



Avian ichnofauna from Sierra de las Cabras tracksite (late Miocene, Jumilla, SE Spain)

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Abstract

The Sierra de las Cabras (Lat. 38° 28' 53"N, Lon. 1° 24' 52"W) is an exceptional ichnofossil site of late Miocene age, located in the Prebetic ranges near the town of Jumilla (Murcia Province, SE Spain). The site contains abundant vertebrate ichnofauna preserved in carbonate facies that were deposited in a semi-arid wetland system with shallow ponds and marshes. The ichnofauna includes diverse mammal footprints and trackways, which have been recently studied, as well as bird ones, which are the target of this paper. We report a total of 51 avian footprints spread over two of the three track-bearing stratigraphic surfaces of the site. The detailed study of these ichnites (footprints and trackways) allows their attribution to the ichnogenus *Fuscinapeda* (Sarjeant and Langston, Texas Memorial Museum Bulletin 36:1–86, 1994), as well as to infer diverse patterns of bird's behavior consistent with shallow water wetlands avifauna. Also, we discuss about the possible trackmakers, which should correspond to walking birds characterized by long legs, with no hallux or a raised one, which could probably belong to the Gruiformes order. The study confirms the presence of *Fuscinapeda* in the Iberian Peninsula and completes the characterization of the vertebrate ichnofauna of Sierra de las Cabras, a site that joins the nearby Hoya de la Sima ichnofossil site to yield the largest and most diverse record of vertebrate ichnites of late Miocene age in southern Iberia.

Keywords Ichnology · Avian footprints · Southeast Iberia · Miocene

Icnofauna aviana del yacimiento de la Sierra de las Cabras (Mioceno superior, Jumilla, SE de España)

Resumen

La Sierra de las Cabras es un yacimiento excepcional de icnofósiles de edad Mioceno superior, situado en la zona prebética, cerca de la localidad de Jumilla (Provincia de Murcia, SE de España). El yacimiento contiene abundante icnofauna, la cual se preserva en facies carbonatadas depositadas en un sistema semiárido de humedales con zonas pantanosas y lagunas poco profundas. La icnofauna se asocia a mamíferos diversos, ésta estudiada recientemente, y a aves, la cual es el objetivo de este trabajo. Reportamos un total de 51 huellas de aves repartidas en dos de las tres superficies estratigráficas que definen al yacimiento. El estudio detallado de estas icnitas (huellas y rastros) permite su atribución al icnogénero *Fuscinapeda* Sarjeant y Langston 1994, así como inferir diversos patrones de comportamiento de las aves, todos consistentes con avifauna de humedales someros. Además, se discute sobre los posibles icnopoyetas de las huellas, que deben corresponder con aves

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zancudas y sin hálux (o con un hálux elevado), probablemente pertenecientes al orden Gruiformes. El estudio confirma la presencia de Fuscinaepeda en la Península Ibérica y completa la caracterización de la icnofauna de vertebrados de la Sierra de las Cabras, un yacimiento que unido al cercano yacimiento de icnofósiles de la Hoya de la Sima proporcionan el mayor y más diverso registro de icnitas de vertebrados del Mioceno superior en el sur de Iberia.

Palabras clave Icnología · Huellas de aves · Sureste de Iberia · Mioceno

1 Introduction

This work focuses on the avian ichnites found in the Upper Miocene Sierra de las Cabras ichnofossil site (Herrero, 2008, 2010), and completes a previous paper dedicated to the mammal ichnites of that location (Herrero et al., 2022). The Sierra de las Cabras site (Lat. 38° 28' 53"N, Lon. 1° 24' 52"W, datum: ETRS89; Fig. 1) is located in the Prebetic ranges, near the town of Jumilla (Murcia province), and joins the neighbor site of Hoya de la Sima (e.g., Herrero, 1997; Perez-Lorente et al. 1997, 1999, 2009; Vilas et al., 2006), located about 9 km to the northeast, to form an exceptional record of vertebrate ichnites of Late Miocene age in south-east Spain (Fig. 1).

The sedimentary succession that hosts the ichnites of Sierra de las Cabras, which has a latest Tortonian or earliest Messinian age (Herrero et al., 2022), consists of carbonates, marls and marly limestones, often showing partial dolomitization. These are stratified in dm- to cm-scale beds that show chalky texture and whitish color. Facies include a variety of freshwater, palustrine and pedogenic carbonates typical of a semi-arid wetland system with shallow ponds, small

swamps, and marshes, that could provide the habitat for the diverse fauna revealed by the footprints. That ichnofauna includes *Hippipeda*, *Rhynoceripeda*, *Canipeda*, *Felipeda*, *Ursipeda*, *Rodentipeda* and possible *Suipeda*, besides the *Avipeda* ichnites studied in this paper. In that environmental frame, fresh water was probably yielded by springs located at the foot of the carbonate hills. The ichnites were imprinted on cohesive, partially consolidated, muddy sediment consisting of marly carbonate, embedded in water at the time the animals left their tracks. Due to the physical state of the carbonate mud at the time of formation, footprints can show evidence of plastic deformation. Vertebrate ichnites are reported from the top of three successive limestone beds, each 10–20 cm thick, that show a strike of N58°E and a dip of 30° SE. For ichnite location reference, the top of the three levels were named surface 1, surface 2 and surface 3, from base to top. Avian ichnites have been reported from surfaces 1 and 3, but not from surface 2.

A more detailed description of the fossil site, including its stratigraphy and sedimentary facies, as well as a discussion about its age, can be found in Herrero et al. (2022).

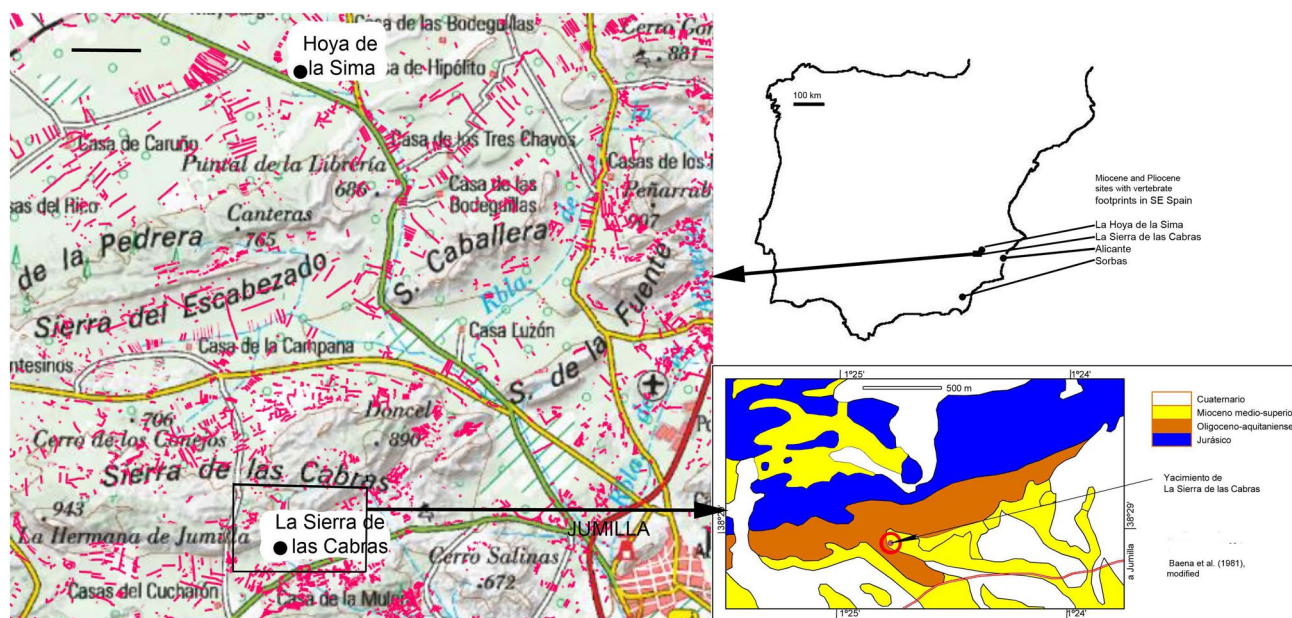


Fig. 1 Geologic and geographic location (from Herrero et al., 2022)

2 Methods and nomenclature

The working method, referencing of footprints, and general terminology and definitions are similar to those described in Herrero et al. (2022) and will be herein only briefly summarized. The 60×60 cm square grid used in Herrero et al. (2022) has been also the basis for this study and is the main reference grid to locate the avian ichnites (Fig. 2). The longer lines of the grid are horizontal and coincide with the strike of the stratification planes, the other lines being perpendicular and coincident to the dip. Photographs were taken over each square, with the aid of a 60×60 cm frame with a 5×5 cm fine rope mesh. The images were processed with Adobe Photoshop® and translated on a scaled plane using AutoCAD®. We used Adobe Photoshop®, Photosynt®, SynthExport®, MeshLab® and Paraview® software for image 3D processing.

We consider a trackway as a sequence of three or more tracks left by the same individual during locomotion (Thulborn, 1990). We use the avian taxobases by de Valais and Melchor (2008) and the avian footprint morphometric and biomorphic quantification proposed by Brown et al. (2003) and García Raguél et al. (2009) (Table 1). Similar approaches can be found in recent papers (e.g., Díaz-Martínez et al. 2011, 2016). We also consider some aspects of Xing et al., (2015), despite this paper focuses in Cretaceous footprints with emphasis in differentiation between bird and small dinosaur footprints.

The reference code given to a footprint consists of the site acronym (CBR), followed by the trackway number, a dot, and the footprint number of those included in that trackway. Avian ichnites have the references CBR1 (which a pair of footprints, CBR1.1 and CBR1.2) to CBR14 (an isolated footprint).

