



OPEN

Aurochs roamed along the SW coast of Andalusia (Spain) during Late Pleistocene

Carlos Neto de Carvalho^{1,2}, Fernando Muñiz³, Luis M. Cáceres^{4✉}, Zain Belaústegui⁵, Joaquín Rodríguez-Vidal⁴, João Belo⁶, Noel Moreira⁷, Mário Cachão^{2,8}, Pedro P. Cunha⁹, Silvério Figueiredo^{10,11}, José María Galán¹², Yilu Zhang¹³, Paula Gómez⁴, Antonio Toscano⁴, Francisco Ruiz⁴, Samuel Ramírez-Cruzado⁴, Francisco Giles-Guzmán¹⁴, Geraldine Finlayson^{14,15,16}, Stewart Finlayson^{14,15} & Clive Finlayson^{14,15,16,17}

In the Iberian Peninsula the fossil record of artiodactyls spans over 53 million years. During the Pleistocene, wild cattle species such as *Bison* and especially *Bos* became common. In Late Pleistocene, the aurochs (*Bos primigenius*) was widespread and the only bovine living along the large river valleys of southern Iberia. Although commonly found in fossil sites and especially in cave bone assemblages, the trace fossil record of aurochs was known worldwide only from the Holocene. Large bovine and roe deer/caprine tracks were found in at least five horizons of the early Late Pleistocene (MIS 5) beach and eolian deposits of Cape Trafalgar (Cadiz Province, South of Spain). The large bovine tracks are formally described as *Bovinichnus uripeda* igen. et isp. nov. and compared with the record of aurochs tracks, large red deer tracks and steppe bison biogeographical distribution in Iberia. Aurochs were the most likely producers of the newly described Trafalgar Trampled Surface (TTS) and some of the large artiodactyl tracks in the Matalascañas Trampled Surface, representing the oldest aurochs track record known. This new evidence, together with comparisons with the record of possible aurochs tracks in the Mid-Late Pleistocene coastal deposits from the Asperillo cliff section in Matalascañas (Huelva Province, SW Spain) and bone assemblages known in Gibraltar, point to a recurrent use of the coastal habitat by these large artiodactyls in SW Iberia.

The artiodactyls are even-toed ungulates belonging to a diversified group of large land mammals that can be found nowadays all over the world, except Antarctica. The oldest fossils of even-toed ungulates date back to the early Eocene and were found in Europe, Asia and North America¹. The oldest bone remains known in Europe were found in the Iberian Peninsula and are dated from this period^{2,3}. However, their record of living activities, known through the study of trace fossils, such as tracks or excrements, is much more scattered, and known only since the late Eocene to early Oligocene in North America and Europe, including Spain⁴⁻⁷ (see the recent attribution of late Paleocene tracks to possible basal artiodactyls or tapiroids⁸).

Fossil tracks, when safely attributed to a specific producer, can be complementary to the osteological record, providing additional data on geographical distribution of species, their paleoecology and biological behaviour.

¹Naturtejo UNESCO Global Geopark, Geology Office of the Municipality of Idanha-a-Nova, Idanha a Nova, Portugal. ²Instituto D. Luiz, University of Lisbon, Lisbon, Portugal. ³Departamento de Cristalografia, Mineralogía y Química Agrícola, Universidad de Sevilla, Sevilla, Spain. ⁴Departamento de Ciencias de la Tierra, Universidad de Huelva, Huelva, Spain. ⁵Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Barcelona, Spain. ⁶Geosciences Center, FlyGIS-UAV Surveys, University of Coimbra, Coimbra, Portugal. ⁷Instituto de Investigação e Formação Avançada, Institute of Earth Sciences (ICT)-Pole of Évora, University of Évora, Évora, Portugal. ⁸Department of Geology, Faculty of Sciences, University of Lisbon, 1749-016 Lisboa, Portugal. ⁹Department of Earth Sciences, MARE-Marine and Environmental Sciences Centre, University of Coimbra, Coimbra, Portugal. ¹⁰Department of Archeology, Conservation and Heritage, CGeo-UC, Polytechnical Institute of Tomar, Tomar, Portugal. ¹¹Centro Português de Geo-História e Pré-História, São Caetano, Portugal. ¹²Centro Administrativo del Acebuche, Parque Nacional de Doñana, Matalascañas, Spain. ¹³Academy of Natural Resources of Henan, Zhengzhou, China. ¹⁴The Gibraltar National Museum, Gibraltar, UK. ¹⁵Institute of Life and Earth Sciences, University of Gibraltar, Gibraltar, UK. ¹⁶Department of Life Sciences, Liverpool John Moores University, Liverpool, UK. ¹⁷Department of Anthropology, University of Toronto, Scarborough Campus, Toronto, Canada. ✉email: mcaceres@uhu.es

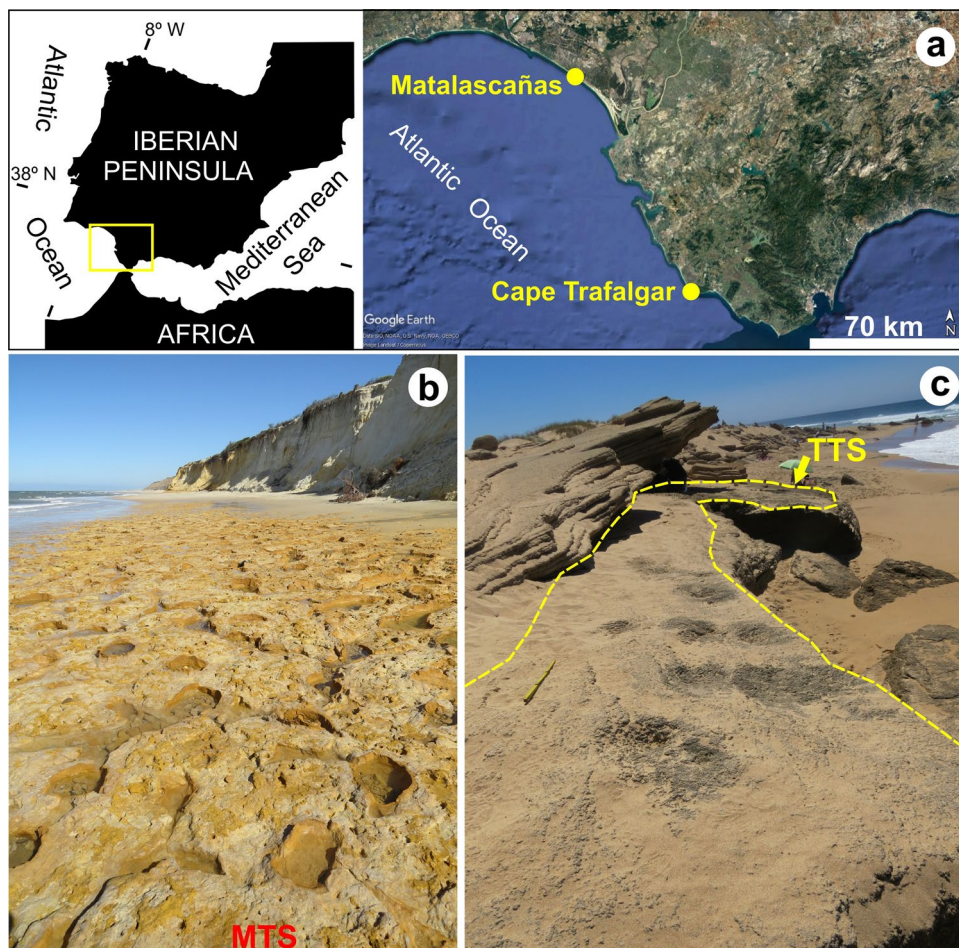


Figure 1. (a) Location of Cape Trafalgar and Matalascañas tracksites in SW Iberian Peninsula, Image adapted from GoogleEarth©; (b) The MTS at Matalascañas, Province of Huelva (SW Spain); (c) the new TTS in Cape Trafalgar (Province of Cadiz). Map in (a) (left) and modifications to the photograph in (c) have been drawn with CorelDraw 12 (<https://www.coreldraw.com/la/>).

The body fossil record of the bovine tribe is relatively common in Quaternary deposits, but rarely have tracks been attributed to these animals. In the Iberian Peninsula, artiodactyl tracks from Pleistocene beds were mostly attributed to goats, cervids, and wild boar^{9–16}. Here we formally describe, for the first time, large artiodactyl tracks from two different sites in SW Spain ascribed to the early Late Pleistocene, safely attributed to aurochs (*Bos primigenius*). During the Late Pleistocene, the aurochs were widespread and the only wild cattle living along the large river valleys in southern Iberia. Artiodactyls are cloven-hoofed animals, which in most cases bear the body weight equally on two of their five toes: the third and fourth. We compare the morphology of very large cloven-hoofed tracks found during the study of Late Pleistocene eolianites in SW Iberia, with the ones of cervids and recent tracks made by *Bos taurus*. Although commonly found in fossil sites and especially in cave bone assemblages^{17–19}, the trace fossil record of aurochs was only known from the Holocene of Great Britain, especially in tidal flat deposits from estuarine areas^{20,21}. In SW Spain, the Cape Trafalgar and Asperillo cliff new tracksites (Fig. 1) provide an opportunity to endorse paleoecological interpretations regarding the recurrent use of the coastal habitats by these massive grazers during the Quaternary.

The track fossil record of artiodactyls in the Iberian Peninsula and the presence of aurochs in the SW

In the Iberian Peninsula, the oldest cloven-hoofed tracks were identified in the Lower Miocene²². The first tracksites were described in the Late Pleistocene (MIS 3) of the Balearic Islands in Mallorca, Menorca and Formentera^{9,11,23}, and attributed to the insular goat *Myotragus balearicus* Bate. Large cervid tracks were described in the Late Pleistocene eolianites of Gorliz (Basque coast, north Spain)¹⁰, in the Late Pleistocene (MIS 5–4) eolianites of SW Alentejo (Portugal)^{12–14}, and in the Late Pleistocene of the Catalan Bay eolianite, in Gibraltar²⁴. However, if the eolianites are confirmed to be MIS 3 in age, the more rounded cervid didactyl tracks from Gorliz could also be compared to those of the reindeer *Rangifer tarandus*, a species commonly found from the bone record in the northern Spain during the Pleniglacial^{25–27}. Recently, the Matalascañas Trampled Surface (MTS)

in the province of Huelva (SW Spain), dated from the early Late Pleistocene (MIS 5), was described showing abundant artiodactyl tracks which were attributed to wild boar, red deer and possibly aurochs^{15,16}.

