4. HUMAN-ELEPHANT INTERACTIONS DURING THE LOWER PALAEOLITHIC: SCRUTINIZING THE ROLE OF ENVIRONMENTAL FACTORS

Maria Rita Palombo[1,*], Eugenio Cerilli[2]

[1]*IGAG-CNR, c/o Department of Earth Science, Sapienza University of Rome, P.le Aldo Moro 5, Rome, Italy*
[2]*Soprintendenza Speciale Archeologia Belle Arti e Paesaggio di Roma, Rome, Italy*
[*]mariarita.palombo46@gmail.com

KEYWORDS | proboscideans; butchery sites; environment; Lower Palaeolithic

ABSTRACT

The human-elephant interactions during the Lower Palaeolithic are an intriguing issue that has been the subject of several studies, however, the multifaceted aspects of the interaction dynamics are still imperfectly known and divide most of the researchers dealing with this topic. Various sources of evidence point out the contemporaneous presence of Palaeolithic humans and proboscideans during the Early and early Middle Pleistocene of Africa and Eurasia in different ecosystems, environments and climatic contexts. This research aims to scrutinize the role (if any) that non-cultural related factors, such as environmental context, resource availability and fauna functional diversity, may have had in regulating the human-elephant interactions from ~1.5–1.4 Ma to 80 ka (approximately MIS 49 to MIS 5), focusing mainly on the Lower Palaeolithic. We analyze by means of some multivariate statistical analyses (cluster analysis, neighbour joining clustering method, PCA) the environmental context and the human behavior at main sites from the Mediterranean area (North Africa, Arabian Peninsula and Southern Europe), as well as at a few selected Western and Eastern European sites, where butchering activities on elephant carcasses have been firmly documented. The obtained results suggest that: i) the butchery behavior did not substantially change in the course of the late Early and Middle Pleistocene; ii) during the Lower Palaeolithic the human-elephant interactions were more affected by chance rather than by cultural/environmental factors; iii) during the Late Pleistocene, conversely, the exploitation of mammoth carcasses was more related to a hunting activity, selectively targeted to young individuals, although other large games were preferred at least by Neanderthal hunters.

4.1   INTRODUCTION

"…. In the forest lashed by the great rain
Father elephant walks heavily, baou, baou,
careless, without fear, sure of his strength…"
(Tracking Father Elephant, translated by Bowra,
1962).

An extraordinary diversity of species, from very specialized to highly ecologically flexible, originated in the course of the long and complex evolutionary history of the polyphyletic and polymorph proboscidean group, which originated in North Africa about 60 million years ago (Gheerbrant, 2009). Proboscidean taxa, including the subfamily Elephantinae, have inhabited the most different environments, such as rain forests, deserts, tundra, savannah, grasslands and bush lands. The higher ecological flexibility a species had, the wider its geographical range was, sometimes attaining a very wide geographic distribution, as in the case for instance of the woolly mammoth *Mammuthus primigenius* (Kahlke, 2015).

The capacity of adaptation, dispersal and diffusion of proboscidean representatives were to some extent similar to the most recent primates and perhaps archaic humans. During the Pleistocene for instance, the recurring climate changes triggered significant modifications in the structure of ecosystems, and the mammal fossil record documents a complex history of dispersal events and species turnovers. The dispersal processes involved different human and proboscidean species. As a result, the geographic range of hominins (Hominina) and proboscideans (i.e., some representative of Mammutidae, Anancinae, Stegodontidae and Elephantidae, in particular elephants belonging to the tribe Elephantini —*Palaeoloxodon*, *Mammuthus* and *Elephas*, as regards to Eurasia) frequently overlapped under a variety of environmental conditions, including even very peculiar ecosystems, such as islands. During the Late Pleistocene for instance, the Flores Island (Indonesia) was inhabited by a dramatically impoverished and unbalanced fauna (Meijer et al., 2010), including the dwarf human

species *Homo floresiensis*. The archaic human from the Liang Bua cave, representative of a long-term population that frequented the cave for about 80 years (95–74 to 12 ka), butchered not only giant rodents (e.g., *Papagomys armandvillei*), but also the dwarf proboscidean *Stegodon florensis insularis*; the behavioral capabilities of Liang Bua humans included also the use of fire (Morwood et al., 2005).

The widespread presence of proboscideans in the territories inhabited by *Homo* spp. may have facilitated the human-proboscidean interactions that go perhaps back to the emergence of our own genus, developing throughout time in different ways, from simple coexistence, to opportunistic exploitation by humans, to highly conflicting relationships as documented in some African and Asian countries today (see e.g., Pant et al., 2016; Evans and Adams, 2018; Anuradha et al., 2019; Hulme et al., 2020; Kitratporn and Takeuchi, 2020; Xu et al., 2020).

The cut marks on equid and bovid bones found at Gona (Ethiopia), dated approximately between 2.58 and 2.1 Ma, provide one of the oldest evidence of human butchery activity in a site where proboscidean remains (*Anancus*) are also recorded (Semaw et al., 1997; Semaw, 2000; Domínguez-Rodrigo et al., 2005). Proboscidean remains were present indeed in archaeological levels of African sites, where lithic artifacts and cut marks on medium- and large-sized mammals have been reported, such as Bouri (~2.5 Ma, Ethiopia; de Heinzelin et al., 1999) and Ain Boucherit (Algeria; Sahnouni et al., 2018; Duval et al., 2019). The lithic artifacts and cut-marked bones found at Ain Boucherit in the layers dated to ~1.9 Ma and 2.4 Ma (Sahnouni et al., 2018; Duval et al., 2019), indicated that scavenging hominins inhabited the North African Mediterranean region earlier than was previously supposed, based on the evidence from the nearby Ain Hanek site (Algeria), dated to ~1.8 Ma (Sahnouni et al., 2013).

In Europe, at sites dated to ~1.5–1.4 Ma, where *Mammuthus meridionalis* is recorded, the presence of cut-marked bones of middle- and large-sized herbivores, as well as of bones broken for marrow

extraction, provides the earliest evidence of archaic human faunal exploitation. In particular, such kind of evidence comes from two Spanish sites located in the Guadiz Baza basin (Barranco León 5 dated to ~1.4 Ma and Fuente Nueva 3 to ~1.2 Ma, on the basis of biostratigraphical, magnetostratigraphical and ESR data, and to ~1.5 Ma based on cosmogenic nuclides for Fuente Nueva 3 (Espigares et al., 2019, this volume and references therein; Rosell and Blasco, this volume), and from the Italian site Pirro Nord 13 (Chelli-Cheheb et al., 2019, 2020).

Although the coexistence of archaic humans and proboscideans is documented in a number of Early Pleistocene sites during time and across continents, the available data are not compelling enough for either proving or rejecting an exploitation of proboscidean carcasses by humans at the earliest butchery sites recording proboscideans remains. In the absence of firm butchery evidence on proboscidean bones, the same uncertainty concerns the majority of Pleistocene sites, where a spatial association of artifacts and elephant bones is documented. The association of stone tools and proboscidean bones —e.g., Mammutinae, *Mammut*; Stegodontidae, *Stegodon*; Elephantinae (Elephantini: *Mammuthus*, *Palaeoloxodon*, *Elephas*; Loxodontini: *Loxodonta*)— is indeed a recurrent phenomenon, distributed across continents and palaeobioprovinces.

Several hypotheses and tentative explanations have been formulated to account for this association. The actual meaning may change depending on a number of factors, such as the spatial distribution of bones and artifacts, the depositional context, the taphonomic signatures, which may suggest that: i) the spatial association of stone artifacts and elephant remains results from a natural accumulation and is not functionally related to any human activity; ii) the place was visited by humans, who accidentally found the carcass they scavenged; iii) the place was located in a territory, where archaic humans hunted on proboscideans; iv) the place was a butchery site, where the carcass obtainment strategy cannot be identified (cf. Yravedra et al., 2010 and references therein). The frequency of the

association and the widespread presence of tools made on elephant bones evidence the important role as a valuable source of food and raw material the proboscideans had for the Lower Palaeolithic humans (e.g., Reshef and Barkai, 2015; Agam and Barkai, 2016; Barkai, 2019a, b). The high nutritional value related to the large amount of flesh and fat a single elephant carcass can provide, could find support in considering that most elephants in central Africa are likely poached nowadays more for their meat rather than for their ivory.

The question whether the Lower Palaeolithic humans were scavengers or hunters is one of the most intriguing and debated issues in literature, and hypotheses and ideas about early human behavior are especially controversial as regards to proboscideans. Although proboscideans were likely pursued and killed by Middle and Upper Palaeolithic hunters in different ways (e.g., by a single individual carrying a spear and stabbing the elephant in the belly or by cooperative hunters as African hunter-gatherers did in historical time) (see e.g., Anzidei et al., 2015 and references therein; Agam and Barkai, 2018; Ichikawa, this volume; Lewis, this volume; Yasuoka, this volume) the debate "hunting vs. scavenging" (which is beyond the scope of our research) is nearly impossible to solve for the majority of the Lower Palaeolithic sites. Moreover, it is worth noting the objective difficulty of detecting whether archaic humans exploited or not elephant remains at several sites recording butchery activity on other large mammals. This is mainly related to the difficulties to identify defleshing traces on elephant bones. It is indeed a challenging task to find such evidence on proboscideans, because the large muscle masses, cartilage, tendons and strong ligaments hamper the contact between stone tool edges and bone surfaces, and if so, the thick periosteum on several bones may prevent any stone tool modification on the bone surface, as confirmed by actualistic butchery observations (Haynes and Klimowicz, 2015).

Firm proofs of the human exploitation of proboscidean carcasses have, however, to be found to avoid misinterpretations in detecting actual butch-

ery sites. The presence of cut marks still remains the most straightforward evidence. Cut marks on mammoth bones have been documented in a number of European Late Pleistocene archaeological sites. During the last decade, detailed studies of faunal remains at various sites led to the identification of butchery activities on elephant remains at some late Early and Middle Pleistocene sites.

The oldest evidence of human butchery activity on proboscideans, however, dates back to the Early Pleistocene of Africa. In the faunal assemblage of HWK EE (Olduvai Gorge, Tanzania), a site older than 1.664 ± 0.0194 (cf. discussion and fig. 2 in McHenry and Stanistreet, 2018), cut marks have been detected mainly on bone surfaces of middle-sized mammals, but also on a proboscidean astragalus (Pante et al., 2018). Later, in East Africa, at the late Early Pleistocene Olorgesaile butchery site (0.99 Ma; Fig. 4.1a, Appendix 4.1), more than 2300 stone artifacts were found surrounding several *Palaeoloxodon recki* bones (Potts, 1989). Sharp flakes could have been used to remove flesh, as shown by cut marks on one elephant rib, some vertebrae and the hyoid bone, where the tongue muscles are attached. In Europe, the oldest proboscidean cut-marked bones (two ribs of *M. meridionalis* about 30 years old) are recorded at the late Early Pleistocene Barranc de la Boella Pit 1 (Spain), together with 125 lithic artifacts including several refitting chert groups (Mosquera et al., 2015; Rosell and Blasco, this volume) (Fig. 4.1a, Appendix 4.1).

Although cut marks on mammoth carcasses are well documented in several Late Pleistocene sites of Europe, very few have been reported in Early and Middle Pleistocene sites. It is interesting to note that, in the course of the Pleistocene the number of elephant butchery sites substantially augmented from the Early to the Late Pleistocene, but the percentage of sites recording cut marks underwent only a moderate increase (Fig. 4.3).

Together with the presence of cut marks and bones intentionally broken for marrow extraction, hints of elephant (i.e., *Mammuthus*, *Palaeoloxodon*) exploitation by archaic humans are also provided by the use-wear analysis of lithic implements and by isotope analysis (e.g., Venditti et al., 2019 and references therein). The spatial association between elephant skeletons (either complete or partially preserved, in anatomical connection or disarticulated showing a moderate dispersion of bones) and artifacts (particularly the presence of refitting) may be considered as an indirect evidence of some butchery activity at the place. At some sites, such as La Polledrara di Cecanibbio (~325 ka, MIS 9, Italy; Anzidei et al., 2012; Pereira et al., 2017), the functionality suggested by the association is confirmed by more firm evidence, e.g., cut marks, use-wear analysis on lithic artifacts, and bones intentionally broken for marrow extraction and artifact manufacturing (Anzidei et al., 2012; Santucci et al., 2016; Cerilli and Fiore, 2018). In some cases, the exploitation can be inferred from the presence of selected elephant body parts carried by humans into their temporary camps, such as the Terra Amata open-air site (~400 ka, MIS 11, France; Valensi et al., 2011), where one of the oldest evidence in Europe of a recurrent exploitation of small fast game is documented (Morin et al., 2019), and caves, such as Spy (MIS 3, Belgium; Germonpré et al., 2014, this volume; Wißing et al., 2016, 2019; Bocherens and Drucker, this volume) (Fig. 4.1a, b, Appendix 4.1).