The main elements and features we have used to discriminate bird tracks, in accordance with Lockley et al. (1992) and Brown et al. (2003), are the following:

- (i) Regarding the digits: number of digits (didactyl, tridactyl or tetradactyl); termination (acuminate); position; interdigital angle **II** ^ **IV** wide open (about 110° or more); length (relatively long and thin, **III** being the longest), convergence zone (digits proximally joined or not); hallux (printed or not, attached to or separated from the foot mark, its location and angle with the rest of the digits).
- (ii) Regarding the pes: footprints wider than long (**a** > **I**); lack of metatarsal mark (in any case, mark of the metatarsal-falanganian pad); the mark of interdigital webs (if exists or not; and in the affirmative case, its relative extension, its number, and its position); the metatarsal-falanganian pad mark (shape, dimension and relative depth).

- (iii) Regarding the trackways: avian trackways are very narrow.

Characterization and classification of bird tracks is not a straightforward task, as there is still strong debate and confusion about ichnotaxonomic assignment procedures. As pointed by Díaz-Martínez et al., (2011), the lack of a normalized methodology is clearly reflected by the large number of corrected names in published works, and in the abundant clarifications and contradictions, as well as in the strong inaccuracies existing in age attributions. Camens and Worthy (2019) expose several contradictions relating to the relevant avian ichnotaxonomy and propose a method for more objectively measuring digit divarication in avian footprints, and particularly in those with curved digital traces. However they de-emphasize other ichnotaxonomic features such as the length and width of the footprints, the presence of hallucal impression, the interdigital angle, and the termination of the digits (round or acuminate). Relevant to our paper, these authors suggest that the tridactyl ichnogenus *Fuscinapeda* Sarjeant and Langston, (1994) (to which we associate the footprints of Sierra de las Cabras, see below) could be a junior synonym of the tetradactyl ichnogenus *Koreanaornis* (Kim, 1969; Kim et al., 2012).

Without entering systematic discussions nor formally proposing any ichnotaxonomic revisions that would be far of the scope of this paper, we must however mention the problems that arise when reviewing the literature dealing with avian footprint assignation. In fact, it is difficult to evaluate if: (1) the features used for ichnotaxonomic determination are real or mimetic structures produced during the formation of the footprint, which can be simple or very complex (Boutakiout et al., 2006), or later structures (such as the collapse structures produced during the K phase (Thulborn & Wade, 1989); (2) there are anatomical foot elements, such as digit pads, hallux or claws, that have not been marked in the footprints because foot penetration has been poor due to the rigidity of the substrate; and (3) the marks are simply undertracks that are not reproductions indicative of the soles of the feet.

In addition, it must be remembered that Neogene fossil birds generally resemble modern taxa, and those that cannot be attributed to a modern genus or species can usually be placed in a modern family with a fair degree of confidence (e.g., James, 2005). In consequence, bird tracks should have also changed very little since the Miocene, an aspect that points to the need for very accurate characterization of fossil tracks. Tiny morphological variations of the ichnotaxonomic characters can be very important to understand morphological changes through time and to identify the trackmakers.

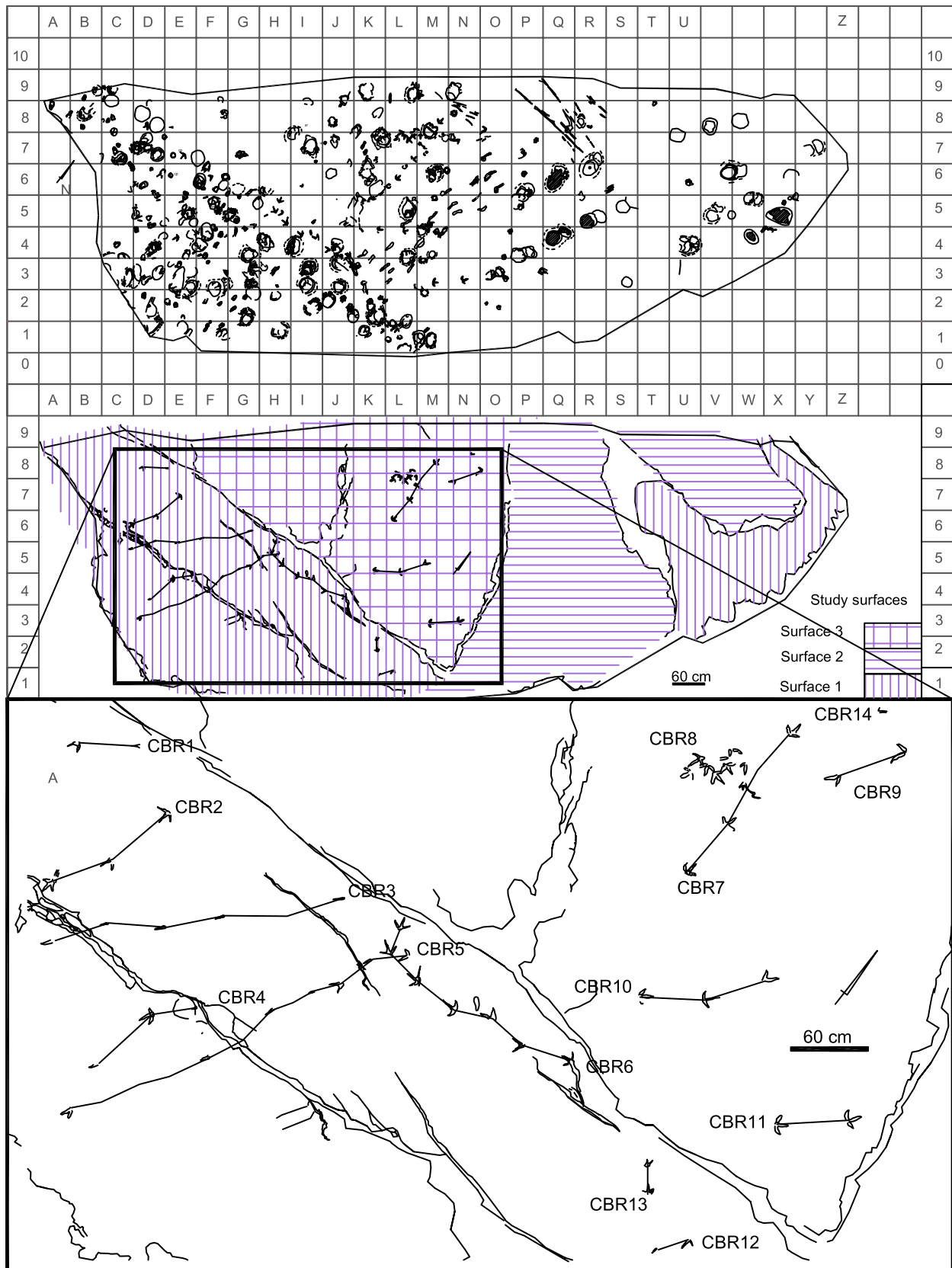


Fig. 2 Above, the Sierra de las Cabras site; mesh of the site with the position of the footprint studied. The light of the mesh used is 60 cm. Center, the three surfaces with traces. Below, avian footprints, pairs and trackways

Table 1 Avian ichotaxonomic characters, scales and nomenclature (from García Raguél et al., 2009)

Footprint length	Size
0 to 25 mm	Very small
25 to 50 mm	Small
50 to 75 mm	Medium
75 to 100 mm	Large
< 125 mm	Enormous
Pes proportion $(l - a)/a$	
< -0.5	Very wide
-0.5 to 0	Wide
0 to 1	Narrow
> 1	Very narrow
Digit length/digit width	
> 4	Delicate
4 to 3	Medium
< 3	Robust
General digits size	
$I < II < IV < III$	
Divarication II^IV	
> 100°	Open, high
< 100°	Low
Didactyl	Proximally joined digits
Tridactyl	Proximally separated digits
Tetradactyl	Protruding central pad
	hallux: separated//joined (incumbent)
Anisodactyl	Three toes forward and one back
Zigodactyl	Two toes forward (II,III) and two back (I, IV)
Heterodactyl	II, IV pointing forward and I, II pointing back
Syndactyl	Two or three toes fused together
Pamprodactyl	I and IV can rotate forward and backward
Webb and lobes	
Totipalmate	All four toes (I-IV) joined by webbing
Bipalmate distal (palmate)	II-III-IV joined by webbing
Bipalmate medial (semipalmate)	Mesial II-III-IV webbing
Bipalmate proximal	Proximal II-III-IV webbing
Monopalmate	Proximal II-III or III-IV webbing
Lobate	Toes (II-IV) are edged by lobes or skin
Footprint asymmetry	
$II \neq IV$	Digit length asymmetry
$II^III \neq III^IV$	Angular asymmetry
I, III parallel but separated	Asymmetric lateral hallux
$I^III \neq 180^\circ$	Asymmetric angular hallux

l footprint length, a footprint width, I, II, III, IV, digit length, II^III , III^IV , II^IV divarication or interdigital angles II-III, III-IV and II-IV

3 Classification adopted for avian footprints

Since the pioneer works of avian footprints by Panin and Avram (1962) and Vialov (1965, 1966) different classifications has been proposed by different authors. In this paper we follow the one proposed by Sarjeant and Langston (1994) as well as the subsequent modifications by Sarjeant and

Reynolds (2001), de Valais and Melchor (2008), Lockley and Harris (2010), Lockley et al. (2012a), McCrea et al. (2014), and Xing et al. (2015).