Aurochs tracks have been studied especially in coastal deposits in England and Wales associated with early Mesolithic to early Bronze Age industries^{20,28–36}. These tracks have been important to understanding the ecology of *Homo sapiens* and its predator–prey interactions, and in determining the onset of cattle domestication. However, they were never formally described from an ichnotaxonomical point of view, and only rarely figured in discussions. At Formby, Sefton Coast (Liverpool) in England, tracks of aurochs, red deer, roe deer, and wild boar have been found in marshland deposits dated from 7.4 to 4.3 ka BP³⁷. The co-existence of red deer, wild boar and aurochs seems to have been a common feature especially in the southern latitudes of Europe during the interglacial periods³⁸. This is exemplified in Gibraltar, where the deposits of Genista I Cave provided remains of *Cervus elaphus*, *Bos primigenius* and *Sus scrofa* (reviewed in³⁹). Coeval to this site is Solana del Zamborino, in Granada (Spain), where *Bos primigenius* was also found⁴⁰. Dated as late Pleistocene (MIS 3), the painting of the Aurochs' Hoofprint of Lascaux, with the clear representation of the dewclaws (digits II and V) in the posterior part of the track as being an important identifying feature when tracking aurochs^{34,41}, is relevant to this study.

Geological setting of the Trafalgar Cape

The Pleistocene coastal deposits of SW Spain are distributed in short sections along the shores of the Gulf of Cadiz (Fig. 2). The Asperillo cliff in the Province of Huelva is one of the longest continuous outcrops of Late Pleistocene-to-Holocene deposits of the region, mostly composed of poorly-cemented eolianites and revealing at the base a paleosol developed over interdune pond deposits with a large trampled surface recently described as the Matalascañas Trampled Surface (MTS)^{15,16}. About 100 km SE of the MTS is Cape Trafalgar, a tombolo connecting the 17 m-high paleodune, oriented WNW-ESE, with the mainland. The last interglacial-Holocene succession between Barbate and Cape Trafalgar rests unconformably on Upper Miocene deposits⁴² (Fig. 2a). The outcrop extends by a maximum area of 600 m by 300 m during low-tide, beneath the lighthouse. The succession (Fig. 2b) is composed of coarse-grained bioclastic sandstones, mostly massive but with a fine, almost horizontal lamination with a NE dip. This unit is truncated by an erosional discontinuity dipping south where abundant large artiodactyl tracks and rhizolith clusters can be found: the Trafalgar Trampled Surface or the TTS. Overlying the TTS and filling the tracks is a 40 cm-thick bed of very coarse, bioclastic sandstones with large broken bivalve shells and balanids, but also with occasional branched rhizoliths, mostly horizontal, up to 4 cm thick (Fig. 2c). The remaining succession is composed of eolianites made of medium-to-fine grained sandstones with planar cross-lamination. Reactivation surfaces are marked by the development of rhizolith horizons, and four (I–IV) highly bioturbated levels with large artiodactyl cloven-hoofed tracks were recognized in a 1.5 m-thick sequence composed of foresets dipping over 20° towards N (Fig. 2a). The succession is then partially covered by the Holocene dune system, but still shows around 2 m of eolianites with similar features to the ones mentioned below, including sparse bioturbation by isolated tracks, horizontal thin rhizoliths and insect burrows (Fig. 2d). This unit ends with a paleosol with a dense vertical rhizoturbation.

The basal beach unit from Cape Trafalgar was dated with U-Th from the last interglacial, MIS 5c (107 ± 2 ka)⁴². This sequence shows a disconformity where the TTS was developed, mostly representing the foreshore. The sand barrier retreat has exposed the TTS to the activity of large artiodactyls in the shoreline. The first eolianite unit was dated by OSL of 99 ± 12 ka⁴² and reveals the progradation of the dune system in a regressive context, including the development of rhizoliths downward to the disconformity and intersecting the tracks. The aggradation deposition of eolian dune sands is marked by high bioturbated levels and the formation of incipient soils with intense rhizoturbation. The second eolianite unit was deposited *circa* 78 ± 8 ka⁴².

When comparing this with the Asperillo cliff reference section in the Bay of Cadiz, according to the few OSL ages presently available⁴³, the MTS was formed during the Last Interglacial warm and seasonal humid period (106 ± 19 ka) as a reddish paleosol (MIS 5), when the sea-level was at highstand position but with frequent fluctuations. Therefore, the TTS may be contemporary of the MTS, and both highlight the presence in the shore of large artiodactyls (see below).

Systematic ichnology

Nomenclatural acts: This study follows the requirements of the International Code of Zoological Nomenclature regarding the registration of the nomenclatural act in ZooBank.

Ichnogenus: *Bovinichnus* igen. nov.

Type ichnospecies: *Bovinichnus uripeda* isp. nov.

Etymology: referring to traces (= *ichnus*) with the morphology of tracks shared by the species of the Tribe Bovini, subfamily Bovinae, which includes besides *Bos*, buffalos, bison, among others.

Diagnosis: Tetractyl, paraxonic and subsymmetrical tracks that are as wide as long; central (III–IV) digit impressions are subparallel, with broad distal end pointing forward, and a narrow, linear interdigital space; internal surfaces of hoofprints flat to slightly concave, external surfaces slightly to markedly convex; hoofprints widest near the heel, but tapering only to minor degree between the heel and the apex; rounded-to-rectangular posterior dewclaw (digits II and V) prints that are much smaller than central digits, printed next to or close to the heel; *manus* and *pes* of closely similar form and size.

Bovinichnus uripeda ichnosp. nov.

ZooBank—urn:lsid:zoobank.org:pub:E834D014-3A20-4721-9B2D-4577B2E10A52.

Koenigswald et al., 1996: Fig. 3E.

Roberts, 2009: Figs. 13, 14.

Neto de Carvalho et al., 2020: Fig. 2A,C,D,E.

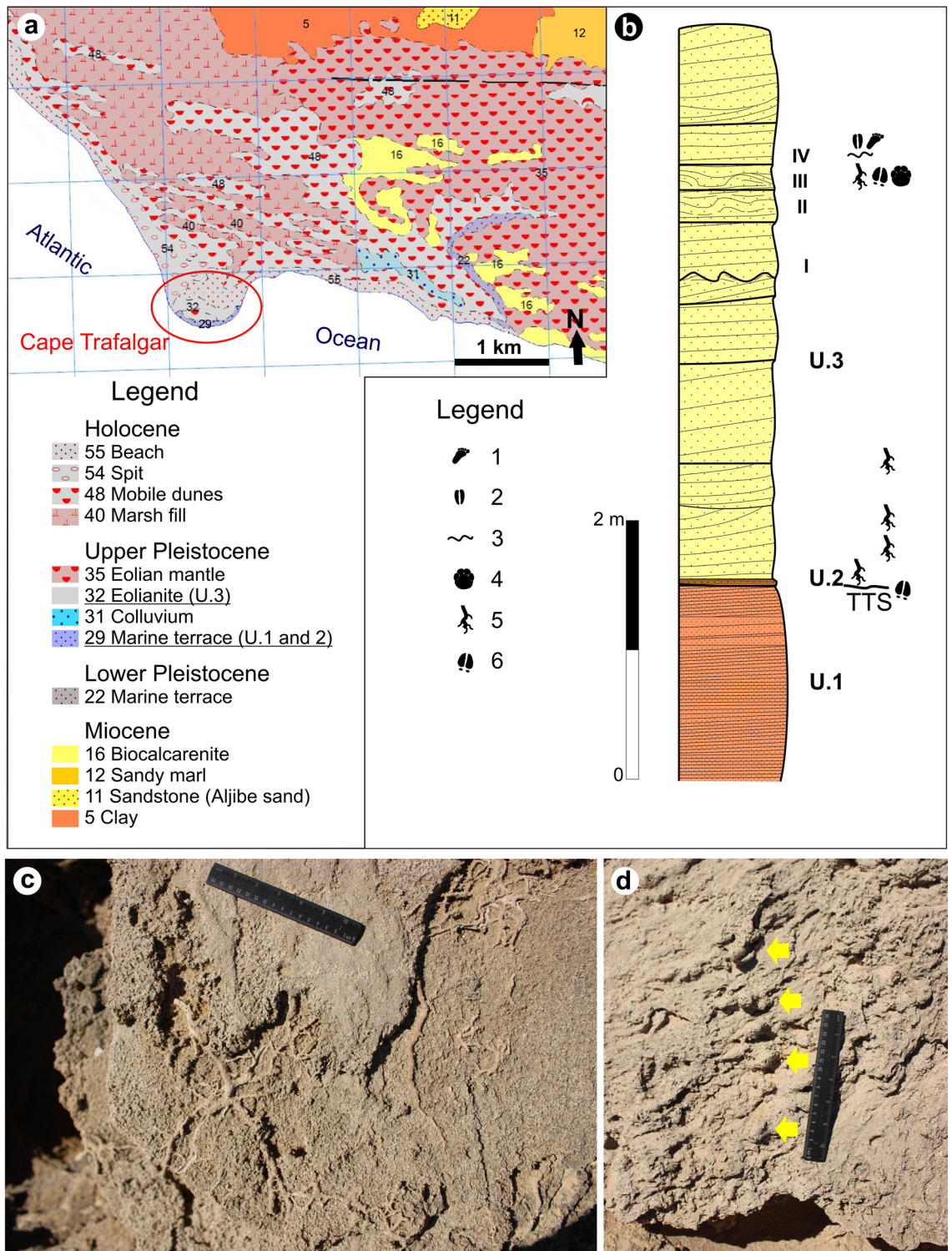


Figure 2. Stratigraphy of the TTS in Cape Trafalgar (Province of Cadiz). (a) Geological map of the Cap Trafalgar area (adapted from the Geological Map of Spain 1:50,000, Map no.1073 Vejer de la Frontera44, source: “© Geological Survey of Spain (IGME)”); (b) detailed stratigraphic column of Cape Trafalgar transition between beach and dune facies and location of the TTS and other trampled horizons (I–IV); rhizolith horizons corresponding to incipient paleosols are indicated (legend: 1—possible hominin footprint; 2—Pecoripeda isp.; 3—bioturbated lamina; 4—large footprint related to *Palaeoloxodon antiquus*; 5—rhizoliths; 6—*Bovininchus uripeda*); (c) thin horizontal and densely branched rhizoliths from the second eolianite unit; (d) insect burrows in linear clusters preserved as convex hyporelief; ruler is 15 cm. Legend in (a), figure (b) and modifications to the photograph (d) have been made with CorelDraw 12 (<https://www.coreldraw.com/la/>).

