

Subsistence Dynamics during the Lower Paleolithic in Gran Dolina Cave (Atapuerca, Spain)

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Abstract: *In recent decades, a large body of evidence has been accumulated to support the view that Middle Paleolithic hominins were regular hunters of large game. The recurrence of primary access to the carcasses, the systematic exploitation of the energy-rich elements, the standardization of mortality patterns and the selection of prey in ecosystems of great diversity observed in many of the archaeological assemblages of the late Middle Pleistocene (MIS 7; <242 ka) suggest the crystallization of a human predatory niche that later came to characterize the “Neanderthal way of life.” However, information concerning the mode and type of access to carcasses, the management of animal resources derived from them, as well as the butchering techniques employed, is scarce before MIS 7. This is especially true in the Palearctic context in which our research is framed. Here we present the zooarchaeological and taphonomic analysis of more than 31,000 faunal remains from the late Middle Pleistocene TD10.1 bone bed and TD10.2 bison bone bed from the site of Gran Dolina, dated from ca. 400-250 ka, to assess the subsistence dynamics of the pre-Neanderthal populations in southwestern Europe. The results obtained for both assemblages suggest that the Lower Paleolithic hominins in Europe were prominent hunters of large game who were able to use diverse hunting strategies, techniques and tactics, such as communal hunting, which at times show a remarkable degree of sophistication. These patterns are linked with the emergence of complex behavioral, social and cognitive capacities.*

Keywords: *Atapuerca, Lower Paleolithic, large game, communal hunting, complex behavior*

Subsistenzdynamik während des Altpaläolithikums in der Gran Dolina-Höhle (Atapuerca, Spanien)

Zusammenfassung: In den vergangenen Jahrzehnten haben sich die Belege zur Untermauerung der Ansicht angehäuft, dass die mittelpaläolithischen Homininen regelmäßig Großwild gejagt haben. Der wiederholte Primärzugriff auf Tierkörper, die systematische Ausbeutung energiereicher Körperteile, die Normiertheit der Mortalitätskurven und die Auswahl der Beutetiere in Ökosystemen hoher Diversität, wie sie in vielen archäologischen Inventaren des späten Mittelpleistozäns (MIS 7; <242 ka) beobachtet werden, sprechen dafür, dass sich für den Menschen eine Raubtier-Nische herauskristallisierte, die später die „Neandertaler-Lebensweise“ charakterisieren sollte. Die Informationen über die Art und Weise des Zugangs zu Tierkörpern, über die Organisation des daraus erschlossenen Umgangs mit tierischen Ressourcen, sowie über die angewendeten Schlachttechniken sind jedoch vor dem MIS 7 spärlich. Dies gilt vor allem in paläoarktischem Zusammenhang, in welchen unsere Studie eingebettet ist. Im vorliegenden Beitrag legen wir die archäozoologischen und taphonomischen Analysen von mehr als 31.000 Faunenresten aus den spätmittelpleistozänen Horizonten „TD10.1 bone bed“ (TD10.1 Knochen-

bett) und „TD10.2 bison bone bed“ (TD10.2 Bisonknochenbett) der Fundstelle Atapuerca in Spanien vor, die zwischen etwa 400.000 und 250.000 Jahre alt sind. Damit können wir die Subsistenzdynamiken vor-neandertalerzeitlicher Bevölkerungsgruppen in Südwesteuropa aufzeigen. Die für beide Inventare erzielten Ergebnisse weisen darauf hin, dass die altpaläolithischen Homininen in Europa bedeutende Großwildjäger gewesen sind, die in der Lage waren, verschiedene Jagdstrategien, -techniken und -taktiken anzuwenden, wie z.B. Gemeinschaftsjagd, die manchmal einen bemerkenswerten Grad an Raffinesse offenbaren. Diese Muster stehen in Verbindung mit dem Aufkommen komplexer verhaltensmäßiger, sozialer und kognitiver Kapazitäten.

Schlagwörter: Atapuerca, Altpaläolithikum, Großwild, Gemeinschaftsjagd, komplexes Verhalten

Introduction

In recent decades enough evidence has been uncovered to demonstrate that Middle Paleolithic hominins were regular hunters of large animals. At least on a regional level, they supplemented their diet by hunting small prey, megafauna and other extractive foods (Speth and Tchernov 1998, 2001, 2002; Conard and Prindiville 2000; Stiner and Munro 2002; Speth and Clark 2006; Yeshurun et al. 2007; Stringer et al. 2008; Villa and Lenoir 2009; Blasco and Fernández Peris 2012b; Conard et al. 2015; Fiorenza et al. 2015; Smith 2015; Yravedra and Cobo-Sánchez 2015, among others). In fact, this evidence, although less frequent, is also consistent for the lower Paleolithic hominins in Europe and the Middle East, and much more numerous in Africa, suggesting that hunting could be closely related to the emergence of the genus *Homo* (Semaw et al. 2003; Egeland et al. 2004; Pickering et al. 2004, 2007; Domínguez-Rodrigo et al. 2007, 2009, 2014; Rabinovich et al. 2008; Saladié et al. 2011, 2014).

The faunal assemblages and the taphonomic inferences derived from them represent the main empirical basis for establishing this hypothesis. The recurrence of primary access to carcasses, the systematic exploitation of energy-rich elements, the standardization of mortality patterns and the selection of prey in areas with a great diversity of resources observed in much of the archaeofaunas dated from the end of the Middle Pleistocene (MIS 7; <242 ka) suggest the crystallization of a human predatory niche at a time characterized by the emergence of other technological and behavioral traits signaling the “Neanderthal way of life” (e.g., Moncel et al. 2011; Fontana et al. 2013). This human predatory niche is characterized by the selective exploitation of big game, resulting in faunal assemblages dominated by prime-adult large ungulates, with one or two species representing the main prey (Stiner 2013: 291). However, the information concerning the mode and type of access to animal carcasses, the management of animal resources derived from them and the butchering techniques employed, is scarce before MIS 7, especially if we move back in time and to the Palaearctic context. As a result, in the European context, there are reasonable doubts about whether the human predatory niche emerges.

Apart from the incontrovertible evidence of hunting found in the archaeological spear horizon of Schöningen in Germany (Thieme 1997; Voormolen 2008; Conard et al. 2015; Rivals et al. 2015; van Kolfschoten et al. 2015) and some specific assemblages, such as Bolomor Cave in Spain with its unusual broad spectrum of prey (Blasco 2011), Boxgrove in England with the exceptionality of its “Pompeian” record (Roberts and Parfitt 1999) or Arago Cave in France with its peculiar diachronic persistence in the occupations (Moigne et al. 2006), few faunal assemblages help us to characterize the predatory behavior of pre-Neanderthals in Europe. This is due in part to the lack of specific

research on subsistence in this context, and in turn, closely related to poor conservation of the oldest records.

The site of Gran Dolina in the Sierra de Atapuerca (Burgos, Spain) has been excavated continuously since the 1990s. During the first decade of the 21st century, the lithological sub-units TD10.1 and TD10.2 were completely excavated, resulting in the richest archaeological layers throughout the whole Sierra de Atapuerca with more than 100,000 coordinate remains. The work here presents the faunal analysis, based on traditional and long-established zooarchaeological methods, of more than 31,000 faunal remains from the “bison bone bed” layer of the TD10.2 sub-unit and from the “bone bed” layer of the TD10.1 sub-unit. For the purposes of this research, I make use of the huge record of Gran Dolina TD10 to shed new light on the subsistence dynamics of the hominins of the Middle Pleistocene while focusing on the tactics and techniques used for subsistence and what these imply on a cognitive and social level.

The Gran Dolina site

Gran Dolina is one of the many karstic formations located in the Sierra de Atapuerca in the northern part of the Iberian Peninsula (Fig.1a). The cave is of phreatic origin and more than 20 m deep with a ‘keyhole’ section morphology. Internal and external deposits fill the cavity, which was discovered in the early 20th century after workers cut through it in constructing a railway. Gran Dolina is now a collapsed structure, with too little of the walls and roof remaining for us to reconstruct at first glance its original geometry. In plan the site presents an oval morphology with more than 100 m² of surface excavation, although the total extension of the original morphology is presently unknown (Ortega 2009).

Eleven stratigraphic units have been identified, from the base to the top (TD1-TD11) (Gil et al. 1987; Parés and Pérez-González 1999; Pérez-González et al. 2001), though these identifications have since been revised (Rodríguez et al. 2011) (Fig.1b and c). The 3-m thick lithostratigraphic unit TD10 is the youngest archaeo-paleontological level and is divided into four lithostratigraphic sub-units named from top to bottom (TD10.1/TD10.4). Geo-chronological studies suggest that the sequence falls within MIS 11–9 (Falgüeres et al. 2001; Berger et al. 2008; Moreno et al. 2015) (Fig.1c). By the summer of 2015, the sub-units TD10.sup, TD10.1, and TD10.2 were fully excavated (~95 m²). The TD10.2 record is composed of 51,000 faunal remains and nearly 9,800 lithic artifacts. Sub-unit TD10.1 is the richest level of the Atapuerca sites, yielding 48,000 faunal remains and 21,200 lithic remains. During fieldwork two main archaeological layers were identified. For the huge concentration of archaeological remains, with its scant vertical thickness and its large horizontal extension and continuity, the archaeological layers were named the TD bone beds, one located in the bottom of TD10.1 and the other in the middle of TD10.2. The posterior archaeo-stratigraphic studies confirmed the integrity of the archaeological layers of both bone beds (Obregón 2012; Rodríguez-Hidalgo 2015).

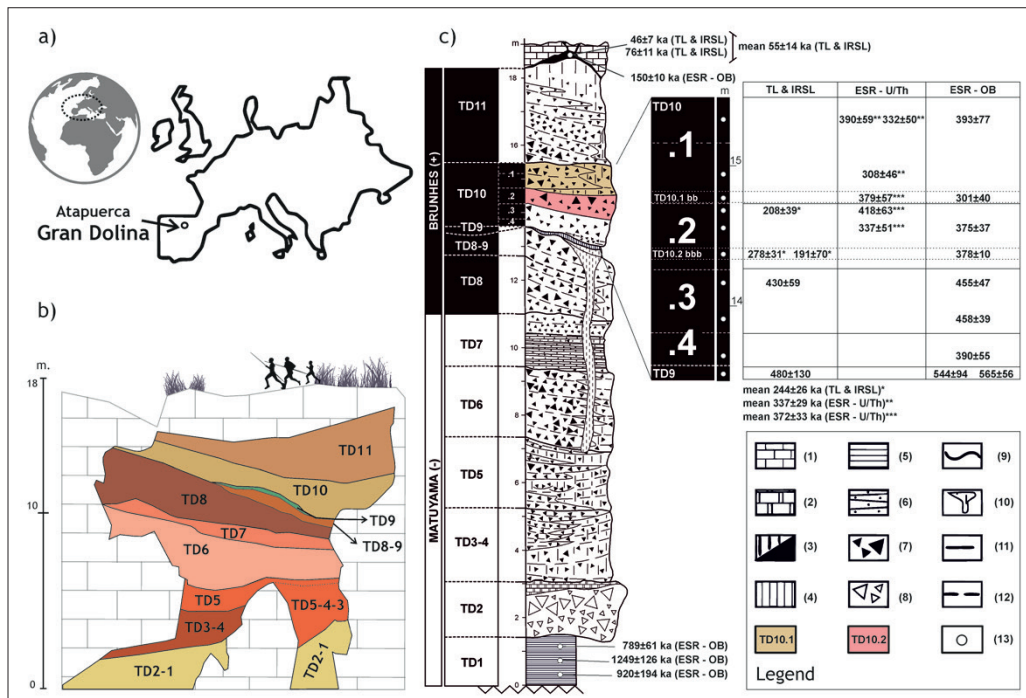


Fig. 1: Location and stratigraphic section of Gran Dolina (Atapuerca): a) location of Gran Dolina in the North of the Iberian Peninsula, b) stratigraphic schematic view of the paleo-morphology of the cave from the railway trench (archaeologically south) section, c) synthetic stratigraphic profile with the locations of the available ESR-U/Th, TL-IRSL and ESR-OB dates from Falguères et al. (1999), Berger et al. (2008) and Moreno et al. (2015). Legend: (1) Mesozoic limestone on the roof of Gran Dolina; (2) speleothem; (3) lutites, clay loam/terra rossa; (4) bat guano; (5) laminated loamy clays; (6) calcilutites and calcarenites; (7) gravel and boulders, clastic flow; (8) arrangement of fallen boulders; (9) main stratigraphic discontinuity; (10) secondary unconformity and loamy-clayey-sandy filling; (11) Matuyama-Brunhes boundary; (12) disappearance of *Mimomys savini* and first occurrence of *Iberomys brecciensis*; (13) location in depth of the samples for dating; in brown the lithostratigraphic sub-unit of TD10.1; in pink the lithostratigraphic sub-unit TD10.2 (modified from Berger et al. 2008: 302). Full color version available online: mgfuopenaccess.org.

