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New Mammal and Bird tracks from the Lower Oligocene of the Ebro Basin (NE Spain): Implications for the Paleogene ichnological record

Martín Linares [a], Mª Aránzazu Luzón [b], Gloria Cuenca-Bescós [a], José Ignacio Canudo [a], Diego Castanera [a,c*]

[a]*Aragosaurus-IUCA, Facultad de Ciencias, Universidad de Zaragoza, 50009, Zaragoza, Spain*

[b] *Geotransfer-IUCA, Facultad de Ciencias, Universidad de Zaragoza, 50009, Zaragoza, Spain*

[c] *Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, c/ Escola Industrial 23, 08201 Sabadell, Barcelona, Spain*

**Corresponding author*

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ABSTRACT

The Ebro Basin (Spain) is one of the few worldwide areas where Paleogene avian and mammal tracksites have been found. A new unpublished tracksite known as La Sagarreta is here described. The tracksite is located in a sandstone-dominated outcrop from the Early Oligocene Peralta Formation in the northern-central sector of the basin. Six different ichnotaxa have been identified. Four belong to mammals, including perissodactyl (cf. *Plagiolophustipus* isp), artiodactyl (*Megapecoripeda* isp. and cf. *Pecoripeda* isp.) and carnivoramorph tracks (cf. *Canipeda* isp.), and the other two to avian tracks (*Aviadactyla vialovi* and *Gruipeda dominguensis*). La Sagarreta presents a high ichnodiversity with the presence of a medium size member (or relative) likely of the genus *Plagiolophus*, one medium and one small sized artiodactyl that probably belong to the family Entelodontidae, one medium size unidentified carnivorous mammal and two types of birds. La Sagarreta tracksite is the most diverse Early Oligocene tracksite at Ebro Basin and one of the few palaeontologic vertebrate records at the central area of the basin.

Key words: Footprints, Perissodactyla, Artiodactyla, Carnivoramorpha, Avian, Peralta Formation

INTRODUCTION

The paleoichnological record provides information about the behavior of extinct animals and is one of the best ways to make ethological inferences based on the fossil record (e.g. Díaz Martínez et al. 2020, Abbassi et al. 2021). Besides, the study of ichnites provides information about the morphology of the autopod of the trackmakers and the paleoecological association, allowing to reveal the presence of particular groups of vertebrates in a specific place and/or time (Ellenberger 1980; Bravo Cuevas et al. 2018; Neto de Carvalho et al. 2020; Abbassi and Dashtban 2021).

Compared with the osteological record, the Paleogene ichnological vertebrate record is scarce in Europe and worldwide, although the abundance of the Cenozoic ichnological record increases progressively with time, being the Paleogene record significantly lower than the Neogene one (McDonald et al. 2007; Hunt and Lucas 2007; Costeur et al. 2009). However, some areas present a high ichnodiversity and a great abundance of Paleogene tracksites, as the case of Spain (Casanovas-Cladellas and Santafé-Llopis 1982; Astiba et al. 2007; Rabal-Garcés and Díaz-Martínez 2010), France (Desnoyers 1859; Ellenberger 1980; Demathieu et al. 1984; Costeur et al. 2009), the western of United States (Sarjeant and Langston 1994; Lockley and Hunt 1995; Lockley et al. 1999; Mustoe 2002; Lucas and Hunt 2007) and Iran (Yousefi Yeganeh et al. 2011; Abbassi et al. 2015; 2016; Abbassi and Maleki 2020). One of these areas with a considerable number of tracksites is the Ebro Basin, in Northeastern Spain which ichnological record spans from the Lower Eocene to the Lower Miocene (e.g.: Díaz-Martínez et al. 2018; Rabal-Garcés et al. 2018). The Paleogene ichnological record of the Ebro Basin is especially significant in order to reconstruct the vertebrate diversity, especially in the central sector of the basin since the osteological record is very scarce (Cuenca et al. 1992).

There are some geological formations where the footprint record is the only vertebrate paleontological evidence (Lockley 1991). This is the case of the Peralta Formation, a Lower Oligocene stratigraphic unit in the northern central area of the Ebro Basin (Senz and Zamorano 1992). It contains one of the first known Cenozoic vertebrate tracksites in Spain, the so called “La Playa Fósil”, with abundant bird footprints (Hernández-Pacheco 1929). In the vicinity of this site a new tracksite called “La Sagarreta”, which stands out by its high ichnodiversity, has been recently found in the same formation. Different fieldwork visits have allowed the recovery of 37 slabs bearing more than 157 footprints. The aim of this study is the description of these new vertebrate footprints focusing on the ichnotaxonomy and the identification of the candidate trackmakers but also highlighting the ichnodiversity and delineating the paleoenvironmental framework until a more exhaustive study is carried out. An evaluation of the significance of this new site for a global understanding of the Oligocene faunas in the Ebro Basin is also provided.

GEOLOGICAL CONTEXT

La Sagarreta site is located in the NE of the Iberian Peninsula, in the Huesca Province. It is close to the La Sagarreta ravine, 2 km away from Peralta de la Sal village and from La Playa Fossil tracksite.

From the geological point of view La Sagarreta site is situated in the northern-central part of the Cenozoic continental Ebro Basin (Figure 1), the younger foreland basin of the Pyrenees (Riba et al. 1983; Burbank et al. 1992; Muñoz et al. 2002). This broadly triangular basin is bounded by the Pyrenees to the north, the Iberian Range to the south and the Catalan Coastal Ranges to the east. From the Late Eocene to the Late Miocene, the Ebro Basin was endoreic and its paleogeographical configuration was characterized by alluvial and fluvial systems sourced in the basin margins that passed to lacustrine areas in the central areas (Muñoz et al. 2002; Pardo et al. 2004).

The stratigraphic rock units cropping out in the study area are shown in figure 1. La Sagarreta site is situated in the topmost part of the Lower Oligocene Peralta Formation (Senz and Zamorano 1992) that has been interpreted as related to the development of a small alluvial fan sourced in the Marginal Sierras. The alluvial deposits grade towards the south to lacustrine evaporite deposits that belong to the Barbastro Formation (Quirantes 1978). These rocks correspond to the T3 genetic unit defined in the Ebro Basin (Muñoz et al. 2002; Pardo et al. 2004; Luzón 2005).

La Sagarreta tracksite (Figure 2) is in a detrital succession made of an alternation of reddish mudstone and sandstone that represents the interference between distal alluvial and shallow lacustrine areas. Several coarsening-upwards cycles, with a lower, mudstone-dominated part, and an upper sandstone-dominated part can be recognized. Variated sedimentary structures as ripples, cross lamination, mud cracks, as well as microbial-related and bioturbation structures are frequently recognized. Interference ripple forms dominate and climbing ripples are common.

The detailed profile of La Sagarreta tracksite (Figure 3) is mainly integrated by orangish siltstone and fine sandstone (rarely medium to coarse) with interbedded brown mudstone. It shows a general coarsening upwards trend. Sandstones and siltstones form tabular or lenticular beds up to 22 cm in thickness, although levels below 10 cm are the most common. They integrate tabular packages which, in turn, are arranged in coarsening upwards cycles, decimetric in thickness. A high variety of sedimentary structures suggesting changes in water velocity and depth can be identified, mainly linguoid ripples, cross and horizontal lamination and trough cross bedding. Ripples are in some cases climbing ripples, revealing high sedimentation rates and heterolithic bedding indicates intermittent flows. Wrinkle and different microbial mat structures are commonly recognized in the top of the strata. Lithology and sedimentary structures indicate a shallow water mass zone with high sedimentary supply and cyclic desiccation. Considering the general stratigraphy in this zone, the environment would correspond to a marginal lacustrine area reached by detrital supplies from close alluvial areas.

No chronological data exists which allow dating the deposits containing the fossil site, but an approximation to its age is possible based on the stratigraphical relation between the Peralta Formation, containing the site, with other stratigraphic units in the area. The upper part of the Barbastro Formation, which is lateral to the Peralta Formation, is capped by a carbonate succession several meters-thick, being both units covered in the study area by the conglomerate and sandstone fluvial Peraltilla Formation In nearby areas to the East (Peraltilla area) the lower part of this formation interbeds several limestone beds that have been dated as middle-upper Rupelian (*Theridomys major*-MP-23) by Álvarez Sierra et al. (1990). Based on these data, an although we are conscious of the possibility that the carbonate beds could not be the exactly the same due to lateral facies changes, a Rupelian age is proposed as very plausible for the studied succession.

MATERIALS AND METHODS

The studied footprints come from a very fine-fine sandstone-mudstone package (Figure 3) located in the upper part of the Peralta Formation. The outcrop is ca. 230 x 50 m and the stratigraphical succession, with several strata and laminae is nearly vertical (Figure 2). Footprints can be recognized in several strata, indicating they were not produced synchronously and not all the strata contain footprints. Most of these beds are strongly fractured and numerous slabs have been detached from the outcrop, being most of the studied ichnites from these fallen slabs. The slabs and the ichnites have been found in five different areas in La Sagarreta outcrop and one isolated ichnite outside the principal outcrop in a lower stratigraphic level (Figure 2). Multiple bird tracks have been identified in-situ in several areas and layers but their study is out of the scope of these paper and a detailed study focused on them will be carried out in the nearly future. On the other hand, few mammal tracks have been identified in-situ and they are included in the present research.

For this study, 37 slabs bearing footprints have been described (see Tables S1 and S2). These slabs are greatly variable in size but they never exceed 50 cm in diameter and 5 cm in thickness. They are housed in the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ, Canudo 2018). The slabs were numbered following the collection numbers from MPZ-2022-147 to MPZ-2022-181 and MPZ-2022-210 and MPZ-2022-211. 157 ichnites have been identified in the surface of the slabs. Almost all the tracks are isolated but some of the avian ichnites form a trackway (e.g.: MPZ-2022-149 and MPZ-2022-157). On the other hand, the ichnites found in situ on the tracksite only the mammal footprints were considered and numbered using LSC (La Sagarreta “Campo” = which means field) as identifier.

In the studied samples, the ichnites are preserved as natural casts (convex hyporeliefs) and true tracks or shallow undertracks (concave epireliefs). The morphological preservation quality has been evaluated according to the scale proposed by Marchetti et al. (2019). These values must be considered in relation to the morphology of the ichnites and the information they can provide. Only the ichnites with a preservation grade of 2 or more have been used for the systematic assignments (Marchetti et al. 2019). The ichnites with low preservation grade do not allow establish new assignments but they could be associated with previously established ichnotaxa. Open nomenclature has been used following Bengtson (1988).

All the slabs and the ichnites were photographed and individually measured using previously established methods for studying the morphology of bird and mammal footprints (e.g.: De Valais and Melchor 2008; Costeur et al. 2009; Melchor et al. 2019). The measurements (Figure 4) taken on the footprints include the footprint length (L), footprint width (W), digit length (L_I, L_{II}, L_{III}, L_{IV}), digit width (W_I, W_{II}, W_{III}, W_{IV}) and the interdigital angles (II^III, III^IV, II^IV, I^IV, I^II). The length and width were taken directly from the footprints in the slabs. In the case of the angles, the software ImageJ (https://imagej.nih.gov/ij/download.html) was used. For the bird ichnites it must be considered that in the case of curved lateral digits the measure of digital divarication could be more subjective (Camens and Worthy 2019). In the case of the trackways, the mean stride (S) and pace length (P) were also measured. In the tridactyl footprints it has been impossible to determine if the individual footprints are the impression of the right or left foot, so the lateral digits were identified according to their position with respect to the central digits. In the case of the tetradactyl footprints, right and left footprints were identified according to the medial location of digit I (hallux).

Digital three-dimensional models of the most significant footprints were obtained from high-resolution digital photogrammetry using a standard protocol for ichnological studies (Matthews et al. 2016; Falkingham et al. 2018). The 3D models were generated from sets of 30-50 pictures taken with a Canon PowerShot SX740HS camera, using Agisoft Metashape Standard Edittion (v.1.6.5.11249. www.agisoft.com). After that the 3D model has been processed in Cloudcompare (V.2.12, https://www.danielgm.net/cc/) to create a false-colour depth map that help in the morphological descriptions of the studied of ichnites. Photogrammetric meshes of the relevant specimens created for this study are available for download in the supplementary information.

SYSTEMATIC ICHNOLOGY

Perissodactyl footprints

Ichnogenus Plagiolophustipus Santamaria et al. 1989-1990

Type ichnospecies: *Plagiolophustipus montfalcoensis* Santamaria et al.1989-1990

Diagnosis: Tridactyl ichnite with a central digit much longer and wider than the laterals, which are slightly asymmetrical. The overall length of the track varies between 5 and 6 cm.

cf. *Plagiolophustipus* isp. (Figure 5)

Material: Eight isolated ichnites (MPZ 2002-147, MPZ 2002-163, MPZ 2002-176, MPZ 2002-179, MPZ 2002-180, MPZ 2002-181, LSC3), three preserved as concave epirelief and five as convex hyporelief. Also, two concave epirelief preserved in situ as a tracksite (LSC4.1 and LSC4.2) (Figure 2, point 4).

Description: Tridactyl mesaxonic footprints with sub-elliptic morphology, longer than wide (8-11 cm length and 5.5-8 cm width). Central digit (III) is considerably larger, rounder and wider and protrudes anteriorly over the lateral digits (II and IV). Lateral digits are more elongated and have a variable anterior morphology with sharply-pointed to rounder tip. The lateral digits are slightly asymmetric being one of them slightly larger and displaced forward. The posterior part of the footprint has a round and wide morphology with a similar width than the central digit. The digits are united with the posterior part and only in the ichnites with the higher morphological preservation quality the central hoof is distinguishable. The digits have similar interdigital angles (30º-45º) between the central digit (II) and lateral digits (II and IV), the footprints being quite symmetric (Figure 5). There are two consecutive tracks (LSC4.1-4.2) that might be part of the same trackway with an approximate pace length of 20 cm.