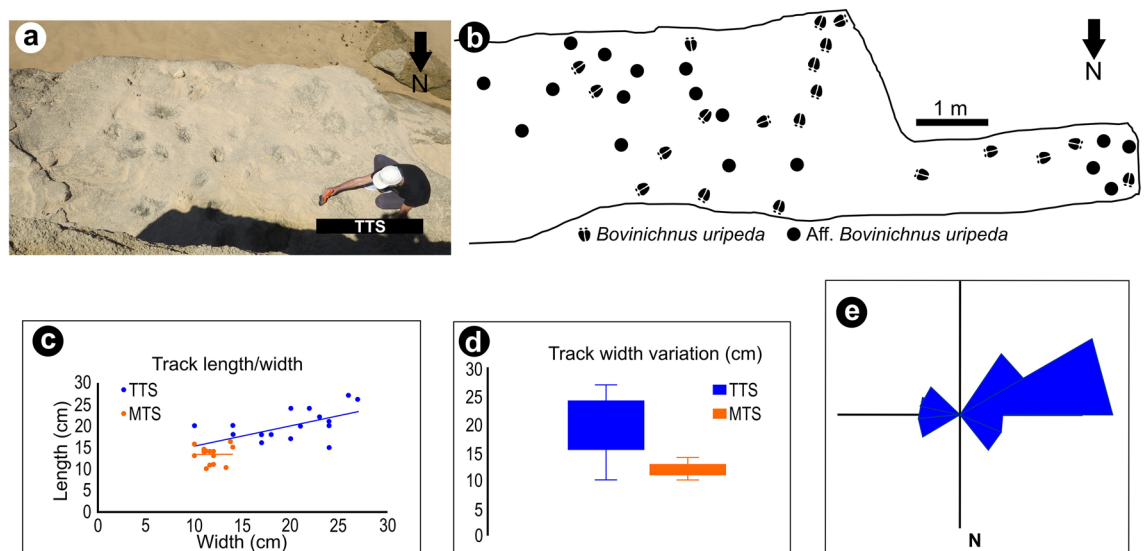


Figure 3. Graphical representation and data on measurements taken in the TTS and the MTS: (a,b) Distribution of tracks in the main area of the TTS; (c) bivariate plot of track length/track width ratio ($n=18$ in the TTS and $n=17$ in the MTS). The track length included dew claw impressions if present; (d) boxplot of track width variation ($n=18$ for the TTS and $n=17$ for the MTS); (e) rose diagram with the orientation of the hoofprints in the TTS ($n=14$). Figure (b) has been drawn with CorelDraw 12. (<https://www.coreldraw.com/la/>).

Holotype and Paratypes: TTS10 (Fig. 5a), and TTS8, TTS13, respectively. They were left in situ but photogrammetric 3D models were produced (Fig. 4).

Type horizon: Trafalgar Trampled Surface (TTS): Fig. 5a–c.

Etymology: In Latin, the prefix *uri-* is the plural word for aurochs and the suffix *-peda* refers to feet.

Type locality: Cape Trafalgar, GPS: $36^{\circ}10'54.92''\text{N}-6^{\circ}02'05.87''\text{W}$.

Diagnosis: The same as for the ichnogenus.

Description: Tracks occur in the TTS in concave epirelief, mostly isolated, or in small *manus-pes* sets up to seven in the same trackway (T3) (Fig. 3a,b). The breadth size range varies between 100 and 270 mm, but with most of the tracks measuring 200–240 mm (Fig. 3c,d). They are mostly oriented towards WSW (Fig. 3e) determined by the tipping of the hoofprints or the location of the dewclaws (Fig. 4a,b). Usually, well-preserved true tracks are tetradactyl and show evidence of pressure pads. The digits III and IV are by far the largest and correspond to crescent-shaped impressions. The posterior part of the prints is deeper than the cleave or digit tips and may reveal rounded-to-rectangular small dew claw imprints proximal to the heel. The outer width measured between dew claw impressions corresponds in size to the posterior width of the hoofprints (Fig. 4). The termination of each hoof impression is blunt and directed forward. In convex hyporelief preservation and cross sections, hoof impressions are separated by a central ridge (Fig. 5b). At least four trampled levels can be seen in cross section in the eolianite beds. The indentation produced by the large rigid hoof over the well-laminated sandstone show soft deformation, composed of marginal upfolds and microfaults, of the underlying laminae and a concave track infill (Fig. 5c,d). The stride length, or distance between footprints from the same foot, calculated for the trackway T3 varies from 210 to 100 cm and is 150 cm in the trackway T1. The pace length, or the distance between two successive footprints, varies from 110 to 45 cm in T3 and is 96 cm in the trackway T2. There is no evidence in trackways for *manus-pes* overprinting and 'direct register', in which pes is placed directly in manus impression, or in the cross sections of the trampled surfaces in the eolianite.

Tetradactyl tracks with the morphology of *Bovinichnus uripeda* were previously described in the MTS¹⁶. They are now synonymized under *B. uripeda* despite showing smaller dimensions (Fig. 3c,d).

The morphotype A1 described in the MTS as *Cervipeda*¹⁵ corresponds to large hoofprints with an average size range of 12–13, 5 cm in length and 7.5 cm broad and some few trackways with measured stride lengths between 100 and 132 cm. However, some tracks are up to 17.8 cm in length and show pace lengths of 100 cm, which are now integrated in the new *Bovinichnus uripeda* (Figs. 3c,d and 6a). The tracks can be rectangular or squared to oval in outline. Impressions of third and fourth toes are central, well-developed mirror images with internal surfaces sometimes in median or posterior contact, straight or concave at the front (Fig. 6b,c); in some examples, they are separated by a continuous interdigital space, usually broadest at the front (Fig. 6d,e). They can be widest near the heel or in the central part, tapering to an apex of angular or sharply parabolic shape, directed forward, or rotated inwards or outwards, to the midline of the trackway. The second and fifth toe impressions (dew claw imprints) can be seen in some tracks, are smaller and subtriangular or rectangular, located immediately behind the hoofprints (Fig. 6e) or separated from them, extending the tracks for extra 30 mm (Fig. 6c). The trackways show no major differences in size between fore feet and hind feet (Fig. 6a). Pressure pads surrounding the track indicate they were imprinted directly on the surface.

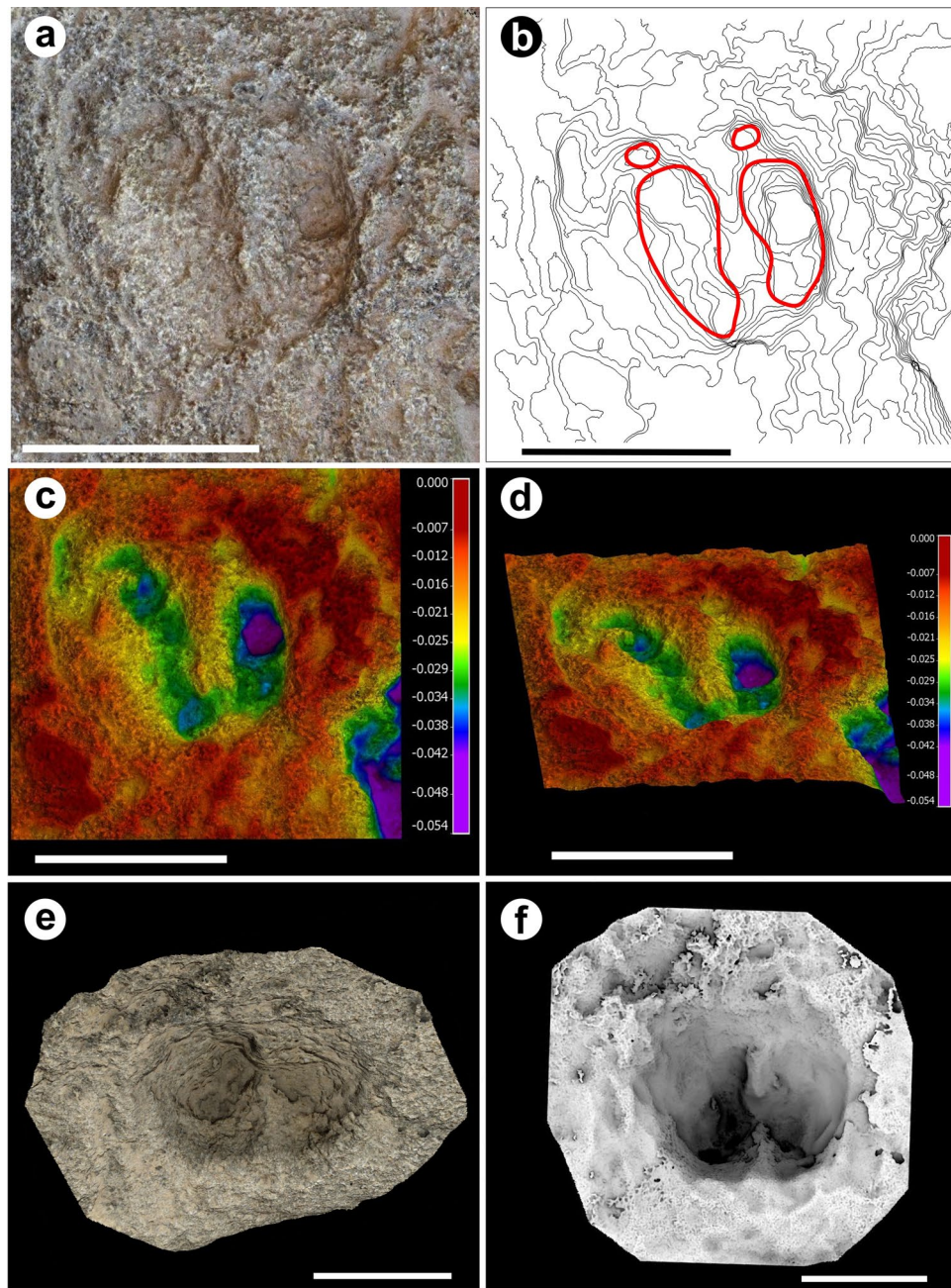


Figure 4. 3D models of the *Bovinichnus uripeda* holotype (TTS10) and paratype TTS8: (a) Orthogonal view of the natural colours textured 3D model of the TTS10 with the general morphology depicted from the contour lines map, equidistance of 1 mm (b); (c) false colour DSM in orthogonal view showing deeper areas in the heel side of the hooves and the tips resulting from the impulse created in the foot-off event. The circular-to-elliptical dew claw imprints are also evident behind the hooves; (d) oblique view of the previous DSM to complement previous observations; (e) oblique view of the textured natural colour 3D model of the paratype TTS 8; (f) orthogonal view of the paratype TTS 8 where the deepest part of the hoofprints is displaced to their anterior part reflecting the pressure angle exerted by the limb on the substrate during the foot-off event. Scale bar is 150 mm. The 3D model of the images (a–d) were produced by the software WebODM 2.1.0, (<https://github.com/OpenDroneMap/WebODM>); MeshLab 2020.12, (<https://www.meshlab.net/>); CloudCompare 2.11.0, (<https://www.danielgm.net/cc/>) and the 3D model of the images (e,f) were produced with the software Meshroom 2021.1.0, (<https://alicevision.org/#meshroom>); MeshLab 2020.12, (<https://www.meshlab.net/>); CloudCompare 2.11.0, (<https://www.danielgm.net/cc/>).