The first characters to be established for classification refer to the interdigital webbing and its extension (Tables 1 and 2). Sarjeant and Reynolds (2001) compiled the avian footprints into three ichnofamilies: Avipedidae, Gruipedidae

Table 2 Classification of bird footprints (Morphofamilies) based on several authors (see text)

Footprint morphology	Morphofamily	
Palmate	Anatipedidae, Sarjeant and Lanston (1994)	
	Charadriipedidae, Sarjeant and Lanston (1994)	
	Ignotornidae, Kim et al. (2006)	
	Undetermined, Lockley and Harris (2010), includes <i>Uhangrichnus</i> Yang et al. (1995)	
Not palmate		
	Tetradactyl	Gruipedidae, Sarjeant and Langston (1994)
		Jindongornipedidae, Lockley and Harris (2010)
	Koreanaornipedidae, Lockley and Harris (2010)	
	Zigodactyl footprints, Lockley et al. (2007)	
Tridactyl	Avipedidae Sarjeant and Langston (1994)	
	Limivipedidae, McCrea et al. (2014)	

and Anatipedidae, the later including the Charadriipedidae ichnofamily. In Anatipedidae, the semi-palmate, palmate and totipalmate footprints (including Charadriipedidae) can be found. Footprints with very small interdigital webbing that extend between the three front digits or between two of them are not included in this category. Additionally, Lockley et al. (2012b) defined Ignotornidae and an indeterminate (webbed) ichnofamily that includes the ichnogenus *Uhangrichnus* (Yang et al., 1955). These two later ichnofamilies are palmate or semi-palmate and tetradactyl. Sarjeant and Reynolds (2001) grouped the non-webbed tetradactyl ichnites (with hallux mark) into the Gruipedidae ichnofamily. However, Lockley and Harris (2010) found some limitations in the classification of Sarjeant and Reynolds (2001), in which, for example, there was no place for the zigodactyl ichnites (Li et al., 2005), these with two digits directed forwards and two backwards.

Lockley et al., (2012b) also defined the Koreanaornipodiidae and Jindongornipodiidae ichnofamilies. Currently, there are several families included in the tetradactyl group (Gruipedidae, Jindongornipedidae, Koreanaornipedidae, and the zigodactyl footprints, see Table 2).

The non-webbed tridactyl ichnites (without hallux mark) were included in the Avipedidae family, currently divided into Avipedidae and Limivipedidae (as defined by McCrea et al., 2014). The Limivipedidae family arises from the modification of *Aquatilavipes currei* (McCrea & Sarjeant, 2001), redefined as *Limivipes currei* (McCrea et al., 2014). Avipedidae and Gruipedidae do not have interdactillary webbing, or in any case they are proximal monopalmate. In both ichnofamilies the three digits (II-III-IV) are directed forward.

Lockley and Harris (2010) highlight the difficulties of ichnogenus classification due to the interpretative approaches

by researchers as well as the extramorphological features described in many traces. They conclude that bird ichnology must be based on the accurate description of ichnites without considering the trackmaker, and always must consider both the footprint assemblage and the footprint bearing sedimentary facies.

For the identification and fundamentally for the definition of new ichnotaxa, some key aspects should be considered, including the recommendations of Peabody (1955) relative to the minimum necessary number of footprints of each type; and those of Sarjeant (1989), Gatesy (2003) and Romero-Molina et al. (2003) regarding the variability of ichnotaxonomic features, type of sedimentary surface, and the fidelity of the reproduction of the autopodium (stamps). Significant variations between footprints of the same trackmaker have been described in birds and other tridactyl animals such as dinosaurs, even in ichnites of the same animal and site (cf. Lallensak et al. 2016; Masrour et al., 2017; Melchor & Valais, 2006; Romero-Molina et al., 2003). There are examples of footprints within a single trackway, where the footprints can show changes in ichnotaxonomic characters large enough to be associated with more than one ichnogenus (Romero-Molina et al., 2003).

All these aspects regarding ichnotaxa determination have been considered in our study of Sierra de las Cabras site, where the avian ichnites show noticeable variability both in shape and dimension. If the above considerations were not taken into account, that variability probably would lead to erroneous identification of multiple ichnogenera.

De Valais and Melchor (2008) consider that the Gruipedidae ichnofamily comprises tetradactyl and tridactyl prints, since the same animal can leave footprints of both types in the same trackway. In this paper we assume that tridactyl footprints cannot be attributed exclusively to the anatomical difference of autopodia, but sometimes to abnormalities or extramorphological variability. This does not discard the tridactyl or tetradactyl character as an ichnotaxonomic feature. We consider that tridactyl footprints associated with tetradactyls in the same trackway (same outcrop and by the same trackmaker) may be included in Gruipedidae. This does not imply that exclusively tridactyl footprint assemblages belong to the Gruipedidae family.

Lockley et al. (2020) assign their Morphotype A (tetradactyl prints) to *Avipeda* because part of them do not have a hallux mark. Thus they do not consider the tridactyl or tetradactyl character as an ichnotaxonomic feature, but the result of differential preservation, or a problem of real traces and undertraces: "... an apparently tridactyl track (without hallux trace) on one surface of a thin slab appears tetradactyl (with hallux) on the other side of the same slab ..." (Lockley et al, 2020, p.5). Our criterion in this case is that Morphotype A is a tetradactyl imprint.

Lockley et al., (1992, p.123) find that both the proximal connection of the digits and the hallux mark are partly a function of preservation: “The degree to which individual digit impressions are interconnected proximally is also in part a function of preservation”. In this paper we consider that digits joined or separated proximally are of the same ichnogenus when they coexist in footprints of the same trackway.

Lockley et al. (1992) considered that the mark of digit pads was of interest for the identification of one of the tridactyl ichnogenera (*Aquatilavipes*). However, this characteristic also depends on the substrate and these marks are rarely preserved (McCrea & Sarjeant, 2001).

Finally, regarding the size of the avian ichnites, it should be noted that some authors consider it as a discriminative ichnogenic character (Brown et al., 2003), despite there are avian ichnogenera that show large size variations.

4 Description of avian footprints of Sierra de las Cabras

A total of 51 footprints are reported in the Sierra de las Cabras site (Table 3). These are distributed as follows: 1 isolated footprint (CBR14), 4 pairs (CBR1, CBR11, CBR12, CBR13; 8 footprints), 8 trackways (CBR2, CBR3, CBR4, CBR5, CBR6, CBR7, CBR9, CBR10; 34 footprints), and 1 group (CBR8; 9 footprints). There are footprints in the lower ichnite level or stratigraphic surface 1 (CBR1, CBR2, CBR3, CBR4, CBR6, CBR12, CBR13) and in the upper ichnite level or stratigraphic surface 3 (CBR7, CBR8, CBR9, CBR10, CBR11, CBR14). No avian footprints have been found in the intermediate level (surface 2).

The footprints are relatively deep, and the outline is usually sharp. There are no deformation structures such as base breccias (Boutakiout et al., 2006), but there are tensional microfractures parallel to the footprint outline, with partial fall of the walls into the hollows of the digits (CBR6.5, Fig. 4) as well as a base incision (Boutakiout et al., 2006).

The average pace length (Table 4) is 42 cm and that of the stride is 73 cm, almost twice the length of the pace. This is consistent with very narrow gauge trackways ($\text{Ar/a} = 0.17 < 0.05$) in which the value of the trackway deviation is low (3.3 cm).

We attribute to skid marks the striae and grooves behind some footprints (for example: CBR2.3, Fig. 3).

It should be noted that most of the ichnites do not show pad marks and some of them do not show a mark of the proximal interdigital web. We consider these facts as related

to the imprinting process, as we found in some cases, even in ichnites of the same trackway,

The presence of pad, claw and interdigital web marks, and syngenetic structures such as microfaults are criteria that allow us to confirm they are not underprints but real (true) footprints and, perhaps in some cases (Fig. 3), stamps (in the sense of photo 1, p. 43 from Brown, 1999).

5 Ichnotaxonomy

Morphofamily Avipedidae

Sarjeant and Lagnston 1984

Diagnosis. Avian footprints showing three digits, all directed forward. Digits united or separate proximally. Webbing lacking or limited to the most proximal part of the interdigital angles.

Ichnogenus *Fuscinapeda*

Sarjeant and Lagnston 1984

Diagnosis. Avian footprints of small to large size, showing three digits, slim or moderately thick (II to IV). Digit III is characteristically more than 25% longer than the lateral digits. Total interdigital span greater than 95° and often exceeds 110°. Digits united proximally, frequently showing a distinct “heel.” Webbing absent or restricted to the most proximal part of the interdigital angles.

Ichospecies *Fuscinapeda* isp

5.1 Description

The footprints are tridactyl, anisodactyl, and show noticeable digit length asymmetry (Fig. 3). They are very long ($\text{I} = 11.5$ cm in average) and very wide ($\text{a} = 13$ cm; in average), with pes wider than long ($(\text{I} - \text{a})/\text{a} = -0.1$). They have long digits that join proximally in a wider part that is sometimes protruding towards the back. Digit II is the smallest ($\text{II} < \text{IV} < \text{III}$; $6 < 6 < 8.5$ cm), III being more than 25% longer than any of the lateral digits. The average length to width ratio for the digits in the trackways ranges between 4.5 and 5, so they can be described as delicate, almost medium digits (Table 1). In some footprints digit III becomes progressively thinner towards the apex (Fig. 3). There are no hallux marks. The divarication of the digits II^IV is high ($> 120^\circ$) and the average values indicate that the ichnites show angular symmetry ($\text{II}^{\text{III}} = \text{III}^{\text{IV}}$). The digit pads are barely distinguishable as a smooth widening of the footprint outline and a slight depression in the sole of the digits (for example CBR4.2, CBR7.1, CBR11.1, Fig. 3). There is a prominent central (metatarsal) pad that forms a heel (in CBR4.1 the area where the three digits meet is bulging). The tip of the

