BIRDS FROM SIMA DEL ELEFANTE, ATAPUERCA, SPAIN: PALAEOECOLOGICAL IMPLICATIONS IN THE OLDEST HUMAN BEARING LEVELS OF THE IBERIAN PENINSULA

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Abstract. Palaeoenvironmental reconstruction of Early Pleistocene sites has a particular interest as it sheds light on how the arriving of the first Europeans occurred, as well as on the nature of the relation between these humans and the ecosystems. Bird remains are useful tools for this purpose, because they are commonly represented in the assemblages and most taxa still exist, allowing a direct comparison between past and extant birds associations. Here we analyse the bird remains from the Early Pleistocene levels of the Sima del Elefante site (1.1 to 1.5 million years old). Almost 10.000 remains belonging to at least 26 different taxa have been included. The assemblage is dominated by corvids and has a mixed origin, with cave-dwelling taxa dying in the cave and other taxa being accumulated by predators. The Sima del Elefante avian assemblage provides the oldest record of several taxa in the Iberian Peninsula (*Haliaeetus albicilla*, *Corvus pliocaenus*). Besides, here we report the oldest evidence of Imperial Eagle in the Iberian Peninsula, prior to the separation of the oriental and Iberian populations. The assemblage composition suggests that open environmental conditions were dominant, with minor presence of woodlands and water bodies, which is congruent with some previous approaches by other proxies. The first humans occupying the Iberian Peninsula inhabited under Mediterranean climate conditions, which gradually deteriorated, as reflected by the avian turnover recorded at the middle Pleistocene Atapuerca assemblages.

INTRODUCTION

The archaeological and palaeontological sites of the Sierra de Atapuerca, located in Burgos (Spain) (Fig. 1a), are widely known for their com-

plete Quaternary archaeological and palaeontological record, which covers nearly one and a half million years of the Earth History and human evolution (Carbonell et al. 1995, 2008; López-García et al. 2010; Rodríguez et al. 2011; Arsuaga et al. 2014; Cuenca-Bescós et al. 2015, 2016; Expósito et al. 2017). Some of the caves that conform the At-
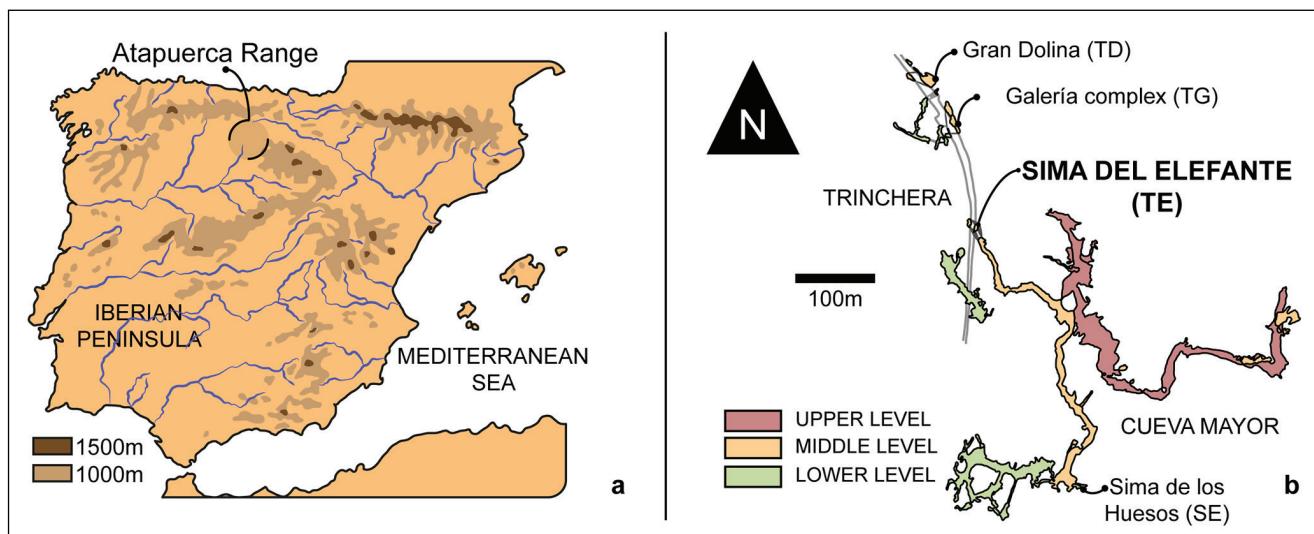
Fig. 1 - Geographical context of the Atapuerca Sites Complex. A) Geographical location of the Atapuerca Range in the Iberian Peninsula. B) Schematic map of Las Torcas Karstic System (modified from Ortega et al. 2013).

apuerca karst complex yield internationally known sites, as Gran Dolina, Galería, Sima de los Huesos and Sima del Elefante. The Sima del Elefante cavity contains the oldest sediment-infill of the Atapuerca complex. The fossil birds recorded there are the object of this work. Some of the Atapuerca cave-sites became exposed thanks to the construction of a railway trench in the XIX century. All these caves belong to the Las Torcas Karstic System, developed in three stages corresponding with three recognized karstic levels. Sima del Elefante belongs to the middle level, the Cueva Mayor complex (Fig. 1b), and the cavity used to be an underground water exit point (Ortega et al. 2013).

What has made this site a worldwide known one are the human remains and lithic industry that have been recovered in the level 9 of this site (Carbonell et al. 2008; Huguet et al. 2013, 2017; Lorenzo et al. 2015; de Lombera-Hermida et al. 2015). The fossil human remains consist of an incomplete mandible with some teeth and a phalanx, assigned to the species *Homo* sp., and dated as 1.2-1.1 million years (Carbonell et al. 2008; Bermúdez de Castro et al. 2011). Also, thousands of small-vertebrate fossil remains have been recovered from the Sima del Elefante sediment, including mammals, reptiles, amphibians and birds (Blain et al. 2011; Cuenca-Bescós et al. 2001, 2010, 2013, 2015; Galán et al. 2016, 2019a).

The fossils of birds in Pleistocene sites appear mainly as bones or eggshells, that is, as direct remains. Also, they play an important rol as accumulator agents of small vertebrates, notably small mammals (Andrews 1990; Laroulandie 2002; Bochenski 2005). Bird remains from the Atapuerca sites have been extensively studied (Sánchez-Marco 1987, 1995, 1999a, 1999b; Núñez-Lahuerta et al. 2016, 2019) and, according to Sánchez-Marco (2018), the most updated faunal list from levels TE7 to TE14 of the Sima del Elefante (Early Pleistocene) is: *Anas* sp., *Haliaeetus albicilla*, *Falco tinnunculus*, *Palaeocryptonyx donnezani*, *Bonasa nini*, *Perdix palaeoperdix*, *Coturnix coturnix*, *Columba livia/oenas*, *Carduelis chloris* and *Corvus antecorax*. Remarkably, the species *Bonasa nini* has been described on the basis of a tibiotarsus recovered in this site (Sánchez-Marco 2009). The objective of this work is to analyze a new set of avian samples recovered in the Sima del Elefante lower levels, different of those remains analyzed previously by other authors, in order to draw an updated paleoenvironmental picture of the area in which the oldest known inhabitants of the Iberian Peninsula appeared.

Sima del Elefante

The Sima del Elefante, from now labelled TE (capital letters of the Trinchera Elefante, T is for sites of the Trinchera, meaning railway trench, in the Sierra de Atapuerca, and E for Elefante), is a colmated cave with a 25 m deep, 15 m wide sediment infill. A section of the infilling is exposed in the railway trench. This infilling is divided into 16 stratigraphic

Fig. 2 - Synthetic stratigraphic column of the Sima del Elefante site. Modified from Carbonell et al. 2008. Age data from Parés et al. 2006; Van der Made 2001; Rosas et al. 2006; López-García et al. 2011; Arnold & Demuro 2015; Cuenca-Bescós et al. 2015; de Lombera-Hermida et al. 2015. NISP: Number of identified specimens.
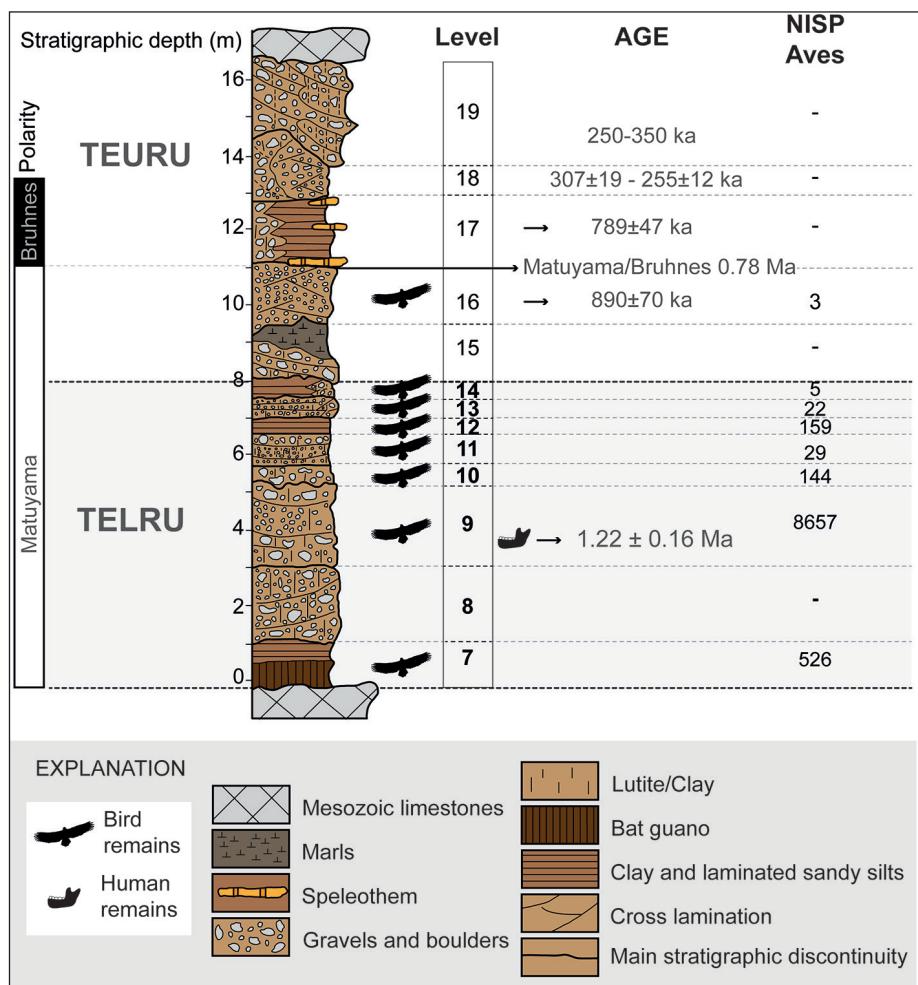
units, named TE7 to TE21 from the oldest to the most modern (Rosas et al. 2006; Huguet et al. 2017) (Fig. 2). The original entrance of the cave during the accumulation of the levels had probably a fissure configuration (Rosas et al. 2006).

The stratigraphic layers in Sima del Elefante are divided into three main sedimentary phases. The oldest phase comprises layers TE7 to TE14 and is called TELRU (Trinchera Elefante Lower Red Unit). The intermediate phase covers layers TE15 to TE19 and is called TEURU (Trinchera Elefante Upper Red Unit). Finally, the upper phase covers layers TE20 and TE21 (Rosas et al. 2006; Carbonell et al. 2008; Cuenca-Bescós et al. 2010, 2016).

The TELRU layers (TE7 to TE14) have allochtonous origins, they were formed as a result of the entry of sediments from the slopes and exterior of the cave. The layers are inclined towards the north, but the slope softens through the upper units. TE9 and TE10 are conformed by gravitational clays forming a cone (Rosas et al. 2006), and the uppermost part of the level TE10 shows a change to a hy-dric regimen (Rosas et al. 2004). These TELRU layers are the object of this work.

The palaeomagnetic analyses show a change in the polarity in the base of the TE17 unit. The lower levels have reverse polarity and have been assigned to the Matuyama Chron, so they are older than 780 ka. Sublevel TE9c has been dated by biostratigraphy, palaeomagnetism and cosmogenic isotopes, yielding an age between 1.3 and 1.1 million years (Parés et al. 2006; Carbonell et al. 2008; Huguet et al. 2017). Units TE7 to TE14 represent the interval between 1.5 and 1.1 million years (Cuenca-Bescós et al. 2001, 2013; Cuenca-Bescos & García 2007). The small mammal assemblage of these levels belongs to the biozone *Allophaiomys*, before the Jaramillo subchron (Cuenca-Bescós et al. 2015, 2016). The ages for the TE16 and TE17 levels have been obtained by TT-OSL, with 789±47 and 890±70 respectively (Arnold & Demuro, 2015). A uranium series (U/Th) analysis of two travertine samples from the roof of level TE18 has yielded two dates, 307 ± 19 ka and 255 ± 12 ka (de Lombera-Hermida et al. 2015) and the

biochronological analysis allowed the attribution of the units TE18 and TE19 to the Middle Pleistocene (250-350ka, OIS9-8) (Van der Made 2001; Rosas et al. 2006; López-García et al. 2011). These results suggest that the chronology of TE19 would be more recent than 255 ka (OIS 7) (Huguet et al. 2017).

The faunal association identified in the Sima del Elefante site also brings biochronological information. Plio-Pleistocene and lower Pleistocene taxa have been recovered at the TELRU section of the site. Rodents and insectivores show primitive conditions comparing with other 1 million-year sites. The first lower molars of the Arvicolinae rodent *Allophaiomys lavocati* recovered in Sima del Elefante show a similar morphology to those in the sites of Fuente Nueva 3 (Spain) or Pirro Nord (Italy), both sites in the same biozone than TELRU (Cuenca-Bescós et al. 2010). Vallaparadis, a site in eastern Spain with a slightly younger chronology, presents some similar faunas as *Allophaiomys lavocati*, though it differs in others (Minwer-Barakat et al. 2011; Cuenca-Bescós et al. 2016). A Plio-Pleistocene carnivore, *Pannonictis nestii,* has been recovered in TELRU, with a similar morphology to the remains of the same species recovered in the Italian site of Pietrafitta, 1.4 ma old (García et al. 2008). Also, the evolution of the insectivorous association points to a warm and wet climate, with some temperature variations (Carbonell et al. 2008).