It is noted a difference in the sample between the morphology of the lateral digits. Three specimens have lateral digits with a rounder morphology (Figure 5 (A-F)) whereas the others have a sharper and elongated morphology (Figure 5 (G-L)). These two morphotypes do not have any other difference. The different morphology of the lateral digits described in our sample coincides with the mode of preservation of the footprints as epirelief or hyporelief, so the epireliefs have rounder lateral digits and the hyporeliefs sharper digit morphology.

Discussion

Firstly, the difference previously mentioned between the two morphotypes identified in the sample could be explained to be product of the different preservation mode of the ichnites (epireliefs vs hyporeliefs) and/or the substrate conditions at the time of track production and/or anatomical differences between manus and pes in the trackmakers. For this last hypothesis is impossible determine if La Sagarreta ichnites are pes or manus since they are isolated specimens. There are not manus and pes differences described in the literature for other *Plagiolophustipus* ichnites although no trackways have been described (e.g. Santamaría et al. 1989-1990; Astibia et al. 2007). It is noteworthy that *Palaeotheriipus sarjeanti* has manus less elongated and a central digit not as developed as in the pes (Ataabadi and Khazaee 2004). However, the manus and pes of *Plagiolophustipus* and their differences are unknown. In addition, the hyporeliefs present a bigger depth than the epireliefs, so their differences could be related to differences in the substrate conditions with a softer substrate when the footprints preserved as hyporeliefs were produced. So, these differences could be the product of the sedimentological characteristics of substrate that give these subtle differences in the lateral digits. It is impossible to determinate which one of these hypotheses is more solid in the current state of knowledge and with the available material. Perissodactyl footprints are known through the different Cenozoic stages and multiple ichnotaxa are described (Vialov 1966; McDonald et al. 2007; Costeur et al. 2009). The key to determine that they are perissodactyls is the mesaxonic character of the footprints (the middle digit bears most of the animal's weight) with usually an odd number of digits (some members show tetradactyl manus; Mustoe 2002). There are four ichnotaxa with similar morphology to the perissodactyl tracks from La Sagarreta, three of them associated to palaeothere mammals (Figure 6): *Palaeotheriipus* from the Eocene of France and Iran (Ellenberger 1980; Ataabadi and Khazaee 2004), *Lophiopus* from the late Eocene of France (Ellenberger 1980), *Moropopus* from the late Eocene of Iran (Abbassi et al. 2016) and *Plagiolophustipus* from the Early Oligocene of Spain (Santamaría et al. 1989-1990). Besides, other perissodactyl ichnotaxa characterized by tridactyl footprints such as *Rhinoceripeda* from the Miocene of Hungary (Vialov 1965; full description in Kordos 1985) and identified in the Oligocene of France (Costeur et al. 2009) have a more oval and rounded morphology and three oval hoof impressions.

Palaeotheriipus has two different ichnospecies *P. similimedius* (Ellenberger 1980) from the late Eocene of France and *P. sarjeanti* (Ataabadi and Khazaee 2004) from the middle Eocene of Iran. *Palaeotheriipus* presents great similarities with the morphology of the studied ichnites, especially *P. sarjeanti.* Main differences of *Paleotheriipus* ichnospecies are in the heel impression (*P. similimedius* has a rounder heel). The ichnospecies *P. sarjeanti* shows similar central digit and metacarpal impressions, however it has larger total size and parallel lateral digits with more symmetry between them. *Lophiopus* has two ichnospecies *L. rapidus* and *L. latus* (Ellenberger 1980). In general, *Lophiopus* has a similar size than the studied ichnites and three digits with smaller lateral digits with a sharp tip. *L. rapidus* has a marked "heel mark" that is not present in *L. latus. Lophiopus,* especially *L. rapidus,* has similarity with La Sagarreta ichnites but the central digit in *Lophiopus* is narrower (in the studied ichnites the width in the central digit is close to the heel width) and the lateral digits are symmetrical. Besides, *Lophiopus* show a greater divergence between their digits (with a total divarication angle II^IV higher than 90º).

Moropopus is a monospecific ichnogenus with only the ichnospecies *M. elongatus* defined (Abbassi et al. 2016). These ichnites present lateral digits more separated and isolated from the central digit, existing a marked separation between them. Also, the digits present a slightly curve to the front part of the footprint that it is absent in La Sagarreta footprint.

In other hand, *Plagiolophustipus* has smaller size, asymmetrical lateral digits that are less rounded than in *Palaeotheriipus*. Ichnites with a great variety in the size and the morphology of the lateral digits have been associated with this ichnogenus. The central digit is rounder and has a similar width to the heel. All these features make this ichnogenus the most similar to La Sagarreta perissodactyla tracks.

There is only one ichnospecies included in the ichnogenus *Plagiolophustipus*, *P. montfalcoensis* (Santamaría et al. 1989-1990). However, *Plagiolophustipus* has been described in other areas of the Ebro Basin showing a great variety of size and morphology of ichnites (Santamaría et al. 1989-1990; Murelaga et al. 2000; Astibia et al. 2007; de Gibert and Sáez 2009; Díaz-Martínez et al. 2018). La Sagarreta ichnites have a slightly larger size (a size range is included in the diagnosis) and more symmetrical lateral digits than the holotype ichnites (Santamaría et al. 1989-1990) but they are not as large as the ichnites described by Murelaga et al. (2000). These ichnites also have even more symmetrical lateral digits and a sharper central digit than those of La Sagarreta. Considering their similarity, but also the aforementioned differences of La Sagarreta ichnites with the holotype, it was decided to classify them with open nomenclature as cf. *Plagiolophustipus* isp. until a revision of the material assigned to this ichnotaxa including the type series is carried out.

Artiodactyl footprints

Ichnogenus: *Megapecoripeda* Kordos, 1985

Type ichnospecies: Megapecoripeda miocaenica Kordos, 1985

Diagnosis: Footprints of a large artiodactyl of composite stature. The print of the inner hoof is usually smaller than it is the case with the outer hoof, being shifted distally. In case of quiet gait and a horizontal, even surface this asymmetry will disappear. The hoof prints grow proximally wider, deviating by 10 to 20 degrees from the axial line.

Megapecoripeda isp. (Figure 7)

Material: one concave hyporelief in the slab (MPZ 2022-177) and one in situ on field (LSC1) (Figure 2, point 2)

Description: didactyl footprint showing two symmetrical and parallel-arranged digits imprints with a slightly union between the digits that allows to see all the digit morphology. They have a large size (7-8 cm long and 7 cm wide) with a marked dominance (around 40-50%) of the length respect to the width of each digit (Figure 7 (A, B)). One of the digits is slightly larger than the other. They have an oval morphology with round shape in the anterior and posterior part. There are not lateral digit impressions even with the great depth of some ichnites.

Discussion: The presence of only two digits and the paraxonic characteristics of the ichnites allow their interpretation as Artiodactyla tracks. This kind of ichnites have a great similarity with its associated ichnotaxa, being only the morphology and size variations the principal differences between them (Lucas and Hunt 2007; Costeur et al. 2009; Abbassi et al. 2015). Abbassi et al. (2015) summarized some of the most important ichnogenus of artiodactyl footprints: *Anoplotheriipus* (Ellenberger, 1980), *Bifidipes*

(Demathieu et al. 1984; emend. Fornós et al. 2002), *Bijugopeda* (Sarjeant and Reynolds 1999), *Bothriodontipus* (Santamaría et al. 1989-1990), *Camelipeda* (Vialov 1984), *Diplartiopus* (Ellenberger 1980), *Dizygopodium* (Sarjeant and Reynolds 1999), *Entelodontipus* (Casanovas-Cladellas and Santafé-Llopis 1982), *Gambapes* (Sarjeant and Langston 1994), *Lamaichnum* (Aramayo and Manera de Bianco 1987), *Megalamaichnum* (Aramayo and Manera de Bianco 1987), *Megapecoripeda* (Kordos 1985), *Odocoileinichnium* (Aramayo and Manera de Bianco 1987), *Paracamelichnum* (Pérez-Lorente et al. 2009) and *Pecoripeda* (Vialov 1965).

The medium artiodactyl footprints from La Sagarreta have visible separated digits which allows to eliminate ichnotaxa attributed to Camelidae footprints, because they have a characteristic union between the digits such as in *Camelipeda*, *Paracamelichnum*, *Megalamaichnum, Lamaichnum*, *Dizygopodium* and *Bijugopeda* (Lucas and Hunt 2007). The French Eocene footprints of the ichnogenus *Anoplotheriipus* and *Diplartiopus* also present that union between their digits making impossible to determinate the morphology of the individual digits (Ellenberger 1980).

Some ichnotaxa associated with Artiodactyla have more than two-digit tracks so they can also be discarded. These are *Bothriodontipus* (Santamaría et al. 1989-1990), *Fustinianapodus* (Díaz-Martínez et al. 2020), *Cervipeda* (Vialov 1965), and *Suidichnus* (Neto dee Carvalho et al. 2020). *Bothriodontipus* and *Fustinianapodus* are tetradactyl ichnites with four-digit impressions oriented anteriorly. On the other hand, *Suidichnus* and *Cervipeda* has two large central digits oriented anteriorly and the impression of two lateral dew claw in the posterior direction.

Entelodontipus, *Bifidipes*, *Pecoripeda, Megapecoripeda* and *Gambapes* (Figure 8) have only two-digit impressions and are the most similar to the studied tracks. *Bifidipes* has subtriangular digit impressions with a high divarication, with divergent margins and separation (Demathieu et al. 1984; Fornós et al. 2002). *Entelodontipus* has small size and subparallel digit impressions with a subelliptic morphology and a posterior part wider than the anterior part (Casanovas-Cladellas and Santafe-Llopis 1982). *Pecoripeda* has two digits that are always separated but sometimes in contact to each other. They have a similar wedge shaped and sharp or round tip, and have a width less than 35% of their length (Sarjeant and Langston 1994). These digits can be convergent, parallel or divergent according to the pace. *Megapecoripeda* has a great similarity to *Pecoripeda* but it has a larger size (Costeur et al. 2009). *Gambapes* is very similar to *Pecoripeda* with the same general morphology, only existing a difference in the relation between length and width, *Gambapes* ichnites has a width greater than 35% than length and a smaller size (Sarjeant and Langston 1994). Nonetheless, *Gambapes* has been suggested to be a junior synonym of *Pecoripeda* (Lucas and Hunt 2007).

Costeur et al. (2009) suggest the use of *Megapecoripeda* for all the large size artiodactyl ichnites with only two digits. Also, the ichnites associated with *Megapecoripeda* present a slightly marked union between their digits, that it is more marked in the posterior part. The aforementioned Camelidae ichnites present also a union between their digits although in *Megapecoripeda* case even with a union in all the length of the digit the inner margin of the digit is identifiable, so, the morphology of the digit is distinguishable. The studied ichnites present a similar size, morphology, and type union between the digits that the ichnites associated with *Megapecoripeda.*

Two different ichnospecies associated to *Megapecoripeda*, *M. miocaenica* (Kordos1985) and *M. velox* (Costeur et al. 2009) have been identified. The latter is a combination between *Bifidipes velox* and *Megapecoripeda*. Both ichnospecies are similar having the same size and morphology, but *M. miocaenica* has an asymmetrical digit and a slightly divarication between the digits. *M. velox* has a great variety of morphologies and interdigital angles, but their digits are symmetrical in comparison with *M. miocaenica.* This makes the ichnites described by Costeur et al. (2009) more similar to the studied ichnites, but the combination proposed by these authors presents problem with respect its ichnotaxonomy validity. Firstly, Costeur et al. (2009) did not establish the diagnostic features at ichnospecies level and the principal reason for the combination was the size of the footprints. Abbassi et al. (2021) commented the doubts of the validity of this approach because the variation in size of footprints is not a valid ichnotaxobase. Thus, with only one well-preserved ichnite in La Sagarreta it is impossible establish an ichnospecific assignation to the studied materials with certainty.

Ichnogenus: *Pecoripeda* Vialov (1965), emmend. Sarjeant and Langston 1994

Type ichnospecies: Pecoripeda gazella

Diagnosis: Artiodactyl footprints of elongated wedge shape, indicating the presence of two hooves in both the manus and pes. Manus and pes of closely similar form, though sometimes of different size. The medial (III) and lateral (IV) hoof prints are always distinct, with axial surfaces sometimes in median or posterior contact, more often separated by continuous interdigital space. The medial and lateral hooves are exact or mirror images in outline; each is broadest posteriorly, tapering anteriorly angular or sharply parabolic apex. Apices of hoof prints directed forward; axes convergent,parallel or divergent according to pace. The maximum breadth of each hoof print is less than 35% of its length (Sarjeant and Langston 1994)

cf. *Pecoripeda* isp. (Figure 7)

Material: one ichnite preserved as a concave epirelief (MPZ 2022-151) in a slab.

Description: Track with two digital impressions with a marked separation between them. It has small size and is considerably longer than wide (2.5 cm and 1 cm respectively, length/width ratio 2.5). The hoof imprint is round and wide at the rear and narrow at the front with a sharp and subacute tip. The inner margin is straight. The anterior tips of the digits diverge more than 40% (Figure 7 (D-F)).

Discussion: Attending the previous discussion, the didactyl character of these footprints allows to discard the tetradactyl ichnotaxa and those assigned to Camelids with a union in their digits. MPZ 2022-151 differs from the *Megapecoripeda* specimens in their smaller size. In artiodactyl tracks, manus imprints are usually smaller than the pes impressions, but in the case of *Megapecoripeda velox* their manus are larger than the pes (Costeur et al. 2009).

The morphology of the ichnite is also different, being more similar to *Pecoripeda* ichnites (Vialov 1965) with only two long and narrow digits that have a larger posterior part and a convergence anteriorly with sharp anterior tips. Nonetheless, the length/width ratio is higher than in *Pecoripeda*. *Entelodontipus* (Casanovas-Cladellas and Santafé-Llopis 1982) also has a wider posterior part, but the digit tips are rounder and subparallel. *Bifidipes* has a similar morphology but they have divergent margins instead of the converging in the studied ichnites (Demathieu et al. 1984; Fornós et al. 2002). *Gambapes* is very similar to *Pecoripeda* but with a higher length/width ratio and as already mentioned has been considered to be a junior synonym of *Pecoripeda* by some authors (Lucas and Hunt 2007). This last ichnotaxa is the association more probable for the studied ichnites but the preservation of the slab, with only one ichnite of this kind and with a fracture that affects it, makes impossible confirm this proposal so the open nomenclature is used.

