

## EARLY MIOCENE SHOREBIRD-LIKE FOOTPRINTS FROM THE EBRO BASIN, LA RIOJA, SPAIN: PALEOECOLOGICAL AND PALEOENVIRONMENTAL SIGNIFICANCE

IGNACIO DÍAZ-MARTINEZ,<sup>1,2</sup> OIER SUAREZ-HERNANDO,<sup>3</sup> BLANCA MARTÍNEZ-GARCÍA,<sup>3</sup> JOSÉ MARÍA HERNÁNDEZ,<sup>4</sup> SALVADOR GARCÍA FERNÁNDEZ,<sup>5</sup> FÉLIX PÉREZ-LORENTE,<sup>2</sup> AND XABIER MURELAGA<sup>3</sup>

<sup>1</sup>CONICET - Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, General Roca 1242, 8332 Fisque Menuco (General Roca), Río Negro, Argentina

<sup>2</sup>Facultad de Ciencias, Estudios Agroalimentarios e Informática, Universidad de La Rioja, Madre de Dios 51-53, 26006 Logroño, La Rioja, Spain

<sup>3</sup>Universidad del País Vasco UPV/EHU, Facultad de Ciencia y Tecnología, Departamento de Estratigrafía y Paleontología, Apartado 644, E-48080 Bilbao, Bizkaia, Spain

<sup>4</sup>Fundación Cristina Enea, Paseo Duque de Mandas 66, 20012 San Sebastián, Gipuzkoa, Spain

<sup>5</sup>Aula Paleontológica de Cenicero, Casa de Cultura Las Monjas, 26350 Cenicero, La Rioja, Spain  
e-mail: [inaportu@hotmail.com](mailto:inaportu@hotmail.com)

**ABSTRACT:** Small shorebird-like footprints have been discovered in Cenicero (La Rioja, Spain). They are preserved in a sandstone block of the transition unit between the Nájera and Haro Formations from the Ebro Basin. This level is positioned in the Y2 local zone (MN2), of Agenian age (early Miocene). The footprints are small, tridactyl or tetradactyl, with slender and proximally unconnected digit impressions. They have phalangeal pads and claw marks, and there is no evidence of a web or metatarsal pad. The footprints are compared with other shorebird-like ichnotaxa and assigned to the Cretaceous ichnotaxon *Koreanaornis* isp., which is herein identified for the first time in the Cenozoic. Other shorebird-like footprints from the late Eocene to early Miocene in the Ebro Basin and the early Miocene ichnotaxa *Aviadactyla media* and *Aviadactyla vialovi* are also related to this ichnotaxon. In addition to the shorebird-like footprints, the Cenicero tracksite has invertebrate traces and sedimentary and organic structures typical of the *Scoyenia* ichnofacies, suggesting a mud-dominated floodplain in a central-distal alluvial fringe as the paleoenvironment. The morphology, habitat, and behavior inferred from the shorebird-like footprints in the Cenicero tracksite are similar to other fossil footprints found in the Mesozoic and Cenozoic as well as to modern shorebird tracks. This is likely due to morphological, ecological, and behavioral convergences among different avian clades from the Early Cretaceous to the present.

### INTRODUCTION

During the construction of a wine cellar in the vicinity of Cenicero (La Rioja, Spain), fourteen sandstone blocks with 142 footprints of early Miocene age (Ebro Basin) were found (Díaz-Martínez et al. 2011). They were assigned to an artiodactyl (*Pecoripeda* isp.), a perissodactyl (cf. *Hippipeda*), and two large avian (*Gruipeda* aff. *maxima* and *Uvaichnites riojana*) ichnotaxa (Díaz-Martínez et al. 2011, 2012a, 2012b). A new block with small shorebird-like footprints found recently at the same locality (the Cenicero tracksite) is examined in this work.

Several shorebird-like footprints have been described in the Cenozoic Ebro Basin (Spain) in recent years. The oldest examples are from the upper Eocene of Liedena (de Raaf et al. 1965; Payros et al. 2000) in the province of Navarra. Oligocene footprints were found in Solsona-Sanaüja (de Gibert and Saez 2009) in Lleida and in Etaio (Murelaga et al. 2007) in Navarra. The youngest ones come from the Oligocene–Miocene interval of Alcanadre (García-Raguel et al. 2009) in La Rioja and the lower Miocene of Los Arcos (Astibia et al. 2007) in Navarra.

Shorebird-like footprints are abundant in the Mesozoic and Cenozoic ichnological record worldwide (see Lockley and Harris 2010, and references therein). They are small, slender tracks with large digit divarication and look just like the tracks of extant shorebirds (Lockley and Rainforth 2002). Beside the morphology, the shorebird-like footprints reflect the same behavior and habitat from the Early Cretaceous to the present (e.g., Genise et al. 2009; Lockley and Harris

2010; Falk et al. 2010, 2014). They are generally associated with lake-basin, fluvial-floodplain, or coastal-plain and marine-shoreline deposits (Lockley and Harris 2010). Traditionally, Mesozoic and Cenozoic bird tracks have been studied and named separately by researchers (see Lockley and Harris 2010), and therefore there are likely synonymies (Anfinson et al. 2009).

The main objective of this work is to describe in detail the new shorebird-like footprints found in Cenicero (early Miocene, Ebro Basin), taking into account their paleoecological and paleoenvironmental implications. Moreover, the similarity of Mesozoic and Cenozoic shorebird-like footprints is also analyzed.

