Swiss Journal of Palaeontology (2026) 145: 597–623 | DOI 10.3897/sjp.145.182523

Research Article

Avian remains from Venta Micena (Baza Basin, Granada Geopark) shed light on the Early Pleistocene wetland environments and trophic dynamics of the Southern Iberian Peninsula

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Academic editor: Analía Forasiepi ♦ **Received** 15 December 2025 ♦ **Accepted** 12 April 2026 ♦ **Published** 13 May 2026

Abstract

The fossil site of Venta Micena (Baza Basin, southeastern Iberian Peninsula), dated to the Early Pleistocene (1.6–1.5 Ma), is renowned for its huge assemblage of skeletal remains of large mammals, most of which were unburied from two roughly coeval excavation quarries, VM3 and VM4. These bone accumulations resulted from the scavenging habits of giant hyaenas (*Pachycrocuta brevirostris*), which transported ungulate carcasses to their maternity dens to consume them. The fossils have enabled detailed reconstructions of Western European faunal communities during the Early Pleistocene, but the remains of small vertebrates, particularly birds, are rare and still poorly understood. Here we describe the first avian remains from Venta Micena and assess their palaeoenvironmental and ecological significance. Three taxa were identified: (i) the Common Shelduck *Tadorna tadorna*; (ii) the Pleistocene Giant Crane *Grus* cf. *primigenia*; and (iii) the Pleistocene subspecies of Common Raven, *Corvus corax antecorax*. The presence of *T. tadorna* and *G.* cf. *primigenia* suggests the existence of a wetland environment characterized by oligohaline waters surrounded by brackish pools in the vicinity of the site. The presence of *C. corax antecorax* is consistent with the abundance of remains of ungulate carcasses exploited by *P. brevirostris*, indicating rich scavenging opportunities. Palaeosynecological modeling suggests that meat consumption by ravens approached those of each of the large carnivores, thus significantly reducing the available carrion for other secondary consumers. Moreover, digestive corrosion and tooth marks on bird bones evidence the consumption of avian remains by carnivores, probably juvenile hyaenas. Altogether, these findings reveal a more complex structure of the faunal community that inhabited Venta Micena than previously recognized.

- First avian remains from Venta Micena are described, including a shelduck, *Tadorna tadorna*, and the oldest records of the large crane *Grus* cf. *primigenia* and raven *Corvus corax antecorax*.
- *Grus* and *Tadorna* support the presence of a mild, oligohaline to brackish wetland environment in the Baza Basin.
- The scavenging habits of *Corvus* add complexity to the trophic interactions in the ecosystem surrounding the Baza palaeolake.

Keywords

Late Villafranchian, meat consumption, Orce, Quaternary birds, scavenging, wetlands

Introduction

Geological and palaeontological setting

The late Early Pleistocene (Late Villafranchian) site of Venta Micena (VM) lies in the Baza Basin (Province of Granada, southeastern Spain), a synorogenetic inland basin located in the northeastern sector of the Guadix-Baza Depression, in the contact between the External and Internal Zones of the Betic Cordillera (Fig. 1A, B). This sedimentary depression shows tectonic subsidence and continental sedimentation, features inherited from a marine basin formed during Late Miocene times in the interior of the Betic mountain range (Sanz de Galdeano and Vera 1992; Platt et al. 2013). The transition from a marine sedimentary regime to a continental one took place 7.5–7.0 Ma ago, being the result of major regional tectonic movements. This caused the isostatic uplifting of the basin (average uplift rate of ~200 m/Ma, estimated from upper Neogene coastal marine conglomerates and coral reefs; Braga et al. 2003), which has continued to the present day leading to an elevation of the basin glacis to a height of 1,000 m above sea level (asl).

Isostatic uplifting resulted in the disconnection of the basin from the Mediterranean Sea. This in turn gave rise to the transition from an exorheic sedimentary regime to an endorheic one, in which the deposition of continental sediments was favoured by intense subsidence (Playà et al. 2000; Palmqvist and García-Aguilar 2011; Guerra-Merchán et al. 2014; Granados 2024). As a result, the Baza Basin preserves a ~600 m thick and relatively continuous record of Late Miocene (latest Turolian) to Middle/Late Pleistocene continental sediments. These sediments represent fluvial and alluvial deposits at the basin margins that change to lacustrine and swampy deposits towards the basin centre. Intercalated with them, there are also deposits linked to hot springs, which are nowadays abundantly represented in the Betic mountain range (Fig. 1A, B) (García-Aguilar et al. 2014, 2015, 2024).

The varied lithological composition of the Orce sub-basin, placed in the northeastern sector of the Baza Basin, with alternations of fluvial red detrital facies and lacustrine carbonate-marly facies that locally show gypsum deposits (restricted to the centre of the lacustrine system in this area) and cherts, points to a palaeogeographic model of fluvio-lacustrine sedimentation highly variable in time and space. This resulted in a wetland environment, with open plains and forest patches in the emerged zone around a shallow fluvio-lacustrine system surrounded by marshy areas (Mendoza et al. 2005; García-Aguilar and Palmqvist 2011; Granados et al. 2021; Palmqvist et al. 2022a, 2022b).

The relatively continuous deposition of continental sediments during most of the Pliocene and Pleistocene led to the generation of many palaeontological sites with fossils of terrestrial fauna, particularly large mammals (e.g., Ros-Montoya et al. 2017, 2018; Granados et al. 2026). Of interest here, two sites of the Orce sub-basin dated to ~1.4 Ma (Palmqvist et al. 2016), Barranco León-D and Fuente Nueva-3, preserve abundant Oldowan tools and skeletal remains of large mammals linked through the presence of anthropogenic cut and percussion marks, as well as a human deciduous tooth in Barranco León-D (Martínez-Navarro et al. 1997; Oms et al. 2000; Espigares et al. 2013, 2019, 2023, 2026; Toro-Moyano et al. 2013; Titton et al. 2021; Palmqvist et al. 2023a, 2024). Moreover, the site of Venta Micena (1.6–1.5 Ma) stands out because it includes an exceptional record of the large mammal community that preceded the first hominin dispersal in the Baza Basin (Arribas and Palmqvist 1999; Rodríguez-Gómez et al. 2016, 2017; Palmqvist et al. 2022a).

Venta Micena, an exceptional window for the Early Pleistocene terrestrial ecosystems

Venta Micena (VM) is an 80–120 cm thick limestone stratum that outcrops over > 2.5 km and preserves a worldwide unique fossil record of large mammals (Moyà-Solà et al. 1987; Martínez-Navarro 1991; Martínez-Navarro and Palmqvist 1995; Palmqvist et al. 1999; Martínez-Navarro and Rook 2003; Martínez-Navarro et al. 2011, 2021; Ros-Montoya et al. 2012; Medin et al. 2017). The VM stratum is formed by micritic limestone beds deposited in the context of a series of short-time events that resulted in highstand to lowstand shallowing sequences of the lake margin, which led to the development of successive palaeosoils (Fig. 1E). These events probably correspond to alternating wet and dry seasons of successive years (Arribas and Palmqvist 1998; García-Aguilar and Palmqvist 2011; García-Aguilar et al. 2013; Granados et al. 2021; Palmqvist et al. 2022a).

The huge fossil assemblage unburied from Venta Micena is composed of ~24,000 skeletal remains of 24 taxa of large mammals. The remains were unearthed from a surface of ~400 m^2 distributed among several excavation quarries, including VM3 and VM4 (Fig. 1C), which represent areas of the VM stratum where very dense concentrations of skeletal remains are observed. These bone accumulations are roughly coeval, although their deposition does not necessarily correspond to the same

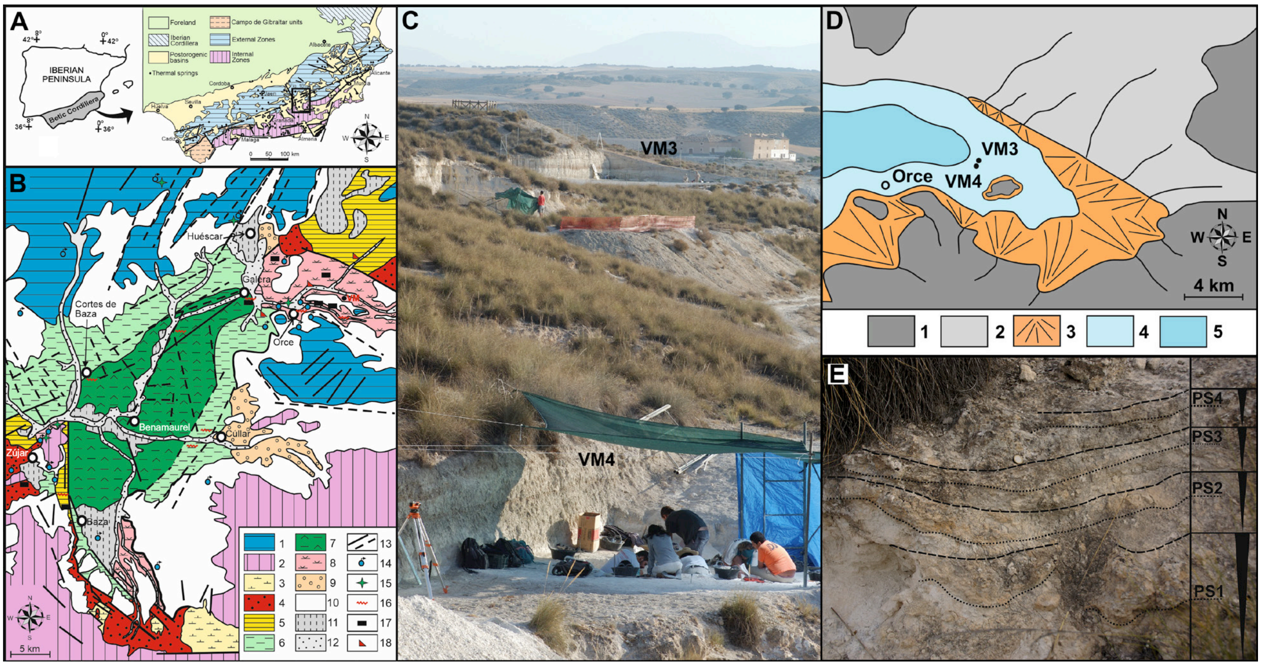

Figure 1. A. High-scale geological context of the Baza Basin (enclosed in a box) in the Betic Cordillera. To the North, this basin is bounded by reliefs of Mesozoic age, mostly carbonates (Tethys type), which belong to the External Zones of the Betic Cordillera. To the South, it is surrounded by reliefs composed of sedimentary and metamorphic rocks of Palaeozoic-Triassic age, which belong to the Internal Zones. To the West, it connects with the Neogene Guadix Basin and to the Southeast with the Neogene Almanzora Corridor Basin. The points mark the hot springs that are currently active in the Betic mountain range; **B.** Geologic map of the Baza Basin. 1-Substrate of the External Zones; 2-Substrate of the Internal Zones; 3-Tortonian, marine facies; 4-Late Turolian-Pliocene, alluvial facies s.l.; 5-Pliocene-Early Villafranchian, mainly lacustrine facies; 6-Early and Middle Villafranchian, distal fluvial facies (sandstones and clays); 7-Early and Middle Villafranchian, marly-evaporitic lacustrine facies; 8-Late Villafranchian-Epivillafranchian, lacustrine and distal fluvial facies; 9-Middle and Late Pleistocene, proximal alluvial and locally lacustrine facies; 10-Glacis surface; 11-Holocene alluvial; 12-Holocene fluvial terraces; 13-Tectonic fractures (in discontinuous traces, those inferred from satellite images); 14-Hot springs currently active in the Baza Basin; 15-Recent travertine buildings; 16-Seismites; 17-Levels of dark clays; 18-Cherts. VM (in red) indicates the position of the late Early Pleistocene site of Venta Micena; **C.** Panoramic view of the Venta Micena stratum, which outcrops in the Orce sub-basin along ~2.5 km, showing the position of two excavation quarries discussed in the text during the summer season of 2005, which was codirected by B. Martínez-Navarro and P. Palmqvist: VM3 (background) and VM4 (foreground). The straight-line distance between VM3 and VM4 is ~350 m; **D.** Palaeogeographical context of the Orce-Venta Micena sector of the Baza Basin during the Late Villafranchian [1, External Zones; 2, Pliocene sediments (emerged relief); 3, Alluvial and fluvial sediments; 4, Extension of the lake during a highstand stage; 5, Extension of the lake in a lowstand stage]. The position of excavation quarries VM4 and VM3 of the Venta Micena site is shown; **E.** Photograph of the 80–120 cm thick micritic limestone stratum of Venta Micena, showing the palaeosoils (PS) that resulted from four successive highstand to lowstand shallowing cycles (the photograph was taken 40 m North of VM4).

years, as explained below. Of these quarries, VM3 and, to a lesser extent, VM4, are the two more intensively excavated during recent decades (Palmqvist et al. 1996, 2011, 2022a; Arribas and Palmqvist 1998; Palmqvist and Arribas 2001).