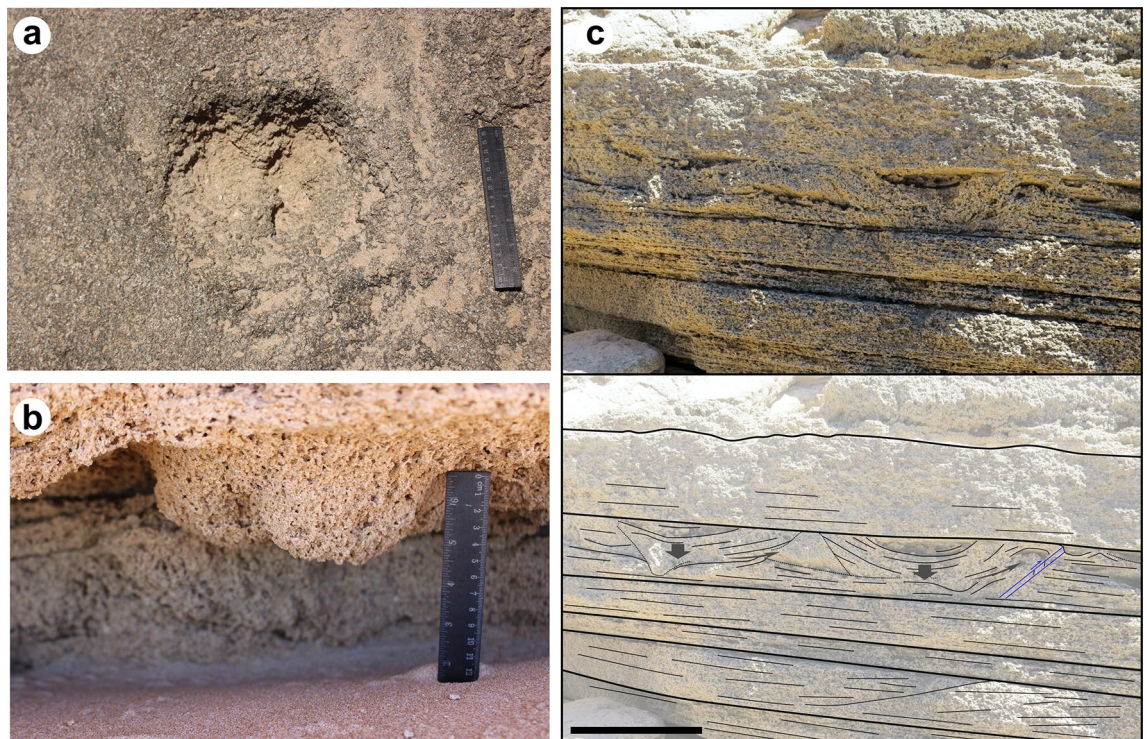


Figure 5. *Bovinichnus uripeda* igen. nov. et isp nov. from the Late Pleistocene (MIS 5c) of Cape Trafalgar: (a) well-preserved track as concave epirelief (holotype TTS10) showing the dewclaws; ruler is 15 cm; (b) convex hyporelief preservation in the trampled horizon I, evidencing the narrow ridge between toes; (c) tramped level IV with large bifid tracks attributed to aurochs in section (above) and interpretation of the sedimentary deformation (below). Scale bar is 15 cm. The interpretation of (c) (below) was drawn with CorelDraw X7 (<https://www.coreldraw.com/la/>).

When not showing dew claw prints, the Matalascañas hoofprints are similar to ichnogenus *Bifidipes* Demathieu et al. They are didactyl footprints organized in homopod trackways with cleaves pointed and hooves diverging and clearly separated, although not so much closer, and wider, to the heel⁴⁵ (Fig. 6e).

Remarks: Sarjeant and Langston⁶ provide an early revision of artiodactyl fossil tracks emphasizing the lack of ichnological description of kidney-shape to crescentic hoofprints of many bovoids. The ichnotaxonomy of artiodactyl tracks is problematic since the hooves are characterised by a wide range of small morphological variations^{6,22}. In this regard, there were attempts to revise the ichnotaxonomy of the artiodactyl tracks⁶ with the last made by Neto de Carvalho et al.¹⁶, and completed in the present work (Fig. 7). In this study the number of digit impressions in the well-preserved true tracks has been considered as the most important ichnotaxobase, thus *Bovinichnus* tracks were compared only with artiodactyl tetradactyl ichnotaxa that are presently valid²². Tetradactyl tracks attributed to artiodactyls are resumed to *Cervipeda* (Vialov), *Bothriodontipus* Casanovas-Cladellas and Santafé-Llopis, *Cervipus* Matsukawa et al., *Fustinianapodus* Díaz-Martínez et al., and *Suidichnus* Neto de Carvalho et al. *Bothriodontipus* has four forward-direct ungual prints while *Bovinichnus* shows two large hoofprints and two posteriorly-located dewclaws. Both *Cervipeda* and *Cervipus* shows slender hoofprints and their largest size is in average much smaller than *Bovinichnus uripeda*. *Fustinianapodus* described recently in the Lower Miocene of Spain²² is recognized by subtriangular dew claw impressions in the *pes* tracks, and elongate ones in the *manus* tracks. Finally, *Suidichnus* described in the MTS are tracks longer than wide, with a general trapezoidal shape, and dew claw impressions conical to comma-shaped, smaller than the main toes, longer than wide, and projected laterally from behind the main toes, with a wider angle in the foreprint comparing with the hindprint¹⁶. Artiodactyl tracks with hooves parallel but with hoof apices almost as rounded as the hind portions, the track having an oval to rounded-rectangular outline, are placed into *Lamaichnium* Aramayo and Bianco⁶. Besides that, the didactyl shape of these tracks attributed to camelids clearly distinguishes it from *Bovinichnus*. Therefore, and following the suggestion of Sarjeant and Langston⁶, *Bovinichnus uripeda* is considered a new artiodactyl ichnotaxon of bovoid morphology.

Slow walking usually keeps *manus* and *pes* separated in the artiodactyls⁴⁶, with *manus* impression lying ahead of the *pes* impression. Stride over 2 m together with the shape of cleaves and the large width of the prints indicate that the TTS were produced by large bovines. In the Sefton Coast and at Peterstone (England), aurochs tracks associated with Chalcolithic industries, show lengths of 220–280 mm³⁷, which are also comparable in shape with *Bovinichnus uripeda* and must be included in the new ichnospecies (see also³⁴). Finally, the Late Paleolithic rock art painting of the Aurochs' Hoofprint of Lascaux (France), with the clear representation of the dewclaws in the posterior part of the track, recognizes the tetradactyl shape of aurochs tracks^{34,41}.

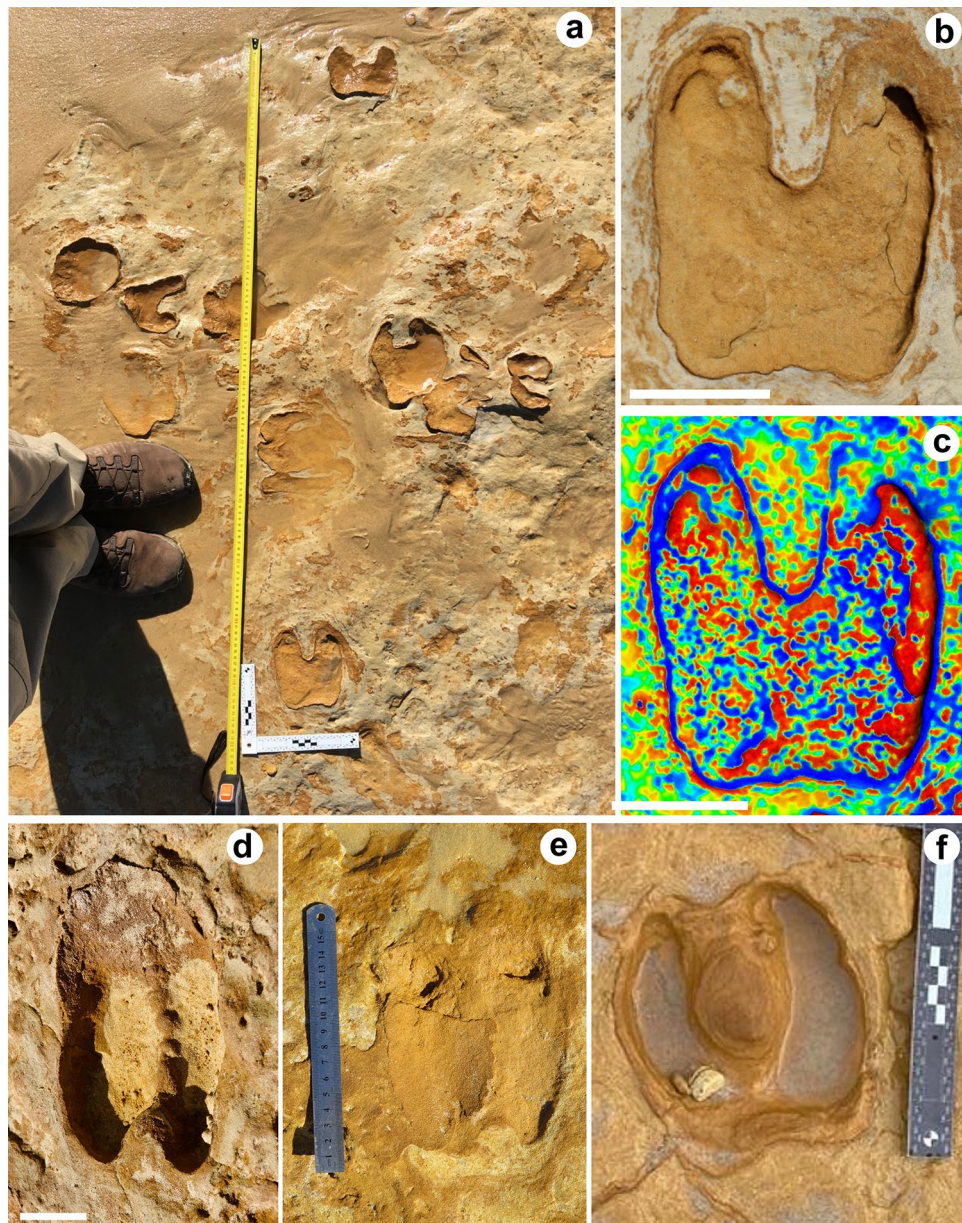


Figure 6. Large artiodactyl tracks from the MTS. (a) Trackway T1 attributed to aurochs based on the large size of the squared tracks and the preservation of the dewclaws as rectangular imprints; (b) 3D model of a tetradactyl track from the MTS interpreted as *Bovinichnus uripeda*, vertical view of the texturized 3D model in natural colours; (c) vertical view from the previous track made of the false colours DSM (cold and hot colours represent depth gradient, from deeper to shallower, respectively); (d) *Bovinichnus uripeda*, large track; (e) *manus-pes* couple, note the dewclaws; (f) large cervid track found in the MTS for comparison, with slender toes with sharp tips, well splayed, with almost linear outlines. Scale bar is 10 cm. The 3D model of the images (b,c) were produced by the software Meshroom 2021.1.0 (<https://alicevision.org/#meshroom>); MeshLab 2020.12 (<https://www.meshlab.net/>); CloudCompare 2.11.0 (<https://www.danielgm.net/cc/>).