### GEOLOGICAL SETTING

The Cenicero site (Fig. 1) is located in the Tertiary Ebro Basin, a large tectonosedimentary depression filled with more than 4,000 m of Oligocene–Miocene sediments (Villena et al. 1996) (coordinates: 42°28'21.99" N latitude and 2°37'42.90" W longitude).

The referenced cross section (Fig. 2) crops out with a bedding orientation striking N45°E and dipping 18°NW (Díaz-Martínez et al. 2011; Díaz-Martínez et al. 2012a, 2012b). The most common facies association is a succession of mainly beige siltstones, which frequently exhibit pseudogley paleosol levels (PiPujol and Buurman 1997), and less usually are interbedded with red or orange lutites showing gley levels (Kraus and Aslan 1993). These detrital fine-grained deposits occasionally

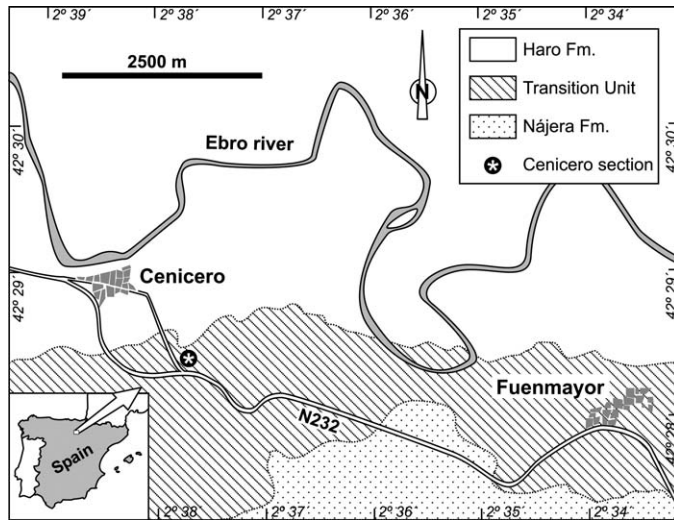


FIG. 1.—Local geological map with the location of the Cenicero section.

include interbedded calcarenitic sandstone, sublitharenites or wackes, in layers less than 30-cm thick. These sediments have sharp bases and horizontal lamination, fining-upward sequences, and vertical root trace levels (Hernández et al. 1997) at the top.

The shorebird-like footprints are found in a fine-grained calcarenitic sandstone block with very thin lamination, labeled 14CN. Centimeter-sized current ripples, wrinkle structures, and invertebrate traces can be seen on the same surface as the bird tracks (Fig. 3, 4). There are simple horizontal trails on the bedding plane, simple horizontal meniscate burrows, and simple vertical burrows related with *Hemithoidichnites*, *Taenidium*, and *Skolithos* respectively. In addition, the block is divided into two distinct superficial patterns; one pattern shows a wrinkled surface with smooth traces, and the other shows a smooth surface with better-preserved traces (Fig. 4).

This main facies assemblage is typical of deposits of a central-distal alluvial fringe or a mud-dominated floodplain. The bioturbation marks suggest subaqueous invertebrate movement, and the pedogenic features indicate subaerial exposure after floods (PiPujol and Buurman 1997). The calcarenitic sandstone interlayers are interpreted as distal erosional channels formed and filled during sediment-bearing floods. The measured paleocurrents suggest a south-dominant flow, and the calcareous composition reflects the materials available in the source area in the Iberian Range (Díaz-Martínez et al. 2011).

An additional paleoenvironmental analysis based on ostracod assemblages (Suárez-Bilbao et al. 2014) indicates shallow, ephemeral ponds in an alluvial or floodplain system, with conditions more favorable for the establishment of ostracod communities in the upper part of the succession (samples CN-7.7 to CN-10; Fig. 2). According to the paleoecological criteria proposed by Meisch (2000), the identified ostracod species (see Suárez-Bilbao et al. 2014) indicate that water temperatures ranged from 12 to 29 °C, and water salinity varied from freshwater to mesohaline water (0.1‰ to 18‰) along the section. The variation in water temperatures and salinity values could be due to changes in the precipitation regime on the floodplain system: the probable seasonal nature of rainfall could have resulted in partial evaporation of the ponds during dry periods, which would have generated the increased salinity values (Suárez-Bilbao et al. 2014).

Stratigraphically, the Cenicero section is located in the informal “Transition Unit” proposed by Díaz-Martínez et al. (2011), and positioned between the Najera Formation (below) and Haro Formation (above) (Fig. 2). The Cenicero section is located 130 m above the

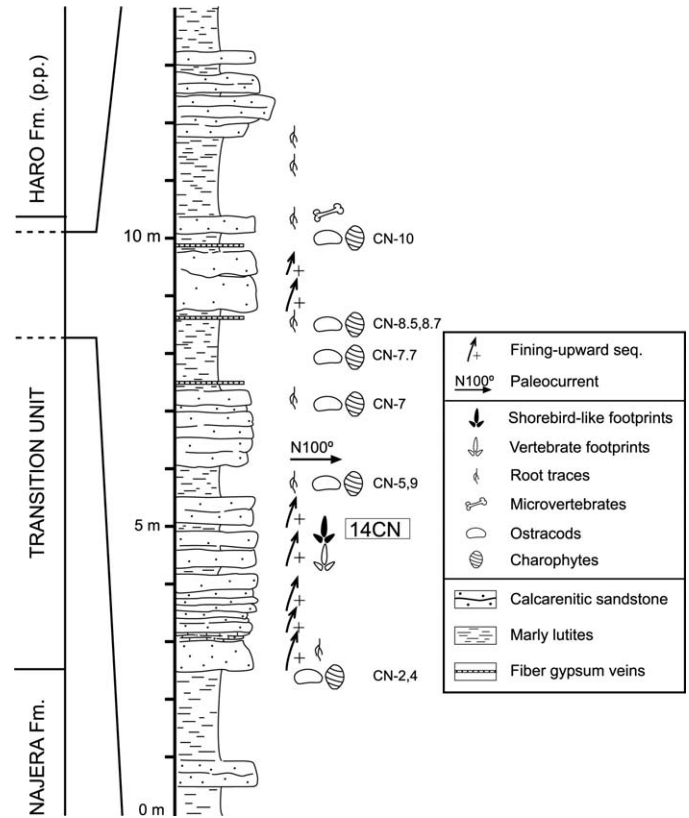


FIG. 2.—Stratigraphic section of the Cenicero tracksite. p.p. = *pro parte*.

