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Pleistocene cave hyenas in the Iberian Peninsula: New insights from Los Aprendices cave (Moncayo, Zaragoza)

Víctor Sauqué, Raquel Rabal-Garcés, Joan Madurell-Malaperia, Mario Gisbert, Samuel Zamora, Trinidad de Torres, José Eugenio Ortiz, and Gloria Cuenca-Bescós

ABSTRACT

A new Pleistocene paleontological site, Los Aprendices, located in the northwestern part of the Iberian Peninsula in the area of the Moncayo (Zaragoza) is presented. The layer with fossil remains has been dated by amino acid racemization to 143.8 ± 38.9 ka (earliest Late Pleistocene or latest Middle Pleistocene). Five mammal species have been identified in the assemblage*: Crocuta spelaea* (Goldfuss, 1823) *Capra pyrenaica* (Schinz, 1838), Lagomorpha indet, Arvicolidae indet and *Galemys pyrenaicus* (Geoffroy, 1811). The remains of *C. spelaea* represent a mostly complete skeleton in anatomical semi-connection. The hyena specimen represents the most complete skeleton ever recovered in Iberia and one of the most complete remains in Europe. It has been compared anatomically and biometrically with both European cave hyenas and extant spotted hyenas. In addition, a taphonomic study has been carried out in order to understand the origin and preservation of these exceptional remains. The results suggest rapid burial with few scavenging modifications putatively produced by a medium sized carnivore. A review of the Pleistocene Iberian record of *Crocuta* spp. has been carried out, enabling us to establish one of the earliest records of *C. spelaea* in the recently discovered Los Aprendices cave, and also showing that the most extensive geographical distribution of this species occurred during the Late Pleistocene (MIS4-2).

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INTRODUCTION

The cave hyena *(Crocuta spelaea)* is a well-known and widespread taxon in the Late Pleistocene of Europe. The first mention of the cave hyena in the paleontological literature dates back to illustrations by Esper (1774) portraying the teeth of animals recovered from the Zoolithen Cave in Bavaria (Germany; Diedrich, 2008, 2011a). Several decades later, Goldfuss (1823) formally erected the new species *Hyaena spelaea* on the basis of an almost complete cranium recovered from Zoolithen Cave. This species was later transferred to the genus *Crocuta* by Soergel (1937). Some scholars consider the cave hyena a subspecies of the living African spotted hyena and refer to *Crocuta crocuta intermedia* (Bonifay, 1971) or *Crocuta crocuta spelaea* (see Kurtén, 1957; Werdelin and Solounias, 1991).

During the Late Pleistocene cave hyenas were the main non-anthropic accumulators of bone remains in caves (Fosse, 1997; Diedrich, 2014). As a consequence of its activity, hundreds of accumulations have been documented in European caves (Fosse, 1997; Fosse et al., 1998; Diedrich and Žák, 2006; Turner et al., 2008; Fourvel, 2012; Diedrich, 2014; Fourvel et al., 2014). In the Late Pleistocene of the Iberian Peninsula, the cave hyena was a common element in large mammal assemblages, being recorded from numerous sites (Arribas et al., 2010; Varela, 2011). Its last Iberian occurrence was in the south of the Peninsula, in Las Ventanas Cave (Granada, Spain) at the end of the Late Pleistocene (ca. 12.780 cal ka BP, Carrión et al., 2001).

Despite their ubiquitous presence in European Late Pleistocene assemblages, complete or even partial skeletons of *Crocuta spelaea* are very rare in the fossil record. The most complete specimens are known from Koněprusy Cave (Czech Republic; Diedrich and Žák, 2006) and from Les Oubliettes (Gargas, France; Cardoso, 1993). The lack of more complete skeletons of this species in the fossil record may be a consequence of their scavenger dietary habits, including cannibalism (Diedrich, 2005, 2011a, 2011b, 2011c, 2011d, 2012a, 2012b, 2014).

During a paleontological survey in 2012 in the Moncayo Massif, several bones of cave hyena were discovered in a cave called Los Aprendices (Zaragoza, Spain). The aim of this paper is to present the former cave and the excavated hyena remains. The studied specimens include the best-preserved skeleton of *Crocuta spelaea* in the Iberian Peninsula, and one of the most complete in Europe. This skeleton allows for a taphonomic study to understand the processes undergone by the carcass and to identify which animals might have scavenged on it. Furthermore, a biometric analysis of such a well-preserved specimen provides a good comparison with other specimens from Iberia and South-Western and Central Europe.

LOS APRENDICES CAVE: THE HISTORY OF ITS DISCOVERY AND ITS GEOGRAPHICAL AND GEOLOGICAL LOCATION

History of Its Discovery

The site of Los Aprendices was discovered in 2012 by members of the University of Zaragoza and the CEA (Centro de Espeleología de Aragón; Speleological Centre of Aragón) in the course of a prospection survey in the caves of the Moncayo Massif ("Prospection of the karstic caves in the Moncayo area located within the municipal areas of Purujosa, Trasobares and Calcena Nº Exp 087/2011"). Los Aprendices Cave was already known in the region and while mapping it in 2005 members of the CEA unblocked a passage leading to a gallery with a detritus cone that probably corresponds to the former entrance to the cave. During

FIGURE 1. 1, Metapodials of *Crocuta spelaea* in anatomical semi-connection. 2, Cranium of *Crocuta spelaea*. 3, Filtering the excavation grid. 4, Excavation of various *Crocuta spelaea* remains from the hyena level.

the work associated with the unblocking of the gallery several large carnivore metapodials in anatomical correspondence were discovered (Figure 1.1). Preliminary study of the recovered remains at the University of Zaragoza suggested that they belong to a cave hyena. Taking that information into account, a systematic field survey was begun in the Los Aprendices Cave in order to extract other bones putatively corresponding to the same specimen.

Description of the Cave and the Infill

Los Aprendices Cave is situated in the Sierra del Moncayo, which is located in the central part of the Iberian Range, northern Spain (Figure 2.1). As a result of the altitude of the Sierra and its geographical location between the Duero and Ebro river basins, the area receives major hydrological input from Atlantic fronts. The entrance of the cave is at an altitude of 910 m in the western slopes of the Peñas del Cabo, among the foothills of the Moncayo, just a few kilometres to the south of the village of Calcena (Zaragoza, Spain) (Figure 2.2-3). The cave extends into the limestone-dolomite breccias and vacuolar dolomites of the Cortes de Tajuña Formation, which is Lower Jurassic in age. It consists of a large sloping gallery comprising a big hall in its initial section, which gradually diminishes in size, with a reduction particularly in the height of the ceiling (Figure 2.4). To reach the gal-

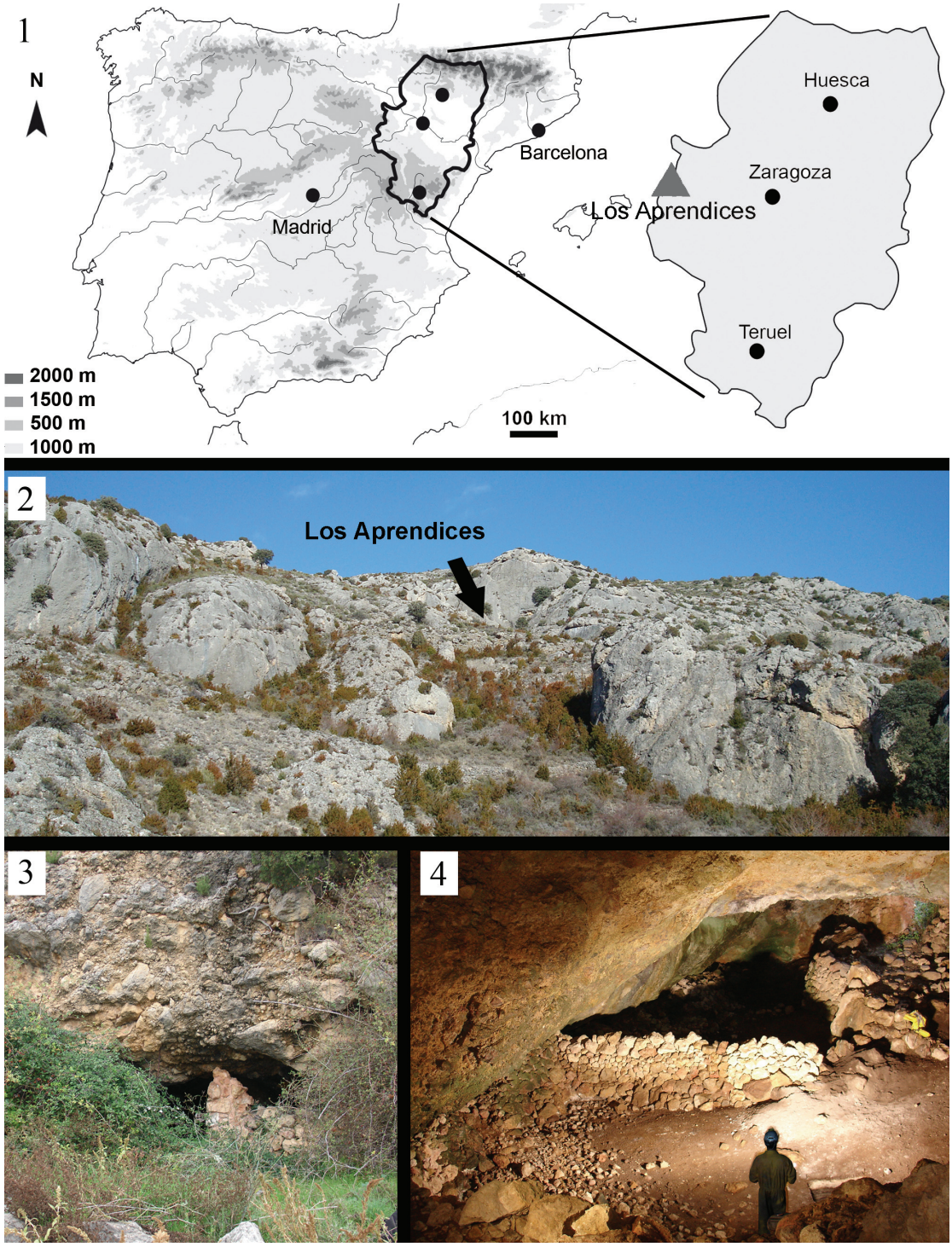

FIGURE 2. 1, Geographical situation of Los Aprendices Cave. 2, Panoramic view of the western slopes of the Peñas del Cabo. 3, Mouth of Los Aprendices Cave. 4, Main gallery of the cave.

lery where the fossil remains were found we have to pass through a narrow aisle (some 50 cm in height) that leads to another gallery at a lower level than the main hall (Figure 3.1-2). At the end of this gallery is the sediment cone that is probably associated with a former entrance to the cave (Gisbert and Pastor, 2009). This former entrance must have been the one used by the animals to reach the cone (Figure 3.5).

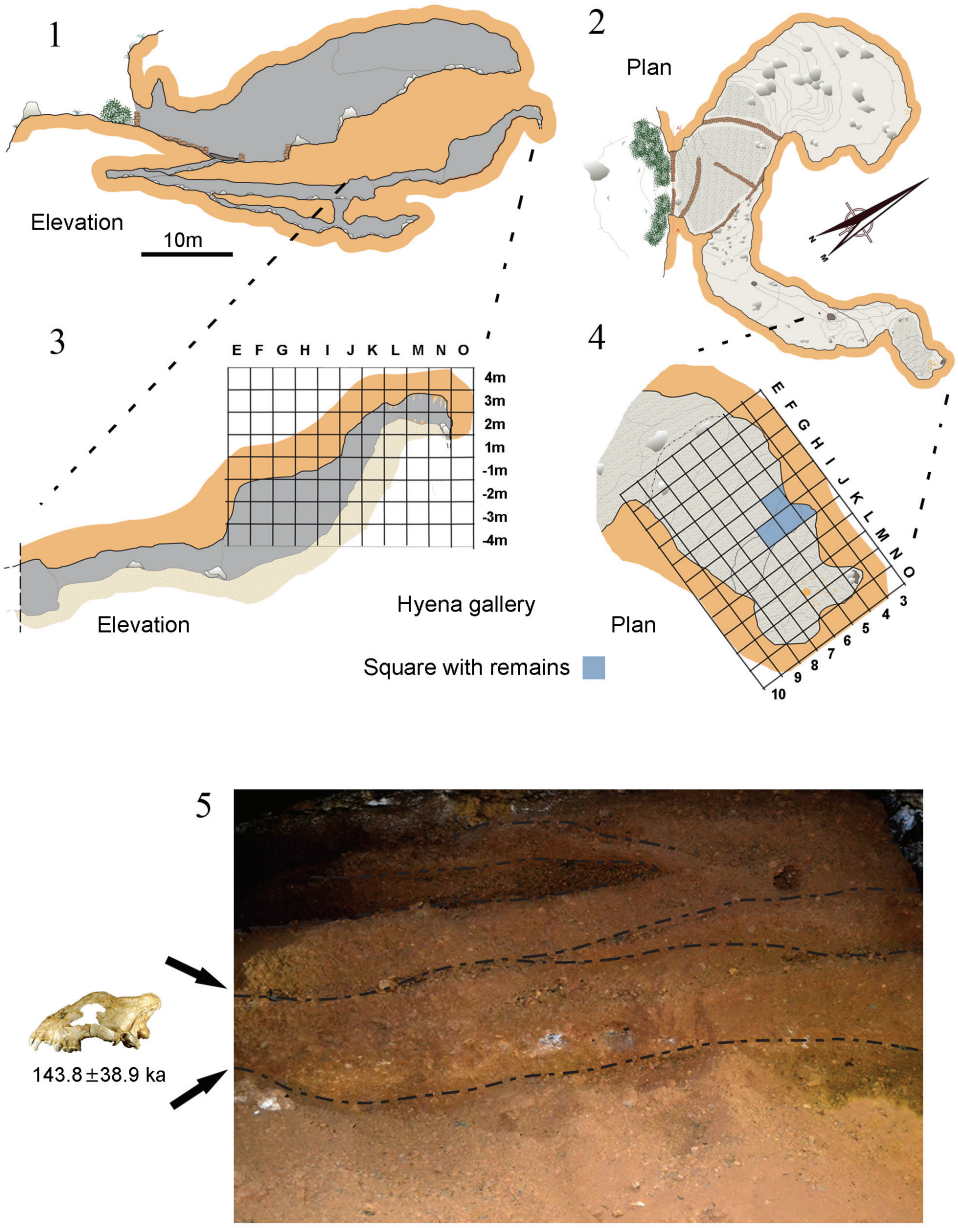

FIGURE 3. 1, Elevation view of Los Aprendices Cave. 2, Plan view of Los Aprendices Cave. 3, Detailed elevation view of the hyena gallery showing the excavation grid. 4, Detailed plan view of the hyena gallery showing the excavation grid as well as how the squares that were excavated were coloured. 5, Sediment cone that blocks off the former entrance to the hyena gallery. Within it one can see the hyena level, from which the skeleton of *Crocuta spelaea* was recovered.

As mentioned above, the sediment cone blocks off a former entrance. It has a depth of 7 m and consists of a superposition of conglomerate levels. The level at which the cave hyena was found is composed of a clayey matrix and clasts with a maximum diameter of 5 cm and an average size of roughly 2 cm. Neither the adjacent nor the overlying levels have reported macrofaunal remains. The level with the cave hyena includes few clasts in the area where the skeleton occurred, but was a conglomerate supported by the clayey matrix (Figure 3.5).