Based on these criteria, we have selected the late Early to early Late Pleistocene sites studied herein. Our idea was to provide a few hints in order to contribute to deconstructing the intriguing issue of the evolutionary dynamics of human-elephant interactions during time and across space, in the light of the profound late Early and Middle Pleistocene environmental changes. Our purpose is two-folded: i) to appraise the role (if any) that either the ecosystem functioning and environmental factors or simple chance may have had in promoting the butchery activity of the late Early and Middle Pleistocene *Homo* representatives on elephant carcasses, and ii) to highlight the similarities/differences in archaic human behavior at each site in the light of the environmental context, resource availability and fauna diversity.

Figure 4.1: Location of the main Early–early Late Pleistocene (**a**) and Late Pleistocene, MIS 4–MIS 2 (**b**) sites recording butchery activity on elephants (*Palaeoloxodon* and *Mammuthus*) (made with Natural Earth, naturalearthdata.com).
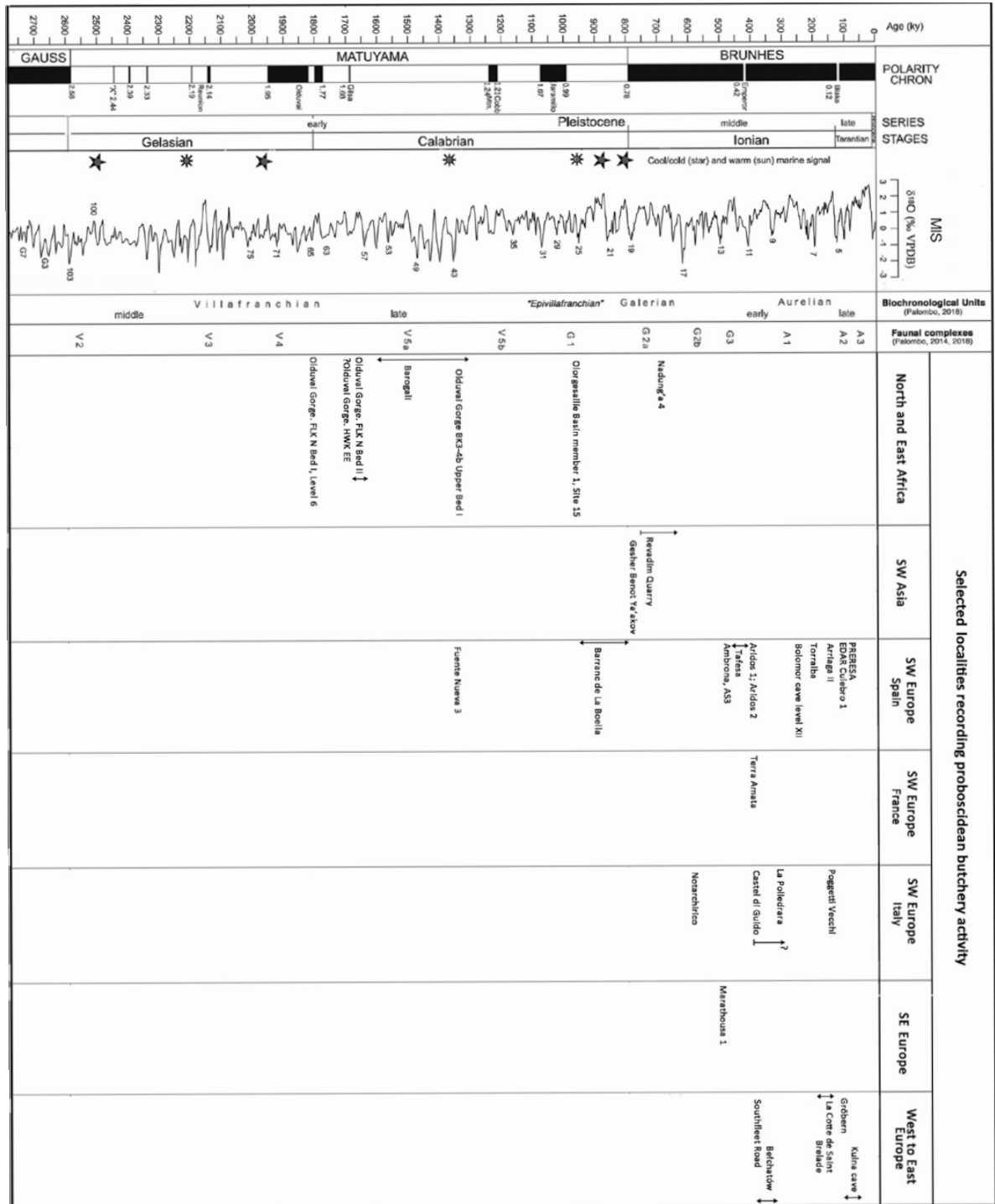
Figure 4.2: Chronological scheme and biochronological setting of the Early, Middle and Late Pleistocene elephant butchery sites selected for this study.

Accordingly, we intend to scrutinize the reliability of the following hypotheses: i) Did the way in which humans exploited elephant carcasses change during the focal time, according to the changing human species and material culture? ii) Did the human butchering activity on elephants depend to any extent on physical/biotic factors, e.g., geographical region, elephant species, vegeta-

tion type, functional diversity/ecological structure of mammalian palaeocommunities (particularly number and strength of top predators), human species and material culture? iii) Was the way in which humans interacted with elephants more affected by chance rather than by cultural/environmental factors?

Aiming to scrutinize whether the biotic and physical environmental factors or a simple chance had any role in promoting the butchery activity on elephant carcasses during the late Early to the early Late Pleistocene, we examined three different scenarios: i) around the time that early human groups moved for the first time from Africa to Eurasia; ii) slightly later, when the global climatic conditions underwent the dramatic reorganization known as EMPT (Early to Middle Pleistocene Transition); iii) from the time that the Acheulean culture spread in Europe until the appearance of the Middle Palaeolithic culture, briefly glancing at the period of climate worsening recorded from MIS 4 to MIS 2.

4.2 MATERIAL AND METHODS

4.2.1. MATERIAL

For a firm detection of elephant butchery localities we selected late Early to early Late Pleistocene (MIS 49–MIS 5; Fig. 4.1a, Appendix 4.1) sites, following in a very rigorous and restrictive way the criteria mentioned above, e.g., presence of cutmarked elephant bones or intentionally broken for marrow extraction; elephant skeletons (from articulated to moderately spatially dispersed) surrounded or associated with lithic implements and presence of refitting; use-wear analysis of the lithic implements and isotopic data related to their organic residues, documenting activities referable to butchering (e.g., cutting meat/soft material and scraping off the meat from the hide); and compelling presence of elephant bones carried by humans at the place. Moreover, we excluded from the analysis sites for which data related to the variables we have considered in the statisti-

cal analysis (see below) were not informative or complete enough. Accordingly, the selected sites represent only a subset of the numerous alleged sites reported in literature; however, the sample can be regarded as adequate for a first investigation about the role that environmental aspects may have had in regulating the human-elephant interactions during the Lower Palaeolithic. A few European Late Pleistocene sites (MIS 4–MIS 2) have been also included in the statistical analysis for comparison purposes (Appendix 4.1). The total number of the considered localities is 39.

Stratigraphical data, absolute geochronology, palaeomagnetism and biochronological principles were applied for ordering the selected sites in a chronological sequence and gathering them into faunal complexes (see e.g., Palombo, 2009, 2018) (Fig. 4.2). Considering that new discoveries and absolute chronological assessments might change any previously established biochronological scheme, the current chronological assessment can be regarded as the "best-fit" allowed by the available data.
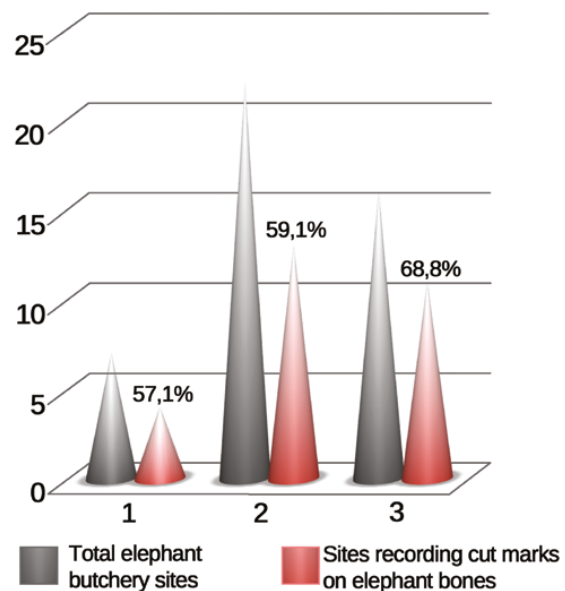
Figure 4.3: Comparison among the number of selected elephant (*Palaeoloxodon* and *Mammuthus*) butchery sites and the percentage of sites recording cut marks on elephant (*Palaeoloxodon* and *Mammuthus*) bones during the Early Pleistocene (1), Middle and early Late Pleistocene (2), and Late Pleistocene (MIS 4 to MIS 2) (3).

4.2.2. METHODS

To estimate the putative influence of physical and biotic aspects on human butchery behavior during time and across space, we performed statistical (univariate and multivariate) analyses by using as cases the selected late Early to Late Pleistocene sites (see above) and a large set of variables.

SELECTED VARIABLES | We selected three main groups of variables for the analysis: 1) variables related to the most general aspects of the site, such as chronology, geographical location and climate; 2) variables considered as appropriate for describing the environmental context and some aspects of the ecosystem functioning, such as the basic different types of landscape (e.g., plain, hill, mountain) and the depositional environments, e.g., the various alluvial contexts, cave, volcanic); of vegetation at the site and/or in the surrounding territory; fauna richness and ecological diversity of the large mammal fauna found at the site (highly, and poorly diversified mammalian fauna assemblage); the species and number of butchered elephants, as well as their ontogenetic age; the amount and spatial distribution of elephant remains; number and power of top predators; 3) and variables related to archaic humans, and their activity and behavior (e.g., human species identified based on human remains or inferred according to the material culture and the age of the site, material culture, cut marks on elephant bones, elephant bones broken for marrow extraction, cut marks and broken bones of other mammals).

We considered the presence of top predators, because it may hamper the access to carcasses by archaic humans and other scavengers [see Konidaris and Tourloukis (this volume) for a discussion on the role of large carnivores in human-elephant interactions]. During the Early Pleistocene for instance, the presence of the saber-toothed cat *Homotherium latidens* and the powerful short-faced hyena *Pachycrocuta brevirostris*, likely hampered human groups to access the carcasses they were scavenging. Therefore, carnivores and humans alternated each

other in exploiting carcasses. The same might have sometimes occurred during the Middle Pleistocene, even if the composition of the carnivore guild had changed. During the Late Pleistocene, more organized and better-equipped hunter groups competed successfully even with the most powerful predator, the cave lion *Panthera spelaea*.

As regards to the vegetation, we considered the classic broad vegetation types (e.g., type of forest —rain, evergreen, deciduous, mixed etc.—, grassland, savannah, tree grassland/savannah, shrubland, tundra, taiga, Mediterranean macchia), which substantially differ each other in structure and plant species richness, as well as in environmental productivity (e.g., Mucina, 1997 and references therein).

It is worth noting that the identification of the *Homo* species interacting with proboscideans may be controversial and debated at some sites. In particular, it is generally accepted that *Homo heidelbergensis*, whatever its phyletic relationships could be, was the human species that spread the Acheulean culture widely in Europe. Recently, the attribution to this species of some key human samples has been questioned. For instance, the human remains from the extraordinary rich Sima de los Huesos (~430 ka, MIS 12, Atapuerca, Spain; Bermúdez de Castro et al., 2019 and references therein) have been identified by some scholar as *H. heidelbergensis*, whereas others regarded them as belonging to the Neanderthal lineage (Stringer, 2012; Buck and Stringer, 2014; Manzi, 2016; Roksandic et al., 2018, 2019; Arsuaga et al., 2019; Bermúdez de Castro et al., 2019). In our database, we indicated the most recent in literature specific name given to the humans acting at each site. Concerning the Late Pleistocene sites, if the human species was not specified, we preferred to indicate it as Anatomically Modern Human (AMH), but we have to be aware that many Eastern European sites fall into a chronological interval in which the overlapping/replacement of *Homo neanderthalensis* and/by *Homo sapiens* was in progress.

To facilitate the comparison, sites have been grouped into three main categories, based on the

completeness of the elephant skeleton(s): 1) sites with a single carcass found in association with stone artifacts, and with some bones in anatomical connection and few others dispersed within a short distance; 2) sites, where a single carcass was butchered, but the bones are characterized by a certain degree of disarticulation, and bones are dispersed over a small area; 3) sites documenting a polyphasic accumulation of portions of carcasses or individual bones.