Fuenmayor 2 paleontological site (Díaz-Martínez et al. 2011), which is positioned in local zone Y1 of Daams and Van der Meulen (1984) (European Neogene Land Mammal unit, MN2) (Martínez-Salanova 1987; Sesé 2006; and Ruiz-Sánchez et al. 2012). Moreover, the occurrence of *Armantomys daamsi* (Álvarez-Sierra et al. 1991) in the study section shows that the Cenicero site is dated concretely in local zone Y2 (MN2) of the Agenian (early Miocene).

#### MATERIALS AND METHODS

This work studies a new block with 26 avian footprints. The footprints are preserved in a sandstone block repositioned in the Paleontological Museum of Enciso (Enciso, La Rioja, Spain). The block was found at the Cenicero tracksite in an upper layer of the same stratigraphic package as the published mammal and large bird footprints (Díaz-Martínez et al. 2011, 2012a, 2012b). The footprints are designated according to convention (e.g., Casanovas et al. 1989; Pérez-Lorente 2001) as follows: first the tracksite identification, second the trackway, and third the footprint. For instance, 14CN4.1 is the first footprint of trackway number 4 of the Cenicero (CN) 14 tracksite.

The measurements (Table 1) and the nomenclature used in this study are mainly based on previous work (Pérez-Lorente 2001; de Valais and Melchor 2008; Díaz-Martínez et al. 2011). The measurements taken were: footprint length (FL), footprint length + hallux length (FL+hx), footprint width (FW), digit II length (II), digit III length (III), digit IV length (IV), angle between digits I and II (I<sup>II</sup>), angle between digits II and III (II<sup>III</sup>), angle between digits III and IV (III<sup>IV</sup>), angle between digits II and IV (II<sup>IV</sup>), pace length (PL), stride length (SL), pace angulation (ANG), trackway deviation (TD), inner trackway width (iTW), and external trackway width (eTW).