The large mammal association recovered from Los Aprendices Cave includes *Capra pyrenaica* and *Crocuta spelaea*. By screening and washing the sediment from the cave, the following microfaunal remains were also recovered: Lago-

morpha indet., Arvicolidae indet., *Galemys pyrenaicus* and Serpentes indet.

To investigate the chronology of the site, two bone samples were initially sent for C^{14} dating at the Poznan Radiocarbon Laboratory (Poland). Unfortunately, there was no collagen in the bones, precluding a successful analysis. Subsequently, samples were sent to be analysed by amino acid racemization. For this purpose, we chose three molars of *Capra pyrenaica*, found in the same level as the hyena. The analysis was carried out at the Laboratory of Biomolecular Stratigraphy (Laboratorio de Estratigrafía Biomolecular; LEB) of the Mines Engineering School Polytechnic University of Madrid. The sample was prepared in accordance with the LEB protocol and analysed in a HPLC-1100 high-performance liquid chromatograph equipped with a fluorescence detector. The age obtained by this process was 143.8 ± 38.9 ka (see Appendix 1 with abundance and racemization relations of various amino acids). Given the associated fauna at the site, we regard it as more coherent for the sigma to be negative, with the site thus dating to the early stages of the Late Pleistocene.

The fossil remains studied in the present paper are housed in the Museo de Ciencias Naturales of the University of Zaragoza (with reference abbreviations from MPZ 2014/574 to MPZ 2014/718). The remains were recovered with the authorization and financial support of the Government of Aragon and the Moncayo Natural Park.

MATERIAL AND METHODS

Identifiable remains and bone fragments larger than 4 cm have been studied. For a general taxonomic identification the following references were followed: Pales and Lambert (1971) and Walker (1985). Measurements were taken with digital calipers (Mitutoyo Digimatic Caliper CD-800 CX, Japan) in accordance with the protocols of Hollister (1918), Bonifay (1971), von den Driesch (1976), Clot (1980), Cardoso (1993) and Blasco and Montes (1997). All measurements are given in millimetres. The Los Aprendices specimen has been compared to individuals of the extant species collected from different localities and stored at the Royal Museum for Central Africa, Belguim (RMCA), the Museu de Ciències Naturals de Barcelona, Spain (MZB); and Museu de Geologia de Barcelona, Spain (MGB), and to Late Pleistocene fossils from Gabasa 1 (Huesca, Northern Spain) stored at the Museo Arqueológico Provincial de Huesca, Spain. In addition, the morphometric data have been compared with collections from western Europe published by Bonifay (1971), Blasco and Montes (1997), Altuna and Mariezkurrena (2000), García (2003), Testu (2006), Fourvel (2012) and others.

In order to assess the skeletal representation in the assemblage from Los Aprendices, we referred to the number of remains (NR), the number of identified specimens (NISP), the minimum number of elements (MNE) and the minimum number of individuals (MNI), which were calculated in accordance with Lyman (1994). To calculate the MNI, the teeth were used, because these are the most common anatomical element, and the degree of eruption and dental wear were also taken into account. The age of the *Crocuta spelaea* specimen was determined in accordance with the revision by Fourvel (2012) of the methods of Mills (1982) and Brugal et al. (1997).

Various types of marks produced by carnivore teeth have been differentiated (pits, punctures, grooves, furrowing, crenulated edges and impact points), following the definitions by Haynes (1980, 1983), Binford (1981) and Sala (2012). The measurements were taken with electronic digital calipers. To identify the carnivore marks, these measurements were compared with data provided by Delaney-Rivera et al. (2009), Domínguez-Rodrigo and Piqueras (2003), Saladié et al. (2013) and Rabal-Garcés et al. (2012).

To ascertain whether the breakage of the bones took place in fresh bone, immediately postmortem, or sometime after burial, as well as the possible causes of this breakage, we follow the criteria proposed by Villa and Mahieu (1991). This method takes into account the delineation (curved, intermediate or transverse), the angle (oblique, right angle or mixed) and the type of edge of the breaks shown by long bones greater than 4 cm in length (irregular or smooth). Further, the breakage index has also been taken into account. This refers to the size of the diaphysis preserved in relation to the total size of the bone in question, both in terms of its length and its circumference. The breakage indices that refer to the length of the diaphysis are L1 (preserved length < 25% of total length), L2 (preserved length between 25% and 50% of total length), L3 (preserved length between 50% and 75% of total length) and L4 (preserved length > 75% of total length). The breakage indices for the circumference are as follows: C1 (preserved circumference < 50% of total circumference), C2 (preserved circumference > 50% of total circumference) and C3 (the circumference is complete or almost complete, at least in some part).

Dentognathic and postcranial abbreviations: Bd, Breadth of the distal end; Bp, Breadth of proximal end; BPC, Proximal articular surface breadth; BM, body mass; c, lower canine; C, upper canine; d, distal; DMD, mesiodistal diameter; DPA, Olecranic maximum depth; DVL, vestibule-lingual diameter; GB, greatest breadth; GL, greatest length; H condyle md, height of mandibular condyle; Hdiast, height of ramus below the diastema; Hm1, height of ramus below m1; Hp4, height of ramus below p4; Hramus, mandibular ramus height; i2, second lower incisive; i3, third lower incisive; I1, first upper incisive; I2, second upper incisive; I3, third upper incisive; FL, femur length; HL, humerus length; l, left; L, length; Lm1, lower carnassial length; max, maximum; min, minimum; Mtc, metacarpus; Mtt, metatarsus; m1, first lower molar; n, sample size; p, proximal; p2, second lower premolar; p3, third lower premolar; p4, fourth lower premolar; P1, first upper premolar; P2, second upper premolar; P3, third upper premolar; P4, fourth upper premolar; r, right; SD, smallest breadth of the diaphysis; SKL, skull length; W, Width; W condyle md, width of the mandibular condyle; X: mean; σ, standard deviation; 1st Pha: first phalanx; 2nd Pha: second phalanx. Sites: Ap, Los Aprendices: L.K, Labeko Koba; S.I, Sima I; Bo, Bolinkoba; Ga, Gabasa; Fo, Fontainhas; Va, Valdegoba; C.B, Cueva del Búho; To, El Toll; Ol, Olopte B; C.O, Cova de l'Or; Mo, Mollet; Ata, Atapuerca; TD 8, Atapuerca Trinchera Dolina 8; LV, Lunel-Viel; Pe, Petralona; Mos, Mosbach; Ka, Kazanka; Context: A, archaeological; P, palaeontological. Chronology: P, Pleistocene; MP, Middle Pleistocene; ELP, early Late Pleistocene; LP, Late Pleistocene; EH, early Holocene; MPal, middle Palaeolithic; EUPal, early Upper Palaeolithic; UPal, Upper Palaeolithic; Ms, Mousterian; Chat, Chatelperronian; Per, Perigordian; Au, Aurignacian; Gr, Gravettian; So, Solutrean; Mg, Magdalenian; Az, Azilian.

RESULTS

A total of 217 remains have been recovered from the site of Los Aprendices, 209 of which have been identified taxonomically. Eight fossils larger than 4 cm that have not been identified taxonomically have also been recovered. The MNE is 120. A total of 194 remains of *Crocuta spelaea* have been recovered, belonging to a single adult individual. The Los Aprendices individual fits into class 4 (6-10 years) according to Fourvel (2012) (Figures 4, 5).The individual was found in anatomical semiconnection in the sediment cone within an area of scarcely two square metres (Figure 3.4-5**,** Table 1). Further, 15 remains belonging to at least two individuals of *Capra pyrenaica* have been recovered, one of the individuals being an adult and the other a neonate (see Table 2).

SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family HYAENIDAE Gray, 1821
Genus CROCUTA Kaup, 1828

Type Species. *Crocuta crocuta* Erxleben, 1777

Crocuta spelaea Goldfuss, 1823
(Figures 4-7)

1823 *Hyaena spelaea* Goldfuss p.456-462, figs. 16, 17.

1993 *Crocuta crocuta spelaea* Cardoso, p. 82-99, figs. 1, 2, 3, 4.

v. 1997 *Crocuta crocuta* Blasco and Montes , p.12, 14, 17-21, pl, 2, 3, 4, 5, 6, 7.

1998 *Crocuta crocuta spelaea* Iñigo, Molero and Maldonado, p. 66, 68, fig. 1.

1999 *Crocuta spelaea* Baryshnikov, p. 167, 168, figs. 2, 3, 4.

2002 *Crocuta crocuta* Davis, p. 54, 55, fig. 21.

2005 *Crocuta crocuta* Arbizu, Álvarez-Lao, and Adan, p. 134, pl, 1..

2006 *Crocuta crocuta spelaea* Diedrich and Žák, p. 248, 249, figs. 5, 6.

2006 *Crocuta crocuta spelaea* Testu, p. 273, 274 , pl, 12, 13

2008 *Crocuta crocuta spelaea* Diedrich, p. 825, fig. 3.

2010 *Crocuta crocuta* Arsuaga, Baquedano, Pérez-González, Sala, García, Álvarez-Lao, Laplana, Huguet, Sevilla, Blain, Quam, Ruiz Zapata, Sala, Gil García, Uzquiano, and Pantoja, p. 63, fig. 9.

2010 *Crocuta spelaea* Rosell, Blasco, Rivals, Cebrià, Morales, Rodríguez, Serrat, and Carbonell, fig. 4.

2012a *Crocuta crocuta spelaea* Diedrich, p. 67-74, figs. 3, 4, 5, 6, 7, 8, 9,10.

2012b *Crocuta crocuta spelaea* Diedrich, p. 173-177, figs. 3, 4, 5.,6,7

v. 2012 *Crocuta crocuta* Martínez-Sánchez, López-García, Alcalá-Ortiz, Blain, and Rabal-Garcés, p. 551, fig. 2.

2014 *Crocuta crocuta* Maroto, fig. 4.

2015 *Crocuta crocuta* Álvarez-Lao, Ruiz-Zapata, Gil-García, Ballesteros, and Jiménez-Sánchez, fig. 5.

2015 *Crocuta crocuta spelaea* Fourvel, Fosse, Fernandez, and Antoine, p. 248, 249, 250, fig. 3.

TABLE 1. List of anatomical elements recovered from the individual of *Crocuta spelaea* from Los Aprendices. L left. R right. NR, number of remains; NISP, number of identified remains; MNE: minimum number of elements.

Elements		MNE	NISP	NR
Cranium		1	12	12
Mandible	R	1	1	1
Mandible	L	1	3	3
Axis		1	4	4
Cervical V.		5	9	9
Thoracic V.		7	26	26
Lumbar V.		4	8	8
Ribs		10	29	29
Scapula	L	1	2	2
Scapula	R	1	2	2
Humerus	R	1	2	2
Ulna	L	1	2	2
Ulna	R	1	4	4
Radius	R	1	3	3
Scapholunate	R	1	1	1
Capitate	R	1	1	1
Unciform	R	1	1	1
Capitate	L	1	1	1
Pisiform	R	1	1	1
Mtc II	R	1	1	1
Mtc III	R	1	1	1
Mtc IV	R	1	1	1
Mtc V	R	1	1	1
Mtc II	L	1	1	1
Mtc III	L	1	1	1
Mtc IV	L	1	1	1
Mtc V	L	1	1	1
Femur	R	1	10	10
Tibia	R	1	2	2
Tibia	L	1	1	1
Talus	R	1	1	1
Calcaneus	L	1	1	1
Calcaneus	R	1	2	2
Cuboid	L	1	1	1
Cuboid	R	1	1	1
Pyramidal	R	1	1	1
Scaphoid	R	1	1	1
Scaphoid	L	1	1	1
Cuneiform	R	1	1	1
Cuneiform	L	1	1	1
Mt II	R	1	1	1
Mtt III	R	1	1	1
Mtt IV	R	1	1	1
Mtt V	R	1	1	1
Mt II	L	1	1	1
Mtt III	L	1	1	1
Mtt IV	L	1	1	1
Mtt V	L	1	1	1
1st phalanx		12	16	16
2nd phalanx		8	9	9
3rd phalanx		4	4	4
Sesamoids		13	13	13
		107	194	194

Holotype. *Hyaena spelaea* Goldfuss, 1823. Incomplete cranium (Goldfuss-Museum Bonn No. M2609).

Type Locality. Zoolithen Cave, Geilenreuth, Wiensent Valley, Bavaria, Germany.

Localities. The species is found in hundreds of Pleistocene caves throughout Europe.

Material. cranium (MPZ 2014/657), one mandible (MPZ 2014/593), one axis (MPZ 2014/589), five cervical vertebrae (MPZ 2014/592, MPZ 2014/605, MPZ 2014/607, MPZ 2014/668, MPZ 2014/675), seven thoracic vertebrae (MPZ 2014/641, MPZ 2014/656, MPZ 2014/661, MPZ 2014/667, MPZ 2014/670, MPZ 2014/674, MPZ 2014/690), four lumbar vertebrae (MPZ 2014/582, MPZ 2014/586, MPZ 2014/701, MPZ 2014/703), ten ribs (MPZ 2014/591, MPZ 2014/604, MPZ 2014/612, MPZ 2014/637, MPZ 2014/646, MPZ 2014/651, MPZ 2014/652, MPZ 2014/658, MPZ 2014/662, MPZ 2014/666), two scapulae (MPZ 2014/584, MPZ 2014/588), one humerus (MPZ 2014/672), two ulnae (MPZ 2014/610; MPZ 2014/676), one radius (MPZ 2014/611), one scapholunate (MPZ 2014/613), two capitate (MPZ 2014/630, MPZ 2014/659) one pisiform (MPZ 2014/614), eight metacarpi (MPZ 2014/575, MPZ 2014/581, MPZ 2014/615,

TABLE 2. Overview of NR, number of remains; NISP, number of identified remains; MNE, minimum number of elements; MNI, minimum number of individuals and the distribution by age of the fossils from Los Aprendices.

					MNI by ages	
Taxa	**NR**	**NISP**	**MNE**	**MNI**	**neonate**	**adult**
Capra pyrenaica	15	15	13	2	1	1
Crocuta spelaea	194	194	107	1		1
Unidentified (>4cm)	8					
Total	217	209	120	3	1	2

MPZ 2014/616, MPZ 2014/617, MPZ 2014/618, MPZ 2014/684, MPZ 2014/685), one femur (MPZ 2014/587), two tibiae (MPZ 2014/671, MPZ 2014/681), one talus (MPZ 2014/682), two calcanei (MPZ 2014/632, MPZ 2014/677), one unciform (MPZ 2014/678), two cuboids (MPZ 2014/ 623, MPZ 2014/ 629), two scaphoids (MPZ 2014/623, MPZ 2014/629), two cuneiforms (MPZ 2014/62, MPZ 2014/628), eight metatarsi (MPZ 2014/633, MPZ 2014/634, MPZ 2014/635, MPZ 2014/636, MPZ 2014/642, MPZ 2014/643, MPZ 2014/644, MPZ 2014/645) and twenty-four phalanxes (MPZ 2014/575, MPZ 2014/576, MPZ 2014/577, MPZ 2014/578, MPZ 2014/579, MPZ 2014/580, MPZ 2014/583, MPZ 2014/590, MPZ 2014/594, MPZ 2014/599, MPZ 2014/600, MPZ 2014/601, MPZ 2014/602, MPZ 2014/603, MPZ 2014/620, MPZ 2014/621, MPZ 2014/622, MPZ 2014/626, MPZ 2014/627, MPZ 2014/631, MPZ 2014/639, MPZ 2014/654, MPZ 2014/655, MPZ 2014/680).