Table 3 Measurements and relations of CBR avian footprints and trackways

Footprint (cm)	l	a	Ar	Lr	P	z	Ap	O	II-III-IV	II [^] III [^] IV [^] II	(1-a)/a	Ar/a	NE
CBR1.1													N242E
CBR1.2	9				0				6,-,-				
CBR2.3	12	12							7-9-5	50,66,116	0		N209E
CBR2.2			4	22	52	105	160	0		..., 52			
CBR2.1	12	15			54				9-10-6	43,77, 120	-0.2		
CBR3.6													N231E
CBR3.5			4		45	88	157						
CBR3.4					44	90	164						
CBR3.3					47								
						94							
CBR3.1													
CBR4.3													N210E
CBR4.2	12		11		53	88	151	5		54,83, 137			
CBR4.1					38								
CBR5.12									6,7,-				N215E
CBR5.8													
CBR5.6													N270E
						35							
CBR5.4													
CBR5.3	25		3			53	155	-24	5,8,-	-, 68			
CBR5.2	9		4		31	57	146	-2	-,7,-	90,-			
CBR5.1	11				28				5,9,-				
CBR6.7	11	12							7,8,6	49,51,100	F	F	N350E
CBR6.6	11	12							6,10,5	58,65,123	-0.1		
CBR6.5	13	14	7	27	22	43	113	5	6,8,95	55,69,124	-0.1	0.5	
CBR6.4	11	17	-1	10	31	67	190	7	6,8,6	48,75,123	-0.3	-0.06	
CBR6.3	11	17	3	21	36	67	156	-11	-,8,7	-,70	-0.3	0.18	
CBR6.2	13		4	21	30	59	152	-4	6,8,7	58,67,125			
CBR6.1	10				32				5,7,7	48,69,117			
CBR7.4	13	12				84			6,11,6	52,55,107	0.1		N7E
CBR7.2									5,8,6	67,67,134			
CBR7.1		13			48				6,8,5	55,51,106			
CBR8.9													
CBR8.8	10									81			
CBR8.7	10												
CBR8.6	12									149			
CBR8.5	11									111			
CBR8.4	9									121			
CBR8.3										128			
CBR8.2	15												
CBR8.1	9									141			
CBR9.2	13								-,10,-				N320E
CBR9.1	14				55				-,13,-				
CBR10.3	13								-,10,6	-,66			N53E
CBR10.2	10	13	1,5	20	49	98	154	-4	6,7,3	81,67,148	-0.15	0.1	
CBR10.1	12	11			50				5,9,6	-,47			
CBR11.2	15	14							6,10,7	64,72,136	0.1		N57E
CBR11.1	10	12			56				6,8,7	59,68,127	-0.2		
CBR12.2									-,7,4				
CBR12.1									-,8,-				

Table 3 (continued)

Footprint (cm)	l	a	Ar	Lr	P	z	Ap	O	II-III-IV	II [^] III [^] IV [^] II	(l-a)/a	Ar/a	NE
CBR13.2													N67E
CBR13.1													
CBR14													
Average	11	13	3	20	42	73	155	-4	6-8,5-6	62-62, 122	-0.1	0.17	

Measurements in cm and sexagesimal degrees

l footprint length; *a* footprint width; *Ar* trackway deviation; *Lr* trackway width; *P* pace length; *z* stride length; *Ap* pace angle; *O* orientation or angle between the axis of the print and the adjacent midline; *I*, *II*, *III*, *IV* digit length; *II[^]III[^]IV[^]II* divarication or interdigital angles II-III, III-IV and II-IV; *(l-a)/a* variation of pes length relative to pes width; *Ar/a* indicate narrow-wide gauge; *NE* trackway direction

Table 4 Average data of measurements and relations of CBR avian footprints and track

Footprint	l	a	Ar	Lr	P	z	Ap	O	II-III-IV	II [^] III [^] IV [^] II	(l-a)/a	Ar/a	Direction
CBR1	9				50				6, -, -				N242E
CBR2	12	14	4	22	53	105	160	0	8, 10, 5	46, 67, 118	-0.1		N209E
CBR3			4		45	90	160						N231E
CBR4	12		11		40	88	151	5		54, 83, 137			N210E
CBR5	12		3		30	48	150	-11	5, 8, -	90, 68, -			N240E
CBR6	11	15	4	20	30	49	153	-1	6, 8, 6	54, 68, 119	-0.2	0.21	N350E
CBR7	13	13			48	84			6, 9, 6	58, 58, 116	0.1		N7E
CBR8	12									-, -, 104			
CBR9	13				55				-, 12, -				N320E
CBR10	12	12	1,5	20	50	98	154	-4	6, 9, 5	81, 60, 148	-0.15	0.1	N53E
CBR11	12	13			56				6, 9, 7	61, 70, 131	-0.1		N57E
CBR13		67											N67E
CBR14													
Average	11	13	3	20	42	73	155	-4	6-8, 5-6	62, 62, 122	-0.1	0.17	

Data in cm and sexagesimal degrees

l footprint length, *a* footprint width, *Ar* trackway deviation, *Lr* trackway width, *P* pace length, *z* stride length, *Ap* pace angle, *O* orientation or angle between the axis of the print and the adjacent midline, *II*, *III*, *IV* digit length, *II[^]III[^]IV[^]II* divarication or interdigital angles II-III, III-IV and II-IV, *(l-a)/a* variation of pes length relative to pes width, *Ar/a* indicate narrow-wide gauge, *direction* trackway direction

digits is acuminate, and the claw mark can be recognized in many of the footprints.

Some footprints are monopalmate, with a proximal web between digits **III-IV** (Figs. 3, 4, 5) neighboring the vertex of the interdigital angle (for example, CBR6 or CBR10). This is a rare feature. Monopalmate footprints have been reported in the literature, but between digits **II-III** (e.g., Falk, 2009). Lockley et al. (2020) cite proximal **III-IV** monopalmate footprints, but in tetradactyl tracks.

5.2 Discussion

Because the avian ichnites of Sierra de las Cabras site are non-webbed tridactyl footprints, they should correspond to Avipedidae or Limiavipedidae ichnofamily (Table 2), but Limiavipedidae is restricted to the Cretaceous, and the age of Sierra de las Cabras ichnites is Late Miocene.

It should be noted that our procedure to get the length of digits (we measure it parallelly to the digit axis, from the hipex to the apex) differs from that by McCrea and Sarjeant (2001), who measure the digits following straight lines from a common point at the back of the footprint to the tip of each digit. Application of that method to our footprints would result in average digit lengths (**II//III//IV**) longer (7.8//11.7//8.8 cm) than we have reported, and also in a larger digit length/width ratio, with an average value of 8 instead of 4.5. This is relevant because the digit length to width ratio was used by McCrea and Sarjeant (2001) to discern between the ichnogenera *Aquatilavipes* (Currie, 1981; McCrea & Sarjeant, 2001) (thinner digits: < 15%, > 6.6) and *Fuscinapeda* (Sarjeant & Langston, 1994; McCrea & Sarjeant, 2001) (wider digits: > 15%, < 6.6).

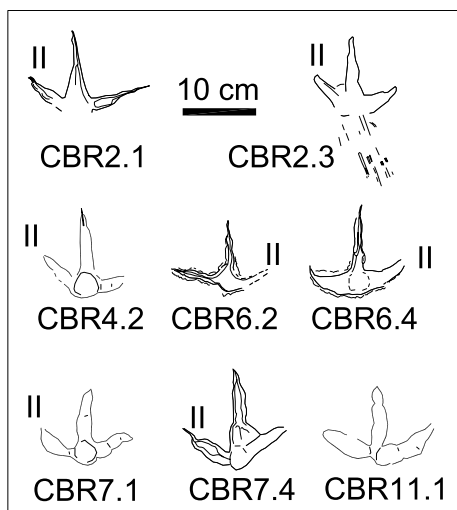


Fig. 3 Significant traces of the CBR site. Outlines (thick) and auxiliary lines (thin) showing digital pads (CBR2.1, CBR7.1, CBR7.4, CBR11.1), slide marks (CBR2.3) and extramorphological deformations (CBR2.1, CBR6.2, CBR6.4, CBR7.4). Well-marked metatarsophalangeal pad in several footprints (CBR4.2, CBR7.1)

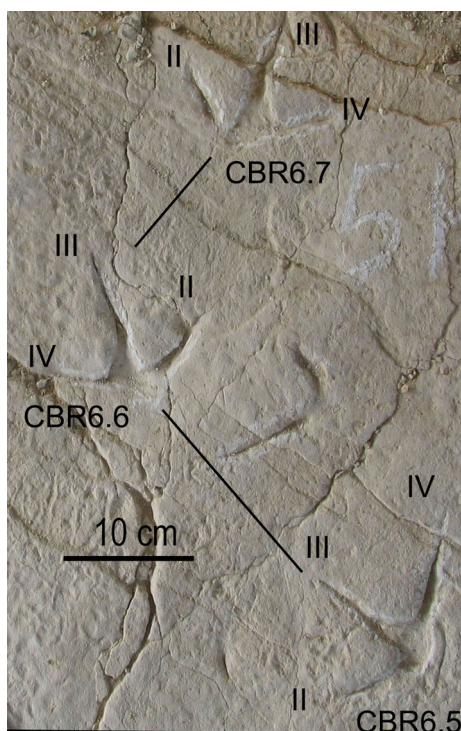


Fig. 4 Part of the CBR6 trackway (CBR6.5-CBR6.6-CBR6.7) showing the position of the web and the general shape of the avian footprints. The paces are indicated by black lines. Collapse of the digit walls in all three footprints. Marked III-IV interdigital web

Avipedidae includes the ichnogenera *Avipeda* (Sarjeant & Langston, 1994), *Aquatilavipes* (Currie, 1981), *Aviadactyla* (Sarjeant and Reynolds 2001), *Fuscinapeda* (Sarjeant & Langston, 1994), *Ornithotarnocia* (Kordos, 1983), and *Uvaichnites* (Díaz-Martínez et al. 2012) [Another two ichnogenera, *Alaripeda* (Sarjeant & Reynolds, 2001) and *Ludricharadripodiscus* (Ellemerger 1980), were also included in this ichnofamily in some works, although we consider this inclusion disputable because of the tetradactyl character of many of *Alaripeda* footprints, and the semipalmate character of *Ludricharadripodiscus*]. The distinctive features of the five ichnogenera are:

- (i) *Aviadactyla* (Sarjeant & Reynolds, 2001) has proximally separated digits and shows no metatarsal pad mark. The middle digit is less than 25% longer than digits II and IV and the interdigital divarication II[^]IV is somewhat greater than 95°.
- (ii) *Avipeda* (Sarjeant & Langston, 1994), consists of small footprints and digits of similar length. The middle digit is not 25% longer than the lateral ones. The digits are partially joined or separated proximally, and the interdigital divarication does not exceed 95°.
- (iii) *Ornithotarnocia* (Kordos, 1983) has much thicker digits than the other Avipedidae ichnogenus footprints.
- (iv) *Uvaichnites* (Díaz-Martínez et al., 2012), has the digits separated proximally and the metatarsal pad well separated.
- (v) *Aquatilavipes* (Currie, 1981; Sarjeant & Langston, 1994). Defined by tiny to small footprints (<4.5 cm) with delicate digits ($I/a > 10$) of acuminate termination, with visible or deducible metatarsal pad. Currie (1981) defined *Aquatilavipes* from more than 200 very small footprints (between 2.0 and 4.4 cm in length) on a single stratigraphic surface of Early Cretaceous age. Even though the Early Cretaceous age and the very small size are for some authors discriminative ichnogenus criteria:
 - (a) *Aquatilavipes* specimens have also been cited in the Upper Cretaceous (Fiorillo et al., 2011), and *A. wallacei* (Zonneveld et al., 2011), which is 1.5 to 3 cm long, was defined in the Oligocene.
 - (b) *A. currei* (McCrea & Sarjeant, 2001) has a medium to large size [$I = 9$ cm]) with relatively thick digits.

The similarity between *Limivipes currei* (formerly *A. currei*) and *Fuscinapeda* (Sarjeant & Langston, 1994) is such that McCrea and Sarjeant (2001) concluded that they

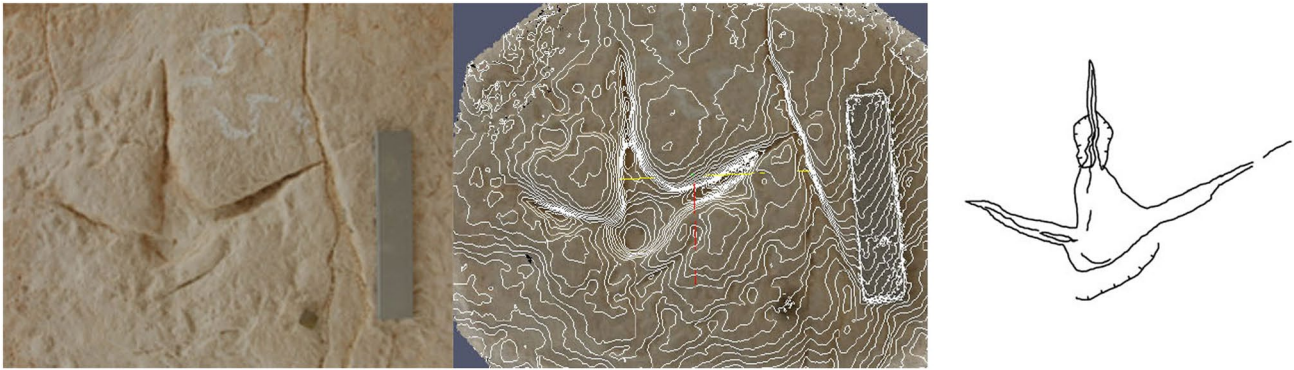


Fig. 5 Images of CBR6.5: photography, topography and drawing of the visible structures. Total or partial collapse of the walls of the digits. Tension tracks on both sides of the III marck -near the web-, and behind the footprint—parallel to the heel-digit outline sector. Scale, 10×2 cm

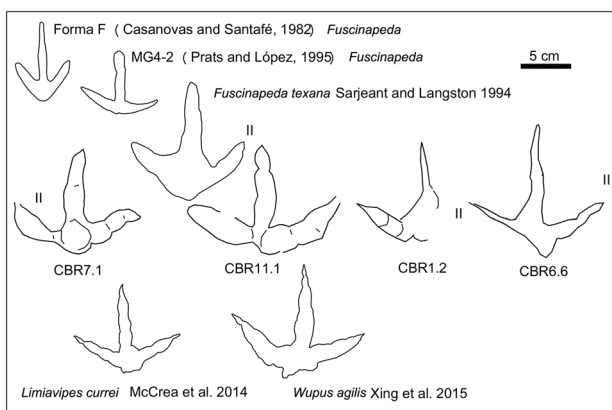


Fig. 6 Representation of the holotype of *Fuscinapeda texana* (Sarjeant & Langston, 1994); two Spanish footprints attributable to *Fuscinapeda*; *Limiavipes currei* (McCrea et al., 2014); *Wupus* (Xing et al., 2015); and four of the CBR footprints

should be distinguished by the relative width of the digits: the ichnogenus *Aquatilavipes* would be defined by a digit length to width ratio larger than 6.6; and that lower values would correspond to *Fuscinapeda*. However Azuma et al. (2002) found in *A. izumiensis* (I = 38 mm, Early Cretaceous) length to width ratios lower than 5.9 for digit III. Despite possible uncertainties associated to different measurement procedures (cf. McCrea & Sarjeant, 2001), and the particularities of each imprint determined by the sedimentary material on which it was marked, it was obvious that a new combination of characteristics would be necessary to clearly separate *Aquatilavipes* and *Fuscinapeda*. McCrea et al. (2014) revised the *A. currei* ichnospecies and assigned it to the new ichnogenus *Limiavipes* and ichnofamily Limiavipedidae. With this change, the ichnogenus *Aquatilavipes* recovers its original definition in which its individuals are small to tiny in size. Limiavipedidae is currently formed by *Limiavipes* (McCrea et al., 2014) and by *Wupus* (Xing

et al., 2015) (Fig. 6). According to Xing et al. (2015) Limiavipedidae is restricted to the Cretaceous and could occupy a similar morphospace that later, in the Cenozoic, would occupy the ichnogenus *Leptostilostipus*, *Culcipeda*, *Gruipeda* and *Fuscinapeda*.

- (vi) *Fuscinapeda* (Sarjeant & Langston, 1994) was defined as a new ichnogenus (and *Fuscinapeda sirin* Sarjeant & Langston, 1994, as its type ichnospecies) from the revision of *Avipeda sirin* (Vialov, 1965). *Fuscinapeda* (Sarjeant & Langston, 1994) is characterized by narrow termination of digits, pointed nails, and digits II and IV inclined towards digit III. The angle II^IV can range between 120 and 135°, depending on the substrate resistance, and the angle II^III is greater than III^IV. Digit pads are often observed: three on digit III and two on II and IV. In the center of the mark of each digit, a channel parallel to the digit axis can exist, that can be continuous or discontinuous. That channel, however, is barely observed when the footprints are superficial. The orientation is slightly negative (sensu Casamiquela et al., 1987), the trackway relatively wide, and the pace, although variable, consistently short. *Fuscinapeda* is characterized by thick to very thick digits.

The ichnological features of these footprints, including size, proximally connected thick digits, asymmetrical digit lengths, visible digit pads, and the digit length to width ratio; allow to include the avian footprints of Sierra de las Cabras within the *Fuscinapeda* ichnogenus. Lucas et al., (2007); cf Abbassi, (2022) doubted the validity of *Fuscinapeda* as an ichnogenus and Abbassi (2022) say that this ichnogenus needs revision because *Avipeda sirin* (*Fuscinapeda sirin*) “differs from both ichnospecies *F. meunieri* and *F. texana*, either by size or by morphology”. The large thickness of digits in *Fuscinapeda* varies among their ichnospecies. The

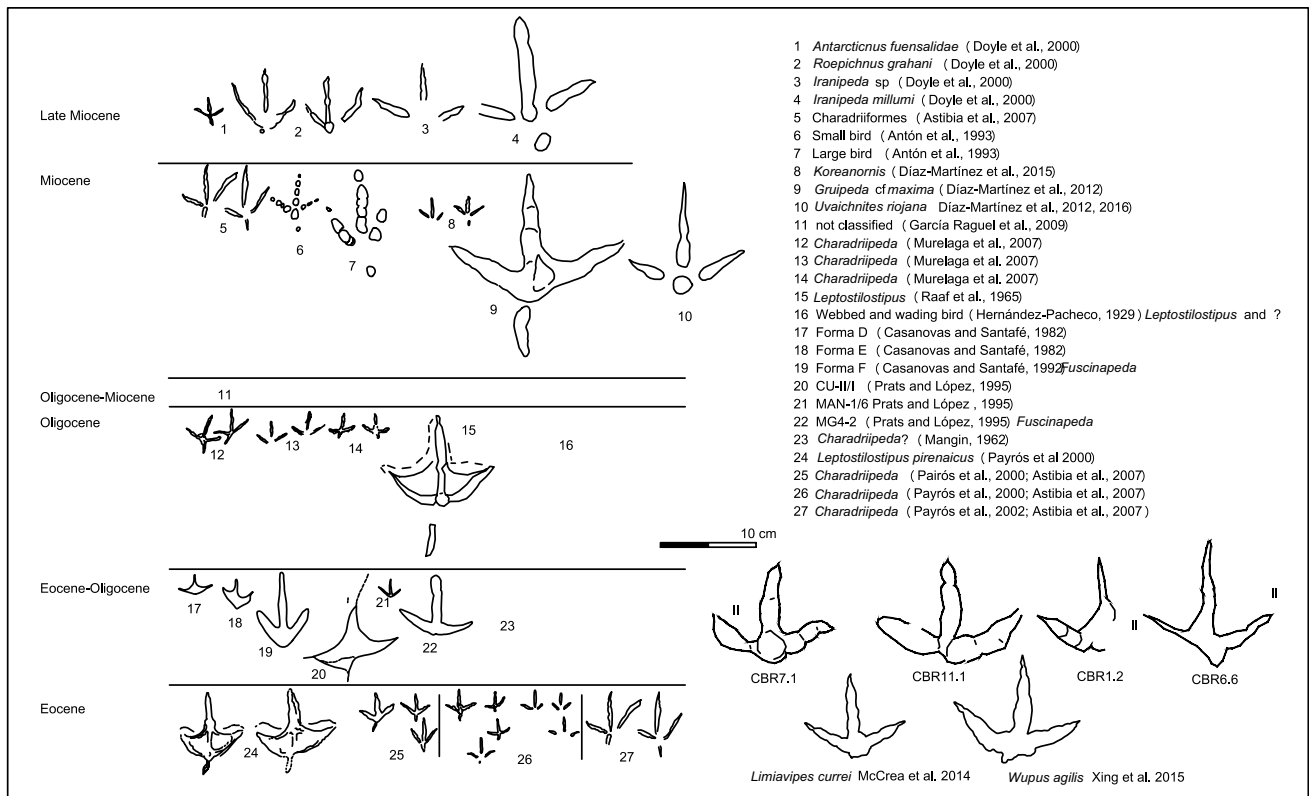


Fig. 7 Diagram of Spanish avian footprints. The numbers without drawing (11, 16, 23) indicate the position of footprints not drawn because there is no image in the references or because the image is not good and does not have a scale