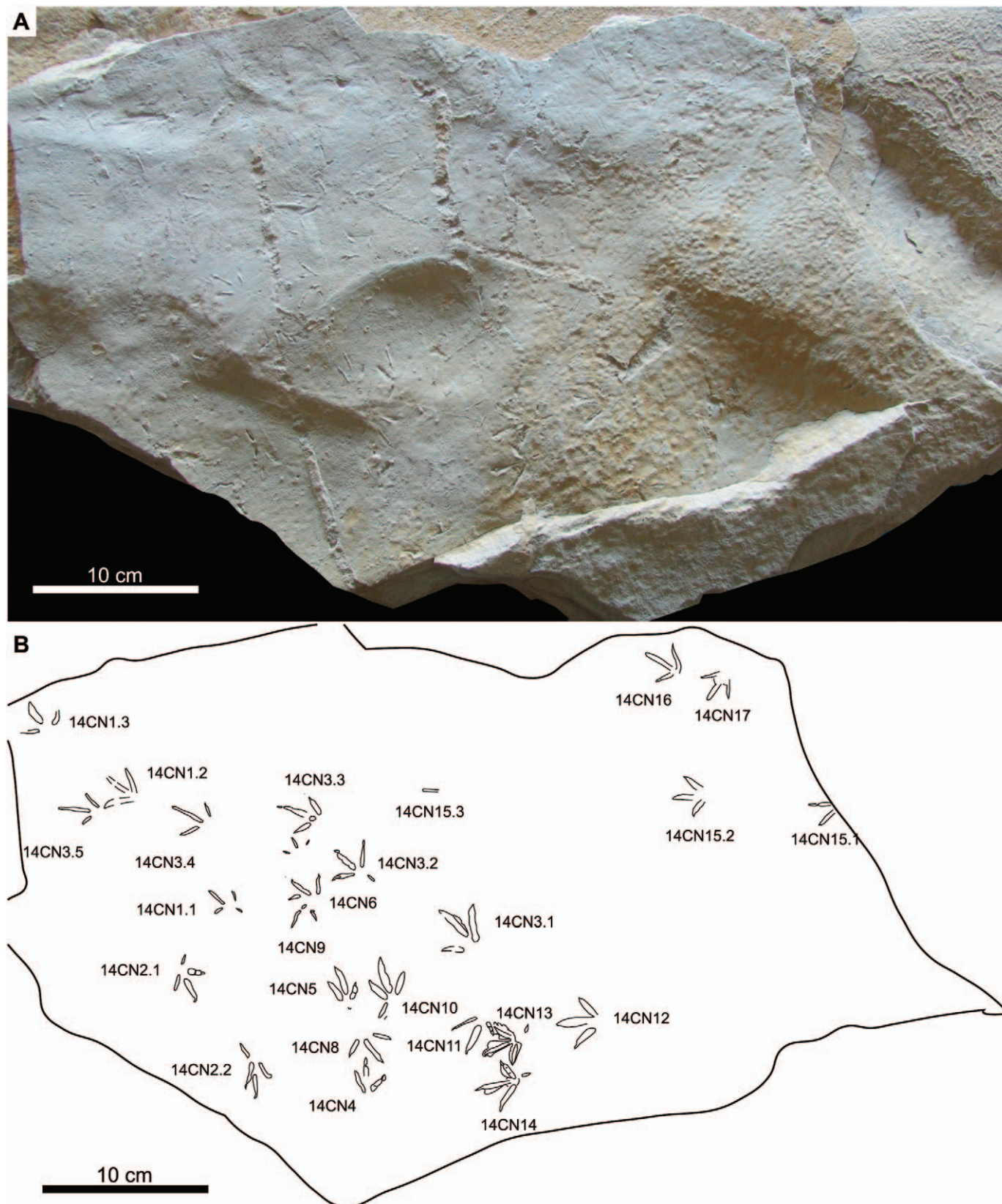


FIG. 3.—A, B) Photograph and sketch of the shorebird-like footprints of block 14CN, respectively.

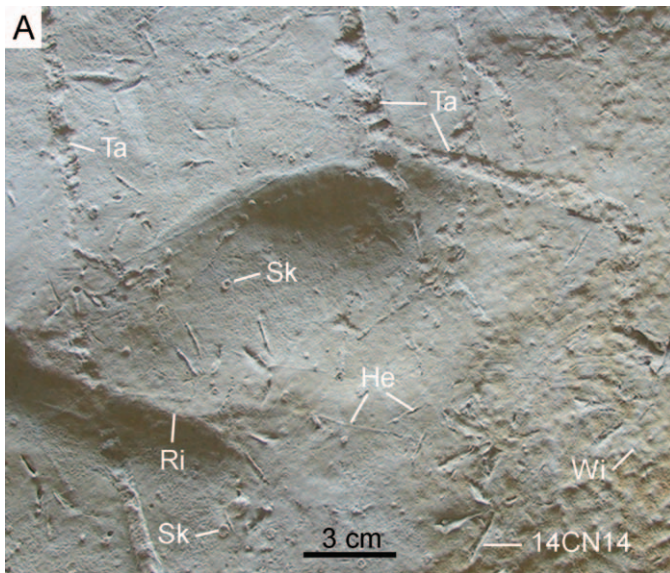


FIG. 4.—Photograph of a section of block 14CN with ripple marks, wrinkle marks, and vertebrate and invertebrate traces. Ta = *Taenidium*; He = *Hemithoidichnites*; Sk = *Skolithos*; Ri = ripple marks; and Wi = wrinkle marks.

#### ICHOLOGICAL DESCRIPTION

Ichnofamily *Koreanaornipodidae* Lockley, Houck, Yang, Matsukawa, and Lim 2006

Ichnogenus *Koreanaornis* Kim 1969  
*Koreanaornis* isp.

**Material.**—Twenty-six footprints: 14CN1.1, 14CN1.2, 14CN1.3, 14CN2.1, 14CN2.2, 14CN3.1, 14CN3.2, 14CN3.3, 14CN3.4, 14CN3.5, 14CN4, 14CN5, 14CN6, 14CN7, 14CN8, 14CN9, 14CN10, 14CN11, 14CN12, 14CN13, 14CN14, 14CN15.1, 14CN15.2, 14CN15.4, 14CN16, and 14CN17. The footprints are preserved as concave epireliefs without clear erosional structures.

**Horizon and Locality.**—Transition unit between the Nájera and Haro Formations of Agenian age (lower Miocene), Ceniceró locality, La Rioja, Spain.

**Description.**—Tridactyl or tetradactyl (hallux impression preserved in some specimens), mesaxononic anisodactyl footprints. They are diminutive to small (see parameters of ichnotaxobases in Díaz-Martínez et al. 2011) from 17 mm to 28 mm (from 24 mm to 35 mm with hallux impression), and wider than long except when the hallux is preserved (average 22 mm long to 25 mm wide without hallux). Digit III is the longest (average 17 mm). Digit II is smaller than IV (11 mm and 13 mm respectively), and digit I, the hallux, is the smallest and quite variable in length. The digit divarication between digits II and IV ranges from 57° to 114°. They have angular asymmetry and the average digit divarication between digits II and III is 41° less than between III and IV, which is 50°. The angle between digits I and II is 81° to 138°.

Digital pad impressions are recognizable in digits II, III and IV in some tracks (14CN2.1, 14CN3.2, 14CN4, 14CN5, and 14CN14). They are generally only slightly visible, although there are very clear bumps on the sole of the footprints marking the lateral outline of the pads. Digit impressions are slender and the proximal ends are not in contact with each other even though they are sometimes very close to the hallux

impression. The proximal part of digit III usually begins more distally than the proximal surface of the other toes. The digit impressions have an acuminate distal end. No evidence of webbed toes nor central pads is preserved.

There are four trackways (14CN1, 14CN2, 14CN3, and 14CN20) and another probable two trackways, one of which is composed of footprints 14CN4, 14CN5, 14CN6, and 14CN7, and the other, composed of footprints 14CN12, 14CN13, and 14CN14. The average pace length and stride length are 70 mm and 130 mm respectively. They are very narrow trackways ( $iTR/FW = 0.2$ ) with high pace angulation (average 157°). The footprints are rotated inward.