During the lowstand stages in the summer season, the adult hyaenas accumulated skeletal remains of the prey scavenged in the vicinity of their maternity dens, which were dispersed across the emerged plain surrounding the lake margins. In the highstand stage of the winter season, the plain was submerged by the rising of the lake water table and the precipitation of micritic limestone capped the bone assemblages, thus contributing to skeletal preservation. This explains why most bones of Venta Micena show weathering stage 0, which indicates a relatively short period of subaerial exposure before burial in the sediment, less than one year (Behrensmeyer 1978). Herbivore taxa dominate in the fossil assemblages from VM3 and VM4, both in number of identifiable specimens and minimal number of individuals. Elements of the appendicular skeleton predominate over cranial and axial elements. The ontogenetic stages estimated for the individuals include calves and juveniles with deciduous teeth as well as prime and past prime adults with fully erupted permanent dentition. More common herbivores show high frequencies of non-adult individuals, while adults predominate among carnivores, except for the giant (~110 kg) Short-faced Hyaena *Pachycrocuta brevirostris* (Gervais, 1850) (Palmqvist et al. 2011), where 50% are juveniles in VM3 (Palmqvist et al. 2022a).

Taphonomic analyses of the fossil assemblage from VM3 showed that *P. brevirostris* was the bone accumulating agent and that loss of palaeobiological information was mostly due to the selective destruction of skeletal remains by these hyaenas during the period when they were exposed on the surface before their burial (Palmqvist et al. 1996, 2011, 2022a; Arribas and Palmqvist 1998; Palmqvist and Arribas 2001; Espigares 2010). More specifically, analysis of mortality patterns for ungulate species, inferred from juvenile/adult ratios and abundance of tooth-wearing classes, indicated that hyaenas scavenged the skeletal remains of animals previously hunted by hypercarnivores such as sabretooths *Homotherium latidens* (Owen, 1846) and *Megantereon whitei* Broom, 1937, jaguar *Panthera gombaszoegensis* (Kretzoi, 1938) and wild dog *Xenocyon lycaonoides* (Kretzoi, 1938). This inference is based on: (i) the positive relationship in herbivorous taxa between the percentage of juveniles and the estimated body mass for adults, which indicates the selection of young and more vulnerable individuals in larger prey species; (ii) the finding of U-shaped, attritional mortality profiles in horse *Equus altidens* (von Reichenau, 1915) and Megacerine deer *Praemegaceros verticornis* (Dawkins, 1872), the two ungulates better represented in the assemblage, which indicates the selection by predators of very young and very old individuals; and (iii) the presence of abundant autopodial bones of ungulates with pathologies that limited the animals' ability to escape from predators (Palmqvist et al. 1996; Arribas and Palmqvist 1998). In addition, the skeletal representation of ungulate taxa in VM3 suggests that hyaenas selectively transported herbivore carcasses and body parts to their maternity den as a function of the mass of the ungulates scavenged (Palmqvist and Arribas 2001). This resulted in the transport of whole carcasses of small to medium-sized ungulates, while the carcasses of large species were dismembered and the limbs that provided higher marrow yields were preferentially transported to the den. Later, fracture and consumption of major limb bones by hyaenas in the denning area was also highly selective, correlating well with their marrow content and mineral density (Arribas and Palmqvist 1998), which resulted in well-defined consumption patterns for each major limb bone (Palmqvist et al. 2011).

Given the bone-cracking abilities of *P. brevirostris*, the fossil assemblages from Venta Micena are predominantly composed of skeletal remains of large mammals, while the remains of other vertebrates (e.g., small mammals and herpetofauna) are largely underrepresented at this site (Palmqvist et al. 1996; Arribas and Palmqvist 1998; Palmqvist et al. 2011, 2022a). In general terms, birds have a low preservation potential due to the small size of most species combined with their lightweight and often pneumatized skeletons, as well as the absence of highly mineralized tissues such as teeth (Turvey and Blackburn 2011). For these reasons, sites preserving rich avifaunas are typically either taphonomically exceptional deposits (i.e., *fossil lagerstätten* preserved in caves) or are dominated by low-pneumaticity, large-bodied "water birds" (Mitchell 2015). This explains that bird remains are scarcely represented in the open-air sites of the Guadix-Baza Depression, with the only exception being of the earliest Middle Pleistocene site of Huéscar-1 (Sánchez-Marco 1989; Alonso-Diago 2003). The wetlands of the Baza Basin included an extensive lacustrine system with oligohaline waters and brackish environments, which was surrounded by an emerged plain with shallow freshwater ponds of variable dimensions that constituted a reservoir of fresh water for the terrestrial fauna (Granados et al. 2021; Palmqvist et al. 2022b). These palaeoenvironments must have been extremely favourable for bird populations. In addition, only a few other Early Pleistocene sites of the Iberian Peninsula preserve avian remains, including Sierra de Quibas (Montoya et al. 1999), Cueva Victoria (Sánchez-Marco 2004), Gran Dolina, and Sima del Elefante of Atapuerca (Rosas et al. 2001; Sánchez-Marco 2005; Nuñez-Lahuerta et al. 2016).

To date, no avian taxa have been conclusively identified in Venta Micena, except for a citation (without any photo or description) on the presence of Charadriiformes indet. (aff. Laridae) in VM3 (Martínez-Navarro 1991). For this reason, in this study, we have performed a survey of the scarce and fragmentary avian remains preserved in the huge osteological collection from VM3 and VM4. The information obtained from the new avian taxa identified in our study, as well as from the marks preserved on some of the bird bones, provides a better understanding of the Early Pleistocene faunal community that inhabited Venta Micena and the interrelationships between the species that comprised it.

Material and methods

Fossil specimens studied

A total of 18 avian remains from Venta Micena, including one fragment of a skull, one axial element, and 16 appendicular bones, were identified and studied at the Museum of Prehistory of Orce (MPO) and the Archaeological Museum of Granada (AMG). Of these remains, 16 were unearthed from quarry VM4 during fieldwork between 2013–2015 and are housed at AMG, while the specimens AMG-VM-84/CIII/D8/NC and AMG-VM-3121 were unburied from quarry VM3 in the years 1984 and 1990, respectively, and were curated in the Museum of Prehistory of Orce during our study. At present, all the avian specimens studied are housed at AMG.

Bone species identification was based on direct comparisons with osteological collections housed at the National Museum of Natural Sciences (MNCN, Madrid) and the Anatomical Museum of the University of Valladolid (MAUV), Spain. Diagnostic characters provided by specialized references (e.g., Cohen and Serjeantson 1996; Mayr 2004; Livezey and Zusi 2006, 2007; Mourer-Chauviré 2025) were also used. Bone measurements were taken with a digital caliper Sylvac S235 (error = +0.1 mm) and using photographs taken with a Canon EOS 6D camera. Bone cortical surfaces were analysed with a stereoscopic binocular microscope (Olympus SZ 11) and a digital microscope (DINO-LITE Model AM4115TL). Postmortem, pre-burial taphonomic attributes such as weathering and abrasion were analysed following the criteria of Behrensmeyer (1978), with adjustments made for birds (Behrensmeyer et al. 2003; Prasak 2011). Carnivoran activity on bones (e.g., tooth marks including pits and scores, furrowing, etc.) was described based on the works of Binford (1981), Blumenschine (1995), Blumenschine et al. (1996), Haynes (1980) and Shipman (1983). Bone breakage patterns were classified following Capaldo and Blumenschine (1994) and Villa and Mahieu (1991). Chemical alterations produced by digestion were documented, which allowed to differentiate five degrees of corrosion (0: null; 1: light; 2: moderate; 3: heavy; 4: extreme) following the methodology used for micromammals by Andrews (1990) and Lloveras et al. (2008).

Palaeosynecological model

We have used here a palaeosynecological model that allows estimating the yearly production of meat resources that would be available to the secondary consumers of a large mammals palaeocommunity and the distribution of these resources among the members of the carnivore guild (for details on this model, see Rodríguez-Gómez et al. 2013, 2016, 2024a). The model, called PSEco, calculates, for each species of primary consumers, the survival and mortality profiles that result in a stable and stationary population in the long term (i.e., these profiles represent the average of population fluctuations over time). For doing so, maximum and minimum subadult mortalities are estimated by the model for each primary consumer, which in turn allows calculation of how many individuals from each different age class can die annually without causing the herbivore population to collapse. These estimates provide the yearly biomass of primary consumers available for the secondary consumers of the palaeocommunity. Once the available meat or Total Available Biomass (TAB) is estimated, the model calculates the demands and consumption profiles of the secondary consumers or Total Demanded Biomass (TDB), which results from the estimates of their annual meat intakes, optimal densities, and prey preferences. The distribution of meat among the species of secondary consumers, based on these demands, allows calculating the degree of satisfaction of their dietary requirements and the intensity of competition for these resources in the carnivore guild.

In this study, we have reassessed the estimates obtained previously with the PSEco model for reconstructing the palaeocommunity of large mammals of Venta Micena (Rodríguez-Gómez et al. 2017) by now including the raven as a member of the secondary consumers guild. To achieve this, we assumed that this species consumed carrion from all ungulate size categories with the same preference. We considered, for adult ravens, a body mass of 1.16 kg, a density of 1.5 individuals per km^2 (Salvador 2023), and a meat consumption per raven of 228.5 g/day, which is the mean value between consumption in winter by modern ravens (415 g/day) when plant resources are scarce (Heinrich 1994), and summer (42 g), when mammalian meat accounts for ~10% of their diet (Engel and Yong 1989; Boarman and Heinrich 1999). With these values, we calculated a yearly meat demand of ravens and the other secondary consumers of Venta Micena (e.g., hyaena *P. brevirostris*, sabretooths *H. latidens* and *M. whitei*, and wild dog *X. lycaonoides*) under optimal ecological conditions, distributing the available biomass of primary consumers among them.

Results

Of the 18 avian remains studied, seven are from wing bones and allow identification of at least three avian taxa, while the remaining fossils are very fragmentary or show no diagnostic characters. Of these bird remains, 88.9% (i.e., 16 out of 18) were unearthed from quarry VM4.

Systematic Palaeontology

Class Aves Linnaeus, 1758
Order Anseriformes Wagler, 1831
Family Anatidae Vigors, 1825
Genus *Tadorna* Boie, 1822

Tadorna tadorna **Linnaeus, 1758**

Referred specimens. Distal epiphysis of a right humerus (AMG-VM-14/D13/10), proximal half of a left ulna (AMG-VM-13/E13/1), and left femoral diaphysis with part of the distal epiphysis (AMG-VM-14/G10/58) from excavation quarry VM4 (Fig. 2A–D, G, H). These three fragments were found in close spatial association. In addition, direct comparison with museum specimens of *T. tadorna* (n = 6; Suppl. material 1) indicates that the humerus, ulna, and femur fragments show mutually consistent relative proportions, based on preserved lengths and epiphyseal/diaphyseal widths, and fall within the observed extant range, supporting the interpretation that they may have belonged to the same individual.