MULTIVARIATE STATISTICAL ANALYSIS | The environmental *sensu lato* based resemblance among elephant butchery sites was evaluated by means of two clustering methods (the classic cluster analysis and the neighbour joining clustering method) and one ordination method (principal component analysis-PCA).

Cluster analysis, a multivariate analysis technique by which it is possible to group cases minimizing the distance within each group and maximizing the distance between groups, is a classification method aimed at grouping cases based on the similarity of their attributes. It is commonly used to group a series of samples based on multiple variables that have been defined from each case. Accordingly, we use the hierarchical clustering routine to explore if and to which extent the selected sites cluster depending on their age, geographical position, and physical and biotic environmental characteristics. As clustering technique, we used the unweighted pair-group average method (UPGMA). In UPGMA, the level at which a member (case, herein a site) joins an existing cluster is based on average similarities of all the existing members, calculated from the original matrix of coefficients. Each member of a cluster, therefore, has an equal weight at all levels of clustering. Clusters are joined based on the average distance between all members in the two groups.

The neighbour joining clustering is an alternative, bottom-up (agglomerative) method for hierarchical cluster analysis originally developed for phylogenetic analysis (Saitou and Nei, 1987), but regarded by some as sometimes superior to

UPGMA for processing ecological data. In the resulting unrooted dendrogram, two branches from the same internal node do not need to have equal branch lengths, because the branch length is proportional to the amount of change.

We carried out the ordination method to further investigate the structure of the data and better understand the main factors influencing the similarities/differences among the analyzed butchery sites. According to this method, the positions of cases (sites) plotted against two or sometimes three axes (each corresponding to a dimension in space) depict the gradient of greatest variation along the "first" axis, the second largest gradient of variation along the "second" axis etc. In particular, the PCA finds new hypothetical variables (linear combinations of the original variables) accounting for as much as possible of the variance in multivariate data. The eigenvalues and eigenvectors of the variance-covariance matrix or the correlation matrix are determined with the SVD algorithm, highlighting the factors (variables) that contribute more to join/separate cases (sites) each other. We used PCA as a descriptive and exploratory multivariate technique, because it is found to be useful in summarizing all the information that describes the similarities of a set of cases in a small number of dimensions, regardless of the statistical proprieties of the data (Hammer and Harper, 2006).

Analyses were executed with the PAST (PAleontological STatistics) 3.16 software (Hammer et al., 2001).

4.3   RESULTS: A CRITICAL OVERVIEW

4.3.1. CLUSTER ANALYSIS

The cluster analysis was performed in three steps. First, we considered all the cases and variables (Fig. 4.4). Second, we performed the analysis by excluding the "geographical setting" and "chronology" variables (Fig. 4.5a), and then by using the variables related to the environment *sensu lato* and to human behavioral/cultural aspects (Fig. 4.5b),

or alternately using one (Fig. 4.5c) or the other (Fig. 4.5d). Third, we considered as cases the sites dated from the late Early to the early Late Pleistocene using either all the variables, or the variables related to the environment *sensu lato* or to human behavioral/cultural aspects.

CLUSTER ANALYSIS OF SITES DATED FROM THE LATE EARLY PLEISTOCENE TO THE LAST GLACIAL MAXIMUM (APPROXIMATELY MIS 49 TO MIS 2) (ALL VARIABLES) |

In the dendogram obtained by using all cases and all variables (Fig. 4.4), a chronological ordering mainly prevails. Two well-separated clusters are detectable. The cluster A that includes nearly all the Early to last interglacial Pleistocene localities, and the cluster B that mainly includes the last glacial localities. In the cluster A, the Early and Middle plus last interglacial Pleistocene localities form two sister clusters (respectively A.1.2 and A1.1), gathered in the group A1. The cluster A includes also, as separate rami, the Spanish sites Fuente Nueva 3 (Early Pleistocene, may be older than 1.4 Ma; 1.50 ± 0.31 Ma according to the cosmogenic nuclide burial age provided by Álvarez-Posada et al., 2015, cf. Espigares et al., 2019 and references therein) and Bolomor Cave (late Middle Pleistocene, 152 ± 23 ka). Fuente Nueva 3 is the oldest site with a partial, articulated skeleton of *M. meridionalis* and lithic artifacts (Espigares et al., 2013, this volume and references therein; Rosell and Blasco, this volume). Bolomor Cave is the only site in the database, where bones and teeth of a butchered young straight-tusked elephant were recovered (Blasco and Fernández Peris, 2012, this volume; Blasco et al., 2013; Rosell and Blasco, this volume). The peculiarity of both Spanish sites is highlighted by the quite great distance they show from all other localities gathered in cluster A.

However, some more departures from the general chronological trend are present. For instance, the post-Jaramillo Early Pleistocene Barranc de La Boella Pit 1 (~0.96–0.78 Ma; Vallverdú et al., 2014; Mosquera et al., 2015) falls into the group of the late Middle Pleistocene (MIS 11–MIS 6) lo-

calities, as does the early Middle Pleistocene Italian site Notarchirico (A1 level, dated to ~660 ka, MIS 16, although the ecological structure of the large mammal fauna suggests temperate climatic conditions) (Pereira et al., 2015 and references therein). This conceivably depends on the presence at both sites of large cutting tools/Acheulean artifacts (Mosquera et al., 2016; Moncel et al., 2019).

At Belchatów (Poland, Middle Pleistocene, MIS 11 or 9? in Pawlowska et al., 2014; MIS 9 in Marks et al., 2019), cut marks, attributed probably to flesh filleting, were detected on a *Mammuthus trogontherii* rib (Pawlowska et al., 2014). Accordingly, the anomalous setting of the site likely relates to the presence of a representative of the genus *Mammuthus*; that is, together with the species *M. primigenius*, the elephant recorded in the last glacial sites, whereas *P. antiquus* is the most common elephant species butchered at the Middle Pleistocene Southern European sites.

The presence in the group B of the late Middle Pleistocene (MIS 6) levels of the long stratigraphic sequence of La Cotte de St Brelade (Jersey, U.K.; spanning in age from ~238 to 40 ka, Scott et al., 2014 and references therein) and the last glacial site of Spy cave (inhabited by *Homo neanderthalensis* until ~33 ka; Semal et al., 2009) accounts for the overall similarity between the British and Belgian sites. Interesting to note is that the Spanish PRERESA site (OSL dated to ~84 ka; MIS 5a), but whose age is debated ranging from early MIS 6 to MIS 5 (see discussion in Yravedra et al., 2019a, b and Moreno et al., 2019), and EDAR Culebro 1 (dated to ~121 ka by the OSL method and ~150–95 by the AAR method; Manzano et al., 2010), show a degree of similarity with the Middle Pleistocene sites higher than that shown by the German sites of Lehringen (well-known due to the presence of a 2.4 m long wooded spear found within the area of the skeleton belonging to an adult male straight-tusked elephant) and Gröbern. The reason behind the apparently anomalous setting of the German sites cannot be easily explained, because both are correlated to the Eemian (MIS 5e), based on the large mammal assemblages and the
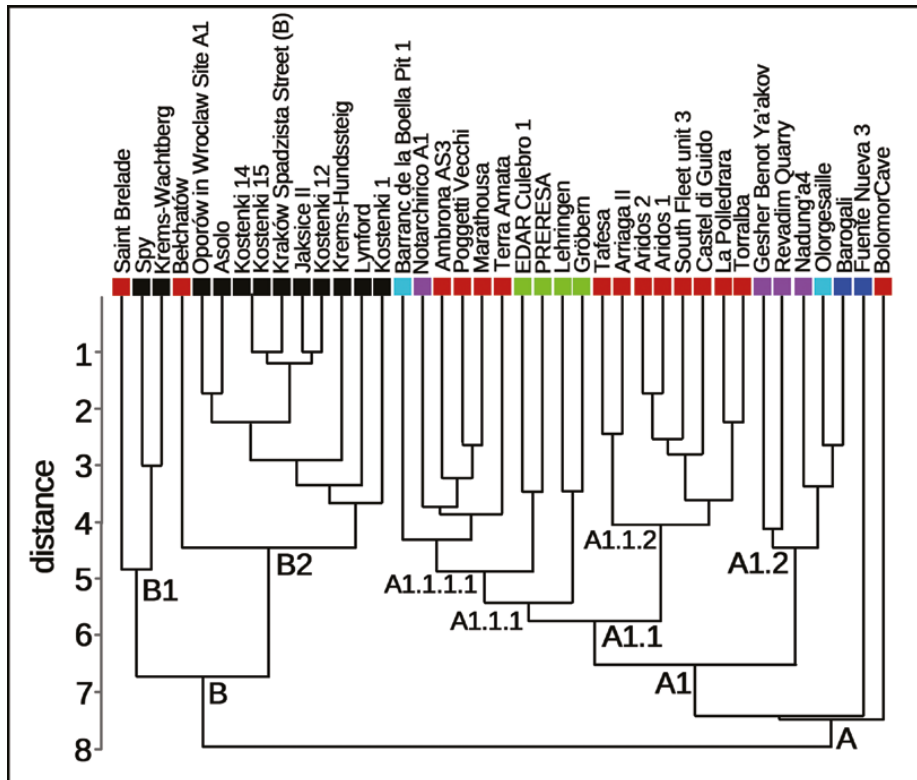
Figure 4.4: Q-mode dendrogram showing how the selected elephant butchery sites ranging from the late Early Pleistocene to the Last Glacial Maximum (from MIS 54–MIS 39 to MIS 2) cluster using all variables. Clusters are joined based on the average distance between all members in the groups (unweighted pair-group average, UPGMA) (for the chronological context see the legend in Fig. 4.7).

vegetation type, which show some similarities to that recorded on various late Middle–early Late Pleistocene European localities (e.g., Litt, 1990; van Kolfschoten, 2000; Weber, 2000). A tentative explanation might relate to the similarity in the geometry of the dispersed elephant bones and in the occasional attendance at the sites of human groups that possibly alternated with carnivores. The same reason could explain the similarity that shows the Middle Pleistocene site of Belchatów with the last glacial sites Asolo, Oporow and Lynford in the cluster obtained by using only the human-related variables (Fig. 4.5d).

All things considered, the results highlight the complex interplay among several factors in regulating the clustering of the butchery sites dated from the late Early Pleistocene to the Last Glacial Maximum. On the one hand, indeed, the geological age of the deposits (on which elephant and human species, and material cultural depend) may be regarded as the variable that mainly contributes to the clustering of the analyzed sites. This is suggested, for instance, by the setting of the most recent

sites that generally show certain homogeneity and some degree of similarity. On the other hand, a number of departures from the chronological ordering have been detected. At some cases, we have tentatively explained anomalous clusterings in terms of environmental context, material culture among sites differing in age, presence/absence of a particular elephant species, fauna structure or the peculiar interplay of more than one factors. However, it is sometimes difficult to find a compelling explication.

CLUSTER ANALYSIS OF SITES DATED FROM THE LATE EARLY PLEISTOCENE TO THE LAST GLACIAL MAXIMUM (APPROXIMATELY MIS 49 TO MIS 2) (ENVIRONMENTAL AND HUMAN RELATED VARIABLES) |