thickest are those of *F. texana* (Sarjeant & Langston, 1994) (Fig. 6), followed by *F. meunieri* (Sarjeant & Langston, 1994) and then by *F. sirin* (Sarjeant & Langston, 1994) (cf. Krapovickas, 2010), which are notably thinner. Also, *F. texana* is larger than the other two ichnospecies and sometimes is monopalmate III-IV (cf. Sarjeant & Langston, 1994; Fig. 6).

According to their characteristics, the avian ichnites of Sierra de las Cabras are closer to *F. texana* than to any of the other two ichnospecies, although their specific attribution to that ichnospecies (or alternatively to a new one) will require of further work. Until now, the only ichnites of *F. texana* (Sarjeant & Langston, 1994) reported in the literature are those of its original definition. It should be noted however that paper Sarjeant and Langston (1994) included in *Fuscinapeda* the specimen “Forma F” by Casanovas-Cladellas and Santafé-Llopis (1982) found in the Oligocene of Lérida, Spain (Fig. 7). Shortly after, Prats and López (1995) reported another specimen (MG4 -2) of similar size and characteristics in the same area, which is similar to *F. texana* in size, morphology of the digits, and the prominent shape of the metatarsophalagian pad. However, MG4-2 is poorly preserved and does not allow the recognition of a possible monopalmate character.

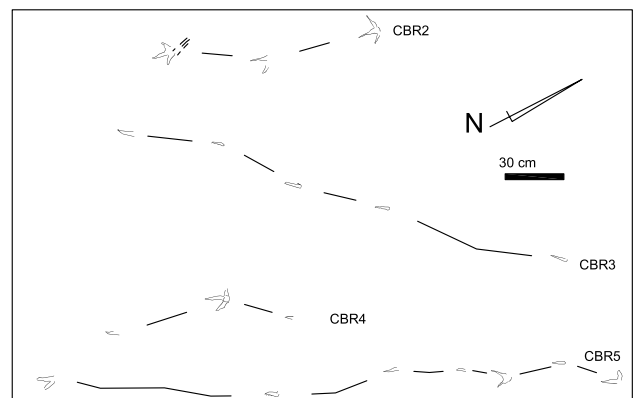
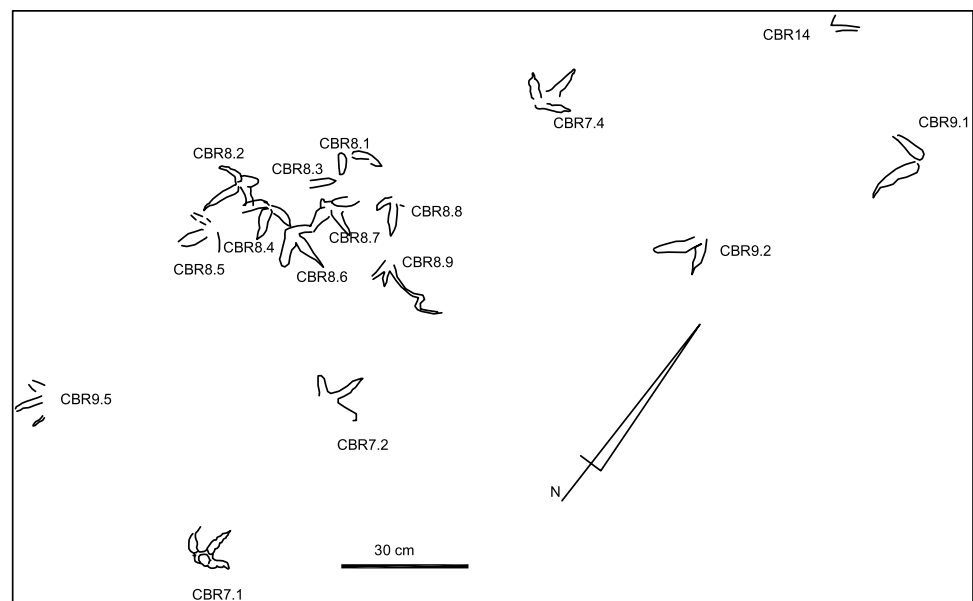


Fig. 8 CBR2, CBR3, CBR4, CBR5. Three parallel trackways with incomplete footprints. Possibly the feet are not completely printed because the viscosity of the mud did not allow it in this sector

6 Behavior inference

Some aspects of the Sierra de las Cabras trackways allow to discuss possible behavior patterns. Among these:

Fig. 9 CBR7 and CBR9 trackways and group CBR8. Possible pairs of tracks in stop stance (CBR8.2- CBR8.4 y CBR8.6- CBR8.7). The CBR7 and CBR9 trackways traverse the sectors without changes in trajectory



- (i) CBR6 trackway: It is formed by complete footprints and that towards the end turns to the right.
- (ii) CBR3, CBR4, CBR5 trackways (Figs. 4, 8): They are partially or totally formed by incomplete footprints in which only the middle digit is marked, are very close to each other, and follow the same direction. It is also possible that the traces of these three trackways result from partial support of the foot, which could be related with walking accompanied by fluttering. It should be noted that the position of the footprints of CBR4 and CBR5 is uncertain and is even possible that some of these may not belong to the trackway to which they are assigned, because they are two almost parallel trackways that intersect each other and in which intermediate footprints are missing.
- (iii) Ensemble of CBR7 and CBR9 trackways and CBR8 group (Fig. 9): The CBR7 and CBR9 trackways intersect in CBR8 and cross it. In this group there are pairs of footprints placed laterally in a position which is congruent with birds that support both feet on the ground (CBR8.3/CBR8.4, and CBR8.6/CBR8.7). Despite the crossing of the CBR7 and CBR9 trackways takes place in the CBR8 group, the tracks of CBR8 do not seem to be related with the birds that made CBR7 and CBR9, because the trajectories of these pass through the area without any variation.

Such diverse patterns of activity, with trackways in several directions, do not suggest a group of birds moving from one point to other, nor that the existence of a water line that determined movement direction due to separation of water from emerged land. Nor is strong variation of depth detected depending on the direction of travel, suggesting a flat and

horizontal walking surface. We assume that the Sierra de las Cabras trackways are congruent with two groups of birds (one producing the footprints on surface 1 of the site and the other on surface 3) and record diverse behaviors, comparable to those of the flocks of *Calibris* studied by Genise et al. (2009).

It is also significant the existence of features in some footprints and trackways that could reveal different response of the sediment to the imprint process. Among these are collapse structures (of greater penetration in the mud); incomplete (partial) mark of the digits (or lack of impression of one or more digits); or, by the contrary, complete mark of all three digits and no deformations. These aspects points to the possibility that the behavior of the mud was different according to sectors, or that the conditions of the mud changed through time. However, no trackway seems to cross sectors with mud showing very different physical conditions (e.g., drier and wetter mud along a pathway). Neither do the trajectories cross each other in any case (i.e. birds stepped on the same sediment at different times), which prevents inferring different behaviors of the sediment through time.

7 Possible trackmakers

The characteristics of footprints produced by a single bird are often very variable (e.g., Fiorillo et al., 2011) and thus, inference of trackmakers from ichnites can be very difficult and problematic, particularly when the number of footprints is limited. The size and the morphological similarities may not be significant; the later including the number of marks of digit pads, the digit divarication, the presence of hallux mark, and the nail marks, among others. With these limitations in mind, our aim in this chapter is to comment some

persistent features of the Sierra de las Cabras avian footprints that could help to discuss the possible types of birds that made them.

The Sierra de las Cabras ichnites show large size, which suggests they were probably generated by birds with long limbs. This inference is similar to that by McCrea and Sargeant (2001) for *Aquatilavipes currei*, which was attributed to large wading birds. Shortly after, Coria et al. (2002) compared *A. currei* with footprints by present-day shorebirds.

Another remarkable aspect is the lack of distal interdigital webbing of the Sierra de las Cabras ichnites. This feature, in large to enormous footprints, is typical of walking birds, probably wading ones (Brown et al., 2003). Walking birds with footprint size comparable to those of Sierra de las Cabras can be Ciconiiformes or Gruiformes (tetra and tridactyls), but the tridactyl character of our ichnites discard the Ciconiiformes, which are tetradactyls, and points towards Gruiformes, and this order includes both tetra and tridactyls. The Gruiformes are characterized by having long or short legs, sometimes mesial palmate digits, sometimes lobed digits, without hallux or with elevated hallux.

In the same way, De Valais and Melchor (2008) assimilate non-webbed (or with a very small web) anisodactyl footprints with hallux greatly reduced or absent (incumbent), to type 2 bird tracks of Elbroch and Marks (2001).