Description. Humeral distal epiphysis AMG-VM-14/D13/10 is almost complete, preserving part of the dorsal surface, which is slightly weathered and lacks the distalmost part of the ventral epicondyle (Fig. 2A). A ventral supracondylar tubercle is present in the ventral margin, proximal to the ventral epicondyle. The ventral condyle is rounded, with the major axis transversely positioned to the shaft. Proximally to this condyle, a fossa for the brachialis muscle is well defined on the cranial surface. The dorsal condyle is obliquely positioned to the shaft. An ectepicondylar prominence (i.e., a weakly developed dorsal supracondylar tubercle) is present on the dorsal surface, at the level of the proximal end of the dorsal condyle.


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Proximal half of ulna AMG-VM-13/E13/1 has the olecranon and ventral cotyla absent but shows a rounded dorsal cotyla (Fig. 2D). It shows the impression for the insertion of the scapulotriceps muscle on the outer face, while it defines the incisura radialis on the inner face. There is also a well-defined impression by the insertion of the brachial muscle, which extends distally with a triangular shape. A nutrient foramen is located near the end of this impression, along the cranial margin.

Femur fragment AMG-VM-14/G10/58 shows a diaphysis slightly flattened mediolaterally, with a subtle linea intermuscular cranialis that ascends proximally from the midshaft (Fig. 2G). The distal epiphysis only preserves a fragmented lateral condyle, while the fossa poplitea and sulcus patellaris are both partially observed in the caudal and cranial face, respectively.

Comparisons and remarks. The overall configuration of the distal humerus (including the ventral supracondylar tubercle, the condylar morphology, and the presence of a well-defined brachialis fossa) is consistent with Anseriformes and, within them, Anatidae (Worthy et al. 2022). Comparison with 22 anatid species (Suppl. material 1) further supports assignment to Tadornini (shelducks), as the distal humerus closely matches *Tadorna* in morphology—specifically, a relatively shallow brachial fossa that is not distomedially deepened and a weakly developed dorsal supracondylar tubercle (Worthy and Pledge 2007)— and in overall distal size (Figs 2A–C, 3A). Two *Tadorna* species currently inhabit the Western Palearctic, the Common Shelduck (*Tadorna tadorna*) and the Ruddy Shelduck (*T. ferruginea* (Pallas, 1764)). The remaining species of *Tadorna* have restricted distributions outside the Western Palaearctic (Australia and New Zealand, southern Africa, and East Asia), making their occurrence in the Pleistocene record of southern Iberia exceedingly unlikely. Accordingly, we restrict detailed comparisons to the two Western Palearctic taxa. Morphologically, only a few subtle characteristics have been observed in the distal humerus that allow these two species to be distinguished, including: (i) the olecranon fossa, which is deeper and transversely positioned to the shaft in *T. tadorna*, rather than longer and vertical to the shaft, as in *T. ferruginea* (Bedetti and Pavia 2013); (ii) the m. brachialis fossa, which in *T. tadorna* is elliptical and well delimited on all sides, while in *T. ferruginea* it is only clearly marked on the sides, but gradually tapers upwards (Soergel 1966); and (iii) a very thin ridge starting from the ectepicondylar prominence and running obliquely towards the m. brachialis fossa, which is present in *T. ferruginea* but not in *T. tadorna* (Mourer-Chauviré 2025) (Fig. 2C). Characters (i) and (ii) do not allow an unambiguous differentiation between both species in the Venta Micena specimens given their state of preservation, but the lack of the ridge of character (iii) seems clear in AMG-VM-14/D13/10. In addition, the dimensions of this bone fragment also agree with the size of *T. tadorna* (Fig. 3A), which is slightly smaller than *T. ferruginea* (Mourer-Chauviré 2025). Taken together the size and shape of AMG-VM-14/D13/10, we assign it to *T. tadorna.*

Although the proximal half of the ulna has limited diagnostic value on its own, its size and morphology are consistent with the anatid sample examined (Suppl. material 1) and do not contradict the identification based on the humerus; it is also morphologically similar to ulnae of *Tadorna*.

The shape and size of the femur fragment agree with femora of *Tadorna* in the comparative series (Suppl. material 1), supporting the identification inferred from the humerus.

Synthesis. The two associated remains from VM4 (ulna AMG-VM-13/E13/1 and femur AMG-VM-14/G10/58) are consistent in size and morphology with the identification of the humerus AMG-VM-14/D13/10 as *Tadorna tadorna*.

Genus *Tadorna* Boie, 1822

Tadorna sp.

Referred specimens. Complete left ulna (AMG-VM-84/CIII/D8/NC) from excavation quarry VM3 (Fig. 2F).

Description. AMG-VM-84/CIII/D8/NC is a complete ulna with the ends of both epiphyses partially eroded (Fig. 2F). Proximally, the ventral and dorsal cotylae, as well as the olecranon, are partially eroded. A well-marked impression for the brachialis muscle is observed on the ventral surface, extending from the ventral cotyla to approximately the first quarter of the bone's length. Near the distal end of this impression, along the cranial margin, a nutrient foramen is present. The diaphysis is only slightly curved. Distally, the dorsal condyle is rounded, whereas the ventral condyle and carpal tubercle are strongly eroded.

Figure 2. Avian appendicular bones identified as *Tadorna tadorna* (**A, D, G**) and *Tadorna* sp. (**F**) from Venta Micena compared to the bones of modern specimen MAUV-3946 (B, E, H). **A.** AMG-VM-14/D13/10, distal epiphysis of a right humerus from VM4; **B.** MAUV-3946, right humerus; **C.** Zoomed detail of distal epiphyses of *T. tadorna* MAUV-3946 and *T. ferruginea* MAUV-309; **D.** AMG-VM-13/E13/1, proximal half of a left ulna from VM4; **E.** MAUV-3946, left ulna; **F.** AMG-VM-84/CIII/D8/NC, left ulna from VM3; **G.** AMG-VM-14/G10/58, diaphysis with partial distal epiphysis of a left femur from VM4; **H.** MAUV-3946, left femur. Abbreviations: bf, fossa brachialis muscle; ct, carpal tubercle; dc, dorsal condyle; ep, ectepicondylar prominence; epr, ridge from ectepicondylar prominence; fp, fossa poplitea; ib, impressio brachialis muscle; ir, incisura radialis; isc, impression of scapulotriceps muscle; lc, lateral condyle; lic, linea intermuscular cranialis; nf, nutrient foramen; of, olecranon fossa; ol, olecranon; pcd, dorsal cotylar process; pcv, ventral cotylar process; prc, papillae remige caudalis; sp, sulcus patellaris; vc, ventral condyle; ve, ventral epicondyle; vst, ventral supracondylar tubercle. Views are indicated in the panels.

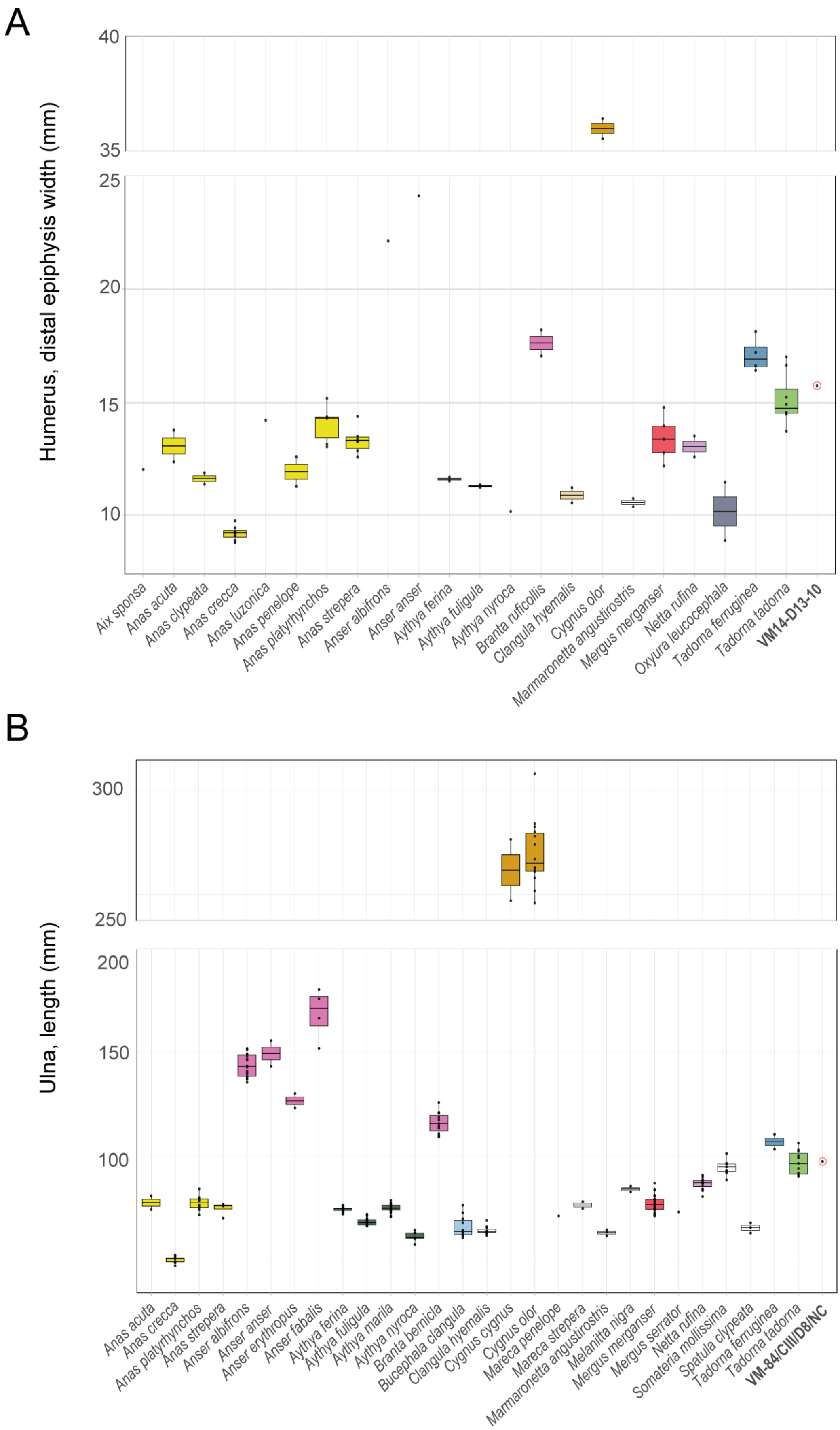

Figure 3. Dimensions of *Tadorna* specimens from Venta Micena compared to the species of ducks (Anseriformes) present in Iberia and Europe today. **A.** Width of distal humeral epiphysis; **B.** Length of ulna. Box and whisker plots show the 25-75% interquartile range with the thick line indicating the median value. Data used for these diagrams from Suppl. material 1.

Comparisons and remarks. In overall morphology, AMG-VM-84/CIII/D8/NC falls within the anatid range represented in our comparative sample (Suppl. material 1) and closely resembles *Tadorna* (Fig. 2E). The carpal tubercle is reported as the only diagnostic character of the ulna to differentiate between both *Tadorna* species present in the Palaearctic region (Zelenkov 2022), but it is strongly eroded in AMG-VM-84/CIII/D8/NC and cannot be assessed. Total bone length is 97.8 mm, a size that falls within the range of *T. tadorna* rather than that of *T. ferruginea* (Fig. 3B). However, the low sample size analyzed of *T. ferruginea* and the absence of any diagnostic character (owing to the erosion) imply that AMG-VM-84/CIII/D8/NC can only be classified as *Tadorna* sp. Given that other bones were conclusively identified as *T. tadorna*, the most parsimonious interpretation would be that all skeletal remains from Venta Micena are from *T. tadorna*, but we cannot discard that future findings at the site will allow identifying *T. ferruginea.*

Order Gruiformes Bonaparte, 1854
Family Gruidae Vigors, 1825
Genus *Grus* Pallas, 1766

Grus cf. *primigenia* Milne-Edwards, 1896

Referred specimens. Left ulna with partial proximal and distal epiphyses (AMG-VM-G13-40) and diaphysis of a left radius (AMG-VM-G13-37). Both specimens were unburied from quarry VM4 (Fig. 4).