Assuming that the most influential variable in the site clustering is their geological age, we attempt to further scrutinize to which extent the other factors may have influenced the similarity among the analyzed sites. We performed cluster analyses first by excluding the "geographical setting" and "chronology" vari-

ables, and then by using either the variables related to the environment *sensu lato* or to human behavioral/cultural aspects.
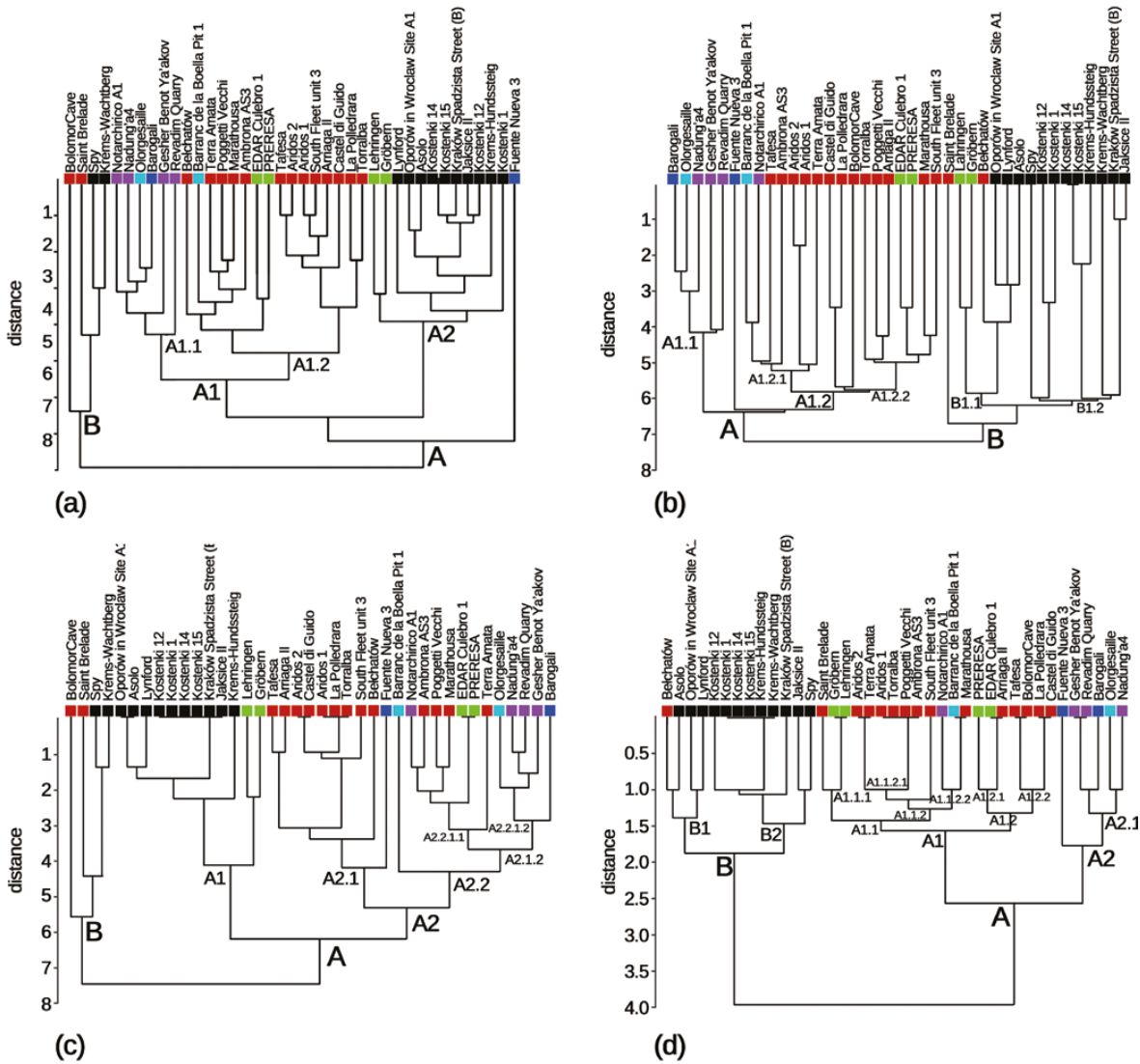
Excluding the variables "geographical setting" and "chronology", the clustering does not substantially change, although few variations can be observed with respect to the results obtained by using all the variables (Fig. 4.5a). Worth noting is the setting of the sites dated to the last glacial (MIS 4–MIS 2) that form a sister group A2 with the group A1. A1 gathers nearly all the other late Early (group A1.1) and Middle–early Late Pleistocene localities (A1.2). The localities gathered in A1.2 show a quite high similarity. This accounts for a considerable affinity in physical and biotic aspects among the sites, in particular as regards to the fauna structure and the human behavior. Some peculiarity in the fauna structure and human behavior might explain the odd position of Bolomor, La Cotte de St Brelade and Spy. These three sites gather together with the Austrian Krems-Wachtberg cave (last glacial, MIS 2) in a separate group (B), which shows a great distance from the group A. The unicity of the Early Pleistocene site Fuente Nueva 3 is further confirmed by its distance from all the other localities. The Fuente Nueva 3 position may in part depend on the absence of cut marks, which are instead recorded on M. meridionalis ribs at Barranc de la Boella (the only other butchery place of the species), the remarkable presence of powerful top predators, including the giant hyena *Pachycrocuta brevirostris* that had access to the same mammoth carcass the humans exploited and may have competed with them, and the very warm and humid climate reconstruction for the site (Espigares et al., 2013, this volume; Blain et al., 2016; Rodriguez-Gomez et al., 2016; Rosell and Blasco, this volume).

It should be furthermore underlined that if on the one hand the early Late Pleistocene Spanish localities (PRERESA and EDAR Culebro 1) still fall in the same group (A1.2), gathering the Middle Pleistocene sites (plus the late Early Pleistocene Barranc de la Boella Pit 1), on the other hand the German Eemian sites Lehringen and Gröbern are

part of the group A2, which includes sites not only more recent, but also characterized by different environmental conditions, in particular as regards to the climate, a variable still included in the analysis. The unexpected position of the two sites seems to be related more to the combined influence of various biotic environmental factors (the large mammal fauna structure is poorly diversified at both sites) rather than to human related aspects.

The comparison among the dendrograms obtained by using as variable either both the environmental and human related (Fig. 4.5b), or the environmental (Fig. 4.5c), or the human related variables (Fig. 4.5d) shows indeed, that the position of the two German sites remains substantially unchanged when the environmental related variables are taken into account, while they gather together with the Middle Pleistocene sites if the dendrogram is based only on the human related variables.

In the dendrogram based on these variables (Fig. 4.5d), the clustering is mainly related to the geological age of the sites and, in turn, firstly to the human species inferred as present at the site, and secondarily to the material culture; however, other aspects interact also in the site clustering, as suggested by the anomalous position of a few localities (some already mentioned above). In the cluster A, the Early–Middle Pleistocene sites gather together in the groups A1 and A2. It is worth noting, however, the peculiar position of Barranc de la Boella (group A.1.1.2.2). The Spanish Early Pleistocene site shows a high similarity with the Middle Pleistocene Greek site Marathousa 1, dated to ~500–400 ka (Konidaris et al., 2018; Tourloukis et al., 2018 and references cited in both), in spite of the different human and elephant species present at the two sites. In addition, the late Middle Pleistocene Italian site Poggetti Vecchi (~171 ka, MIS 7), recording the presence of H. neanderthalesis (Arangunen et al., 2018, 2019; Capalbo et al., 2018), gathers together with the quite older Spanish sites Áridos 1 and Ambrona A3 (group A.1.1.2.1), as well as Áridos 2 and Terra Amata (France), correlated to MIS 12–MIS 11. At the latter sites, the

Figure 4.5: Q-mode dendrograms showing how the elephant butchery sites ranging from the late Early Pleistocene to the Last Glacial Maximum (from MIS 54–MIS 39 to MIS 2) cluster excluding from the variables the geographical position and the chronology (**a**); using the environmental and human related variables (**b**), the environmental related variables (**c**), and human related variables (**d**) (for the chronological context see the legend in Fig. 4.7).

presence of *H. heidelbergensis* (or perhaps humans close to those present at the penecontemporaneus site of Sima de los Huesos, see above) has generally been accepted, based on the chronology and geographical position of the sites (e.g., de Lumley et al., 2009; Panera et al., 2011; Santonja et al., 2018 and references therein). The similarity may relate to the human activities at these sites interpreted as residential or butchery places, where humans had an early access to a carcass in a non-competitive situation.

The cluster B includes the sites correlated to MIS 4–MIS 2 recording the presence of *H. neanderthalesis* or Anatomically Modern Human/H. sapiens. They form two sister clusters based mainly on the chronology. B1 includes the MIS 4 and MIS 3 sites, and B2 the late MIS 3/MIS 2 ones. Once again Belchatów (likely MIS 9) shows an anomalous position, gathering together with the localities of B1, close to the Italian MIS 4 site Asolo (Mussi and Villa, 2008), probably due to the aspects discussed above.

It is worth noting that the distance among groups (and sites) progressively decreases as the number of variables reduces and that the similarity increases performing the analysis only using the human related variables. This suggests that, despite all sets of factors contribute to the clustering structure by differentiating the sites even if in different ways, the difference are less pronounced regarding the human behavior, as highlighted by the prevailing influence of variables, such as the human species and material culture, rather than butchery activities.

CLUSTER ANALYSIS OF SITES DATED FROM THE LATE EARLY PLEISTOCENE TO THE EARLY LATE PLEISTOCENE (APPROXIMATELY MIS 49 TO MIS 5) | In the attempt to scrutinize better the factors that might have influenced the butchery activity of early humans, we decided to repeat the analysis focusing on the Early to early Late Pleistocene elephant sites, thus leaving outside the last glacial ones (MIS 4–MIS 2) (Fig. 4.6).

Overall, the dendrogram obtained by using all the variables (Fig. 4.6a) shows a clustering structure rather comparable to those obtained in the previous analyses, but somehow either chronologically (extra-European sites) or geographically (European sites) more consistent. As regards to the chronological setting, some of the inconsistencies showed by the dendrograms obtained including all the localities (Figs. 4.4, 4.5) are still present. Bolomor and La Cotte de St Brelade gather together in a separate cluster (B), the similarity of Fuente Nueva 3 with the other localities included in cluster A is very low, and Barranc de la Boella Pit 1 is close to Acheulean sites ranging in age from MIS 16 to MIS 11, but also the Middle Palaeolithic site Poggetti Vecchi that confirms its peculiarity. The group A1.1. includes also both the Spanish and German early Late Pleistocene, possibly because the multiple influence of a number of variables, including the environmental characteristics.

It has to be noted that excluding the influence of the last glacial sites, Belchatów is positioned in the group A1.2 together with British, Spanish and Italian sites ranging in age from MIS 12 to MIS 7, even though showing the lowest degree of similarity. A high similarity characterizes the Italian site Castel di Guido (Boschian et al., 2019 and references therein) and La Polledrara di Cecanibbio (Anzidei et al., 2012; Santucci et al., 2016; Pereira et al., 2017), which are located in the same territory, are possibly close in age, but show minor differences in the fauna structure and perhaps human behavior.

A few changes can be detected if the chronology and geographical position are removed from the variables (Fig. 4.6a, b, c), although the environmental and/or human-related factors seem to have a major influence in the clustering. This is suggested for instance by the high similarity shown by some couples of sites that differ in age, such as the couples of La Polledrara di Cecanibbio (MIS 9) plus Torralba (MIS 7), and Arriaga II (MIS 6) plus Tafesa (MIS 12–11). La Polledrara di Cecanibbio plus Torralba share a fauna dominated by straight-tusked elephants and aurochs. At Arriaga II and Tafesa, the traces of human activity may result from isolated occupation events related to the processing of elephant carcasses, deer and auroch (Villa, 1990; Anzidei et al., 2012; Panera et al., 2014; Pineda and Saladié, 2019; Yravedra et al., 2019a and references therein; Rosell and Blasco, this volume). The hypothesis finds some support in the way they group together in the dendrogram resulting from the analysis performed by using only the environmental related variables (Fig. 4.6c), where the clustering of sites does not substantially change. We note the reduced distance among group that reaches its lowest value in the dendrogram resulting from the analysis performed by using only the human related variables (Fig. 4.6d). In this case, chronology and human species seem to have a fundamental role in the clustering, although other "human" characteristics, such as artifact technology, anthropogenic modifications and use of sites, also contribute to the group organization. This could confirm the chronological/human species similarity, as well as explain the anomalous positions of some sites. For instance, human species
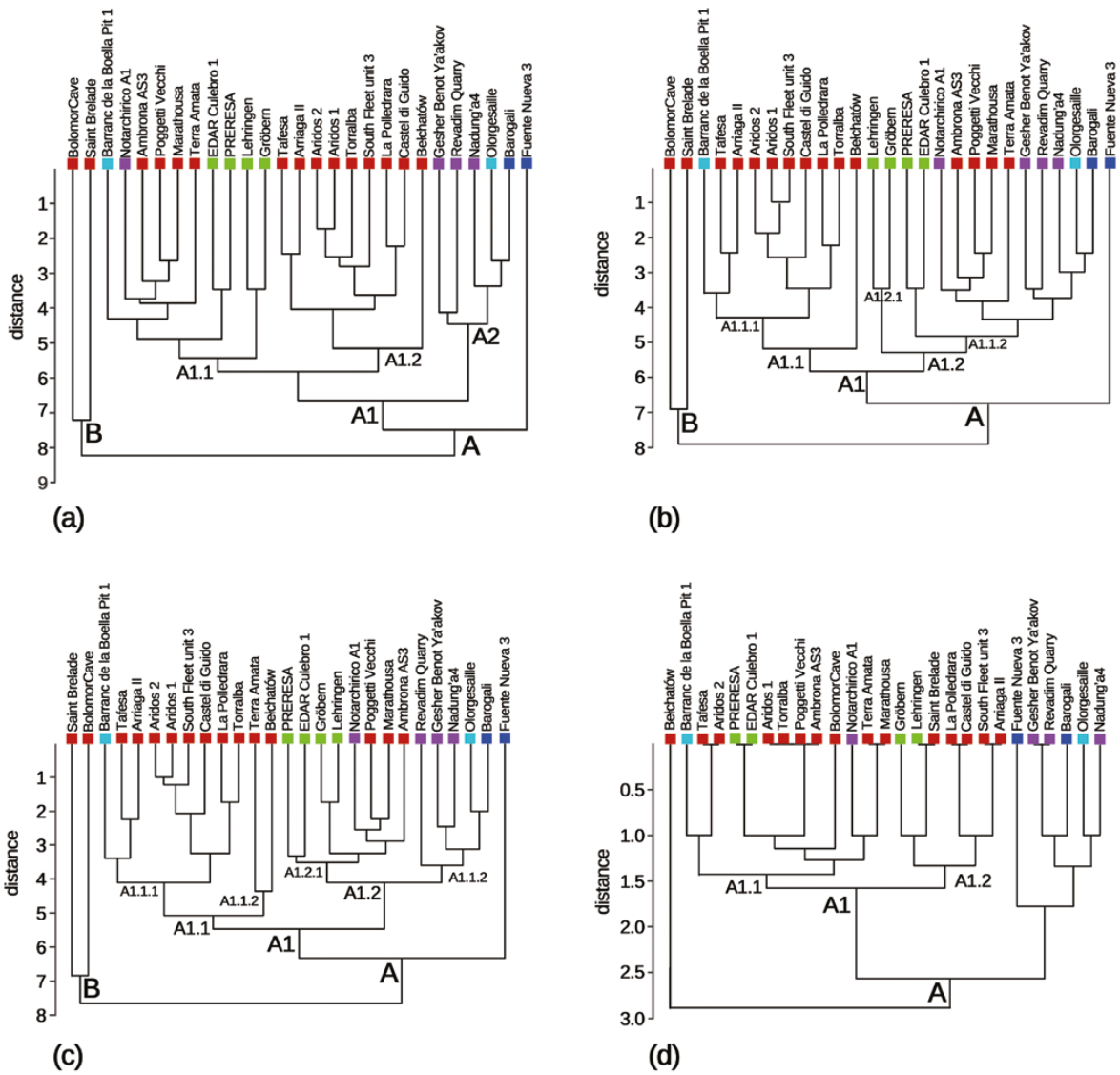
Figure 4.6: Q-mode dendrograms showing how the elephant butchery sites ranging from the late Early to the early Late Pleistocene (from MIS 54–MIS 39 to MIS 5) cluster using all the variables (**a**); using the environmental and human related variables (**b**), the environmental related variables (**c**), and human related variables (**d**) (for the chronological context see the legend in Fig. 4.7).