Paleoenvironmental data do not reflect significant changes in terms of paleoclimate or diversity throughout the TD10 sequence (García-Antón and Sainz-Ollero 1991; Blain et al. 2009; Cuenca-Bescós et al. 2011; Rodríguez et al. 2011). The proxies generated by the micro-vertebrates are certainly contradictory. Rodents suggest a very open and dry steppe-type environment (Cuenca Bescós et al. 2005), while the herpetofauna indicates always a moist environment and the woodiest landscape of the whole sequence of Gran Dolina (Blain et al. 2008). Blain and colleagues suggest that these differences may be due to large fluctuations between the seasons, with very cold and dry winters (indicated by small mammals) and mild, wet summers (suggested by the herpetofauna) (Blain et al. 2008). Most notable here is the absence of extreme glacial conditions and the regularity of the paleo-environmental record, common in the Pleistocene of Iberia. Meanwhile, the pollen spectra indicate a continuous presence of conifers, mesophilic trees and Mediterranean trees along the sequence, with a constant presence of Poaceae, indicative of open habitats. The combination of proxies, the abundance of megaherbivores and the absence

of mammals adapted to closed forest areas, as well as the structure of mammalian paleo-communities, all indicate a landscape indicative of the Mediterranean savanna (Rodríguez et al. 2011).

Certain characteristics of the technological transition from Mode 2 to Mode 3 are observable along the sedimentary succession of TD10. These include a progressive curating in the production of prepared core flakes, and the decreasing degree of shaping of large tools that is reflected in a higher incidence of small flake tools, which progressively increase in standardization and morphological diversity (Menéndez Granda 2010; Terradillos-Bernal and Díez-Fernández-Lomana 2012; Ollé et al. 2013, 2016; García-Medrano et al. 2015). While throughout TD10 the lithic assemblages seem to share a similar pattern for procurement strategies defined by the decisive selection and management of raw materials, TD10.2 reveals a strikingly marked specialization: chert overwhelmingly dominates all other raw materials, accounting for 95% of the assemblage. There is no evidence for the use of fire and no examples of burnt lithics or burnt bones in the entire sequence (Ollé et al. 2013).

Previous zooarcheological investigations have focused on the upper part of TD10.1, analyzing the faunal remains as coming from one unit while they, as turned out later, actually belong to several archaeo-levels (Rosell 2001; Blasco 2011). These studies proposed using Gran Dolina as a referential site. Hominins are the main accumulators and modifiers of faunal remains, while carnivores, to a very limited extent, have been proposed as modifiers of the remains abandoned by humans. The primary and immediate access to the carcasses of large ungulates through hunting would be the main access model, but the scavenging of large carcasses is inferred as well. The anatomical pattern showed differential transport based on weight of the animals (here, of transport of complete carcasses for deer and smaller animals), with elements selected for their high nutritional value in animals over 100/150 kg. The main interpretative differences found in these works concern the nature of the occupations and the dietary spectrum. For Rosell (2001), butchery processes are highly standardized and diet is based on large ungulates (mainly red deer), while Blasco concludes that butchering is highly random, reflecting a broad-spectrum diet in which leporids and birds carry considerable weight. As a result, Rosell interprets the site as a long-term central camp used for large hominin groups (Rosell 2001), while Blasco considers the assemblage to be a product of very short, expeditious occupations conducted by small groups of hominins with diverse cultural traditions (Blasco 2011).

Materials and Methods

Our study is based on two faunal assemblages coming from the main archaeological layers of the Gran Dolina cave site: the TD10.2 bison bone bed and the TD10.1 bone bed. For our investigations, more than 31,000 faunal remains plotted in 3D were analyzed. During the excavation of Gran Dolina TD10, all the macrofaunal remains longer than 2 cm and all identifiable remains (i.e., every single tooth) were recovered and plotted in three dimensional space through the 3COORsystem (Canals et al. 2008). The excavation protocol does not typically piece-plot mesovertebrate remains (e.g., leporids, small birds) as a general rule. These remains were recovered in bone collection bags per day along with non-identifiable macromammal remains less than 2 cm. The contents of

these bone collection bags are not included in this investigation but have been analyzed and reported in Rodríguez-Hidalgo (2015). Nevertheless, although several specialists assisted the excavation team in determining the faunal remains during the course of fieldwork, mesovertebrate remains (mainly complete bones of rabbits) were occasionally recovered *in situ* and piece plotted. We have included these remains in this paper to signify the role of small taxa in the accumulation, but specific research on these finds is still in progress.

Data described for all faunal remains include anatomical element, taxa, size, age, portion and side. We used five measures of abundance: Number of Specimens (NSP), which includes the total amount of faunal remains independent of their identification grade (Grayson 1984); Number of Identified Specimens (NISP); Minimal Number of Elements (MNE); Minimal Animal Units (MAU) and standardized %MAU, and Minimal Number of Individuals (MNI) (Binford 1984; Lyman 1994). Following Domínguez-Rodrigo (1997) for skeletal part representation, carcasses were divided into anatomical segments: head (horn, cranium, mandible, hyoid and tooth), axial (vertebrae, ribs) and appendicular (limb bones). For many taphonomic analyses, coxa and scapulae were lumped with axial segment, given that their responses to taphonomic processes are similar to those of axial elements (Yravedra and Domínguez-Rodrigo 2009). Furthermore, in the case of the pelvis, it is usually processed as part of the axial skeleton (e.g., Binford 1978, 1981). Long bones were divided into upper limb bones (humerus and femur), intermediate limb bones (radius/ulna and tibia) and lower limb bones (metapodials).

We calculated the Shannon evenness index to explore taxonomic diversity in the assemblage: $(E) = -(\sum pi * \ln pi) / \ln S$, where S is the number of species and pi is the standardized proportion of specimens of the i-th species (Magurran 1988). The calculation for non-overlapping taxa follows the protocol of Grayson and Delpech (1998, 2003). Non-identified specimens have been included in type of bone categories (long bones, flat bones or articular bones) and in weight-size categories (Saladié et al. 2011). The five weight-size categories include the following: a) very large-sized animals weighing more than 800 kg, equivalent to size 5 in African zooarchaeological methodologies (see Brain 1981; Bunn and Ezzo 1993; Bunn 2001); b) large-sized animals weighing between 300 and 800 kg equivalent to size 4; c) medium-sized animals weighing between 50 and 200 kg, equivalent to size 3; d) small-sized animals weighing between 10 and 50 kg, equivalent to size 2-1B; e) very small-sized animals that correspond to mesovertebrates (leporids and birds in this work).

To calculate MNE we have taken into account the overlapping of anatomical landmarks, considering age, side or other features that can help researchers estimate a minimum of elements in the assemblage. In the case of long bones, we follow the recommendations of Marean and Spencer (1991), modified by Saladié et al. (2011: Fig. 1), and for the ribs we follow the method explained in detail in Rodríguez-Hidalgo et al. (in press). To calculate MNI we have considered complete dental series and isolated teeth, taking into account their grade of eruption and wear (Smuts et al. 1978; Levine 1982; Mariezkurrena 1983; Węgrzyn and Serwatka 1984; Hillman-Smith et al. 1986; Hillson 1986) and skeletal development patterns, epiphysation and ossification following Barone (1976).

Following Stiner (1990, 1994), we have clustered the estimated individuals into three age groups: young, prime-adults and old individuals. Dental replacement of dP4 by P4

indicates the transition to maturity, and the loss of infundibula in M1/M2 has been used to infer the presence of old individuals. For bison we have taken into account the considerations of Driver and Maxwell (2013) about the young age category defined as animals less than two years old. The results have been plotted in modified triangular graphs, which plot the proportional representation of three age classes at 95% confidence interval (Steele and Weaver 2002). In some instances we use the mortality categories proposed by Bunn and Pickering (2010), who subdivide the category of young into a young juvenile sub-stage (newborn through yearling) and sub-adult juvenile sub-stage, based on wear patterns of deciduous molars.

Spearman's rank order was used to test correlations between %MAU and bone mineral density, while taking into account the MNE of each portion of the elements. We used data on caribou for medium-sized animals and bison for large-sized animals (Kreutzer 1992; Lam et al. 1999). The significance of the Spearman correlation coefficient used in this research is 95% (0.05) and 99% (0.01). We subsequently correlated the %MAU with the Standard Food Utility Index [(S)FUI] proposed by Metcalfe and Jones (1988), the Utility Index and Marrow Index from Emerson (1993), the logarithm of the Meat Drying Index (MDI) from Friesen (2001), and the Unsaturated Marrow Index (UMI) from Morin (2007). The resulting scatter plot is then interpreted in the general middle-range theoretical context from Binford (1978: 81) and his ethnoarchaeologically-derived skeletal part abundance curves (Hill 2008). Finally, we calculated the Shannon evenness index on the basis of Faith and Gordon (2007). Tests conducted by these researchers show that correlation analysis may be highly sensitive to interactions between sample size and the uniformity of the distribution of skeletal items. Non-significant correlations may be artefactual even where sample sizes are small. They suggested that a more or less uniform representation of skeletal parts in a series reflects transportation and butchering strategies. These studies suggest that the Shannon evenness index can be successfully applied as a quantitative means of distinguishing assemblages with different transport characteristics (Faith and Gordon 2007).

Following Villa and Mahieu (1991), shaft circumference, shaft length, and the fracture outline, angle, and edge were listed to explore the nature of fragmentation observed in the assemblage. For flat bones we observed the same criteria when enough cortical tissue and medullary cavity made this possible as in the case of scapular neck or costal angle in the ribs. Spiral fractures in proximal ribs and proximal blade sections have been considered as green fractures (Hill 2008).

The occurrence of bone surface modifications (butchering marks and carnivore-induced marks) was used to assess the implications of different actors in the archaeological assemblage. All faunal remains were inspected macroscopically and microscopically (OPTHEC 120 Hz model) according to Blumenschine et al. (1996). For detailed bone surface observation, an ESEM Fei Quanta 600 was used (low vacuum mode, using both secondary and back-scattered electron detectors). The distribution and incidence of modifications were recorded. Hominin- and carnivore-induced damage was noted in terms of the anatomical area and the region (portion and side) of the modifications. Identified anthropogenic modifications included cut marks, breakage (percussion marks and peeling) and human tooth marks. Cut marks were identified based on the criteria of Binford (1981), Potts and Shipman (1981), Shipman (1981), Shipman and Rose (1983), Noe-Nygaard (1989) and Domínguez-Rodrigo et al. (2009). Four types of cut mark have been

identified: incisions or slicing marks, sawing marks, scraping marks and chop marks. Saw marks (Noe-Nygaard 1989) are produced through a repetitive and bi-directional motion (Fisher 1995) employed to cut hard tissues such as tendons or ligaments (personal observation). Recording the type, delineation, situation and position of the cut marks by element allows us to infer several butchering activities. For this purpose we have used ethnoarchaeological sources (Binford 1978; Abe 2005), experimental data (Frison 1974; Nilssen 2000) and our own butchering experiments conducted with several kinds of animals (red deer, roe deer, fallow deer, reindeer, bison, horses, carnivores, primates, leporids, birds) and several research goals (e.g., Saladié et al. 2015). Surface modifications during the anthropic breakage of bones were also analyzed and recorded in terms of presence or absence for each remain. These include percussion pits (Blumenschine and Selvaggio 1988), conchoidal scars and flakes, and adhered flakes (Capaldo and Blumenschine 1994) and peeling (White 1992; Pickering et al. 2013). Descriptions include the location of damage on the remains. Conchoidal scars and flakes were assumed to be anthropogenic when associated with percussion pits.