#### DISCUSSION

All the 14CN footprints have the same main features: slender digit impressions, absence of metatarsal pad impression, base of digit III impression set more distally than digits II and IV, clear phalangeal pad and claw impressions, and no evidence of webbing. Nevertheless, the number of digit impressions preserved and the divarication between digits II and IV is variable. Even the same trackway can contain both tridactyl and tetradactyl footprints and/or differences up to 27° in the divarication between digits II and IV (14CN1 and 14CN3) (Table 1). Variations in substrate hardness and the flexibility of the digits (Sarjeant and Reynolds 2001) as well as the behavior of the trackmaker (Belvedere and Mallison 2014; Marty et al. 2014) may produce these morphological differences. Therefore, we consider that all the footprints belong to the same ichnotype.

The shorebird-like tracks of the Ceniceró tracksite are similar to others found in the Mesozoic and Cenozoic ichnological record. Traditionally, Mesozoic and Cenozoic avian footprints have been assigned to a different ichnotaxa (see Lockley and Harris 2010, tables 1, 2). Only de Valais and Melchor (2008) applied a name initially given to a Cenozoic ichnotaxon to Mesozoic specimens (Lockley and Harris 2010), and Mansilla et al. (2012) assigned Cenozoic tracks to a Mesozoic ichnotaxa. Anfinson et al. (2009) suggested that there had never previously been any explicit attempt to compare these Mesozoic and Cenozoic tracks, and that therefore there could be synonymies between them.

Small unwebbed shorebird-like footprints have been classified into different ichnogenera (Fig. 5): *Koreanaornis* Kim 1969 (Early Cretaceous, Korea); *Aquatilavipes* Currie 1981 (Early Cretaceous, Canada); *Ludicharadripodiscus* Ellenberger 1980 (Eocene, France); *Antartichnus* Covacevich and Lamperein 1972 (Oligocene–middle Miocene, Antarctica); *Avipeda*, Vialov 1965 (Miocene, Ukraine); *Aviadactyla* Kordos 1983 (early Miocene, Hungary); and *Fuscinapeda* Sarjeant and Langston 1994 (Miocene, Ukraine).

In *Aquatilavipes*, *Ludicharadripodiscus*, *Antartichnus*, *Avipeda* (*sensu* Sarjeant and Langston 1994), and *Fuscinapeda* (*sensu* Sarjeant and Langston 1994), the impressions of digits II, III, and IV are united proximally, whereas in 14CN the footprints are separated.

The *Koreanaornis* ichnospecies (*K. hamanensis* Kim 1969; *K. dodsoni* Xing, Harris, Jia, Luo, Wang and An 2011; and *K. sinensis* (Zhen, Li, Chen, and Zhu 1995)); *Aviadactyla media* Kordos 1983; and *Aviadactyla vialovi* (Kordos and Prakfalvi 1990) present the same main features as the 14CN footprints (slender, proximally unconnected digits, pad and claw impressions, etc.) (Fig. 6). These five ichnotaxa are very similar and differ from each other mainly in the number of digits impressed and in the divarication between digits II and IV. *Koreanaornis hamanensis* was initially defined as tridactyl (Kim 1969), but Lockley et al. (1992) emended the diagnosis and proposed faint hallux impressions preserved in some specimens. The divarication between digits II and IV averages about 120° (range 105°–125°) (Lockley et al. 1992). The ichnotaxon *K. sinensis*, previously considered *Aquatilavipes sinensis* (Zhen et al. 1995), is tridactyl or tetradactyl and presents similar divarication as *K. hamanensis*

TABLE 1.—Measurements of the shorebird-like footprints of Cenicero. Abbreviations: FL = footprint length; FL+hx = footprint length + hallux length; FW = footprint width; II = digit II length; III = digit III length; IV = digit IV length; I^II = angle between digits I and II; II^III = angle between digits II and III; III^IV = angle between digits III and IV; II^IV = angle between digits II and IV; PL = pace length; SL = stride length; ANG = pace angulation; TD = trackway deviation; iTW = inner trackway width; and eTW = external trackway width.

	FL	FL+hx	FW	II	III	IV	I^II	II^III	III^IV	II^IV	PL	SL	ANG	TD	iTW	eTW
14CN17	20	-	21	-	-	-	-	-	-	81	-	-	-	-	-	-
14CN16	22	-	25	-	-	-	-	-	-	94	-	-	-	-	-	-
14CN15.3	-	-	-	-	-	-	-	-	-	-	-	148	-	-	-	-
14CN15.2	20	24	24	-	-	-	-	52	38	90	80	-	-	-	-	-
14CM15.1	-	-	-	-	-	-	-	-	43	-	-	-	-	-	-	-
14CN14	27	35	30	14	22	18	106	66	43	109	-	-	-	-	-	-
14CN13	23	33	25	-	16	13	81	52	56	110	-	-	-	-	-	-
14CN12	26	-	31	-	-	-	-	32	57	89	-	-	-	-	-	-
14CN11	21	-	25	8	18	16	-	35	50	85	-	-	-	-	-	-
14CN10	26	32	23	15	22	14	99	24	41	65	-	-	-	-	-	-
14CN9	18	-	22	07	16	7	-	31	66	97	-	-	-	-	-	-
14CN8	21	-	27	11	18	11	-	39	67	106	-	-	-	-	-	-
14CN7	-	-	17	-	-	-	-	46	62	108	-	-	-	-	-	-
14CN6	17	-	-	12	13	-	-	52	-	-	-	-	-	-	-	-
14CN5	21	27	18	13	17	10	-	15	42	57	-	-	-	-	-	-
14CN4	21	-	19	12	-	13	-	30	43	73	-	-	-	-	-	-
14CN3.5	23	-	19	07	18	11	-	39	49	88	68	-	-	-	-	-
14CN3.4	24	-	25	08	21	12	-	43	56	99	63	131	169	-25	4	24
14CN3.3	24	-	23	11	20	12	-	54	35	89	41	95	131	8	10	44
14CN3.2	20	30	31	16	17	14	130	50	55	105	80	120	-	-6	3	34
14CN3.1	28	-	30	13	23	23	-	44	34	78	-	-	-	-	-	-
14CN2.2	22	34	27	16	14	12	-	-	-	-	72	-	-	-	-	-
14CN2.1	20	29	21	10	15	10	-	-	-	-	-	-	-	-	-	-
14CN1.3	19	-	27	09	15	14	-	54	60	114	71	-	-	-	-	-
14CN1.2	24	-	30	-	-	-	-	45	35	80	84	154	170	-10	3	29
14CN1.1	17	24	27	06	12	6	138	27	72	99	-	-	-	-	-	-
Mean	22	30	25	11	17	13	111	41	50	91	70	130	157	-8	5	33