The tetradactyl A1 morphotype described in the MTS shows some differences that allow to separate into two different morphotypes (Fig. 6). Despite the preservational variation in morphology that can be found in the MTS¹⁵, and the fact that in average A1 tracks have the same size, there are subtle differences that suggest different producers. The larger tracks, blunt shape of cleaves without separation in the proximal area and their convex outline, making many of them rounded or squared, with circular to oval dew claw imprints, can be compared with *Bovinichnus uripeda* from Cape Trafalgar and the tracks of the aurochs known in the Holocene deposits of Great Britain^{34,47} (Fig. 6a–e). On the other hand, cervid prints are slenderer with the previous half of each foot tapering to a point, for example, in red deer (*Cervus elaphus*) the forefoot generally creates splayed tracks, especially in soft and/or sandy grounds (Fig. 6f).

SCHEMATIC DIAGRAM	ICHOGENUS	AGE & LOCALITY	SCHEMATIC DIAGRAM	ICHOGENUS	AGE & LOCALITY
	<i>Cervipeda</i> (Vialov 1965)	Lower Miocene, Pliocene, Late Pleistocene (USA, Ukraine, S Spain)		<i>Lamaichnum</i> Aramayo & Manera de Bianco 1987	Late Eocene - Late Pleistocene (Argentina, USA)
	<i>Pecoripeda</i> Vialov 1965	Late Eocene - Recent (Ukraine, USA, Argentina, Hungary, Iraq, Iran)		<i>Cervipus</i> Matsukawa et al. 2007	Pliocene - Lower Pleistocene (Japan)
	<i>Anoplotheriopus</i> Ellenberger 1980	Upper Eocene (France, N Spain)		<i>Elaphuriformipes</i> Matsukawa et al. 2007	Pliocene - Lower Pleistocene (Japan)
	<i>Diplartiopus</i> Ellenberger 1980	Late Eocene (France)		<i>Paracamelichnum</i> Pérez-Lorente et al. 2009	Upper Miocene (Spain)
	<i>Bothriodontipus</i> Casanovas-Cladellas & Santafe-Llopis 1982	Oligocene (N Spain)		<i>Fustinianapodus</i> Díaz-Martínez et al. 2020	Lower Miocene (Spain)
	<i>Bifidipes</i> Demathieu et al. 1984	Lower Oligocene, Late Miocene - Pliocene - Late Pleistocene (France, Spain, Portugal, Sardinia)		<i>Suidichnus</i> Neto de Carvalho et al. 2020	Late Pleistocene (Spain)
	<i>Megapecoripeda</i> Kordos 1985	Early Oligocene, Lower to Late Miocene (Hungary, France, Spain)		<i>Bovinichnus</i> (this contribution)	Late Pleistocene (Spain)

Figure 7. Revision of the valid artiodactyl ichnogenera¹⁶ with visual comparison of morphologies, age and locality (country). All tracks have been redrawn from the original references where they were described for the first time. (m) manus, (p) pes. *Anoplotheriopus* left pes; *Diplartiopus* left pes; *Bothriodontipus* pes (not indicated which side); *Lamaichnum* manus (not indicated which side); *Paracamelichnum* right manus; *Fustinianapodus* left manus and pes; *Suidichnus* overprinting of left manus by corresponding pes; *Bovinichnus* right track; for other ichnogenera autopods were not specified/shown no morphological distinction in the references. This figure has been drawn with CorelDraw X6 (<https://www.coreldraw.com/la/>).

Discussion

The difference between red deer, domestic cattle and aurochs tracks. Despite red deer, domestic cattle and aurochs tracks may show a tetradactyl preservation, red deer tracks are slenderer, with sharp cleave anteriorly, and cattle leave rounded tracks with convex outlines, when compared to aurochs. Large artiodactyl hoofprints attributed to cervids have been described in the Late Pleistocene of the Iberian Peninsula, including Gorniz in northern Spain, SW Portugal and the MTS^{10,13–15}. These longer-than-wide tracks composed of hoofprints that are more slender than those of *Bovinichnus uripeda*, can reach up to 150 mm in length; the tracks from Gorniz attributed by Flor¹⁰ to *Cervus elaphus* (see its Fig. 5) reach 130 mm in length but are rounded and could have been produced by the reindeer (with the widest and roundest tracks of all deers) or the European Bison. In the Sefton Coast, the red deer tracks dated from the Neolithic are 100–150 mm in length³⁷, while modern average of a full-grown red deer stag's fore print is 80–90 mm long and 60–70 mm wide⁴⁶. Pointed cleaves of the red deer contrast in this area to the more rounded and larger hooves of the aurochs. Also, the outer edge of the cleaves curve evenly towards the tip. In red deer, the dewclaws are rounded impressions. Straddle is relatively narrow, with a stride length for adult varying between 80 and 150 cm⁴⁶.

Barr and Bell²⁰ interpreted rectangular hoof prints, ranging from 120 to 180 mm in length, as made by red deer and the larger square hoof prints, ranging from 200 to 260 mm in length, as made by aurochs. When showing similar sizes, aurochs differ from cervid tracks by the blunt tips and wider hooves, besides the smaller space enclosed between the two hooves in aurochs⁴⁸.

Despite being broadly bovoid rounded tracks, there is a marked difference in size, especially in length, between *Bos taurus* and *Bos primigenius*. Tracks of extant, fully grown cattle are $\sim 100 \times 95$ mm in size²⁰, which is less than half the size of the very large bovine tracks found in Cape Trafalgar. For the purpose of comparing the morphology (but not taphonomic variation) of extant domestic cattle hoofprints with Cape Trafalgar and Matalascañas tracks, a bull 1128 kg in weight was invited to walk in a dry fine sand substrate. He left rounded tracks measuring 180 mm long which are nevertheless more rounded than aurochs tracks. Moreover, the hooves outside are convex and the inner edge is concave at the front and convex at the back⁴⁶.

Aurochs vs. Bisons as producers of *Bovininchnus* in SW Iberia. Aurochs and Steppe Bisons coexisted in Iberia during the Late Pleistocene. Since these two bovines were in size and morphologically very similar, these would rise the possibility that steppe bisons could be likely producers of *Bovininchnus*. Therefore, it is vital to understand the biogeographical distribution of the two species in order to be sure about the most likely producer of *Bovininchnus uripeda* in SW Spain.

The origin of the aurochs is not clear, although it is thought to have Indian ancestry, dating back to about 2 Ma⁴⁹. The aurochs were first reported in Europe during the Middle Pleistocene at Venosa-Notarchirico, Italy, and finally became extinct in Poland in 1627 AD³⁸. Aurochs finds are less numerous during the Pleistocene than during the Holocene, but a large distribution area is represented nonetheless, from SW Iberia to southern Scandinavia, North Africa to Korean peninsula and Japan⁵⁰. In the Eemian (MIS 5e), they expanded towards northern territories, where their skeletons were found, e.g., in excavations made in the Trafalgar Square at central London⁵¹. During the early Holocene (Mesolithic and Neolithic cultural phases in Europe) the species seems to have increased in number, probably due to increasingly favorable mild and wet conditions after the end of the Last Ice Age⁵⁰. Its early appearance in Spain dates back to 0.7 Ma⁵². Remains of aurochs dated from the Middle or Late Pleistocene have been uncovered in Great Britain, France, Spain, Portugal, Italy, and Germany. The distribution of the aurochs has fluctuated with the changing climate during the Pleistocene, being more widely dispersed in interglacials and interstadials⁵⁰. During the Pleniglacial, with the European northern ice cap boundary having a southerly course, and with the Iberian and Italian peninsulas being used as refugial areas⁵³, aurochs became rare or completely disappeared during colder periods in many areas of Europe. At Gibraltar, taking advantage of the milder climate in the southernmost Europe during the MIS 3, *Cervus elaphus*, *Sus scrofa* and *Bos primigenius* were found related to habitats of stone pine/juniper woodland, savannah, shrubland with patches of grassland⁵⁴.

The long-horned *Bison priscus* (Bojanus), or steppe bison, is the earlier form of *Bison*, thought to have become extinct in Europe at the end of the Pleistocene⁵⁵. As the aurochs, the steppe bison had also a wide distribution across Europe, from the Iberian Peninsula, through central and eastern Europe and into Siberia, crossing the Bering strait into North America during the early Holocene^{56,57}. The steppe bison was able to adapt to a wide range of environments, both glacial and temperate⁵³, by performing long migrations. Of the two species, *Bison priscus* is thought to be particularly problematic in terms of its skeletal distinction from *Bos primigenius*^{58,59}. The problem is enhanced by the fact that *Bison priscus* was relatively abundant during the Pleistocene, and seems to appear alongside *Bos primigenius* on several sites. Nevertheless, the steppe bison is known only from MIS 3–2 from northern and central Spain^{18,26,60} during which it was found together with *B. primigenius*²⁵. During this period, the expanding territories of *B. priscus* related to colder and steppe environments may have reached the southern latitudes of Granada⁶¹. *B. priscus* appears in the cave art from North (Altamira, Altxerri, Santimamiñe and Ekain) and Central Spain (La Hoz and Siega Verde) during the Last Glacial Maximum, where representations of aurochs are rare¹⁸. Bison are absent from the long and well-studied Late Pleistocene sequences in Gibraltar, and elsewhere in SW Iberia. Thus, the aurochs were the only bovines existing during the MIS 5 in SW Iberia and we can confidently attribute the *Bovininchnus uripeda* tracks from Cape Trafalgar and Matalascañas to aurochs.

The only fossil tracks related to *Bison sensu lato* that are known were described⁶² in dune and interdune deposits from Nebraska (USA). However, they are found mainly in cross sections, as concave-up deformation structures or undertracks, circular to oval in plane, ranging from 70 to 160 mm in diameter. Due to this kind of preservation, it is not possible to compare the Nebraska tracks with *Bovininchnus uripeda*. However, if we compare the tracks produced by the extant *Bison bonasus* with *Bovininchnus uripeda* we realize they are wider than long and, therefore, do not present the more rectangular morphology (slightly longer than wide) evidenced in *Bovininchnus*. Therefore, the track length/width ratio can be very useful to distinguish between the presence of aurochs and steppe bisons in the track fossil record.

“The Beach Bulls”: large aurochs tracks in the TTS. Aurochs have reached their maximum body size in the early Late Pleistocene interglacial^{38,61}. There is an increase in size of the metapodial bones preserved in levels dated as Middle Pleistocene to early Late Pleistocene and a decrease of the same during the Late Pleistocene to early Holocene³⁸. This trend is also found for other large mammals in Europe such as the red deer⁶³ and the wild boar⁶⁴ (see evidence from tracks in¹⁶). After that, there is a general size decrease between the Late Pleistocene and the early Holocene^{52,58,64,65}, with a size increase recorded after beginning of the Holocene⁶⁶. The Last Glacial was responsible for a decrease in size of the aurochs^{47,67}. There is also clear evidence of a size reduction in red deer at the end of the Pleistocene in Iberia^{67,68}. In the case of the aurochs, the body size increase during the early Late Pleistocene may be related to predation pressure since during this period these animals were prey for a large array of large carnivores, including Neanderthals. The large track size recorded in the early Late Pleistocene from Cape Trafalgar (Fig. 8) is comparable with the records of up to 280 mm in length from the lower Holocene of western England^{37,47}, which correspond to the largest track record attributed to aurochs. This increase in size of aurochs recorded in tracks during the Holocene has been attributed to predation pressure and husbandry^{20,69}.