Carnivore tooth marks were also present in the TD10 assemblage. The morphological traits of the punctures (deep, multicuspid, with a bowl-shaped transversal section) and the scoring (deep, with the base and walls creating an irregular path, often associated with pits with an oval or angular morphology) (Bunn 1981; Shipman 1981; Blumenschine 1995; Fisher 1995; Domínguez-Rodrigo and Barba 2006), together with the presence of other major modifications such as furrowing or breakage on bones of large animals, allowed us to infer the activity of carnivores in the assemblage. We noted the presence of licking, pitting, scoring, furrowing and scooping out, and of digested bones (Haynes 1980, 1983; Binford 1981). We further noted the measurements of the pits, punctures and scores using the criteria of Domínguez-Rodrigo and Piqueras (2003) and Andrés et al. (2012) and compared them with experimental data from Selvaggio (1994), Delaney-Rivera et al. (2009), Andrés et al. (2012) and Saladié et al. (2013a, b). Tooth marks bearing no clear diagnostic criteria for attribution to a particular taphonomic agent (human or carnivore) were left out of the study.

Since the assemblage exhibits both anthropogenic marks and damage generated by carnivores, we have taken into account the coincidence of these modifications (Egeland 2007), and specifically the overlapping of these modifications, in order to establish the degree of interdependence between agents in the formation of the assemblage. We use the term interdependence for finds exhibiting hominid and carnivore use of the same carcass at any stage of assemblage formation (*sensu* Egeland et al. 2004). Furthermore, considering the existence of a rich carnivore guild during the European Middle Pleistocene (Turner 1992; Croitor and Brugal 2010) and the critical role that interspecific competition may have played in the use of carcasses by carnivores (Binford 1981; Blumenschine et al. 1994; Domínguez-Rodrigo 1994, 1999, 2001), we have implemented a number of taphonomic indices that allow us to estimate the degree of carnivore ravaging of the assemblage. We considered the ratio of specimens with shaft fragments (NISP) of limb bones against epiphyseal specimens (Marean and Spencer 1991; Blumenschine and Marean 1993), the percentage of change in the epiphysis of the long bones $[(MNE \text{ before ravaging} - MNE \text{ after ravaging}) / (MNE \text{ before ravaging}) * 100]$ using the NME according to Domínguez-Rodrigo et al. (2002), the ratio of axial (ribs + vertebrae) elements relative to the long bones (MNE) and the ratio of proximal humerus + distal radius from the distal humerus + proximal radius (MNE) (Domínguez-Rodrigo and Organista 2007).

Results

The TD10.2 bison bone bed of Gran Dolina

We analyzed 24,216 faunal remains (NSP) belonging to a wide variety of taxa (18 taxonomic groups), including ungulates, carnivores, large rodents, leporids, birds, and reptiles. Despite this, as the name of the bone bed indicates, bison dominate the assemblage (22,532 or 98.4% NISP). What is critical in understanding the taxonomic features of the assemblage is that the other 17 taxa range down to 1% NISP, and are always represented by less than 60 specimens (Table 1). Among the indeterminable remains,

Taxa	TD10.1 Bone Bed			TD10.2 Bison Bone Bed		
	NISP	%NISP	MNI	NISP	%NISP	MNI
<i>Bison sp. (small)</i>	-	-	-	22,532	98.1	60
<i>C. elaphus/D. dama clactoniana</i>	1,484	79.6	8	48	0.2	4
<i>Cervus elaphus priscus</i>	22	1.2	7	-	-	-
<i>Dama dama clactoniana</i>	9	0.5	2	-	-	-
<i>Bison schoetensacki</i>	136	7.3	2	-	-	-
<i>Equus sp.</i>	132	7.1	1	55	0.2	5
<i>Equus ferus</i>	2	0.1	2	-	-	-
<i>Equus cf. hydruntinus</i>	1	0.1	1	-	-	-
<i>Stephanorhinus cf. hemitoechus</i>	46	2.5	1	-	-	-
<i>Hemitragus bonali</i>	3	0.2	1	-	-	-
<i>Capreolus priscus</i>	5	0.3	1	4	0.02	2
<i>Panthera leo spelaea</i>	1	0.1	1	12	0.05	2
<i>Canis lupus</i>	-	-	-	7	0.03	3
<i>Cuon alpinus europaeus</i>	-	-	-	3	0.01	1
<i>Canis/Cuon sp.</i>	2	0.1	1	51	0.2	4
<i>Lynx cf. pardinus</i>	-	-	-	8	0.03	2
<i>Vulpes vulpes</i>	-	-	-	29	0.1	3
Mustelidae indet cf. <i>Meles meles</i>	-	-	-	4	0.02	1
<i>Mustela putorius</i>	-	-	-	1	0.004	1
<i>Felis silvestris</i>	1	0.1	1	-	-	-
Carnivora indet.	-	-	-	9	0.04	0
<i>Castor fiber</i>	-	-	-	16	0.07	2
<i>Hystrix sp.</i>	-	-	-	2	0.01	1
<i>Marmota marmota</i>	-	-	-	5	0.02	1
<i>Oryctolagus sp.</i>	16	0.9	3	58	0.3	6
<i>Erinaceus europaeus</i>	-	-	-	3	0.01	1
<i>Testudo hermanni</i>	-	-	-	1	0.004	1
Aves	4	0.2	2	41	0.2	4
Total NISP- MNI	1,864	-	34	22,889	-	104
Very Large size	12	-	-	-	-	-
Large size	1,119	-	-	-	-	-
Medium size	1,759	-	-	-	-	-
Small size	148	-	-	13	-	-
Very Small size	0	-	-	12	-	-
Indeterminate	2,092	-	-	1,302	-	-
Total NSP	6,994	-	-	24,216	-	-

Table 1: Taxonomic determination, NISP, (%NISP, NSP and MNI of the fauna from the TD10.1 bone bed and TD10.2 bison bone bed of Gran Dolina.

only 0.1% of NSP are compatible with small size and very small-sized adult animals, and 5.4% are totally indeterminable (taxonomically and anatomically). The Shannon Evenness indicates that this is an extremely uneven assemblage ($E=0.024$). Thus, the TD10.2 bison bone bed can be considered as monospecific since 99% of NISP for ungulates is represented by a single species. With this feature as the main characteristic of the assemblage, and the absolute lack of anthropogenic modification in the faunal remains other than bison, the data presented below refer to the bison sub-set.

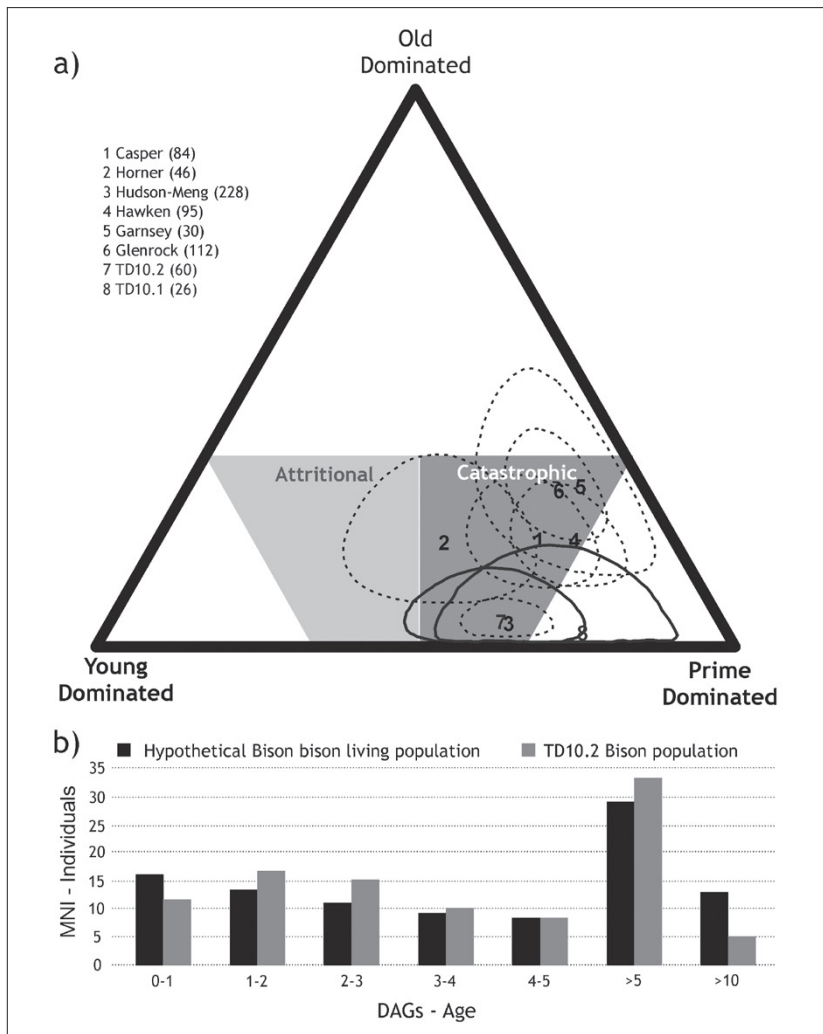


Fig. 2: Mortality pattern of the ungulates for TD10.1 and TD10.2 bison assemblages. In the modified ternary plot (a), the overlap of the 95% confidence ellipsis of the TD10.2 bison mortality pattern with data from other bison dominated sites (from Driver and Maxell 2013) and into the catastrophic mortality area of the triplot can be seen. The TD10.1 ungulate mortality overlaps with the prime-dominated area of the tri-plot. The bar chart graphic (b) shows the structure population in terms of the dental age groups (DAGs) of the bison from TD10.2 bone bed which closely resembles a living population structure (after Reher 1970).

The bison set is composed of 22,532 specimens representing at least 60 individuals as derived from the mandibular molars. Of these, 21 were young, 36 were prime-adults, and 3 were old, overlapping with the triplot zone of catastrophic mortality (Fig. 2). The structure of the population inferred through 47 mandibular series is very close to a living population (Frison and Reher 1970) (Fig. 2). The estimation of seasonal mortality inferred through eruption, wear and microwear indicates a bimodal pattern in which most deaths are concentrated in two seasonal windows that match with late spring/early summer and early fall (Rodríguez-Hidalgo et al. 2016a).

The anatomical profile is characterized by the common occurrence of the axial skeleton, especially heads and ribs. The ribs are very abundant (41% NISP or 3,892), followed by isolated teeth (17.9% NISP or 1,699), vertebrae (14.5% NISP or 1,380), fragments of skull (7.7% NISP or 732), and mandibles (7.1% NISP or 673). All other skeletal elements are represented by very low values, ranging between 1.3% and 0.1% of the NISP (125 NISP or less). Especially striking is the lack of long bones. Remains totaling 13,026 finds have not been assigned to a specific anatomical element. These include fragments of indeterminate flat bones (36.7% NISP or 8,207), with fragments of ribs and vertebral apophysis (5,739) most prevalent. Unidentified long bone fragments represent 10.7% of the NISP, most of them shaft fragments (1,720 *vs.* 64 distal end fragments) and indicative of the prevalence of the densest portions of the limbs in the bison set. Considering together all specimens belonging to the axial skeleton (except for teeth), they total more than 15,000 remains (67% NISP), while all anatomically determinable or indeterminable fragments of long bones (including metapodials) total little more than 3,000 specimens.