The cave hyena is the predominant taxon in Los Aprendices. As the elements were found in

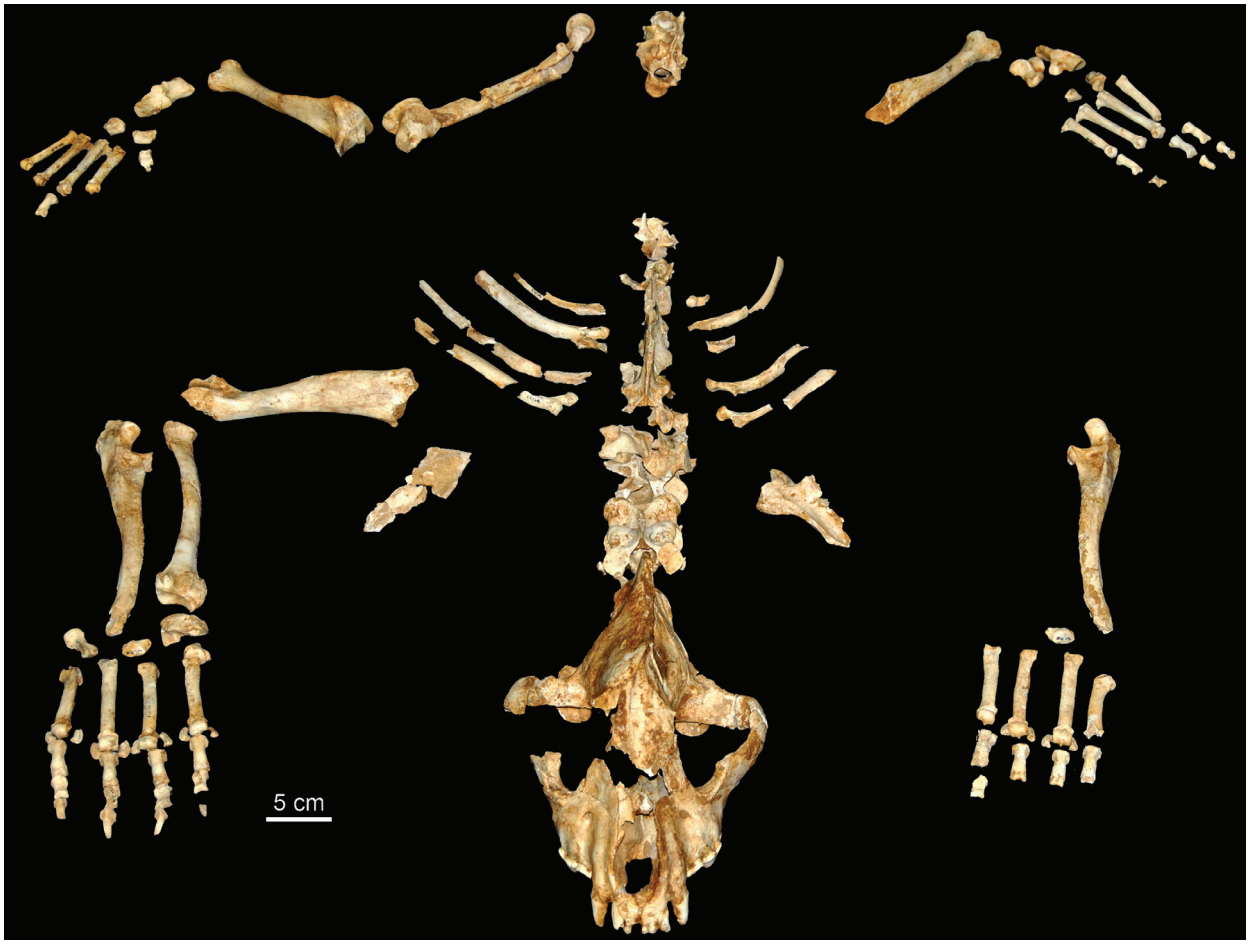

FIGURE 4. Panoramic photo of the skeleton of *Crocuta spelaea* from Los Aprendices.

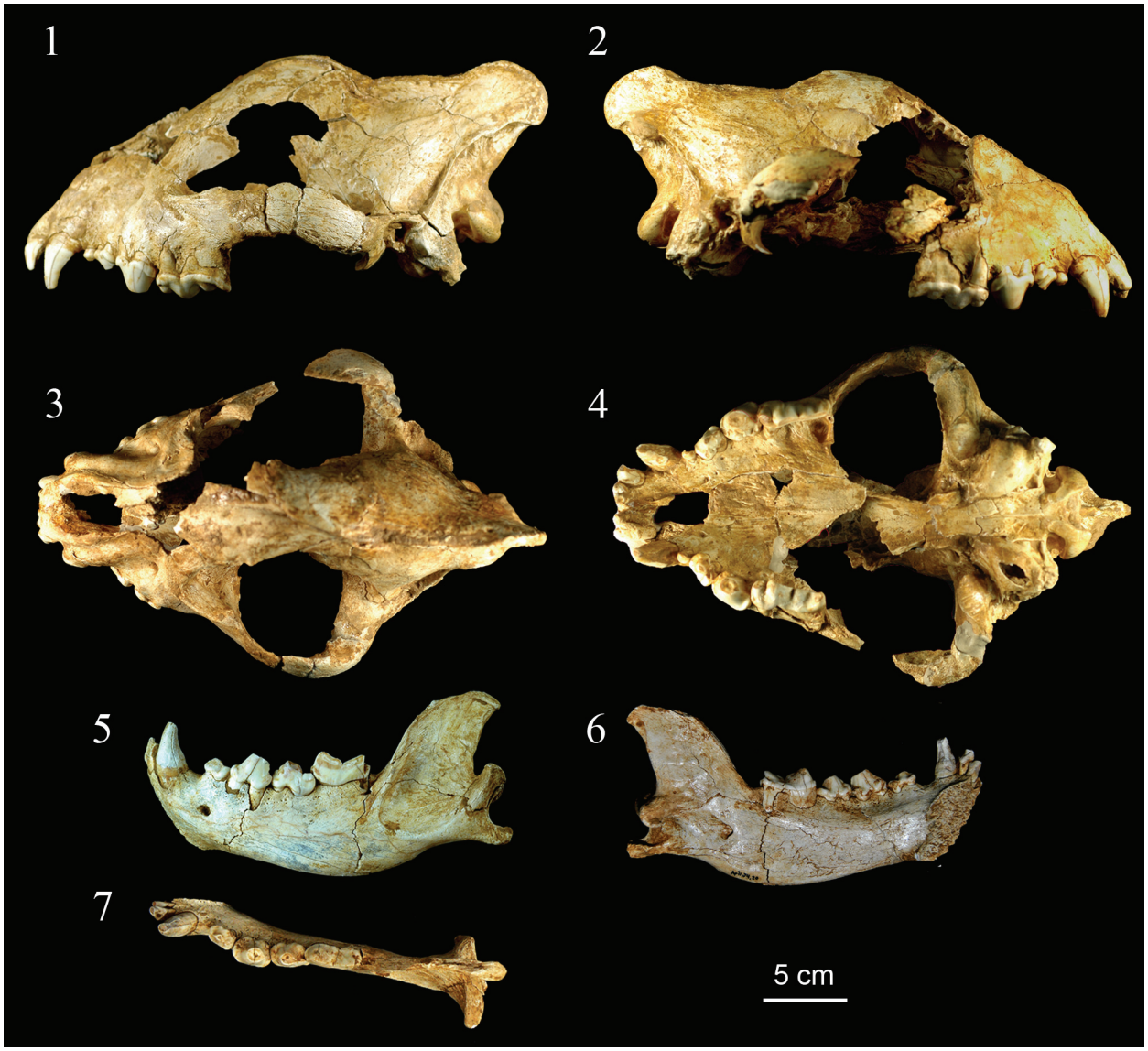

FIGURE 5. Photograph of the cranium (1-4, MPZ 2014/657) and hemi-mandible (5-7, MPZ 2014/593) of *Crocuta spelaea*: 1-2, lateral view; 3, dorsal view; 4, occlusal view; 5, buccal view; 6, lingual view; 7, occlusal view.

anatomical position and, presumably because there is no duplication of elements, they have been assigned to a single individual. We here describe the cranium, mandible, teeth, because these are elements of great taxonomic importance.

Description

Cranium. The cranium (MPZ 2014/657) is almost complete, lacking a fragment of the right zygomatic arch and part of the nasals including a fragment of the right side. The sagittal crest is slightly deformed, and the left side of the neurocranium is flattened (Figure 5). The diastema between the canine and P1 is reduced, and P1 and P2 are in contact (Figure 5.4). In extant *Crocuta crocuta,* P1-P2 are separated by a distance of several mm. The infraorbital foramen is located above the point of contact between P2 and P3. The dental series displays the moderate curvature typical of *C. spelaea* (García, 2003). The palate is wide at the P4, and even though it is broken a pronounced concavity characteristic of the genus Crocuta can be observed (Morales et al., 1987). The cranium has a wide snout with a slight post-canine constriction. The rostral region (splanchnocranium) is short and wide, conferring upon it a “U”-shape in dorsal view, whereas in *Hyaena* it is “V”-shaped (García, 2003). One of the most notable characteristics of the cra-

FIGURE 6. *Crocuta spelaea* forelimb remains from Los Aprendices. 1, left scapula in dorsal view (MPZ 2014/584). 2, left humerus in cranial view (MPZ 2014/672). 3, right radius in palmar view (MPZ 2014/611). 4, left ulna in medial view (MPZ 2014/610). 5, right ulna in medial view (MPZ 2014/676). 6, right Mtc V in dorsal view (MPZ 2014/618). 7, right Mtc IV in dorsal view (MPZ 2014/617). 8, right Mtc III in dorsal view (MPZ 2014/616), 9, right Mtc II in dorsal view (MPZ 2014/615). 9, left Mtc II in dorsal view (MPZ 2014/685). 10, left Mtc III in dorsal view (MPZ 2014/684). 11, left Mtc IV in dorsal view (MPZ 2014/ 581). 12, left Mtc V in dorsal view (MPZ 2014/575). 13, right scapholunate in proximal view (MPZ 2014/613). 14, right pisiform in proximal view (MPZ 2014/614). 15, trapezoid (MPZ 2014/619). 16, right cuneiform in dorsal view (MPZ 2014/659). 17, unciform (MPZ 2014/678) 18-26, first phalanx in dorsal view (MPZ 2014/576, 577, 578, 583, 621, 622, 626, 631). 27-34, second phalanx in lateral view (MPZ 2014/594, 599, 600, 601, 627, 639, 654, 655). 35-37, third phalanx in dorsal vier (MPZ 2014/590, 603, 680).

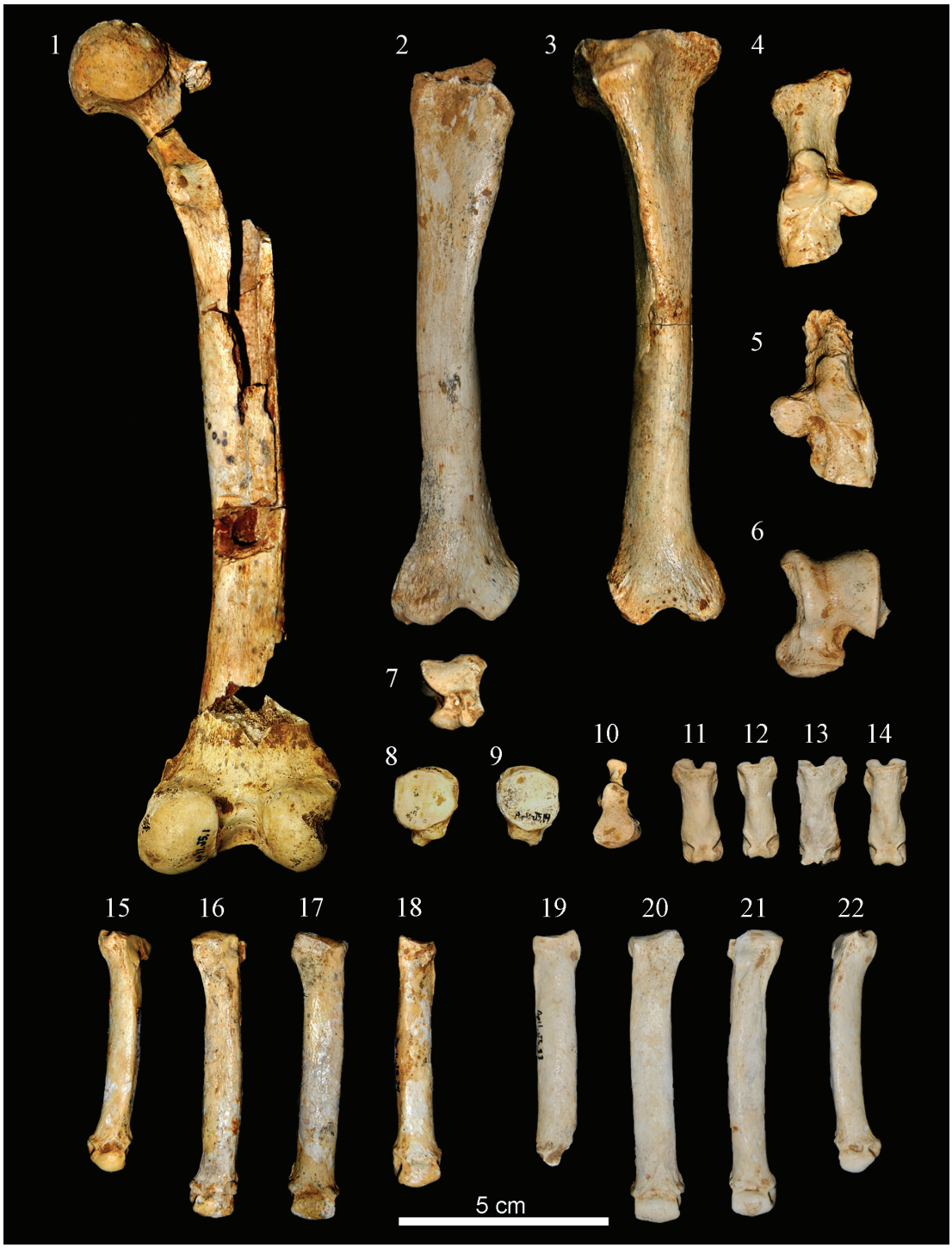

FIGURE 7. *Crocuta spelaea* hind limb remains from Los Aprendices. 1, right femur in caudal view (MPZ 2014/587). 2, left tibia in cranial view (MPZ 2014/681). 3, right tibia in cranial view (MPZ 2014/671). 4, left calcaneus in dorsal view (MPZ 2014/677). 5, right calcaneus in dorsal view (MPZ 2014/632). 6, left astragalus in dorsal view (MPZ 2014/682). 7, left navicular in lateral view (MPZ 2014/625). 8, right cuboid in proximal view (MPZ 2014/ 623). 9, left cuboid in proximal view (MPZ 2014/ 629). 10, left first cuneiform in proximal view (MPZ 2014/62). 11-14, first phalanx in dorsal view (MPZ 2014/579, 580, 620, 624). 15, right Mtt V in dorsal view (MPZ 2014/636). 16, right Mtt IV in dorsal view (MPZ 2014/635). 17, right Mtt III in dorsal view (MPZ 2014/634). 18, right Mtt II in dorsal view (MPZ 2014/633). 19, left Mtt II in dorsal view (MPZ 2014/642). 20, left Mtt III in dorsal view (MPZ 2014/643). 21, left Mtt IV in dorsal view (MPZ 2014/644). 22, left Mtt V in dorsal view (MPZ 2014/645).