In summary, the Sierra de las Cabras avian footprints were made by walking birds, whose large tridactyl footprints are compatible with birds of the Gruiformes order characterized by long legs, sometimes with webbed digits at the base, sometimes edged, and with no hallux or a raised one. The Gruiformes adapted to semi-arid wetland systems as those inferred for the Sierra de las Cabras site (with shallow ponds, small swamps, and marshes; Herrero et al., 2022) include a diversified group that have developed a series of adaptations such as lobed and long digits to move in those environments. Cranes, coots, and bustards are among the present-day members of this order.

8 Conclusions

A new site of avian ichnites is described from Sierra de las Cabras (Jumilla, Murcia), a tracksite that shows an exceptional variety of vertebrate footprints. This site provides the second description and ichnogenus assignation of avian footprints in Messinian sediments of the Iberian Peninsula.

This paper confirms that in Iberia there are footprints of *Fuscinapeda*, an ichnogenus tentatively inferred for certain ichnites found in Agramunt (Lérida). It is however the first time that the ichnogenus is formally described in the area.

The avian ichnites of the Sierra de las Cabras are the largest among those found in Spain, which allows us to determine, for now, the maximum size of the Paleogene and Neogene fossil birds in the country.

The grouping of avian footprints and their orientation do not imply that the trackmaker birds had gregarious behavior, although the likelihood is that there were groups that visited or inhabited those places. The diversity of trackway directions both within the trackways of the same ichnotype and the total of those found, speak of some animals that roamed the area, in principle without a defined direction, but with the presence of defined natural conditions (water presence of a pond). It is possible but not likely that the prints of birds imply family groups because the accumulation of shorebird footprints may involve other behavior.

The geological location of the avian tracks of the Sierra de Las Cabras in the Southeast of the Iberian Peninsula, reaffirms the spatial–temporal distribution model of Paleogene–Neogene vertebrate ichnites.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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References

Abbassi, N. (2022). *Miocene wildlife of Zanjan*. University of Zanjan.

- Antón, M., López, G., & Santamaría, R., (1993). Estudio preliminar de la icnofauna miocena del yacimiento de Salinas de Añana (provincia de Álava). In *Comunicaciones de las IX Jornadas de Paleontología, Málaga* (pp. 23–28).
- Astibia, H., Pereda, X., Payros, A., Murelaga, X., Berreteaga, A., Bacta, J. I., & Badiola, A. (2007). Bird and mammal footprints from the Tertiary of Navarre (Western Pyrenees). *Ichnos*, 14, 175–184. <https://doi.org/10.1080/10420940601049917>
- Boutakiout, M., Hadri, H., Nouri, J., Caro, S., & Pérez-Lorente, F. (2006). The syngenetic structure suite of dinosaur footprints in finely laminated sandstones. Site nº 1 of Bin El Ouidane (IBO; Central Atlas, Morocco). *Ichnos*, 13, 39–42. <https://doi.org/10.1080/10420940600739781>
- Brown, R., Ferguson, J., Lawrence, M., & Lees, D., 2003. *Huellas y señales de las aves de España y de Europa Ed* (p. 334). Omega
- Brown, T. 1999. *The science and art of tracking* (p. 219). Berkley Books
- Camens, A. B., & Worthy, T. H. (2019). Pliocene avian footprints from the Lake Eire Basin, South Australia. *Journal of Vertebrate Paleontology*. <https://doi.org/10.1080/02724634.2019.1676764>
- Casanovas-Cladellas, M. L., & Santafé-Llopis, J. V. (1982). Icnofauna oligocena de Agramunt (Lérida, España). *Acta Geológica Hispánica*, 17, 113–119.
- Coria, R. A., Currie, P. J., Eberth, D., & Garrido, A. (2002). Bird footprints from the Anacleto Formation (Late Cretaceous) in Neuquén Province, Argentina. *Ameghiniana*, 39, 453–463.
- Currie, P. J. (1981). Bird footprints from the Gething Formation (Aptian, Lower Cretaceous) of northeastern British Columbia, Canada. *Journal of Vertebrate Paleontology*, 1, 257–264.
- de Raaf, J. F. M., Beets, C., & Korternbout, G. (1965). Lower Oligocene bird tracks from northern Spain. *Nature*, 207, 146–148.
- De Valais, S., & Melchor, R. N. (2008). Ichnotaxonomy of bird-like footprints: An example from the Late Triassic-Early Jurassic of northwest Argentina. *Journal of Vertebrate Paleontology*, 28, 145–159. [https://doi.org/10.1671/0272-4634\(2008\)28\[145:IOBFAE\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2008)28[145:IOBFAE]2.0.CO;2)
- Díaz-Martínez, I., García-Fernández, S., Hernández, J. M., Murelaga, X., & Pérez-Lorente, F. (2011). Icnitas de aves y mamíferos del Mioceno temprano de La Rioja (Cuenca del Ebro, España). *Ameghiniana*, 48, 139–153.
- Díaz-Martínez, I., Hernández, J. M., García-Fernández, S., Murelaga, X., & Pérez-Lorente, F. (2012). *Uvaichnites riojana*: A new crane-like bird ichnotaxon from the lower Miocene of La Rioja (Ebro Basin, Spain). *Proceedings of the Geologists' Association*, 123, 464–470. <https://doi.org/10.1016/j.pgeola.2012.02.003>
- Díaz-Martínez, I., Suarez-Hernando, O., Martínez-García, B. M., Hernández, J. M., García-Fernández, S., Pérez-Lorente, F., & Murelaga, X. (2015). Early Miocene shorebird-like footprints from the Ebro Basin, La Rioja, Spain: Paleoenvironmental and paleoenvironmental significance. *Palaios*, 30, 424–431. <https://doi.org/10.2110/palo.2014.078>
- Díaz-Martínez, I., Suarez-Hernando, O., Martínez-García, B. M., Larrasoña, J. C., & Murelaga, X. (2016). First bird footprints from the lower Miocene Lerín Formation, Ebro Basin, Spain. *Palaeontologia Electronica*. <https://doi.org/10.26879/604>
- Doyle, P., Wood, J. L., & George, G. T. (2000). The shorebird ichnofacies: An example from the Miocene of southern Spain. *Geological Magazine*, 137, 517–536. <https://doi.org/10.1017/S0016756800004490>
- Elbroch, M., & Marks, E. (2001). Tracks and trails. In M. Elbroch & E. Marks (Eds.), *Bird tracks and sign: A guide to North American species* (pp. 13–165). Stackpole Books Mechanicsburg.
- Falk, A.R. (2009). *Interpreting behavior from early Cretaceous bird tracks and the morphology of bird feet and trackways* (p. 140). Master's thesis, University of Kansas
- Fiorillo, A., Hasiotis, S., & Kobayashi, Y. (2011). Bird tracks from the Upper Cretaceous Cantwell Formation of Denali National Park, Alaska: A new perspective on ancient northern polar vertebrate biodiversity. *Journal of Systematic Paleontology*, 9, 33–49. <https://doi.org/10.1080/14772019.2010.509356>
- García Raguél, M., Cuevas González, I., Díaz-Martínez, I., & Pérez-Lorente, F. (2009). Fragmentos de roca con huellas de ave en el terciario de Alcanadre (La Rioja). Descripción, estructuras y problemas de identificación. *Zubia*, 27, 81–158.
- Gatesy, S. M. (2003). Direct and indirect tracks features: What sediment did a dinosaur touch? *Ichnos*, 10, 91–98. <https://doi.org/10.1080/10420940390255484>
- Genise, J. F., Melchor, R. N., Archangelsky, M., Bala, L. O., Straneck, R., & de Valais, S. (2009). Application of neoichnological studies to behavioural and taphonomic interpretation of fossil bird-like tracks from lacustrine settings: The Late Triassic-Early Jurassic Santo Domingo Formation, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 143–161. <https://doi.org/10.1016/j.palaeo.2008.08.014>
- Hernández-Pacheco, F. (1929). Pistas de aves fósiles en el Oligoceno de Peralta de la Sal (Lérida). *Memorias de la Real Sociedad Española de Historia Natural*. XV (pp. 379–382).
- Herrero, C. (1997). Las huellas fósiles de La Hoya de la Sima. *El Picarcho*, 93, 21–22.
- Herrero, C., Herrero, E., Martín-Chivelet, J., & Pérez-Lorente, F. (2022). Vertebrate ichnofauna from Sierra de las Cabras track-site (Late Miocene, Jumilla, SE Spain). Mammalian ichnofauna. *Journal of Iberian Geology*, 48, 241–279. <https://doi.org/10.1007/s41513-022-00192-5>
- Herrero, E. (2008). Nuevo yacimiento de icnitas de la Sierra de las Cabras (Jumilla, Murcia). In M. Lechuga Galindo, P. E. Collado Espejo, M. B. Sánchez González (Eds.), *XIX Jornadas de Patrimonio Cultural de la Región de Murcia: [celebradas en] Cartagena, Alhama de Murcia, La Unión y Murcia Vol. 1* (Paleontología, Arqueología, Etnografía) (pp. 39–40).
- Herrero, C. (2010). Cubierta de protección en el yacimiento de icnitas de la Sierra de las Cabras, Jumilla (Murcia). In *Proceedings of the XIX jornadas de patrimonio cultural de la Región de Murcia* (pp. 41–42).
- James, H. F. (2005). Paleogene fossils and the radiation of modern birds. *The Auk*, 122, 1049–1054. <https://doi.org/10.1093/auk/122.4.1049>
- Kim, B. K. (1969). A study of several solemarks in the Haman Formation. *Journal of the Geological Society of Korea*, 5, 243–258.
- Kim, J. Y., Lockley, M., Seo, S. J., Kim, K. S., Kim, S. H., & Baek, K. S. (2012). A paradise of Mesozoic birds: The world's richest and most diverse Cretaceous bird track assemblage from the Early Cretaceous Hanman formation of the Cajinn tracksite, Jinju, Korea. *Ichnos*, 19, 28–42.
- Kordos, L. (1983). Ujabb adatok az ipolytarnoci also-miocen homokko labnyomaihoz. *Magyar Allami Foldtani Intézet Evi Jelentése*, 1985, 453–465.
- Krapovickas, V. (2010). *El rol de las trazas fósiles de tetrápodos en los modelos de icnofacies continentales en ambientes de climas áridos-semiáridos* (p. 343). Universidad de Buenos Aires.
- Lallensak, J. N., Van Heteren, A. H., & Wings, O. (2016). Geometric morphometric analysis of intratrackway variability: A case study on theropod and ornithopod dinosaur trackways from Münchehagen (Lower Cretaceous, Germany). *PeerJ*. <https://doi.org/10.7717/peerj.2059>
- Leonardi, G., (Ed.) (1987). *Glossary and manual of tetrapod footprint palaeoichnology* (p. 75). Departamento Nacional da Produção Mineral, Brasilia, Brazil