We have estimated 1,197 elements (MNE), the most numerous of which belong to low survival elements such as ribs (MNE = 402) and vertebrae (MNE = 272). The long bones are scarce in MNE, especially the upper limbs (humerus=18 MNE; femur=11 MNE). The high representation of some rare items in many Pleistocene assemblages such as the hyoid is particularly remarkable. The relative abundance of these elements (%MAU) attenuates the over-representation of the ribs (Fig. 3). Nevertheless, the only anatomical

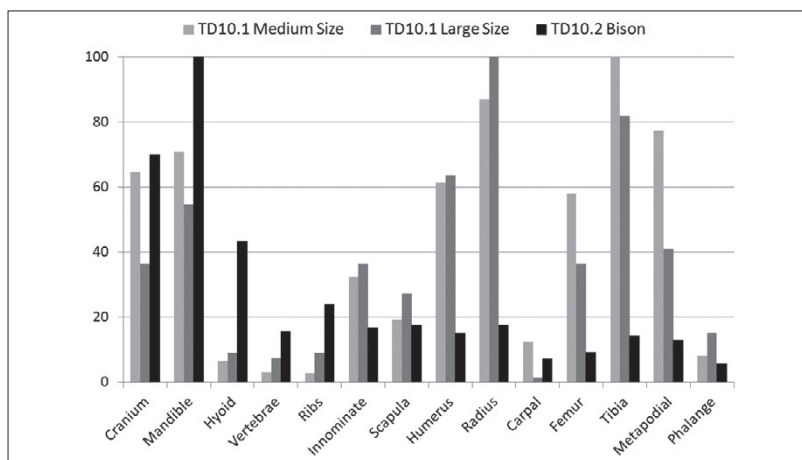


Fig. 3. %MAU distribution by element for large size animals and medium size animals from TD10.1 bone bed assemblage and for bison remains from TD10.2 bison bone bed assemblage.

elements that exceed 20% of MAU continue to belong to the axial skeleton, particularly the cranial segment and ribs. The %MAU of the limb suggests a marked loss, especially among the distal bones such as the metapodials and phalanges. The scarcity of the epiphysis from the shafts of long bones, and especially the least dense epiphyseal, suggests mineral density was mediated through attrition processes in the formation of the assemblage. In contrast, the high representation of the hyoid (43%MAU) suggests that the cranial remains are not over-represented by attritional processes associated with mineral density (Kreutzer 1992). Despite this, and due to significant bias in anatomical representation, we have tested for possible differential destruction. The results show a weak linear correlation ($r_s=0,295$; $p=0.0001$) indicating that the destructive processes associated with mineral density are implicated but are not a major cause of the anatomical representation in the bone bed (Table 2).

The relationship between the anatomical profile and the economic utility of the elements for assessing economic transport strategies is ambiguous. Although the result is not statistically significant in the majority of cases (Table 2), the linear correlation between the %MAU and (S)FUI is similar to the reverse bulk utility curve (Binford 1978; Metcalfe and Jones 1988; Marean 1997; Faith and Gordon 2007) (Fig. 4), in which high utility elements have been transported away from the site and low utility elements have been abandoned.

Layer	Taxon/Size	(S)FUI ¹	(S)AVGFUI ²	UMI ³	(S)AVGMAR ⁴	MDI ⁵	BMD ⁶
TD10.2	<i>Bison</i> sp.	$r_s = -0.09$	$r_s = 0.28$	$r_s = 0.34$	$r_s = -0.02$	$r_s = -0.14$	$r_s = 0.2^*$
TD10.1	Very Large size	$r_s = 0.11$	$r_s = 0.02$	$r_s = 0$	$r_s = 0.06$	$r_s = -0.03$	-
	Large size	$r_s = 0.09$	$r_s = -0.05$	$r_s = 0.42$	$r_s = 0.72^{**}$	$r_s = -0.58^*$	$r_s = 0.2$
	Medium size	$r_s = -0.25$	$r_s = -0.18$	$r_s = 0.53$	$r_s = 0.68^{**}$	$r_s = -0.83^{**}$	$r_s = 0.351^{**}$
	Small size	$r_s = 0.64$	$r_s = 0.6^*$	$r_s = 0.44$	$r_s = 0.19$	$r_s = 0.04$	-
	Very Small size	$r_s = 0.47$	$r_s = 0.4$	$r_s = 0.37$	$r_s = 0.60$	$r_s = -0.24$	-

Table 2: Statistical correlation between %MAU, utility indices and bone mineral density (BMD) by size weight categories in the faunal assemblage of Gran Dolina TD10.1 bone bed and between %MAU and the same indices for bison remains of TD10.2 bison bone bed. The significance of Spearman (r_s) correlation coefficient is indicated through asterisk (* $p < 0.05$; ** $p < 0.01$). ¹Standard Food Utility Index (Metcalfe and Jones 1988), ²Food Utility Index (Emerson 1993), ³Unsaturated Marrow Index (Morin 2007), ⁴Standardized Average of Marrow Fat (Emerson 1993), ⁵Meat Drying Index (Friesen 2001) and ⁶Bone Mineral Density for Rangifer tarandus (Lam et al. 1999) and for Bison bison (Kreutzer 1992).

Using indicators that reduce the effects of biotic or physical post-depositional depletion of cancellous bones, long bones are unevenly represented. The evenness index (0.799) indicates low anatomical diversity in the bison set, supporting the interpretation that carcasses were selectively transported, either because the transport was over a longer distance, because the carcasses were acquired at long distances from the “final deposition site” or because several carcasses were transported at the same time, increasing the transport weight. Given that the sample size is large (MNE = 200), this value is compatible with an unbiased strategy, in which skeletal elements are transported in direct proportion to their economic utility.

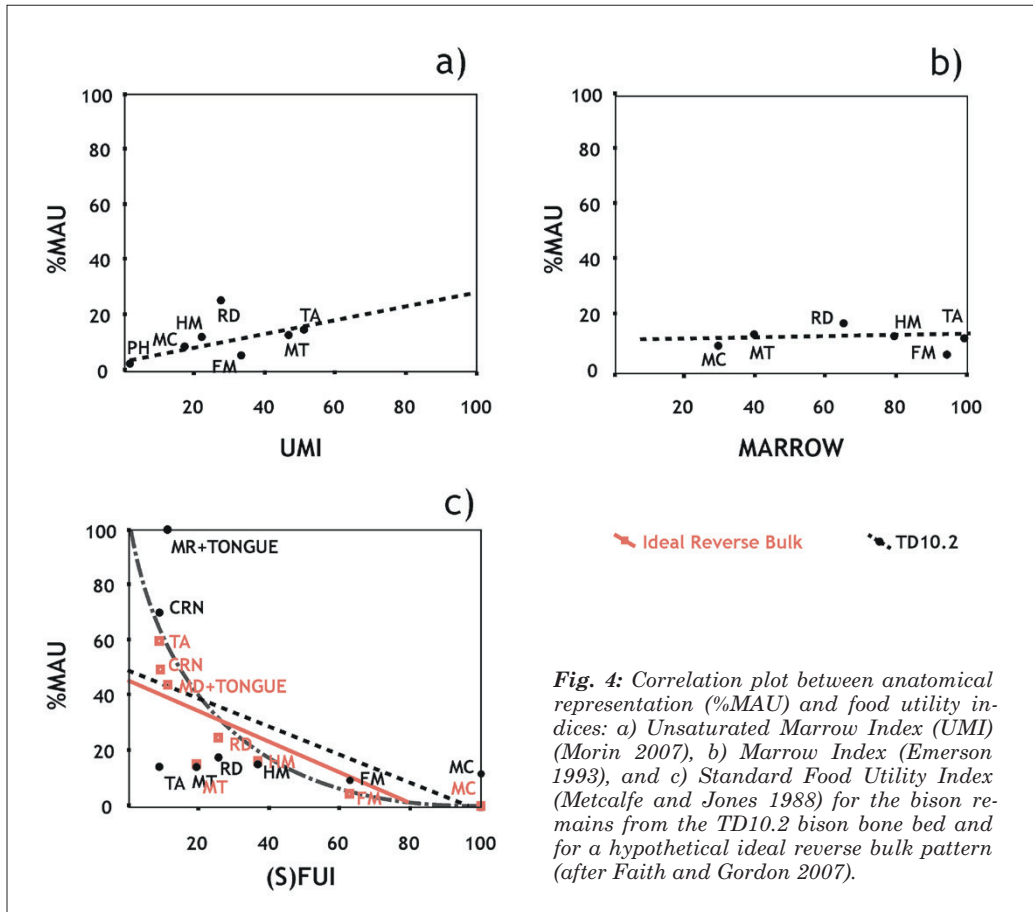


Fig. 4: Correlation plot between anatomical representation (%MAU) and food utility indices: a) Unsaturated Marrow Index (UMI) (Morin 2007), b) Marrow Index (Emerson 1993), and c) Standard Food Utility Index (Metcalf and Jones 1988) for the bison remains from the TD10.2 bison bone bed and for a hypothetical ideal reverse bulk pattern (after Faith and Gordon 2007).

Fragmentation analysis has been applied to a total of 2,098 long bones. The results show that 84% of them are less than $\frac{1}{4}$ of the length of the shaft and less than $\frac{1}{3}$ of its section. In the set there are no diaphyseal cylinders (long bones which retain more than a quarter of the original length of the shaft and the entire section). Among the 3,647 planes of fracture, curved (57%) and longitudinal (31%) are most common, and angles of fractures are mostly oblique (51%), with smooth surfaces predominating (84%), and coinciding with a green fracture of most long bones. The relationship between NISP and MNE (Klein and Cruz-Urbe 1984) of bones such as ribs gives us an idea of the high fragmentation of this element (3,892 *vs.* 402). An important number of fractures on ribs are considered to be green ($n=523$), although most of the rib fractures, and those on flat bones, appear to be due to post-depositional processes (including abundant fractures due to excavation processes, $n=898$).

Cut marks are present on 4.5% of bison specimens, and with the high number of cut marks (1,019 cut-marked specimens and more than 3,200 individual signals), the TD10.2 bison bone bed constitutes a Lower Paleolithic assemblage with the highest number of

cut marks and cut-marked specimens thus far documented (Fig. 5 and Table 3). Cut marks are present on most of the elements and are absent only on underrepresented bones and those of low utility, such as carpals, tarsals, and distal phalanges. Regarding cut-marked bones, most of the cut marks are documented on rib fragments (35.7%), indeterminate long bone fragments (17.3%) and indeterminate flat bone fragments (15.2%), which is not surprising when taking into account the anatomical representation in the NISP. However, if we consider cut-marked specimens and the NISP of each element, intermediate appendicular (38.7%) and proximal appendicular bones (28.6%) show the highest frequencies (Fig. 5). If we consider the portions of the bone that are marked, we can see that 76% of the cut marks are on the shafts, 18% on portions near the epiphysis and only 4% on the epiphyses.

Taxa	TD10.1 Bone Bed						TD10.2 Bison Bone Bed					
	Cut Marks		Anthrop. breakage		Carnivore marks		Cut Marks		Anthrop. breakage		Carnivore marks	
	n	%	n	%	n	%	n	%	n	%	n	%
<i>Bison sp. (small)</i>	-	-	-	-	-	-	1,019	100	295	100	1,436	95.0
<i>Cervus/Dama</i>	397	44.0	167	51.9	88	28.8	-	-	-	-	14	0.9
<i>Bison schoetensacki</i>	40	4.4	11	3.4	11	3.6	-	-	-	-	-	-
<i>Equus sp.</i>	27	3.0	8	2.5	10	3.3	-	-	-	-	5	0.3
<i>S. cf. hemitoechus</i>	3	0.3	2	0.6	-	-	-	-	-	-	-	-
<i>Capreolus priscus</i>	1	0.1	-	0.0	-	-	-	-	-	-	2	0.1
<i>Panthera leo</i>	-	-	-	-	1	0.3	-	-	-	-	-	-
<i>Canis/Cuon</i>	1	0.1	-	0.0	-	-	-	-	-	-	4	0.3
<i>Vulpes vulpes</i>	-	-	-	-	-	-	-	-	-	-	3	0.2
<i>Castor fiber</i>	-	-	-	-	-	-	-	-	-	-	3	0.2
Carnivora indet.	-	-	-	-	-	-	-	-	-	-	2	0.1
<i>Oryctolagus sp.</i>	-	-	-	-	2	0.7	-	-	-	-	33	2.2
Aves	-	-	-	-	-	-	-	-	-	-	9	0.6
Very Large size	2	0.2	1	0.3	1	0.3	-	-	-	-	-	-
Large size	167	18.5	58	18.0	75	24.5	-	-	-	-	-	-
Medium size	208	23.1	68	21.1	83	27.1	-	-	-	-	-	-
Small size	12	1.3	2	0.6	1	0.3	-	-	-	-	-	-
Indeterminate	44	4.9	5	1.6	34	11.1	-	-	-	-	-	-
Total	902		322		306	-	1,019	-	295	-	1,511	-

Table 3: Taxonomic distribution of the specimens (NISP/NSP) and frequencies with anthropic (Anthrop.) induced modifications (cut marks and anthropogenic breakage) and carnivore induced modifications (tooth marks, carnivore breakage and digested bones) for the assemblages studied in this work.