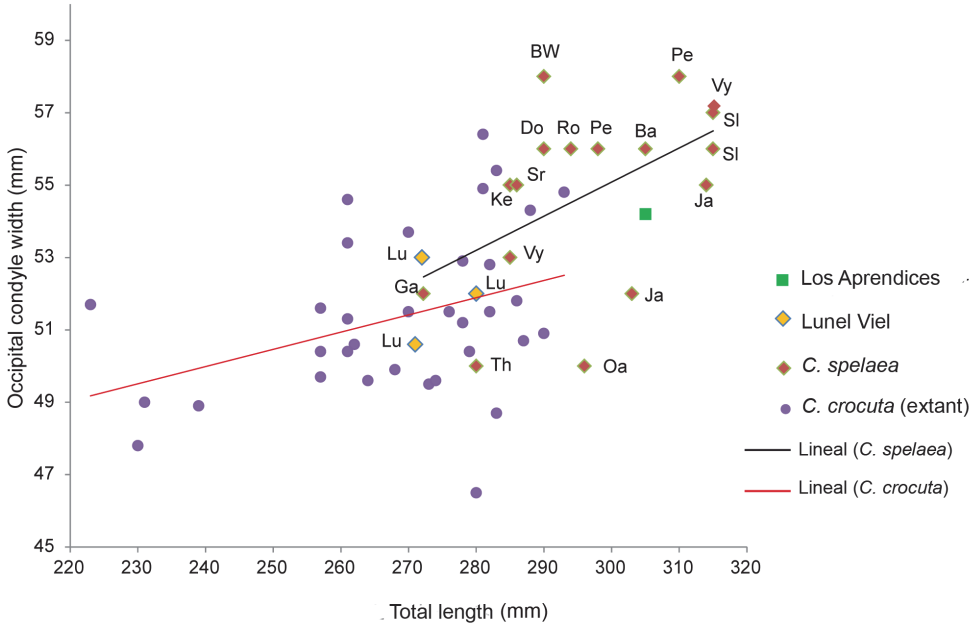

FIGURE 8. Bivariate graph representing the width of the condyles in relation to the total length of the cranium. Abbreviations:Ba, Badel Cave; BW, Bad Wildungen; Do, Döbritzer Cave; Ja, Jaurens; Ke, Ketsch; Pe, Perick Caves; Ro, Rösenbecker Cave; Th, Thiede; Oa, Oase Cave; Sr, Srbsko Cave; Vy, Výpustek Cave (Diedrich, 2011a); Sl, Sloup Cave (Diedrich, 2012b); Ga, Gargas (Cardoso, 1993); Lu, Lunel Viel (Bonifay, 1971). The measurements of the crania of extant *C. crocuta* specimens were taken by J.M.-M of the Royal Museum for Central Africa (RMCA) of Belgium.

nium is the absence of M1. This element is generally lacking in the genus *Crocuta* but is present in *Hyaena,* in which M1 has three cuspids (Kurtén, 1957; Werdelin and Solounias, 1991; García, 2003).

The cranium has a total length of 305 mm, which lies clearly outside the range of extant *Crocuta crocuta* (see Figures 5, 8; Appendix 2). However, it matches the size documented for cave hyenas and is larger than the *C. c. intermedia* (Serres et al., 1828) of Lunel Viel (Bonifay, 1971). In general terms the measurements of the skull of Los Aprendices are similar but lightly larger than those of *Crocuta crocuta praespelaea* from Mosbach, Kazanka and Petralona (Kurtén, 1962; Kurtén and Poulianos, 1981; Schütt, 1971; Baryshnikov, 2014). The specimen from Los Aprendices is similar in size to cave hyenas from central Europe at the sites of Badel Cave, the Perick Caves, and Rösenbecker Cave (Diedrich, 2011a), as well as at the French site of Jaurens (Ballesio, 1979). In comparison with other crania from the Iberian Peninsula, the specimen from Los Aprendices is clearly smaller as compared with the specimen from Fontainhas (L=317 mm) in Portugal (Cardoso, 1993), and slightly larger than the cranium from Gabasa 1 (L=294mm) (Blasco and Montes, 1997). Furthermore, it is larger than the latest Early Pleistocene cranium from Gran Dolina TD4W (L=265mm), which is ascribed to *C. crocuta* (García and Arsuaga, 1999).

Upper dentition. C1. The length and width of the upper canines from Los Aprendices are within the range of variation of extant *Crocuta crocuta* but are clearly larger than average (Appendix 3).

P1. P1 is a small simple tooth, the crown of which forms a low cone crossed by a ridge that transversely divides it into two.

P2. Mesial and distal accessory cusps are present and clearly developed. The outline of the tooth is rectangular, with the distal part buccolingually wider than the mesial part. The length and width of P2 from Los Aprendices fall within the range of extant *Crocuta crocuta* but close to the maximum values. The P2 from Los Aprendices is clearly larger than the P2 from the cranium of *C. crocuta* from Gran Dolina TD4W. The P2 from Los Aprendices is larger than *C. crocuta* spp. from Petralona (Baryshnikov and Tsoukala, 2010) and the *C. c praespelaea* from Kazanka and Mosbach (Baryshnikov, 2014), which according to Baryshnikov (2014) has the largest P2 of the *spelaea* forms. It is remarkable that the Los Aprendices P2 is the larg-

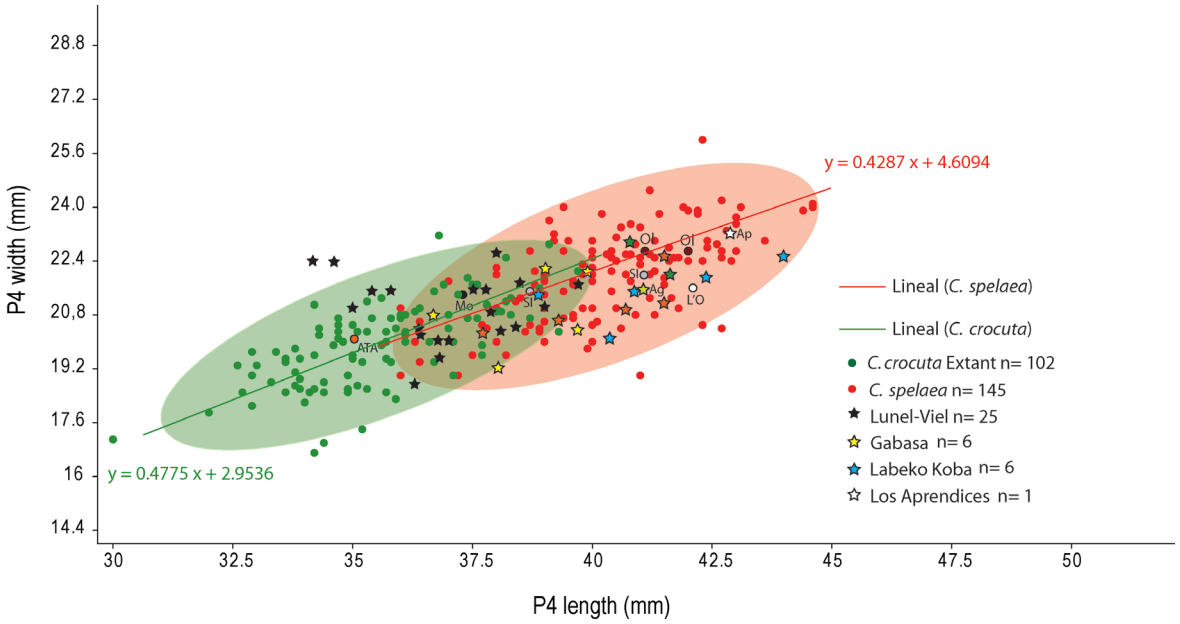

FIGURE 9. Graph representing total length versus total width of P4 of extant and cave hyaena from several sites. The comparative measurements have been extracted from, Reynolds, 1902; Bonifay, 1971; Ballésio, 1979; Clot, 1980; Argant, 1991; Cardoso, 1993; Blasco and Montes, 1997; Fosse, 1997; Castaños, 1987; Baryshnikov, 1999; Altuna and Mariezkurrena, 2000; García, 2003; Testu, 2006; Fourvel, 2012; and J.M.-M personal commun., 2015. Abbreviations: ATA, Atapuerca; Ag, Aguilón P-7; Ap, Los Aprendices; Mo, Mollet; Ol, Olopte B; L'Or Cova de l'Or; SI, Sima I. Confidence ellipses with confidence interval (0.95) are figured.

est premolar recovered in the Iberian Peninsula of fossil record of *Crocuta* genus.

P3. P3 is characterized by the great development of the protocone, which is surrounded by a well-developed cingulum and lacks accessory cusps. This tooth is an important part of the process of bone crushing (Schütt, 1971), and therefore its structure can be used to evaluate the degree of adaptation the dentition to feeding on carrion (Baryshnikov, 2014). This tooth presents an extremely high crown, which is also seen in other populations of *Crocuta spelaea.* It indicates a *Crocuta spelaea* specialization for breaking bones related to scavenging. The length and width values of P3 from Los Aprendices are within the range of variation of the Iberian Pleistocene cave hyena and exceed the measurements of extant *C. crocuta* (Appendix 3).

P4. The anterior face of the protocone is approximately level with the anterior face of the parastyle, which is typical of the genus *Crocuta* (Wederlin and Solounias, 1991) Its greatest length and width markedly exceed those of extant *C. crocuta* and *C. c. intermedia* (Cardoso, 1993), and it is also larger than the *C. crocuta* from the Middle Pleistocene of Gran Dolina TD4W (García, 2003). The Los Aprendices specimen is of similar length and width as *C. c. praespelaea* from Kazanka (Baryshnikov, 2014) and is slighty larger than *C. c. praespelaea* from Mosbach (Bayshnikov, 2014) and *C. crocuta* spp. from Petralona (Baryshnikov and Tsoukala, 2010). Therefore, its values are similar to those of *C. spelaea* from the Iberian Peninsula, such as Gabasa 1 (Blasco and Montes, 1997), Fontainhas (Cardoso, 1993), Sima I, Kobaedaerra (Castaños, 1987), Labeko Koba (Altuna and Mariezkurrena, 2000), El Toll, Olopte B and Cova de l'Or (J.M.-M personal commun., 2015.) (Appendix 3). The extreme metrical variability of dental remains (Figure 9, Appendix 3) most likely coincides with ecomorphotypic variation, so it is not recommended to use cave hyenas for biochronological purposes (e.g., Kurtén, 1957; Kurtén and Poulianos 1977; Klein and Scott 1989; Baryshnikov 1999, Fourvel et al., 2015).

Mandible. The left hemimandible from Los Aprendices is well preserved and practically complete. The corpus preserves the i1, i2, c1, p2, p3, p4 and m1, all showing wear. The ramus has a complete and well preserved coronoid process, articular and angular apophyses. The corpus presents a basal edge that in lateral view is strongly convex at the level of m1 (Figure 5.5-6). This feature is characteristic of *Crocuta* (Bonifay, 1971; Testu, 2006). The hemimandible is mesiolingually curved. In buc-

cal view, the ramus in its distal part shows a deep, subtriangular masseteric fossa that extends from the protoconid of m1 to the angular process and the condyle. The single mental foramen is placed at the level of p2. The arrangement of the first two premolars (p2 and p3) is not overlapping, and p4 and m1 overlap as in *Crocuta* (Testu, 2006). The disposition of the premolars in the dental series is clearly curved (Figure 5.7); this curvature is caused by the increase in size and is a distinctive feature of *C. spelaea* (García, 2003).

Los Aprendices hemimandible is larger mesiodistally as compared with extant *Crocuta crocuta* (Appendix 4). It is also far larger than fossil hyenas from the Middle Pleistocene, such as Atapuerca TD 8 (García, 2003) and Lunel Viel (Bonifay, 1971). However, the distance c1-m1 is smaller than in *C. c. praespelaea* from Kazanka (Baryshnikov, 2014). On the other hand, the mandible fits perfectly within the range of *C. spelaea* and is one of the largest specimens of the Iberian Peninsula (Appendix 4). The biometric analysis of the hemimandible further reinforces the inclusion of the studied specimen in the hypodigm of *C. spelaea*.

Lower dentition. c1. The c1 is within the range of variation shown by the population of Pleistocene cave hyenas and larger than extant *Crocuta crocuta* (Appendix 5).

p2. The main cusp, the protoconid, is buccolingually wide and mesially surrounded by a well-developed cingulum. The distal accessory cusp is well-developed and separated from the protoconid by a transverse groove. The p2 of Los Aprendices is clearly larger than the average for extant *C. crocuta*, *C. c. intermedia* and *C. c. praespelaea* from Petralona (Appendix 5). On the other hand, its values fit perfectly with the *C. spelaea* from Labeko Koba (Altuna and Mariezkurrena, 2000) and are slightly smaller than the individual of *C. c. praespelaea* from Kazanka (Baryshnikov, 2014). It is also slightly larger than the population of *C. spelaea* form Gabasa (Blasco and Montes, 1997).

p3. The protoconid has a slightly distal tilt, and shows a marked cingulum on the mesial and distal edges. No accessory cusps are developed. The p3 of Los Aprendices is the largest from the Iberian fossil record and definitely larger than extant *Crocuta crocuta* (Appendix 5).

p4. p4 displays well-developed accessory cuspid with the distal one being mesiodistally longer than the mesial one. As in p3, the protoconid displays a slight distal tilt. The p4 fits perfectly within the range of Late Pleistocene cave hyenas, being larger than extant *Crocuta crocuta* and *C. c. intermedia,* which we classified as a *C. crocuta* from the Middle Pleistocene. Furthermore, the measurements from Los Aprendices are similar to the *C. c. praespelaea* (Appendix 5).

m1. The paraconid is clearly mesiodistally larger than the protoconid, a taxonomic character only seen in *Crocuta* among Middle to Late Pleistocene bone-cracking hyaenas (Werdelin and Solounias, 1991). The m1 presents a well-developed cingulum on the lingual side that extends up to the anterior edge. Distally, a mesiodistally short talonid is evident, which is a character typical of the genus *Crocuta*. Finally, the distolingual part of the protoconid displays a small but well-marked metaconid. Several scholars consider the presence of well-developed metaconid in the m1 as an ancestral character in the genus *Crocuta*, barely present in the last European spotted hyaenas. However, the extreme variability in the development and presence of m1 metaconid in extant and extinct representatives of the genus *Crocuta* prevent its use for taxonomic proposes (Werdelin and Solounias, 1991; García, 2003).

The length and width of m1 from Los Aprendices are within the range of variation of the Iberian Pleistocene cave hyena and exceed the measurements of extant *Crocuta crocuta* (Appendix 5). In Figure 10, it can be observed that there are two distinct populations: one for the *C. spelaea* and another population made up of extant *C. crocuta* and the specimens of *C. crocuta* from the Middle Pleistocene, such as *C. c. intermedia* (Bonifay, 1971) *C. crocuta* from Gran Dolina (García, 2003).

Forelimbs. The forelimb bones (Figure 6; Appendix 6) include both incomplete scapulae, one nearly complete humerus, both complete ulnas, one complete radius, some carpals such as the scapholunar, pisiform, cuneiform and unciform, and all eight metacarpals except the Mtc I.

Humerus. The proximal epiphysis of the humerus is broken and the head is missing. In cranial view, the diaphysis is straight laterally flattened, with caudal bending in the proximal third. The deltoid crest is very prominent and connected with the humeral crest. The distal trochlea is wide and the condyle is broken. Above this there is a well-developed oval supratrochlear foramen. In the distal part of the diaphysis, there is a deep and well-developed olecranon fossa. As a consequence of the broken or absent epiphysis, is not possible to metrically compare the humerus with other known samples.