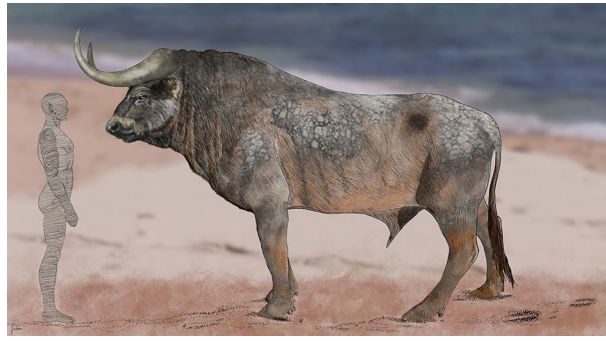


Figure 8. Reconstitution of the size of the aurochs based on the maximum size of the tracks found in the TTS, in a context of beach environment where they were produced (artwork of José María Galán).

Aurochs visiting the beach. Aurochs was typically a “wetland specialist” which preferred to live in marshy forests, near estuarine areas and floodplains for grazing during the day^{50,69}. According to these authors, aurochs lived in small herds and were grazers, not browsers like many deer species, thus requiring open landscapes composed of grasslands. For this main reason, herds of aurochs were roaming the coastal areas of southern Europe during the Late Pleistocene. Pandolfi et al.³⁸ have described remains of aurochs together with red deer and wild boar in southern Italian coast referable to early Late Pleistocene. In Portugal, *Bos primigenius* osteological remains are found in the Atlantic coastal caves of Figueira Brava (MIS 5), Furninha (MIS 4–2?), Lapa da Rainha (MIS 2), and Algar de Cascais, besides close to the alluvial plains of Tejo River, at Foz do Enxarrique and Salemas quarry (MIS 3), and further south, Vale de Boi and Lapa do Picareiro sites (MIS 3–2)^{17,70–72}. As described before, aurochs were also found in caves of Gibraltar, not far from Cape Trafalgar, in contemporary and later Pleistocene deposits (MIS 5–3)^{39,54}. In the Mediterranean coast of Málaga, Zafarraya (MIS 3) and Nerja (MIS 2) caves show the already rare presence of aurochs, besides being pictured in the rock art from Navarro (MIS 2) coastal cave^{73,74}. Finally, the Valencian coast shows the long presence of aurochs between MIS 9–2 in the caves of Bolomor, Cova Negra, Beneito, El Salt, and Abric del Pastor⁷⁵. The aurochs tracks from early Late Pleistocene of the TTS and the MTS add two more coastal sites to the ones listed in southern Iberia.

The aurochs track record and skeletal remains are abundant in Late Pleistocene to Holocene estuarine paleoenvironments in Great Britain^{20,34,47} where they were preserved in intertidal deposits^{30,70}. Glades may have attracted the animals to graze not far from the dense coastal woodland^{37,70}. The TTS and the MTS are located not far from the marshlands of Cadiz, and the Guadalquivir and Odiel rivers, respectively. But their association to beach and dune-interdune deposits, not in direct relation with fluvial environments, requires further explanation. This explanation may be found in a modern analogue example from the Doñana National Park, by comparing the behaviour of wild cattle (*Bos taurus*) regarding resources partitioning between seasons.

Doñana feral cattle has been living under free-ranging conditions since the thirteenth century⁷⁶. High quality habitats in Doñana National Park include lagoon meadows and the lower grassland of the ecotone zone between the scrubland and the marshland, which are most used by the active habitat selection of the feral cow-herds⁷⁶. Land sand dunes found in large areas in the coast of Doñana (primary or covered by a xerophytic community of shrubs) are considered a low-quality habitat where the availability of the forage is low and therefore avoided by the cattle. Most of the tracks in the MTS likely attributed to aurochs are smaller in size than *Bovininchnus uripeda* described in the TTS. This track size difference in coeval deposits may be explained by habitat difference/preference and the strong sexual dimorphism known for aurochs. Lagoon meadows related with interdune drying ponds was the most likely environment described in the MTS^{15,16}. Aurochs, especially cow-herds would have centred their movements around food patches of high availability and quality of food, such as the MTS. This could happen especially at the end of spring and during summer, providing enough food for the offspring. However, in the coastal beach and dunes of Trafalgar Cape the aurochs presence recorded by larger-sized tracks and trackways, in the TTS showing a preferential orientation of movement towards the shoreline. The well-drained sandy substrate certainly resulted in the virtual absence of an herbaceous layer in this beach area, where also the eolianites show a sparse rhizoturbation.

Among dimorphic mammals, males have higher metabolic needs than females and are usually relegated to low quality habitats, resulting in male greater seasonal home range⁷⁶. The tracks in the TTS are mostly from large bulls and may indicate this wide dispersion to poor-quality coastal habitats. But there are few tracks 100 mm in length that can be related with the presence of cows. In Doñana National Park, this occasional presence of both cows and bulls together in coastal habitats usually happens in autumn, when rut is in its peak and the bulls were associated with the cow-herds⁷⁶. Nevertheless, cow-size tracks in the TTS are rare comparing with the large tracks and trackways, showing mostly the same orientation, which can only be attributed to bulls walking together in herd. Therefore, while the MTS may record the presence of a cow-herd, the five trampled horizons in Cape Trafalgar may have resulted from the occasional but recurrent procurement of the shore by small herds of bulls.

It is relatively common nowadays to find feral cattle visiting the shores across the world. The Xhosa beach cattle, the “beach-loving cows” in South Africa, even became a tourist attraction. They come down to the shores usually to curl up on the sand and chew the cud. Other examples of recurrent visits of herds to the shores across the world may be found in Hong Kong or Corsica. The Cape Trafalgar’s TTS might represent the arrival of a

“beach-loving” aurochs herd of bulls for enjoying digestion while controlling possible predators in open landscape, or have a short moment of rest from parasites.

Conclusions

The dated early Late Pleistocene (MIS 5) coastal deposits from SW Iberia show the presence of artiodactyl track-sites. The new Cape Trafalgar site (TTS) together with the recently described Matalascañas site (MTS) record the recurrent trampling by large cloven-hoofed ungulates, being the oldest record of aurochs locomotion. *Bovichnus uripeda* igen. et isp. nov. is formally described and safely attributed to aurochs, after size and morphological comparisons with coeval large red deer tracks and the biogeographical distribution of the steppe bison, only present in southern Spain during the MIS 3. Other artiodactyl tracks, together with elephant and human tracks (see Supplementary Material I) help to provide a perspective of the aurochs ecological community, both in the TTS and the MTS. The unexpected paleoenvironments where the trampled horizons occur, i.e., beach and dune deposits, in the TTS, and interdune pond deposit, in the MTS, suggest a resource partitioning comparable with the cow-herds vs. bull-herds found nowadays in close related feral cattle (*Bos taurus*) living in the nearby Doñana National Park. Smaller tracks in average found in the MTS may represent cow-herds grazing in a high-quality food patch related with the retreating seasonal pond and development of meadows. The large tracks from the TTS described as *B. uripeda* and showing mostly the same direction of movement, are better interpreted as a bull-herd slowly walking towards the shoreline and looking for some peace, as it presently happens with feral cattle visiting the shores in different parts of the world.

Materials and methods

Field campaigns in the Cape Trafalgar section, made between 2020 and 2021, produced 2D cartography, 3D photogrammetric models of the most representative tracks and a detailed stratigraphic log. This data was then compared qualitatively with the large artiodactyl tracks that have been described in the MTS^{15,16}.

The ichnological material. The Cape Trafalgar section provides at least five stratigraphic horizons with large cloven-hoofed tracks. The upper four horizons can be seen mostly in section as undertracks and preserved as true tracks in bedding soles. There, it was not possible to identify trackways. The TTS is exposed for an area of at least 70 m² and 36 tracks were positively identified. Tracks are concentrated in the eastern sector of the TTS, but at least 9 tracks can be found towards west, with at least two of them belonging to the same trackway (T1). Six short trackways, composed of two to seven tracks sets, were determined in total. Each track was provided with a code (TTSx) and measured (Table 1). Well-preserved hoofprints were measured regarding length, the breadth of the widest part of the print, length and breadth of the dewclaws whenever present, orientation, pace and stride when organized in trackways. Track length/width ratio was calculated and may be used to distinguish artiodactyl tracks in the fossil record with comparable morphologies, e.g., *Bison*. Track depth was indicated only for the deep tracks since most of the tracks show no more than 20–30 mm in depth. However, several tracks are just rounded prints without evidence of toes. In these cases, only rarely measurements were obtained using the pressure pads to orientate the track.

The track length/width ratio and orientation patterns were examined by plotting, in bivariate and boxplot graphs, and in a rose diagram, respectively, the information of individual tracks (Fig. 3).

The storm surge of the spring 2020 exposed for a short period large area of the MTS, cleaning over 1.5 m of beach. Since the outcrop is located in the intertidal zone of Matalascañas beach, i.e., an area affected by intense tidal gradients, data recovery was limited in time and mainly consisted of taking photographs for photogrammetry and making casts for some of the tracks. The recognized tracks and trackways have been grouped in four morphotypes for mammals and three for birds. Likewise, insect traces have been recognized, as well as rhizoliths.

Photogrammetry. Digital photogrammetry and GIS techniques have been used to produce safeguard records and highlight the morphological features of some of the tracks in both the TTS and the MTS. *Bovichnus uripeda* holotype and paratypes were interpreted and described based on the field observations, measurements and analysis of the digital 3D models. Photos were made with a Canon PowerShot SX50HS camera with a zoom lens 50x/4.3–215 mm 1:3.4–6.5 VSM. The photogrammetric models were processed using the software Meshroom 2021.1.0⁷⁷ and ODM 2.1.0⁷⁸, post-processed, analysed and highlighted in Meshlab v2020.12⁷⁹ and CloudCompare v2.11.0⁸⁰. The results obtained enabled to highlight with false colors the 3D morphology of the tracks^{81,82}, making visual interpretation more effective.