Due to the abundance of axial elements, we have been able to document butchering tasks that are usually scarce in Pleistocene assemblages. In this sense, the presence of a large number of slicing marks on the lingual surface of the mandibles (20%) and on the hyoids (5%) suggests a recurrent exploitation of the tongue. As regards the trunk, 28.7% of the cut marks are located on the medial side of the rib. This situation is invariably associated with evisceration (Binford 1981; Nilssen 2000).

Other tasks such as disarticulation and dismemberment can be inferred here, for example, when we observe the long and deep cuts in the area surrounding the acetabulum, on the iliopubic eminence, and on the pectineus surface of an *os coxa* of an adult bison, or in the neck and head of ribs, although the scarcity of epiphyses of long bones contributes to its lower archeological visibility. The same holds true for skinning, inferred through cut marks on the skull and metapodials since the remains of the former are fragmentary and the latter scarce. Cut marks related to skinning are located on the frontal, orbital, and nasal portions of the skull and on the anterior side of the metapodials.

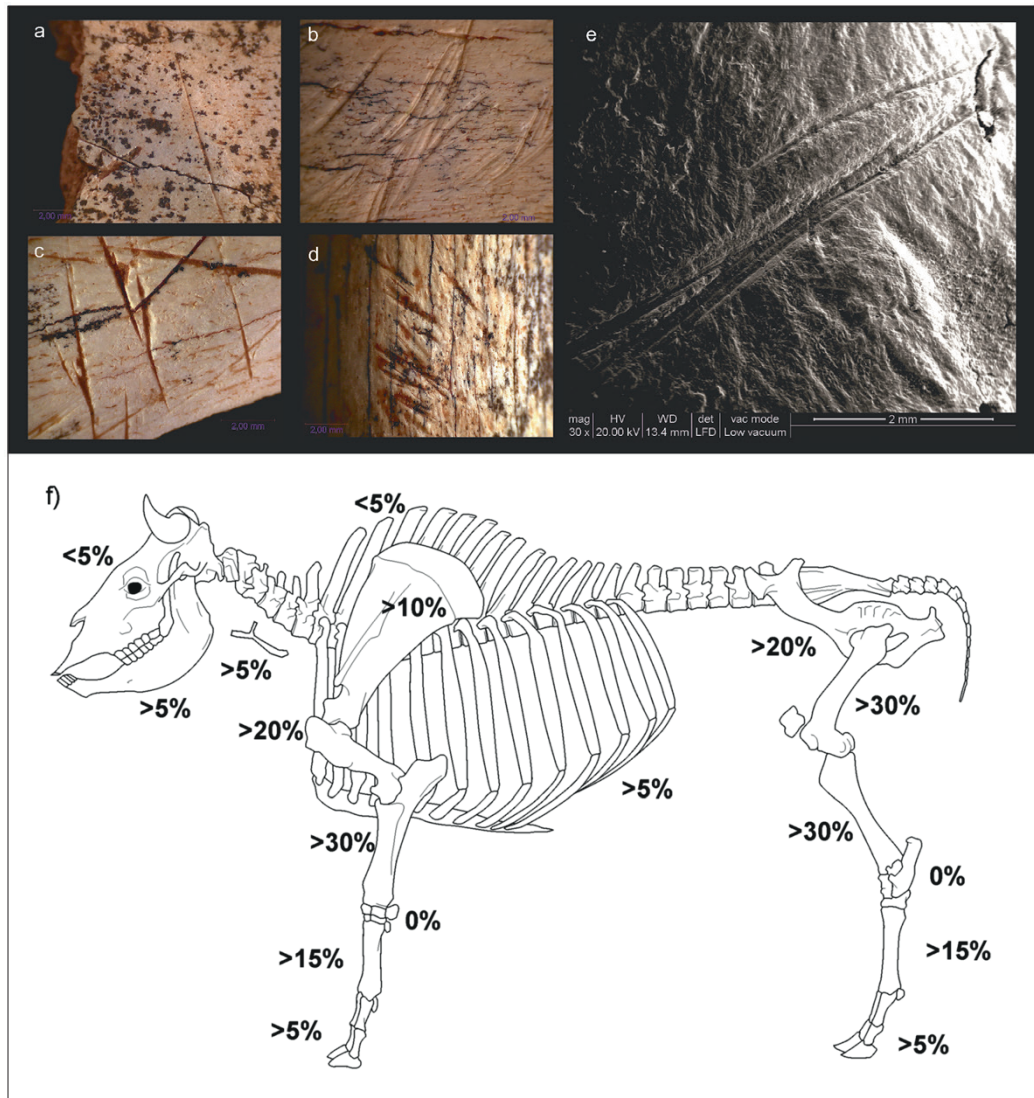


Fig. 5: Examples of cut marks in the bison assemblage of TD10.2 bison bone bed (a, b, c, d and e), and frequency of cut-marked bones by anatomical elements (f).

The skinning of the heads must have been carried out for alimentary purposes (the exploitation of the brains) or for the extraction of the hides. Regardless of the aim in skinning the heads, the difficulty in handling them, and the high cost in time and energy that is required in removing their skin (personal observation) indicates that, at least sometimes, hominids were interested in obtaining skinned skulls or the skin of the skull. Finally, in six different (MNE) phalanges (four first phalanges and two second phalanges), slicing marks have been observed that can be related to skinning of the shanks.

The bison set preserves evidence of anthropogenic breakage by percussion and peeling on 390 specimens (NISP). The breakage involves both long and flat bones. The diagnostic features are related to the use of tools for percussion such as anvils, hammer stones and choppers (NISP=295), and to the bending of flat bones generating modification in the form of peeling (NISP=95). Percussion bone breakage is observed mainly on bones with high marrow content (NISP=216; 73%), and especially common on the femur and radius/ulna. A total of 114 specimens from indeterminate long bones complete the group (4.7 %NISP).

The percussion marks are situated on the ends of the diaphysis, near the metaphyseal area. The pattern is especially repetitive on ulnae, humeri, radii, and femora. Adhered flakes (NISP=63) and conchoidal scars (NISP=18) have also been observed. The bone flakes attributed to anthropogenic breakage amounted to 51 finds, although another 596 finds with green fracture outlines have no diagnostic characteristics to attribute to a particular agent. The abundant display of percussion breakage on long bones that has been recorded for the set suggests that many of these fragments are likely to be anthropogenic. In addition to the fracture of long bones, we have also observed the intentional fracture of some elements with low medullary yield such as ribs and proximal phalanges. On ribs we have recorded percussion fractures on the costal angle area in 30 cases as a means to access the inner red marrow (Binford 1981; Pickering et al. 2013). We also observed crushing and anvil damage on the opposite side and cracks extending from the area of percussion along the shaft. However, ribs were broken mainly through peeling (NISP = 66). As we have described above, 523 rib fragments display features of green breakage. In the case of proximal rib fragments displaying spiral fractures (NISP = 74), archaeological analogy suggests that these were probably snapped during detachment from the vertebrae (Hill 2008).

As for the proximal phalanges, we found no diagnostic criteria in the form of percussion marks for ascribing the fractures to hominin activity. However, the recurrence of the breakage pattern (30% of phalange 1), consisting in longitudinally-split phalange 1 that do not refit among them (Fig. 6), and the archaeological and experimental parallels (e.g., Hill 2008; Jin and Mills 2011) point to an anthropogenic origin.

We have been able to determine the activity of carnivores through tooth marks, carnivore breakage, and digested bones on 6.1% of the specimens (NISP = 1,436). We have documented pits, scores, and perforations (98.4%), furrowing (10.2%), and scooping-out (1.3%). Sometimes, the tooth marks are numerous, generating pitting on 9.7% of the chewed remains (Table 3).

Among the long limb bones, epiphyseal and near epiphyseal fragments revealed marks more frequently than shaft fragments (24.8%, 18.1% *vs.* 6.2%). As stated above,



Fig. 6: Examples of breakage patterns on bison first phalanges from the TD10.2 bison bone bed. The arrow indicates slicing marks on the distal articular surface of a first phalange: (a) posterior and lateral proximal surface of two second phalanges (b) related to disarticulation prior to breakage.

the less dense portions of long bones are scarce in the bison set. The loss of the epiphysis may relate to the ravaging of carnivores (Blumenschine 1986; Marean et al. 1992) as suggested by the distribution of modifications on these bone portions. Heavy furrowing affected 7% of bones chewed by carnivores (0.6% of total of NISP). In four cases (two metacarpals, one femur, and one indeterminate long bone), scooping-out was observed. Pitting has been recorded mainly on ribs ($n=42$), flat bone fragments ($n=28$), and long bones ($n=24$). The fractures attributed to carnivores are scarce ($n=52$) and affect different elements, especially ribs (NISP=11) and long bones (NISP=19) (Table 3). Digested remains are scarce ($n=26$). Most include fragments of long bones or unidentified fragments that

have been assigned to bison based on size. The few determinable pieces consist of sesamoids and fragments of teeth. Over 90% of these remains were moderately to heavily digested. The average length is 23 mm. No coprolites were found in the assemblage.

We have measured more than 1,200 tooth marks. The mean of the width on cortical bones is 1.45 mm, while that on cancellous bones is slightly larger (1.95 mm). The maximum values for the width of perforation punctures and pit marks (7.3 mm on cortical bone and 8.69 mm on cancellous bone) clearly indicate the involvement of large carnivores with the carcasses. All metric parameters considered together suggest the involvement of large and/or medium-sized carnivores such as large canids and hyenas (Fig. 7). However, we cannot dismiss the intervention of smaller carnivores, such as foxes, whose traces could be deleted or marked by the signals of larger animals. In the same way we cannot rule out the intervention of large carnivores such as bears. The data about type, location, frequency and intensity of gnawing combined with measurements of tooth marks suggest that durophagous carnivores were involved in the modifications found in the assemblage. The relative abundance of remains of large canids, the absence of remains of hyaenids and coprolites point to the former as the main carnivore bone modifiers in TD10.2. Nevertheless the intensity of some modifications and the large size of the bison carcasses suggest the intervention of hyenas too.