Carnivoramorph footprints

Ichnogenus: *Canipeda* Panin and Avram 1962

Type Ichnospecies: Canipeda longigriffa Panin and Avram 1962

Diagnosis: Digitigrade to semidigitigrade, tetradactyl, paraxonic, longer than wide footprints; arranged in quadrupedal and homopodial trackways. Elliptic, similar-sized and clawed digital pads form an arc in front of, and are well separated from, a large metapodial pad. Metapodial pad rounded to triangular or trapezoidal. *Felipeda* is distinguished by having footprints wider than long, lacking claw marks and with digital pad impressions that tend to be subcircular. (Emend Melchor et al. 2019).

cf. *Canipeda* isp. (Figure 7)

Material: One concave epirelief in the slab (MPZ 2022-168) and one epirelief on the field (LSC2) (Figure 2, point 5, La Sagarreta outcrop).

Description:

Tetradactyl ichnites that are longer than wide (6.7 and 6.7 cm of length, 5 and 3 cm of width) showing four digital impressions separated of the metapodial pad. The digital pads have an ovoidal to elongated shape oriented antero-posteriorly, with a length between 2-3 cm and width about 1 cm. The central digits are longer and more advanced than the lateral ones. The central pads are parallel and the laterals present a slightly divergence. All the digits present claw marks that are not connected with the pad. The claw marks are poorly impressed and have a circular-elliptical morphology. The metapodial pad is large sized (2.5 cm of length and 2 cm of width) showing only one clear pad with a subrectangular-subovoidal shape (Figure 7 (G-I)).

Discussion: The ichnological record in relation to Paleogene carnivorous mammals is very scarce and is mostly composed of pentadactyl (Ellenberger 1980; Demanthieu et al. 1984; Sarjeant and Wilson 1988; Sarjeant and Langston 1994; McCrea et al. 2004; Costeur et al. 2009) and tetradactyl ichnogenera (Casanovas-Cladellas and Santafé-Llopis 1974; Santamaria et al. 1989-1999; Rabal-Garcés and Díaz-Martínez 2010).

There are three large tetradactyl ichnogenera associated with creodonts: *Creodontipus* (Santamaria et al. 1989-1990), *Tetrastoibopus* (Sarjeant and Langston 1994) and *Quiritipes* (Sarjeant, et al. 2002) (Figure. 9), which have slightly similar footprint morphology to the studied specimens although none of them coincide perfectly with the footprints from La Sagarreta. *Creodontipus* has ichnites that are wider than long with digital impressions with an acuminate (pointed) morphology and very close digits. *Tetrastoibopus* has lateral digits with larger dimensions than the central ones, and *Quiritipes* does not preserve claw marks, (although Melchor et al. 2019 doubt this interpretation), and presents digit impressions with multiple pads. The former has a metapodial pad with similar morphology to the studied ichnites whereas the latter two show a triangular metapodial pad. There are other ichnotaxa associated with creodonts: *Dischidodacylus stevensi* (Sarjeant and Wilson 1988), *Hyaenodontipus praedator* (Ellenberger 1980), *Sarcotherichnus enigmaticus* (Demanthieu et al. 1984), *Sarjeantipes whitea* (McCrea et al. 2004) and *Zanclonychopus cinicalcator* (Sarjeant and Langston 1994). However, all this ichnotaxa have five digits so they do not coincide with the tetradactyl morphology of the studied specimens.

The most common tetradactyl ichnotaxa generally associated to carnivores are grouped into three main ichnogenera *Bestiopeda* (Vialov 1965), *Felipeda* (Panin and Avram 1962) and *Canipeda* (Panin and Avram 1962). A great variety of morphologies have been grouped in *Bestiopeda*, with pentadactyl and tetradactyl footprints included. *Canipeda* and *Felipeda* have tetradactyl footprints and presents three major differences between them. The latter has a width greater than or similar to the length compared to *Canipeda* in which the length dominates; *Canipeda* has clear claw impressions that tend to be absent in *Felipeda*, and the digital pads are elongated in an anterior-posterior direction compared to the subcircular pads of *Felipeda* (Melchor et al. 2019). All these main *Canipeda* characteristics are seen in the studied ichnites from La Sagarreta so this ichnite can be related to *Canipeda.*

Melchor et al. (2019) reviewed the record of canid and canid-like footprints from the Early Eocene to Holocene. This record includes ichnotaxa that are similar to *Canipeda* (e.g.: *Quiritipes* and *Creodontipus*), ichnites with a dubious association to *Canipeda (*e.g.: cf. *Canipeda* isp. from the Late Eocene of Jaca (Spain); Rabal-Garcés and Díaz- Martínez 2010) and ichnites belonging to *Canipeda* ichnospecies. There are multiples ichnospecies included in *Canipeda* that range with certainty from the Lower Miocene to the Pleistocene: *C. longigriffa* (Panin and Avram 1962): *C. gracilis* (Vialov 1965): *C. therates* (Remeika 1999) y *C. sanguinolenta* (Vialov 1966) (Figure 9). All these ichnospecies differ with the studied ichnites: *C. longigriffa* and *C. sanguinolenta* have a triangular metapodial pad and usually bilobate; *C. therates* has a similar metapodial pad than the previous ichnotaxa and smaller central digits than the lateral ones; *C. gracilis* has smaller size (near to 3.5 cm) with a length/width ratio close to 1 and a subtriangular metapodial pad in the manus and subrounded to elliptical in the pes. This makes *C. gracilis* the ichnotaxa more similar to studied ichnites but *C. gracilis* presents a higher divergence between their digits and the metapodial pad impression is slightly different.

All those features make the aforementioned ichnotaxa different from La Sagarreta ichnites. Interestingly, the tracks from La Sagarreta are similar to the ichnites described by Rabal-Garcés and Díaz- Martínez (2010) from the Late Eocene of Jaca (Spain). They have a similar metapodial pad impression with subelliptic morphology, subparallel digits with large central digits and longer than wide ichnites. They classified the tracks as cf. *Canipeda* and have been subsequently classified as *Canipeda* isp by Melchor et al. (2019). although the authors did not associate them to a specific ichnospecies. Considered the previous discussion we classify the tracks as cf. *Canipeda* isp taken into account the few material in our sample (just 2 specimens) and the similarities with *Canipeda* but also the differences in the metapodial pad impression morphology.

Avian footprint

Morphofamily: Avipedidae, Sarjeant and Langston 1994

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

Discussion:

Sarjeant and Langston (1994) establish four avian morphofamilies: Anatipedidae, Guipedidae, Charadriipedidae and Avipedidae. Gruipedidae and Anatipedidae are tetradactyl, also Anatipedidae and Charadriipedidae have digits united by webbing in all their length or only in part of them. On the other hand, Avipedidae does not have webbing or it is only present in the proximal part of the footprints and they are tridactyl.

Ichnogenus: Aviadactyla Kordos 1985

Type ichnospecies: Aviadactyla media Kordos 1985

Diagnosis: Avian footprints of small to moderate size composed of three digital impressions. Digits of slender to moderate width, tapering distally and sometimes exhibiting distinct, slender claws but typically without, or with only feeble indication of digital pads or interpad spaces. Length of central digit (III) is less than 25% greater than that of the lateral digits. Total interdigital span exceeds 95°. Digits convergent proximally but are usually isolated (though digit II may have a minimal contact with digit III). There is no indication of a metatarsal pad or of webbing between digits (emend. Sarjeant and Reynolds 2001).

Aviadactyla vialovi Kordos and Prakfalvi 1990 (Figure 10)

Diagnosis: Avian footprints of small to moderate size, having slender and flexible digits (II to IV) with slender claws whose inclination is only slightly divergent from the digit axis. The digits lack interpad spaces. Interdigital span is variable according to pace and substrate, ranging from about 80° to over 155°. The interdigital angle between digits II and III is slightly less than between digits III and IV. Proximally the digits converge with digit II sometimes in slight contact with digit III, but digit IV is always separated and neither webbing nor a metatarsal pad is present. The digits are of comparable length, with digit III slightly longer than the others. Trackway of moderate width; stride of moderate length (emend. Sarjeant and Reynolds, 2001).

Materials: 2 concave epirelief footprints in the slabs (MPZ 2022-156 and MPZ 2022-210) and 11 convex hyporeliefs in the slabs (MPZ 2022-148, MPZ 2022-162, MPZ 2022-171, MPZ 2022-172, MPZ 2022-174.A)

Description: tridactyl ichnites of small sized birds, that are wider than long. The footprint length and width mean value is 1.8 cm and 2.4 cm respectively. They have the digital impressions without a union between them and any trace of webbing. The digital imprints are slender and pointed with a wide central section. The ichnites with the higher morphological preservation claw impressions at their distal end can be identified. The central digit impression (III) is similar or longer to the lateral digits (II and IV).

Interdigital angles (II^III and III^IV) have a great disparity (35º min, 65º max) with a 51º average, and the total interdigital angle (II^IV) usually exceed the 90º with a mean of 112º. II^III angles are slightly higher than III^IV (Figure 10).

Discussion: There are numerous ichnogenera in the fossil record with tridactyl footprints which can be associated to Avipedidae morphofamily. Sarjeant and Langston (1994) and Sarjeant and Reynolds (2001) established: *Aquatilavipes* (Currie 1981), *Avipeda* (Vialov 1965), *Aviadactyla* (Kordos 1985), *Ludicharadripodiscus* (Ellenberger 1980), *Fuscinapeda* (Sarjeant and Langston 1994) and *Ornithorarnocia* (Kordos 1985). Other studies have included a new ichnogenus to this morphofamily such as *Uvaichnites* (Díaz-Martínez et al. 2012) (Figure 11). *Fuscinapeda* and *Ornithorarnocia* have more thick digits united proximally. Something similar happens with *Aquatilavipes* that has slender digits but still united. *Ludicharadripodiscus* could present a hallux and interdigital webbing. *Avipeda* has also united proximally the digit impressions. *Uvaichnites* has separated digits, but they are thicker, the central digit being much larger than the laterals and also shows a marked central metatarsal pad.

Sarjeant and Reynolds (2001) recognize three different *Aviadactyla* ichnospecies: *Aviadactyla media (*Kordos 1985), *Aviadactyla panini* (Kordos and Prakfalvi 1990) and *Aviadactyla vialovi* (Kordos and Prakfalvi 1990). Both, *A. panini* and *A. vialovi* were in origin part of the ichnogenus *Carpathipeda* but this ichnogenus was considered subsequently an invalid ichnotaxon (Sarjeant and Reynolds 2001).

Aviadactyla media has a large size, is slightly asymmetric and their digits have rounded tips. On the other hand, *Aviadactyla vialovi* and *Aviadactyla panini* have smaller size and are more similar to studied ichnites, also showing slender digits and sharp end tips. The principal difference between *A. vialovi* and *A. panini* is the interdigital angle between digits II and IV. *A. vialovi* has a higher interdigital angle ranging from 80º to 150º.

Considering the original description *A. panini* has a lower interdigital angle below to 70º. The total interdigital angle in the studied ichnites is higher than 85º so *A. vialovi* is the association more probable from them.

Morphofamily: Gruipedidae Sarjeant and Langston 1994

Diagnosis: Avian footprints showing four digits, three of which (II to IV) are directed forward and the fourth (I) directed posteriorly, its axis either coinciding with, or at an angle to that of digit III. Digits united or separate proximally. Webbing absent or limited to the most proximal part of the interdigital angle (Sarjeant and Langston, 1994).

Discussion: Sarjeant and Langston (1994) established Gruipedidae as a morphofamily of tetradactyl and anisodactyl avian ichnites without a web joining the anterior digits or being that web only present in the proximal part. Other tetradactyl morphofamilies such as Anatipedidae (Sarjeant and Langston 1994) have a web that link the digits. Others such as Ignotornidae (Lockley et al. 1992) and Jindongornipodidae (Lockley et al. 2006) are normally used to refer to Mesozoic footprints and some authors have doubt about their use in Cenozoic ichnites (e.g.: Kim et al. 2006; Lockley et al. 2006) although others have used it for Cenozoic footprints (e.g.: Abbassi and Dashtban 2021). However, they have been considered and their characteristics do not coincide with the studied ichnites. Ignotornidae usually are asymmetrical and have a semi-palmate web (Kim et al. 2006). Jindongornipodidae has larger footprints with a clear longer digit IV than II (in the case of La Sagarreta they are similar in length).

Ichnogenus: Gruipeda Panin and Avram 1962

Type Ichnospecies: Gruipeda maxima Panin and Avram 1962 emend. De Valais and Console 2019

Diagnosis: Footprints showing four digits imprints, three of which (II to IV) are directed forward and larger, the fourth (I), directed backward, spur-like and short. The interdigital angles between digits II and III and between digits III and IV are commonly less than 70º. The hallux imprint is posteromedially directed; the interdigital angle between digits I and II being smaller than that between digits I and IV. When present, digital pad traces displaying the relation I: 2, II: 2, III: 3, IV: 4. Webbing trace absent. (Emend. De Valais and Console 2019)

Ichnospecies: *Gruipeda dominguensis*, De Valais and Melchor 2008

Diagnosis: Gruipeda preserved as tridactyl or tetradactyl footprints, commonly with a footprint length smaller than 50 mm, and length/width ratio of 0.7-0.9. Bipedal trackways displaying a zero to inward rotation with relation to the midline, pace angulation ranging from 150º to 182º, and a stride length from 2.5 to 5 times the footprint length. Footprints slightly asymmetric, typically with the angle between digits II-III larger than those of digits III-IV, and a larger divarication of digits II-IV in the range 90º-135º. Relative digit length is I<II<IV<III. Hallux impression present in almost half of the footprints with a posterior to posteromedial position. Occasional rhomboid to rounded sole.