(*sensu* Lockley and Rainforth 2002, fig. 17.5B; Lockley et al. 2012, fig. 8B). *Koreanaornis dodsoni* is tridactyl and the divarication angle between digits II and IV averages about 87° (range 58°–109°) (Xing et al. 2011). The ichnotaxon *A. media* is tridactyl and the angle between II and IV ranges from 81° to 125° (Kordos 1983). And finally, *A. vialovi* is tridactyl with variable II–IV divarication ranging from about 80° to over 155° (Sarjeant and Reynolds 2001). The differences among these ichnotaxa are the same as we identify above for the footprints of 14CN within the same trackway. The divarication can be variable depending on pace and substrate hardness (Sarjeant and Reynolds 2001), and the absence or presence of a hallux impression in most *Koreanaornis* tracks may be the result of variable preservation and the inherently small size of the hallux (Anfinson et al. 2009). Therefore, the hallux trace and the divarication angle are not consistent morphological features in this case (although in other cases the divarication is a good criterion for distinguishing bird tracks, see Falk et al. 2011). As a result, we propose that ichnospecies *A. media* and *A. vialovi* belong to ichnogenus *Koreanaornis*, and the possible synonymy of all *Koreanaornis* ichnospecies (*A. media* and *A. vialovi* included) should be revised in order to select the valid ichnotaxa and adapt their diagnosis on the basis of useful ichnotaxobases regardless of age (Mesozoic or Cenozoic). This problem would need detailed ichnotaxonomical analyses of described examples and further systematic discussion, which is beyond the scope of this paper.

Based on their morphological features and the ichnotaxonomical discussion, we classified the 14CN footprints within *Koreanaornis*; however, we have not assigned them to any of its ichnospecies until the validity and systematic relationships are discussed.

Several footprints in the Ebro Basin from the late Eocene to the early Miocene (and assigned to different ichnotaxa) could be classified within *Koreanaornis*. Such is the case of *Charadriipeda* isp. 1 and 2 from the late

Eocene of Navarra (Payros et al. 2000, figs. 6–10), *Gruipeda* isp. from the Oligocene of Lleida (de Gibert and Saez 2009, fig. 6A–B), small wading bird tracks from the early Oligocene of Navarra and Zaragoza (de Raaf 1965, fig. 1), morphotypes 1 and 3 from the Oligocene of Navarra (Murelaga et al. 2007, fig. 4.3), avian tracks from the late Oligocene–early Miocene of La Rioja (García-Raguel et al. 2009, figs. 34–38, 40), and bird tracks from the early Miocene of Navarra (Astibia et al. 2007, fig. 11h–i).

Traditionally, *Koreanaornis* has been considered a Mesozoic ichnotaxon and it is identified in this work for the first time in the Cenozoic ichnological record. These footprints and other similarly shaped Mesozoic and Cenozoic ones have been compared with extant shorebirds (e.g., Lockley et al. 1992, 2006; Lockley and Harris 2010; Falk et al. 2010; Contessi and Fanti 2012). This assumption is based on footprint shape (the Early Cretaceous tracks are similar to extant shorebirds) and the sedimentary facies (indicating a water-margin environment) (e.g., Currie 1981; Lockley et al. 2001; Lim et al. 2000). Mesozoic and Cenozoic shorebird-like footprints have already been compared to Charadriiform birds (Doyle et al. 2000; Lockley and Rainforth 2002; Lockley and Harris 2010). The oldest remains of the order Charadriiformes, although highly fragmentary, are from the Campanian–Maastrichtian (Chiappe 1995; Case and Tambussi 1999); the diversification of the crown is restricted to the Cenozoic based on mitochondrial DNA (Brown et al. 2008). Therefore, the trackmakers of Mesozoic and Cenozoic *Koreanaornis*-like tracks could be different taxonomically. For instance, Falk et al. (2014) suggested that early Ornithurine birds likely produced Early Cretaceous tracks as they are the dominant water birds of that age (Zhou and Zhang 2007), and Doyle et al. (2000) affirmed that some Miocene tracks are typical of many wading shorebirds of the Charadriiformes, particularly sandpipers and snipes of the Charadriidae.