Description. The two bone remains were found very close to each other, which suggests that they may have belonged to the left wing of the same individual. The ulna is long and slightly curved (Fig. 4A), with a total length of > 286 mm (missing part of the proximal end) and a craniocaudal cross-section at midshaft of 11 mm. The proximal epiphysis is almost lost, except for the proximal widening at the caudal surface. The insertion of the brachialis muscle is marked at this proximal section. The diaphysis presents a nutrient foramen that is ventrally located in the line that limits cranially the impression of the brachial muscle (Fig. 4D, G). The caudal face of the distal epiphysis preserves part of the dorsal and ventral condyles, but their cranial face and the carpal tubercle are both missing. The radius diaphysis is straight, with a craniocaudal cross-sectional diameter of 7.9 mm (Fig. 4J).

Comparisons and remarks. In general terms, the size and overall morphology of both limb bones—including diaphyseal straightness, the size and position of the nutrient foramen, and the shape of the distal epiphysis of AMG-VM-G13-40—are all consistent with the anatomy of Gruidae, based on published descriptions (Cohen and Serjeantson 1996) and direct comparison with extant individuals of the Eurasian Crane, *Grus grus* (Linnaeus, 1758) (N = 10), Sandhill Crane, *Antigone canadensis* (Linnaeus, 1758) (N = 3) and Siberian Crane, *Leucogeranus leucogeranus* (Pallas, 1773) (N = 1) (Suppl. material 1). The ulna AMG-VM-G13-40 is only comparable in size to the largest extant gruid, the Asian Sarus Crane, *Antigone antigone* (Linnaeus, 1758) (Fig. 5). Populations of this species are mainly sedentary, restricted to areas south of the Himalayas, SE Asia, and NE Australia (Archibald et al. 2020b), and have breeding tied to monsoon climates (Johnsgard 1983). This makes the presence of *A. antigone* in the Pleistocene of Europe unlikely (Stewart 2007), particularly in Venta Micena during the Late Villafranchian. The only member of Gruidae present today in the Western Palearctic is *G. grus*. Compared to individuals of *G. grus*, AMG-VM-G13-40 is notably larger in size (Fig. 5). An extinct crane larger than *G. grus*, *G. primigenia*, has been described as differing from the extant species primarily in size, with no clear diagnostic morphological distinctions, and is recorded from the Middle and Late Pleistocene to Holocene of Europe, including Britain (Harrison and Cowles 1977; Northcote and Mourer-Chauviré, 1985, 1988; Stewart, 2007; Tyrberg, 2009). Moreover, the holotype of *G. primigenia* is a distal tibiotarsus and the available referred material (Northcote and Mourer-Chauviré, 1985, 1988) does not include an ulna. For this reason, we could not make a direct comparison of our ulnar specimen with *G. primigenia.* In any case, the identity of large European Quaternary cranes is debated, particularly whether *G. primigenia* is conspecific with *G. grus* (i.e., representing large individuals of the Eurasian Crane) or instead a distinct, notably larger species (see Stewart, 2007 for a review). Accordingly, and given that *G. primigenia* is still regarded as a valid species, we tentatively assign here the associated wing bones AMG-VM-G13-40 and AMG-VM-G13-37 to *Grus* cf. *primigenia*. If this interpretation is correct, Venta Micena may represent the oldest known record of the Giant Crane in Europe, placing its first occurrence in the late Early Pleistocene.

Order Passeriformes Linnaeus, 1758
Family Corvidae Vigors, 1825
Genus *Corvus* Linnaeus, 1758

Corvus corax antecorax Mourer-Chauviré, 1975

Referred specimens. Distal half of a right humerus (AMG-VM-3121) from quarry VM3 (Fig. 6).

Description. The humeral diaphysis is slightly curved (Fig. 6), with craniocaudal and dorsoventral midshaft cross-sections of 6.8 and 7.9 mm, respectively. A nutrient foramen is present on the caudal face of the proximal extreme of the shaft. The distal epiphysis is well preserved except for the dorsal supracondylar process at the dorsal margin, which is broken. In the cranial face, the dorsal condyle is oblique, and the ventral condyle is perpendicular to the shaft axis. The major axis is slightly shorter in the dorsal condyle (7.2 mm) than in the ventral condyle (7.8 mm). The tubercle for the insertion of the superficialis pronator muscle is positioned immediately proximal to

Figure 4. Forearm bones AMG-VM-G13-40 and AMG-VM-G13-37 from VM4. These specimens, identified as a left ulna (**B, C, E, G, H**) and a left radius diaphysis (**J**) of *Grus* cf. *primigenia*, respectively, are compared to modern *G. grus* specimens MNCN-26485 (**A**) and MNCN-23812 (**F, I**). Abbreviations: ct, carpal tubercle; dc, dorsal condyle; ib, impressio brachialis muscle; nf, nutrient foramen; ol, olecranon; pcd, dorsal cotylar process; prc, papillae remige caudalis; vc, ventral condyle. Views are indicated in the panels.

the dorsal condyle. The fossa for the brachialis muscle is well-marked and located at the cranioventral margin, proximal to the flexor process.

Comparisons and remarks. The length ratio for both condyles, the presence of the tubercle for the superficialis pronator muscle and the position of the fossa brachialis are diagnostic for Passeriformes (Mayr 2004; Livezey and Zusi 2006, 2007). Among modern passerines, the overall morphology— including the size and position of the nutrient foramen— and large size of AMG-3121 are only consistent with the Eurasian Raven, *Corvus corax* Linnaeus, 1758, based on direct comparison with extant individuals (N = 29; Suppl. material 1). However, the dimensions of the diaphysis and distal epiphysis of AMG-VM-3121 are noticeably smaller than in a sample of modern ravens. According to the size ranges provided by Mourer-Chauviré (1975: table 32), AMG-VM-3121 falls into the range of the *C. corax* subspecies *C. c. antecorax*, a raven recorded in several fossil sites of the European Late Pliocene to Middle Pleistocene (Sánchez-Marco 2004). The first record of this taxon in the Iberian Peninsula is from the late Early Pleistocene site of Sima

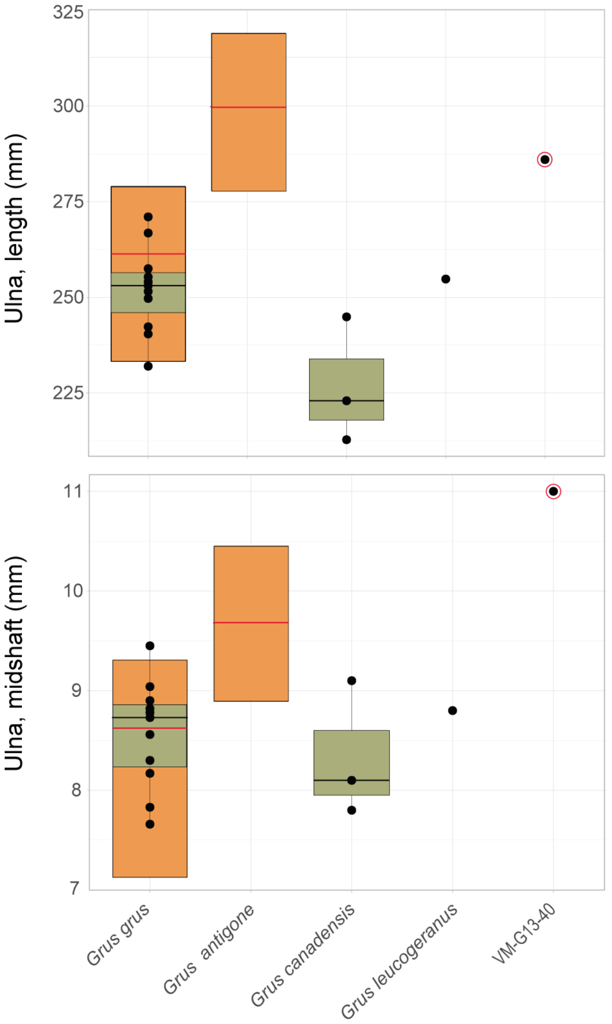

Figure 5. Length and craniocaudal midshaft dimensions of ulna AMG-VM-G13-40, identified as *Grus* cf. *primigenia*, compared to four extant crane species: *G. grus* (n = 40), *Antigone antigone* (n = 8), *A. canadensis* (n = 3), *Leucogeranus leucogeranus* (n = 1). Green boxes and whiskers show the 25–75% interquartile range with the thick black line indicating the median value from individual measurements. Orange boxes and thick red line show, respectively, the minimum-maximum range and mean values provided by Stewart (2007). Data used for these diagrams from Suppl. material 1.

del Elefante level TE7 (Núñez-Lahuerta et al. 2016), which is dated to 1.3–1.2 Ma (Carbonell et al. 2008). Given that the site of Venta Micena is older (1.6–1.5 Ma; Martínez-Navarro 1991), this implies that AMG-VM-3121 represents the earliest occurrence of *C. c. antecorax* in the Iberian Peninsula.

Aves indet.

Referred specimens. Partial skull corresponding to the posterior part of the cranial vault (mostly the parietal region with the sagittal and nuchal crest) (AMG-VM-14/I13/57), proximal fragment of a left ulna (AMG-VM-13/G13/62), partial distal epiphysis of a right ulna (AMG-VM-14/I13/22), fragmented ulnar diaphysis (AMG-VM-13/G13/63), associated partial epiphyses of proximal and distal tibiotarsi (AMG-VM-15/F12/62 and AMG-VM-15/F12/63), diaphysis and partial distal epiphysis of a left tibiotarsus (AMG-VM-14/F12/13), tarsometatarsus (AMG-VM-15/E11/20), distal portion of a pedal phalanx (AMG-VM-13/H10/4), and partial right pelvis preserving the preacetabular portion of the ilium and the acetabulum (AMG-VM-15/H14/28) (Fig. 7). All these bone remains were unburied from quarry VM4 and are preserved in a very fragmentary condition, which precludes their taxonomic identification. In addition, the fragment of a hollow long bone AMG-VM-14/F13/15 could not be identified either anatomically or taxonomically.

Bone marks

Of the bird remains analysed in this study, 55.5% (i.e., 10 out of 18; Table 1) show alterations in their cortical surface compatible with digestive damage (nine specimens, 50% of the remains) or with carnivore tooth marks (four specimens, 22.2% of the remains). All bone specimens are unweathered (i.e., they show weathering stage 0 according to criteria in Behrensmeyer 1978) and none show evidence of abrasion by fluvial transport. The bone fragments attributed to Common Shelduck, *T. tadorna*, from VM4 (i.e., AMG-VM-14/D13/10, AMG-VM-13/E13/1 and AMG-VM-14/G10/58) show digestive corrosion in the distal epiphyses, and pits and scores (0.4–0.7 mm width) appear in the diaphysis of the ulna and femur (Fig. 8A–C). The ulna identified as *Tadorna* sp. (AMG-VM-84/CIII/D8/NC) from VM3 also evidences the two types of taphonomic alterations, digestive corrosion in both epiphyses and narrow scores in the diaphysis (Fig. 8D–F) with an average width of 0.5 mm. The distal half of humerus AMG-VM-3121, assigned to *C. c. antecorax*, is also altered by digestion (Fig. 8I, J), but to a lesser extent than the shelduck bones. In the case of the ulna and radius of *G.* cf. *primigenia* (AMG-VM-G13-40 and AMG-VM-G13-37, respectively), no digestive marks were identified. We tentatively interpreted the linear marks of the cortical surface of the ulnar diaphysis as tooth marks (Fig. 8G). Concerning the bone fragments of Aves indet., signs of digestive corrosion appear in skull fragment AMG-VM-14/I13/57, partial pelvis AMG-VM-15/H14/28, and pedal phalanx AMG-VM-13/H10/4 (Fig. 8H, K, L).