Material and methods

The material included in this work consists of unpublished bird fossil remains recovered from the TELRU sections (levels TE7 to TE14) during the field campaigns performed since 1998. The remains have been photographed using a photo camera Sony α100 and measured using a digital caliper (Mitutoyo Digimatic Caliper CD-8^CX) and the software ImageJ.

Systematic palaeontology

The anatomical nomenclature follows Baumel & Witmer (1993). The osteological analysis of Woolfenden (1961), Woelfle (1967), Kraft (1972), Fick (1974), Gilbert and collaborators (1985), Jánossy (1983a), Moreno (1985), Solti (1980, 1981, 1996), Tomek and Bochenski (2000, 2009), Wójcik (2002) and Bochenski and Tomek (2009) have been used to

identify the remains. The reference collections used were those from the Laboratorio de Arqueociencias de Lisboa (LARC) and the Estación Biológica de Doñana (EBD).

For the revision of the paleontological record of the identified taxa the synthesis works of Mlíkovský (2002), Tyrberg (1998), Hernández-Carrasquilla (1993, 1994) and Pimenta and collaborators (2015) have been used.

The laboratory work was carried out in the Centro Nacional de Investigación sobre Evolución Humana (CENIEH) and in the Institut Catalá de Paleoecologia Humana i Evolució Social (IPHES), Universidad de Zaragoza (UNIZAR) and Museo de Ciencias Naturales de la Universidad de Zaragoza (MCNUZ) facilities. The material is stored in the CENIEH and IPHES facilities.

Paleoenvironmental reconstructions

For the paleoenvironmental reconstruction the Habitat Weighting method has been used (Evans et al. 1981; Andrews 2006), following the modifications proposed by Rodríguez et al. (2011). Four main habitats have been distinguished: Wooden (WO), Open Humid (OH), Open Dry (OD) and Water Areas (WA). The reason of the utilization of this modification is to compare the obtained results with those of the works that cover the Sima del Elefante sequence for several faunal groups (Blain et al. 2010; Rodríguez et al. 2011; Galán et al. 2016). For the scores, the data from the extant representatives of each taxa have been used.

Abbreviations

TE-Trinchera Sima del Elefante; TELRU- Trinchera Sima del Elefante Lower Red Unit; MNI-minimum number of individuals; NISP-number of identified specimens; MNE-minimum number of elements.

COR-coracoid; SCA-scapula; RAD-radius; HUM-humerus; ULN-ulna; CMC-carpometacarpus; Fem-femur; TBT-tibiotarsus; TMT-tarsometatarsus; CRA-cranium; MAN-mandible; VER-vertebra; PDA-phalanx digitorium majoris alae; PEL- pelvis; STE-sternum; PHA-pedal phalanx; P.UN-ungueal phalanx; QUA-os quadratum; FUR-furcula.

Results and discussion

We analyzed 9542 bird fossil remains. The fossils belong to at least 26 different bird taxa, from levels TE7, TE9, TE10, TE11, TE12, TE13 and TE14 of the TELRU Unit of the Early Pleistocene section of the Sima del Elefante site (Tab. 1).

	TE14	TE13	TE12	TE11	TE10	TE9a	TE9b	TE9c	TE9d	TE9e	TE9	TE7	TOTAL
Spatula clypeata								1					1
Anas crecca												1	1
Anatini indet.			2 (1)				1	2 (1)					5 (4)
Anseriformes indet						1		4			1	1	7
Coturnix coturnix			1									4 (1)	5 (2)
Palaeocryptonyx donnezani	1	1		1	4 (1)	2 (2)	3	37 (5)	1		1	1	52 (15)
Bonasa nini								2 (1)					2 (1)
Galliformes indet.						1		1	2			5	9
Columba livia	1	1			1			4(1)					7 (4)
Columba livia/oenas	1	3(2)			1			4(1)	1			1	11 (7)
Rallus aquaticus								3(2)					3(2)
Gallinula chloropus								1					1
Calidris sp.								1					1
Gallinago sp.							1	1					2 (2)
Charadriiformes indet.						1							1
Aquila cf. *heliaca/adalberti*						17 (2)		10 (2)	15 (1)				42 (5)
Aquila/Hieraaetus									5(1)				5(1)
Aquila sp.			2 (1)		2 (1)			1	9			1	15 (6)
Haliaeetus albicilla			4 (1)		4 (1)	1	25 (1)	78 (5)	7 (2)		6 (1)	27 (2)	152 (14)
Accipitridae indet.			4	1	14	7	4	34	19		2	10	95
Athene vallgornerensis							1	2			1		4 (3)
Falco tinnunculus		1						1					2 (2)
Falco rusticolus								1					1 (1)
Falco sp.												2 (1)	2 (1)
Corvus pliocaenus		11(1)	127(12)	24(2)	97 (7)	219(15)	135 (12)	868 (367	324(19)	25(2)	113(8)	218(16)	8161 (461)
Corvidae indet.		1	1		6	6		311	19		3	17	364
Paridae indet.								2					2
Alaudidae indet.												3	3
Turdus viscivorus/pilaris												2(2)	2(2)
Turdus philomelus/iliacus/merula												4(4)	4(4)
Turdus sp.		1	2				1	1					5 (4)
Muscicapidae indet.												1	1
Motacillidae indet.												2	2
Coccothraustes coccothraustes								1					1
Passeriformes indet.	2		16	3	7	5	5	46	3		2	85	174
Aves		3			8	13	5	221	4	2		141	397
TOTAL	5	22	159	29	144	273	181	7638	409	27	129	526	9542

Tab. 1 - Number of identified remains (NISP), and minimum number of individuals (MNI) in brackets of the birds recovered in each level of the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain.

The assemblage is dominated by Corvidae remains (Fig. 3a), followed by diurnal birds of prey (Accipitriformes and Falconiformes) and Columbiformes (Fig. 3b).

Most of the anatomical elements have been recovered and considered for study. Most of the remains appear complete in the site, nevertheless the characteristics of the sediments and the fragile nature of bird bones hampers the extraction, making almost impossible the extraction of complete bones.

Systematic palaeontology

Order **Anseriformes** Wagler, 1831
Genus *Spatula* Boie, 1822

Spatula clypeata Linnaeus, 1758
Fig. 4c

Material: TE9c, proximal humerus.

Description. In the humerus, the fossa pneumoanconea is open and well developed (Woolfenden 1961), and the crista deltopectoralis is relatively short (Bochenski & Tomek 2009). The morphology of the bone fits with a middle sized Anatini. The proximal width of the bone is 16.9 mm, and that fits with both *Mareca penelope* and *Spatula clypeata*. The position of the foramen pneumaticum, which is very proximal, allows the assignation of the bone to *Spatula clypeata* (Woefle 1967).

Remarks. The oldest record of *Spatula clypeata* comes from the Late Miocene of Čebotarevka, in Ukranie (Mlíkovský 2002). The Sima del Elefante site provides the oldest record of the taxon in the Iberian Peninsula, also present at the Early-Middle Pleistocene site of Huéscar (Sánchez-Marco 2002). *Spatula clypeata* inhabits margins of wetlands with submergent vegetation, and grasslands (Dubowy et al. 2020).
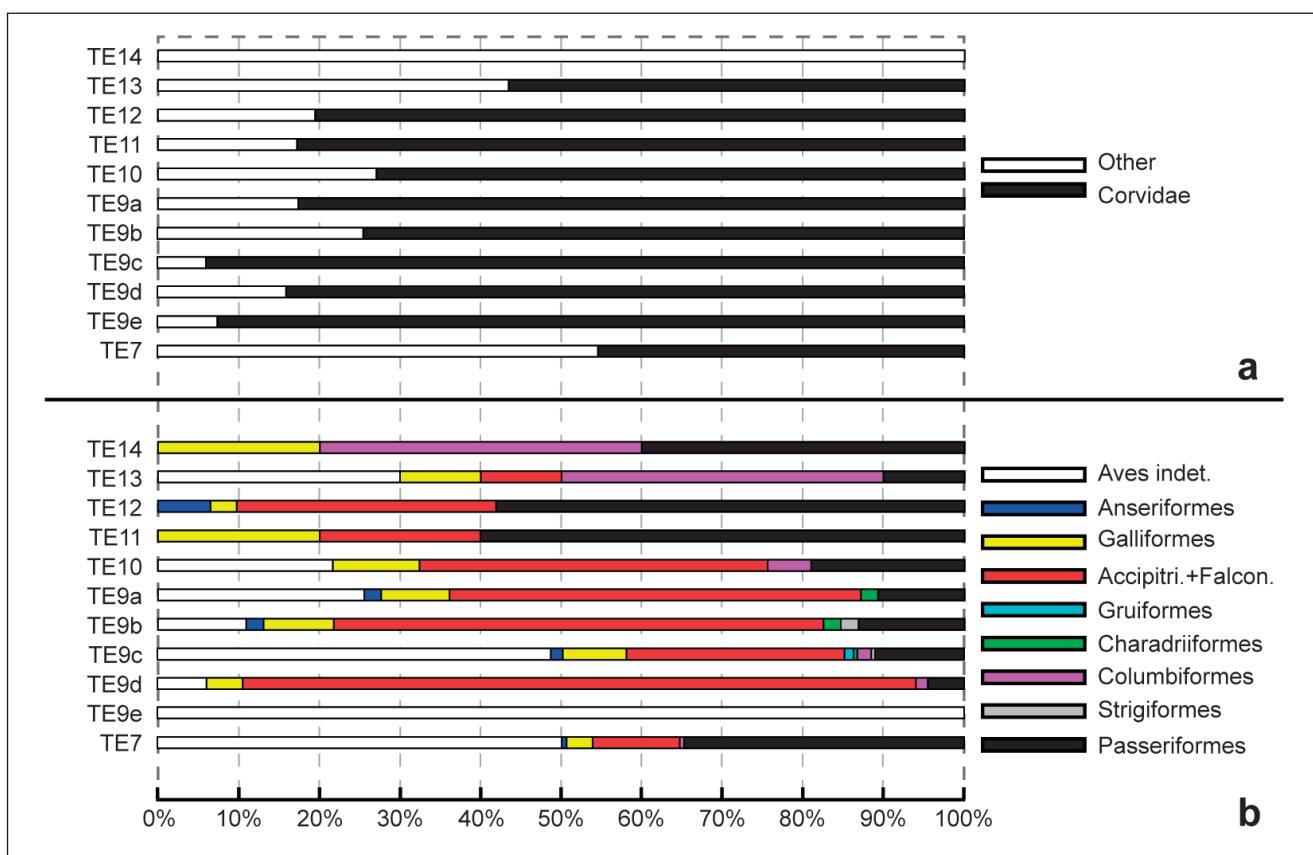
Fig. 3 - Relative abundance of the different groups of Aves identified in the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. a) Relative abundance of corvids within the whole assemblage; b) relative abundance among the non-corvid groups.

Genus *Anas* Linnaeus, 1758

***Anas crecca* Linnaeus, 1758**

Material: TE7, proximal humerus.

Description. The humerus shows an open and well-developed fossa pneumoanconea and a short crista deltopectoralis (Woolfenden 1961; Bochenski & Tomek 2009). The general morphology fits with an Anatini member. The proximal width of the bone (13.5 mm) fits both with *Spatula querquedula* and *Anas crecca*. The tuberculum dorsale is not highly developed, allowing the assignation of the bone to *Anas crecca*.

Remarks. *Anas crecca* is recorded in the Late Miocene of Sokolov in Ukranie (Mlíkovský 2002) and it is common in Pleistocene sites all over Europe (Tyrberg 1998). The Sima del Elefante site provides the oldest record of the taxon in the Iberian Península (Núñez-Lahuerta et al. 2016). It has also been cited in other sites of the Atapuerca complex, as in the Early Pleistocene of Gran Dolina and

the Middle Pleistocene of Galería (Sánchez-Marco 2004). *Anas crecca* inhabits a variety of habitats related preferably with eutrophic waters and herbaceous surroundings (Johnson et al. 2020).

Tribe **Anatini** Leach, 1820
Fig. 4b

Material: TE9c, distal carpometacarpus, proximal tarsometatarsus; TE9b, distal ulna; TE12, distal coracoid, distal ulna.

Description. The general morphology of the remains fits with a small sized Anatidae of the Tribe Anatini (Woelfle 1967). The coracoid lacks the coracoidal foramen, and the ventral edge of the facies articularis humeralis projects ventrally (Fig. 4b) (Gilbert et al. 1985). The proximal tarsometatarsus has four hypotarsal crests (Gilbert et al. 1985).

Remarks. The species of the tribe Anatini are linked to water bodies, mostly breeding on fresh water (Winkler et al. 2020).

Fig. 4 - Anseriform and galliform remains from the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. a) Anseriformes indet., premaxilar, dorsal view (TE9c); b) *Anas* sp., left coracoid, dorsal view (TE12); c) *Spatula clypeata*, right humerus, caudal view (TE9c); d) *Bonasa nini*, left tibiotarsus, cranial view (TE9c); e) *Coturnix coturnix*, left humerus, caudal view (TE12). *Palaeocryptonyx donnezani* remains: f) right coracoid, ventral view (TE9c); g) left humerus, caudal view (TE9c); h) right carpometacarpus, ventral view (TE9c); i) left femur, caudal view (TE10); j) right tarsometatarsus, dorsal view (TE9); k) left tarsometatarsus, dorsal view (TE9c); l) right tarsometatarsus, dorsal view (TE9a); m) left tarsometatarsus, dorsal view (TE10).

Anseriformes indet.

Fig. 4a

Material: (all partial remains), TE7, 1 remain; TE9, 1 remain; TE9c, 4 remains; T9a, 1 remain.

Remarks. The remains show the general characteristics of the Anseriformes, but the state of conservation hampers the assignation to the bones beyond the order level.

Order **Galliformes** Temminck, 1820
Genus *Coturnix* Garsault, 1764

Coturnix coturnix (Linnaeus, 1758)

Fig. 4e

Material: TE7, proximal humerus, distal humerus, two distal tarsometatarsi; TE12, complete humerus.