Radius. The proximal epiphysis has an oval outline. The bicipital tuberosity is prominent, oval and

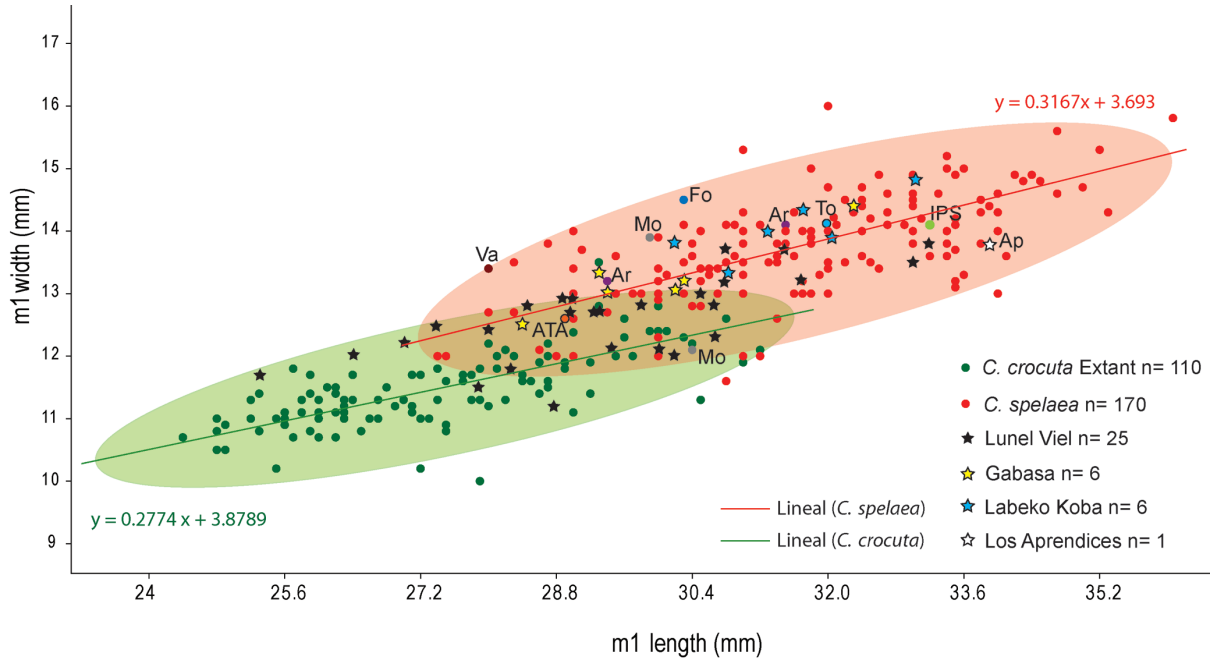

FIGURE 10. Graph representing total length versus total width of m1 of extant and cave hyaena from several sites. The comparative measurements (in mm) have been extracted from, Reynolds, 1902; Bonifay, 1971; Ballésio, 1979; Clot, 1980; Argant, 1991; Cardoso, 1993; Blasco and Montes, 1997; Fosse 1997; Castaños, 1987; Baryshnikov, 1999; Altuna and Mariezkurrena, 2000; García, 2003, Testu, 2006; Fourvel, 2012 and J.M.-M personal commun., 2015. Abbreviations: ATA, Atapuerca; Ap, Los Aprendices; Ar, Arbreda; Fo, Fontainhas; IPS, Institut de Paleontologia M. Crusafont de Sabadell; Mo, Mollet; To, El Toll; Va, Valdegoba. Confidence ellipses with confidence interval (0.95) are figured.

is placed on the proximolateral part of the diaphysis. The diaphysis has a semicircular cross section and is anteroposteriorly flattened. It shows strong torsion in the distal part of the bone. The distal epiphysis is mediolaterally wider than the diaphysis and has a very marked styloid process that is pointed and projected distally. The radius length of the Los Aprendices specimen (227 mm) is within the range of variation of Iberian Pleistocene cave hyenas. Its length also lies within the range of extant *Crocuta crocuta*, but is slightly below average (Appendix 6, Figure 11.1). Despite being shorter than that of extant *C. crocuta,* it is moderately mediolaterally wider, which gives a characteristic robust aspect to *C. spelaea* (Kurtén, 1957).

Ulna. The proximal part of the olecranon process is not preserved and the diaphysis displays more curvature and robusticity as compared with extant *Crocuta crocuta*. The triangular area below the lesser semilunar notch is deep and connected to the depressed area for the interosseous ligament, which can be seen on the lateral part of the diaphysis. The styloid process is robust with a rounded articular circumference that projects posteriorly.

Metacarpals. The metacarpals are clearly shorter than the average in extant *Crocuta crocuta* and are mediolaterally robust (Appendix 6, Figure 11.2). The length and width of MtcpIII falls outside the range of variation of extant *C. crocuta,* being closer to the minimum values for proximodistal length and close to the maximum values for mediolateral breadth (Appendix 6).

Hindlimbs. Of the hindlimbs (Figure 7; Appendix 6), only one broken femur and both tibiae are more or less complete. One astragalus and both calcanei complete some tarsals have also been recovered: one navicular, both cuboids, one first cuneiform and all eight metatarsals except Mtt I.

Femur. The diaphysis is straight in the proximal part and slightly anterioposteriorly curved in the distal part. It has a circular cross-section, which becomes oval in the distal part. The proximal epiphysis is broken and the great trochanter is missing. The neck is complete and connects the diaphysis with the head, which is spherical shape and presents an oval fovea capitis. The distal epiphysis of femur consisted of two similar condyles. The lateral one is partially broken. The condyles are similar, situated at the same level and

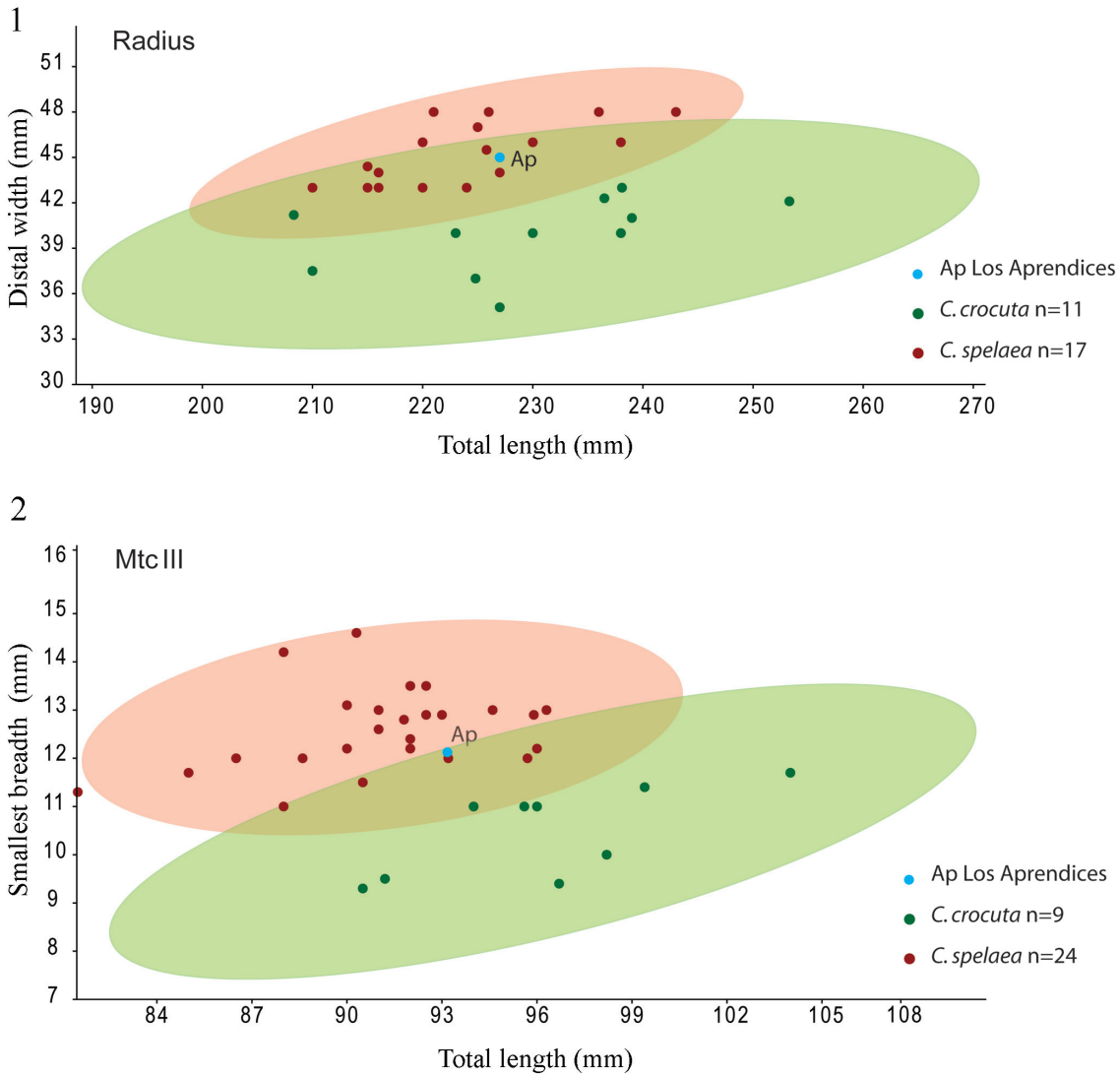

FIGURE 11. 1, Graph representing total length of radius versus distal width of extant and cave hyaena from several sites. The comparative measurements (in mm) have been extracted from Ehrenberg, 1940; Cardoso, 1993; García, 2003; Diedrich, 2011e; and J.M.-M personal commun., 2015. 2, Total length of third metacarpus versus smallest breadth of the diaphysis (SD) of extant and cave hyaena from several sites. The comparative measurements (in mm) have been extracted from Ehrenberg, 1940; Cardoso, 1993; García, 2003; Fourvel, 2012, and J.M.-M personal commun., 2015. Confidence ellipses with confidence interval (0.95) are figured.

separated by a intercondyloid fossa. The femur length of the Los Aprendices specimen is within the range of variation of extant *Crocuta crocuta* but very close to the maximum values and clearly greater than the average (Appendix 6). The distal epiphysis mediolateral width is outside the range of variation of extant *C. crocuta* (Appendix 6). The femur from Los Aprendices is similar in size to the femur from Labeko Koba (Altuna and Mariezkurrena, 2000) and larger than the femur from TD5, which belongs to *C. crocuta* (García, 2003). In Figure 12.1, it can be observed that there are two clusters that differentiate *C. spelaea* from extant *C. crocuta*.

Tibia. The tibia is short and robust. It is slightly convex on the proximomedial side. The proximal epiphysis has a triangular cross-section, and this morphology continues throughout the diaphysis except for the distal portion, where it is oval. The tibial crest is wide and well-developed. The distal epiphysis is subrectangular, with a well differentiated, laterally projecting medial rounded malleolus. The length and width of tibia from Los Aprendices are within the range of variation of the cave hyena

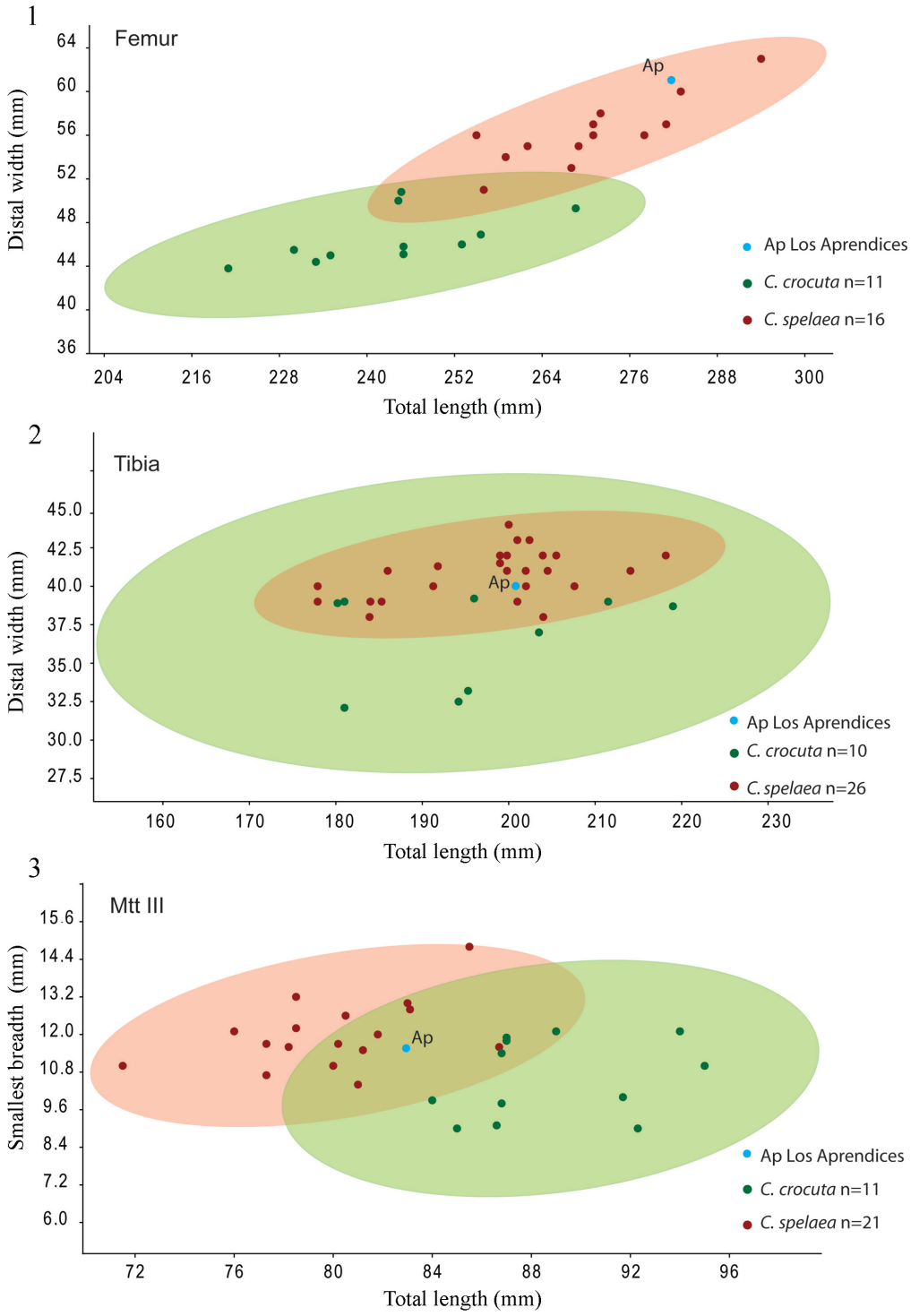

FIGURE 12. 1, Graph representing total length of femur versus distal width of extant and cave hyaena from several sites. The comparative measurements have been extracted from Ehrenberg, 1940; Cardoso, 1993; Altuna and Mariezkurrena, 2000; Diedrich, 2011e. 2, Total length of tibia versus distal width of extant and cave hyaena from several sites. The comparative measurements have been extracted from Reynolds, 1902; Ehrenberg, 1940; Cardoso, 1993; Diedrich, 2011e; Fourvel, 2012. 3, Total length of third metatarsus versus smallest breadth (SD) of the diaphysis of extant and cave hyaena from several sites. The comparative measurements have been extracted from Ehrenberg, 1940; Cardoso, 1993; García, 2003; Fourvel, 2012. Confidence ellipses with confidence interval (0.95) are figured.

and extant *Crocuta crocuta* (Appendix 6, Figure 12.2).