and material culture account for the new position of Fuente Nueva 3, which gathers with the Early Pleistocene sites (A2), while Barranc de la Boella is still included in the group gathering the Middle– early Late Pleistocene sites (A1).

4.3.2. NEIGHBOUR JOINING METHOD

The results obtained by applying the neighbour joining method roughly support the supposition

that all the variables contribute to the clustering structure, even if some environmental and human related aspects are among the most influencing variables (Fig. 4.7). The peculiar position of some sites, such as Fuente Nueva 3, characterized by a rich mammalian fauna with a high diversity of secondary consumers (Espigares et al., 2013, this volume; Blain et al., 2016; Rodríguez-Gómez et al., 2016), might account for the influence of variables related to the environment *sensu lato* characteristics in the neighbour joining. We need to
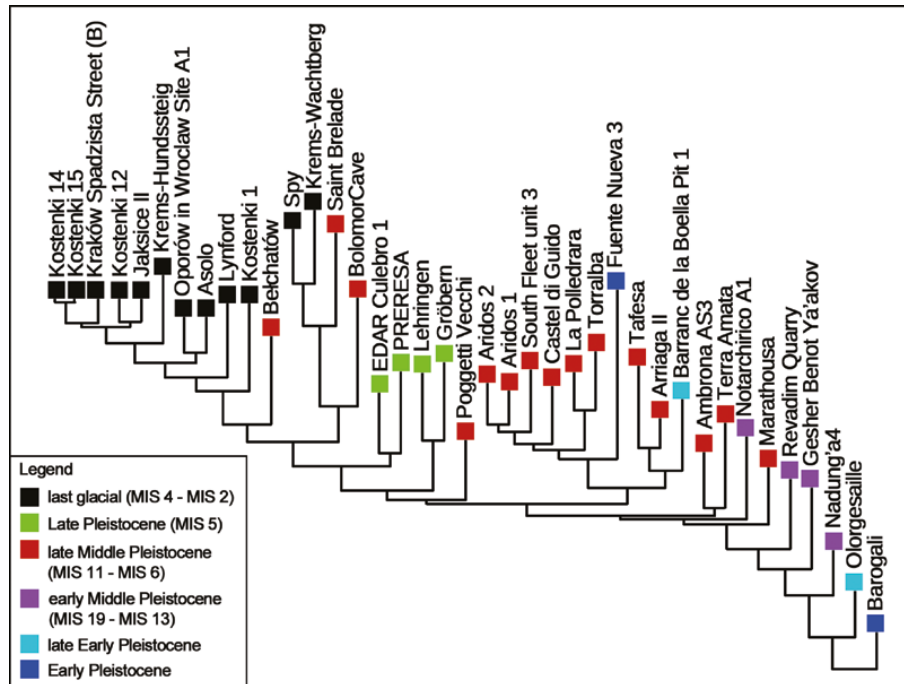
Figure 4.7: Hierarchical clustering tree of the elephant butchery sites resulting from the neighbour joining clustering analysis performed by using all variables.

note, however, that Bolomor Cave, where a generalist human exploited a broad spectrum of prey including young elephants (Blasco et al., 2013; Sañudo et al., 2016; Blasco and Fernández Peris, this volume), is not separated as in the classic clustering analysis (see Fig. 4.4), but joins with La Cotte de St Brelade and Spy, suggesting that the human behavior contributed also to the clustering of these sites.
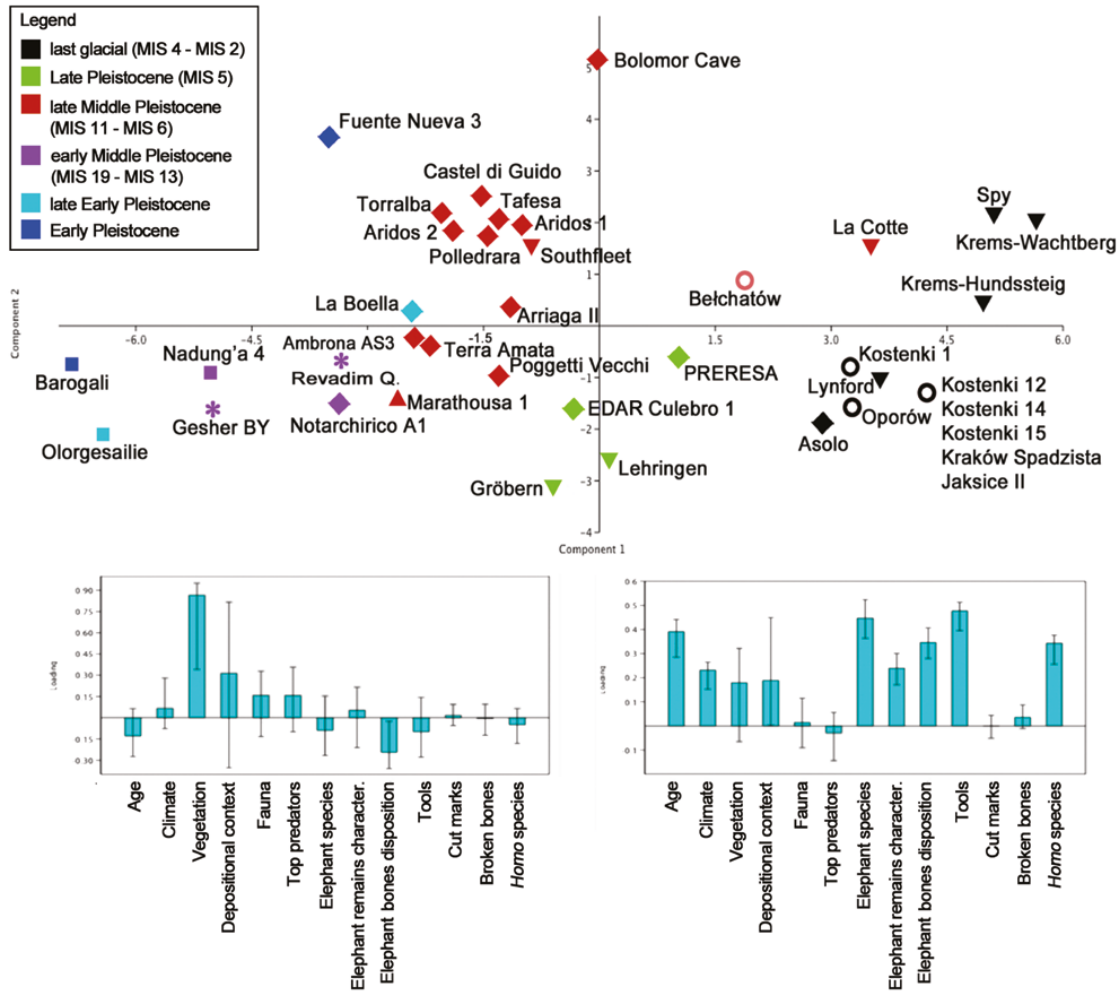
4.3.3. PRINCIPAL COMPONENT ANALYSIS

The PCA was computed using all the variables, first considering the entire set of sites (Fig. 4.8) and subsequently only the sites dated from the late Early to the early Late Pleistocene (approximately MIS 49 to MIS 5) (Fig. 4.9).

The PCA results obtained from the total dataset roughly confirm some influence of the chronology in the site distribution, but also evidence that of the climate or climate related factors (e.g., vegetation type, which has the highest weight on the first component) (Fig. 4.8). Conversely, some biological factors, such as the fauna characteristics, the num-

ber and power of top predators, and human signatures on bones (cut marks and intentional breakage for marrow extraction), are the variables with the lowest weight on the second component, and seem to have negligible influence. Variables related to the butchered elephants, such as species and spatial distribution of bones, and humans (*Homo* species and lithic tool technology) have a major influence in the second component, as well as the chronology of the site to which the human and elephant species are actually related. A chronological assessment is also evident as regards to the first axis. However, the PCA results cannot be regarded as compelling on account of the low values of the two first principal components. The variance accumulated by the first principal component, which accounts for as much as possible of the variability in the data, and the second component, reaches only 35.196% and 15.695%, respectively. Accordingly, the total variance accumulated by the two components is roughly the same percentage reached by the succeeding components, accounting for as much as possible of the remaining variability.

The PCA results obtained reducing the case to the Early to early Late Pleistocene butchery sites
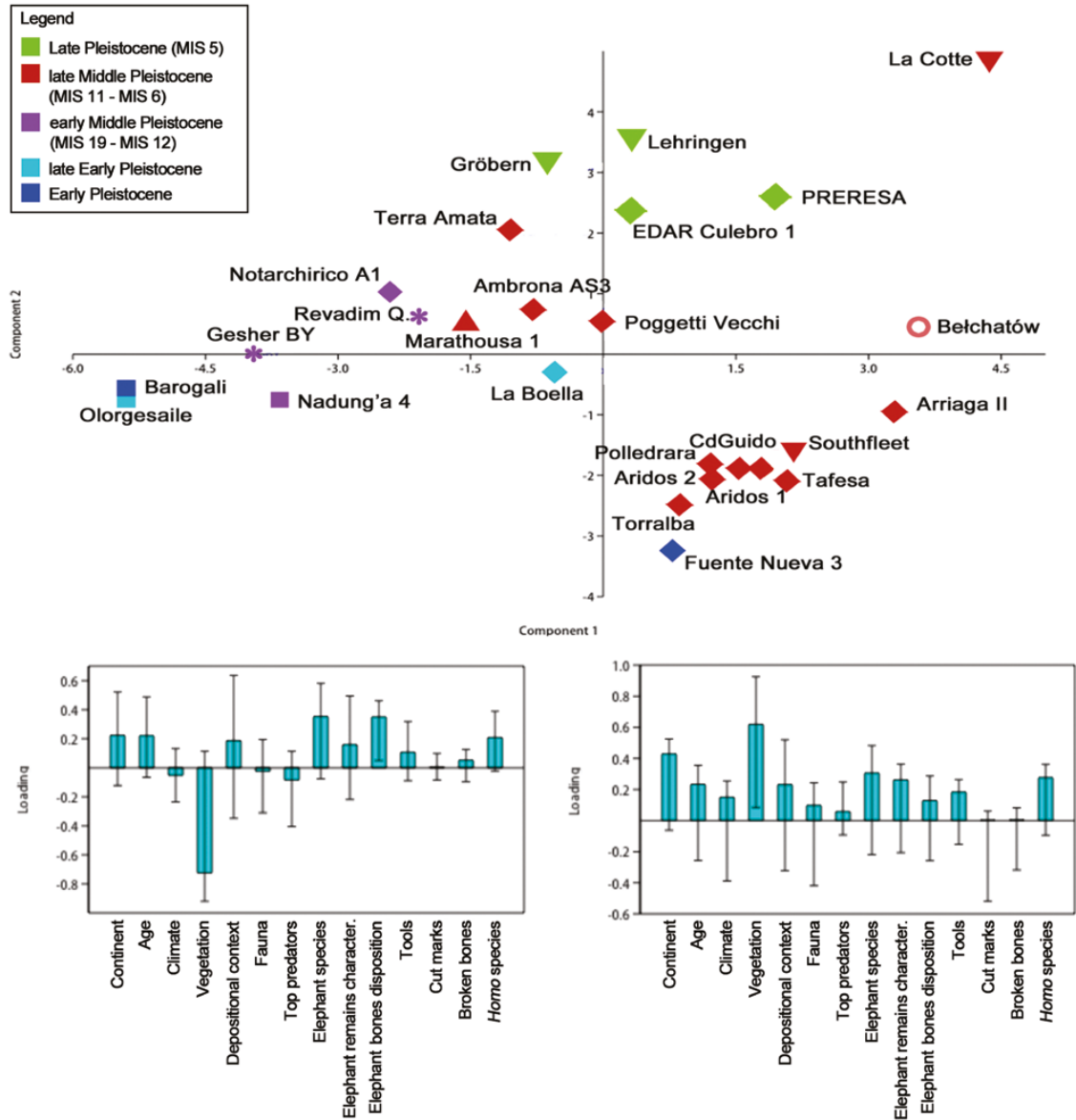
Figure 4.8: Diagram resulting from the principal components analysis (PCA) computed by using all variables and the elephant butchery sites ranging from the late Early Pleistocene to the Last Glacial Maximum (from MIS 54–MIS 39 to MIS 2). The component loadings (below) show the degree to which the different original variables enter into the components 1 (on the left) and 2 (on the right).