Discussion

On the preservation of skeletal remains in Venta Micena

The late Early Pleistocene site of Venta Micena preserves a huge assemblage of large mammals. Most skeletal remains were unburied from VM3 and VM4, the two main excavation quarries of the site. By the year 2020, the

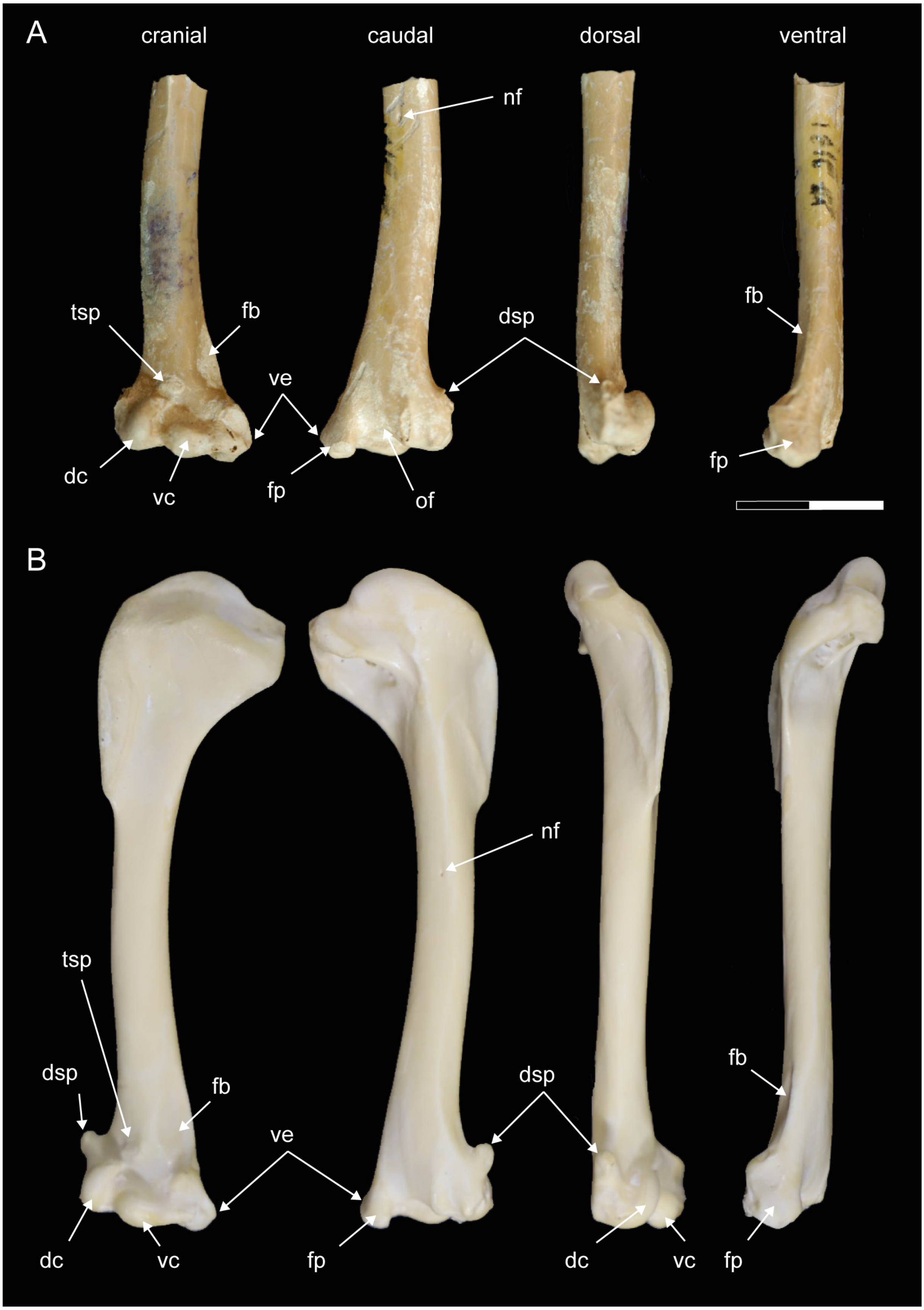

Figure 6. Distal half fragment of a right humerus AMG-VM-3121 from VM3 identified as *Corvus corax antecorax* (**A**), compared to modern specimen MNCN-26548 of *C. corax* (**B**). Abbreviations: bf, fossa brachialis muscle; dc, dorsal condyle; dsp, dorsal supracondylar process; fp, flexor process; nf, nutrient foramen; of, olecranon fossa; tsp, tubercle for superficialis pronator; vc, ventral condyle; ve, ventral epicondyle. Views are indicated in the panels. Scale bar: 20 mm.

Figure 7. Avian remains from VM4 identified as Aves indet. **A.** Partial skull AMG-VM-14/I13/57 corresponding mostly to the parietal region (the arrows mark the position of the sagittal and nuchal crest); **B.** Proximal fragment of left ulna AMG-VM-13/G13/62; **C.** Partial distal epiphysis of right ulna AMG-VM-14/I13/22; **D.** Fragmented diaphysis of ulna AMG-VM-13/G13/63; **E.** Diaphysis with partial distal epiphysis of left tibiotarsus AMG-VM-14/F12/13; **F.** Partial proximal epiphysis of left tibiotarsus AMG-VM-15/F12/62; **G.** Fragments of distal epiphysis of left tibiotarsus AMG-VM-15/F12/63; **H.** Partial right pelvis AMG-VM-15/H14/28; **I.** Tarsometatarsus AMG-VM-15/E11/20 embedded into the rock matrix; **J.** Proximal portion of pedal phalanx AMG-VM-13/H10/4. Arrows highlight key anatomical features. Abbreviations: ac, acetabulum; cex, canalis extensorius; cf, crista fibularis; cns, crista nuchalis sagittalis; dc, dorsal condyle; int, incisura tendinosa; mep, medial epicondyle. Views are indicated in the panels.

number of identified specimens (NISP) of large mammals was 8,150 in VM3 and 1,578 in VM4 (Palmqvist et al. 2022a: table 1). In contrast, other vertebrates are poorly represented at the site. This is the case with birds, as we have unequivocally identified only 18 bone remains in this study. However, it should be noted that although the fossils of large mammals from VM4 barely represent ~20% of those unburied from VM3, 16 out of 18 bird

Table 1. Bone specimens showing evidence of digestive abrasion and tooth marks in the avian remains from Venta Micena. NR, number of remains; MNE, minimum number of elements; MNI, minimum number of individuals.

Species	Quarry	NR	MNE	MNI	Digestive damage (%)	Pits & scores (%)
C. c. antecorax	VM3	1	1	1	1 (100%)	-
Tadorna sp.	VM3	1	1	1	1 (100%)	1 (100%)
T. tadorna	VM4	3	3	1	3 (100%)	2 (66.7%)
G. cf. *primigenia*	VM4	2	2	1	0 (0%)	1?
Aves indet.	VM4	11	6	4	4 (36.4%)	-
Total		**18**	**13**	**8**	**9 (50%)**	**3-4 (~20%)**

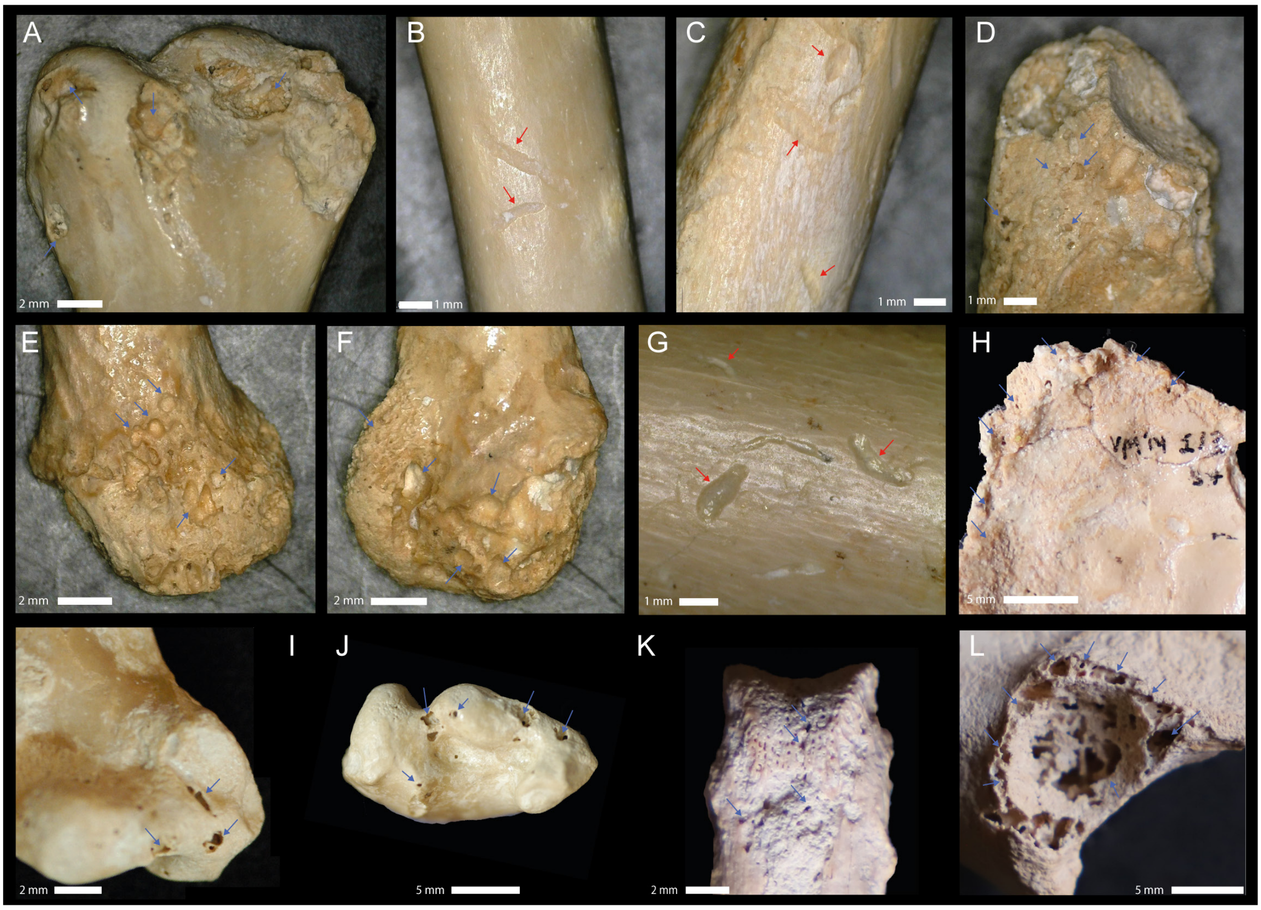

Figure 8. Examples of avian remains from Venta Micena showing evidence of damage by digestive abrasion (**A, D–F, H–L**; blue arrows) or tooth marks (scores and pits) by carnivores (**B, C, G**; red arrows). **A.** AMG-VM-14/D13/10, distal humerus of *Tadorna tadorna* in caudal view; **B.** AMG-VM-4/13-E13-1, proximal region of an ulnar diaphysis of *T. tadorna*; **C.** AMG-VM-14/G10/58, distal region of a femoral diaphysis of *T. tadorna*; **D.** AMG-VM-84-CIII-D8-NC, proximal epiphysis of an ulna of *T. tadorna* in ventral view; **E.** AMG-VM-84-CIII-D8-NC, distal epiphysis of an ulna of *T. tadorna* in dorsal view; **F.** AMG-VM-84-CIII-D8-NC, distal epiphysis of an ulna of *T. tadorna* in ventral view; **G.** AMG-VM-14/G13/63, ulnar diaphysis of Aves indet; **H.** AMG-VM-14/I13/57, anterior region of a skull fragment of Aves indet; **I.** AMG-VM-3121, flexor process of a humeral distal epiphysis of *Corvus corax antecorax* in cranial view; **J.** AMG-VM-3121, distal epiphysis of a humerus of *C. c. antecorax* in sagittal view; **K.** AMG-VM-13/H10/4, proximal epiphysis of a pedal phalanx of Aves indet; **L.** AMG-VM-15/H14/28, region of the acetabulum in a partial pelvis of Aves indet. The blue arrows mark those areas of the cortical bone surface where the effects of digestive abrasion are more intense.

remains (~90%) identified in this study come from VM4. Therefore, the question is: even though the abundance of avian remains is extremely low in Venta Micena, how can we explain that they are comparatively much more represented in quarry VM4 than in quarry VM3?

