; see Marty et al., 2009) in taphonomic studies.

In this context, a suggestive image would be to be able to identify herds of different kinds of dinosaurs, as is currently the case with wildebeest and zebras in Africa. However, although there are sites in which the gregarious behavior of ornithopod and sauropod dinosaurs have been proposed in the same tracking surface (see Fig. 5A, the Late Jurassic Las Cerradicas tracksite; Castanera et al., 2011, 2013a; the Lower Cretaceous La Era del Peladillo tracksite, Spain; Pérez-Lorente, 2015) it has not been possible to demonstrate their synchronicity because they show some of the groups overstepping the tracks of the other.

5.2 Depredation. How did the dinosaurs hunt?

On the other hand, another type of synecological inference is the predator–prey relationship. In the Lower Cretaceous of the USA, a theropod trackway was found close to and in the same direction as a sauropod trackway and was interpreted as a possible hunting scene (Farlow et al., 2012; Thomas & Farlow, 1997). Thulborn and Wade (1989) suggested that a large hunting theropod dinosaur produced a stampede of small theropod and ornithopod dinosaurs (mid-Cretaceous, Australia) (see Romilio et al., 2013 and above in Sect. 4.1.3 for other interpretation). Paik et al. (2020) pointed out the possibility that a solitary theropod was stalking a herd of ornithopods (Upper Cretaceous, Korea). It has also been proposed that a dromaeosaurid-troodontid may have been left to hunt a mammal, burrowing using its hypertrophied claw (Simpson et al., 2010).

6 Track formation-preservation and paleoenvironment. Where did the dinosaurs live?

As suggested before, dinosaurs are a cosmopolitan clade that has been adapted to live in many environments. Dinosaur tracks have been found in fluvial, lacustrine, alluvial, volcanic, aeolian, or coastal settings (e.g. Nadon, 1993; Houck & Lockley, 2006; Milàn & Loope, 2007; Paik et al., 2010; de Souza Carvalho et al., 2013; Cónsole-Gonella et al., 2017, 2021; Castanera et al., 2022, 2023). Moreover, footprints themselves provide very valuable information on particular characteristics of the paleoenvironment such as moisture content, bathymetry, paleocurrents, subaqueous substrates, zonations in lacustrine margins and the presence of alkaline lakes (Melchor, 2015). But, in order to use vertebrate tracks as precise paleoenvironmental proxies are mandatory the identification and characterization of tracked surfaces (e.g. Castanera et al., 2023), subsurfaces, and types of footprint (e.g. true track, elite track, underprint, undertrack, natural cast, undertrack cast, overtrack, internal overtrack, deep track, and penetrative track) following concepts and definitions in Leonardi (1987), Lockley (1991), Allen (1997), Fornós et al. (2002), Milàn et al. (2004), Piñuela et al. (2012), Marty et al., (2009, 2016) and Gatesy and Falkingham (2020).

Fossil tetrapod tracks are originally impressed on palaeosurfaces, which are related to subaerial exposure or under a little sheet of water during track formation (Marty et al., 2016; Melchor, 2015). A further term, analogous to paleosurface, is tracking surface, which is the actual surface on which the producer trampled, i.e. the sediment/foot interface (Fornós et al., 2002). It is necessary to identify the tracking surface to be able to relate the producer with the environment in which that surface was formed and to determine what footprints were formed at the same time (ichnocoenosis or trace fossil assemblage). This is important because the same tracksite can bear tracks preserved and observed on the same stratigraphic horizon, but actually related to different, overlying, tracking surfaces (e.g. true tracks, underprints and undertracks).