(Fig. 4.9) are more compelling than those obtained including the few last glacial sites selected for the purpose of comparison (Fig. 4.8), because the first and second components account respectively for the 45.6% and 42.5% (total 88.1%) of the variance.

The vegetation type is the most influential variable both in the first and second components, as expected due to the key role that the vegetation cover plays in the ecosystem structure and functioning. Conversely, the biological factors (fauna, number and power of top predators, and particularly human modifications on elephant bones) seem to be less influential.

4.3.4. UNIVARIATE ANALYSIS

A further attempt to find any potential trend during time was made by comparing the number of, and the anthropogenic modifications on elephants and other animal bones at the elephant butchery localities (Figs. 4.10, 4.11). The results have to be considered with caution, because the sites (39) we selected in a very rigorous and exclusive way are only a subset of the numerous alleged sites reported in literature. The "absence of evidence", such as cut marks and/or intentionally broken bones at some sites recording elephant remains associated with artifacts, cannot be considered as the "evidence of

Figure 4.9: Diagram resulting from the principal components analysis (PCA) computed by using all variables and the elephant butchery sites ranging from the late Early to the early Late Pleistocene (from MIS 54–MIS 39 to MIS 5). The component loadings (below) show the degree to which the different original variables enter into the components 1 (on the left) and 2 (on the right).

absence" of elephant exploitation by humans, especially if this kind of activity is documented in other mammals found at the site. Moreover, we include in the analysis only a few among the sites dated to the last glacial (MIS 4–MIS 2) present in the literature, because for most of the sites the basic information, especially related to taphonomic analysis, is missing or not exhaustively provided.

The results (Fig. 4.10) highlight an augment of sites recording anthropogenic modifications on elephant bones (cut marks, percussion marks, fractured bones) from the Early to the Middle Pleistocene and a decrease in the Late Pleistocene, at least regarding the sites selected for the analysis. The significant increase of anthropogenic modifications in the Middle Pleistocene relates possibly to some augment of the exploitation of elephant carcasses, even if it is a challenging task to assert whether this tendency
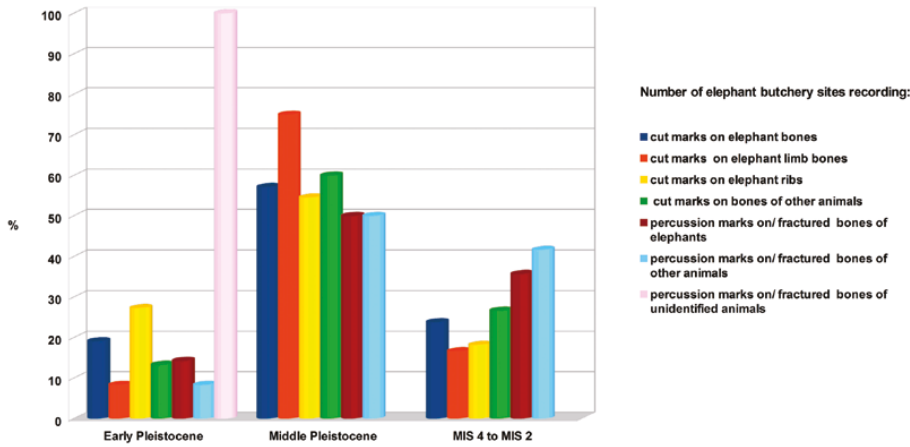
depends mainly on some change in the human behavior or on the interaction of other factors, such as an increase in the occupancy by archaic humans and the need to exploit a large spectrum of resources.

During the Middle Pleistocene, there is also a marked increase in both the percussion marks and bones of elephants and other animals intentionally broken for marrow. Cut marks have especially been detected on ribs, mostly located on their ventral or lateral sides, likely created during the removal of organs or flesh filleting (Fig. 4.11).

The exploitation of elephant carcasses is sometimes associated to that of other mammals. The latter, documented by cut-marked and fractured bones, tends to be dominant in the Late Pleistocene (Fig. 4.11). This fact suggests that the exploitation of proboscideans, in particular of *M. primigenius,* was an important component in subsistence strategies, but secondary to the exploitation of other small and large mammal species.

4.3.5. REMARKS

Overall, the results obtained by processing site characteristics by means of multivariate statistical analyses (cluster analysis, neighbour joining clustering method, PCA) suggest that the butchery behavior did not substantially change in the course of the late Early and Middle Pleistocene.

The environment characteristics, particularly the vegetation type, had, however, an indirect effect on animal and human occupancy, because they affected the productivity, the amount of available resources, the faunal structure, and, in turn, the presence and consistency of human groups in a territory. Conversely, the geographical location and the butchered elephant species likely had a marginal effect. We need to note that in the Early Pleistocene humans and predators succeeded each other in exploiting elephant remains. Nearly the same occurred during the Middle Pleistocene, although the composition of the carnivore guild changed. During the last glacial, better-equipped and organized AMH hunter groups successfully competed with top predators.

The results obtained by processing site characteristics, such as number of compelling butchery elephant sites, and the anthropogenic modifications on elephants and other animal bones by means of univariate statistical analyses, suggest that: i) in the course of the Pleistocene the number of compelling elephant butchery sites significantly augmented; ii) at the oldest sites, cut marks on elephant bones are mainly documented on ribs and scapulae; iii) cut marks on elephant long bones are reported since the Middle Pleistocene; iv) percussion marks and intentionally broken elephant bones prevail in the sites dated to the last glacial phases, apparently in agreement with a progressively increasing systematic exploitation of elephant carcasses during time.

Considering the results of both multivariate and univariate analyses, the hypothesis that during the Lower Palaeolithic the human-elephant
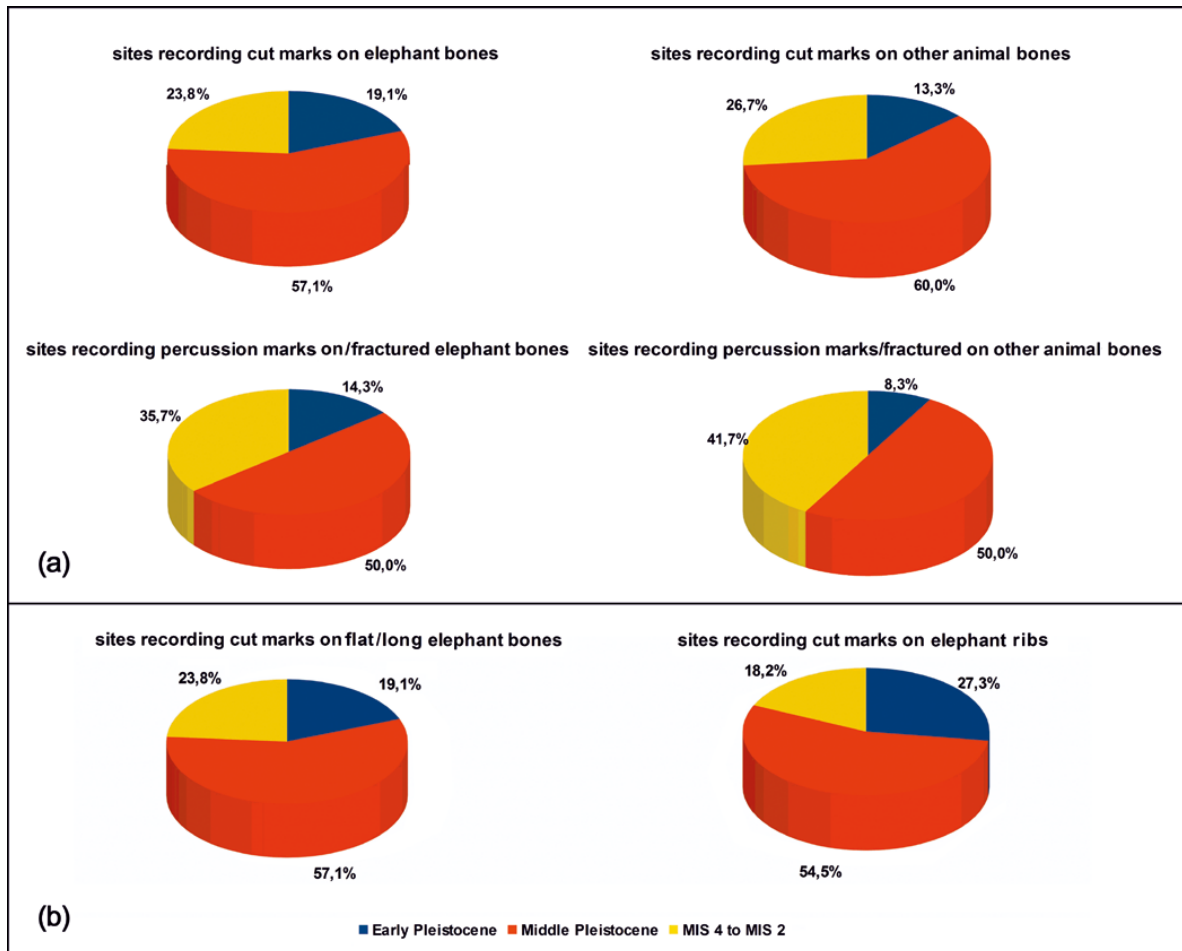
Figure 4.11: Pie charts showing the variation of anthropogenic modifications on elephant and other animal bones (**a**), and on elephant bones (**b**) at the elephant butchery sites ranging from the late Early Pleistocene to the Last Glacial Maximum (from MIS 54–MIS 39 to MIS 2)

interactions were more affected by chance rather than by cultural/environmental factors seems to be conceivable, at least based on the analysis of the available data from the sites selected for this research. During the Late Pleistocene, conversely, the exploitation of mammoth carcasses was more related to hunting activity, selectively addressed to young individuals, although other large games were preferred at least by Neanderthal hunters (see e.g., Germonpré et al., this volume).

4.4   DISCUSSION

During the last couple of decades, the increasing interest on early human behavior in resource ex-

ploitation, and the determination to contribute to the debate on scavenging vs. hunting large game, by providing firm evidence supporting one or the other theory, promoted the development of research and a considerable increase in striking data. However, the question of human-proboscidean interactions remains a challenging issue, difficult to deconstruct especially as regards to the Lower Palaeolithic. This is in particular due to: i) the discontinuity and incompleteness of the fossil record in time and space; ii) the defective information available for some sites (for instance the localities discovered, excavated and studied several decades ago, and the nowadays no longer accessible or available collections); and iii) the objective impossibility to identify all the sites, where archaic humans actually
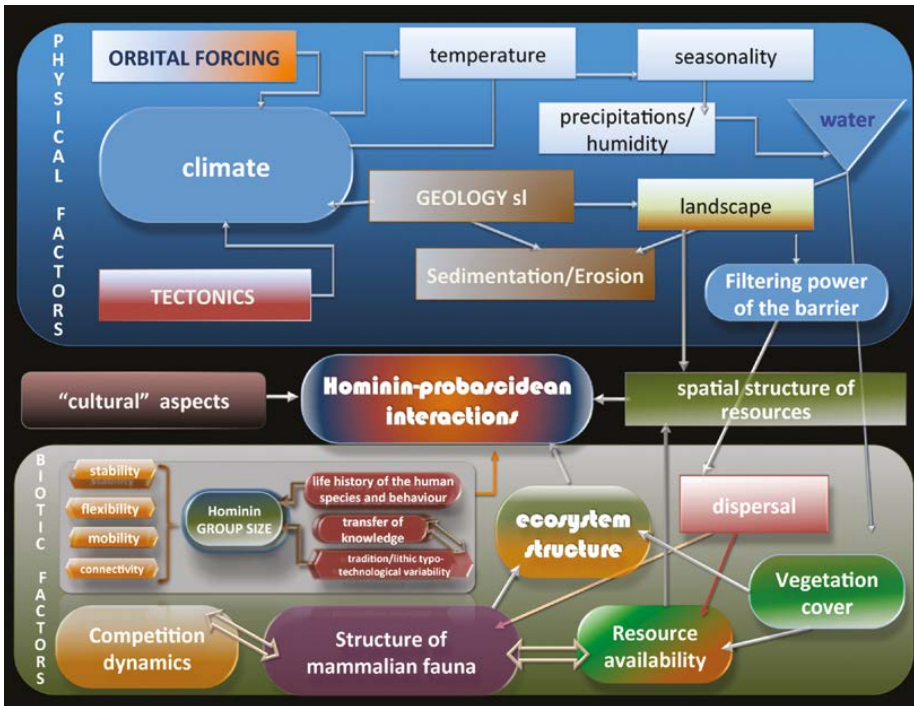
exploited proboscidean carcasses for meat. It is the case, for instance, of the numerous sites recording both proboscidean remains and butchery activity on large and small animals, or where dispersed proboscidean remains are associated with artifacts, as it frequently occurs in alluvial depositional contexts.