As explained before, the bone assemblage accumulated in VM3 has been interpreted as the result of the activity of a hyaena clan, which scavenged the ungulate prey hunted by hypercarnivores and accumulated the prey carcasses and body parts in the vicinity of their maternity den, where the adult hyaenas selectively fractured many of these bones to access their medullary cavities. As a result, the fossil assemblage is biased against small vertebrates like birds (Palmqvist et al. 1996, 2011; Arribas and Palmqvist 1998; Palmqvist and Arribas 2001; Espigares 2010). The comparatively low preservation potential of bird bones, resulting from their small size and hollow condition (Turvey and Blackburn 2011), would explain the scarcity of avian fossils in Venta Micena compared to the abundance of skeletal remains of large mammals.

The bone assemblages from VM3 and VM4 are generally similar, except for some minor differences in taxa abundance (Luzón et al. 2021; Palmqvist et al. 2022a): remains of megaherbivores (i.e., elephant *Mammuthus meridionalis* (Nesti, 1825), rhino *Stephanorhinus hundsheimensis* (Toula, 1902), and hippo (*Hippopotamus antiquus* Desmarest, 1822) and carnivores (excluding hyaenas) are represented in VM4 by somewhat higher frequencies than in VM3, whereas horse remains are slightly more abundant in VM3. More specifically, and according to data in Palmqvist et al. (2022a: table 1), megaherbivores and carnivores account for 8.9% and 14.2% of the remains of large mammals in VM4, respectively, and for 3.5% and 6.4% in VM3, respectively, while *E. altidens* represents 31.6% of the remains in VM4 and 49.4% in VM3. In addition, there are some taphonomic differences between VM4 and VM3, including: (i) the frequency of unweathered skeletal remains (*sensu* Behrensmeyer 1978), higher in VM4 (90.8%) than in VM3 (75.9%), which suggests that the bones preserved in VM3 were exposed for longer before being buried in the sediment; (ii) the abundance of anatomically connected skeletal elements, which is lower in VM3 than in VM4; and (iii) the frequency of bones with carnivore toothmarks, higher in VM3 (29.4%) than in VM4 (5.5%), indicating that the remains in VM3 were more thoroughly exploited by hyaenas compared to those in VM4 (Palmqvist et al. 2022a). Given these differences, Luzón et al. (2021) suggested the possibility that a different carnivore other than *P. brevirostris* was the taphonomic agent involved in the bone accumulation process at VM4.

According to Palmqvist et al. (2022a), however, sedimentological analysis of the VM stratum and a comparative taphonomic study of VM3 and VM4 pointed to an alternative interpretation, that the bone assemblages preserved at VM4 and VM3 were accumulated by different hyaena clans on the plain surrounding the lake during the dry seasons of different years. Specifically, the VM stratum is composed of limestone beds deposited during the wet season over several consecutive years, as recorded in the VM stratum by five or six highstand to lowstand shallowing sequences of the lake margin that resulted in the development of successive palaeosoils (Fig. 1E) (Arribas and Palmqvist 1998; García-Aguilar and Palmqvist 2011; García-Aguilar et al. 2013; Granados et al. 2021; Palmqvist et al. 2022a). During the lowstand stages in the summer season, the adult hyaenas accumulated skeletal remains in the vicinity of their maternity dens, which were dispersed across the emerged plain surrounding the lake margins. After the subsequent rising of the lake water table in the highstand stage of the winter season, this plain was submerged and the precipitation of micritic limestone capped the bone assemblages, thus contributing to skeletal preservation. This explains why most bones of Venta Micena show weathering stage 0, which indicates a relatively short period of subaerial exposure before burial in the sediment, less than one year according to Behrensmeyer (1978) in the case of the bones of Amboseli National Park in Kenya, where annual rainfall is ~350 mm (however, the bones may continue unweathered even after 2.5 years of exposure in more humid environments like Doñana in Southern Spain, where rainfall is ~580 mm per year; see Pizarro-Monzo et al. 2025).

With this in mind, it is reasonable to conceive that during the years in which the accumulation of the bone assemblage from VM3 took place, the rise of the water table in the rainy season probably occurred several months later than during those that correspond to the accumulation of skeletal remains detected in VM4. This would have left the skeletal remains of VM3 more time exposed before being buried in the sediment, which would explain why they are more affected by atmospheric weathering and show evidence of a more intense modification by hyaenas, including a higher frequency of carnivore tooth-marks and a lower abundance of bones in anatomical connection. Moreover, this interpretation also helps to clarify why the entire VM stratum, outcropping over 2.5 km, appears to be littered with fossils of large mammals, as it is difficult to conceive a *P. brevirostris* "mega-denning site" that extended over several squared kilometres: as proposed by Palmqvist et al. (2022a), the surface covered by the VM stratum would be inhabited by different hyaena clans during several consecutive years, which would explain why this stratum is riddled with skeletal remains. This taphonomic interpretation is based on the differences of preservation between the remains of large mammals in VM3 and VM4. In the case of the scarce avian remains identified in both bone assemblages, all these remains are unweathered and unabraded, which indicates their quick burial after the death of the birds. Moreover, most of the avian remains (~90%) are from VM4, which agrees with the conditions more favourable for preservation of skeletal remains in this quarry, as evidenced also in the taphonomic attributes of the skeletal remains of large mammals.

Despite the fact that the bone assemblages preserved at VM4 and VM3 are broadly contemporary, except for a difference of a few years in their accumulation by the hyaenas, it must be noted that they are positioned only ~350 m apart (Fig. 1D). This is also an argument against the possibility of two neighbouring hyaena clans: In Serengeti, where Spotted Hyaenas (*Crocuta crocuta* (Erxleben, 1777)) engage in prolonged clashes with neighbouring clans, the permanent territory defended by a clan around the communal den fluctuates between 2.6 and 5.7 km^2 (Hofer and East, 1993). This results in a minimum distance of 910–1220 m between two neighbouring hyaena clans, which is 2.6–3.5 times the distance between VM3 and VM4, which suggests that the bone accumulations preserved in both quarries were not coeval but correspond to separate accumulation events during different years. Furthermore, a study of a Spotted Hyaena clan in the Masai

Mara showed that hyaenas used different communal den sites over a ten-year period, with a mean distance between consecutively used dens of 1.5 ± 0.1 km (Boydston et al. 2006). Given that the distance between VM4 and VM3 is nearly five times less than the one expected when adult Spotted Hyaenas move their cubs to a new denning site, this suggests that VM4 and VM3, although roughly coeval, do not represent a residential relocation of the same hyaena clan. Therefore, the most parsimonious interpretation is that different hyaena clans accumulated diachronically the skeletal remains of the prey scavenged on the emerged plain surrounding the Baza palaeolake during the dry seasons of different years (Palmqvist et al. 2022a).

The fact that the rising of the water table in the depositional years of VM4 took place earlier than in those of VM3, which left the skeletal remains of VM4 less time exposed before being buried in the sediment, explains their less thorough consumption by the hyaenas (Palmqvist et al. 2022a). As a result, it is not surprising that most avian remains preserved at Venta Micena are from VM4, because the small size of these bone remains combined with their pneumatic condition would translate into much lower preservation integrity compared to large mammal bones, which would result in their preservation only under truly exceptional conditions.

Although most interpretations on the taphonomic context of Venta Micena have been derived from the huge assemblage of large mammals preserved at the site, the taphonomic characteristics of the scarce fossil record of birds provide additional information. As noted above, all avian remains are unweathered and unabraded, which suggests that the time elapsed until their burial was very short. Despite that, half of these remains show evidence of digestive corrosion and/or pits and scores produced by the teeth of small to medium-sized carnivores, most probably the juvenile hyaenas or the jackal-sized wolf *Canis orcensis* (Martínez-Navarro et al. 2021; Palmqvist et al. 2023b). Moreover, we cannot discard that ravens participated in the consumption of the bird remains, although no taphonomic evidence indicates their involvement.

Finally, despite the low quantity of avian remains preserved and their low preservational integrity, the identification of at least three avian taxa in this study provides new clues on the palaeoenvironments of the Baza Basin during the late Early Pleistocene and the interactions among the members of the faunal palaeocommunity that inhabited it.

Palaeoenvironmental implications of the avian remains from Venta Micena

Evidence from the composition and geochemistry of the sedimentary deposits, as well as from the presence of fossil invertebrates like molluscs (e.g., the gastropods *Bithynia tentaculata* (Linnaeus, 1758), *Hydrobia acuta* (Draparnaud, 1805), *Melanoides tuberculata* (Müller, 1774), and *Gyraulus laevis* (Say, 1817); the bivalve *Euglesa casertana* (Poli, 1791), and ostracods *Candona* Baird, 1845 sp. and *Cyprideis torosa* (Jones, 1850)) indicate that the Baza Basin was home to an extensive (~1,125 km^2) and permanent palaeolake during the Early Pleistocene with oligosaline (3–5‰) waters, which was surrounded by a wide, emerged plain with fresh water ponds. This palaeolake was subject to seasonal variations in the water table between the dry and rainy seasons (Anadón et al. 1994; García-Aguilar et al. 2013, 2024; Albesa and Robles 2020; Granados et al. 2021; Palmqvist et al. 2022b). Such a wetland environment is also evidenced in Venta Micena by the presence of the giant, fully aquatic hippo (*Hippopotamus antiquus*), a species that fed exclusively on submerged vegetation according to isotopic biogeochemistry (Palmqvist et al. 2003, 2008a, 2008b, 2022d).

A similar palaeoenvironment was proposed for Huéscar-1, a site from the Baza Basin dated to the Early-Middle Pleistocene (Epivillafranchian) boundary (Ros-Montoya et al. 2018), which preserves a rich fossil avifauna dominated by waterfowl (Sánchez-Marco 1989). The ornithological palaeocommunity of Huéscar-1 includes fourteen bird species of Anatidae (*Anas crecca* Linnaeus, 1758/ *Spatula querquedula* (Linnaeus, 1758), *A. platyrhynchos* Linnaeus, 1758, *S. clypeata* (Linnaeus, 1758), *Mareca strepera* (Linnaeus, 1758), *Anas* Linnaeus, 1758 sp., *Netta rufina* (Pallas, 1773), *Aythya farina* (Linnaeus, 1758), *Ay. nyroca* (Güldenstädt, 1770), *Ay. fuligula* (Linnaeus, 1758), and *Aythya* Boie, 1822 sp.), Podicipedidae (cf. *Tachybaptus ruficollis* (Pallas, 1764)), Phasianidae (*Perdix perdix* (Linnaeus, 1758)), Rallidae (*Crex crex* (Linnaeus, 1758)), and Strigidae (*Bubo bubo* (Linnaeus, 1758)) (Sánchez-Marco 1989). Of these species, 78.6% are aquatic, which agrees with the presence of an extensive wetland environment in the Baza Basin during most of the Plio-Pleistocene, when the basin was subject to endorheic drainage (Palmqvist et al. 2022b; García Aguilar et al. 2024). The presence in Venta Micena of the Common Shelduck (*T. tadorna*) and a large crane (*G.* cf. *primigenia*) in the Early Pleistocene of the Baza Basin is consistent with the wetland habitats preferred by these species in the present (Archibald et al. 2020a; Carboneras and Kirwan 2020).