Metatarsals. The metatarsals are shorter than those of extant *Crocuta crocuta* and more robust (Appendix 6, Figure 12.3). As occurs with Mtc III, the length and width of Mtt III is outside the range of variation of extant *C. crocuta,* but close to the length minimum and wider than the maximum value (Appendix 6, Figure 12.3).

TAPHONOMY

The recovered specimen of *Crocuta spelaea* displays several gnaw marks and fractures putatively corresponding to carnivore activity and for this reason a detailed taphonomic study was carried out.

Breakage

Breakage of the long bones was analysed in accordance with the protocol of Villa and Mahieu (1991). The delineation of the fractures of the bones tends to be transverse (70%). The predominant angles are right angles (80%), and the edges are mainly irregular (85%) (Figure 13.1). With regard to the length and section of the preserved diaphysis there is a predominance (30%) of bones with a length greater than a quarter but less than half of the total length of the bone (L2), and a complete diaphysis (C3). Second in frequency (21.8%) are bones with a length less than a quarter of the total and a complete diaphysis section (C3). It is noteworthy that only 34% of the bones have a diaphysis section of less than a third of the total (C1). Likewise, bones with a length of less than a quarter of the total only represent 21.8% of the total (Figure 13.2). The presence of a high number of bones with transverse delineation, right angles and irregular edges is related to fracturing when the bone is dry, and this pattern indicates that the bone has been broken due to sedimentary pressure.

Gnaw Marks

The skeleton of the hyena from Los Aprendices displays modifications produced by carnivores, showing evidence of scavenge. Twenty bones with bite marks have been found, which – with a NISP of 191 – yields of percentage of 10.5%. The part of the skeleton with the greatest modification is the zeugopod-stylopod region, with 25% of the remains altered. The axial skeleton also presents a considerable degree of alteration, with 11.5% of the remains altered, while the autopods show a much lower level of alteration, amounting to just

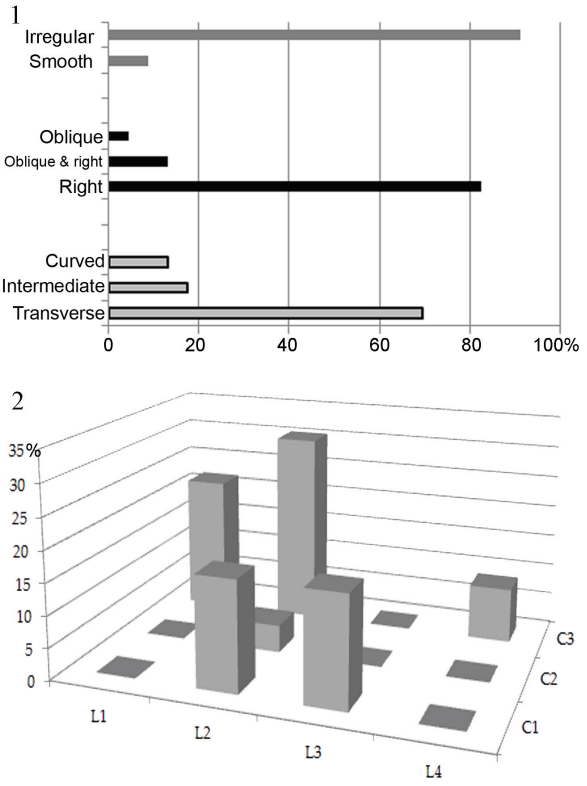

FIGURE 13. 1, Analysis of the breakage of the long bones from the skeleton of *Crocuta spelaea* from Los Aprendices, showing the abundance of each type of fracture according to the criteria analysed: angle, delineation and edge of the breaks. 2, Analysis of the breakage of the diaphyses in terms of circumference (C1, C2, C3) and length (L1, L2, L3, L4) for the skeleton of *Crocuta spelaea* from Los Aprendices.

4.2%. The low modification of the autopodium could be related to low bone consumption intensity, which also is supported by the fact that no ingested bone flakes have been recovered. (Table 3, Figure 14).

Table 4 presents the data for the different types of bite marks documented and their distribution among the different bone elements. The main

TABLE 3. Cave hyena remains (NISP) affected by carnivore bites in the skeleton of *Crocuta spelaea* from Los Aprendices.

	NISP	Modified NISP	% Modified
Axial skeleton	96	11	11.5
Zeugopod-stylopod	24	6	25
Autopod	71	3	4.2
Total	191	20	10.5

FIGURE 14. Photographs of the various types of marks (indicated by white arrows) present on the skeleton of *Crocuta spelaea* from Los Aprendices. 1, detailed image of the proximal epiphysis of the right humerus (MPZ 2014/672). 2, humerus in cranial view (MPZ 2014/672). 3, humerus in lateral view (MPZ 2014/672). 4, right ulna (MPZ 2014/676) showing "furrowing" on the proximal epiphysis, as well as a "puncture". 5, left ulna (MPZ 2014/610) showing "furrowing" on the proximal epiphysis. 6, right tibia (MPZ 2014/681) showing "furrowing" on the proximal epiphysis. 7-8, lateral and dorsal views of a left calcaneus (MPZ 2014/677) showing "furrowing" and grooves on the calcaneal tuberosity. 9, rib (MPZ 2014/591) showing a "puncture". 10, lumbar vertebra (MPZ 2014/582) in caudal view showing "furrowing" on the vertebral body. 11, lumbar vertebra (MPZ 2014/582) in ventral view showing three pits, corresponding to the incisors of a medium-sized carnivore. 12-13, lateral and caudal views of a dorsal vertebra (MPZ 2014/674) showing how the vertebral body has been torn off by a bite.

TABLE 4. Number of cave hyena remains (NISP) affected by different types of bites in the skeleton of *Crocuta spelaea* from Los Aprendices.

	"Groove"	"Pit"	"Puncture"	Crenulated edge	Impact point	"Furrowing"	"Scoping out"
Cervical V.						2	
Thoracic V.						1	
Lumbar V.		3		2		1	
Indet. V.		1	1	1	1	2	
Scapula			1			1	
Ribs		1	1	2		2	
Humerus	1	1	1		1		1
Ulna		1	1		1	2	
Femur	1					1	
Tibia	1	1	2			1	1
Tarsal	1					1	
Phalanx						2	
NISP	4	8	7	5	3	16	2

conclusion from the analysis is that the most abundant type of mark on the hyena bones is “furrowing”, which appears on 15 remains, followed by “punctures” and “pits”, which in total appear on 12 remains (Figure 14). In terms of bone consumption sequence, the skeleton of Los Aprendices shows low bone consumption.

Measurements have been taken on the tooth marks produced by carnivores (“pits”, “punctures” and grooves). All the marks measured were found on spongy bone or fine cortical bone. The mean width of the depressions (“pits” and “punctures”) is 2.91 mm, and the mean length is 3.77 mm. The grooves have a mean width of 1.60 mm and a mean length of 5.70 mm (Table 5).

DISCUSSION

The Iberian Record of *Crocuta*

The earliest European occurrence of *Crocuta crocuta* is from the latest Early Pleistocene layer TD4-5 of Gran Dolina in the Sierra de Atapuerca (Spain) (ca. 0.9 Ma; García and Arsuaga, 1999). The presence of the taxon is almost continuous in the TD sequence. The sequence from TD3-4-TD8 is dated to between 473 ±130 and 900±150 ka (Moreno et al., 2015). A closer age, but just after the Brunhes-Matuyama boundary is shown by the record from Casal Selce in Italy (Sardella and Petrucci, 2012). The arrival of *C. crocuta* and the extinction of *Pachycrocuta brevirostris*, last recorded in layer EVT7 of Vallaparadís Estació (ca. 0.85 Ma; Madurell-Malapeira et al., 2010), mark the beginning of the Galerian Mammal Age in

TABLE 5. Measurements of the “pits”, “punctures” and grooves found in the skeleton of *Crocuta spelaea* from Los Aprendices. Abbreviations: min, minimum; max, maximum; σ, standard deviation; n, sample size; L, length; W, width.

	Pits in cancellous bone			Punctures in cancellous bone			"Pits" & "punctures" in cancellous bone			Grooves in cancellous bone	
	Width	Length	L/W	Width	Length	L/W	Width	Length	L/W	Width	Length
Mean	2.38	3.21	1.35	3.61	4.49	1.2	2.91	3.77	1.31	1.6	5.7
σ	0.76	1.27	1.67	1.32	1.46	1.1	1.14	1.46	0.26	0.57	1.48
Min.	1.49	1.59	1.07	2.19	3.33	1.5	1.49	1.59	0.92	1.01	3.66
Max.	3.35	5.16	1.54	6.4	7.42	1.2	6.4	7.42	1.73	2.33	7.55
n	9	9		7	7		17	16	16	8	8

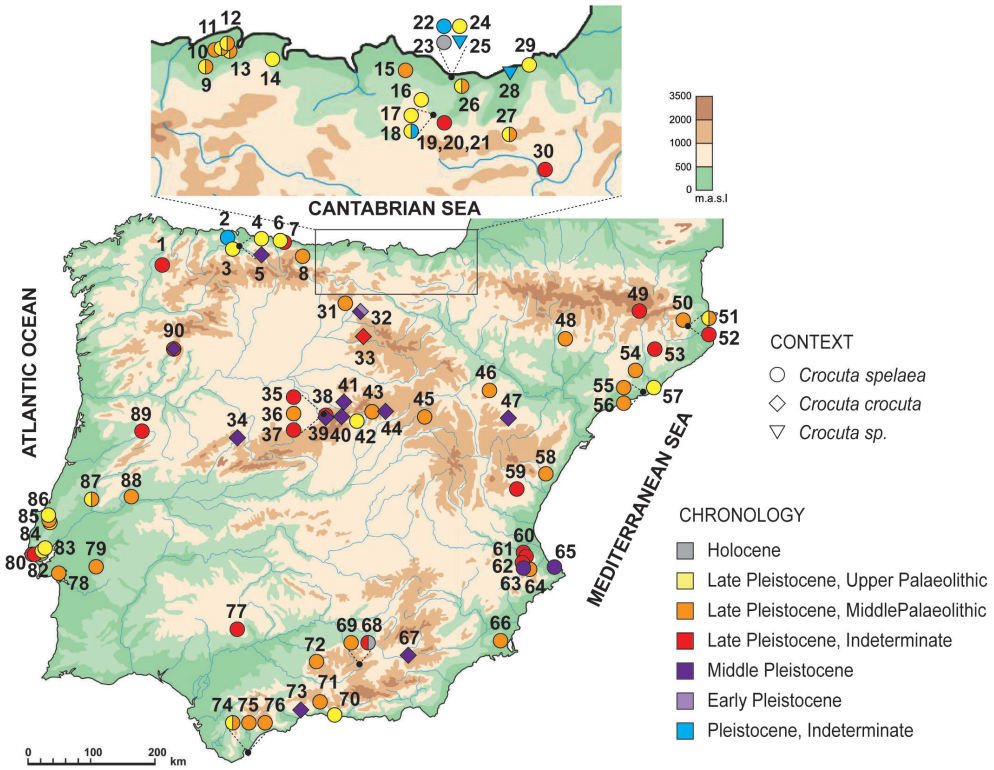

FIGURE 15. Palaeogeographic and diachronic distribution of the *Crocuta* in the Iberian Peninsula. The numbers refer to the sites listed in Appendix 7.

Europe. This faunal turnover has been called "the *Crocuta crocuta* event" (Martínez-Navarro, 2010).

During the Middle Pleistocene, *Crocuta crocuta* was the most common hyaenid recorded in the Iberian Peninsula. According to the paleontological literature fossils of *C. c. intermedia* have been recovered from a variety of sites in the Iberian Peninsula (Figure 4, Table 1), such as Atapuerca TD4 (Aguirre, 1987), the Cueva del Congosto (Carrión et al., 2006; Arribas et al., 2010), the Cuevas de Pedraza (Carrión et al., 2006; Arribas et al., 2010), Pinilla del Valle (Arribas et al., 2010), Villacastín (Carrión et al., 2006) and Cúllar (Carrión et al., 2006). In fact, the subspecies *C. c. intermedia* has been subject to broad criticism, as the specimens of *C.c. intermedia* and modern-day *C. crocuta* present a similar morphology and cannot be biometrically distinguished (Bonifay, 1971; García, 2003; Arribas et al., 2010). This is due to the fact that their metric parameters lie within the range of the present-day *C. crocuta* population (Kurtén, 1957; García, 2003). For some authors the hyaenid from Atapuerca TD4 in fact belongs to *C. crocuta* (García and Arsuaga, 1999; García, 2003) as does the one found at Pinilla del Valle (Arsuaga et al., 2012).

Crocuta spelaea is first recorded in Western Europe around 300 ka (Baryshnikov and Tsoukala, 2010). It is not until the Middle-Late Pleistocene boundary that the larger cave hyena from appears (Arribas et al., 2010). *C. spelaea* is craniodentally larger than *C. crocuta* and also displays a relative shortening of the distal limb segments, especially the radius, tibia, metacarpals and metatarsals (Kurtén, 1957).

The cave hyena enjoyed notable success, becoming a ubiquitous taxon in European faunal associations of the Late Pleistocene from the Urals to the Iberian Peninsula (Figure 15, Appendix 7) (Arribas et al., 2010; Carrión et al., 2006, Stuart and Lister, 2014). Some authors hold that there are anatomical differences that are not sufficient for making a taxonomic distinction between individuals from the Eurasian Pleistocene and those from Africa (Turner et al., 2008). Results of studies of ancient DNA of these fossil remains suggest that the populations of European spotted hyena are a subset of the African population and not a distinct species (Rohland et al., 2005). Other authors suggest that there are still discrepancies between molecular and paleontological data. These authors suggest that the evolutionary timescale of spotted

hyenas is not fully resolved, so further analyses are needed in order to reconcile the molecular and morphological data (Sheng et al., 2014).In the Iberian Peninsula there are numerous sites associated with the accumulating activity of cave hyenas, sites such as the Cueva del Búho (Iñigo et al., 1998), Torrejones (Arribas, 1997; Carrión et al., 2006) Gabasa 1 (Blasco and Montes, 1997), Las Ventanas (Carrión et al., 2001), Nerja (Arribas et al., 2004), Zafarraya (Geraads, 1995 Arribas et al., 2010) and Gorham (Carrión et al., 2008). The presence of *Crocuta spelaea* extended throughout the Late Pleistocene, lasting almost to the LGM (Last Glacial Maximum) as also the case in northern Eurasia (Stuart and Lister, 2014). However in Cueva de las Ventanas there is an indirect record (coprolites) that is dated to ca. 12 780 cal yr BP (Carrión et al., 2001), which is one of the latest records of this taxon in Europe. The reason for the disappearance of cave hyenas from Europe may be related to climatic factors or to other factors, such as reduced availability of prey or the ecological impact of hominids on the physical environment (Varela et al., 2010; Varela, 2011; Stuart and Lister, 2014).