- Li, R., Lockley, M. G., & Liu, M. (2005). A new ichnotaxon of fossil bird track from the Early Cretaceous Tiajialou Formation (Barremian-Albian), Shandong Province, China. *Chinese Science Bulletin*, 50, 1149–1154.
- Lockley, M. G., Yang, S. Y., Matsukawa, M., Flemming, F., & Lim, S. K. (1992). The track record of Mesozoic bird: Evidence and implications. *Philosophical Transactions of the Royal Society of London*, 336, 113–114.
- Lockley, M. G., Li, R., Harris, J., Matsukawa, M., & Liu, M. (2007). Earliest zygodactyl bird feet: evidence from early Cretaceous Road Runner-like traces. *Naturwissenschaften*, 94, 657–665.
- Lockley, M. G., Li, J., Matsukawa, M., & Li, R. (2012a). A new avian ichnotaxon from the Cretaceous of Nei Mongol, China. *Cretaceous Research*, 34, 84–93. <https://doi.org/10.1016/j.cretres.2011.10.006>
- Lockley, M. G., Lim, J. D., Kim, J. Y., Kim, K. S., Huh, M., & Hwang, K. G. (2012b). Tracking Korea's early birds: A review of Cretaceous avian ichnology and its implications for evolution and behavior. *Ichnos*, 19, 17–27. <https://doi.org/10.1080/10420940.2012.660409>
- Lockley, M., Kim, K. S., Lim, J. D., & Romilio, A. (2020). Bird tracks from the Green River Formation (Eocene) of Utah: ichnotaxonomy, diversity, community structure and convergence. *Historical Biology*. <https://doi.org/10.1080/08912963.2020.1771559>
- Lockley, M. G., & Harris, J. D. (2010). On the trail of early birds: a review of the fossil footprint record of avian morphological and behavioral evolution. In P. K. Ulrich et al., (Eds.), *Trends in ornithology research* (pp. 1–63).
- Lucas, S. G., Kelly, S. A., Spielmann, J. A., Lockley, M. G., & Connell, S. D. (2007). Miocene bird footprints from Northern New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, 42, 169–176.
- Mangin, J. P. (1962). Traces de pattes d'oiseaux et flute-casts associés dans un "facies-flysch" du Tertiaire Pyrénéen. *Sedimentology*, 1, 163–166. <https://doi.org/10.1111/j.1365-3091.1962.tb00033.x>
- Masrou, M., Lkebir, N., & Pérez-Lorente, F. (2017). Anza palaeoichnological site. Late Cretaceous. Morocco. Part II. Problems of large dinosaur trackways and the first African Macropodosaurus trackway. *Journal of African Earth Sciences*. <https://doi.org/10.1016/j.jafrearsci.2017.04.019>
- McCrea, R. T., & Sarjeant, W. A. S. (2001). New ichnotaxa of bird and mammal footprints from the Lower Cretaceous (Albian) Gates Formation of Alberta. In K. Carpenter, D. H. Tanke, & M. W. Skrepnick (Eds.), *Mesozoic vertebrate life* (pp. 453–478). University of Indiana Press.
- McCrea, R. T., Buckley, L. G., Plint, A. G., Currie, P. J., Haggart, J. W., Helm, C. W., & Pemberton, S. G. (2014). A review of vertebrate track-bearing formations from the Mesozoic and the earliest Cenozoic of the western Canada with a description of a new theropod ichnospecies and reassignment of an avian ichnogenus. *New Mexico Museum of Natural History and Science Bulletin*, 62, 5–93.
- Melchor, R. N., De Valais, S., & Genise, J. F. (2002). Bird-like fossil footprints from the Late Triassic. *Nature*, 417, 936–938. <https://doi.org/10.1038/nature00818>
- Melchor, R. N., & de Valais, S. (2006). Ichnotaxobases for bird-like footprints: towards a uniform approach. *3rd Workshop on ichnotaxonomy*. Prague and Jevicko (Czech Republic) (pp. 17–18).
- Murelaga, X., Astibia, H., Baceta, J. I., Almar, Y., Beamud, B., & Larascaña, J. C. (2007). Fósiles de pisadas de aves en el Oligoceno de Etaio (Navarra, Cuenca del Ebro). *Geogaceta*, 41, 139–142.
- Panin, N., & Avram, E. (1962). Noe urme de pas de vertebrate in Miocenul Subcarpatilor Ruminestkya. *Studie Si Cercetari De Géologie, Géophysica, Si Géografie, Serie Géologie*, 7, 455–484.
- Payrós, A., Astibia, H., Cearreta, A., Pereda-Suberbiola, X., Murelaga, X., & Badiola, A. (2000). The Upper Eocene South Pyrenean coastal deposits (Liedana Sandstone, Navarre): Sedimentary facies, benthic foraminifera and avian ichnology. *Facies*, 42, 107–132. <https://doi.org/10.1007/BF02562569>
- Peabody, F. E. (1955). Taxonomy and the footprints of Tetrapods. *Journal of Paleontology*, 29, 915–918.
- Pérez-Lorente, F., Rodríguez, T., Mancheño, M. A., Serrano, F., & Romero, M. (1997). Pisadas fósiles de mamíferos en el Mioceno Superior de la Hoja de la Sima (Jumilla, Murcia, España). *Memorias De Arqueología*, 12, 15–28.
- Pérez-Lorente, F., Serrano, F., Rodríguez, T., Mancheño, M. A., & Romero, M. (1999). Pisadas fósiles de mamíferos en el mioceno superior de La Hoya de la Sima (Jumilla, Murcia, España). *Revista Española De Paleontología*, 14, 257–267.
- Pérez-Lorente, F., Herrero, C., Herrero, E., & Montoya, P. (2009). *Paracamelichnum jumillensis*, n. ichnogen. n. ichnosp., Upper Miocene Camelidae Ichnites from the Hoya de la Sima site (Murcia, Spain). *Ichnos*, 16, 208–219. <https://doi.org/10.1080/10420940802686087>
- Prats, M., & López, G. (1995). Síntesi de la Icnofauna del Sinclinal d'Agramunt, entre el Meridià d'Agramunt i el riu Segre (Prov. de Lleida). *Paleontologia i Evolució*, 28–29, 247–267.
- Romero-Molina, M. M., Pérez-Lorente, F., & Rivas, P. (2003). Análisis de la parataxonomía utilizada con las huellas de dinosaurio. In *Dinosaurios y otros reptiles mesozoicos de España*, vol 26 (pp. 13–32). Instituto de Estudios Riojanos, Ciencias de la Tierra
- Sarjeant, W. A. S. (1989). "Ten paleoichnological commandments": A standardized procedure for the description of fossil vertebrate footprints. In D. D. Gillette & M. G. Lockley (Eds.), *Dinosaur tracks and traces* (pp. 369–370). Cambridge Univ. Press.
- Sarjeant, W. A. S., & Langston, W. (1994). Vertebrate footprints and invertebrate traces from the Chadronian (Late Eocene) of West Texas. *Texas Memorial Museum Bulletin*, 36, 1–86.
- Sarjeant, W. A. S., & Reynolds, R. E. (2001). Bird footprints from the Miocene of California. In R. E. Reynolds, (Ed.), *The changing face of the Mohave desert*, Abstracts from the 2001 Desert Symposium (pp. 21–40).
- Thulborn, R. A. (1990). *Dinosaur tracks*. Chapman and Hall.
- Thulborn, R. A., & Wade, M. (1989). A footprint as a history of movement. In D. D. Gillette & M. G. Lockley (Eds.), *Dinosaur tracks and traces* (pp. 51–56). Cambridge Univ. Press.
- Vialov, O. S. (1965). *Stratigrafiya neogenovix molass Predkarpatskogo progiba*. Naukova Dunka (K), Kiev
- Vialov, O. S. (1966). *Sledy zhiznedeyatel'nosti organizmov I ikh paleontologicheskoe znachenie* (p. 219). Akademii Nauk Ukranian
- Vilas, L. Arias, C., Rozycki, A., Herrero, C., & Martínez-Abellán, R. (2006). El yacimiento de icnitas de vertebrados de la Hoya de la Sima (Mioceno terminal). Jumilla, Murcia, España. *De Re Metallica* (pp. 1–6).
- Xing, L., Buckley, L. G., McCrea, R. T., Lockley, M. G., Zhang, J., Piñuela, L., Klein, H., & Wang, F. (2015). Reanalysis of Wupus agilis (Early Cretaceous) of Chongqing, China a large avian trace: differentiating between large bird and small non-avian theropod tracks. *PLoS One*, 10(5), e0124039. <https://doi.org/10.1371/journal.pone.0124039>
- Zonneveld, J. P., Zaim, Y., Rizal, Y., Ciochon, F. L., Bettis, E. A., Aswan, A., & Gunnell, G. F. (2011). Oligocene shorebird footprints, Kandi, Ombilin Basin, Sumatra. *Ichnos*, 18, 221–227. <https://doi.org/10.1080/10420940.2011.634.228>