Description. The remains have the morphology of a small sized Phasianidae (Kraft 1972). They are smaller than the ones belonging to genus *Perdix* and only slightly smaller than *Palaeocryptonyx donnezani*. In the humerus the ventral side of the fossa pneumotricipitalis is weakly pneumatized and the incisura capitis is broad. The caput humeri and the

CORACOID	Lenght from angulus medialis to the top	Shaft minimum width	Facies articularis humeralis width	Lenght from facies articularis humeralis to the top	Sternal facet lenght	Proximal width	Proximal depth
Plioperdix ponticus [1]	-	-	2.2	9	-	-	-
Francolinus capeki [2]	25.1-28.8 (14)	-	-	-	7.2-8.8 (32)	5.3-6.4 (46)	3.9-4.5 (40)
Chauvireria balcanica [3]	27.6-28.2	-	-	-	-	5.4-6	3.5-7
Palaeocryptonyx donnezani [7]	-	-	-	-	-	-	-
Palaeocryptonyx donnezani (TE)*	32	3.1	2.9	10.7	7.9	5.9	4.2
Palaeocryptonyx novaki (Higueruelas)*	-	3	2.5	9.1	-	5.7	3.2
P. donnezani FSL 92890 [7]	29.8	-	-	-	-	6.1	-
P. donnezani FSL 92894-1 [7]	30.2*	-	-	-	-	5.7	-
P. donnezani TE9c I29	34.5	-	-	-	-	-	-
P. donnezani TE9c J30	33.5	-	-	-	-	-	-
P. donnezani TE9c K29	33.5	-	-	-	-	-	-

HUMERUS	Maximum lenght	Proximal width	Distal width	Distal depth	Ulnar condyle width	Shaft width (at midpoint)
Plioperdix ponticus [1]	-	-	6.9-7.1 (4)	3.8-4.2 (5)	2.3-2.5 (5)	-
Francolinus capeki [2]	40-43.4 (7)	10.8-12 (8)	7-8.6 (7)	-	-	3.7-4.6 (8)
Chauvireria balcanica [3]	39.2-44.6 (9)	10.1-11.3(39)	6.8-8.1(53)	-	-	-
Palaeocryptonyx donnezani [5]	-	11.4	8.2	-	-	-
Palaeocryptonyx donnezani [4]	43.1	11.9	8.8	-	-	-
Palaeocryptonyx donnezani [3]	38.2	9.8-10.3	7.1-8.3 (4)	3.9-4.9 (4)	-	3.3-3.7
Palaeocryptonyx donnezani (Quibas)*	39.3	11.2	7.8	4.5	-	3.8
Palaeocryptonyx donnezani (Quibas)*	38.4	10.9	7.3	3.8	-	3.8
Palaeocryptonyx donnezani (Quibas)*	-	-	7.3	4.1	-	3.4
Palaeocryptonyx donnezani (TE)*	-	11.5	-	-	-	4.1
Palaeocryptonyx donnezani (TE)*	-	11.8	-	-	-	-
Palaeocryptonyx donnezani (TE)*	-	-	7.6	4.4	2.6	3.5
Perdix palaeoperdix [6]	47.5 (108)	12.9 (106)	9.6 (106)	-	-	4.7 (108)
P. donnezani FSL 92891-1 Lectotype [7]	38.3	10.2	7.5	-	-	-
P. donnezani FSL 92891-1 [7]	-	10	-	-	-	-
P. donnezani FSL 92891-2 [7]	-	-	7.1	-	-	-
P. donnezani FSL 92891-3 [7]	-	-	7.4	-	-	-
P. donnezani TE9c I29 (1)	42	-	-	-	-	-
P. donnezani TE9c I29 (2)	41.8	11.2	8	-	-	-
P. donnezani TE9c J29	-	-	7.8	-	-	-

CARPOMETACARPUS	Maximum lenght	Carpal trochlea diameter	Proximal width	Distal width	Metacarpal majus width (at midpoint)
Plioperdix ponticus [1]	20.9	2.3-2.5	5.6-5.7	-	-
Francolinus capeki [2]	23.3-24 (3)	-	6.6-6.8 (3)	4-4.8 (3)	2.2-2.3 (3)
Chauvireria balcanica [3]	20.3-22.8 (27)	-	6.1-7 (40)	3.9-4.6 (31)	1.8-2.2 (45)
Palaeocryptonyx donnezani [5]	22.4-26.1 (3)	-	6.6-7.4 (4)	4.2-5.4 (3)	-
Palaeocryptonyx donnezani [4]	24	-	6.9	-	-
Palaeocryptonyx donnezani [3]	21.6	-	5.9	4.1	1.9
Palaeocryptonyx donnezani (TE)*	22.9	3.4	6.8	4.8	2.2
Palaeocryptonyx donnezani (TE)*	22.9	3.4	6.6	4.1	2.3
Palaeocryptonyx donnezani (TE)*	23.1	3.5	6.7	4.7	2.2
Perdix palaeoperdix [6]	26.1 (112)	-	7.5 (110)	5.2(110)	2.4(112)
Coturnix coturnix (TE)*	19.6	2.4	5.1	3.2	1.8
P. donnezani FSL 92891-3 [7]	21.6	-	-	-	-
P. donnezani TE9 G29	21.9	-	-	-	-
P. donnezani TE9d H24	23.4	-	7	-	-

TARSOMETATARSUS	Maximum lenght	Proximal width	Proximal depth	Distal width	Shaft width (at midpoint)	Minimum shaft depth	Shaft depth (at midpoint)
Plioperdix ponticus [1]	28.4	5.2	-	5.2-5.5 (3)	2.3	1.4-1.6 (5)	-
Francolinus capeki [2]	36-39.2 (4)	5.8-6.7 (3)	-	7-7.6 (15)	3-4.2 (4)	-	-
Chauvireria balcanica [3]	27-29.9 (6)	5.2-6 (33)	-	5.1-6.2 (25)	-	-	-
Palaeocryptonyx donnezani [4]	-	-	-	7.7	-	-	-
Palaeocryptonyx donnezani [5]	-	-	-	7.9-8.1	-	-	-
Palaeocryptonyx donnezani [3]	ca 34.5	7.1	-	-	3.4	-	2.4
Palaeocryptonyx donnezani (Quibas)*	-	-	-	6.2	3.6	2	2.4
Palaeocryptonyx donnezani (TE)*	35.7	6.3	-	7	3.2	2.2	2.4
Palaeocryptonyx donnezani (TE)*	35.3	5.9	5.8	6.4	2.9	2	2.2
Palaeocryptonyx donnezani (TE)*	-	6.2	6.3	-	2.9	2.1	2.4
Palaeocryptonyx donnezani (TE)*	-	6.5	6	-	-	-	-
Palaeocryptonyx donnezani (TE)*	-	-	-	7	-	2.1	-
Palaeocryptonyx donnezani (TE)*	-	-	-	6.9	-	2	2.4
Palaeocryptonyx donnezani (TE)*	-	-	-	6.8	-	-	-
Perdix palaeoperdix [6]	41.3 (112)	7.4 (110)	7.3 (53)	8(101)	3.5(112)	-	-
P. donnezani TE9 F30	36.4	-	-	7	3.1	-	-
P. donnezani TE9c F30	36	-	-	6.7	-	-	-
P. donnezani TE9c G30 (1)	35.5	6	-	6.5	2.9	-	-
P. donnezani TE9c G30 (2)	-	6.5	-	-	-	-	-
P. donnezani TE9c I28	38.2	-	-	7.2	-	-	-
P. donnezani TE9c I29 (1)	-	-	-	6.6	-	-	-
P. donnezani TE9c I29 (2)	36.4	6.5	-	6.8	3	-	-
P. donnezani TE9c I29 (3)	35.5	6.4	-	6.6	-	-	-
P. donnezani TE9c J29	-	6.3	-	-	-	-	-
P. donnezani TE9c J30	37.5	6.5	-	6.7	-	-	-
P. donnezani TE9c K30	35	6.7	-	6.7	-	-	-
P. donnezani TE9b L30 (1)	-	-	-	6.7	-	-	-
P. donnezani TE9b L30 (2)	-	-	-	6.7	-	-	-
P. donnezani TE9a+ J31	37.5	-	-	6.8	3	-	-
P. donnezani TE10 K31	38	-	-	7	-	-	-

Tab. 2 - Measurements of the coracoids, humeri, carpometacarpi and tarsometatari of several species of Galliformes from the Early Pleistocene of Europe and the remains of *Palaeocryptonyx donnezani* recovered in the Early Pleistocene levels of the Sima del Elefante. Measurements expressed in millimeters. Data from Sánchez-Marco 2009. (1) Bochenski & Kurochkin 1987; (2) Jánossy 1974; (3) Boev 1997: (4) Mlíkosvský 1996; (5) Mlíkovsky 1998; (6) Mourer-Chauviré 1975; (7) Pavia et al. 2012; (*) Original measurements from Sánchez-Marco 2009). Modified from Sánchez-Marco 2009.

processus supracondylaris are more pointed than in *Palaeocryptonyx*, as described by Pavia and colleagues (2012) (Fig. 4e).

Remarks. The common quail has been already cited in the Sima del Elefante levels (Sánchez-Marco 2018). It usually avoids well-wooded areas and wetlands, appearing in open habitats (McGowan et al. 2020). The oldest record of *Coturnix coturnix* comes from the Early Pleistocene of Pedrera de S´Onix site in the Balearic Islands (Alcover et al. 1981), in the Iberian Peninsula the oldest record is the presence in the Early Pleistocene of Quibas (Sánchez-Marco 2009).

Genus *Palaeocryptonyx* Depéret, 1892

Palaeocryptonyx donnezani Depéret 1892

Figs 4f, 4g, 4h, 4j, 4k, 4l, 4m

Material: TE7, distal femur; TE9, complete tarsometatarsus; TE9d, complete carpometacarpus; TE9c, five complete coracoids, one distal coracoid, three complete humeri, one distal humerus, one complete ulna, two distal ulnae, three complete carpometacarpi, two proximal carpometacarpi, one distal tibiotarsus, eight complete tarsometatarsi, four proximal tarsometatarsi, five distal tarsometatarsi; TE9b, distal coracoid, two distal tarsometatarsi; TE9a, one complete tarsometatarsus, two distal tarsometatarsi; TE10, distal carpometacarpus, complete femur, complete tarsometatarsus, distal tarsometatarsus; TE11, coracoid fragment.

Description. The morphology of the remains fits with a small sized Galliformes (Kraft 1972). The size of the remains fit with other remains of *Palaeocryptonyx donnezani,* recovered in the Sima del Elefante (Sánchez-Marco 2009) being smaller than *Perdix perdix* and larger than *Coturnix coturnix* (Tab. 2). The morphology of the bones fits with the description of this taxon given by other authors (Sánchez-Marco 2009; Pavia et al. 2012). In the coracoid the facies articularis clavicularis is slanting ventrally (Fig. 4f), and the processus acrocoracoideus is wider than in *Palaeocryptonyx novaki* (Sánchez-Marco 2009). In the humerus the proximal end is wider than the distal one, the pneumatic dorsal fossa is shallow and the ventral one is large and has a poorly developed crista deltopectoralis (Fig. 4g), there are no characters that allow the differentiation of the humeri of *P. novaki* and *P. donnezani* (Sánchez-Marco 2009). The ulna is relatively straight and has a prominent condylus ventralis, larger than the condylus dorsalis ulnae, and a small tuberculum carpalis. In the carpometacarpus the internal muscular depression is deep, unlike *Palaeocryptonyx novaki*, in which it is

shallow (Sánchez-Marco 2009) (Fig. 4h). In the tarsometatarsus the sulcus extensorius is narrow and small, in contrast with the bigger sulcus extensorius of *Palaeocryptonyx novaki* (Sánchez-Marco 2009) (Fig. 4j,k,l,m).

Remarks. *Palaeocryptonyx donnezani* is relatively common in the Pliocene and Early Pleistocene of Western Europe and appears in localities as Perpignan (where was described by Depéret 1892), Chlum 6 (Mlíkovský 1996), Deutsch-Altenbburg (Mlíkovský 1998), Quibas (Sánchez-Marco 2009), Cava-Sud (Pavia & Bedetti 2013) and Pirro Nord (Bedetti & Pavia 2013). It is noticeable the absence of *Perdix perdix* (or *Perdix palaeoperdix*) among the analyzed remains, as it was mentioned as present in the general assemblage of the cave (Rosas et al. 2001), but the revision of the material included in the mentioned paper here performed allowed the reasignation of the remains to *P. donnezani*.

Genus *Bonasa* Stephens, 1819

Bonasa nini Sánchez-Marco, 2009
Fig. 4d

Material: TE9c, distal humerus, distal tibiotarsus.

Description. The bones show the typical morphology of a medium sized Phasianidae (Kraft 1972). The humerus has a distal width of 10,3 mm. The morphology of the condylus ulnaris extends distally, being separated from the condylus radialis. In the tibiotarsus (6.3 mm distal width) the pons supratendineus is narrow, and the sulcus extensorius has a relatively central position (Kraft 1972) (Fig. 4d). Those characters along to the size allow assigning the remains to the genus *Bonasa*, the total length of the bone could not be measured, but the species *Bonasa nini*, which comes from the same site shows a similar size, thus, the remains are assigned to *Bonasa nini*.

Remarks. The extinct species *Bonasa nini* has been described on the basis of Sima del Elefante level TE13 remains (Sánchez-Marco 2009). The main difference of *Bonasa bonasia* with *Bonasa nini* lies in the length of the tibiotarsus, a parameter that has not be possible to measure in this study, nevertheless the remain analyzed here probably belongs to this species. Nowadays *Bonasa bonasia* occurs in mixed coniferous deciduous woodland with understorey (de Juana & Kirwan 2020). Before the

analysis of the Sima del Elefante remains, the oldest records of the *Bonasa* genus came from the site of Kozi Grzbiet, in Poland (Middle Pleistocene in age) (Bochenski 1984) and Stránská Skála in the Czech Republic (MQ4 biozone in age) (Mlíkovský 1995). Sánchez-Marco (2009) identified *Bonasa* in the Early Pleistocene of the TE13 level of Sima del Elefante. The record in the TE9c represents the oldest global record of the genus *Bonasa*.

Galliformes indet.

Material: (all partial remains), TE7, 5 remains; TE9d, 2 remains; TE9c, 1 remain; TE9a, 1 remain.

Order **Columbiformes** Latham 1790
Genus *Columba* Linnaeus, 1758

Columba livia Gmelin, 1789
Figs 5f, 5g, 5h

Material: TE9c, complete coracoid, proximal humerus, complete carpometacarpus, distal tarsometatarsus; TE10, complete humerus; TE13, complete tarsometatarsus; TE14, distal tarsometatarsus.