Although the taxon is present at many sites, this is often in the form of teeth, either from adult or juvenile individuals, and isolated bones, or indirect evidence as coprolites (Carrión et al., 2001, 2006; Álvarez-Lao, 2002; Arsuaga et al., 2012). As a result of their gregarious, scavenging and cannibalistic behaviour, remains of *Crocuta spelaea* tend to be highly modified by gnawing, and associated skeletal remains are extremely rare (Diedrich, 2005, 2011a, 2012b, 2014). Up to now, the best-preserved remains of *C. spelaea* in the Iberian Peninsula were the crania from Gabasa 1 (Blasco and Montes, 1997) and the cranium from Fontainhas (Cardoso, 1993). Within Europe the most complete fossil is the one from Les Oubliettes (Gargas, France) (Cardoso, 1993) and the skeleton from Koněprusy Cave (Czech Republic) (Diedrich, 2012a). As a result of its taphonomic history, the *C. spelaea* skeleton from Los Aprendices is one of the most complete and best-preserved in Europe, and certainly the best-preserved in the Iberian Peninsula (Figure 15).

Taxonomic Attribution of the Studied Material

The characteristics of *Crocuta spelaea* have been described by other authors based on observations from isolated remains of cave hyena (Reynolds, 1902; Kurtén, 1957). The Los Aprendices skeleton provides a unique opportunity to study the anatomical proportions of cave hyenas based on a semi-complete individual. The Los Aprendices skeleton presents some characteristics of *C. spelaea,* such as the short diastema between C and P1, and P1 and P2 in contact, while in extant *C. crocuta* P1 and P2 are separated by a diastema. The dental series displays a moderate curvature in the maxillary and mandible, which is characteristic of *C. spelaea* (García, 2003). Furthermore, the skeleton has a huge skull, a powerful mandible and long proximal hindlimb elements (femur) compared to other cave hyenas. By contrast, medium and distal hindlimb parts are more robust and shorter than those of extant *C. crocuta*. In the fossil record, there are few articulated *C. spelaea* skeletons, in fact only three have been recovered so far. The skeleton of Koněprusy Cave (Czech Republic; Diedrich and Žák, 2006), Les Oubliettes (Gargas, France; Cardoso, 1993) and Los Aprendices. Despite the scarce material of *C. spelaea*, these skeletons present a similar femur length and metatarsus length ratio. This pattern is different from extant *C. crocuta* (Figure 16). These features agree with those previously reported for *C. spelaea* and support the idea that *C. spelaea* and *C. crocuta* are different species (Kurtén, 1957; Baryshnikov, 1999; Vinuesa et al., 2015) (Table 3, Figure 12). The biometric analysis of cranial elements reveals that there are two clearly distinct populations: one is formed by the extant *C. crocuta,* and the other by the cave hyena *C. spelaea,* which is the species characteristic of the Eurasian Late Pleistocene (Figures 7, 8, 12). On the other hand, there are no morphological or metrical criteria to distinguish *C. c. intermedia* from extant *C. crocuta* (Kurtén, 1957; García, 2003). Therefore, the cave hyena could be considered as a Late Pleistocene form that evolved from the *C. crocuta,* which arrived to the Iberian Peninsula in "the *Crocuta crocuta* event" (Martínez-Navarro, 2010). In this context, the Los Aprendices skeleton is the first skeleton in the Peninsula, which clearly belongs to *C. spelaea*. Furthermore, the level where it was found has been dated to 143.8 ± 38.9 ka, meaning that we are dealing with one of the oldest – if not the oldest – and most complete records of *Crocuta spelaea* in the Iberian Peninsula (Figure 15, Appendix 7).

Paleobiological Inferences from the Studied Material

The size of the Los Aprendices skeleton, as well as the size of *Crocuta spelaea,* were obtained using published regression equations for body mass on postcranial measurements in modern car-

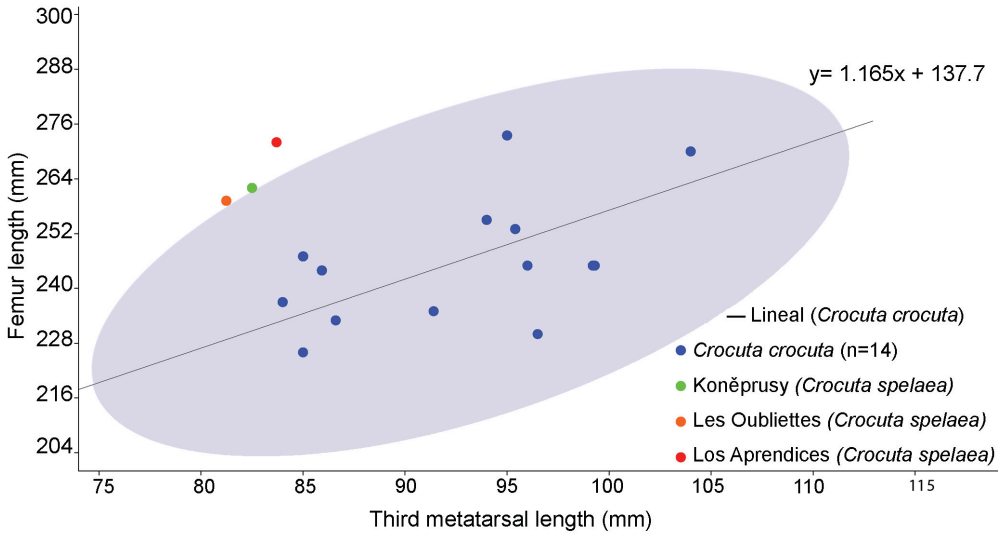

FIGURE 16. Graph representing total length of femur versus total length of third metatarsal in the same individual of extant *Crocuta crocuta* and the three unique complete skeletons of *Crocuta spelaea* from three sites Koněprusy Cave (Diedrich, 2012a); Gargas (Cardoso, 1993) and Los Aprendices this work. Comparative measurements (in mm) have been extracted from Ehrenberg, 1940; Cardoso, 1993; and J.M.-M personal commun., 2015. Confidence ellipse with confidence interval (0.95) is figured.

nivores (Anyonge, 1993; Christiansen, 1999), as well as equations that provide mass estimates from craniodental variables (Van Valkenburgh, 1990) (Table 6).

Regression equations with craniodental variables, such as skull length (SKL) and lower carnassial length (Lm1; equation recalculated with data from Van Valkenburgh, 1990), were used to estimate the body mass of *Crocuta spelaea* and compared it with the mass estimates for extant *C. crocuta* obtained by Palmqvist et al. (2011). In Table 6, it can be observed that the equations overestimate the size of extant *C. crocuta,* and it is likely that this is also the case in *C. spelaea*. On the other hand, the regression equations for body mass (BM) on limbs, including humerus length (HL) and femur length (FL), offer a better correlation between the real body mass of spotted hyenas and the results obtained by regression equations (Palmqvist et al., 2011).

The study of Palmqvist et al. (2011) shows that the most accurately estimated body mass was obtained with the mean of all estimated masses. The mean mass calculated for *Crocuta spelaea* is 88 kg, which is 60% more than the extant *C. crocuta*. This increase in size of *C. spelaea* from the *C. crocuta* from the Middle Pleistocene may have been due to climatic factors, for different sizes are detected in glacial and interglacial periods. It is not possible to distinguish these periods on the basis of the size of the hyenas, but it seems clear that temperature and mean body size are inversely related in accordance with Bergmann's rule (Kurtén, 1957; Kurtén and Poulianos, 1977; Klein and Scott, 1989, Fourvel et al., 2015).

In the case of Los Aprendices, the estimated body mass is 103 kg, which makes it one of the largest cave hyenas ever recorded. However, the body mass could only be estimated but some of equations cited, due to the incompleteness of the studied humerus. According to the later data, the body mass could be overestimated as a consequence of the observed deviations for the regression equations based only on cranial values.

The crural index (tibia length/femur length) in the skeleton of Los Aprendices is 0.74, which is similar to the values of *Crocuta spelaea* (0.75) and *Pachycrocuta brevirostris* (0.74) and clearly lower than in extant *C. crocuta* (0.82) (Palmqvist et al., 2011). The shortening of the tibia of *C. spelaea* suggests a less cursorial lifestyle. Also, such shortening could provide great power and more stability to dismember and carry large parts of carcasses without dragging (Spoor, 1985; Turner and Antón, 1996; Palmqvist et al., 2011).

Crocuta spelaea was a heavier and more powerful animal than extant *C. crocuta*, so *C. spelaea* could use its weight and strength to reduce larger prey. Consequently, this huge carnivore was capable of accumulating bones of large prey like horses (*Equus ferus*), woolly rhinos (*Coelodonta antiquitatis*), giant deer (*Megaloceros giganteus*)

TABLE 6. Regression equations used for estimating the body mass of *Crocuta spelaea* and estimates of size obtained with them for the living hyenas modified of Pamlqvit et al*.,* 2011. Deviations between estimated and actual masses for extant species [(mass estimate)/mass*100] are shown between brackets. Abbreviations: X, mean; min, minimum; max: maximum; BM, body mass; SKL, skull length; Lm1, lower carnassial length; HL, humerus length; FL, femur length.

References	Equation	Los Aprendices	*Crocuta spelaea*				*Crocuta crocuta* (55 kg)		*Pachycrocuta brevirostris*
			N	X	min	max	N		
Van Valkenburgh, 1990	log10 (BM)= 3.13log10 (SKL) - 5.59	145.6	22	140	107.2	173.1	72	63 (14.5%)	176
	log10 (BM)= 2.72log10 (Lm1) - 2.03	135.6	177	112.6	73	165		62 (12.7%)	92
Anyonge, 1993	log10 (BM)= 2.93log10 (HL) - 5.11		19	75.3	58.9	93.5	28	54 (-1.9%)	115
	log10 (BM)= 2.92log10 (FL) - 5.27	67.5	15	69.7	57.1	86.6		52 (-5.5%)	86
Christiansen, 1999	log10 (BM)= 2.88log10 (HL) - 5.15		19	65.7	51.65	81.3	30	48 (-12.7%)	89
	log10 (BM)= 2.86log10 (FL) - 5.15	63.6	15	65.6	54	81.2	199	49 (-10.9%)	80
Andersson, 2004	log10 (BM)= 2.55log10 (TC) - 0.6							62 (12.7%)	110
Average		103		88.15				56 (1.8%)	108

and woolly mammoth (*Mammuthus primigenius*) (Diedrich, 2012b, 2014).

In the last years, actuo-taphonomic studies show that *Crocuta crocuta* seldom creates large accumulations of bones despite having the ability. On the contrary, it is thought that the cave hyena made large accumulations of bones during the Late Pleistocene throughout Europe (Turner et al., 2008; see references in Diedrich, 2014; Fosse, 1997; Fourvel, 2012, Fourvel et al., 2015). Therefore, apart from the morphological differences between *C. spelaea* and *C. crocuta,* ethological differences might exist as well. Another point that supports the separation of *C. crocuta* and *C. spelaea* into two different species is the morphology of their brains, which may be related to the differences in behaviour of these carnivores (Vinuesa et al., 2015). However, it should be borne in mind that behavioural differences could also be due to climatic factors, as well as availability of prey (Fourvel and Mwebi, 2011).

Taphonomy

The characteristics of the breakage in the specimen from Los Aprendices are typical of sites at which the fractures were produced after deposition and with the bone in a dry state, as at Sarrians, Besouze (Villa and Mahieu, 1991) or Coro Tracito (Rabal-Garcés, 2013). This type of breakage is produced by trampling or alternatively by the pressure of sediment or falling blocks (Villa and Mahieu, 1991). In the case of Los Aprendices, it is more likely to have been produced by the weight of the sediment of the cone than by trampling, given how inaccessible the area is. At sites where the breakage is produced on fresh bones and where the accumulation is due to anthropic activity or to carnivores such as hyenas, by contrast, the breaks are characterized by a curved delineation, gentle angles and regular edges. This pattern is observed at Fontbrégoua (Villa and Mahieu, 1991), Gran Dolina stratum Aurora TD-6 (Díez et al., 1999), Abric Romaní L.B., Vanguard Cave (Cáceres, 2002), and the Cueva del Camino (Arsuaga et al., 2012).

The cranium presents a deformed sagittal crest. This type of deformation, without breaking the cranium, suggests that the carcass underwent rapid burial while the individual still preserved some of its soft tissues and the bone had collagen that endowed it with plasticity.

The length of the bones recovered and the sections of diaphysis suggest that the accumulation does not correspond to remains accumulated by bone-breaking carnivores such as hyenas, which destroy the bones and leave abundant

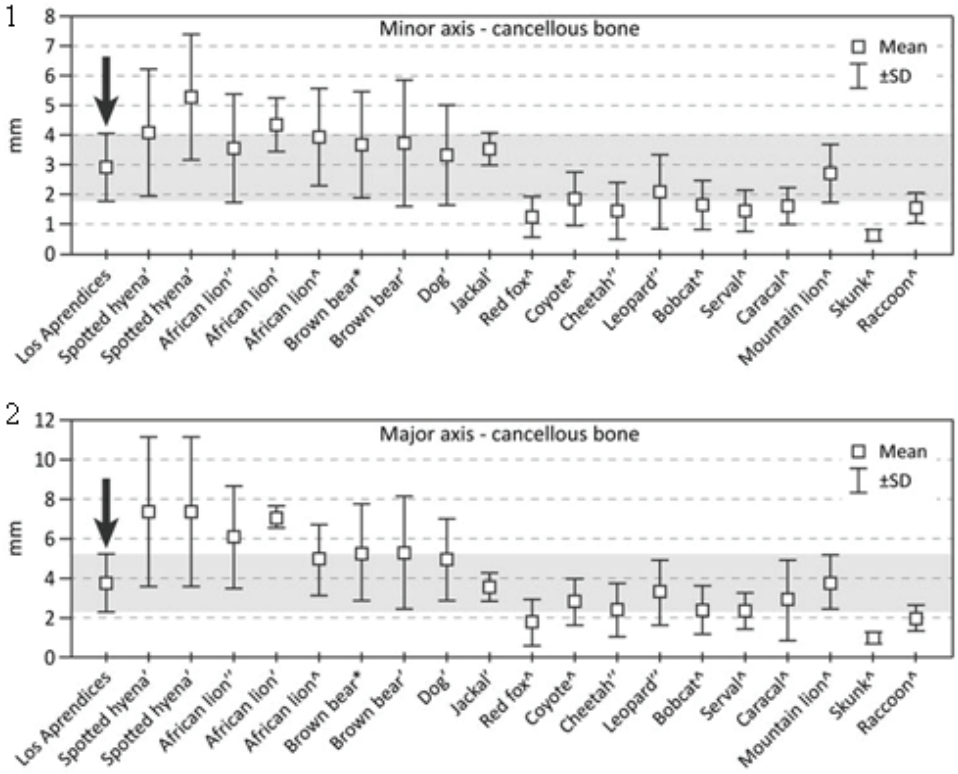

FIGURE 17. Means (square) and standard deviations (DS) of the values for the width (1) and the length (2) of pits on the epiphyses of long bones for various modern-day carnivores, together with the data from Los Aprendices (arrows). Key to the data: "Selvaggio and Wilder, 2001; ' Domínguez-Rodrigo and Piqueras, 2003; ^ Delaney-Rivera et al., 2009; * Saladié, 2009.

diaphysis fragments with an incomplete circumference (L1-L2 and C1-C2) (Villa and Mahieu, 1991; Díez et al., 1999; Cáceres, 2002). The specimen from Los Aprendices presents a predominance of complete diaphyseal sections. However, modified remains may also take the form of diaphyseal cylinders (C3) from which the two epiphyses are lacking. This is observed in various dens in central Europe such as Balve Cave (Diedrich, 2011b), Koněprusy Caves–Prošek Dome, Nad Kačákem, Turská Maštal Cave (Diedrich and Žák, 2006), Bottrop (Diedrich, 2012b) and Westeregeln (Diedrich, 2007).