The extensive wetland of the Guadix-Baza Depression disappeared to a large extent during the Middle Pleistocene (earlier than ~600 ka: García-Tortosa et al. 2024) or in Late Pleistocene times (100–17 ka: Calvache and Viseras 1997; 42 ka: Azañón et al. 2006), when the basin hydrographic network was captured by the Guadiana Menor River, a tributary of the Guadalquivir River. This led to the transition to an exorheic regime, in which erosion dominated over sedimentation. As a result, a badlands landscape predominates now in the sedimentary depression, linked to a mean annual precipitation (MAP) of only ~300 mm in its innermost part. However, climate was more humid during the late Early Pleistocene, with an estimated MAP of 830–940 mm for Venta Micena based on the δ^{15}N values measured in the bone collagen of large mammals (García-Aguilar et al. 2014; Palmqvist et al. 2022c).

Even today, when most of the sedimentary depression shows an exorheic character and rainfall is barely one-third of what it was during the late Early Pleistocene, there are some small salt marshes in the interior of the Baza Basin, which are fed by permanent emanations of groundwater and by the contribution of meteoric waters during the winter and spring seasons. This is the case of a semi-endorheic, hyposaline (~2.5 g/l) lagoon called El Baíco, which is situated at an elevation of 700 m asl between the towns of Baza and Benamaurel, showing a stable water table throughout the year colonized by halophilic vegetation (Orduña et al. 2010). The current extent of this wetland is very small, ~0.7 km^2, although it probably covered 2–5 km^2 at the beginning of the XIX century. Despite its limited extent, the wetland is regularly frequented in the rainy years by more than fifty bird species, many of which use it to breed, including ducks, wading birds, and even migrant flamingos (Fig. 9). Interestingly, *T. tadorna* (occasionally) and *G. grus* (more frequently) have been observed wintering in El Baíco (José A. Rodríguez, pers. comm.). From the sixties onwards this lagoon has been artificially desiccated with drainage channels, locally called ‘sangradores’ (bleeders), which discharge in the Baza River a water flow of ~1,000 l/s. Moreover, attempts have been made to level the lagoon basin with soil from the surrounding hills, with the intention of making the land suitable for agricultural use. For this reason, presently, the wetland of El Baíco is only naturally recovered during the wet season of the rainiest years, being a crypto-wetland (i.e., a place where the water sheet is very small and temporary, but the water level in the subsoil is close to the surface; see Orduña et al. 2010) most of its surface during regular years. The diversity of birds that today inhabit this small wetland suggests that the few species identified at the fossil site of Venta Micena represent only a very small sample of the rich avifauna that inhabited the lacustrine and marshy environments of the Baza Basin during late Early Pleistocene times, when the extent of the lacustrine system exceeded 1,100 km^2 (Palmqvist et al. 2022b).

The living populations of Common Shelduck and Eurasian Crane of the Iberian Peninsula are formed by wintering individuals coming after breeding in North Europe, except for a small contingent of resident individuals of *T. tadorna* (Román 2019; Robledano 2022). However, the scarce avian specimens preserved at Venta Micena, a site in which the accumulation of bones by hyaenas occurred during the dry season of several consecutive years (Palmqvist et al. 2011, 2022a), suggests the presence of breeding populations of *T. tadorna* and *G.* cf. *primigenia* in the ancient basin.

The finding of *T. tadorna* at Venta Micena also supports the presence of marshy environments with euryhaline waters in the surroundings of the Baza palaeolake. The reason is that modern populations of Common Shelduck live in coastal mudflats and lagoons, estuaries and riverine environments linked to salt or brackish waters, where they mainly feed on aquatic invertebrates (i.e., molluscs, insect larvae, and small crustaceans), with special predilection for the saltwater snail *Peringia ulvae* (Pennant, 1777) (Carboneras and Kirwan 2020), an euryhaline species that can survive in waters with salinities up to 39‰ (Britton 1985). Mollusc shells are scarcely preserved in VM3, including *B. tentaculata* and *Stagnicola palustris* (Müller, 1774). In the nearby site of Barranco León, which is slightly younger than Venta Micena, molluscs are more abundantly preserved and include *H. acuta*, *B. tentaculata*, *M. tuberculata*, *S. palustris*, *G. laevis*, and *E. casertanum*. All these species are indicative of the presence of oligohaline (~3‰) to euryhaline (5–40‰) conditions in the lacustrine environments of the Baza Basin (Albesa and Robles 2020; Palmqvist et al. 2022b). As explained before, these lacustrine systems were fed by alluvial inputs from meteoric waters and by contributions from thermal springs. In the surrounding marshy areas, which were subject to more intense evaporation, salinity values would be higher (García-Aguilar et al. 2014, 2024; Granados et al. 2021; Palmqvist et al. 2022b). Moreover, the finding in Venta Micena of ostracods *Ilyocypris bradyi* Sars, 1890 and *I. gibba* (Ramdohr, 1808) provides additional information on the palaeoenvironment: The former species is typical of high-energy streams with abundant underwater vegetation, which would correspond to the rainy season, while the latter lives on shallow lake shores with warm, fresh to oligohaline waters, a sandy substrate, and lush vegetation (Granados et al. 2021; Palmqvist et al. 2022b).

Finally, the Eurasian Crane *G. grus* has resident populations throughout northern Europe and Asia, as well as in Turkey and the Caucasus, nesting in a wide variety of shallow natural and artificial wetlands, including wooded swamps (especially birch and alder), sedge meadows, and peat bogs (Archibald et al. 2020a). Throughout their winter range, they forage in agricultural fields and pastures. In the Iberian Peninsula and northern Africa, the Eurasian Crane is a wintering species (Román 2019), as recorded every year in the Baza Basin (Román, 2019; José Ángel Rodríguez, pers. comm.). According to Díaz et al. (1996), most of the western European crane population winters in the “dehesas” of the Iberian Peninsula, which are former wooded pastures composed of grasslands, cereal crops, and Mediterranean scrub, densely interspersed with Holm Oak (*Quercus ilex* L.) in a savanna-like landscape, where cranes feed on fruits, seeds, fish, insects, and snails (see also Franco et al. 2008). Everywhere, feeding is diurnal and flocks roost at nearby wetlands or other shallow waters. Undisturbed wetlands not impacted by hunting and sufficiently distant from human activities are primarily selected as roost-sites (Végvári and Barta 2015). This represents an open wetland habitat with tree patches like that inferred for Venta Micena from the palaeosynecological analysis of the large mammal fauna (Mendoza et al. 2005; see also Pla-Pueyo and Gierlowski-Kordesch 2025). In addition, a study by Boisseau and Yalden (1998) of place names of England that included some reference to cranes showed that more than half of these names were associated with other water-related toponymic elements

Figure 9. 'El Baíco' wetland in the Baza Basin during the spring of 2010, a very rainy year. **A.** Photograph showing a couple of Black-winged Stilts (*Himantopus himantopus* (Linnaeus, 1758)) at the left of the image, a Little Egret (*Egretta garzetta* (Linnaeus, 1766)) at the centre, and three specimens of Cattle Egret (*Ardea ibis* (Linnaeus, 1758)) at the right; **B.** View of a group of Greater Flamingos (*Phoenicopterus roseus* Pallas, 1811). Photographs kindly provided by José Ángel Rodríguez.

(e.g., rivers, springs, pools, marshes, lakes, moors, and flood plains), which represents indirect evidence for the historical association of cranes with aquatic habitats in the past environments, less affected by human activity than at present. Although the food and habitat preferences of the extinct Giant Crane (*G.* cf. *primigenia*) are unknown, they were likely broadly analogous to those of extant cranes —i.e., opportunistic omnivores typically associated with wetlands— within Pleistocene landscapes.

Wetlands have played an important role in providing resources for hominins in the ecosystems in which they lived. Not surprisingly, the relationship between ancient human populations and wetlands has been documented in many archaeological sites, including those of the Olduvai Gorge in Tanzania and the fluvio-lacustrine sites of the Guadix-Baza Depression in Spain (see review in Pla-Pueyo and Gierlowski-Kordesch 2025). During the late Early Pleistocene, annual rainfall in the Baza Basin (~900 mm) was higher than today (~300 mm) and the combination of a rainier climate with a more intense hydrothermal activity favoured the presence of extensive wetlands in the basin (García-Aguilar et al. 2014, 2015, 2024; Palmqvist et al. 2022b, 2022c).

Palaeosynecological implications of the avian remains from Venta Micena

Most avian remains from Venta Micena show alterations that evidence the consumption of these birds by predators (Fig. 8). Evidence of digestive corrosion is present, in varying degrees, in most bones of *T. tadorna*, *C. c. antecorax*, and Aves indet., although it hardly allows identifying the agents responsible of such alterations. In contrast, the pits and scores found in the diaphyses of the ulna and femur of *T. tadorna*, as well as the probable tooth mark in the ulna of *G.* cf. *primigenia*, indicate that they were produced by a small to medium-sized carnivore. Palmqvist et al. (2023b) hypothesized that these types of pits and scores might have been produced by juvenile hyaenas, whose milk teeth are sharper, more feloid in shape than those of adults, and their nibbling of bones results in abundant tooth marks, as confirmed at the site of Dmanisi in Georgia (Martínez-Navarro et al. 2025). Following this reasoning, although the involvement of other small to medium-sized carnivores present at Venta Micena like the canid *C. orcensis* (Martínez-Navarro et al. 2021) cannot be discarded (Palmqvist et al. 2023b), the producers of the small tooth marks were most probably juvenile hyaenas (however, in a recent study most tooth marks from VM3 are interpreted as from adult hyaenas; see Yravedra et al. 2025). Regardless of the specific predator, the tooth marks and digestive marks found in these remains indicate that shelducks and cranes were preyed and/or scavenged by carnivorous mammals in Venta Micena, contributing as a previously unknown source of food for this guild of the Baza Basin during Early Pleistocene times. This agrees with observations of modern Spotted Hyaenas, which have occasionally been seen predating on birds (Kruuk 1972; Holekamp et al. 1997; Nasirwa 2000; Portas and Krofel 2024).

The finding of raven cf. *C. corvus antecorax* in Venta Micena adds a new agent in the competition for meat resources among the members of the carnivore guild. Ravens consume small vertebrates and invertebrates, as well as variable amounts of seeds and grains, and are opportunistic scavengers of animal carcasses (Boarman and Heinrich 2020). Modern North American populations track wolf packs, being ubiquitously present at carcasses killed by wolves (Hayes et al. 2000; Stahler et al. 2002) —an adaptive strategy when other resources are scarce, particularly in winter (Vucetich et al. 2004). The Pleistocene raven *C. c. antecorax* co-occurred with a pack hunting canid in Venta Micena, *X. lycaonoides* (Palmqvist et al. 1999). Moreover, the presence of other large-sized predators (e.g., the sabretooths *H. latidens* and *M. whitei*, and the jaguar *P. gombaszoegensis*) and the scavenging hyaena *P. brevirostris* indicates that the meat available in the Baza Basin during Early Pleistocene times was not scarce (Palmqvist et al. 2003, 2008a, 2008b, 2010, 2022b). Individuals of *C. c. antecorax* could have fed on carcasses of medium to large-sized ungulates hunted by these predators, as well as on smaller prey caught by medium-sized carnivores like *C. orcensis* and *Lynx* cf. *pardinus* (Temminck, 1827) (e.g., lagomorph *Oryctolagus* Lilljeborg, 1873 spp.; Agustí et al. 2010). This would have allowed a year-round population of *C. c. antecorax* in the Baza Basin during the Early Pleistocene —modern ravens are resident in almost all terrestrial biomes of the northern hemisphere (Boarman and Heinrich 2020)— thus adding a new competitor for meat into the food web of Venta Micena. Indeed, the digestive marks on the humerus of *C. c. antecorax* from VM3 (Fig. 8I) evidence that this individual was consumed by a predator.