Description. The coracoid has the hook like morphology of the facies articularis humeralis in ventral view, and the edge of the processus supracoracoideus does not protrude in medial view. The humeri show a broaden proximal epiphys and a triangular crista deltopectoralis (total length 46.0 mm) (Fig. 5f). In the proximal part of the bones (proximal width 17 mm) there is a pronounced crest that projects beyond the dorsal margin of the bone, a character present only in some specimens of *C. livia* (Tomek & Bochenski 2009). In the carpometacarpus (total length 30.8 mm), the ventral side of the os metacarpalis minus is separated from the edge of the trochlea carpalis, and in the distal part, the sulcus tendineus is close to the spatium metarpalis (Fig. 5g). In the tarsometatarsus (total length 30.6 mm), the trochlea metatarsalis II is medially narrowed (Fig. 5h), and in lateral view, the knob of the medial side of the trochlea metatarsi II projetcts medially in distal view (Fick 1974; Tomek & Bochenski 2009).

Remarks. *Columba livia* inhabits rocky areas and caves near open scrub vegetation (Lowther et al. 2020). The oldest record of *Columba livia* comes

from the Early Pleistocene of Quibas (Montoya et al. 1999).

Columba livia/oenas Gmelin, 1789/Linnaeus, 1758
Fig. 5e

Material: TE7, distal humerus; TE9d, complete ulna; TE9c, distal humerus, sternum fragment, two distal femora; TE10, complete ulna; TE13, complete coracoid, distal coracoid, complete ulna; TE14, distal carpometacarpus.

Description. The recovered remains show the morphology of the Columbidae family (Fick 1974). In the coracoid, the facies articularis clavicularis shows a hook-like morphology in ventral view, and in medial view the edge of the processus supracoracoideus does not protrude more than the edge of the facies articularis clavicularis (Fig. 5e). In the distal part of the humeri the ectepicondylar processs is located proximally (Gilbert et al. 1985). In the ulna the olecranon is straight, without inflexion in the contact with the cotylus ventralis. In the distal part of the carpometacarpus, the sulcus tendineus is close to the spatium metacarpalis. In the tarsometatarsus, the trochlea metatarsalis II is medially narrowed. The size of the recovered bones does not allow the distinction between *Columba livia* and *C. oenas*, thus the remains have been assigned to the complex *Columba livia/oenas* (Fick 1974; Tomek & Bochenski 2009).

Remarks. *Columba livia* inhabits mostly rock faces, while *C. oenas* inhabits open country and borders between open country and forests (Baptista et al. 2020; Lowther et al. 2020). The oldest record of the genus *Columba* in the Iberian Peninsula comes from the the site of Higueruelas (Sánchez-Marco 2005).

Order **Gruiformes** Bonaparte, 1854
Genus *Rallus* Linnaeus, 1758

Rallus aquaticus Linnaeus, 1758
Fig. 5a

Material: TE9c, complete humerus, two distal humeri.

Description. The humeri show the typical morphology of the Rallidae, with a narrow distal epiphysis, the processus flexorius extents more dis-
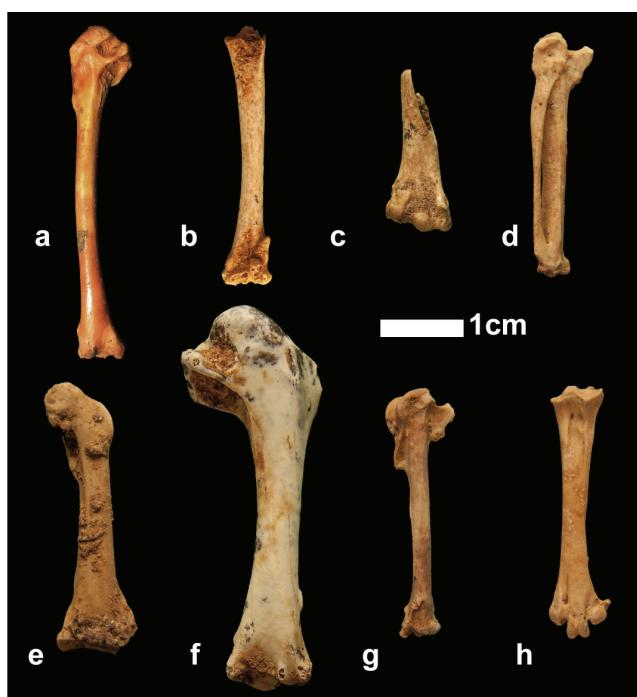
Fig. 5 - Gruiform, charadriiform and columbiform remains from the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. a) *Rallus aquaticus*, left humerus, caudal view (TE9c); b) *Gallinago* sp., left humerus, cranial view (TE9c); c) *Gallinula chloropus*, right humerus, cranial view (TE9c); d) *Calidris* sp., right carpometacarpus, ventral view (TE9c); e) *Columba livia/oenas,* left coracoid, ventral view (TE13); *Columba livia* remains: f) right humerus, caudal view (TE10); g) right carpometacarpus, dorsal view (TE9c); h) right tarsometatarsus, dorsal view (TE13).

tally than the condylus ventralis (Gilbert et al. 1985), the end of the crista that borders the attachment of the musculi brachialis shows a small tuberculum (Cohen & Serjeantson 1996) (Fig. 5a). The total length of the humerus is 39.9 mm, it fits with the medium values for the species of 38.9±1.7 mm (Alcover et al. 2015) and the use of comparative anatomy collections allowed the assignation of the remains to *Rallus aquaticus*.

Remarks. *Rallus aquaticus* inhabits dense riparian and aquatic vegetation with muddy ground (Taylor & Christie 2020). The oldest record of the species comes from the MN15 Hungarian site of Csarnóta 2 (Jánossy 1979). Until this analysis the oldest record of *R. aquaticus* in the Iberian Peninsula came from, the Middle Pleistocene of Galería, also from the Atapuerca Complex (Sánchez-Marco 1999a). The record of *R. aquaticus* in the Early Pleistocene represents the oldest record of the species in the Iberian Peninsula.

Genus *Gallinula* Brisson, 1760

Gallinula chloropus (Linnaeus, 1758)
Fig. 5c

Material: TE9c, distal humerus.

Description. The general morphology fits with a Rallidae (Fig. 5c). The distal part of humerus is narrow, the processus flexorius extends distally further than the condylus ventralis, and the fossa brachialis is shallow (Gilbert et al. 1985). Also, the proximal end of the condylus dorsalis extends over the condylus ventralis, a character of the genus *Gallinula* (Brodkorb 1967). Both the size (7.7 mm distal width) and the morphology allowed the assignation of the remains to *Gallinula chloropus*.

Remarks. *Gallinula chloropus* inhabits freshwater wetlands with emergent vegetation (Taylor et al. 2020). The oldest record of this taxon comes from the Upper Pliocene of Vărșec in Bulgaria (Boev 2000). In the Iberian Peninsula the oldest record comes from the MN16 site of Bobila Ordis (Mayr & Gregor 1999).

Order **Charadriiformes** Huxley, 1867.
Genus *Calidris* Merrem, 1804

Calidris sp.
Fig. 5d

Material: TE9c, complete carpometacarpus.

Description. The carpometacarpus is narrow and flattened, typical of Charadriiformes (Gilbert et al. 1985) (Fig. 5d). The outline of the processus supracondylaris dorsalis is convex, different from the genus *Tringa*, in which is straight or slightly concave (Pavia 2013). The use of the comparative anatomy collections allowed the assignation of the remain to a big-sized member the genus *Calidris*.

Remarks. The species of the genus *Calidris* inhabit areas close to water bodies. The oldest world record of *Calidris* comes from the Miocene of the Czech Republic (Mlíkovský 2002). In the Iberian Peninsula the oldest record known so far came from the Middle Pleistocene of Galería, also in the Atapuerca Complex (Sánchez-Marco 1999a), now the appearance of the genus in the Iberian Peninsula advances to the Early Pleistocene of the Sima del Elefante.

Genus *Gallinago* Brisson, 1760

Gallinago sp.

Fig. 5b

Material: TE9c, distal humerus; TE9b, distal humerus.

Description. The distal humeri have the morphology of the Charadriiformes, the dorsal supracondylaris processus is prominent, and the fossa brachialis is shallow (Gilbert et al. 1985) (Fig. 5b). The size and the morphology allow the assignation of the remains to the genus *Gallinago*.

Remarks. Species of the genus *Gallinago* are typical of wet meadows. The first record of the genus comes from the Hungarian Miocene (Mlíkovský 2002). The oldest record in the Iberian Peninsula came from the Middle Pleistocene of Galería in Atapuerca (Sánchez-Marco 1999a), thus the presence of *Gallinago* in the Early Pleistocene of Sima del Elefante represents the oldest record of *Gallinago* in the Iberian Peninsula.

Charadriiformes indet.

Material: TE9a, 1 remain.

Order **Accipitriformes** Vieillot, 1816
Genus *Aquila* Brisson, 1760

Aquila cf. *heliaca/adalberti* Savigny, 1809/Brehm, 1861

Figs 6d, 6i

Material: TE9d, distal tarsometatarsus, nine pedal phalanxes, five ungual phalanxes; TE9c, three proximal carpometacarpi, distal ulna, distal tarsometatarsus, three pedal phalanxes, two ungual phalanxes; TE9a, ulna fragment, radius fragment, proximal carpometacarpus, two distal tibiotarsi, complete tarsometatarsus, four pedal phalanxes, seven ungual phalanxes.

Description. The morphology and size of the fossil bones belongs to a large-sized Accipitridae (Bochenski & Tomek 2009) in the size range of *Aquila heliaca, Aquila adalberti, Aquila fasciata, Aquila nipalensis, Aquila nipaloides* and some other species from genus *Hieraaetus* (Louchart et al. 2005). In the carpometacarpus the processus extensorius is more rounded, with a strong processus alularis (Trail 2017), the proximal width of the carpometacarpus (23 mm) is outside the range of *A. fasciata, A. rapax* and *A.*

nipaloides (Louchart et al. 2005). The tarsometatarsus shows a fossa in the cotylus lateralis (Fig. 6d), and it is sturdier than the ones of *Aquila fasciata* and *Aquila nipalensis*, and smaller than the tarsometatarsus in *A. nipaloides* (Tab. 3) (Louchart et al. 2005). The proximal foramen is more developed than those of *Hieraeetus*, a characteristic of genus *Aquila*. Also, the tuberositas musculi tibiocranialis forms a short crest in *Aquila*, as it can be observed in the remains here recovered. Those characters, along to the measurements of the phalanx I of digit II (Fig. 6i) (Rodríguez-Hidalgo et al. 2019) (Fig. 7, Tab. 4) fit with both *Aquila adalberti* and *Aquila heliaca*. The remains have been assigned to *Aquila* cf. *heliaca/adalberti* due to the genetic analysis of the species complex, wich points to a separation of both taxa and apparition of *A. adalberti* during the Late Pleistocene (Martínez-Cruz & Godoy 2007).

Remarks. *Aquila heliaca* inhabits most of the Palearctic medium/lower latitudes (Ueta and Ryabtsev, 2001), appearing in forested wet areas near to water bodies (Katzner et al. 2005). *Aquila adalberti* appears in the Iberian Peninsula and inhabits forested areas (Meyburg et al. 2020). The oldest record of *Aquila* cf. *heliaca* comes from the Early Pleistocene (MNQ20 in age) of Somssich-hégy 2, in Hungary (Jánossy 1983b). The oldest record of the taxa with complete assignation (excluding cf. and aff.) comes from the Middle Pleistocene of the Chinese locality of Zhoukoudian (Hou 1993), and the next record comes from the beginning of the Upper Pleistocene of Binagady, in Azerbaijan (Panteleyev & Burchak-Abramovich 2000).

The first record of *Aquila adalberti* is considerably more modern, until recently it came from the Holocene (González 2008), but recently Rodriguez-Hidalgo and collaborators (2019) proved the presence of cf. *Aquila adalberti* in the Upper Pleistocene of Cova Foradada, in Spain.

Initially *Aquila adalberti* was considered a subspecies of *Aquila heliaca*, later some authors supported the idea of *Aquila adalberti* being a separated species (Hiraldo et al. 1976; González et al. 1989; González 2016). Nowadays the identity of *Aquila adalberti* as a separated species is still under debate. The first genetic analysis pointed to a separation of both taxa in the Early Pleistocene, 1 ma ago (Seibold et al. 1996), a similar age than the Sima del Elefante deposit. The last genetic analysis places the separation of both taxa at the end of the Late Pleistocene or the beginning of the Holocene, with some hybrid-

Tab. 3 - Tarsometatarsi measurements of different Accipitriformes taxa, compared with the tarsometatarsi recovered in the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. (1) García-Matarranz, 2013; (2) McNall (On line); (3) Boessneck 1985; (4) Olson & James 1991; (5) Alcover et al. 2004; (6) Guerra-Rodríguez 2015; (7) Jánossy 1985; (8) Louchart et al. 2005; (9) Mourer-Chauviré & Bonifay 2018. Measurements expressed in millimeters.