Seilacher (1964) realized that some ichnocoenoses of marine invertebrate traces were found recurrently in specific facies with a long geological range, that is, the ichnofacies paradigm. In this way, by identifying a certain ichnocoenosis, it would be possible to infer the paleoenvironmental and bathymetric factors in which they were formed. The Seilacher's original concept has been later introduced in the field of terrestrial vertebrates by Lockley et al. (1994), who defined vertebrate ichnofacies as "recurrent ichnocoenoses that are associated with particular ancient environments (preserved as distinctive lithofacies)" (Lockley et al., 1994, p. 244), and further discussed by Lockley and Meyer (2000), Hunt and Lucas (2006, 2007) and Lockley (2007). In this context, the identification of recurrent vertebrate ichnocoenoses would be a useful proxy in order to determine a continental/transitional paleoenvironment. Indeed, the ichnocoenosis of *Caririchnium* from clastic marine shorelines (Lockley et al., 1994), or the ichnocoenosis of *Parabrontopodus* from lacustrine shorelines (Hunt & Lucas, 2007; Lockley et al., 1986) are part of the *Brontopodus* ichnofacies that represent coastal plain-marine shoreline environments and some lacustrine shorelines (Hunt & Lucas, 2016). Continental vertebrate ichnofacies present, however, various theoretical issues questioning its application (Santi & Nicosia, 2008). For instance, the criteria used for the recognition of invertebrate ichnofacies (e.g. water turbidity, water salinity, depositional rates, oxygenation, temperature) (MacEachern et al., 2012), are not the same as those applied to vertebrate ichnofacies because the factors controlling the distribution of vertebrate trace fossils are poorly known (Buatois & Mángano, 2011). For that, Melchor (2015) suggested that most of these proposed vertebrate ichnofacies are better considered as ichnocoenoses (Hunt & Lucas, 2016), because they represent biological communities with restricted temporal and geographical ranges (Melchor et al., 2006, 2012). Previous analyses about formational and preservational biases of dinosaur tracks in different palaeoenvironments are propaedeutic to terrestrial vertebrate ichnofacies application, playing a similar role to that biostratinomy plays in palaeoecological analyses. In this way, studies about biases in the dinosaur ichnological record are promising. They can likely suggest whether and which tracks can be 'ichnofacies marker', i.e. can be likely related to producers that are ecologically related to a specific substrate. In other words, the narrower the preservational windows, the more effective the ichnofacies marker will be.

7 Final remarks

Since the first discoveries of dinosaur remains, researchers and amateur palaeontologists interested in these animals have asked themselves many questions about them. For instance, Owen (1841) related dinosaurs to aquatic ecosystems. Indeed, sauropods had been restricted to inhabiting the water (aquatic or semiaquatic) due to their immense size and their particular anatomical features (see Romer, 1966; Coombs, 1975), and hadrosaurs were considered amphibious that fed in swampy pools or at their margins taking into account their cranial and appendicular anatomy (see Osborn, 1912; Romer, 1966).

Since the observations made by paleontologists based primarily on osteological descriptions, until recently with the use of new technologies, much has been learned about life of dinosaurs with respect to their locomotion, functional anatomy and ethology (e.g. Carrano, 1998; Coria, 1994; Farlow et al., 2000; Ostrom, 1972, 1994; Salgado & Bonaparte, 1991). Microscopical techniques have provided information about the color of the feathers and eggs (Wiemann et al., 2018; Zhang et al., 2010), growth patterns and osteohistology (e.g. Cerda et al., 2022; Chinsamy-Turan, 2019; Erickson, 2005), egg structure (e.g. Choi et al., 2022; Fernández et al., 2022) and paleopathologies (e.g. Cruzado-Caballero et al., 2021; Rothschild et al., 2020), among others. Three-dimensional reconstructions made by photogrammetry, laser scanner, or computed tomography allow to discuss the body mass estimation (e.g. Bates et al., 2012; Campione & Evans, 2020), the locomotion patterns (e.g. Bishop et al., 2021; Otero et al., 2019) or neuroanathomy (Cerroni & Paulina-Carabajal, 2019; Paulina-Carabajal et al., 2022). Even isotopic studies reveal valuable information about diet (Martin et al., 2022) and habitat (Goedert et al., 2016).

As we have shown in this text, the ichnological record greatly complements the body fossil record, helping to better understand diverse aspects of dinosaurs' life. Dinosaur footprints offer important clues about foot anatomy (e.g. size and relative proportions between digits, phalangeal counting, type of ungual phalanges, position of phalangeal pads), their stance and gaits, intra- and inter-specific interactions, and relationships of paleocommunities in relation to the palaeoenvironment that preserved their traces. The study of dinosaur tracks and traces also provides significant information about substrate conditions during and after trampling (e.g. moisture), paleoshoreline orientations, bathymetry, etc. Nevertheless, there are numerous challenges to be solved in the future. For instance, to use the dinosaur footprints within the ichnofacies studies, it would be necessary to deepen the ecological relationship of each clade of dinosaurs with their environment. In addition, there are still many questions that could be answered with the ichnological evidence on reproduction, initiation of flight, diving, maximum speeds, intraspecific social behavior, among others.

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