Gruipeda dominguensis (Figure 12)

Material: 50 convex hyporelief in the studied slabs of the collection (MPZ 2022-149, MPZ 2022-152, MPZ 2022-153, MPZ 2022-155, MPZ 2022-157, MPZ 2022-161, MPZ 2022-162, MPZ 2022-169, MPZ 2022-173, MPZ 2022-178, MPZ 2022-210 b and MPZ 2022-211) and 56 concave epirelief (MPZ 2022-152, MPZ 2022-154, MPZ 2022-156, MPZ 2022-158, MPZ 2022-159, MPZ 2022-160, MPZ 2022-161, MPZ 2022-162, MPZ 2022-164, MPZ 2022-165, MPZ 2022-166, MPZ 2022-167, MPZ 2022-168).

Description: Avian footprints that have four slender digits with sharp tips, three oriented forward (II-IV) and one oriented backward (I). The three frontal digits are slender with a central digit (III) longer than the laterals (II and IV) which are very similar in size but usually one of the digits (digit IV) is slightly longer. They are usually connected to each other with absence of webbing. The interdigital angles between II-III and III-IV have a great variety but in most of the cases they do not overcome 70º and usually the angle II^III is higher than III^IV. The angle II-IV has great range variation (90º-140º) but the mean is 115º. The fourth digit (I) is significantly smaller and has a spoon-like morphology. The fourth digit is slightly medially displaced with respect to the central digit axis. The ichnites have a small size with a mean length of 2.3 cm and a mean width of 2.2 cm, the length/width ratio being 0.97. Two trackways have been identified that have a stride length of 6 and 14 cm, being 2.75 and 6,1 times the footprint length (MPZ-2022-149 and MPZ-2022-153) (Figure 12).

Discussion: Gruipeda was established by Panin and Avram (1962) as avian ichnites with three frontal digits and one short digit in the opposite direction. Posterior authors (Sarjeant and Langston, 1994; De Valais and Melchor, 2008) have reviewed this ichnotaxon. De Valais and Melchor (2008) emended the diagnosis of *Gruipeda* as tetradactyl anisodactyl avian footprints in which the interdigital angle I-IV is higher than the angle I-II. This difference between the angles makes *Gruipeda* different from other tetradactyl ichnites such as *Iranipeda* (Lambrecht 1938) and *Ardeipeda* (Panin and Avram 1962) (Figure 13), that have the hallux in the same axis that the central digit (III) and with I^II angle similar to I^IV. Also, some studied ichnites present a similarity with *Persiavipes* an ichnogenus of Ignotornidae (Abbasi and Dashtban 2021) (Figure 13). Nevertheless, this ichnogenus is characterized by semi-palmate footprints, a feature not visible in the studied ichnites

Most of the studied ichnites have a small hallux oriented medially that is diverted from the central digit axis and usually separated from the rest of the footprint having an angle close to 20º. In the few cases of preserved trackways with high morphological preservation quality, it seems that the angle I^II is smaller than I^IV (MPZ 2022-149, MPZ 2022-157, MPZ 2022-178).

However, some of the studied ichnites present a large hallux that it is united with the rest of the track and also showing a higher interdigital angle (Figure 12 (C)). This makes these footprints similar to *Ardeipeda,* although these characteristics could be product of extra-morphological factors linked to differences in the substrate and locomotion of the trackmaker (Falk et al. 2017). The influence of this kind of external process and the variation that they produce could be seen in other *Gruipeda* footprints (Abbassi et al. 2015).

Abbassi et al. (2015) summarized twelve different ichnospecies associated to *Gruipeda*: *Gruipeda abeli* (Lambrecht 1938), *Gruipeda becassi* (Panin and Avram,1962), *Gruipeda calcarifera* (Sarjeant and Langston 1994), *Gruipeda diabloensis* (Remeika 1999), *Gruipeda disjuncta* (Panin and Avram 1962), *Gruipeda dominguensis* (De Valais and Melchor 2008), *Gruipeda filiportatis* (Vialov 1965), *Gruipeda intermedia* (Panin 1965), *Gruipeda lambrechti* (Ataabadi and Khazaee 2004), *Gruipeda maxima* (Panin and Avram 1962), *Gruipeda minima* (Panin and Avram 1962), *Gruipeda minor* (Panin 1965).

G. abeli, G. maxima and *G. lambrechti* present a larger size than the herein studied ichnites. *G. becassi* has thicker digits with the impression of digital pads (Sarjeant and Langston 2001). *G. calcarifera* has digits II and I separated from each other with a biconvex outline. *G. diabloensis* has four slender digits, the digits II and IV have a slightly curve anteriorly and an asymmetry between the interdigital angles. *G. filiportatis* has been assigned by Sarjeant and Langston (1994) to the ichnogenus *Gruipeda* but posterior studies reassign it to *Ardeipeda* (Lockley and Harris 2010). It also has a large size with a great hallux (Lockley et al. 2021). *G. intermedia* has slender digits that sometimes are separated with a circular heel impression conserved (Abbassi et al. 2015). *G. minima* has asymmetrical digits with a hallux twice longer of the length of the footprint (De Valais and Melchor 2008). *G. minor* does not conserve the impression of the hallux and have a thick central digit (Abbassi et al. 2015). *Gruipeda dominguensis* has the greatest similarities with the studied ichnites. This ichnotaxon has a small size tridactyl or tetradactyl ichnites with slender digits that do not present an interdigital web. This footprint has a slightly asymmetry between their interdigital angles (with the angle II-III higher than III-IV). *G. diabloensis* is very similar to *G. dominguensis* but the asymmetry is greater between the angles II-III than III-IV (more than 20º) and have curvy digits (De Valais and Melchor 2008). The studied footprints present straight digital digits and a less asymmetry between their interdigital angles, so the tracks are classified as *G. dominguensis*.

DISCUSSION

Implications for the diversity during the Early Oligocene in the Ebro Basin

The Ebro Basin mammal footprint record ranges from the Early Oligocene to the Early Miocene (e.g., Díaz-Martínez et al. 2018; Rabal-Garcés et al. 2018), which includes most of the sedimentary record in the basin, with tracksites identified in most of the stages. At a global scale, the Paleogene footprint record is very scarce (McDonald et al. 2007), however, the Ebro Basin presents a great number of trackistes, especially in the Lower Oligocene (Table S3). This situation makes this basin a key area for the study of the evolution of European ichnofauna during this era, when most of the modern mammal groups appeared and had their more primitive representatives (Blondel et al. 2001; Hooker et al. 2009; Costa et al. 2011).

A total of 24 different tracksites have been described in the Lower Oligocene of the Ebro Basin (Figures 14, 15; Table S3). They are located in three main areas of the northern part of the basin: western (Navarre Province), central (Huesca Province) and eastern areas (Lleida; Barcelona and Tarragona provinces). For paleoecological studies the concept of ichnodiversity is used to measure the richness of species in a site or a region (Buatois and Mángano, 2013). Thus, these Early Oligocene tracksites altogether present a high ichnodiversity, with 11 different ichnogenera recognized and a total 16 ichnospecies identified. These ichnotaxa belong to the main groups of mammals (artiodactyl, perissodactyl, carnivoramorphs) and different birds present during this epoch in Europe. The sites in the central and eastern areas present the higher diversity of ichnites, with 10 ichnotaxa identified in 3 tracksites and a minimum of 18 ichnotaxa in 17 tracksites, respectively (Figures 14, 15). Interestingly, in the tracksites located in the three areas herbivore mammals (both artiodactyl and perissodactyl) dominate the ichnoassemblages, but each area has its own peculiarities. Looking into the distribution of the ichnotaxa at the different areas *Plagiolophustipus*-like tracks are present in all the areas at the Ebro Basin and is the most common morphotype, being present at 11 tracksites in the Lower Oligocene. On the other hand, the ichnogenus *Bothriodontipus,* despite having been found at 7 tracksites and being the second most common morphotype, has been only located at the Eastern area. The western area presents tracksites with only one type of ichnites and the lowest ichnodiversity, with only three ichnotaxa represented (*Plagiolophustipus*, *Entelodontipus* and *Charadriipeda/Koreanornis*). On the other hand, in the sites in the central area of Ebro Basin there is a dominance (both in number of footprints and number of morphotypes) of artiodactyl ichnites (data biased by the presence of hundreds of footprints and 3 ichnotaxa in the Fondota tracksite, Linares et al. 2021), but carnivoramorph and perissodactyl are also present with also a great presence of avian ichnites. The Eastern area is also dominated by artiodactyl (*Bothriodontipus*, *Entelodontipus* and Artiodactyla indet) and perissodactyl (*Plagiolophustipus*) footprints, also with the presence of creodont ichnotaxa (*Creodontipus*).

In this context, La Sagarreta tracksite, presents a significantly high ichnodiversity, with a total of 6 ichnotaxa represented related with, at least, four main groups of animals (birds, artiodactyls, perissodactyls and carnivoramorphs (Figures 14, 15). Interestingly, the eastern area also shows tracksites where the ichnodiversity is considerably high (e.g.: Montagay, Cubells and Agramunt sites, with 5 ichnotaxa). Although the same groups are identified in both areas (central and eastern), the ichnoassemblages are slightly different in the artiodactyl (*Megapecoripeda*/cf. *Pecoripeda* vs *Bothriodontipus*/*Entelodontipus*) and carnivoramorph (cf. *Canipeda* vs *Creodontipus*) ichnoassociation and in the eastern area most of the avian footprints have not been assigned to any ichnotaxa (*Gruipeda* has been described in Sanauja section, by Gibert and Saez 2009 and classified as *Koreanornis* by Díaz-Martínez et al. 2015). From these data La Sagarreta tracksite stands out as the most richness and diverse tracksite of the Ebro Basin, and one of the most richness in the world for the Lower Oligocene (McDonald et al. 2007; Costeur et al. 2009; Abassi et al. 2015).

The information provided by the ichnological record is especially important where the osteologic record is absent or reduced (e.g. Lockley 1991), as it is the case in the Ebro Basin. It is important to emphasize that the ichnodiversity does not reflect with a great certainty the biodiversity and generally does not allow identification to a specific species to be the producer. In the Ebro Basin a total of 24 mammal fossil sites with osteological remains from the Early Oligocene have been described (Cuenca et al. 1992; Estadella Serra 2020). Interestingly, most of them only containing micromammal remains. The avian record during the Oligocene in the Ebro Basin is restricted to their footprints

(Sánchez Marco 1996). Considering only the groups which ichnites are represented in La Sagarreta, Cuenca et al. (1992) reported 9 different artiodactyls (with a dominance of anthracotherids and anoplotherids but also entelodonts), 2 perissodactyls (all of them members of the paleotherids) and 2 carnivore mammals (one mustelid and one amphicyonid). In contrast to these 13 taxa identified in the osteological record, the Early Oligocene ichnite record presents a slightly higher icnhodiversity with a minimum number of 16 ichnotaxa identified plus numerous indeterminate tracks that could considerably raise the total ichnodiversity. These data are especially significant in the case of the central area of the basin where in all the osteologic sites reported by Cuenca et al. (1992) only micromammals are represented. Thus, the only Early Oligocene record of the large mammal and bird fauna in the central area of Ebro Basin are the tracksites.

The scarcity of sites with osteological remains of large mammals and birds and the absence of descriptions of well-known autopods difficult to determine the producer of the studied ichnites with certainty. Among perissodactyls, paleotheres have been proposed as the most probable trackmakers of numerous footprints belonging to *Plagiolophustipus* in the Ebro Basin (Casanovas-Cladellas and Santafé-Llopis 1982; Santamaria et al. 1989-1990; Prats and López 1995; Murelaga et al. 2000; Astibia et al. 2007; Gibert and Saez 2009; Díaz-Martínez et al. 2018). *Plagiolophus* is the only genus member of the family Palaeotheriidae that survive to "*La Grande Coupure*" after the Eocene-Oligocene transition (Blondel 2001; Remy 2004) and they present tridactyl autopods with a great similarity of studied ichnites., *P. huerzeleri* is present at the Montalbán site, located in the Montalban Basin, in the Iberian Range (Remy 2000; Remy 2004), with an age close to La Sagarreta (MP23, early Oligocene). Hence, *Plagiolophus huerzeleri* or another member of the genus *Plagiolophus* (Perales-Gogenola et al.2022) with a medium or large size are the most probable producers of the ichnites of La Sagarreta.

The artiodactyls present a great similarity in their autopod morphology that is reflected in their ichnites (Lucas and Hunt 2007; Costeur et al. 2009). Generally, didactyl *Pecoripeda*-like tracks described in younger (Miocene) tracksites of the Ebro Basin have been related to members of Pecora (Díaz-Martínez et al. 2018). Its attribution to the La Sagarreta footprins presents a problem in relation with the age, since the first occurrence of Pecora with certainty is during the Late Oligocene-Early Miocene (De Miguel et al. 2014). Demathieu et al. (1984) proposed the “gelocids” as possible producers of *Bifidipes velox*. The “gelocids” were small to medium size hornless ruminants that are suggested to be the sister group of Pecora (Janis and Theodor 2014). Entelodonts have been associated with didactyl tracks (e.g.: *Entelodontipus*) during the Early Oligocene (Casanovas-Cladellas and Santafé-LLopis 1982; Díaz-Martínez et al. 2018). Several artiodactyl taxa have been described in the eastern Ebro Basin (Cuenca et al., 1992). The Talladell 3 site has yielded several artiodactyl taxa such as the anthracotheriid *Elomeryx cluae* and the tylopods *Cainotherium gracile* and *Cainotherium commune.* Besides, the large size species *Entelodon magnus* has been found in the “Rocallaura” site (Lleida, Spain) and an undetermined member of the family Entelodontidae at the “Canal Segarra-Garrigues” site (Lleida, Spain), (Blaya et al., 2017; Estadella Serra 2020 and references therein). Although the absence of lateral digit impressions in the studied ichnites could be due to the substrate conditions that make that lateral digit did not generate impressions, they present a great depth and a general good preservation so probably the producers did not have lateral digits. This allows to discard artiodactyl groups described by the osteological record such as the antracotherids (with tetradctyl autopods (Clifford 2010; Cartanyá and Colldefons 1996 and references therein). Members of Tylopoda can be discarded despite their didactyl tracks because they present a union between their digits

(Lucas and Hunt 2007; Linares et al. 2021). Thus, entelodonts are possibly the best candidates to be the producers of the artiodactyl tracks.