With regards to the tooth marks at Los Aprendices, it is difficult to establish which animal produced them, since the modifications in question were produced on the carcass of an isolated hyena. The accumulations generated by hyenas tend to show a great number of carnivore tooth marks (Diedrich, 2011a, 2011b, 2011c, 2012b), with 60-100% of the sample altered. At fossil sites where alterations to remains have been attributed to hyenas (Blumenschine, 1986; Blumenschine and Marean, 1993; Domínguez-Rodrigo, 1994; Marean and Kim, 1998; Yravedra, 2006; Villa et al., 2010), the percentage of bones with tooth marks is greater than 40%. By contrast, accumulations produced by medium-sized carnivores result in a percentage of altered remains of no more than 25% (Brain, 1981; Sauqué et al., 2014). This criterion might suggest the activity of a medium-sized carnivore at Los Aprendices.

The sizes of the marks ("pits" and "punctures") found on the hyena from Los Aprendices were compared with data obtained in experiments undertaken by Selvaggio and Wilder (2001), Domínguez-Rodrigo and Piqueras (2003), Saladié (2009) and Delaney-Rivera et al. (2009) (Figure 17). The sizes of the marks from Los Aprendices show great similarity to those of the puma, with the mean values, maxima and minima almost the same. Judging by the size of the marks, other carnivores with a size range from ca 10 kg to 50 kg could be responsible. There is no evidence of the existence of any other carnivore in Los Aprendices Cave, making it difficult to propose a reliable ascription of the bite marks in question. Nonetheless, it is most likely that these were caused by a

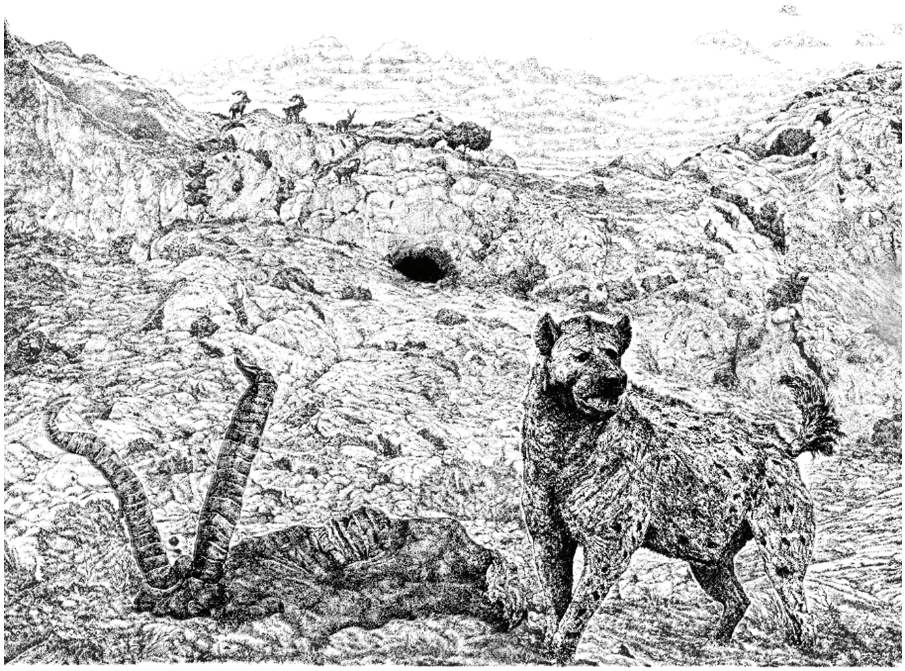

FIGURE 18. Reconstruction of *Crocuta spelaea* in the vicinity of Los Aprendices Cave, feeding on the carcass of a specimen of *Capra pyrenaica* (illustration by Gianfranco Mensi).

large- to medium-sized carnivore. The sizes of the marks as well as the patterns of alteration are very similar to those found at the sites of Los Rincones (Sauqué et al., 2014).

One factor to keep in mind is that cannibalistic behaviour is very common in *Crocuta crocuta* (Frank, 1994). Present-day hyenas accumulate bones from individuals of their own species, as has been observed in Africa (Cooper, 1993; East et al., 1989). This behaviour has also been recorded in *Crocuta spelaea*; in numerous hyena dens crania have been found with bite marks and with jugal arches torn off and mandibles broken (Diedrich, 2005, 2011a, 2011c). Examples are seen in the material from Perick Cave (Diedrich, 2005), Sloup Cave (Diedrich, 2012b), Koněprusy and Chlum Komin Cave (Diedrich and Žák, 2006).

The frequency of individual marks on each bone also varies greatly depending to the accumulating agent in question. Leopards rarely (<5%) leave more than 10 marks on a bone, whereas in the case of hyenas it is common for bones to present numerous individual marks, as many as 42 on a single bone (Selvaggio, 1994; Domínguez-Rodrigo and Pickering, 2010). At Los Aprendices there are no elements with more than seven marks on a single bone (see humerus MPZ 2014/672).

In summary, the low level of post-depositional breakage, the high number of elements represented, the presence of these elements in anatomical semi-connection, the fact that no element is repeated, as well as the left-right mirror symmetry of the elements and the low degree of modification caused by teeth, suggest that the hyena from Los Aprendices was in a complete state when it reached the sediment cone blocking the former entrance to the cave. Once dead, its carcass was presumably scavenged by a medium-sized carnivore. Both the modification pattern and the size of the marks are very similar to those that could have been produced by either a wolf or a European leopard. The presence of both these taxa has been established at a Late Pleistocene site in the vicinity of the site of Los Rincones (Sauqué et al., 2014, 2016a, 2016b). Moreover, taphonomic analysis of the hyena indicates that the marks were not produced by another cave hyena, suggesting that it is most likely that the animal met its death in a solitary context. In other words, if the hyena had been with a clan of cave hyenas at the time of its death, these other hyenas would have scavenged on its carcass, causing a large part of the skeleton to disappear and dispersing the bones (Figure 18). Cannibalistic and scavenging activities of this sort have been recorded in many central European sites (Diedrich, 2005, 2011a, 2011b, 2011c, 2011d, 2012a, 2012b, 2014; Villa et al., 2010).

CONCLUSIONS

Los Aprendices Cave (Zaragoza Province, Spain), has yielded a partially complete skeleton of *Crocuta spelaea* associated with *Capra pyrenaica*, Lagomorpha indet., Arvicolidae indet. and *Galemys pyrenaicus.*

The skeleton is the best preserved Pleistocene *Crocuta* specimen in the Iberian Peninsula and one of the most complete specimens in the European fossil record. Cave hyena fossils are usually fragmentary, and it is difficult to establish the relationships between the different features of the cranial and postcranial elements. For this reason we consider that the skeleton form Los Aprendices may be a reference for future studies. A mass of 103 kg has been estimated for Los Aprendices skeleton, making it one of the largest *C. spelaea* in the European record. This skeleton presents the characteristic features of *C. spelaea* such as: P3 with an extremely high crown, short diastema between C and P1, P1 and P2 in contact, disposition of the premolars in the dental series clearly curved, relative shortening of the distal parts of the extremities and larger size compared with *C. crocuta*. These features could be related with its behaviour as the main non anthropogenic bone accumulator during Pleistocene.

The *Crocuta spelaea* from Los Aprendices preserves 56 % of the total skeleton, providing critical information on the final moments of its life that suggest that it was solitary at the time of death. The skeleton is partially complete and 107 anatomical elements and a total of 194 remains have been recovered. The hyena from Los Aprendices died in the sediment cone that led to the cave, and it was subsequently modified by a large-medium-sized carnivore (probably a wolf or leopard). The pattern of modification and the type of bite marks, as well as the size of these marks, suggest that it was not scavenged by another cave hyena, as habitually occurs among this species (see references in Diedrich, 2014).

The level from which the skeleton was recovered has been dated by amino acid racemization to 143.8 ± 38.9 ka, which would place it either in the Middle Pleistocene or in the early Late Pleistocene, suggesting that Los Aprendices is one of the oldest records of *Crocuta spelaea* in the Iberian Peninsula.

The greatest expansion of the cave hyena in the Iberian Peninsula took place during the Late Pleistocene, between MIS 4 and MIS 2. Furthermore, the species may have survived longer in this area than in other parts of Europe, with records dated close to the Holocene. In our review of cave hyena distribution in the Iberian Peninsula we reallocated some *Crocuta crocuta* to *C. spelaea* mainly based on morphometry. In this review we included 90 sites with presence of cave hyena, which makes the Iberian Peninsula one of the areas with the highest density of sites containing cave hyena remains in Europe.

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APPENDIX 1.

Abundance, racemization relations of aspartic acid (Asp), glutamic acid (Glu), serine (Ser) and age of the samples from Los Aprendices. D: dextro; L :levo; ka: kilo annum; mg: milligram; pmol: picomol. All appendix files are available at the website as zipped spreadsheet files at palaeo-electronica.org/content/2017/1786-crocuta-spelaea-in-iberias.

APPENDIX 2.

Cranial measurements (in mm) of cave hyena from the Iberian Peninsula compared to other European individuals and extant individuals. Abbreviations: L, Length; H, height; W, width; Ap, Los Aprendices; Ga, Gabasa; Fo, Fontainhas; Ga, Gargas; Ch, Châtillon Saint Jean; Ja, Jaurens; Bi, Binagady; Jav, Javorka Cave; Sl, Sloup Cave; Ka, kazanka; Mo, Mosbach; LV, Lunel-Viel; TDW, Atapuerca Trinchera Dolina, extant *Crocuta crocuta*; A, Blasco and Montes, 1997; b, Cardoso, 1993; c, J.M.-M personal commun., 2015; d, Baryshnikov, 2014; e, Bonifay, 1971; f, García, 2003; g, Baryshnikov and Tsoukala, 2010. Note:? denotes uncertainity in the measure due to a fracture in the bone. All appendix files are available at the website as zipped spreadsheet files at palaeo-electronica.org/content/2017/1786-crocuta-spelaea-in-iberias.

APPENDIX 3.

Upper dentition measurements (in mm) of Los Aprendices *Crocuta spelaea* compared to other fossil hyenas and extant *Crocuta crocuta.* Abbreviations: X: mean; min; minimum; max: maximum; DMD, Mesiodistal diameter; DVL, vestibulo-lingual diameter; Ko, Kobaederra;Fo, Fontainhas; Ag, Aguilón; Ka, Kazanka; Mo, Mosbach; a, Altuna and Mariezkurrena , 2000; b, Castaños, 1987; c, Blasco and Montes, 1997; d, Iñigo et al., 1998; e, Cardoso, 1993; f, J.M.-M and personal commun., 2015; g, García, 2001; h, Bonifay, 1971; I, Kurtén and Poulianos, 1981; j, Kurtén, 1962; k, Schütt, 1971; l, Baryshnikov, 2014; m, Turner, 1984; n, Hollister, 1918. All appendix files are available at the website as zipped spreadsheet files at palaeo-electronica.org/content/2017/1786-crocuta-spelaea-in-iberias.

APPENDIX 4.

Mandible measurements (in mm) of Los Aprendices *Crocuta spelaea* compared to other fossil hyenas and extant *Crocuta crocuta*. Abbreviations: X: mean; min; minimum; max: maximum; Hramus, mandibular ramus height; Hdiast, height of ramus below the diastema; Hm1, height of ramus below m1; Hp4, height of ramus below p4; H condyle md, height of mandibular condyle; W condyle md, width of the mandibular condyle; Ap, Los Aprendices; Ga, Gabasa; Va, Valdegoba; S.Ab, Sima de Abraham; Ca, Caldeirao; Gar, Gargas; Eh, Ehringsdorf; Te, Teixoneres; TR, Terrasses des Canyars; Ka, Kazanka; a, Blasco and Montes, 1997; b, García, 2001; c, Altuna and Mariezkurrena, 2000; d, Martínez-Sánchez et al., 2012 e, Davis, 2002; f, Cardoso, 1993; g, Rosell et al., 2012; h, Daura et al., 2013; i, Baryshnikov, 2014; j, Bonifay, 1971; k, J.M.-M personal commun., 2015. All appendix files are available at the website as zipped spreadsheet files at palaeo-electronica.org/content/2017/1786-crocuta-spelaea-in-iberias.

APPENDIX 5.

Lower dentition (in mm) of Los Aprendices *Crocuta spelaea* compared to other fossil hyenas and extant *Crocuta crocuta*. Abbreviations: X: mean; min; minimum; max: maximum; DMD, Mesiodistal diameter; DVL, vestibulo-lingual diameter; Ap, Los Aprendices: L.K, Labeko Koba; S.I, Sima I; Bo, Bolinkoba; Ga, Gabasa; Fo, Fontainhas; Va, Valdegoba; C.B, Cueva del Búho; To, El Toll; Ol, Olopte B; C.O, Cova de l'Or; Mo, Mollet; Ata, Atapuerca; LV, Lunel-Viel; Pe, Petralona; Mos, Mosbach; Ka, Kazanka; a, Altuna and Mariezkurrena , 2000; b, Castaños, 1987; c, Blasco and Montes, 1997; d, Cardoso, 1993; e, García, 2001; f, Iñigo et al., 1998; g, J.M.-M personal com-

mun., 2015; h, Bonifay, 1971; I, Kurtén and Poulianos, 1981; j, Schütt, 1971; l, Turner, 1984; m, Hollister, 1918. All appendix files are available at the website as zipped spreadsheet files at palaeo-electronica.org/content/2017/1786-crocuta-spelaea-in-iberias.

APPENDIX 6.

Postcranial measurements (in mm) of Los Aprendices *Crocuta spelaea* compared to other fossil hyenas and extant *Crocuta crocuta.* Abbreviations: X: mean; min; minimum; max: maximum, Bd: Breadth of the distal end; Bp: Breadth of proximal end; BPC, Proximal articular surface breadth; DPA, Olecranic maximum depth; GB: Greatest breadth; GL: Greatest length; SD: smallest breadth of the diaphysis; Mtc: metacarpus; Mtt: metatarsus; 1st Pha: first phalanx; 2nd Pha: second phalanx; Ap, Los Aprendices; L.K, Labeko Koba; S.I, Sima I; Ga, Gabasa; To, El Toll; TD 8, Atapuerca Trinchera Dolina 8; LV, Lunel-Viel; A, Altuna and Mariezkurrena , 2000; b, Blasco and Montes, 1997; c, Castaños, 1987; d, García, 2001; e, J.M.-M personal communication., 2015; f, Cardoso, 1993; g, Bonifay, 1971; h, Ehrenberg, 1940. Note: ? denotes uncertainity in the measure due to a fracture in the bone. All appendix files are available at the website as zipped spreadsheet files at palaeo-electronica.org/content/2017/1786-crocuta-spelaea-in-iberias.

APPENDIX 7.

Palaeontological and archaeological sites of the Iberian Peninsula with hyena remains. The numbers refer to the sites of Figure 1. Abbreviations: Context: A, archaeological; P, palaeontological. Chronology: P, Pleistocene; MP, Middle Pleistocene; ELP, Early Late Pleistocene; LP, Late Pleistocene; EH, Early Holocene; MPal, Middle Palaeolithic; EUPal, Early Upper Palaeolithic; UPal, Upper Palaeolithic; Ms, Mousterian; Chat, Chatelperronian; Per, Perigordian; Au, Aurignacian; Gr, Gravettian; So, Solutrean; Mg, Magdalenian; Az, Azilian. All appendix files are available at the website as zipped spreadsheet files at palaeo-electronica.org/content/2017/1786-crocuta-spelaea-in-iberias.