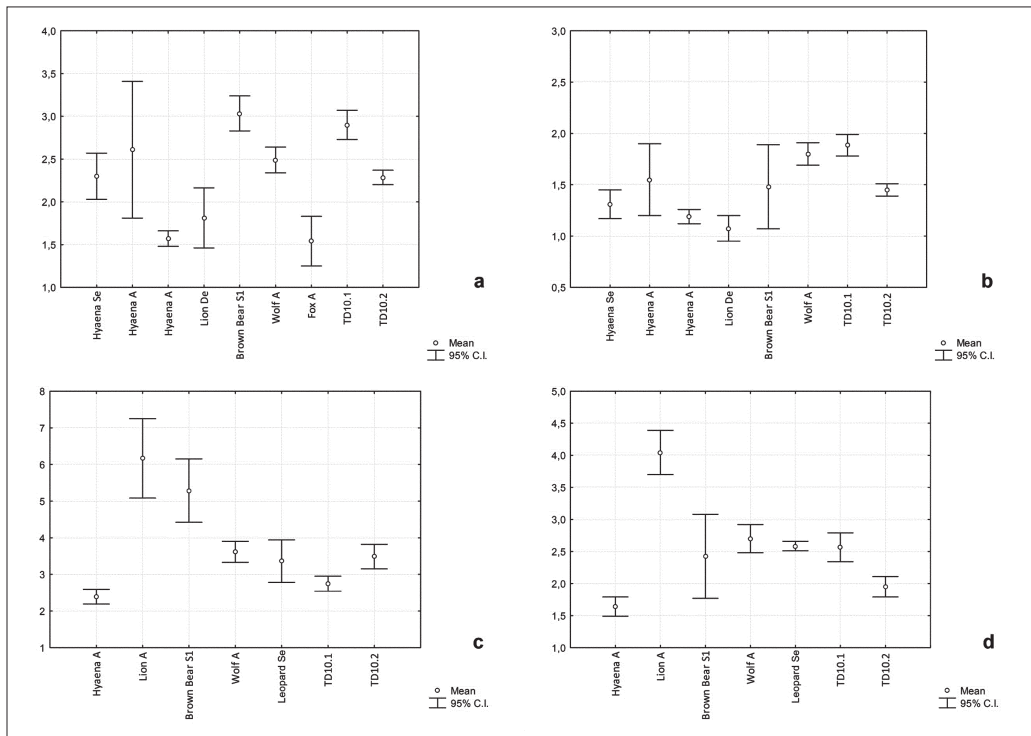


Fig. 7: Measurements for carnivore tooth marks on TD10.2 bison bone bed and TD10.1 bone bed on cortical bone tissue (up) and cancellous bone tissue (down) (mean and 95% confidence intervals in mm; length: left; width: right). The results are compared with those of actualistic studies. Legend: Se = Selvaggio (1994); De = Delaney-Rivera et al. (2009); A = Andrés et al. (2012); S1 = Saladié et al. (2013a).

Co-occurrence of human and carnivore modifications has been observed on long bones (0.5% NISP) and ribs and vertebrae (0.5% NISP) (total 91 NISP). This very low coincidence suggests independence in the formation of the set, but we must consider that this result could be altered by the different distribution of damage along portions of the bones (Saladié et al. 2014). Carnivore tooth marks and cut marks overlap on seven remains. In all cases carnivore marks are superimposed over the cut marks, providing evidence of secondary access by the former.

The results of the estimation of carnivore ravaging through taphonomic indices indicate a moderate to high ravaging, when we consider the indices that reflect the epiphysis to shaft ratios, and very light ravaging, according to the axial to appendicular index. These results are contradictory because they indicate a strong loss of epiphyses of the long limb bones by carnivore ravaging, an observation that does not correspond to what we might expect for the axial skeleton ravaging, which should be high. Nevertheless, the results are similar when we take into account other sites where large ungulates predominate. Such occurrences are interpreted as kill sites in which it is supposed that whole carcasses are represented prior to anthropogenic selective transport and carnivore ravaging (Fig. 8). These results suggest that, when given anthropogenic mass predation events of large ungulates, subsequent carnivore ravaging hardly affects the representation of the axial skeleton, probably due to its abundance in the complete skeleton. This seems to be the case in the TD10.2 bison bone bed in Gran Dolina.

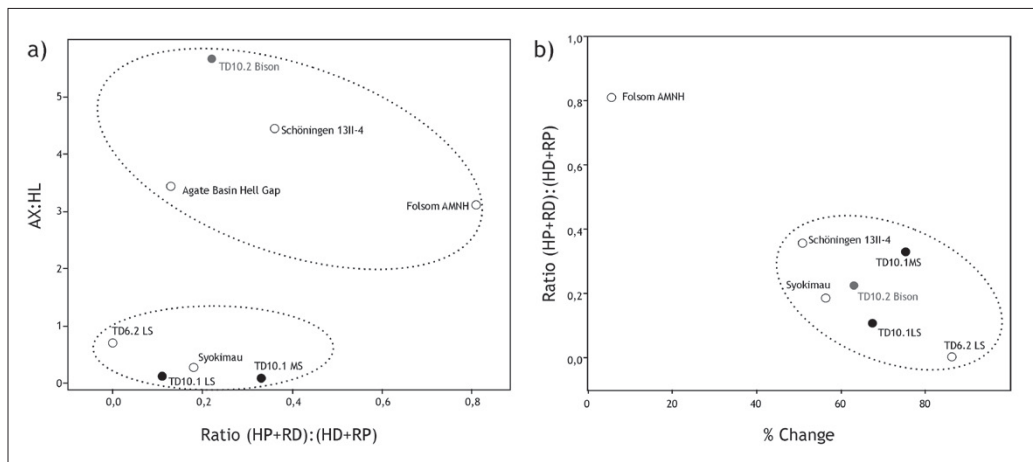


Fig. 8: Correlation between taphonomic indices of ravaging applied to the TD10.2 bison set, TD10.1 bone bed by categories of weight size (Large Size and Medium Size) and other control assemblages (from Hill 2008; Egeland et al. 2008; Voormolen 2008; Saladié et al. 2011; Folsom AMNH data collection by the author). The correlation of AX:HL to (HP+RD):(HD+RP) shows significant divergence between the assemblages dominated by large size ungulates and/or mass mortality profiles and assemblages dominated by small and medium size ungulates and/or individual predation. As a result, the AX:HL ratio is not interpretable for carnivore ravaging in these cases. The correlation of %Change to (HP+RD):(HD+RP) shows moderate to heavy ravaging in the TD10.2 bison set.

Only about 1% of the faunal remains of the bison bone bed belong to other taxa (NISP=357). The most abundant taxon is rabbit (*Oryctolagus* sp.) (NISP=58), followed by equids (NISP=55), large canids (NISP=61) (*Canis lupus* NISP=7 and *Cuon alpinus*

NISP=3), medium-sized cervids (*Cervus/Dama* NISP=48), and Aves (NISP=41). Other taxa are represented by less than 30 specimens. Carnivores are diverse and abundant in terms of NISP and MNI. The scarcity of individuals prevents mortality interpretations, although immature individuals are common throughout these species (Table 2).

The anatomical representations are highly biased for ungulates, carnivores, and mesovertebrates. Both the ungulates and carnivores among the macromammals are mainly represented by isolated teeth and small and compact bones of the feet. Due to the high bias in the skeletal features, the ratio between MNE and MNI is very high for these animals (Lyman 2008).

With regard to the modifications on bone surfaces, there is no anthropogenic activity except on a radius shaft of a medium-sized bird.

By contrast, signals of carnivore activity are abundant (11.2%) and affect all taxa. Preserved distal portions of the long bones of rabbits and birds, as well as the high proportion of tooth-marked and digested remains of these two taxa (21%) and the absence of anthropogenic activity, indicate their origin is likely related to the activity of non-human predators, probably small terrestrial carnivores and birds of prey (Lloveras et al. 2008, 2009, 2012; Rodríguez-Hidalgo et al. 2013, 2016b), but we should use caution before advancing an interpretation of the finds until the mesovertebrates have been more extensively studied (work in progress).

The TD10.1 bone bed of Gran Dolina

We analyzed 6,994 remains belonging to macro- and mesovertebrates from 11 taxonomic groups. The NISP of 1,864 is mainly composed of deer remains (*Cervus elaphus* and *Dama dama*) (NISP 79.6%), *Bison schoetensacki* (NISP 7.3%), Equidae (*E. ferus/E. cf. hydruntinus*) (NISP 7.1%) and *Stephanorhinus cf. hemitoechus* (NISP 2.5%). The remaining taxa are represented by less than 1% of the NISP (Table 1). The sample shows a moderate value of taxonomic diversity ($E=0.581$). Carnivore remains are extremely scarce in the assemblage (NISP 0.2% or 4 NISP). Most of the indeterminate fragments (NSP 5,130) show characteristics of size, wall thickness and diameter compatible with medium-sized deer remains (NSP 34%), as is reasonable considering the balance of the NISP. The estimated MNI is 34, highlighting the predominance of individuals of red deer and fallow deer (17 MNI or 50%), followed by horses (4 MNI or 11.8%), rabbits (3 MNI or 8.8%), bison and birds (2 MNI or 5.9%). The anatomical distribution of the sample in NSP shows the predominance of long limb bone fragments (NSP 1,852 or 37.9%). The mortality pattern indicates the predominance of prime-adult individuals in the sample (76.5%), followed by young individuals (20.6%) and a few old individuals (2.9%). Regarding the ungulate prey mortality, 19 individuals are prime adults, six are young and one is an old animal (Fig. 2). For the medium-sized deer, which is the main taxonomic group in the sample, a clear prime-dominated pattern is apparent, with 12 prime adults, four young animals and one old individual. Among the six young ungulate individuals, four can be considered sub-adult juveniles and only two of these (red or fallow deer) represent animals that are small in size and relatively more vulnerable as prey. The total number of elements in the sample is 511, of which 466 elements (91.2%) correspond to ungulates, especially medium-sized deer (71.1%). All the skeletal elements are represented. The most common among these are small bones (carpals, tarsals, sesamoids and patellae)

(MNE 70), metapodials (MNE 60), phalanges (MNE 49), tibiae (MNE 41), radius (MNE 40) and mandibles (MNE 31). The least common elements are ribs (MNE 3) and pelvic and shoulder girdle bones (9 scapula and 7 coxae). The relative proportion of the anatomical representation expressed in %MAU clustered by size categories is virtually identical for large and medium-sized animals, showing high frequency of intermediate and upper limbs and cranial bones and scarce representation of the axial postcranial skeleton. The results of the Spearman coefficient between %MAU and mineral density indicate a moderate positive correlation for medium-sized animals ($r_s=0.351$; $p<0.01$) and no significant correlation for large-sized animals ($r_s=0.2$; $p>0.05$) (Table 2).

The surfaces of the bones in the TD10.1 bone bed are exceptionally well preserved. Post-depositional modifications are scarce in this assemblage, except for black stains from manganese oxide deposits found on 30.6% of the remains. Trampling, sub-aerial weathering, root etching or other modifications altering the bone surfaces are especially infrequent (less than 3% of NSP). The few if any incidences of modifications related with bone-destroying, post-depositional processes such as weathering, dissolution or corrosion suggest that, although they were active in modifying the material, their impact on bone-mediated attrition is minimal. A major role for post-depositional processes in mineral density attrition, resulting in the skeletal bias observed in the sample, can therefore largely be discounted as having any significant impact on the anatomical representation observed in the assemblage. Similarly, the results of a fragmentation analysis indicate scarce breakage due to post-depositional processes. Nevertheless, the analyzed sample shows high fragmentation. Only 2.3% of the specimens are complete. Most of the diaphyses preserved less than 1/4 of their original length (96.7%) and less than 1/3 of their original circumference (95.3%). Analysis of broken long bones shows that curved/V-shaped fragments predominate (59.9%), along with oblique angles (89%), and smooth edges (98.6%). The most common combination of features shows a predominance of curve, oblique and smooth fractures (59.9%). These characteristics indicate the predominance of green breakage in the sample.

The coefficients of several utility indices and %MAU show no significant correlation for the majority, independent of the body size of the animals (Table 2). The only coefficients that can be considered in behavioral terms are those for marrow yield in large ($r_s=0.72$; $p<0.01$) and medium-sized categories ($r_s=0.68$; $p<0.01$), indicating a high correlation between productivity of marrow for medium-sized and large animals and its representation in the sample (Fig. 9). In addition, the MDI index shows statistically significant high negative correlation with %MAU in medium-sized animals ($r_s=-0.83$; $p<0.01$) and weaker but significant strong correlation for large animals ($r_s=-0.58$; $p<0.05$). The Shannon evenness index for large and medium-sized animal elements falls within the range of both bulk and unconstrained carcass transport strategy (Large size $E=0.98$; NME 49; Medium size $E=0.98$; NME=179). However, non-significant rank-order correlation between %MAU and utility (FUI) suggests an unconstrained pattern in both weight category sizes.