	Total lenght	Proximal width	Shaft width (at midpoint)	Distal width
Gypaetus barbatus [1]	93.4-98.6	-	-	-
Aegypius monachus [1]	119.5-141.3	-	-	-
Gyps fulvus [1]	104.3-120.0	-	-	-
Halieetus leucocephalus [2]	84.9-97.2	19.4-23.7	-	23-25.6
Haliaeetus albicilla [3]	93.0-106.0	19.5-24	10.0 -12.0	22.2-27.5
Haliaeetus albicilla (Oahu-Molokai) [4]	90.4	-	12.9	25.2
Haliaeetus albicilla (Maui) [4]	90.6	21.4	12.4	24.2
Haliaeetus albicilla (Formentera) [5]	95.64	22.5	-	24.5
Haliaeetus albicilla (Es Pouas) [6]	102.7-107-2	-	-	-
Haliaeetus albicilla [7]	92-107.7	-	-	-
Aquila chrysaetos [2]	95.9-106.9	20.9-24.5	-	22.9-28.8
Aquila chrysaetos [8]	95-112.1	19-25.6	8.4-12.5	21.8-27.3
Aquila chrysaetos [1]	101-121.4	-	-	-
Aquila audax [9]	101-114.4	19.3-22.9	11.2-13.4	22-25.7
Aquila adalberti [1]	90.9-100.5	-	-	-
Aquila heliaca/adalberti [8]	92-95.6	17.8-21.1	8.4-10.2	19.5-23.1
Aquila verreauxii [9]	110	20.8	12.2	23
Aquila fasciata [1]	94.6-107	-	-	-
Aquila fasciata [8]	92.8-105.6	17-19.8	7.8-10	18.7-21.9
Aquila nipaloides [8]	104-120	19.6-24	9.8-11.3	22.3-24.8
Aquila nipalensis [8]	90.3-103.4	17.9-21.3	8.4-10.4	19.5-23.1
Aquila rapax [8]	80.8-81.2	15.1-15.9	7.5	16.9-18.9
Circaetus gallicus [1]	86.3-100.8	-	-	-
Aquila claudeguerini [9]	132	-	16.3	31.3
Haliaeetus albicilla (TE9d F26)	-	-	-	22.1
Haliaeetus albicilla (TE9d G26)	-	-	-	25.6
Haliaeetus albicilla (TE9d G27)	-	-	-	25
Haliaeetus albicilla (TE9d I31)	-	21	-	-
Haliaeetus albicilla (TE9c I31)	-	21	-	-
Haliaeetus albicilla (TE9c J31)	-	-	-	24.6
Haliaeetus albicilla (TE9c K29)	-	23.4	-	-
Haliaeetus albicilla (TE10 I22)	-	23.4	-	-
Haliaeetus albicilla (TE12 E30)	102	23	11.5	25.9
Aquila cf. **heliaca/adalberti** (TE9d G30)	-	-	-	20.5
Aquila cf. **heliaca/adalberti** (TE9a K30)	97	19.5	10.5	20
Aquila sp. (TE9c K30)	-	-	-	24.9
Aquila sp. (TE12 G30)	122	22	11.3	-

Tab. 4 - Measurements of the phalanx I of the digit II of big-sized Accipitridae recovered in the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. Measurements expressed in mm.

	Lenght	Proximal width	Taxa	n° in figure 6
TE7 H23	32.5	17	*Haliaeetus albicilla*	1
TE9d G27	32	17	*Haliaeetus albicilla*	2
TE9c I26	33	17.5	*Haliaeetus albicilla*	3
TE9b L31	33	18	*Haliaeetus albicilla*	4
TE9c K29	34.5	18.9	*Haliaeetus albicilla*	5
TE9a K30	27	12.5	*Aquila* cf. *heliaca/adalberti*	6
TE10 G27	26.7	13	*Aquila* cf. *heliaca/adalberti*	7
TE7c L28	30	14.5	*Aquila* cf. *heliaca/adalberti*	8
TE9d G29 (1)	31.1	14	*Aquila* cf. *heliaca/adalberti*	9
TE9d H29	31.5	14.5	*Aquila* cf. *heliaca/adalberti*	10
TE9d G29 (2)	31.9	15	*Aquila* cf. *heliaca/adalberti*	11

ization taking place later (Martínez-Cruz & Godoy 2007). The genetic analysis, along with the analysis of the paleontological record of the two taxa support the theory of *A. adalberti* being a subspecies of *A. heliaca* (González 2008). The record of this taxon in the Sima del Elefante site represent the oldest record of the Imperial Eagle in the Iberian Peninsula, being practically contemporary to the first trace of the Imperial Eagles in Somssich-hégy 2. Both records could appertain to the common ancestor of the complex *Aquila heliaca/adalberti*.

Genus *Aquila* Brisson, 1760/ Genus *Hieraaetus* Kaup, 1844

Aquila/Hieraaetus

Material: TE9d, distal coracoid, distal ulna, distal radio, proximal carpometacarpus, proximal femur.

Fig. 6 - Birds of prey remains from the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. a) *Haliaeetus albicilla*, right humerus, caudal view (TE7); b) *Haliaeetus albicilla*, right coracoid, ventromedial view (TE7); c) *Haliaeetus albicilla*, left tarsometatarsus, proximal and dorsal views (TE12); d) *Aquila* cf. *heliaca/adalberti*, left tarsometatarsus, proximal and dorsal views (TE9c); e) *Falco rusticolus*, right humerus, cranial view (TE9c); f) *Falco tinnunculus*, left humerus, cranial view (TE9c); g) *Athene vallgornerensis*, right tarsometatarsus, dorsal view (TE9c); h) *Haliaeetus albicilla*, phalanx 1 of the digit I, superior view (TE9c); i) *Aquila* cf. *heliaca/adalberti*, phalanx 1 of the digit I, superior view (TE9d).

Description. The shape of the remains fits with a medium sized Accipitridae. In the ulna the condylus ventralis is narrow and does not project distally, also the distal margin of the tuberculum carpale curves proximally (Bochenski & Tomek 2009). In the carpometacarpus the metacarpal process is proximal and the pisiform process is more reduced than in Falconidae (Gilbert et al. 1985). In the proximal femur there is an opening near the the crista trochanteris, and the linea intermuscularis cranialis has a medial position with respect to this opening.

Remarks. The remains belong to a medium sized member of the subfamily Aquilinae. The general size of the remains fit with several taxa from genus *Aquila* and *Hieraaetus*, both raptors are common in the Pleistocene of Europe (Tyrberg 1998)

Aquila sp.

Material: TE7, complete tarsometatarsus; TE9d, distal humerus, distal carpometacarpus, proximal femur, distal tibiotarsus, distal tarsometatarsus, two pedal phalanxes; TE9c, complete tarsometatarsus; TE10, phalanx digiti majoris alae, distal ulna; TE12, complete tarsometatarsus, ungual phalanx.

Remarks. the remains belong to a big-sized member of the genus *Aquila,* but they are smaller than those from the recently described *Aquila claudeguerini* (Mourer-Chauviré & Bonifay 2018).

Genus *Haliaeetus* Savigny, 1809

Haliaeetus albicilla Linnaeus, 1758
Figs 6b, 6c, 6h

Material: TE7, two complete coracoids, complete scapula, complete humerus, distal humerus, distal radius, complete carpometacarpus, alular phalanx, pelvis fragment, distal tibiotarsus, proximal tarsometatarsus, two distal tarsometatarsis, six pedal phalanxes, eight ungual phalanxes; TE9, two proximal coracoids, distal coracoid, distal ulna, sternum fragment, quadratum; TE9d, three proximal tarsometatarsi, two distal tarsometatarsi, two phalanxes; TE9c, complete coracoid, two proximal coracoids, four distal coracoids, three proximal scapulas, distal radius, two proximal humeri, distal humerus, two proximal ulnas, three distal ulnas, four proximal carpometacarpi, distal carpometacarpus, two proximal femora, two distal tibiotarsi, two complete tarsometatarsi, two proximal tarsometatarsi, four distal tarsometatarsi, two quadratums, twenty six pedal phalanxes, sixteen ungual phalanxes, distal furcula, eight vertebras; TE9b, coracoid fragment, proximal coracoid, sternum fragment, humerus fragment, distal humerus, proximal humerus, ulna fragment, proximal ulna, distal ulna, complete carpometacarpus, proximal carpometacarpus, distal carpometacarpus, distal tarsometatarsus, eight pedal phalanxes, three ungual phalanxes; TE9a, ungual phalanx; TE10, distal ulna, proximal carpometacarpus, proximal femur, proximal tarsometatarsus; TE12, proximal tibiotarsus, distal tibiotarsus, complete tarsometatarsus, pedal phalanx.

Description. The remains belong to a big-sized Accipitridae. The coracoid is robust, and the processus acrocoracoideum is thin (Fig. 6b), the small protrusion close to the impressio ligamenti coracoidei which appears in the genus *Aquila* is absent here, and the space between the facies articularis humeralis and the impression acrocoracoidei is extended (Pavia et al. 2018). In the ulna posterior view, the condylus dorsalis has a rounded morphology, unlike in genus *Aquila*. In the carpometacarpus, the processus extensorius is more irregular and angular than in *Aquila*, and the processus pisiformis is smaller and curved towards the bone (Pavia et al. 2018). In the proximal part of the tarsometatarsus, the fossa in the cotylus lateralis that appears in *Aquila* is absent (Fig. 6c) (Trail 2017), and the crista medialis is thin, as it is in *Haliaeetus* (as noted by Pavia and colleagues 2018). The phalanxes 1 of the digit I have been measured following the work of Rodriguez-Hidalgo and colleagues (2019), fitting with the proportions of *Haliaeetus albicilla* (Fig. 6h, 7; Tab. 4). The size, along with the morphological characteristics, allows assigning these remains to *Haliaeetus albicilla*.

Remarks. The presence of *Haliaeetus albicilla* has been already cited in the Sima del Elefante sequence (level TE10) (Rosas et al. 2001). It is a large-sized bird of prey which inhabits aquatic areas, in lakes rivers or marshes (Orta et al. 2020a). The oldest record of the taxon comes from the Early Pleistocene (MN17) of Tegelend, in the Netherlands (Junge 1953). The presence of *Haliaeetus albicilla* in the level TE7 of the Sima del Elefante is the oldest evidence of the taxa in the Iberian Peninsula.
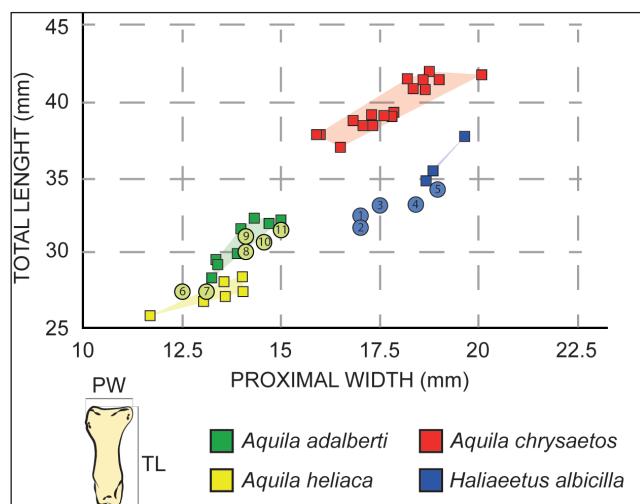

Fig. 7 - Diagram showing the total length vs. proximal width of the phalanx 1 of the digit I of genera *Aquila* and *Haliaeetus* recovered in the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain, compared with the measurements presented by Rodríguez-Hidalgo et al. 2019. Circles represent the data from Table 5. Extracted and modified from Rodríguez-Hidalgo et al. 2019.

Accipitridae indet.

Material: (partial remains), TE7, 10 remains; TE9, 2 remains; TE9d, 19 remains; TE9c, 34 remains; TE9d, 4 remains; TE9a, 7 remains; TE10, 14 remains; TE11, 1 remain; TE12, 4 remains.

Order **Strigiformes** Wagler, 1830
Genus *Athene* Boie, 1822

Athene vallgornerensis Guerra, Alcover & Bover, 2011

Fig. 6g

Material: TE9, distal tibiotarsus; TE9c, complete tarsometatarsus and distal tarsometatarsus; TE9b, distal tarsometatarsus.

Description. The remains belong to a small-sized strigiform bird. The pons supratendineus is absent in the tibiotarsus, and in the tarsometatarsus, the trochlea metatarsi III has a similar length than the other trochleas (Gilbert et al. 1985). The shape of the bone is similar to *Athene*, is smaller than those of *Strix* or *Asio* and more robust than in genus *Otus*. Also, the bone is longer and slenderer than the ones belonging to genera *Surnia, Aegolius* and *Glaucidium*. The sulcus hypotarsi is deep and there are two foramen vasculare distale, allowing the assignation of the bone to the genus *Athene* (Guerra et al. 2012). The size of the bone (total length 29.8

mm, proximal width 6.3 mm, distal width 7.2 mm), along with the mentioned characteristics, allow to assign the bones to _Athene vallgornerensis_ (Fig. 6g).

Remarks. _Athene vallgornerensis_ was described in the Early Pleistocene of Mallorca (MN17) and has been considered an insular taxon related to other species from the Mediterranean islands (Guerra et al. 2012). The Sima del Elefante report represents the oldest and only record in the Iberian Peninsula. _Athene noctua_ inhabits a variety of semi-open habitats, avoding dense vegetation (Holt et al. 2020), nevertheless the absence of other remains of the _A. vallgornerensis_ hampers the possibility of understanding its adaptations to a more terrestrial life (Pavia & Mourer-Chauviré 2002; Louchart 2005; Guerra et al. 2012).

Order **Falconiformes** Sharpe, 1874
Genus _Falco_ Linnaeus, 1758

Falco rusticolus Linnaeus, 1758
Fig. 6e

Material: TE9, distal humerus.

Description. The humerus shows the morphology of Falconiformes (Bochenski & Tomek 2009). The attachment of the musculi pronator brevis is located near to the anterior margin of the epicondylus ventralis, and the attachment of brachial muscle is wide and oriented parallel to the shaft (Fig. 6e) (Solti 1981). The distal length (20 mm) fits with se size of a large falconiform (Solti 1980; Bedetti & Pavia 2007). The shape of the processus supracondylaris dorsalis is not pronounced and is not as close to the condylus dorsalis as it is in _F. cherrug_, thus the bone can be assigned to _Falco rusticolus_.

Remarks. _Falco rusticolus_ today inhabits an ample variety of habitats, including riverine areas, open and forested habitats, in the arctic region (breeding) and also boreal (wintering) (Booms et al. 2020). The oldest record of the species comes from the Early Pleistocene of the Czech Republic site of Stránská Skála (Mlikovský 2002), and the oldest record known so far in the Iberian Peninsula came from the upper Pleistocene of Urtiaga and Cueva del Volcán del Faro (Davidson 1989; Elorza 1990), thus the Sima del Elefante report represents the oldest record of _Falco rusticolus_ in the Iberian Peninsula.

Falco tinnunculus Linnaeus, 1758
Fig. 6f

Material: TE9c, distal humerus; TE13, distal ulna.

Description. The remains belong to a small-sized falconiform. The humerus has a distal width of 10mm, that fits with several taxa, such as _F. subbuteo, F. columbarius_ and F. _tinnunculus_. It shows a shallow fossa musculi brachialis and a smalltuberculum supracondylaris dorsalis, which allows the assignation of the humerus to _F. tinnunculus_ (Solti, 1996). The ulna has a distal width of 6.3 mm, which fits with _F. columbarius_, _F. tinnunculus_ and _F. vespertinus_. It has big tuberculum carpale and condylus ventralis, and the condylus dorsalis is small, those characters fit with _F. tinnuculus_ (Solti 1996) (Fig. 6f).