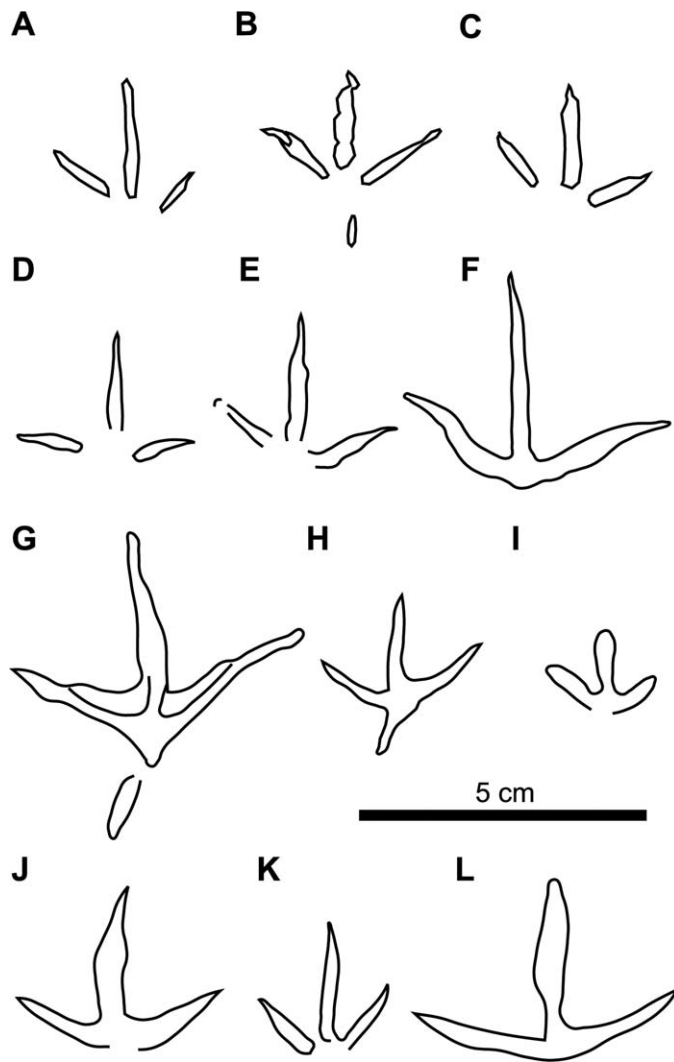


FIG. 5.—Comparison among sketches of 14CN tracks and other bird ichnotaxa. A) 14CN3.4. B) 14CN3.2. C) 14CN8. D, E) *Koreanaornis* (redrawn from Lockley et al. 1992). F) *Aquatilavipes* (redrawn from Currie 1981). G) *Ludicharadripodiscus* (redrawn from Ellenberger 1980). H) *Antartichnus* (redrawn from Covacevich and Lamperein 1972). I) *Avipeda phoenix* (redrawn from Lockley and Harris 2010). J) *Avipeda sirin* (redrawn from Lockley and Harris 2010). K) *Aviadactyla vialovi* (redrawn from Sarjeant and Reynolds 2001). L) *Fuscinapeda* (redrawn from Lockley and Harris 2010).

#### PALEOENVIRONMENTAL AND PALEOECOLOGICAL IMPLICATIONS

The vertebrate (shorebird-like) and invertebrate (*Helminthoidichnites*, *Taenidium*, and *Skolithos*) traces, together with the sedimentary and organic structures found in block 14CN, define it as the *Scoyenia* ichnofacies (Seilacher 1967) according to Frey et al. (1984) and Buatois and Mangano (1995). Moreover, these avian footprints could be related with the shorebird ichnofacies proposed by Lockley et al. (1994), who defined some vertebrate ichnofacies with the aim of temporally dividing the archetypical continental ichnofacies proposed by Seilacher (1967). Melchor et al. (2006) and de Gibert and Saez (2009) affirmed that the shorebird ichnofacies is a subset (ichnosubfacies) of the *Scoyenia* ichnofacies.

Frey and Pemberton (1986, 1987) proposed that the *Scoyenia* ichnofacies occurs in low-energy deposits periodically exposed to air or