Butchering marks (cut marks and percussion marks) have been located in 16.3% of the faunal remains. The modifications are concentrated on ungulate remains, mainly on deer (Table 3). Cut marks are present on 12.9% of the remains (NSP=902). Cuts appear on most of the taxa identified, especially on medium-sized deer, bison and horse remains.

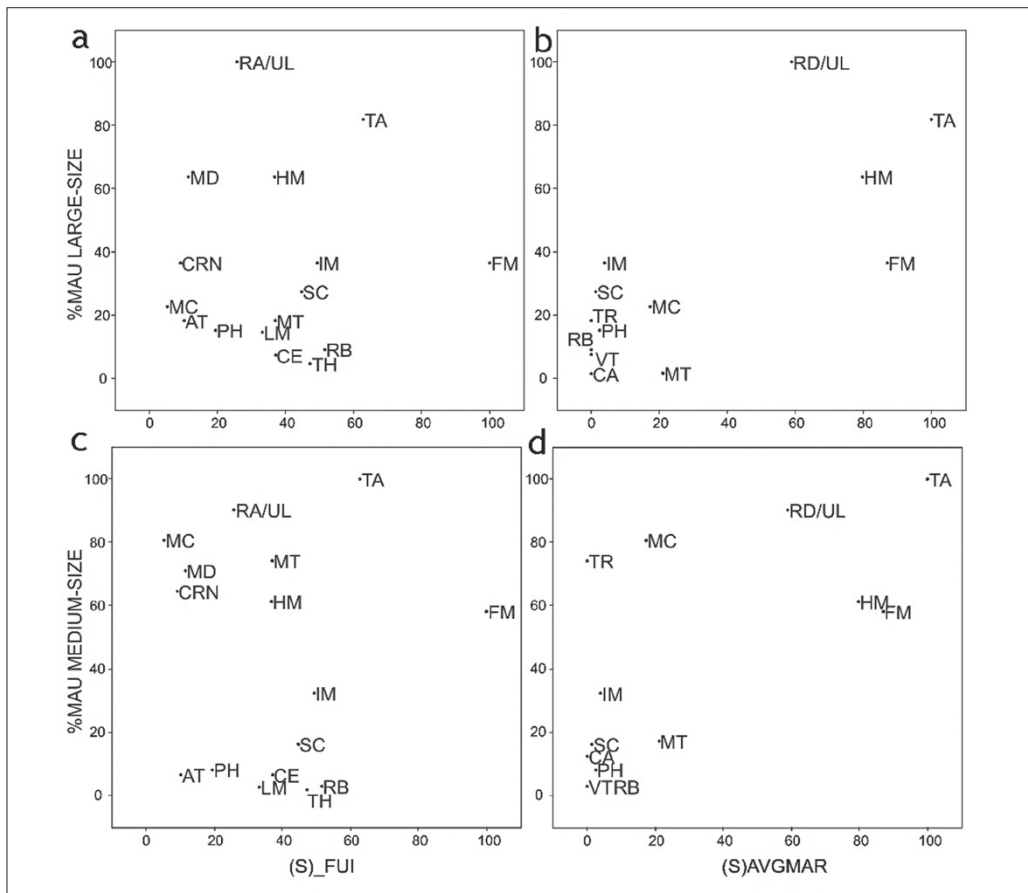


Fig. 9: Scatter plots of skeletal representation in % MAU (ordinate), (S)_FUI (Metcalf and Jones 1988), Marrow Index (S)AVGMAR (Emerson 1993) and mineral density BMD (Lam et al. 1999) for large-sized (up) and medium-sized animals (down) for the TD10.1 bone bed sample.

The presence of cuts on some remains of rhinoceros and roe deer reveals an anthropogenic component to all ungulates in the sample except for *H. bonali*, possibly due to the low NISP of this taxon. Furthermore, there are cut marks on one carnivore specimen, reflecting the exploitation of *C. lupus/C. alpinus* for meat. No rabbit or bird remains show cut marks. Cut marks are present on all anatomical elements, including the skull and axial segment bones, although they are most abundant on appendicular bones (66%, NISP=597) (Fig. 10). In these bones, 83% of the cut marks are on shaft fragments, 13% on near-epiphysis areas and 3.4% on epiphyses. For anatomical segments, cut marks are more common in the intermediate limb bones, followed by the upper limb bone elements (Fig. 10). We have not observed notable differences in the distribution of cut marks with regard to the groups by size or weight or different treatment by species. The butchering activities identified in this sample through the cut marks include skinning, defleshing, disarticulation, dismembering, evisceration and periosteum removal. The location, position and relationship between marks reflect a systematic butchering process.

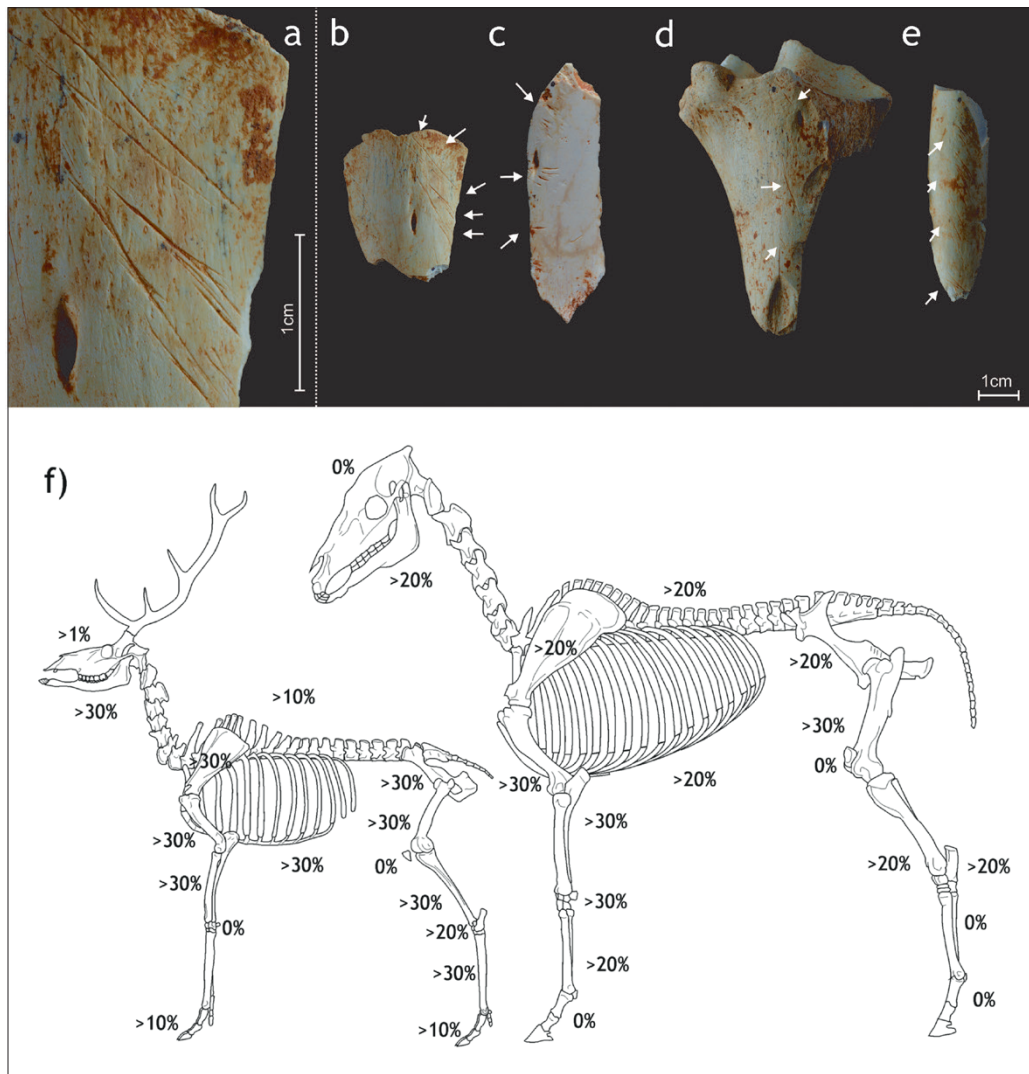


Fig. 10: Examples of cut marks in ungulate remains of TD10.1 bone bed (a, b, c, d and e) and frequency of cut-marked bones by anatomical elements for the Medium size (deer) and Large size (horse) remains (f).

Evidence of anthropic breakage is present in the assemblage in long and flat bones (NSP=351). The damage to bone surface related to anthropic breakage is derived from stone-hammer inflicted percussion (91.7% of fractured bones, NSP=322) and peeling (8.3%, NSP=29). Percussion bone breakage is found mainly in long bones (NSP=292) although it is also present in mandibles (NSP=9) and ribs (NSP=4) belonging to large-sized animals. Regarding the three phalanges of red deer that are present in the assemblage (two first phalanges and one second phalange), anthropogenic fractures have resulted in a standard breakage of the bones in the form of a longitudinal split. This characteristic breakage is equally visible on a further set of 11 phalanges (6 of indeterminate medium-sized

deer, 2 of bison and 1 of horse) but they have no percussion marks. The recurrence of this pattern suggests that they are also the product of anthropogenic fracture.

As is common in Middle Pleistocene faunal assemblages of the Sierra de Atapuerca, we have not identified any burnt bone.

Carnivore-induced modifications were present on 306 specimens. The types of bone surface modification caused by carnivores include pits, punctures and scores (98%), furrowing (5.5%), crenulated edges (2.6%), corrosion by gastric acid (1.9%) and/or pitting (1.6%). Furthermore, the indentations caused by tooth cusps on the fracture edges have been observed on 62 remains (4.3% of the set), indicative of carnivore breakage. According to the relative frequency of each weight-size, the most affected category was that of animals of very small size, and the least affected was that of animals of very large size (very large size 1.7%; large size = 6.8%; medium size = 5.3% and small size = 0.6% and very small size = 9.5% with carnivore-induced modifications) (Table 3).

The carnivore tooth marks were located most frequently on epiphyseal fragments, with 14.1% of these bearing tooth marks versus the 9.1% documented on near-epiphysis areas and the 4.8% present on shaft fragments. The Fisher's exact test ($p < 0.01$) reveals that these differences are statistically significant.

Given their average dimensions and 95% confidence interval (Fig.7), the pits and puncture marks seem to have been made by a large or medium-sized carnivore. Compared to modern experimental samples (Selvaggio 1994; Delaney-Rivera et al. 2009; Andrés et al. 2012; Saladié et al. 2013a), pit length and width on dense cortical shafts and cancellous bone reveal that the carnivore pit and puncture mark samples are similar to those documented for large or medium-sized carnivores.

Anthropogenic and carnivore modifications have been demonstrated on 56 specimens (0.8%). These remains have at least one cut mark and one carnivore tooth mark (explicitly overlapping in five cases). There are also percussion pits on five specimens. This low frequency, as proposed by Egeland et al. (2004), seems to indicate greater independence between agents, which would suggest that they did not act on the same carcasses. However, the low frequency of low survival portions and elements suggests that the ravaging by carnivores could actually be much higher. The values of the ratios that have allowed us to evaluate this possibility are presented in Fig. 8. All values indicate important scenarios of ravaging carnivores, which would act on the bones first processed intensively by hominins.

Discussion and conclusions

Our study points to hominins as the taphonomic actors primarily responsible for the faunal accumulations at Gran Dolina. The huge concentration of archaeological remains represents thin, well-defined archaeo-stratigraphic layers in which no significant post-depositional processes took place. In this sense, the bone beds represent *in situ* levels where hominins performed tasks related to subsistence, and interpreted here through the faunal record. Taking into account the scarcity of well-preserved anthropogenic faunal accumulations dated to the Middle Pleistocene, the two layers studied above represent valuable sources in which to discover the narratives on the evolutionary past of our genus.