Remarks. _Falco tinnunculus_ appears in a great variety of wooded habitats, with herbaceous vegetation or shrubbery (Orta et al. 2020b). The oldest record of _F. tinnunulus_ comes from the Hungarian site of Beremend 15 (MN16 in age) (Jánossy 1987). It is common in the palentological record of the Iberian Peninsula (Tyrberg 1998), and its record on the Early Pleistocene levels of Sima del Elefante represents its oldest record in this area.

Falco sp.

Material: TE7, proximal tibiotarsus, distal tarsometatarsus.

Remarks. The remains belong to a small sized falconiform.

Order **Passeriformes** Linnaeus, 1758
Family Corvidae Leach, 1820
Genus _Corvus_ Linnaeus, 1758

Corvus pliocaenus (Portis, 1889)
Figs 8a, 8b, 8c, 8d, 8e, 8f

Material: TE7: 218 remains; TE9: 113 remains; TE9e: 25 remains; TE9d: 324 remains; TE9c: 6868 remains; TE9b. 135 remains; TE9a: 219 remains; TE10: 97 remains; TE11: 24 remains; TE12: 127 remains; TE13: 11 remains; TE16: 3 remains. (Tab. 5).

Description. the remains belong to a big sized corvid, smaller than _Corvus corax antecorax_ and bigger than _Corvus frugilegus_ and _Corvus corone_. _Corvus pliocaenus_ shows some overlap with the former, albeit the bigger differences appear in the tarsometatarsus

	COR	SCA	RAD	HUM	ULN	CMC	FEM	TBT	TMT	MAN	VER	PDA	PEL	STE	PHA	P.UN	QUA	FUR
TE7	19	7	2	35	45	22	19	23	19		10	5	5	1	1	3	1	1
TE9	7	6	1	9	10	20	10	13	11		6	1	1		6	7	5	
TE9e	5	1	2	2	6	3	2		2					1				1
TE9d	23	6	8	41	69	53	32	29	36		4	6				10		3	4
TE9c	475	236	114	614	1223	893	671	673	939	15	322	143	41	39	203	147	87	33
TE9b	11	1		12	35	17	12	16	18		2	3			2	6		
TE9a	26	3	1	18	35	28	16	24	34		13	4		4	6	5	2	
TE10	7	6	3	6	14	8	3	15	19			3		3	3	5	2	
TE11	1			3	5	1	3	2	3		1	2			1	1	1	
TE12	10	4	1	13	29	16	12	13	15		3	3		2	2	3		1
TE13					2	2	2	1	1			2			1			

Note: In TE9d the value **4** appears under VER and **3**, **4** under QUA, FUR respectively.

Tab. 5 - Remains of *Corvus pliocaenus* recovered in the different TELRU levels of the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain expressed in number of identified specimens (NISP). Abbreviations in section 3.3.

Tab. 6 - Measurements of the different *C. pliocaenus* bones recovered in the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. Measurement taken according to Tomek & Bochenski (2000). Data expressed in millimeters. n: number of specimens; Min: minimum value; Max: maximum value; Mean: mean value; SD: standard deviation.

		n	Min	Max	Mean	SD
Coracoid	a	4	47.5	50	48.9	0.9
	b	12	42.1	47.5	45.2	1.6
	c	16	9.5	11	10.4	0.5
	d	24	3.5	4.7	4	0.3
	e	6	17.4	19.8	18.7	0.8
	g	11	10.6	14.1	12.6	1.2
	h	16	4.1	5.4	4.6	0.4
Scapula	b	9	11.2	14.6	13.3	1
	c	25	9.5	11.8	10.9	0.6
	d	10	6.5	7.9	7.2	0.6
	e	4	2.3	2.6	2.4	0.1
	f	4	4.7	5.5	5	0.3
Humerus	a	5	71	78.3	75.8	2.8
	b	14	19.6	22.3	21.2	0.8
	c	7	6	6.9	6.3	0.4
	d	5	18	19.7	18.6	0.7
	e	5	4.2	5.8	4.9	0.7
	f	3	5.7	6.5	6.2	0.4
	g	6	7.1	8	7.5	0.4
	h	36	15.9	17.7	16.9	0.6
	i	37	8.2	10.4	9.5	0.5
	j	28	7	8.6	8	0.4
Radius	b	8	3.8	4.1	4	0.1
	c	9	4.2	4.9	4.7	0.3
	d	9	2.9	4	3.5	0.4
	f	11	5.2	7.4	6.6	0.8
Ulna	a	7	92	97.1	94.2	2
	b	40	11	13	12	0.4
	c	29	12	14.4	13.3	0.6
	d	29	5	6.9	5.8	2.5
	e	12	5.3	5.9	5.5	0.2
	f	60	9.2	12	10.8	0.6
	g	60	7.2	10.3	9.2	0.7
	h	68	6.2	8.3	7.6	0.4

		n	Min	Max	Mean	SD
Carpometacarpus	a	8	52.2	58.4	56.2	2
	b	8	47.5	54.2	52.3	2.2
	c	82	8.2	10.6	9.4	0.5
	d	83	5.8	7.5	6.5	0.4
	e	42	10.8	13.5	12.6	0.6
	f	36	6.5	8.8	7.6	0.5
	g	38	5.2	7.8	7	0.5
	h	10	7.6	8.8	8.3	0.4
	i	13	11.8	13.2	12.4	0.4
	j	20	5	7	5.9	0.5
F.D.M.A	a	9	23	25.7	24.5	1
	b	6	5.7	7.7	7	0.7
	c	1			5	
	d	1			3.1	
Femur	a	19	55.2	62.7	59.2	2.3
	b	56	11.2	13.7	12.3	0.5
	c	42	4.4	6.2	5.3	0.3
	d	3	5.3	5.6	5.4	0.2
	e	2	5	5.1	5.1	
	f	53	12.5	14.6	12.8	0.6
	g	31	6.9	8.6	7.6	0.4
	h	40	8.5	11.4	9.9	0.6
	i	42	6.4	8.7	8.5	2
Tibiotarsus	b	8	11.1	12.6	11.7	0.5
	c	8	14	17	15.6	0.9
	d	2	13.7	14.2	14	
	e	3	7.4	9.2	8.4	0.9
	f	2	4.4	4.7	4.5	
	g	3	5	5.2	5.1	0.1
	h	51	8.9	10.9	10	0.5
	i	41	9.2	10.5	9.7	0.4
	j	72	9	11.4	10.4	0.5
Tarsometatarsus	a	6	69.5	74.2	71.6	1.7
	b	47	10.2	12.5	11.3	0.5
	c	6	4.1	4.5	4.4	0.2
	d	61	6.8	9.6	8.2	0.5
	e	53	4.3	6.4	5.1	0.4
	f	51	2.7	3.4	3.1	0.2

length. The size is similar to *C. pliocaenus janossyi,* this one being more robust. The medium size of the remains resembles that of *Corvus pliocaenus* described in Pirro Nord and Cava Sud (Tab. 6), in the Early Pleistocene of Italy (Bedetti & Pavia 2013; Pavia & Bedetti 2013). In contrast with *C. corone,* the acrocoracoid process of the coracoid is not pointed, and the facies articularis furcularis is elongated, making an open arch between its end and the shaft (Tomek & Bochenski 2000) (Fig. 8a). The humerus is shorter than those of *C. c. antecorax* and *C. p. janossyi* (Fig. 8b) (Mourer-Chauviré 1975). In the ulna, the notch on the olecranon is not very visible, and the incisura tendinosa is deep as in the remains described from
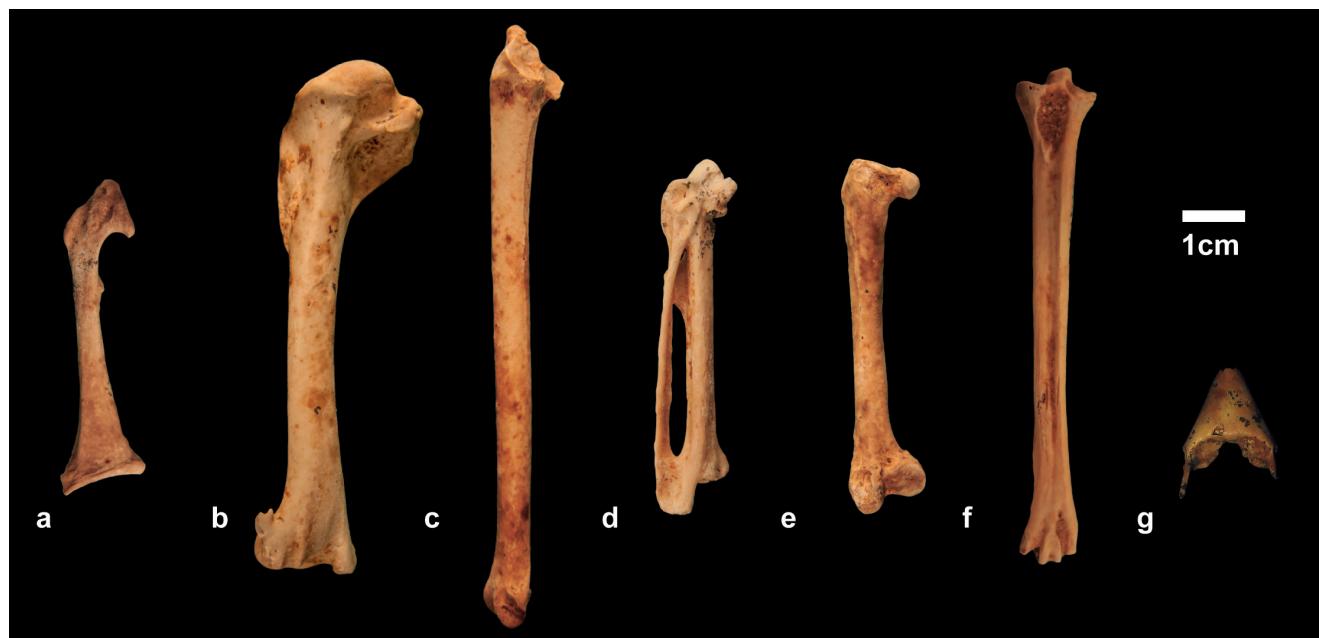
Fig. 8 - Passeriform remains from the Early Pleistocene TELRU levels from the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. *Corvus pliocaenus* remains: a) right coracoid, ventral view (TE9c); b) left humerus, caudal view (TE9c); c) left ulna, ventral view (TE9c); d) left carpometacarpus, dorsal view (TE9c); e) left femur, caudal view (TE9c); f) left tarsometatarsus, dorsal view (TE9c); g) *Coccothraustes coccothraustes* mandible, dorsal view (TE9c).

Italy (Pavia & Bedetti 2013) (Fig. 8c). In the carpometacarpus, the processus intermetacarpalis is pronounced and reaches only the end of the spatium intermetacarpalis (Fig. 8d). In the femur, the condylus medialis is elongated, and the nodule between the muscular imprint and the fibular part of the condylus lateralis is visible (Fig. 8e). The tarsometatarsus is longer and slenderer than in *C. corax* and the other European extant taxa (Tab. 6) (Fig. 8d).

Remarks. *Corvus pliocaenus* was described on the basis of Early Pleistocene remains from Valdarno (Portis 1889), lately the species was synonymized with *Corvus corone* because of their similar size (Mlíkovský 2002). Recently, the remains described in Italy (Bedetti & Pavia 2013; Pavia & Bedetti 2013) supported the validity of *Corvus pliocaenus* as an independent taxon (Kessler 2020). The subspecies *Corvus pliocaenus janossyi* was described on the basis of Middle Pleistocene remains from several sites from France (Mourer-Chauviré 1975), it was described as a subspecies of *C. pliocaenus* due to the similar size of the bones. Nevertheless, the proportions are clearly different between both taxa, *C. pliocaenus* being slenderer. Thus, the status of *C. pliocaenus janossyi* as a subspecies must be revised, and maybe it should be given the status of species, according to its unique anatomical characteristics. The record of *Corvus plio-*

caenus in the Early Pleistocene of Sima del Elefante is its only record in the Iberian Peninsula for now. A deeper morphological and morphometrical analysis of *Corvus pliocaenus* anatomy and its comparison with other taxa is currently in progress.

Corvidae indet.

Material. TE7, 17 remains; TE9, 3 remains; TE9d, 19 remains; TE9c, 311 remains; TE9a, 6 remains; TE10, 6 remains; TE12, 1 remain; TE13, 1 remains.

Family Paridae Vigors, 1825
Paridae indet.

Material: TE9c, two proximal humeri.

Description. the humeri have the two fossae well developed separated by the medial bar, the fossa tricipitalis is pneumatized (Jánossy 1983a).

Family Alaudidae Vigors, 1825

Material: TE7, three proximal humeri.

Description. humeri of passeriform. It with a well-developed fossa pneumoanconea and a reduced fossa tricipitalis. The fossa penumoanconea

is pneumatized, a characteristic that allows the assignation of the bones to the Alaudidae (Jánossy 1983a), specifically the humeri belong to big sized Alaudidade (Moreno 1985).

Family Turdidae Rafinesque, 1815
Genus *Turdus* Linnaeus, 1758

Turdus viscivorus/pilaris Linnaeus, 1758/
Linnaeus, 1758

Material: TE7, two proximal humeri.

Description. the humeri have the characteristics of the Turdidae family humeri, with the medial bar reduced, and which does not separate the dossae (Jánossy 1983a). The size of the bone fits with *T. pilaris*, but the shape of the fossa pneumoanconea points to *T. viscivorus*, which is slighty bigger in size. The similitudes in both size and shape of the representatives of genus *Turdus* (Wójcik 2002) hamper the assignation of the remains to a species.

Remarks. birds of the genus *Turdus* appear generally in forested areas. Both *Turdus pilaris* and *Turdus viscivorus* inhabit mixed areas with woodlands and open landscapes (Collar 2020a, 2020b).

Turdus philomelos/iliacus/merula Brehm, 1831/
Linnaeus, 1766/Linnaeus, 1758

Material: TE7, four proximal humeri.

Description. the humeri show the general morphology of the genus *Turdus*, with a rounded shape of the crista deltopectoralis (Jánossy 1983a). The overlapping on the size of *T. philomelos, iliacus* and *merula* prevents us to assign the fragments of bone to a single taxon (Wójcik 2002).