Reference	Length (cm)	Width (cm)	L/W ratio	Depth (cm)	Shape	Orientation	Trackway
TTS1	14	10	1.4	–	Hoofprint	230°SW	–
TTS2	10	20	0.5	–	Hoofprint	80°E	–
TTS3	20	24	0.83	9	Hoofprint	275°W	T2
TTS4	17	16	1.06	14	Hoofprint	303°NW	
TTS5	17	18	0.94	–	Hoofprint	109°E	
TTS6	27	26	1.04	–	Hoofprint	259°W	T3
TTS7	21	20	1.05	–	Hoofprint	259°W	T3
TTS8	20	17	1.18	2.3	Hoofprint	259°W	T3
TTS9	24	20	1.2	–	Hoofprint	122°SE	–
TTS10	22	24	0.92	2.7	Hoofprint	250°W	T4
TTS11	24	15	1.6	–	Circular	–	T4
TTS12	23	22	1.05	–	Hoofprint	250°W	–
TT13	24	21	1.14	4.7	Hoofprint	225°SW	T5
TT14	–	18		–	Hoofprint	–	T5
TT15	14	20	0.7	–	Hoofprint	247°SW	T6
TT16	14	18	0.78	–	Hoofprint	–	–
TTS17	26	27	0.96	–	Circular	–	–
TTS18	–	–		–	Circular	233°SW	–
MTS1	15.7	10	1.57	–	Hoofprint	n.d	–
MTS2	15	14	1.07	–	Hoofprint	n.d	T1
MTS3	16.3	13.8	1.18	–	Hoofprint	n.d	T1
MTS4	11	12	0.92	–	Hoofprint	n.d	–
MTS5	10	11.3	0.89	–	Hoofprint	n.d	–
MTS6	14.5	11	1.32	–	Hoofprint	n.d	–
MTS7	13	12	1.08	–	Hoofprint	n.d	–
MTS8	14	11.6	1.21	–	Hoofprint	n.d	–
MTS9	14.2	11	1.29	–	Hoofprint	n.d	–
MTS10	10.8	11.6	0.93	–	Hoofprint	n.d	–
MTS11	10.2	13.3	0.77	–	Hoofprint	n.d	–
MTS12	14	11	1.27	–	Hoofprint	n.d	–
MTS13	14	12	1.17	–	Hoofprint	n.d	–
MTS14	13	10	1.3	–	Hoofprint	n.d	–
MTS15	14	11	1.27	–	Hoofprint	n.d	–
MTS16	17.8	15.7	1.13	–	Hoofprint	n.d	–
MTS17	15	11	1.36	–	Hoofprint	n.d	–

Table 1. Track measurements in the TTS and the MTS.

Data availability

All data generated or analysed during this study are included in this published article and its supplementary information files.

Received: 27 January 2022; Accepted: 16 May 2022

Published online: 14 June 2022

References

- Theodor, J. M., Erfort, J. & Métais, G. The earliest artiodactyls: Diacodexidae, Dichobunidae, Homacodontidae, Leptochoeridae and Raoellidae. in *Evolution of Artiodactyls* (eds. Prothero, D.R. & Foss, S. E.). 32–58. (Johns Hopkins University, 2007).
- Badiola, A. *et al.* The role of new Iberian finds in understanding European Eocene mammalian paleobiogeography. *Geol. Acta* 7(1–2), 243–258 (2009).
- Boivin, M. *et al.* New material of *Diacodexis* (Mammalia, Artiodactyla) from the early Eocene of Southern Europe. *Geobios* 51(4), 285–306 (2018).
- Ellenberger, P. Sur les empreintes de pas des gros mammifères de l'Eocene supérieur de Garrigues-Ste-Eulalie (Gard). *Palaeovertebr. Mém. Jubil. R. Lavocat*. 13, 37–78 (1980).
- Santamaría, R. L. G. & Casanovas-Cladellas, M. L. Nuevos yacimientos con icnitas de mamíferos del Oligoceno de los alrededores de Agramunt (Lleida, España). *Paleont. Evol.* 23, 141–152 (1990).
- Sarjeant, W. A. S. & Langston, W. Jr. Vertebrate footprints and invertebrate traces from the Chadronian (Late Eocene) of Trans-Pecos. *Texas. Mem. Mus. Bull.* 36, 1–86 (1994).
- Costeur, L., Balme, C. & Legal, S. Early Oligocene mammal tracks from southeastern France. *Hist. Biol.* 16(4), 257–267. <https://doi.org/10.1080/10420940902953197> (2009).

8. Wroblewski, A.F.-J. & Gulas-Wroblewski, B. E. Earliest evidence of marine habitat use by mammals. *Sci. Rep.* **11**, 8846. <https://doi.org/10.1038/s41598-021-88412-3> (2021).
9. Fornós, J. J. & Pons-Moya, J. Icnitas de *Myotragus balearicus* del yacimiento de Ses Piquetes (Santanyi, Mallorca). *Bol. Soc. Hist. Nat. Balears* **26**, 135–144 (1982).
10. Flor, G. Estructuras de deformación por pisadas de cérvidos en la duna cementada de Gorliz (Vizcaya, N de España). *Rev. Soc. Geol. Esp.* **2**(1–2), 23–29 (1989).
11. Fornós, J. J., Bromley, R. G., Clemmensen, L. B. & Rodríguez-Perea, A. Tracks and trackways of *Myotragus balearicus* Bate (Artiodactyla, Caprinae) in Pleistocene eolianites from Mallorca (Balearic Islands, Western Mediterranean). *Palaeogr. Palaeoecol. Palaeoecol.* **180**, 277–313 (2002).
12. Neto de Carvalho, C. Vertebrate tracksites from the Mid-Late Pleistocene eolianites of Portugal: The first record of elephant tracks in Europe. *Geol. Q.* **53**(4), 407–414 (2009).
13. Neto de Carvalho, C., Saltão, S., Ramos, J. C. & Cachão, M. Pegadas de *Cervus elaphus* nos eolianitos pliocénicos da ilha do Pessegueiro (SW Alentejano, Portugal). *Ciênc. Terra* **5**, 36–40 (2003).
14. Neto de Carvalho, C., Figueiredo, S. & Belo, J. Vertebrate tracks and trackways from the Pleistocene eolianites of SW Portugal. *Commun. Geol.* **103**(1), 101–116 (2016).
15. Neto de Carvalho, C. *et al.* Paleoeological implications of large-sized wild boar tracks recorded during the Last Interglacial (MIS 5) at Huelva (SW Spain). *Palaios* <https://doi.org/10.2110/palo.2020.058> (2020).
16. Neto de Carvalho, C. *et al.* First vertebrate tracks and palaeoenvironment in a MIS-5 context in the Doñana National Park (Huelva, SW Spain). *Quat. Sci. Rev.* <https://doi.org/10.1016/j.quascirev.2020.106508> (2020).
17. Cardoso, J. L. Les grands mammifères du Pléistocène supérieur du Portugal. Essai de synthèse. *Geobios* **29**(2), 235–250 (1996).
18. Sala, M. T. N., Pantoja, A., Arsuaga, J. L. & Algaba, M. Presencia de bisonte (*Bison priscus* Bojanus, 1827) y uro (*Bos primigenius* Bojanus, 1827) en las cuevas del Búho y de la Zarzamora (Segovia, España). *Munibe* **61**, 43–55 (2010).
19. Figueiredo, S. D. & Sousa, M. F. O registo de bovídeos pliocénicos em Portugal. in *Livro de Resumos das IV Jornadas de Arqueologia do Vale do Tejo*. Vol. 10. (Centro Português de Geo-História e Pré-História, 2017).
20. Barr, K. & Bell, M. Neolithic and Bronze age ungulate footprint-tracks of the Severn Estuary: Species, age, identification and the interpretation of husbandry practices. *Environ. Archaeol.* **22**(1), 1–15 (2017).
21. Bell, M. *Making One's Way in the World* (Oxbow Books, 2020).
22. Díaz-Martínez, I. *et al.* Multi-aged social behavior based on artiodactyl tracks in an early Miocene palustrine wetland (Ebro Basin, Spain). *Sci. Rep.* **10**, 1099. <https://doi.org/10.1038/s41598-020-57438-4> (2020).
23. Quintana, J. Descripción de un rastro de *Myotragus* e icnitas de *Hypnomys* del yacimiento cuaternario de Ses Penyes d'es Perico (Ciutadella de Menorca, Balears). *Paleont. Evol.* **26–27**, 271–279 (1993).
24. Muñiz, F. *et al.* Following the last Neanderthals: Mammal tracks in Late Pleistocene coastal dunes of Gibraltar (S Iberian Peninsula). *Quat. Sci. Rev.* **217**, 297–309 (2019).
25. Altuna, J. Fauna de mamíferos de los yacimientos prehistóricos de Guipúzcoa. Con catálogo de los mamíferos cuaternarios del Cantábrico y del Pirineo occidental. *Munibe* **24**, 1–464 (1972).
26. López González, F., Vila Taboada, M. & Grandal d'Anglade. Sobre los grandes bóvidos pleistocenos (Bovidae, Mammalia) en el NO de la Península Ibérica. *Cad. Lab. Xeol. Laxe* **24**, 57–71 (1999).
27. Sommer, R. S., Kalbe, J., Ekström, J., Benecke, N. & Liljengren, R. Range dynamics of the reindeer in Europe during the last 25,000 years. *J. Biogeogr.* **41**, 298–306. <https://doi.org/10.1111/jbi.12193> (2014).
28. Whittle, A., Antoine, S., Gardiner, N., Milles, A. & Webster, A. Two Later Bronze Age occupations and an Iron Age channel on the Gwent foreshore. *Bull. Board Celt. Stud.* **36**, 200–223 (1989).
29. Aldhouse-Green, S. *et al.* Prehistoric human footprints from the Severn Estuary at Uskmouth and Magor Pill, Gwent, Wales. *Archaeol. Camb.* **141**, 4–55 (1992).
30. Allen, J. R. L. Subfossil mammalian tracks (Flandrian) in the Severn Estuary, S.W. Britain: Mechanics of formation, preservation and distribution. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **352**(1352), 481–518 (1997).
31. Bell, M. Prehistoric coastal communities: the Mesolithic in western Britain. in *CBA Research Report*. Vol. 149. (Council for British Archaeology, 2007).
32. Bell, M. The Bronze Age in the Severn estuary. in *Research Report*. Vol. 172. (Council for British Archaeology, 2013).
33. Scales, R. Footprint tracks of people and animals. in *Prehistoric Coastal Communities: The Mesolithic in Western Britain* (ed. Bell, M.). Vol. 149. 139–147. CBA Research Report 149. (Council for British Archaeology, 2007).
34. Roberts, G. Ephemeral, subfossil mammalian, avian and hominid footprints within Flandrian sediment exposures at Formby Point, Sefton Coast, North West England. *Ichmos* **16**, 33–48 (2009).
35. Waddington, C. Low Hauxley, Northumberland: A review of archaeological interventions and site condition. *Archaeol. Res. Serv.* **2010/25** (2010).
36. Eadie, G. & Waddington, C. Rescue recording of an eroding inter-tidal peat bed at Lower Hauxley, Northumberland (6109). *Archaeol. Res. Serv.* **2013/17** (2013).
37. Burns, A. The prehistoric footprints at Formby. in *Sefton Coast Landscape Partnership Scheme* (2014).
38. Pandolfi, L., Petronio, C. & Salari, L. *Bos primigenius* Bojanus, 1827 from the Early Late Pleistocene deposit of Avetrana (southern Italy) and the variation in size of the species in southern Europe: Preliminary report. *J. Geol. Res.* <https://doi.org/10.1155/2011/245408> (2011).
39. Currant, A. P. A review of the Quaternary mammals of Gibraltar. in *Neanderthals on the Edge: 150th Anniversary Conference of the Forbes' Quarry Discovery, Gibraltar* (eds. Stringer, C. B., Barton, R. N. E. & Finlayson, J.C.). 201–206. (Oxbow, 2000).
40. Penela, A. J. M. Los grandes mamíferos del yacimiento acheulense de la Solana del Zamborino, Fonelas (Granada, España). *Antr. Paleoeol. Hum.* **5**, 29–187 (1988).
41. Bataille, G. *Prehistoric Painting. Lascaux or the Birth of Art* (MacMillan, 1980).
42. Zazo, C. *et al.* Palaeoenvironmental evolution of the Barbate-Trafalgar coast (Cadiz) during the last ~140 ka: Climate, sea-level interactions and tectonics. *Geomorphology* **100**, 212–222 (2008).
43. Zazo, C. *et al.* Landscape evolution and geodynamic controls in the Gulf of Cadiz (Huelva coast, SW Spain) during the Late Quaternary. *Geomorphology* **68**, 269–290. <https://doi.org/10.1016/j.geomorph.2004.11.022> (2005).
44. García de Domingo, A., González Lastra, J., Hernaiz Huerta, P. P., Zazo Cardeña, C. & Goy Goy, J. L. *Mapa Geológico de la Hoja No. 1073 (Vejer de la Frontera). Mapa Geológico de España a Escala 1:50.000. Segunda Serie (MAGNA)*. <http://info.igme.es/cartografiadigital/geologica/Magna50Hoja.aspx?Id=1073&language=es> (©Instituto Geológico y Minero de España (IGME), 1990).
45. Demathieu, G., Ginsburg, L., Guérin, C. & Truc, G. Étude paléontologique, ichnologique et paléocéologique du gisement oligocène de Saignon (bassin d'Apt, Vaucluse). *Bull. Mus. Natl. Hist. Nat.* **6**(2), 153–183 (1984).
46. Bang, P. & Dahlström, P. *Animal Tracks and Signs* (Oxford University Press, 2001).
47. Wright, E. *The History of the European Aurochs (Bos primigenius) from the Middle Pleistocene to Its Extinction: An Archaeological Investigation of Its Evolution, Morphological Variability and Response to Human Exploitation*. (PhD. Thesis, University of Sheffield, 2013).
48. Koenigswald, W. V., Sander, P. M. & Walders, M. The Upper Pleistocene tracksite Bottrop-Welheim (Germany). *Acta Zool. Cracov.* **39**(1), 235–244 (1996).