The results from the TD10.2 bison bone bed indicate that it is virtually a monospecific assemblage. Remains of at least 60 bison were accumulated together with several thousand lithic tools. Distribution and frequency of butchering marks indicate early, primary, and recurrent access to the carcasses by hominins as well as systematic butchering and intensive exploitation. No evidence of secondary access has been recorded. The catastrophic mortality profile and the concentration of death at two seasonal peaks point strongly to mass predation as the hunting technique for bison procurement and the origin of the assemblage through overlapping events of multiple kills. The anatomical representation, with a dominance of axial elements, suggests the use of Gran Dolina as a kill-butchering site and the recurrent transport of high yield portions of the carcasses (mainly the limbs) somewhere outside the cave. Heavy carnivore ravaging has been recorded. In this scenario, the lack of “low survival” elements such as vertebrae and ribs is understandable (Marean and Spencer 1991; Marean et al. 1992; Marean and Assefa 1999; Marean and Cleghorn 2003). However, the large amount of carcasses accumulated in each kill event paradoxically favored the high survival of “low survival” elements.

Evidence that is commonly used to infer communal hunting in the Middle and Upper Paleolithic as well as in more recent times includes monospecific faunal assemblages dominated by large ungulates that exhibit a high number of animals slaughtered, catastrophic mortality profiles, seasonal mortality, systematic exploitation of carcasses, and transport of elements of high utility (e.g., Wheat 1972; Reher 1973; Frison 1974, 1987; Forbis 1978; Speth 1983, 1997; Todd 1987; Olsen 1989; Driver 1990; Reeves 1990; Byers and Hill 2009; Rendu et al. 2012; Santiago and Salemme 2016; White et al. 2016). These characteristics are fully consistent with those observed in the faunal assemblage of the TD10.2 bison bone bed, suggesting that cognitive, social and technological capabilities required for successful communal hunting of large ungulate prey was fully developed in the pre-Neanderthal populations of Atapuerca as early as *circa* 400 ka (Rodríguez-Hidalgo 2015; Rodríguez-Hidalgo et al. 2016a, in press).

In the case of the TD10.1 bone bed, our results also point to an assemblage highly dominated by large ungulates. Bison, horses, fallow deer but especially red deer were the main prey exploited by hominins. No evidence of small game has been uncovered. Distribution and frequencies of butchering marks on skeletons indicate again early access to the carcasses by hominins as well as systematic butchering for intensive exploitation. We have not seen any evidence of secondary access. Regarding the age at death of the ungulate prey, the TD10.1 bone bed is dominated by prime-age animals, suggesting that ambush hunting and/or stalking (cooperative or not) was the main hunting tactic employed by the hominins (Stiner 1990; Bunn and Gurtov 2014). In addition, the primary access to formidable prey such as rhinoceros, bison and horses points to the use of other cooperative tactics as well. The skeletal representation dominated by “high survival” elements suggests the systematic transportation of the carcasses from the kill site to Gran Dolina. Carcass transport decisions are difficult to infer due to the modifications of carnivore ravaging in the original anatomical profiles. Notwithstanding, such decisions must have been standardized enough to generate very similar skeletal profiles between animals of different weights (large and medium-sized). In this sense, the data support a somewhat preferential transport of elements with a high marrow yield (principally long bones), indicating a fundamental economic strategy.

From an archaeological point of view based specifically on the taphonomy, the huge concentration of faunal remains, the high number of individuals inferred from an assemblage taxonomically dominated by prime-aged ungulates, the extreme scarcity of carnivore remains, the high frequency of butchering marks, the high fragmentation of remains and the high representation of the more valuable parts of the carcasses are all characteristics supporting the residential base camp hypothesis for the archaeological horizon of the TD10.1 bone bed (Yeshurun et al. 2007; Clark 2008; Stiner et al. 2009, 2011; Stiner 2013). Hominins systematically carried animal remains to the base camp during very intensive and probably long-term occupations to exploit animal resources, and probably to share them among group members who did not participate in the kill events (Rodríguez-Hidalgo 2015; Rodríguez-Hidalgo et al. 2015). This is consistent with a primordial division of labor, at least between the group members who hunted and the group members who remained in the Gran Dolina base camp.

Although the two assemblages studied here show similarities in their taphonomic history regarding the anthropogenic pathway (early access to the carcasses by hunting, intensive butchering, systematic transport from the kill to the base camps, etc.), the differences regarding the taxonomic representation, the mortality profiles and anatomical representation are significant. These differences are particularly noteworthy because not too much geological time has passed between the formations of the layers and because, at least presumably, the hominins responsible for both accumulations must have been phylogenetically and culturally closely related. Nevertheless, our interpretation of the functionality of the site and the length of the occupations recognizes these differences. Gran Dolina was used as a kill-butcher site for very specific activities, in behavioral terms, with short occupations during the formation of the TD10.2 bison bone bed; it was used as a reference campsite for long and extensive occupations during the formation of the TD10.1 bone bed. As a result, the management of resources is very different among the layers. Both hunting and lithic resources reveal a hyper-specialization in TD10.2 due to the fact that we are looking only at a very short-term and specific activity (the communal hunting/butchering events) among the broad spectrum of activities developed by hominins in their day-to-day lives. This management becomes more flexible or perhaps more generalist in TD10.1 as a consequence of the great variety of subsistence activities developed in long-term and more intensive occupations.

The integration of zooarchaeological data previously reported for Gran Dolina TD10.1 (Rosell 2001; Blasco 2011) with the results from this study provides valuable information for interpreting the subsistence dynamics along the Gran Dolina TD10 covering the second half of the Middle Pleistocene.

Previous and ongoing research confirms that the Atapuerca hominins based their intake of animal resources on the regular hunting of large ungulates. In the different samples studied, the evidence indicates the selection of prey, the intensive and systematic processing of carcasses and the transport of the meat supply to reference camps. Other strategies such as scavenging have also been proposed (Rosell 2001: 177; Blasco 2011: 235, 260-261). However, the data supporting the role of scavenging are anecdotal and can be interpreted in different ways. It is true that this strategy and especially non-confrontational scavenging can be an efficient foraging technique, as observed in ethnographic studies (O'Connell et al. 1988), but it only represents one more option in

predatory economies (Stiner 1994; Conard and Prindiville 2000; Ferraro et al. 2013). None of the main criteria commonly put forward to infer scavenging has been observed throughout the TD10 sequence. These criteria include the distribution of cut marks on the epiphysis and diaphysis, their frequency in different appendicular elements, high incidence of tooth marks on the diaphysis, attritional mortality profiles and the prevalence of heads and distal ends of the limbs in the anatomical representation, among others (Binford 1981, 1984, 1985; Blumenschine 1986; Stiner 1994; Domínguez-Rodrigo 1999; Domínguez-Rodrigo and Yravedra 2009). We must then assume that if scavenging were a paleoeconomic strategy, it has no real archaeological visibility in Gran Dolina TD10.

Given the above, the taphonomic data suggest that the Lower Paleolithic hominins of Gran Dolina TD10 were efficient hunters who based their diet on large ungulates, mainly bison, deer and horses. The exploitation of other taxa informs us about their flexibility in hunting tactics and techniques and about their control of the cave's surrounding environments. This flexibility is presented as a constant throughout the sequence of TD10, although the broad variation of exploited prey is too large and the recurrence too small to be used as an appropriate proxy to establish generalizations. One of the most important generalizations, in our opinion, is the constant reference to the use of carcasses of megafauna (rhinoceros), which have low archaeological visibility as a result of transport constraints. In fact most of the access to this type of very large animal in the European context occurs in open-air sites (Bratlund 1999; Yravedra et al. 2010, 2012, 2014; Smith 2015), probably in relation to butchering sites. Another example is the evidence of butchering carnivores (Rosell 2001; Blasco et al. 2010; Rodríguez-Hidalgo et al. 2015), which is sporadic and difficult to interpret, but revealing of the position of hominins in the ecosystems as top predators. The use of small prey, mainly rabbits but birds as well, appears to be important in the TD10.1 sample analyzed by Blasco (Blasco 2011; Blasco et al. 2013). However, in the absence of data for the top of the sequence (Rosell 2001: 123), and taking into account the negative evidence of anthropic use described above for the TD10.1 and TD10.2 bone beds, we propose being cautious in interpreting the weight of small game in the diet of hominids who occupied TD10, especially when some of the key arguments suggesting an important use of small prey by hominins in TD10.1 are based on breaking patterns of the long bones (Blasco 2011: Fig. 6.16; Blasco et al. 2013: Fig. 2), which are subject to problems of equifinality (see Rodríguez-Hidalgo et al. 2013: Fig. 7).

The main objective of this work was to establish the origin of the two main faunal accumulations of the Gran Dolina site: the TD10.2 bison bone bed and TD10.1 bone bed. Our hypothesis was that these accumulations were caused by the activity of hominins. To test this, we relied on the zooarchaeological and taphonomic analysis of more than 30,000 faunal remains. This research confirms the initial hypothesis of an anthropogenic origin for the two main archaeological horizons in the Gran Dolina TD10 unit. Hominins were the main accumulators and modifiers of animal remains, using the cave site for a variety of activities. The contribution of nonhuman predators was very limited. However, the data collected here indicate that, although they were not relevant accumulators, large carnivores were important modifiers of the TD10 archaeological remains.

In confirming the main hypothesis, we are able to establish some inferences about how hominins obtained animal carcasses. We also can suggest the techniques and tactics

they used to acquire the prey, and what dynamics were in motion that influenced the subsistence and bases of the paleoeconomy for the hominins who occupied the cave. Our data demonstrate hunting as the only archaeologically verifiable means for obtaining these animal carcasses. Hunting is presented as the basic fundament for activities at the site throughout the sequence. We observe a focus on tasks dealing with the game itself, such as the processing of carcasses and the consumption of prey. The data do not support the use of scavenging as a complementary strategy, which is a point of contrast with sites of similar age.

The hunting techniques and tactics suggested by the record and based on the taxonomic and mortality data vary widely, but all indicate a high degree of cognitive, social and technological sophistication. Chances are that prey was captured mainly through simple predation events. Individual hunting events were characterized by ambush or stalking, either through cooperative hunting using these methods or others. The TD10.1 bone bed reflects a high capacity for selecting prey, a fact that is in line with the concept of a human predator niche (Stiner 2013; Stiner and Kuhn 2016). Our study expands this concept on a chronological and cultural level. Other sites, which were close in time but far away in space and environmental contexts, present the same pattern. These include Bolomor (Blasco and Fernández Peris 2012a, b; Blasco et al. 2013), Schöningen (Thieme 1997; Voormolen 2008; Conard et al. 2015; van Kolfschoten et al. 2015), Misliya (Yeshurun et al. 2007), Boxgrove (Parfitt and Roberts 1999; Roberts and Parfitt 1999) and Qesem (Stiner et al. 2009, 2011). This suggests that Middle Pleistocene hominids in the Euro-Mediterranean area were efficient hunters and that the human hunting niche probably was fully developed among the pre-Neanderthal populations.

Among the hunting techniques employed, our research has enabled us to observe mass predation, with the oldest case of communal hunting in the history of human evolution (Rodríguez-Hidalgo et al. in press). In this sense, this work sheds new light on the flexibility of hunting behavior, in terms of type of prey as well as technique.

Finally, we have established a series of hypotheses on the use of Gran Dolina during the formation of the assemblages studied and the character of the occupations.

We argue that the cave was used as a kill-butcherer site during the formation of the TD10.2 bison bone bed and as a residential camp during the formation of the TD10.1 bone bed. The change in use of the site carries important consequences in terms of composition and taphonomy of the assemblages: in the oldest level, we are given only one facet, probably exceptional, of subsistence and daily life of the hunter-gatherers who inhabited the Sierra de Atapuerca; in the more recent level, we are provided a sample of everyday life. In the case of TD10.2, seasonal use of one location in the territory for the development of specific tasks integrates logistical models, while the presence of a residential camp at the time of formation of the TD10.1 bone bed offers important implications for key issues in research on human evolution, in the distribution of food, the division of labor and interdependence among group members for subsistence.

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