Remarks. *T. philomelos* inhabits temperate patched forests with bushes and grassland open areas (Collar 2020c), *T. iliacus* appears in mosaic landscapes with forests and open country, specially in river basins or floodplains (Collar et al. 2020), and *T. merula* inhabits preferentially forests (Collar & Christie 2020).

Turdus sp.

Material: TE9c, complete humerus; TE9b, complete humerus; TE12, two proximal humeri; TE13, complete humerus.

Description. The humeri belong to a passeriform. The medial bar is reduced and does not separate the two fossae completely. The size of the bones allows assigning them to the genus *Turdus* (Jánossy 1983a). Nevertheless, their assignation to one of the species of the *Turdus* genus has not been possible, due to the degree of overlapping in the size (Wójcik 2002).

Remarks. The species of the genus *Turdus* are relatively common in the Quaternary paleontological record (Tyrberg 1998). The first record of the genus *Turdus* comes from the Hungarian Miocene (Mlíkovský 2002).

Family Muscicapidae Flemming, 1822
Muscicapidae indet.

Material: TE7, proximal humerus.

Description. The humerus has the two fossae well developed and separated by the medial bar. The fossa tricipitalis is shallower than the fossa pneumoanconea (Jánossy 1983a).

Family Motacillidae Horsfield, 1821

Material: TE7, two proximal humeri.

Description. Humeri with two confluent fossae, which is characteristic of several groups of Passeriformes. The size of the bones and the morphology allows the assignation of these fragments to Motacillidae indet. (Jánossy 1983a).

Family Fringillidae Leach, 1820
Genus *Coccothraustes* Brisson, 1760

Coccothraustes coccothraustes (Linnaeus, 1758)
Figure 8g

Material: TE9c, mandible.

Description. robust mandible, with mandibular fenestra, and a characteristic profile described by Moreno (1985) (Fig. 8g).

Remarks. *C. coccothraustes* inhabits old deciduous woodland (Clement & Christie 2020). The oldest global record of the taxon comes from la Pedrera de d´Onix (Alcover et al. 1981). The record in the Sima del Elefante is the oldest record of *C. coccothraustes* in the Iberian Peninsula.

Fig. 9 - In situ *Haliaeetus albicilla* fossil remains in the level TE7 of the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. Photo: Xosé Pedro Rodríguez, from the EIA.

Passeriformes indet.

Material: TE7, 85 remains; TE9, 2 remains; TE9d, 3 remains; TE9c, 46 remains; TE9b, 5 remains; TE9a, 5 remains; TE10, 7 remains; TE11, 3 remains; TE12, 16 remains; TE14, 2 remains.

Taphonomic remarks

Lagomorpha and Aves are the most abundant remains in the TELRU sequence, with the birds representing more than the 50% of the total number of remains at some levels (Huguet et al. 2013, 2017). Most of the recovered bird remains in the Sima del Elefante site are broken, but these fractures occurred during the excavation and extraction processes, due to both environmental change in the conditions (exposing the remains to the dryer atmospheric conditions) and the fragility of bird bones. These factors hamper the optimal recovering

of the fossils (Huguet 2007), when actually most of the remains outcropped complete at the site (Fig. 9). Most of the bird skeletal elements have been recovered, including skulls (Rosas et al. 2001). That, along with the high number of elements recovered, indicates a high potential for bone preservation in these layers (Huguet et al. 2017).

The state of conservation of the bird remains is constant all over the sequence. As mentioned above, most of the remains appear complete in the site. Some remains show black manganese patinas (Fig. 10c), related with the presence of humidity in the cave (Courty et al. 1989). No cut marks have been observed in the analyzed remains, but their presence has been observed in remains from TE9 (Huguet 2007). Less than the 10% of the remains show marks produced by predation which correspond to whether carnivores or bird of prey punctures (Fig. 10a). Also, marks made by rodents have been observed in a small percentage of the sample (less than 10%) (Fig. 10d). Finally, thin unidentified marks have been observed in the diaphysis of some long bone remains, their presence having been already cited although the origin remains unknown (Huguet 2007) (Fig. 11b).

The dominance of cave-dwellings taxa as *Corvus pliocaenus* and *Columba livia* (Fig. 3), sometimes appearing in anatomical connection and without signals of digestion or predation marks, suggests that these taxa occupied the cavity walls around the entrance and died naturally, then were accumulated within the cavity. It is interesting that the cave dwelling nature of *Corvus pliocaenus* contrasts with *Corvus corax*, which rarely inhabit caves, but inhabit cliffs regularly (Marzluff 2019). Also, some pathologies have been observed in the *Corvus pliocaenus* remains. Three pedal phalanxes show a growth anomaly of the bone (Fig. 10f), and a distal tarsometatarsus possibly affected by polydactyly has been recorded (Fig. 10e). This pathology is related to stress during the embryonic development or with the presence of mutations in the parents (Crosta et al. 2002).

The accumulation of other bird groups could be the result of the action of birds of prey, remains of birds that usually prey on small birds have been recovered in the Sima del Elefante TELRU assemblage (Huguet et al. 2017), as the Common kestrel *Falco tinnunculus* (Orta et al. 2019b), the Imperial eagle *Aquila* cf. *heliaca/adalberti*, which would not nest in the cave but could have nested in the vicin-
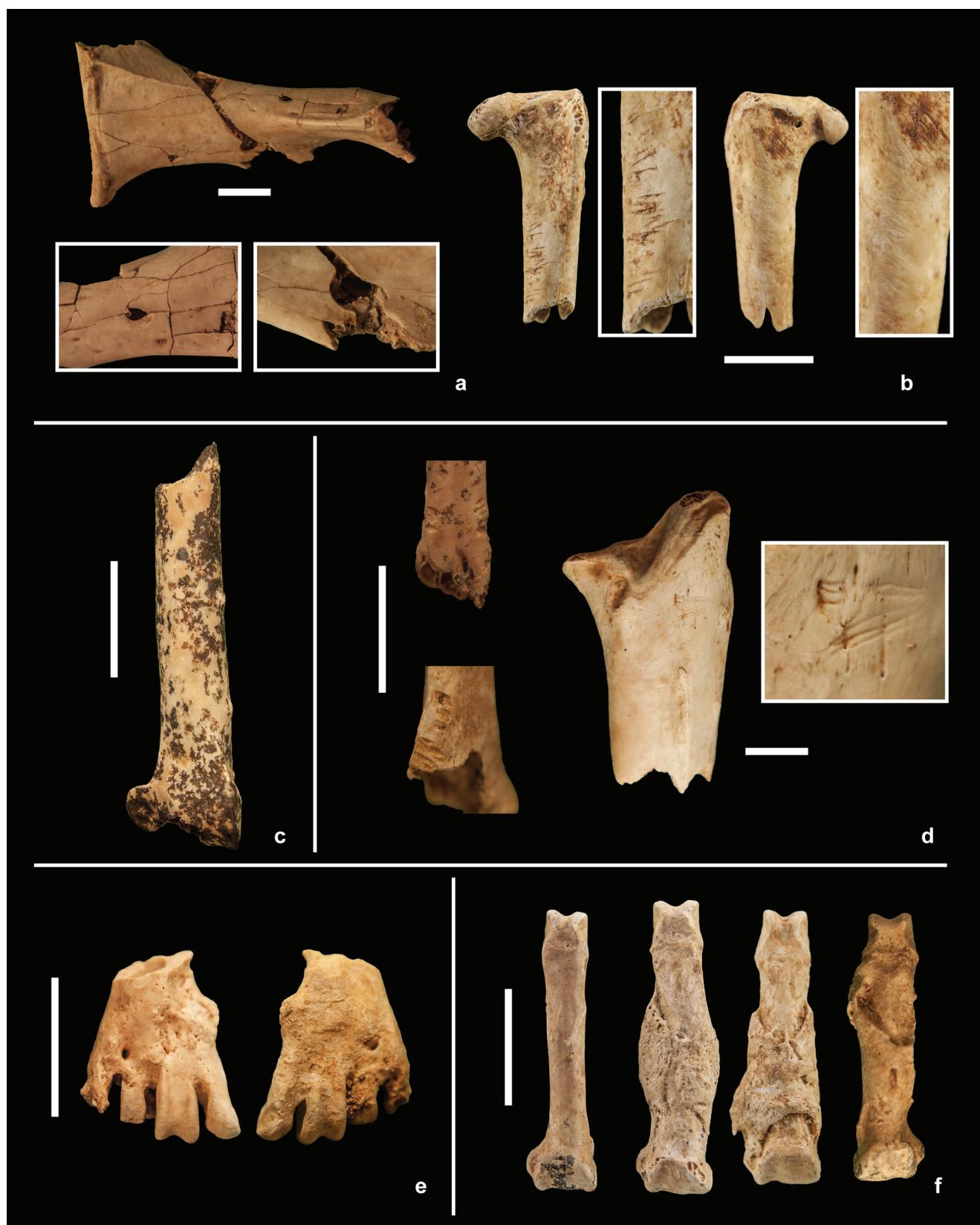
Fig. 10 - Taphonomic remarks and pathologies observed in the bird remains from the Early Pleistocene Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. a) Accipitriformes coracoid with a puncture; b) *Corvus pliocaenus* proximal femur with the unidentified linear marks; c) Manganese patina in a *Corvus pliocaenus* distal ulna; d) scavenging marks in bird long bones and in a proximal ulna of *Haliaeetus albicilla*; e) *Corvus pliocaenus* affected by polydactyly; f) pedal phalanxes with abnormal bone growing (along with a normal phalange). The scale bar represents 1cm in all cases.

ity of the cave (Meyburg & Kirwan 2019), or the dominant *Corvus pliocaenus* (Marzluff 2019). Also, the Raven must also be considered as a potential accumulator of the small mammals remains, as the modifications produced by Ravens are similar to those left by nocturnal birds of prey (Laudet & Selva 2005). A deeper taphonomic analysis is currently being carried out.

Palaeoenvironmental reconstruction

Several publication have shown the palaeoenvironmental reconstructions of the lower units (TELRU) of the Sima del Elefante site (Blain et al. 2010; Rodríguez et al. 2011; Galán et al. 2016, 2019a; Expósito et al. 2017). Some of these works use the Habitat Weighting method (Evans et al. 1981; Andrews 2006), using five habitats (Blain et al. 2010): Wooden (WO), Open Humid (OH), Open Dry (OD), Rocky areas (RO) and continental Water Areas (WA).

Similar methodologies involving a scoring for each habitat in bird taxa have been developed in order to inquire into the past landscapes, and they have also been applied to Atapuerca Early Pleistocene assemblages (Sánchez-Marco 1999b and references therein). Nevertheless, these approaches based on scoring need to be taken with caution, as the habitat preferences of the taxa can nowadays change geographically and could have changed during the Pleistocene. Moreover, birds usually present wider geographical mobility than other faunal groups, as e.g., small mammals or amphibians. Neverthelessthese methodologies can be useful in this context by allowing the comparison between different proxies and the observation of tendencies along a sequence.

The scores for each habitat type have been assigned to each taxon following the habitat preferences described from the Birds of the World (Cornell Lab of Ornithology) references and International Union for Conservation of Nature web pages (Fig. 11a). Only the taxa identified at species level and with extant representative have been considered, with some exceptions. Taxa identified at a genus level have been used as if all the extant representatives share a preferred habitat. Also, *Corvus pliocaenus* has been included, applying in this case the scoring of *Corvus corax*. The bird diversity in the assemblage is dominated by the cave and cliff dweller taxa, as observed by Pavia (2020) in the Plio-Pleis-

tocene site of Kromdraai (South Africa). Due to the inhabitance of *Corvus pliocaenus* and *Columba livia* within the cave walls and entrance, the analysis has been performed twice, both including and excluding these two taxa.

The results point to a landscape dominated by open dry areas with water bodies and woodland patches (Fig. 11c).

The bird association in the TE7 unit is characterized by the abundance of *Corvus pliocaenus*, but it is also noticeable the presence of the *Haliaeetus albicilla*. The affinities of *C. pliocaenus* are still under analysis, but it was probably an ancestor (or a relative) of the common raven *Corvus corax*. The habitat preferences of *Corvus corax* are ample, appearing in almost every ecosystem, but it shows preferences for open environments (Boarman & Heinrich 2020). The record of *Haliaeetus albicilla* reflects the presence of aquatic areas in the nearby (Orta et al. 2020a). The assemblage points to a landscape dominated by open dry and rocky areas, with the presence of some scattered woodlands, and minor water bodies (Fig. 11c). Only chiropters have been analyzed in unit TE7 with paleoenvironmental purpose, the association of these flying mammals reflecting a quite different landscape: one dominated by woodland and woodland margins, with some rocky areas and, in a lesser extent open, environment, (both dry and humid) (Galán et al. 2016).

The TE9 unit is the richest in terms of bird abundance. However, it must be considered that TE9 is also the thicker unit and, as explained above, it is divided in several subunits. As the rest of the TELRU units, the TE9 is clearly dominated by *Corvus pliocaenus*. The next taxon in order of abundance is again *Haliaeetus albicilla*, followed by *Palaeocryptonyx donnezani* and the Imperial eagle *Aquila* cf. *heliaca/adalberti*. The presence of the *Haliaeetus albicilla*, along with the presence of other taxa usually related to water bodies (as the ducks, *Gallinula chloropus* or *Rallus aquaticus*) is again a signal of the presence of water bodies in the nearby. No great differences have been observed in the reconstruction of the different subunits of TE9. They show a clear dominance ofopen dry and rocky landscape, with minor presences of water bodies and woodlands, and open humid areas in a lesser extent (Fig. 11c). Several faunas have been deeply analyzed from unit TE9 (Cuenca-Bescós & Rofes 2004; Rofes & Cuenca-Bescós 2006, 2009; Blain et al. 2010; Rodríguez

et al. 2011; Cuenca-Bescós et al. 2013, 2017; Galán et al. 2016; Rofes et al. 2016; Huguet et al. 2017). All the reconstructions point to a similar climate (warm Mediterranean), but differ in terms of landscape distribution. The open humid landscape predominates for the small mammals (Rodríguez et al. 2011), while woodland is the most represented environment for bats (Galán et al. 2016). The herpetofauna reflects a more mixed environment (Blain et al. 2010). It is noticeable how the presence of water bodies shows a similar tendency in avian and herpetofaunal based approaches through levels TE9c to TE10. TE9b is the one with more water signal within the TE9 context, with a similar proportion than TE10.