Manifold factors could interact each other and contribute to promote and shape the way that archaic humans exploited food resources in a variety of environments, from open savannah and grasslands to riparian woodlands. It is indeed a challenging task to deconstruct the conceivable causal factors, remote and proximate, relating to the human behavior and the type of interaction they had with the elephant populations inhabiting their own territory due to the complexity of the interplay network, and related feedback loops (Fig. 4.12).

The behavior of early humans was obviously driven, like in all other living organisms, by the need to maximize the foraging rate and minimize the energetic cost for exploiting available resources and surviving. However, it is a challenging task to hypothesize a univocal evolutionary pattern of human behavior over time and across space. The mo-

dalities of human active participation in the ecosystem dynamics actually evolved over time, but the archaic human ability to perceive and adapt to the changing physical and biotic environmental conditions and the varying of its equilibrium, may also have changed during the same slice of time even across the same geographic area. On the one hand, physical and some biotic factors (such as dispersal, turnovers, resource availability, competition dynamics, faunal structure and functional diversity) could have had a major influence in constraining the presence and the occupancy of both archaic human and proboscidean species in a territory. On the other hand, the human-elephant interaction dynamics were likely affected mainly by the archaic human behavior, habits, group size and their dispersion/diffusion on the territory, as well as by any kind of inter- and intra-group cooperation, and material cultural aspects.

Specific evidence and several lines of reasoning suggest that the environmental scenario and its changes throughout time played a significant role in regulating time and mode of human evolution and constraining population dynamics. However, we are far from deconstructing the complex network

of causal factors (climate driven environmental changes, catastrophic events, resources availability, geomorphology, landscape characteristics, competition, demographic pressure, cultural aspects such as technology, cognition, communication among others), which may have constrained the human dispersal towards and settlement in any territory during the Early (2.6–0.78 Ma; MIS 103–MIS 19) and early Middle Pleistocene (0.78–0.47 Ma; MIS 19–earliest MIS 12) and, consequently, the conceivable fluctuation in the distribution and density of human groups across space during this time. Periods of dramatic changes in climate regimes and distribution of Palaearctic biota may have played a crucial role in generating adaptive patterns within the primitive human populations, perhaps exerting some influence on human behavioral flexibility in exploiting resources and aggregating either into small groups or rather large bands. However, it remains difficult to answer the somehow speculative question regarding the extent to which such environmental factors may have affected the structure, size, cohesion and intra-group social interactions of the Pleistocene archaic human groups (e.g., Zhou et al., 2005; Hamilton et al., 2017). It is rationale to suppose that physical/environmental factors and "cultural" aspects synergistically act in shaping and regulating prehistoric population size, particularly group size. Disentangling the relationship between the group cohesion/fission and cooperation, and competition due to intrinsic motivation or external factors, is somehow difficult for extant hunter-gatherer populations, and becomes barely possibly regarding the Early Pleistocene humans, as it is to hypothesize the dynamics of intra-group social interactions.

Although it is widely accepted that cooperation among individuals facilitates to achieving optimal results in foraging, and reduces time and energy expenditure in any kind of human activity, a number of questions arise, related to the "cause-effect relationships" among demography, occupancy, productivity, resource exploitation and partitioning, and human behavior and the spillover effects on human-elephant interactions. Consequently, a number of issues deserve to be attentively scrutinized and discussed in more detail. For instance, the matter whether the potential effect exerted on the exploitation and partitioning of resources by the augment of human territory occupancy, and the increase in number and size of populations may have promoted any significant modification of the archaic human behavior. Moreover, the strict selective criteria we have adopted might have led to the exclusion of a number of potential butchery sites, and this may question the hypothesis that during the Lower Palaeolithic the human butchery activity on elephant carcasses was mainly affected by chance. Therefore, the intriguing question arises whether the augment of the number of sites from the Early to the Middle Pleistocene merely related to the increased population density, or due to any beginning of some hunting activity.

Moreover, it is rational to suppose that the group size could have influenced the intra-group cooperation and in turn hunting behavior, but it is a challenging task to find any evidence suitable for inferring the inter-group cooperation dynamics even for the Middle Palaeolithic hunters.

Other intriguing issues deal with the role that the technological innovation, tool efficiency and the progressive developing of archaic human skills may have exerted in shaping the way in which humans interacted with elephants.

Based on the data available in literature, and at least as regards to the sites analyzed herein, no compelling evidence supports the existence of any relationship between the typology and the amount of tools found at a site and potential presence and characteristics of the anthropogenic signatures on elephant bones (cut and percussion marks, intentionally broken bones). In particular, the presence/absence, number and shape of handaxes seem to not correlate with the presence and characteristics of cut marks. It could actually be an expected result due to the scarce likelihood that any kind of cutting tool may leave on elephant bones a signature suitable to persist after taphonomic and diagenetic processes (see e.g., Haynes and Klimowicz, 2015).

A number of studies highlight the key role of small tools in carcass exploitation activities since the Lower Palaeolithic (Venditti et al., 2019 and references therein), although this does not necessarily imply the exclusive use of such kind of tools in sites where also handaxes are present. For instance, at the Middle Pleistocene site of Revadim Quarry (Israel) the use-wear and residual analyses of lithic implements demonstrate the large employment of small flakes in the butchery processes, but also a possible utilization of heavier tools (e.g., handaxes, bifaces, large flakes) for the heavy-duty butchery operations (Venditti et al., 2019; Marinelli et al., this volume). Additionally, the late Middle Pleistocene site La Polledrara di Cecanibbio, where bifaces are absent, is among the sites where small flakes (mainly obtained from a simple reduction sequence and sometimes not or slightly retouched) were systematically employed in the butchering activities (Santucci et al., 2016).

At La Polledrara, as well as in other sites differing in age, human species and elephant butchered species (e.g., Fuente Nueva 3), lithic implements (cores, tools, flakes, some with wear traces testifying for their use on soft animal tissues, and working debris) were associated with an elephant skeleton, documenting the human exploitation of the carcass, likely by scavenging (Espigares et al., 2013, this volume; Santucci et al., 2016).

However, the presence of an elephant skeleton surrounded by tools could have different implications as regards to the origin of the carcass (a hunted elephant? a carcass incidentally discovered? a carcass found during a systematic survey by archaic humans across their home range?). In addition, the spatial connection between skeletal remains and lithic industry may be not enough to indisputably identify a butchery site. An accurate analysis of the depositional context (e.g., stratigraphy, sedimentology, faunal association, spatial distribution of the skeleton bones, particularly presence of skeletal elements in anatomical connection/physiological position, degree of disarticulation and their origin —natural, due to animal intervention and dispersion, or anthropogenic— and taphonomy, with

particular attention to the reconstruction of biostratinomic processes) could provide clues valuable to answer the questions.

La Polledrara provides a valuable case study, which documents the cause of death of an adult straight-tusked elephant and the scavenging activity of a human group (likely *H. heidelbergensis*), including a child 5–10 years old (Anzidei et al., 2012). The *P. antiquus* skeleton lies gently bent on its left side with the preserved forelimb bones in anatomical connection, some of them in physiological position. The front limbs bend on themselves, while the left hind limb lies in a sub-horizontal position, stretched backwards. This peculiar position suggests that the elephant slid on the mud-covered bank at the edge of a palustrine zone and was trapped in the muddy sediments of a puddle, where it died. The skeleton is surrounded on both sides by hundreds of lithic implements, produced *in situ* (as the refitting of various flint flakes proves) and used for cutting soft tissues (meat and hide), as indicated by the use-wear analysis (Santucci et al., 2016). Overall, evidence from La Polledrara suggests that the human group scavenged an elephant carcass, which died from natural causes, as it likely occurred at Poggetti Vecchi (MIS 6), where *H. neanderthalensis* butchered the carcasses of straight-tusked elephant (see Aranguren et al., 2019). Moreover, at La Polledrara the distal epiphyses of both femurs are intentionally broken for marrow extraction. On the broken right femur the still in place percussion flake offers further evidence of human exploitation at the site (Santucci et al., 2016), suggesting that the archaic human groups may have visited time after time the zone surrounding the swampy La Polledrara area. The idea that during the late Middle Pleistocene this territory and its resources were attractive for humans is supported by the evidence provided by the neighbouring butchery site of Castel di Guido. At this site, several stone and some bone tools show clear evidence of recycling, suggesting that the bones of large mammals, mostly elephant, were part of a complex subsistence system characterized by hunting and scav-

enging during a quite long time of permanence or perhaps several phases of human presence at the site (Boschian and Saccà, 2015).

Other sites may represent a single and short phase of use (e.g., Barogali, Olorgesailie basin member 1-Site 15, Gesher Benot Ya'akov, Notarchirico A1 level, Southfleet Road unit 3, Gröbern (?), Áridos 1, Áridos 2, Marathousa 1, and perhaps Asolo), whereas for some others recording an elephant skeleton associated with lithic implements, data are not enough to propose any reasonable hypothesis, as for instance Ficoncella (Italy; MIS 13; Aureli et al., 2015, 2016). Although at the latter site some remains of an adult *P. antiquus* (thus far only partially retrieved from the sediments) were found in close spatial connection with small lithic artifacts showing an original reduction sequence, the sedimentary context, the small thus far investigated area and the rarity of accompanying fauna remains hamper to properly infer the characteristics of this potential butchery site.

All things considered, evidence of elephant flesh and bone marrow consumption, as well as bone artifacts from various Lower Palaeolithic sites, attests that the elephant carcasses constituted a valuable resource for food and raw material, exploited by humans for a slice of time, which could vary from a place to another in an unpredictable way. In the wild, indeed, a number of physical and biotic factors (e.g., temperature, humidity, rain, predator and scavenger animal activity) account for the time that could elapse from the death of an animal and the exposure of skeletal bones.

In the case of Lower Palaeolithic archaeological sites, where there is evidence that archaic humans have exploited elephant carcasses for both meat/marrow and raw material in bone tool production, it is a challenging task to ascertain whether these activities took place or not in a short period of time. This is particularly true considering that bone breakage for marrow consumption did not necessarily occurred immediately after the removal of soft tissues, due to the low rate of marrow fat degradation, still edible after about two months of exposure (Blasco et al., 2019). The arduous to solve issue therefore

arises as whether an elephant carcass was intentionally visited many times by the same human group, or by different groups at different times.

Available data on the one hand do not enable us to answer some questions, on the other highlight some issues, which deserve to be scrutinized in depth, as, among others, the association "artifacts-proboscidean bones" in alluvial depositional context. What is, for instance, the actual significance of fluvial deposits, recording elephant remains, bone artifacts and lithic tools (including some used to cut flesh), in the light of the very rare findings of elephant bone fragments with cut marks in this depositional context? For example, at La Polledrara a single cut-marked bone (a diaphysis fragment) was identified among more than 40 elephant bones (analyzed in a selected area of 100 square meters not far from the butchered skeleton) accumulated both on the bottom of the river during flooding events and in the filling deposit (Cerilli and Fiore, 2018; Cerilli et al., 2019). To date, no cut marks have been detected among the remains found in the sediments deposited during the swampy phase giving rise to areas with stagnant and muddy waters, where some elephants became trapped. Accordingly, as mentioned above, the number of butchery sites could be sensibly higher that the number of sites providing firm indisputable evidence of proboscidean carcass exploitation.

The issues discussed above are only a few among the aspects potentially influencing the way in which Lower Palaeolithic humans interrelated with probo scideans, although many others are worth considering and debating, stressing once again the multifaceted, intriguing aspects of the human-proboscidean interaction dynamics during the Early and Middle Pleistocene.