The impact of competition between ravens and terrestrial carnivores is not anecdotal, as they scavenge substantial amounts of wolf-killed prey (Hayes et al. 2000) and are strong competitors for large mammal carcasses (Kaczensky et al. 2005). Specifically, it has been estimated that while wolves are feeding on a carcass, they routinely lose 2–20 kg of food per day to ravens (Vucetich et al. 2004), with some groups reaching 37 kg of daily losses (Promberger 1992). A small wolf pack can lose up to 75% of an ungulate carcass due to scavenging by ravens (Kaczensky et al. 2005). This impact varies with pack size, being strikingly lower for large wolf packs, because some wolves are always present at the kill site and actively chase away ravens. As a result, although wolves living in large packs suffer reduced foraging returns, the loss of food to scavenging ravens may have been behind the evolution to greater sociality and larger pack size in wolves (Vucetich et al. 2004).

How did the raven population of Venta Micena affect the meat resources available for the carnivore guild? According to our palaeosynecological model PSEco, the population of *C. c. antecorax* of Venta Micena would have also had a noticeable impact on the availability of meat resources (Fig. 10). As indicated before, given the adult body mass, population density, and daily meat consumption in winter and summer of modern ravens, the estimate of their yearly meat demands is 125 kg per km^2. In contrast to this estimate, PSEco calculated an average annual consumption by ravens

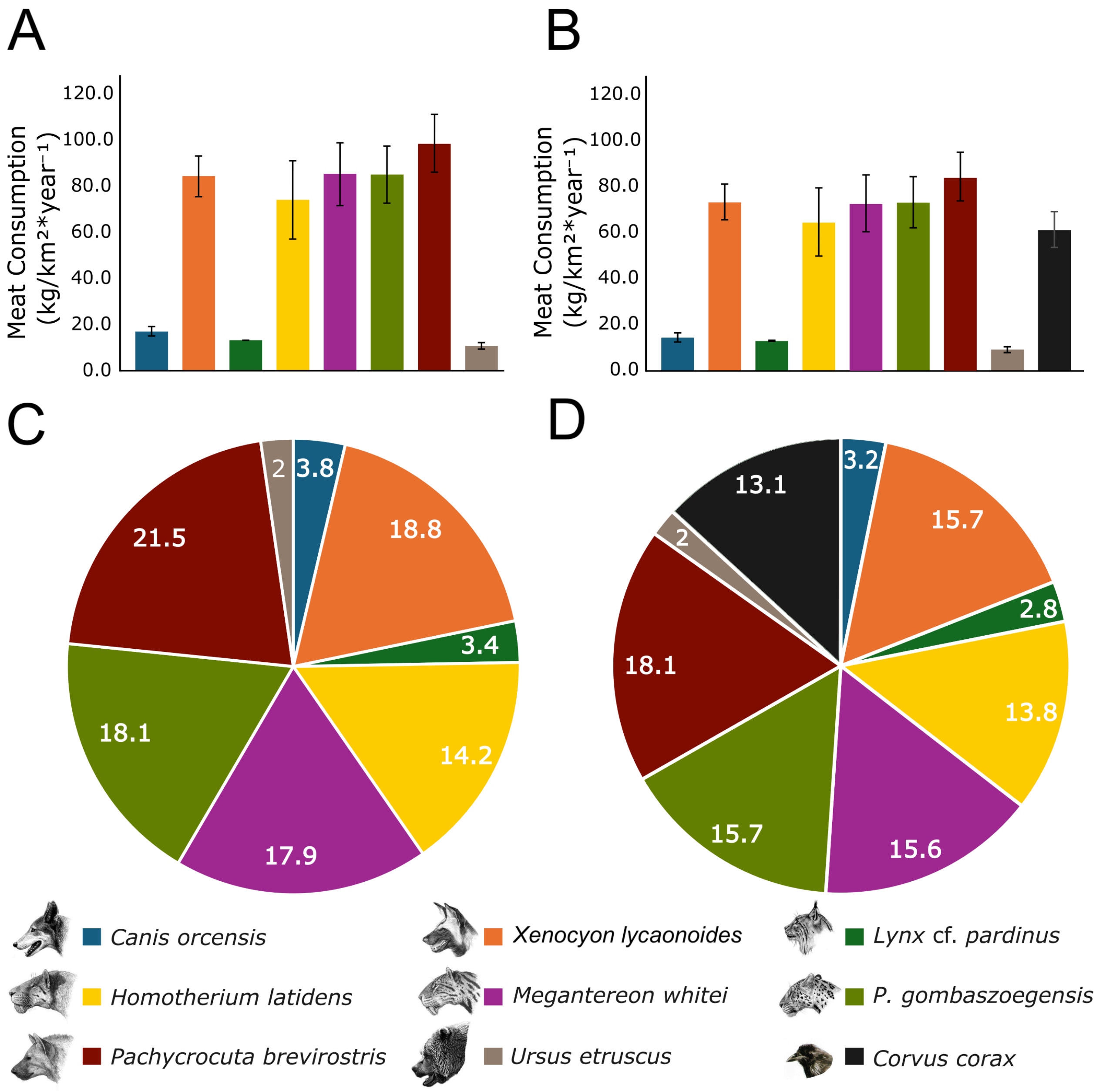

Figure 10. Distribution of meat consumption and consumption percentages by the members of the carnivore guild of Venta Micena (**A, C**, respectively; data from Rodríguez-Gómez et al. 2017) and the corresponding values when a population of common raven is included in the model (**B, D**). The estimates of available meat (Total Available Biomass, TAB) to the secondary consumers were obtained using the PSEco palaeoecological model (see Materials and Methods), based on the average mortality profiles of different prey species. The consumption ranges shown in **A, B** reflect the minimum and maximum estimates of available meat (TAB-min and TAB-max).

of 62 kg of meat per km^2, a figure which is approximately half of their demand under optimal ecological conditions. This value represents 13.2% of the total biomass of ungulates available to the carnivores of the VM palaeocommunity, which was estimated by Rodríguez-Gómez et al. (2024b) as 468 kg/km^2. The percentage of meat consumption by ravens is only 1–5% lower than the estimates obtained for the main large carnivores of the site (e.g., *P. brevirostris*, *H. latidens*, *M. whitei*, *P. gombaszoegensis*, and *X. lycaonoides*), and 4–5 times higher than those of other secondary consumers (e.g., *C. orcensis*, *Lynx* cf. *pardinus*, and *Ursus etruscus* Cuvier, 1823). These results indicate that the presence of ravens would imply that a lower proportion of meat would be available to each of the other secondary consumers (Fig. 10), which would affect their population densities. For example, in the case of the hyaena *P. brevirostris* the decline in consumption from 21.0% to 18.1% would imply that the population density of hyaenas, estimated previously as 6 individuals per 100 km^2 by Rodríguez-Gómez et al. (2017), would decrease to 5 individuals per 100 km^2 (i.e., a decrease of 17%).

Our PSEco model is based on the biomass provided by ungulates —the main source of biomass of primary consumers in Venta Micena— and does not include other

Figure 11. New reconstruction of the wetland environments of Venta Micena during the late Early Pleistocene, illustrating the avian taxa described in this study—*Tadorna tadorna* (foreground left), *Grus* cf. *primigenia* (foreground right), and *Corvus corax antecorax* (in flight above)—together with the giant hyena *Pachycrocuta brevirostris*, two individuals of elephant *Mammuthus meridionalis* (background center), and a group of horses (*Equus altidens*) in the background to the left. Illustration by O. Sanisidro.

potential foods typically consumed by ravens (e.g., small vertebrates and invertebrates, seeds and grains; Boarman and Heinrich 2020). This means that our value of meat consumption by ravens could be somewhat overestimated. However, the high percentage of meat consumption obtained with the model is robust enough to consider that ravens played a significant role in the competition for resources within the guild of secondary consumers of the Baza Basin during the Early Pleistocene.

Palaeosynecological modeling indicates that *C. c. antecorax* played a significant scavenging role, exerting a noticeable impact on the carnivore guild by competing for meat resources with the large mammalian carnivores and particularly with the hyaena *Pachycrocuta brevirostris*. Altogether, the avian evidence reveals a more complex structure of trophic interactions at Venta Micena than previously recognized, in which birds contributed significantly to the ecological dynamics of the lacustrine ecosystem during Early Pleistocene times (Fig. 11), resembling patterns observed in modern wetland environments.

Conclusions

At least three avian taxa were identified from Venta Micena, including the Common Shelduck *Tadorna tadorna*, a large crane interpreted as *Grus* cf. *primigenia*, and the Pleistocene subspecies of the Common Raven *Corvus corax antecorax.* If our tentative assignment for the identification of the Giant Crane proves correct, this record of *G.* cf. *primigenia* would represent the oldest occurrence of large cranes in Europe, while *C. corax antecorax* is the oldest occurrence of this raven in the Iberian Peninsula. The presence of shelducks and cranes supports the existence of a wetland environment with brackish waters and a mild climate in the Baza Basin during the Early Pleistocene. These two taxa (as well as *C. c. antecorax*) and others classified here as Aves indet. were predated by the carnivores of Venta Micena, contributing to the availability of meat resources within the ecosystem.

Acknowledgements

We thank Manuel Ramos (Archaeological Museum of Granada, Spain), Juan F. Pastor (University of Valladolid, Spain) and Diana Ríos (MNCN, Madrid, Spain) for providing access to the collections under their care. We also thank Nikita Zelenkov and Antonio Sánchez-Marco for their help in the identification of the fossils studied in this paper. Gala Gómez-Merino and Ainhoa Rodríguez-Rueda restored the avian fossil specimens from excavation quarry VM4 of Venta Micena. Last but not least, we gratefully acknowledge the insightful comments and suggestions provided by reviewer Federico Javier Degrange and an anonymous reviewer, as well as from editor Analía Forasiepi.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

Funding

This research was funded by PAIDI research group RMN-456 (Junta de Andalucía), Projects CNS2023-145050 (F.J. Serrano) and PID2024-155435NB-I00 (O. Sanisidro) of the Spanish Ministry of Science, Innovation and Universities, Spanish Ministry of Science and Innovation through a "María de Maeztu" excellence accreditation (CEX2024-01485-M/funded by MICIU/AEI/10.13039/501100011033) (CEX2019-000945-M) and Generalitat de Catalunya, 2021SGR 01238 (AGAUR), Comunidad de Madrid and Universidad Complutense de Madrid (Ref. PR27/21–004) through a postdoctoral grant 'Atracción de Talento Investigador César Nombela' to G. Rodríguez-Gómez (Ref. 2023-T1/PHHUM-29222).

Author contributions

Conceptualization (FJS, PP), data curation (FJS, GR-G, JCT), formal analysis (FJS, MPE, GR-G), funding acquisition (FJS, BM-N, PP), investigation (FJS, MPE, GR-G, PP), methodology (FJS, MPE, GR-G), project administration and supervision (FJS, BM-N, PP), visualization (FJS, MPE, GR-G, SR-M, JCT, OS), writing – original draft (FJS, PP), writing – review and editing (all authors).

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary information

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Data type: xlsx

Explanation note: Measurements taken on modern specimens of Gruiformes and Anseriformes: anteroposterior diameter at midshaft, Ulna (mm); maximum length, Ulna (mm); dorsoventral width of distal epiphysis, Humerus (mm).

Link: https://doi.org/10.3897/sjp.145.182523.suppl1