Identifying the producers of the Carnivoramorphs is a complex case. Generally. *Canipeda* has been assigned to members of the order Carnivora, more specifically to members of the family Canidae, as their possible producers (Melchor et al. 2019). However, by the comparison between extant footprints, some of the material related to the ichnogenus *Canipeda* could have also been produced by members of either the family Herpestidae or the family Hyaenidae (Antón et al. 2004; Rabal-Garcés and Díaz-Martínez 2010; Melchor et al. 2019). However, neither of the three groups were present in Europe during the Early Oligocene. Herpestidae and Hyaenidae did not appear in the osteological record until the Miocene (Barycka 2007). The Canidae appear in North America during the Late Eocene where they stayed isolated until the Late Miocene (Turolian) (Wang et al. 2004). Other carnivoramorph groups present during the Early Oligocene can be discarded because they present either pentadactyl manus and pes or by their plantigrade condition (e.g.: Amphicyonids, Hemycionids, and Credonts, Sarjeant et al. 2002; Bjork 2002; Wang et al. 2009; Sole et al. 2022). The “Miacidae” are a group of carnivoramorphs with a similar size and morphology to modern genets that are recognized as primitive true carnivore mammal (Spaulding and Flynn 2009). However, they present retractable claws (Wesley and Flynn 2003; Spaulding and Flynn 2009), so they are unlikely to be the producers in La Sagarreta. In the Ebro Basin, an unidentified member of the genus *Amphicyon* (an amphicyonid) and a primitive mustelid (*Plesisctis filholi)* described at “Pedreres de Talladell” (Tarrega, Lleida), are the only records of carnivoramorphs during the Early Oligocene (Cuenca et al. 1992; Estadella Serra 2020 and references therein). In summary, the studied ichnites are relatively similar (slightly differences in the metapodial pad morphology) to modern canids, but the age of the ichnites makes difficult that the trackmaker was a true canid, so the most probable trackmaker belonged to other carnivoramorph group with autopods relatively similar to modern canids.

Generally, avian footprints cannot be associated with a specific taxonomic group since the morphologies of their foot depend on their behavior and the ecological niche they occupied in the ecosystem, so only in particular cases the trackmakers could be determined with confidence (Sarjeant and Langston 1994). Furthermore, most of the extant avian groups were present during the Paleogene, usually in primitive forms, and they were already present in Europe during the Early Oligocene (James 2005). Therefore, a comparison with the footprints of modern avian groups has been established. In the case of *Aviadactyla vialovi,* Sarjeant and Reynolds (2001) suggest a wading bird, probably a common sandpiper (*Actitis hypoleucos*) or a red-backed sandpiper (*Calidris alpina*), as the trackmaker of this kind of ichnite. However, other modern wading birds as the plovers (*Charadrius*) or sanderlings (*Calidris*) have more similar morphology to studied ichnites because they do not have a hallux impression (or it has a smaller size) and the metatarsal area is poorly marked or absent (Elbroch and Marks 2001). So, the most likely producer of the ichnites in La Sagarreta was a bird with similar foot morphology and habits to members of these groups within the order Charadriiformes. *Gruipeda* has been assigned to three different orders of birds by Sarjeant and Langston (1994): Gruiformes (Gruidae and Rallidae), Charadriiformes and Ciconiiformes. Modern cranes (member of the family Gruidae) footprints do not have a hallux impression, being different from the studied ichnites (Brown et al. 2003). Nonetheless, the members of Rallidae present a small hallux slightly displaced from the central axis (Brown et al. 2003). The Charadriiformes present a great variety of feet morphology, some of them have webbed digits and other lack of them (Elbroch and Marks 2001). The species without a digital web are very similar in their morphology to Rallidae. All this makes impossible to determine if the studied ichnites belong to Rallidae or Charadriiformes, but a member of these groups are the most probable trackmakers.

CONCLUSIONS

The Early Oligocene La Sagarreta tracksite, at the central sector of the Ebro Basin (Peralta Formation) in Spain, is described for the first time. It represents a valuable paleontological record due to the scarcity of ichnological Paleogene record as well as the high ichnodiversity it contains. This new site is one of the best indicators of the biodiversity present during the Early Oligocene at the Ebro Basin. Six different ichnotaxa have been differentiated, which makes the tracksite the most richness and diverse of the Early Oligocene in the basin. Most of the studied ichnites belongs to birds and two different types of avian tracks have been identified (*Aviadactyla vialovi* and *Gruipeda dominguensis*) that were possibly produced by members of the order Charadriiformes. Less common are the footprints of a medium-sized perissodactyls (cf. *Plagiolophustipus* isp.*)*, which most probably producer was a medium-sized member of the genus *Plagiolophus.* Even rarer are the footprints of artiodactyls (*Megapecoripeda* isp. cf. *Pecoripeda* isp.), possibly produced by entelodonts, and carnivoramorphs (cf. C*anipeda* isp.) which trackmaker cannot be identified with certainty. The sedimentological features of the site indicate that correspond to a shallow marginal lacustrine area, with available water, but commonly desiccated, and a sedimentary surface dominated by fine detrital sediments. These conditions probably favored the production of the footprints and the appearance of a diverse fauna in the same locality. This new contribution provides valuable information that complements the scarce knowledge of the Early Oligocene faunas in the Ebro Basin, especially at the central sector where the record of some groups of large mammals (e.g. perissodactyls and carnivoramorphs) had not been previously reported and the other identified groups had been only reported by their footprints.

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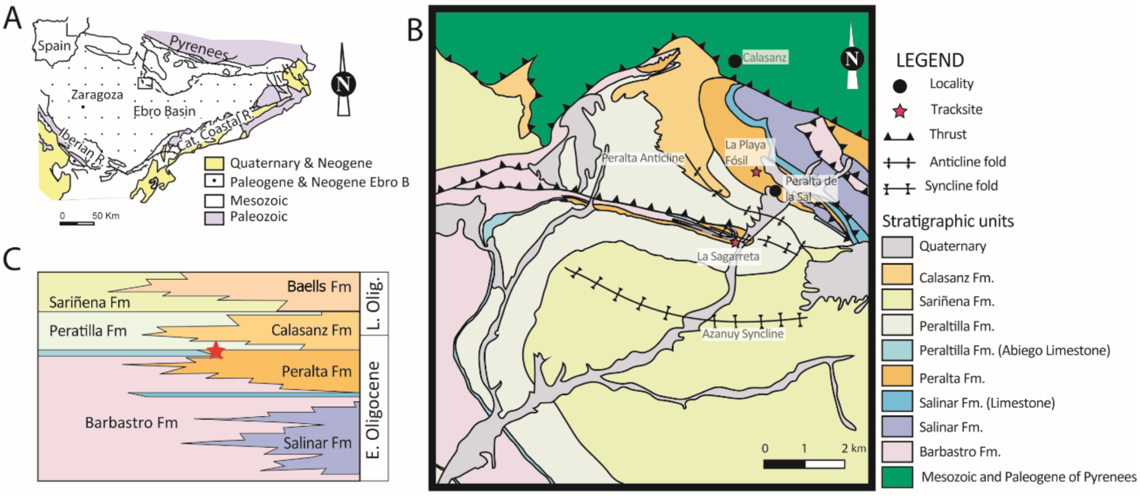

Figure 1. Geographic and geological setting of La Sagarreta tracksite. **A.** Geographical and geological setting of the Ebro Basin. **B.** Geological map in the north-central Ebro Basin with the stratigraphic rock units in the area where the tracksite is located (modified from Senz and Zamorano, 1992). **C.** Stratigraphic relation between the lithological units at the surroundings of the tracksite (modified from Senz and Zamorano, 1992).

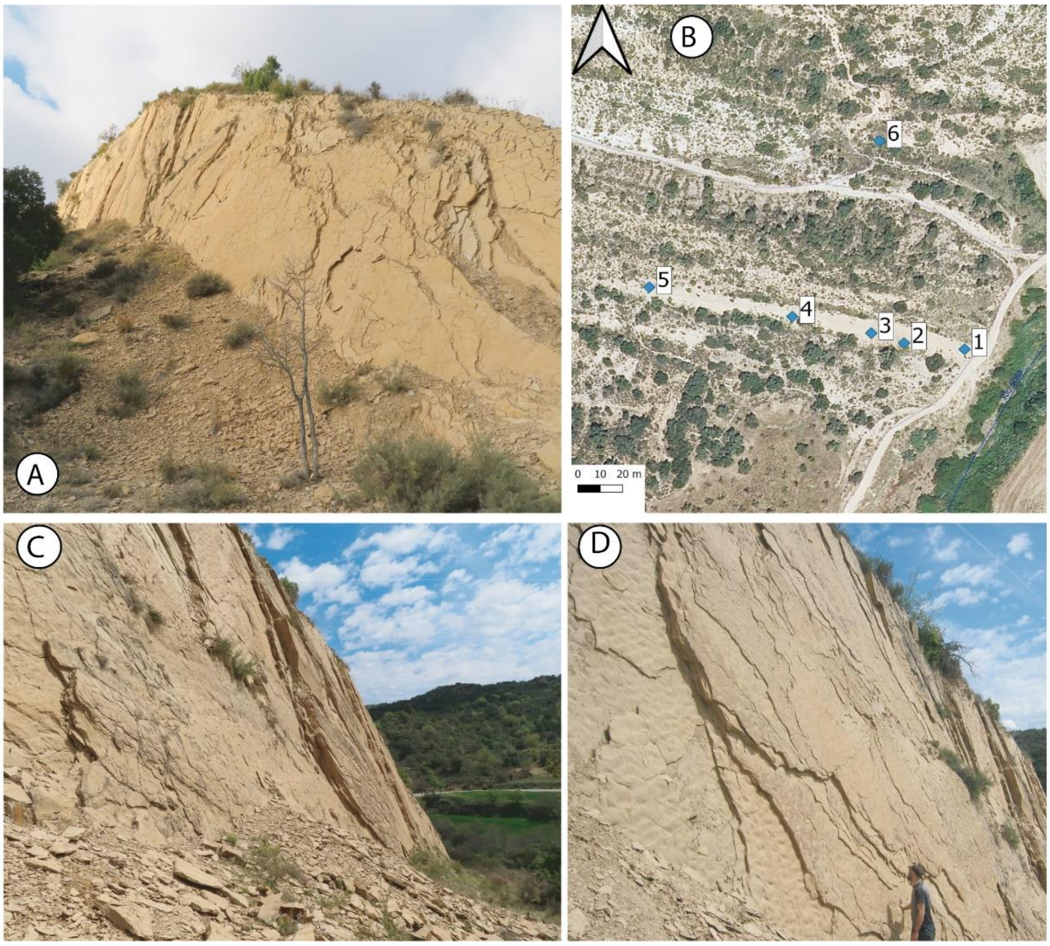

Figure 2. **A**. Panoramic view of the main outcrop of La Sagarreta tracksite (points 1 and 2). **B.** Location of the areas where the slabs with footprints have been collected. **C.** Close-up picture of one outcrop (point 3) of La Sagarreta tracksite with many slabs detached from it in the ground. **D.** Close-up picture of one outcrop (point 3) of La Sagarreta tracksite showing the laminated structure of the La Sagarreta profile and the presence of different types of ripples at the surface of some levels.

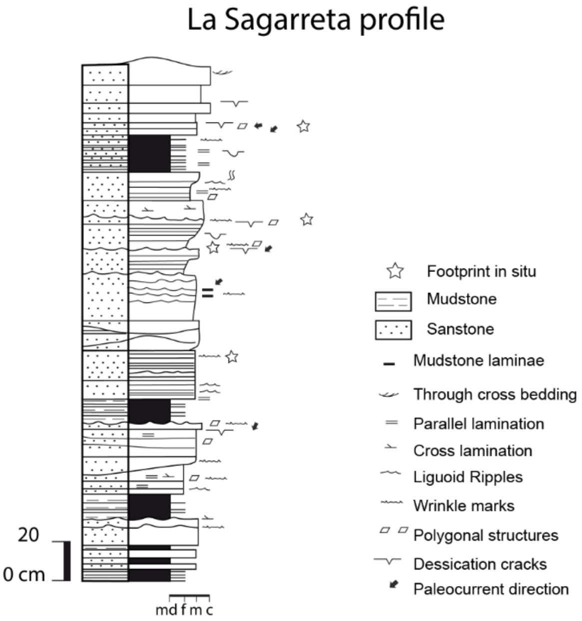

Figure 3. Detailed sedimentary profile corresponding to the La Sagarreta tracksite.