49. Martínez-Navarro, B., Rook, L., Papini, M. & Libsekal, Y. A new species of bull from the Early Pleistocene paleoanthropological site of Buia (Eritrea): Parallelism on the dispersal of the genus *Bos* and the Acheulian culture. *Quat. Intern.* **212**(2), 169–175. <https://doi.org/10.1016/j.quaint.2009.09.003> (2010).
50. Van Vuure, C. *Retracing the Aurochs: History, Morphology and Ecology of an Extinct Ox* (Coronet Books, 2005).
51. Franks, J. W. Interglacial deposits at Trafalgar Square, London. N. *Phytologist* **59**(2), 145–152 (1960).
52. Estévez, J. & Saña, M. Aurochsenfunde auf der Iberischen Halbinsel. in *Archäologie und Biologie des Aurochsen* (ed. Weniger, G.-C.) (Neanderthal Museum, 1999).
53. Mona, S. *et al.* Population dynamic of the extinct European aurochs: Genetic evidence of a north-south differentiation pattern and no evidence of post-glacial expansion. *BMC Evol. Biol.* **10**, 1–13 (2010).
54. Rodríguez-Vidal, J. *et al.* Undrowning a lost world—The Marine isotope stage 3 landscape of Gibraltar. *Geomorphology* **203**, 105–114 (2013).
55. Pfeiffer, T. Systematic relationship between the Bovini with special references to the fossil taxa *Bos primigenius* Bojanus and *Bison priscus* Bojanus. in *Archäologie und Biologie des Aurochsen* (ed. Weniger, G.-C.). 59–70. (Neanderthal Museum, 1999).
56. Zazula, G. D. *et al.* A late Pleistocene steppe bison (*Bison priscus*) partial carcass from Tsiightchic, Northwest Territories, Canada. *Quat. Sci. Rev.* **28**(25–26), 2734–2742 (2009).
57. Boeskorov, G. G. *et al.* The Yukagir Bison: The exterior morphology of a complete frozen mummy of the extinct steppe bison, *Bison priscus* from the early Holocene of northern Yakutia, Russia. *Quat. Intern.* **406**, 94–110. <https://doi.org/10.1016/j.quaint.2015.11.084> (2016).
58. Ekström, J. *The Late Quaternary History of the Urus (Bos primigenius Bojanus 1827) in Sweden*. PhD. Thesis. (Lund University, 1993).
59. Grange, T. *et al.* The evolution and population diversity of *Bison* in Pleistocene and Holocene Eurasia: Sex matters. *Diversity* **10**(3), 65. <https://doi.org/10.3390/d10030065> (2018).
60. Castaños, J., Castaños, P. & Murelaga, X. First complete skull of a Late Pleistocene Steppe Bison (*Bison priscus*) in the Iberian Peninsula. *Ameghiniana* **53**(5), 543–551. <https://doi.org/10.5710/amgh.03.06.2016.2995> (2016).
61. Álvarez-Lao, D. J., Kahlke, R.-D., García, N. & Mol, D. The Padul mammoth finds: On the southernmost record of *Mammuthus primigenius* in Europe and its southern spread during the Late Pleistocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **278**(1–4), 57–70 (2009).
62. Loope, D. B. Recognizing and utilizing vertebrate tracks in cross section: Cenozoic hoofprints from Nebraska. *Palaios* **1**, 141–151 (1986).
63. Albarella, U., Dobney, K. & Rowley-Conwy, P. Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environ. Archaeol.* **14**, 103–136 (2009).
64. Davis, S. J. M. The effects of temperature change and domestication on the body size of Late Pleistocene to Holocene mammals of Israel. *Palaeobiology* **7**, 101–114 (1981).
65. Cerilli, E. & Petronio, C. Biometrical variations of *Bos primigenius* Bojanus 1827 from middle Pleistocene to Holocene. in *Proceedings of the International Symposium on 'Ongulés/Ungulates'*, Toulouse. 37–42. (1991).
66. Davis, S. J. M. & Mataloto, R. Animal remains from Chalcolithic of São Pedro (Redondo, Alentejo): Evidence for a crisis in the Mesolithic. *Rev. Port. Arqueol.* **15**, 47–85 (2012).
67. Mariezcurrera, K. & Altuna, J. Biometría y diformismo sexual en el esqueleto de *Cervus elaphus* wüirmiense, postwüirmiense y actual del Cantábrico. *Munibe (Antr.-Arkeol.)* **35**, 203–246 (1983).
68. Davis, S. J. M. The mammals and birds from the Gruta do Caldeirão, Portugal. *Rev. Port. Arqueol.* **5**, 29–98 (2002).
69. Barr, K. *Prehistoric Avian, Mammalian and H. sapiens Footprint—Tracks from Intertidal Sediments as Evidence of Human Palaeoecology*. PhD. Thesis. (University of Reading, 2018).
70. Hall, J. G. A comparative analysis of the habitat of the extinct aurochs and other prehistoric mammals in Britain. *Ecography* **31**, 187–190 (2008).
71. Bicho, N. F., Gibaja, J. F., Stiner, M. & Manne, T. L. Paléolithique supérieur au sud du Portugal: Le site du Vale do Boi. *L'Antropologie* **114**, 48–67 (2010).
72. Bicho, N. & Haws, J. The Magdalenian in central and southern Portugal: Human ecology at the end of the Pleistocene. *Quatern. Int.* **272–273**, 6–16 (2012).
73. Cortés-Sánchez, M. *et al.* Palaeoenvironmental and cultural dynamics of the coast of Málaga (Andalusia, Spain) during the Upper Pleistocene and early Holocene. *Quatern. Sci. Rev.* **27**, 2176–2193 (2008).
74. Bohórquez, A. M., Ruiz, C. B., Caparrós, M. & Moigne, A. M. Una aproximación a la comprensión de la fauna de macromamíferos de la Cueva de Zafarraya (Alcaucín, Málaga). *Menga Rev. Prehist. Andalucía* **3**, 83–105 (2012).
75. Ripoll, M. P. & Maroto, J. L. fauna mediterránea durante el Pleistoceno superior del Mediterráneo Ibérico. *Kobie Serie Anejo* **18**, 27–38 (2021).
76. Lazo, A. Ranging behaviour of feral cattle (*Bos taurus*) in Doñana National Park, S.W. Spain. *J. Zool.* **236**(3), 359–369. <https://doi.org/10.1111/j.1469-7998.1995.tb02718.x> (1995).
77. AliceVision. Meshroom: V2021.1.0. GNU-GPL. <https://alicevision.org/> (2020).
78. OpenDroneMap Authors ODM. *A Command Line Toolkit to Generate Maps, Point Clouds, 3D Models and DEMs from Drone, Balloon or Kite Images*. *OpenDroneMap/ODM GitHub Page*. <https://github.com/OpenDroneMap/WebODM> (2020).
79. Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F. & Ranzuglia, G. MeshLab: an open-source mesh processing tool. in *Sixth Eurographics Italian Chapter Conference*. 129–136. MeshLab V. 2020.12. <https://www.meshlab.net/> (2008).
80. CloudCompare. V2.11.0. GNU-GPL. <https://www.cloudcompare.org> (2020).
81. Zhukov, S., Iones, A. & Kronin, G. An ambient light illumination model. *Render. Tech.* **98**, 45–55 (1998).
82. Vergne, R., Pacanowski, R., Barla, P., Granier, X., & Schlick, C. Radiance scaling for versatile surface enhancement. in *Proceedings of the 2010 ACM SIGGRAPH Symposium on Interactive 3D Graphics and Games*. 143–150. (2010).

Acknowledgements

Fieldwork was partially supported by the Research Groups RNM-293, University of Huelva & Junta de Andalucía and Naturtejo, E.I.M., to CNC. Research work of SF is supported by the FCT (Science and Technology Foundation), through projects UID/Multi/00073/2020 Geosciences Center-Coimbra University. N. Moreira (ICT) is financed by FCT—Fundação para a Ciência e a Tecnologia, I.P., under the programmatic project Ref. UIDB/04683/2020. We acknowledge the contributions of the Editor and the two reviewers that greatly improved the text.

Author contributions

The individual contributions of each co-author to the article are as follows: C.N.C. coordinated the manuscript and participated in the field work. F.M. and L.M.C. participated in the manuscript and field work. Z.B., J.M.G., P.G., F.R., A.T. and S.R.C. compiled the data acquisition and participated in the field work. J.B., N.M., M.C., P.P.C.

S.F. and Y.Z. analysed the tracks. J.R.V. designed the project. F.G.G., G.F., S.F. and C.F. provided contextual data. All authors discussed and commented on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-022-14137-6>.

Correspondence and requests for materials should be addressed to L.M.C.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2022