The TE10 unit bird assemblage reflects a similar environment to the ones obtained in the previous levels, but dominated by rocky taxa, instead of dry-open landscape taxa, also with presence of water bodies and woodlands (Fig. 11c). The herpetofauna assemblage points to a similar landscape, with more presence of open-humid areas, but with a similar proportion of water bodies and woodlands (Blain et al. 2010). In the case of both non-flying small mammals and chiropters, the proportion of woodlands strongly differs, representing a small proportion in the case of small mammals (Rodríguez et al. 2011), and dominating the landscape in the case of the bats (Galán et al. 2016).

No birds apart from *Corvus pliocaenus* have been analyzed from level TE11. *Corvus pliocaenus* points to a landscape dominated by open dry areas and woodlands. A similar response appears in the herpetofauna assemblage, in which the sequence changes, developing open dry areas linked to the regression of open-humid areas, and a drop in the water signal (Blain et al. 2010). The response of small mammals also reflects an increase of open dry areas (Rodríguez et al. 2011).

In the unit TE12, the water-related taxa reappear (with the presence again of Anatini ducks, and *Haliaeetus albicilla*) and the woodland proportion does not show big changes (Fig. 11c). The herpetofauna shows that a trend to open-dry meadows development is maintained (Blain et al. 2010). The chiropters signal also points to a dryer landscape than in other units (Galán et al. 2016).

The avian assemblage of unit TE13 reflects again a disappearance of the water bodies, but the results must be considered carefully due to the low number of remains recovered at this level. The herpetofauna, though, reflects an increase in open humid areas and water bodies, with a similar proportion of woodlands (Blain et al. 2010). There are no bat remains in this unit. The non-flying small mammals reflect a slight increase in open dry areas and a regression in the proportion of woodlands (Rodríguez et al. 2011).

Only five bird remains have been recovered from level TE14. It is remarkable that this is the only level of TELRU that does not present Corvidae remains. According to other faunas, the level TE14 would be the coldest one, but climate conditions would still have been warmer than nowadays, and this drop in temperatures could be related to the climate deterioration occurred 1.1-1.0 my ago, detected in other sites of similar age, such as Cueva Victoria, Almenara-Casablanca 3 and Cal Guardiola (Blain et al. 2010).

According to the palynological analysis, the conditions during the deposition of units TE7 to TE10 were humid and there were erosive processes. The paleobotanic assemblage fits with the humid conditions reflected by the avian assemblage and other faunas (Expósito et al. 2017), and with the Mediterranean climate reflected by the herpetofauna and chiropters (Blain et al. 2010; Galán et al. 2016). On the other hand, dryer conditions are reflected by palynological analysis in the upper levels TE10, TE11 and TE12, or at least arid episodes in a general humid context (Expósito et al. 2017). This situation is also reflected by the avian assemblage, with the disappearing of water-related taxa in some levels. Also, the herpetofauna analysis reflects a similar situation, with the development of open-dry meadows in some units (Blain et al. 2010).

The reduction in the bird diversity towards the upper part of the TELRU sequence, along with the tendency of aridification of the climate indicated by with the avian assemblage, as well as by the herpetological and palynological analysis (Blain et al. 2010; Expósito et al. 2017), could be reflecting the climate deterioration occured during the Epivillafranchian (Madurell-Malapeira et al. 2014; Bellucci et al. 2015). This event could have led to a change in the landscape, triggering a takeover not only in the big mammal assemblages, but also in the bird assemblages. This would explain the absence of several bird taxa in the other more recent Atapuerca´s sites, as it is the case of the Imperial eagle

Aquila cf. *heliaca/adalberti, Palaeocryptonyx donnezani,* or *Corvus pliocaenus,* which was replaced by *Corvus corax antecorax* in the Atapuerca assemblages aged Middle Pleistocene (Sánchez-Marco 2005). This has already been proposed as explanation for the turnover between *Aquila claudeguerini,* from the Early Pleistocene of France and the later replacement by the Golden eagle *Aquila chrysaetos,* as the climate change could have led to a scarcity of preys (Mourer-Chauviré & Bonifay 2018).

The differences observed in the habitat proportions between the different analyzed faunas can be due to several factors. One that needs to be considered is the difference in the displacement capacity of each group of faunas, and their predators (Fig. 11b). The obtained results for the paleoenvironmental reconstructions will represent areas of different sizes. For example, the maximum range of movement of the most common amphibian taxa in the sequence, whose origin in the accumulation points to in-situ mortality, *Bufo calamita* (Blain et al. 2010) is approximately 1.5 km (Beebe 1979). And about 25-29 km for *Myotis myotis* and *Miniopterus schreibersii* (Arlettaz 1996; Vincent et al. 2011)*,* the most abundant bats in the association (Galán et al. 2016).

On the other hand, the maximum range of movement of some of the other identified taxa can reach 40 km, that is the case of the birds that acted as predators (Fig. 11b),

Another factor that must be considered is the origin of the accumulation. In the case of the herpetofauna and chiropters, the main accumulation factor is the natural death of the individuals in the cave (Blain et al. 2010; Galán et al. 2016). In the case of the non-flying small-mammals, however, the taphonomic analysis points to they being accumulated by a bird of prey, *Strix aluco* (Bennàsar et al. 2016), which hunts in a radius of approximately 0.5 km from the nest (Sunde & Bølstad 2004). Nevertheless, it is noticeable that no remains of *Strix aluco* have been identified in the assemblage in this work nor in previous ones. As mentioned above, the origin of the accumulation of the birds in the Sima del Elefante TELRU assemblage is mixed, with most of the individuals naturally dying, and some of them being accumulated by birds of prey. Except for *Falco tinnunculus,* the birds of prey recovered in the assemblage shows also big radius of movement (Fig. 11b), thus the area represented by the avian assemblage is

bigger than the one represented by other faunas. In the case of taxa living and dying inside the cave, the high number of individuals recovered will hamper the paleoenvironmental reconstruction, as signaled by Galán and colleagues (2016). In the case of birds, the clear dominance of raven remains makes their preferred habitat overrepresented. The differences in the results of the analysis including the whole association and removing *Corvus pliocaenus* and *Columba livia* are outstanding (Fig. 11c). Also, it must be taken into account that the environmental affinities of *Corvus pliocaenus* are not clear, and the preferences of *Corvus corax* have been applied for the analysis. Nevertheless, the affinities of the taxon are still not clear. In the case of the bat-based paleoenvironmental approach, the overrepresentation of woodland habitat is probably related to the origin of the accumulation: as far as the recorded bats were accumulated by natural death within a cave, the high dominance in the record of two cave-dwelling, large colony-forming especies (as *Myotis myotis* and *Myotis schreibersii*) may not accurately reflect the real composition of the bat community living in the area by that moment (Galán et al. 2016, 2019b).

Conclusions

This work adds new data to the knowledge of Early Pleistocene bird assemblages, with 9542 new remains from the Sima del Elefante assemblage. At least 26 different taxa have been identified in the assemblage, from levels TE7 to TE14, all of them belonging to the Sima del Elefante Lower Red Unit, with an age between 1.1 and 1.5 million years. The identified taxa are: *Spatula clypeata, Anas crecca,* Anatini indet., Anseriformes indet., *Coturnix coturnix, Palaeocryptonyx donnezani, Bonasa nini,* Galliformes indet., *Columba livia, Columba livia/oenas, Rallus aquaticus, Gallinula chloropus, Calidris* sp., *Gallinago* sp., Charadriiformes indet., *Aquila* cf. *heliaca/adalberti, Aquila/Hieraaetus, Aquila* sp., *Haliaeetus albicilla,* Accipitridae indet., *Athene vallgornerensis, Falco tinnunculus, Falco rusticolus, Falco* sp., *Corvus pliocaenus,* Corvidae indet., Paridae indet., Alaudidae indet., *Turdus viscivorus/pilaris, Turdus philomelos/iliacus/merula, Turdus* sp., Muscicapidae indet., Motacillidae indet.*, Coccothraustes coccothraustes,* Passeriformes indet and Aves indet. This assemblage provides us a deeperunderstanding of the conditions under which the
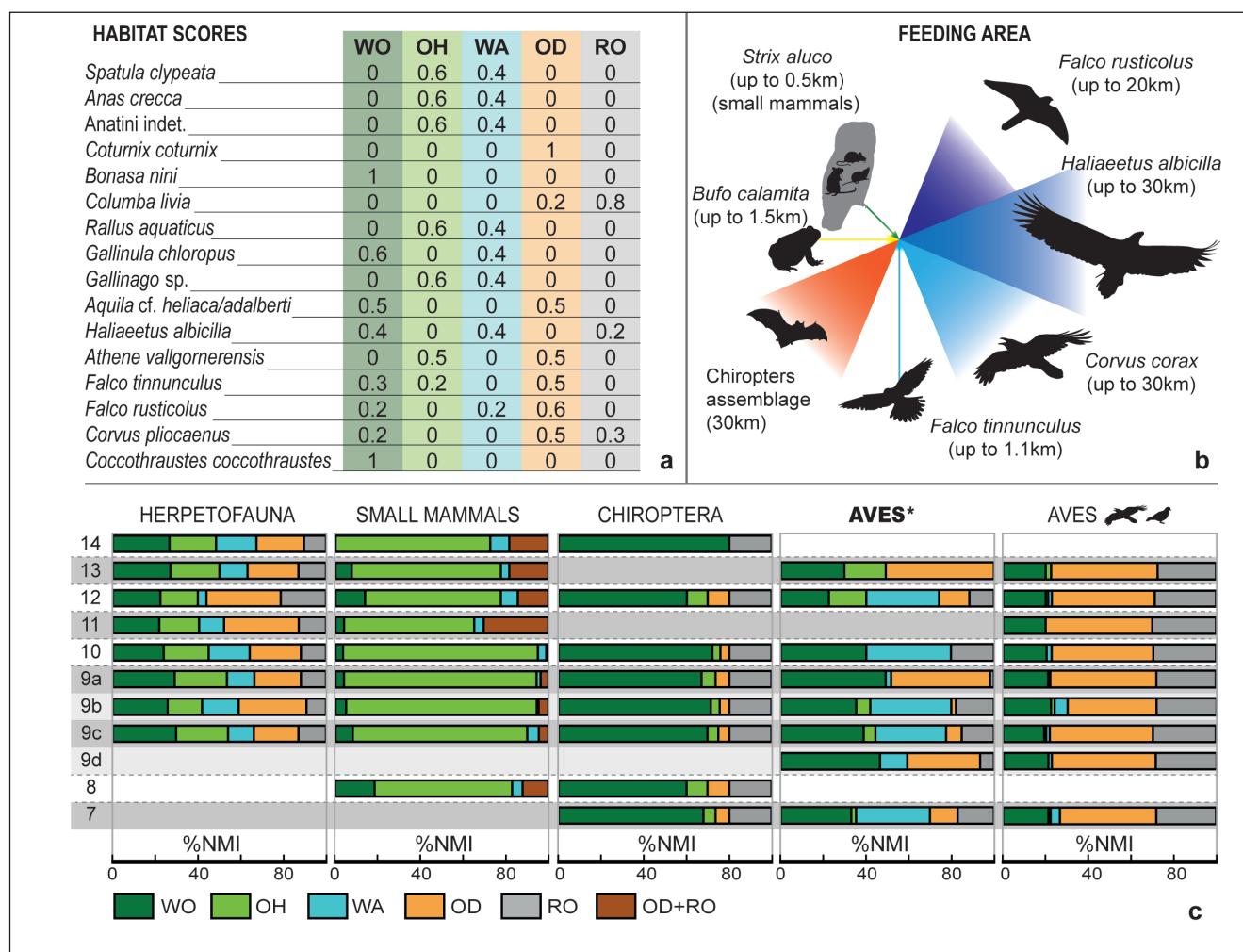
Fig. 11 - Habitat weighting analysis performed with the bird assemblages of the Early Pleistocene levels of the Unit TELRU of Sima del Elefante, Atapuerca, Burgos, Spain. a) Habitat scores for each bird taxa included in the Habitat Weighting analysis. B) Graphic representation of the areas covered by different taxa for feeding. Results from the analysis of the microfauna fossil remains from TELRU of Sima del Elefante.c) Results of the Habitat weighting analysis. WO: woodland areas; OH: Open humid; WA: water; OD: open dry; RO: rocky; NMI: minimum number of individuals. Aves* does not include the cave dwelling taxa *Corvus pliocaenus* and *Columba livia*; Aves includes all the taxa from figure 11a. Herpetofauna data from Blain et al. 2010. Non-flying small mammals data from Rodríguez et al. 2011. Data from chiropters from Galán et al. 2016.

oldest human bearing levels in Atapuerca were accumulated.

The record of some of these taxa represents their oldest record in the Iberian Peninsula (*Haliaeetus albicilla*, *Falco tinnunculus*, *Falco rusticolus*, *Rallus aquaticus*, *Calidris* sp., *Gallinago* sp., *Athene vallgornerensis*, *Corvus pliocaenus* and *Coccothraustes coccothraustes*). The record of the Imperial eagle (*Aquila* cf. *heliaca/adalberti*) in the Sima del Elefante also represents the oldest record of the taxon in the Iberian Peninsula, before the separation of the oriental (*Aquila heliaca*) and Iberian (*Aquila adalberti*) populations.

The taphomic analysis performed here points to a mixed origin of the accumulation, with most of the remains belonging to cave-dwelling taxa, whose individuals probably died naturally in the caves or

the vicinity (highlighting *Corvus pliocaenus*, that represents up to the 90% of the remains in some levels). The small birds could be accumulated by the action of birds of prey, some of them also registered in the assemblage. At this point, the possible action of *C. pliocaenus* as an accumulator agent must be taken into account for the future research not only of the bird accumulation origin, but also for the small mammals.

Regarding the paleoenvironmental reconstructions, the assemblage mostly includes taxa related with open areas, with some representation of woodlands and water bodies. The use of the Habitat Weighting methodology allowed the comparison with the analysis made based on other faunal groups, even if yielding different results. It is im-

portant to consider that there are some factors that hampered the use of this methodology on bird remains, and also that each faunal group represents a different area around the site.

Generally, the analysis points to a degradation of the climate towards the upper part of the the Early Pleistocene Unit TELRU of Sima del Elefante (Atapuerca, Burgos, Spain) sequence. This tendency, that is also reflected by several other proxies, could be one of the reasons of the changes in the avian faunas observed between the Early and the Middle Pleistocene of Atapuerca.

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