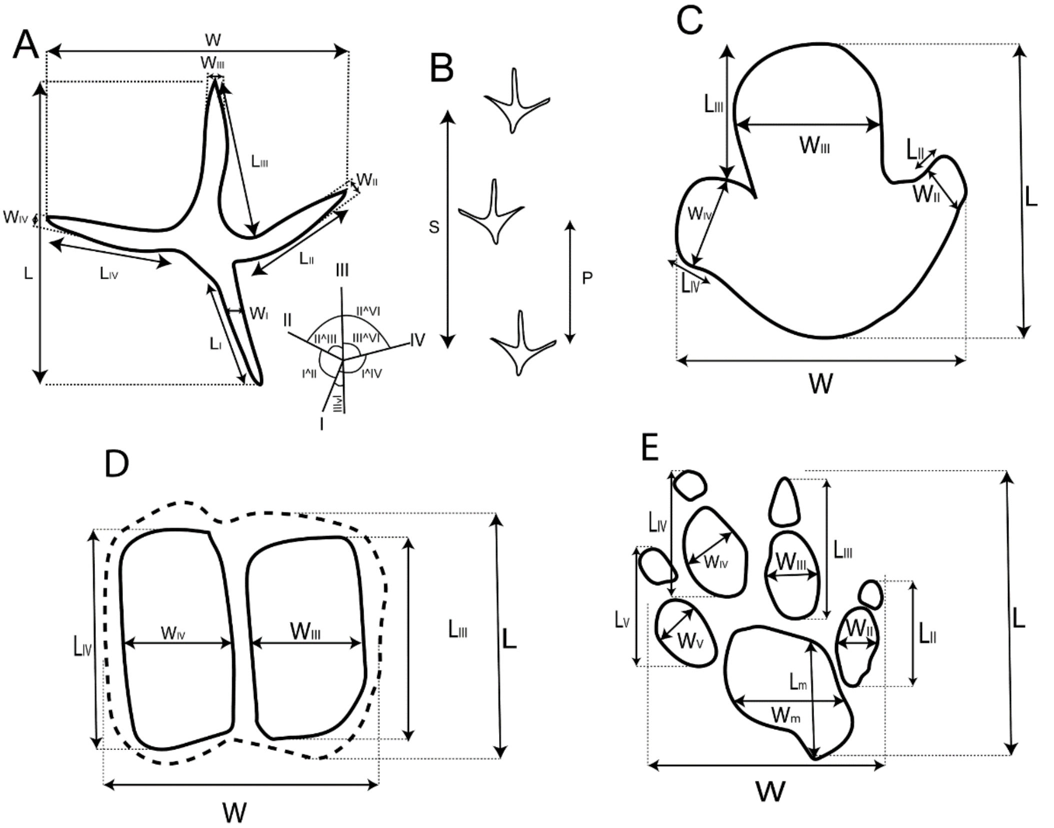

Figure 4. Measurement parameters for the bird and mammal footprints and trackways. **A.** Measurements taken in the individual avian footprints (modified from De Valais and Melchor 2008). **B**. Measurements taken in the avian trackways (modified from De Valais

and Melchor 2008). **C.** Measurements taken in the individual perissodactyl footprints. **D**. Measurements taken in the individual artiodactyl footprints. **E**. Measurements taken in the individual carnivoramorph mammal footprints. Total footprint length (L), total footprint width (W), digit length (LI, LII, LIII, LIV), digit width (WI, WII, WIII, WIV), interdigital angles (II^III, III^IV, II^IV, I^II, I^III, I^IV), pace (P), Stride (S). In the case of carnivoramorph footprint length and width of the metapodial pad (Lm, Wm).

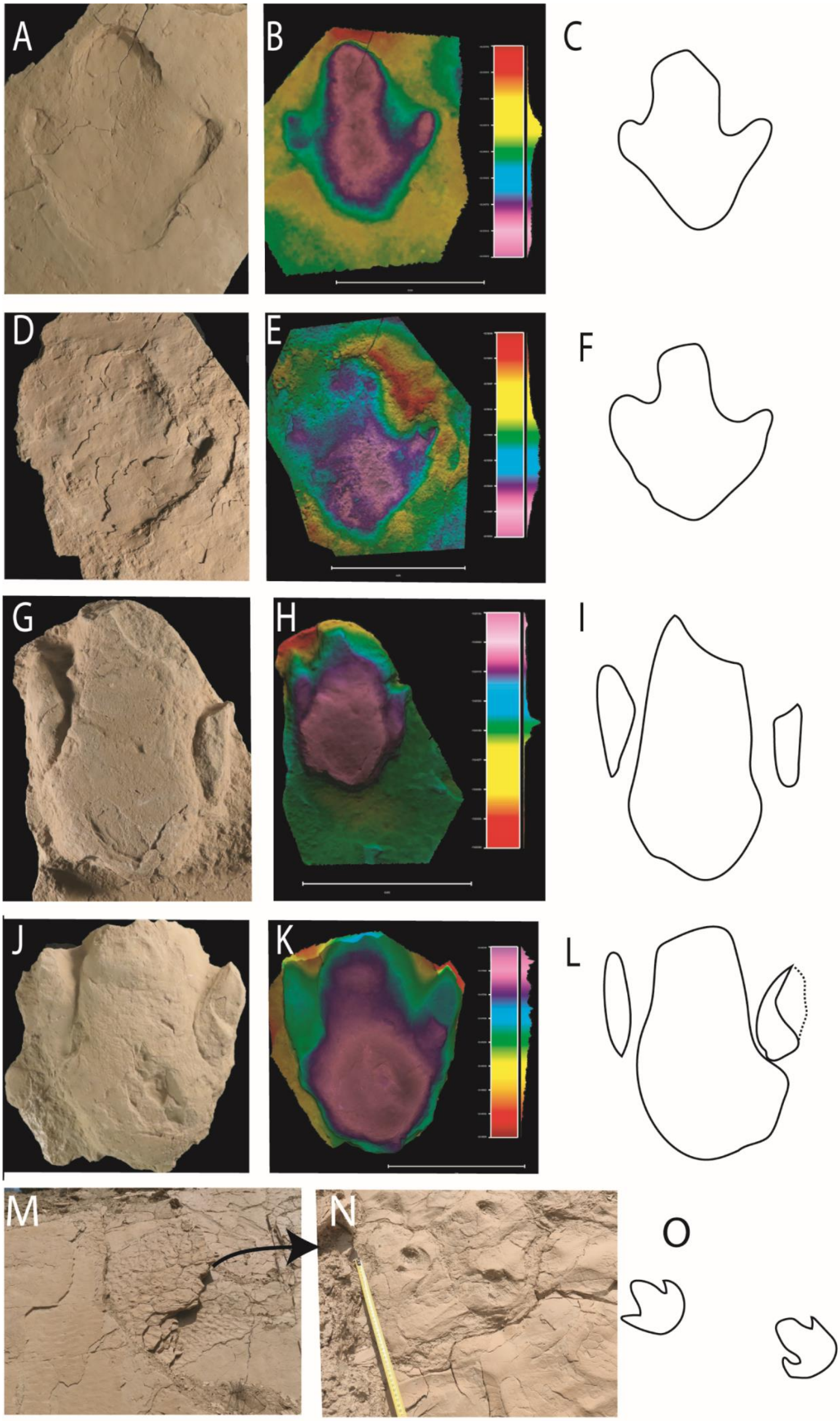
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Figure 5. Perissodactyl footprints (cf. *Plagiolophustipus* isp.) from La Sagarreta tracksite. **A.** Photo of footprint MPZ-2022-147 preserved as concave epirelief. **B.** False-colour depth map of the footprint. **C.** Outline of the footprint. **D.** Photo of footprint MPZ-2022-181 preserved as concave epirelief. **E**. False-colour depth map of the footprint. **F**. Outline of the footprint. **G.** Photo of footprint MPZ-2022-180 preserved as convex hyporelief. **H.** False-colour depth map of the footprint**. I.** Outline of the footprint. **J.** Photo of footprint MPZ-2022-179 preserved as convex hyporelief. **K**. False-colour depth map of the footprint. **L.** Outline of the footprint. Note that in the latter two footprints the central digit is partially broken. **M**. Picture of an outcrop (point 4) with two perissodactyl tracks preserved *in situ*. **N.** Detail picture of the perissodactyl tracks. **O.** Outline of the perissodactyl tracks.

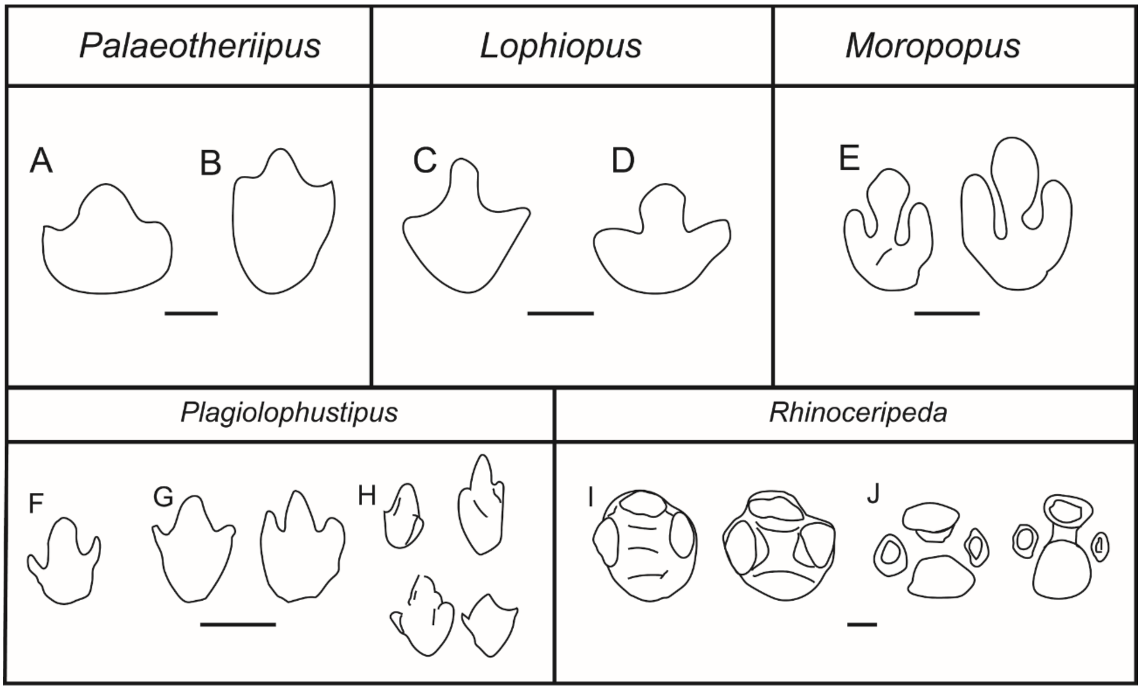

Figure 6. Outlines of the main perissodactyl ichnotaxa related to the studied specimens. **A.** *Palaeotheriipus similimedus* (Ellenberger 1980); **B.** *Palaeotheriipus sarjeanti* (Ataabadi and Khazaee 2004); **C.** *Lophiopus rapidus* (Ellenberger 1980); **D.** *Lophiopus*

latus (Ellenberger 1980); **E.** *Moropopus elongatus* (Abbassi et al. 2016); **F.** *Plagiolophustipus montfalcoensis* (Santamaria et al. 1989-1990); **G.** *Plagiolophustipus* cf. *montfalcoensis* (Murelaga et al. 2000); **H.** *Plagiolophustipus* isp. (Astibia et al. 2007); **I**. *Rhinoceripeda tasnadyi* (Kordos 1985); **J.** *Rhinoceripeda voconcense* (Costeur et al. 2009). Scale bars equal 5 cm.

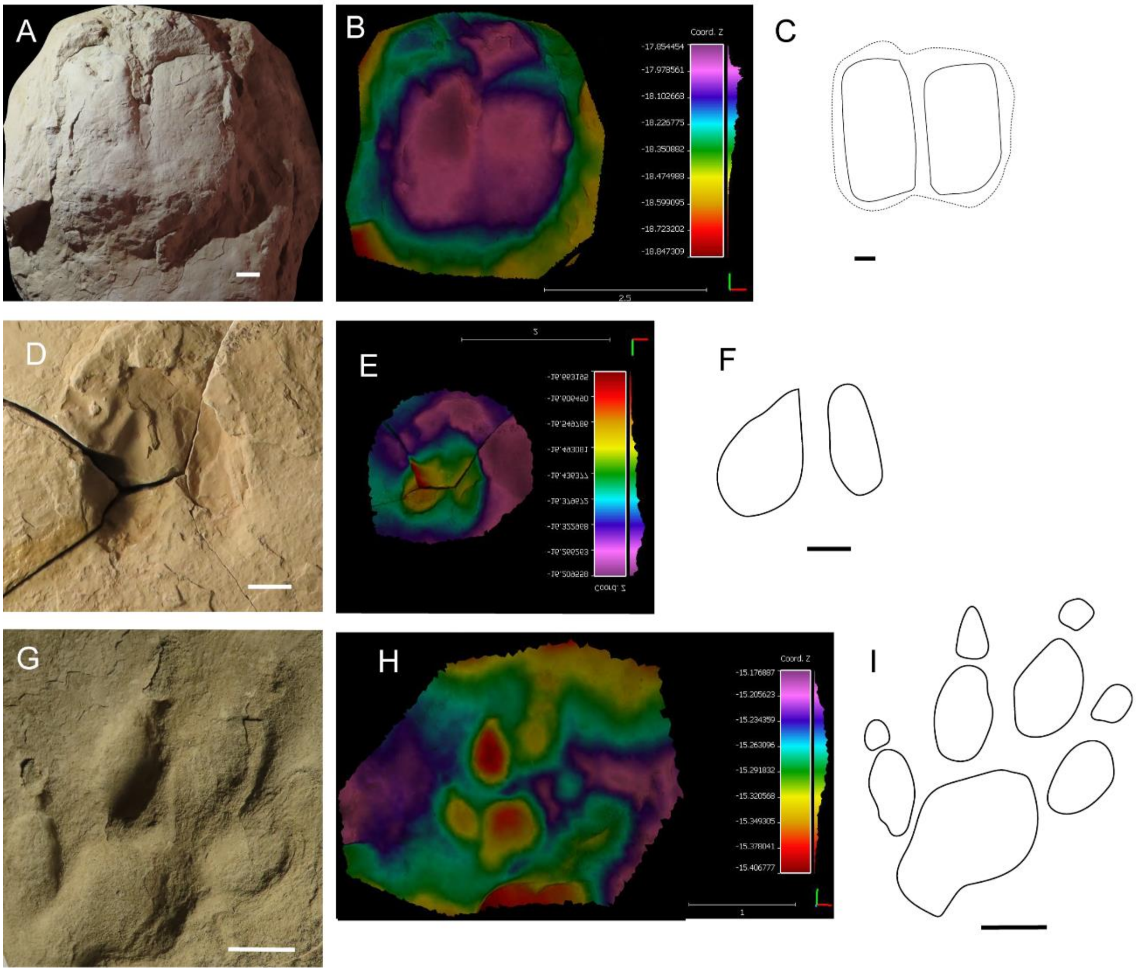

Figure 7. Non-perissodactyl mammal footprints from La Sagarreta tracksites. **A**. Photo of footprint MPZ-2022-177, a medium artiodactyl (*Megapecoripeda* isp.) footprint. **B.** False-colour depth map of the footprint. **C.** Outline of the footprint. **D.** Photo of footprint MPZ-2022-151 a small artiodactyl (cf. *Pecoripeda* isp) footprint. **E.** False-colour depth map of the footprint. **F.** Outline of the footprint. **G.** Photo of footprint MPZ-2022-168, a

carnivoramorph (cf. *Canipeda* isp.) footprint. **H**. False-colour depth map of the footprint. **I.** Outline of the footprint.