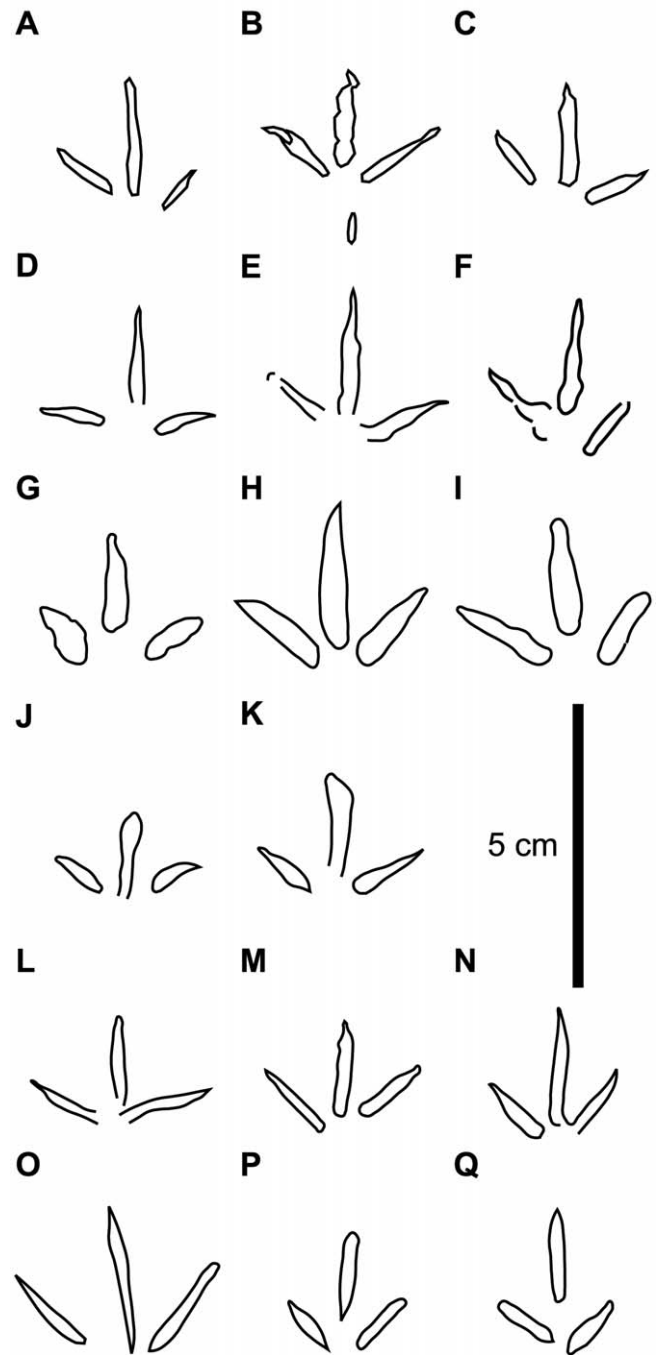


FIG. 6.—Comparison among sketches of 14CN tracks and other bird ichnotaxa. A) 14CN3.4. B) 14CN3.2. C) 14CN8. D–F) *Koreanaornis hamanensis* (redrawn from Lockley et al. 1992). G–I) *Koreanaornis dodsoni* (redrawn from Xing et al. 2011). J, K) *Koreanaornis sinensis* (redrawn from Lockley et al. 2012). L–N) *Aviadactyla vialovi* (redrawn from Sarjeant and Reynolds 2001). O–Q) *Aviadactyla media* (redrawn from Kordos 1983).

periodically inundated and intermediate between aquatic and nonaquatic environments. In fluvial systems, this ichnofacies is present in floodplain deposits, covering a wide variety of subenvironments such as ponds, levees, and crevasse splays (Frey et al. 1984; Frey and Pemberton 1986, 1987; Buatois and Mangano 1995). These data agree with the sedimentological studies of 14CN, which indicate the footprints are

preserved in a sandstone bed of a central-distal alluvial fringe with a mud-dominated floodplain (Díaz-Martínez et al. 2012a). In addition, the arrangement of wrinkle marks (on the right part of the block) on the study layer suggests that 14CN footprints were likely impressed on the banks of a pond with a sufficiently long-lived moist part to support the development of microbial mats (Melchor et al. 2006). Finally, the absence of mudcracks indicates that the shorebird-like footprint track-makers walked upon a surface in which complete desiccation did not occur (Melchor et al. 2006).

The shorebird-like footprints of 14CN are monoichnospecific, with a random pattern and very high track density. Lockley and Harris (2010) identified these features in other Mesozoic and Cenozoic tracksites and proposed that it indicates gregarious behavior. On the other hand, footprints 14CN13 and 14CN14 are placed together as in a standing position after a walk (Figs. 3, 4). The footprints are well marked and deeper than 14CN12, which is behind them and could belong to the same trackway. Moreover, there are no tracks in the trackway after these paired tracks. This sequence of footprints has been related with a simple takeoff based on neoichnological studies (Genise et al. 2009, fig. 7R). Several authors (e.g., Genise et al. 2009; Lockley and Harris 2010; Falk et al. 2014) have suggested that the behavior inferred from shorebird-like footprints (gregariousness, takeoff, landing, feeding, etc.) is similar among Mesozoic, Cenozoic, and current tracks, and it has been identified from at least the Early Cretaceous.

Lockley and Harris (2010) explained that the similarities between Mesozoic and Cenozoic tracks could be related to the selective pressures and/or inherent morphodynamics that produced not only similar foot morphologies but even similar sizes and behaviors of birds in similar niches through time. Several studies with extant birds (e.g., Lennerstedt 1975; Kambic 2008) have confirmed that the structure and size of the foot bones, pads, and papillae correlate with life habits. Moreover, Korner-Nievergelt (2004) found relationships between habit (substrate), locomotion, behavior, and plantar morphology in passerines and suggested that they are an adaptive function of the plantar integument to locomotion and substrate. Hence, the Mesozoic and Cenozoic avian track records reflect the convergent evolution of adaptive morphologies to particular lifestyles in specific ecosystems, without a need to match tracks to members of particular clades (Lockley and Harris 2010).

#### CONCLUSIONS

The early Miocene small shorebird-like footprints found at the Cenicero tracksite (Ebro Basin) are classified as *Koreanaornis* isp. This ichnotaxon, defined in the Early Cretaceous, is identified for the first time in the Cenozoic ichnological record in this work. Moreover, several footprints found in the Ebro Basin from the late Eocene to the early Miocene and the ichnotaxa *Aviadactyla media* and *Aviadactyla vialovi* defined in the early Miocene are related to *Koreanaornis*. Further studies should discuss the validity and systematic relationship of *Koreanaornis* ichnospecies.

The assemblage of vertebrate and invertebrate traces, in conjunction with sedimentary and organic structures found on the track-containing block, ascribes it to the *Scoyenia* ichnofacies (shorebird ichnosubfacies). The ichnological, sedimentological, and stratigraphical data of the Cenicero tracksite indicate that the shorebird-like footprints were likely produced in a pond on a mud-dominated floodplain in a central-distal alluvial fringe.

The shorebird-like footprints described in this work show similarities in morphology, behavior, and ecology with other fossil footprints found in the Mesozoic and Cenozoic and with modern bird tracks. This is likely due to morphological, behavioral, and ecological convergences among different avian clades from the Early Cretaceous to date.

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