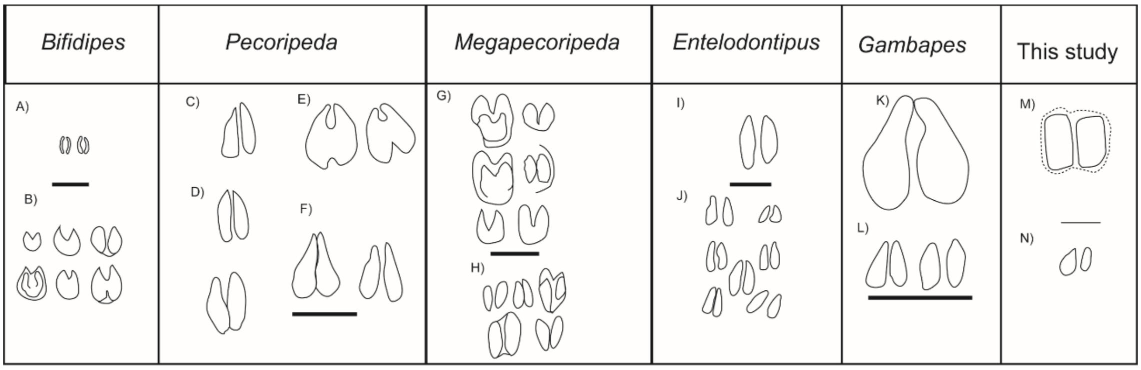

Figure 8. Sketches of the main didactyl artiodactyl ichnotaxa. **A.** *Bifidipes aeolis* (Fornós et al. 2002); **B.** *Bifidipes velox* (Demathieu et al. 1984); **C**. *Pecoripeda amalphaea* (Vialov 1965); **D.** *Pecoripeda djali* (Vialov 1965); **E.** *Pecoripeda diaboli* (Vialov 1965); **F.** *Pecoripeda gazella* (Vialov 1965); **G.** *Megapecoripeda velox* (Costeur et al. 2009); **H.** *Megapecoripeda miocaenica* (Kordos 1985); **I.** *Entelodontipus viai* (Casanovas-Cladellas and Santafé-Llopis 1982); **J.** *Entelodontipus* cf. *viai* (Astibia et al. 2007); **K.** *Gambapes satyri* (Vialov 1965); **L.** *Gambapes hastatus* (Sarjeant and Langston 1994); **M.** MPZ-2022-177; **N.** MPZ-2022-151. Scale bars equal 5 cm.

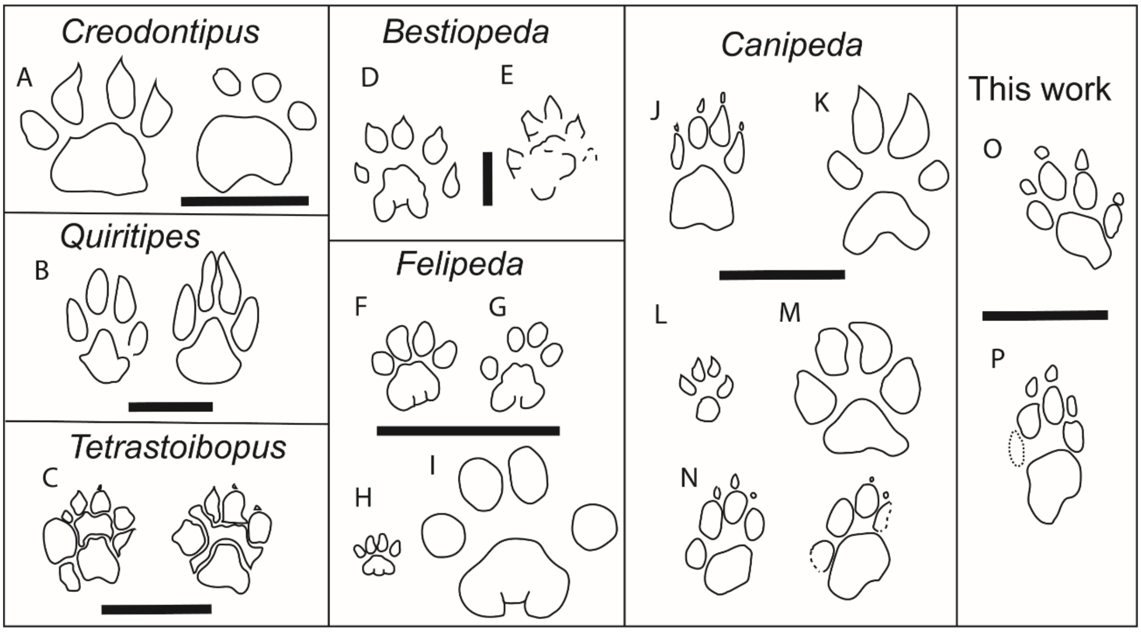

Figure 9. Sketches of the main tetradactyl ichnotaxa assigned to creodont and carnivore mammals. **A.** *Creodontipus* (redrawn from Santamaría et al. 1989-1990); **B.** *Quiritipes* (redrawn from Sarjeant et al. 2000) (Manus left, pes right); **C.** *Tetrastoibopus* (redrawn from Sarjeant and Langston 1994) (Manus left, pes right); **D.** *Bestiopeda guloides* (redrawn from Thenius1967); **E.** *Bestiopeda* isp. (redrawn from Costeur et al. 2009); **F.** *Felipeda milleri* (redrawn from Remeika 1999); **G.** *Felipeda lynxi* (redrawn from Antón et al. 2004); **H.** *Felipeda miramarensis* (redrawn from Agnolin et al. 2018); **I.** *Felipeda parvula* (redrawn from Anton et al. 2004); **J.** *Canipeda longigriffa* (Panin and Avran 1962); **K.** *Canipeda sanguinolenta* (Vialov 1965); **L.** *Canipeda therates* (Remeika 1999); **M.** *Canipeda gracilis* (Vialov 1965); **N.** cf. *Canipeda* isp. (Rabal-Garcés and Díaz-Martínez 2010) (Manus left, pes right); **O.** Outline of MPZ-2022-168; **P.** Outline of LSC2. Scale bar equal 5 cm.

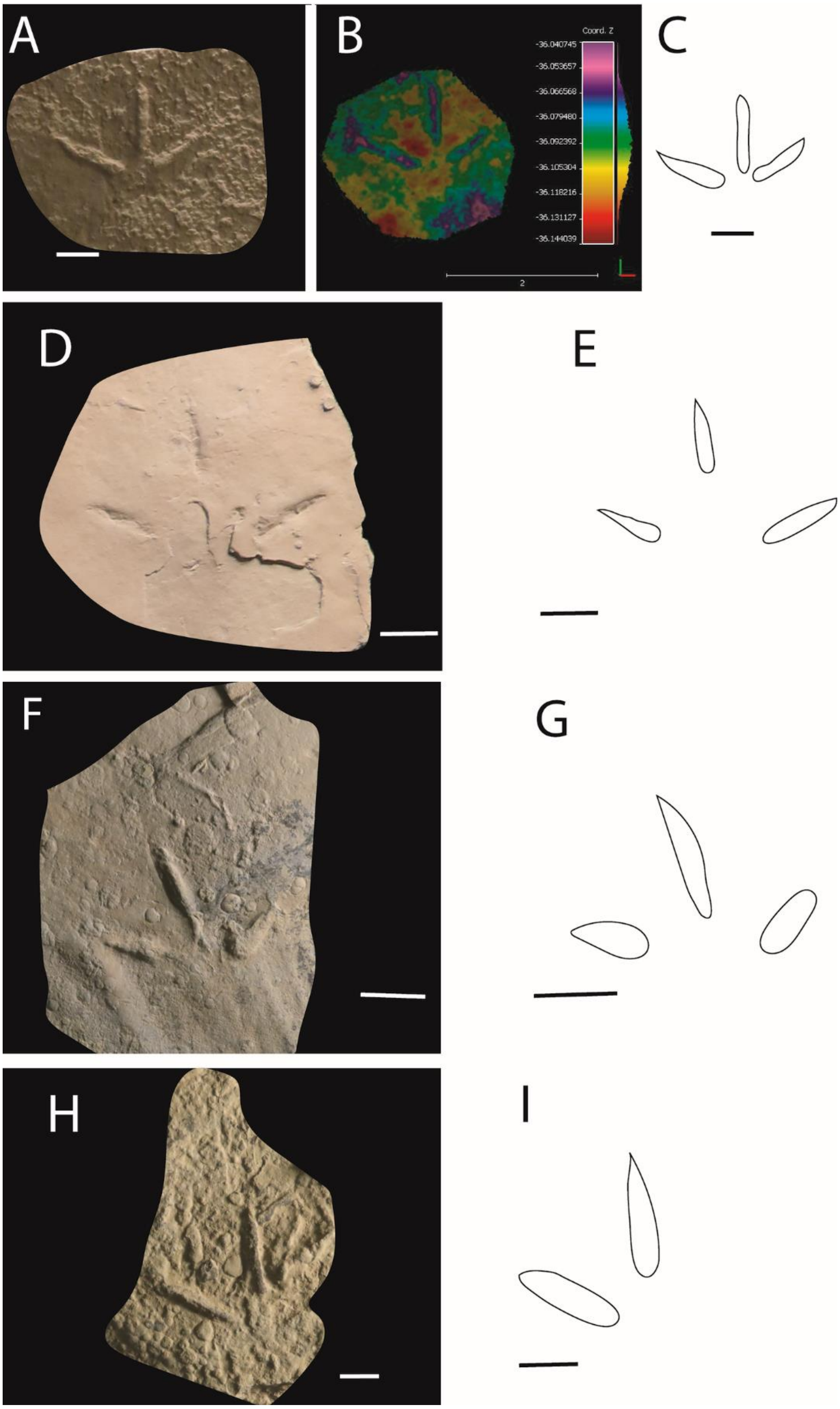

Figure 10. Bird footprints with isolated digits and without hallux impression (*Aviadactyla vialovi*) from La Sagarreta tracksite. **A.** Photo of footprint MPZ-2022-175. **B.** False-colour depth map. **C.** Outline of footprint. **D.** Photo of footprint MPZ-2022-210. **E.**

Outline of the footprint. **F.** Photo of footprint MPZ-2022-148. **G.** Outline of footprint. **H.** Photo of the footprint MPZ-2022-171. **I.** Scale bar equals 1 cm.

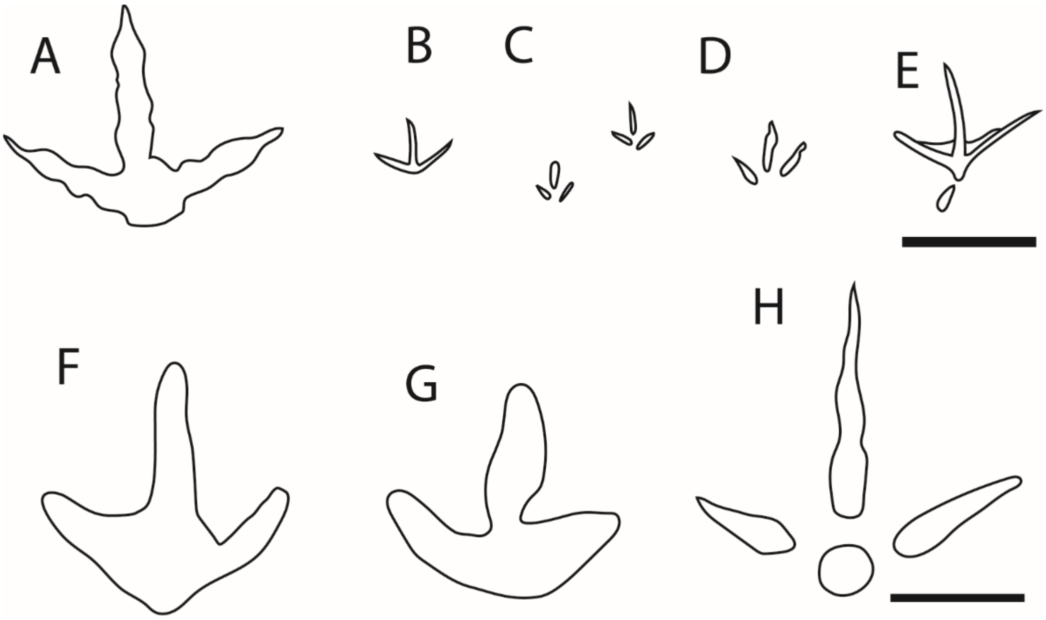

Figure 11. Outline of the main ichnogenus in Avipedidae morphofamily. **A**. *Aquatilavipes curriei* (redrawn from McCrea and Sarjeant 2001). **B**. *Avipeda griponyx* (redrawn from Sarjeant and Reynolds 2001).**C.-E.** *Aviadactyla media* (redrawn from Kordos 1985). **D.** *Aviadactyla vialovi* (redrawn from Sarjeant and Reynolds 2001). **E.** *Ludicharadripodiscus edax* (redrawn from Ellenberger, 1980). **F.** *Fuscinapeda texana* (redrawn from Sarjeant and Langston 1994). **G.** *Ornithotarnocia lambrechti* (redrawn from Sarjeant and Reynolds 2001). **H**. *Uvaichnites riojana* footprint (redrawn from Diaz-Martinez et al. 2012). Scale bar 5 cm.

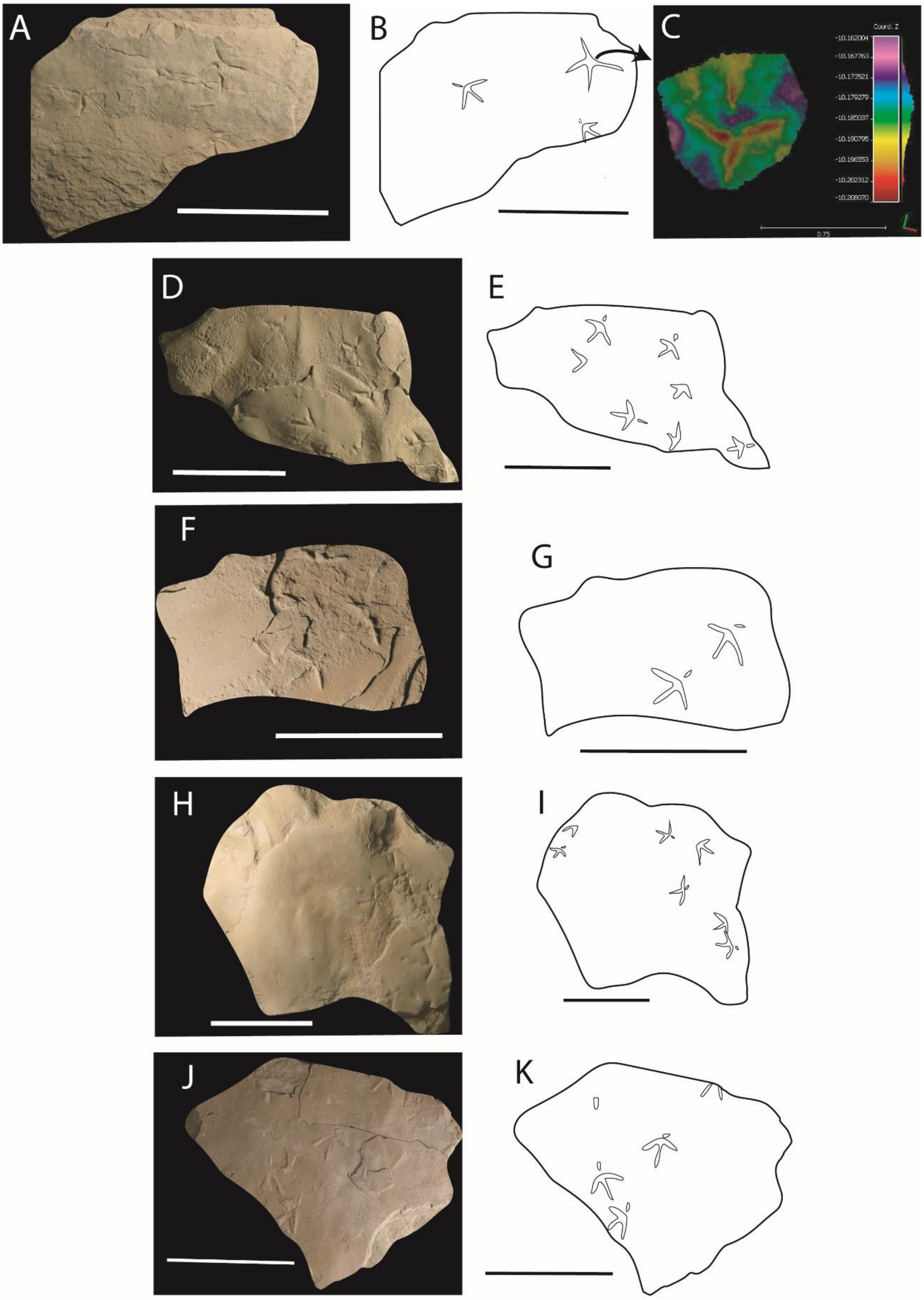

Figure 12. Bird footprints from La Sagarreta tracksite showing clear evidence of hallux impressions (*Gruipeda dominguensis*). **A.** Photo of slab MPZ 2022-159. **B**. Drawing of the slab showing the outlines of the footprints. **C**. False-colour depth map of one footprint

in MPZ 2022-159.1 **D.** Photo of slab MPZ 2022-164. Note that the footprints are in two different layers. **E.** Drawing of the slab showing the outlines of the footprints. **F.** Photo of slab MPZ 2022-178. **G.** Drawing of the slab showing the outlines of the footprint. **H.** Photo of the slab MPZ 2022-154. **I.** Drawing of the slab showing the outlines of the footprints. **J**. Photo of slab MPZ 2022-153. **K.** Drawing of the slab showing the outlines of the footprints. Scale bar equals 10 cm.

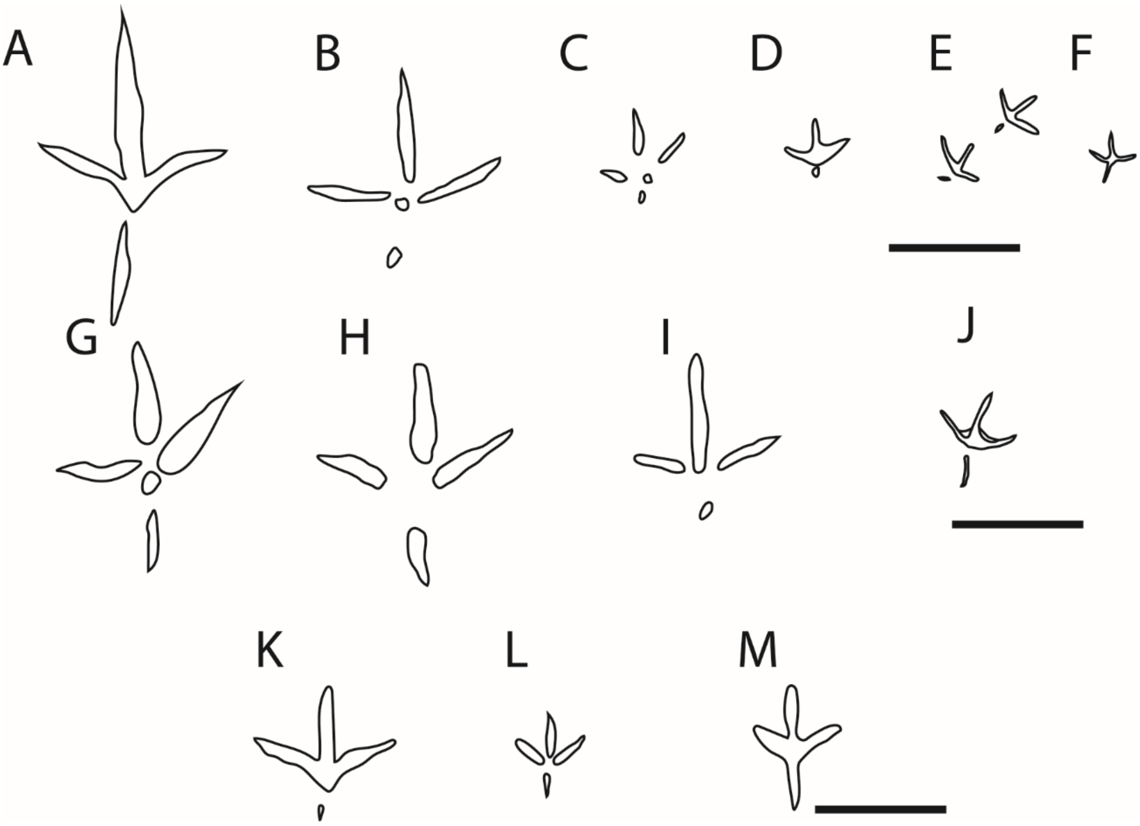

Figure 13. Outline drawings of the main ichnogenus/ichnospecies cited in the text, mainly from Gruipedidae morphofamily. **A** *Gruipeda intermedia* (redrawn after Panin 1965). **B** *Gruipeda maxima* (redrawn from Panin and Avram 1962). **C**. *Gruipeda intermedia* (redrawn from Abbassi et al. 2015). **D.** *Gruipeda dominguensis* (De Valais and Melchor 2008). **E-F**. *Gruipeda dominguensis* from La Sagarreta. **G-H**. *Iranipeda abeli* (redrawn from Abbassi et al. 2021). **I**. *Iranipeda millumi* (redrawn from Doyle et al. 2000). **J.**

Persiavipes gulfi (redrawn from Abbassi and Dashtban, 2021). **K**. *Ardeipeda gigantea* (redrawn from Panin and Avram, 1962). **L.** *Ardeipeda egretta* (redrawn from Panin and Avram, 1962). **M.** *Ardeipeda incerta* (redrawn from Vialov, 1965). Scale bars equals 10 cm.

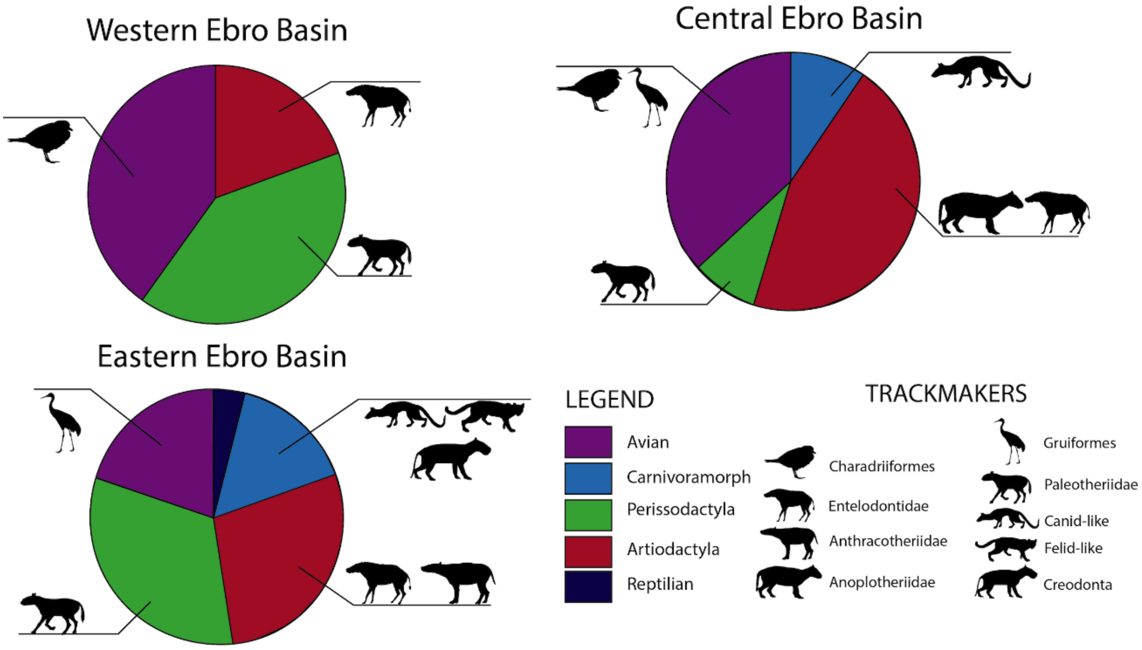

Figure 14. Pie chart showing the ichnodiversity in the three main areas with Early Oligocene tracksites in the Ebro Basin.

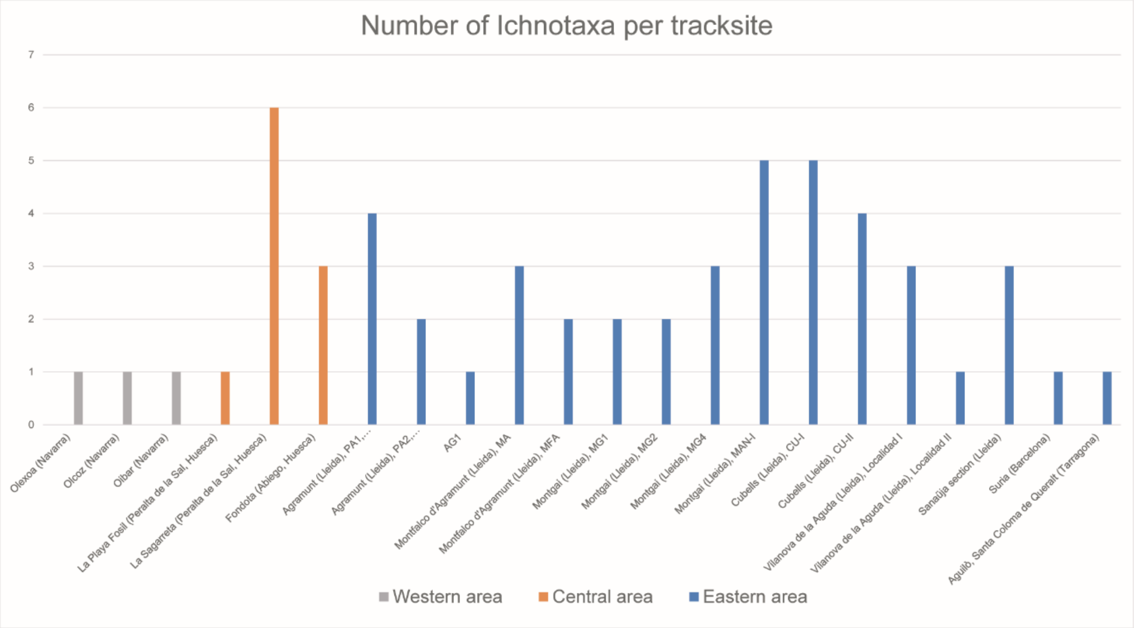

Figure 15. Bar chart showing the number of ichnotaxa per tracksite in the Ebro Basin. Information and references in the table S3.