4.5   CONCLUSIONS

Evidence provided by the palaeontological and archaeological record clearly indicates that different proboscidean species coexisted with different archaic human species in different environments,

varying in climatic conditions, landscapes, vegetation cover, faunal structure and availability of resources. Accordingly, this study aimed to explore whether and to which extent physical and biotic environmental aspects may have affected human-proboscidean (mainly Elephantini) interactions during time and across space, either as remote and proximate causal factors. To this goal, we analyzed the critically revised environmental context at selected elephant butchery sites (chosen following very critical selection criteria) by processing data by means of statistical analyses.

Taken together, the results support as conceivable the hypothesis that during the Lower Palaeolithic the human-elephant interactions were more affected by the chance to find a carcass, rather than were strictly dependent on environmental factors and/or cultural aspects (*sensu lato*). We are aware, however, that the sites analyzed are only a subset of all the potential late Early–early Late Pleistocene sites, and the results cannot be regarded as exhaustive and conclusive. Although we need more research and data to properly deconstruct the mode and extension of such interaction, the results of this research provide some food for thought.

On the one hand, the chosen statistical approach certainly provides some informative results and fresh clues for setting the matter of the archaic human behavior towards elephants, and the casualty vs. intentionality of elephant carcass processing. On the other hand, the lack of compelling evidence supporting a purported butchery activity on elephants may depend on an unpredictable number of factors that hamper the possibility to know the original environmental context of the human-elephant interactions. In addition to the objective difficulty of creating cut marks on elephant bones, there exist also biases related to biostratinomic and taphonomic processes that may sensibly reduce the amount of information, and the disparity in the amount of sites and information during time and across space. For instance, the Early to early Late Pleistocene archaeological sites yielding elephants remains (mainly belonging to *Palaeoloxodon* and subordinately to *Mammuthus* species) are much more numerous than those, where the characteristics of the elephant remains can be indisputably associated with human exploitation of carcasses. Finally, we do not have, of course, solid data on butchery places that may exist, but have not been found yet.

Keeping these limitations in mind, we can try to answer our focal questions. Regarding the question "did the way in which humans exploit proboscidean carcasses change during time, according to the changing human species and material culture?", the obtained results suggest that the archaic human butchery behavior did not substantially change in the course of the late Early and Middle Pleistocene. The augment in the number of sites seems to be related to the increased demography and territory occupancy, although we are aware that occupancy statistics in palaeontology are biased upward by the intrinsic incompleteness of the fossil record. The magnitude of this bias increases as the number of sites investigated decreased. Moreover, based on the analyzed data, we are unable to conclude on some issues, such as whether any relationship may exist between tools and cut marks, and its potential relevance.

As regards to the question "did the human butchering activity on elephants depend in any extent on one or the other physical/biotic factors", focusing on the late Early to early Late Pleistocene, the results underline the role of environment characteristics, particularly the vegetation type. The latter, in particular, had likely an indirect effect on occupancy, because on vegetation depends the primary productivity, and in turn the faunal structure, the amount of available resources, and, consequently, the presence of human groups in a territory. We could speculate that the higher the amount of resources was, the higher distribution and density a human population had, having as a feedback an impact on the resources partitioning, which may have in turn promoted some changes in human behavior. Concerning the matter of the competition with top predators, the available data suggest that during the Early Pleistocene humans and predators succeeded each other in exploiting elephant remains, as sometimes occurred during the

Middle Pleistocene, although the carnivore guild had changed. During the last glacial (MIS 4–MIS 2), better equipped and organized AMH hunter groups successfully competed with top predators.

Finally, concerning the question whether the human butchery activity on elephants depended mainly on casualty or was in some way related to cultural *sensu lato* and/or environmental aspects, the results seem to support the hypothesis of prevailing accidental findings, at least as regards to the elephant carcasses butchered by Lower Palaeolithic humans. The chance to find a carcass is expected to augment in the course of time, depending on the factors discussed above. Conversely, during the Late Pleistocene the exploitation of mammoth carcasses was more related to a hunting activity, selectively addressed to young individuals, even if other large games were preferred at least by Neanderthal hunters.

Overall, this study highlights once again the complexity of the evolutionary dynamics of human-elephant interactions, and the need to explore all the diverse aspects, even those apparently marginal, in order to be able to answer the many questions still remaining unsolved.

ACKNOWLEDGEMENTS

REFERENCES

AGAM, A., Barkai, R., 2016. Not the brain alone: the nutritional potential of elephant heads in Paleolithic sites. Quaternary International 406, 218–226.

AGAM, A., Barkai, R., 2018. Elephant and mammoth hunting during the Paleolithic: a review of the relevant archaeological, ethnographic and ethno-historical records. Quaternary 1, 3.

ÁLVAREZ-POSADA, C., Parés, J. M., Granger, D., Duval, M., Sala, R., Toro, I., 2015. New magnetostratigraphic and numerical age of the Fuente Nueva-3 site (Guadix-Baza basin, Spain). Quaternary International 389, 224–234.

ANURADHA, J. M. P. N., Fujimura, M., Inaoka, T., Sakai, N., 2019. The role of agricultural land use pattern dynamics on elephant habitat depletion and human-elephant conflict in Sri Lanka. Sustainability 11, 2818.

ANZIDEI, A. P., Bulgarelli, G. M., Catalano, P., Cerilli, E., Gallotti, R., Lemorini, C., Milli, S., Palombo, M. R., Pantano, W., Santucci, E., 2012. Ongoing research at the late Middle Pleistocene site of La Polledrara di Cecanibbio (central Italy), with emphasis on human-elephant relationships. Quaternary International 255, 171–187.

ANZIDEI, A. P., Bulgarelli, G. M., Cerilli, E., Fiore, I., Lemorini, C., Marano, F., Palombo, M. R., Santucci, E., 2015. Strategie di sussistenza nel Paleolitico inferiore a La Polledrara di Cecanibbio (Roma): lo sfruttamento di una carcassa di *Palaeoloxodon antiquus*. 50° Riunione Scientifica dell'Istituto Italiano di Preistoria e Protostoria "Preistoria del Cibo", Rome.

ARANGUREN, B., Revedin, A., Amico, N., Cavulli, F., Giachi, G., Grimaldi, S., Macchioni, N., Santaniello, F., 2018. Wooden tools and fire technology in the early Neanderthal site of Poggetti Vecchi (Italy). Proceedings of the National Academy of Sciences 115, 2054–2059.

ARANGUREN, B., Grimaldi, S., Benvenuti, M., Capalbo, C., Cavanna, F., Cavulli, F., Ciani, F., Comencini, G., Giuliani, C., Grandinetti, G., Mariotti Lippi, M., Masini, F., Mazza, P. P. A., Pallecchi, P., Santaniello, F., Savorelli, A., Revedin, A., 2019. Poggetti Vecchi (Tuscany, Italy): a late Middle Pleistocene case of human-elephant interaction. Journal of Human Evolution 133, 32–60.

Arsuaga, J. L., Martinón-Torres, M., Santos, E. 2019. Homo steinheimensis, a comparison between the Steinheim skull and the Atapuerca Sima de los Huesos fossils. 9th Annual Meeting of the European Society for the study of Human Evolution, p. 7.

Aureli, D., Contardi, A., Giaccio, B., Jicha, B., Lemorini, C., Madonna, S., Magri, D., Marano, F., Milli, S., Modesti, V., Palombo, M. R., 2015. *Palaeoloxodon* and human interaction: depositional setting, chronology and archaeology at the Middle Pleistocene Ficoncella site (Tarquinia, Italy). PloS ONE 10, e0124498.

Aureli, D., Rocca, R., Lemorini, C., Modesti, V., Scaramucci, S., Milli, S., Giacco, B., Marano, F., Palombo, M. R., Contardi, A., 2016. Mode 1 or mode 2? "Small tools" in the technical variability of the European Lower Palaeolithic: The site of Ficoncella (Tarquinia, Lazio, central Italy). Quaternary International 393, 169–184.

Barkai, R., 2019a. When elephants roamed Asia: The significance of proboscideans in diet, culture and cosmology in Paleolithic Asia, in: Kowner, R., Bar-Oz, G., Biran M., Shahar, M., Shelach-Lavi, G. (Eds.) Animals and human society in Asia. Palgrave Macmillan, Cham, pp. 33–62.

Barkai, R., 2019b. An elephant to share: rethinking the origins of meat and fat sharing in Palaeolithic societies, in: Lavi, N., Friesem, D. E. (Eds.), Towards a broader view of hunter-gatherer. McDonald Institute Conversations, Cambridge, pp. 153–167.

Bermúdez de Castro, J. M., Martinón-Torres, M., de Pinillos, M. M., García-Campos, C., Modesto-Mata, M., Martín-Francés, L., Arsuaga, J. L., 2019. Metric and morphological comparison between the Arago (France) and Atapuerca-Sima de los Huesos (Spain) dental samples, and the origin of Neanderthals. Quaternary Science Reviews 217, 45–61.

Berthelet, A., 2002. Barogali et l'Oued Doure. Deux gisements représentatifs du Paléolithique ancien en République de Djibouti. L'Anthropologie 106, 1–39.

Blain, H. A., Lozano-Fernández, I., Agustí, J., Bailon, S., Granda, L. M., Ortiz, M. P. E., Sos-Montoya, S., Jiménez Arenas, J. M., Toro-Moyano, I., Martìnez-Navarro, B., Sala, R., 2016. Refining upon the climatic background of the Early Pleistocene hominid settlement in western Europe: Barranco León and Fuente Nueva-3 (Guadix-Baza basin, SE Spain). Quaternary Science Reviews 144, 132–144.

Blasco, R., Fernández Peris, J., 2012. Small and large game: human use of diverse faunal resources at Level IV of Bolomor Cave (Valencia, Spain). Comptes Rendus Palevol 11, 265–282.

Blasco, R., Fernández Peris, J., this volume. From tortoises to elephants: the impact of elephants in the broad spectrum diet at Bolomor Cave (MIS 9–5 Spain).

Blasco, R., Rosell, J., Fernández Peris, J., Arsuaga, J. L., de Castro, J. M. B., Carbonell, E., 2013. Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). Quaternary Science Reviews 70, 124–144.

Blasco, R., Rosell, J., Arilla, M., Margalida, A., Villalba, D., Gopher, A., Barkai, R., 2019. Bone marrow storage and delayed consumption at Middle Pleistocene Qesem Cave, Israel (420 to 200 ka). Science Advances 5, eaav9822.

Bocherens, H., Drucker, D. G., this volume. Isotopic insights on ecological interactions between humans and woolly mammoths during the Middle and Upper Palaeolithic in Europe.

Bosch, M. D., 2012. Human-mammoth dynamics in the mid-Upper Palaeolithic of the middle Danube region. Quaternary International 276, 170–182.

Boschian, G., Saccà, D., 2015. In the elephant, everything is good: Carcass use and re-use at Castel di Guido (Italy). Quaternary International 361, 288–296.

Boschian, G., Caramella, D., Saccà, D., Barkai, R., 2019. Are there marrow cavities in Pleistocene elephant limb bones, and was mar-

row available to early humans? New CT scan results from the site of Castel di Guido (Italy). Quaternary Science Reviews 215, 86–97.

BOWRA, C. M., 1962. Primitive song. World Publishing, NewYork.

BUCK, L. T., Stringer, C. B., 2014. *Homo heidelbergensis*. Current Biology 24, R214–R215.

CAPALBO, C., Mazza, P. P. A., Masini, F., Savorelli, A., 2018. Palaeoecology and taphonomy of the straight-tusked elephant late Middle Pleistocene site of Poggetti Vecchi (Southern Tuscany, Italy). Alpine and Mediterranean Quaternary 31, 43–48.

CERILLI, E., Fiore, I., 2018. Natural and anthropic events at La Polledrara di Cecanibbio (Italy, Rome): some significant examples. Alpine and Mediterranean Quaternary 31, 55–58.

CERILLI, E., Fiore, I., Santucci, E., Marano, F., Anzidei, A. P., Bulgarelli, G. M., Lemorini, C., Palombo, M. R., 2019. Strategie di sfruttamento delle risorse animali a La Polledara di Cecanibbio (Pleistocene medio-superiore, Roma), in: De Grossi Mazzorin, J., Fiore, I., Minniti, C. (Eds.), Atti dell' 8th Convegno Nazionale di Archeozoologia, Lecce, pp. 21–30.

CHELLI-CHEHEB, R., Arzarello, M., Arnaud, J., Berto, C., Cáceres, I., Caracausi, S., Colopi, F., Daffara, S., Montanari Canini, G., Huquet, R., Karambatsou, T., Sala, B., Zambaldi, M, Berruti, G. L. F., 2019. Human behavior and *Homo*-mammal interactions at the first European peopling: new evidence from the Pirro Nord site (Apricena, Southern Italy). The Science of Nature 106, 16.

CHELLI–CHEHEB, R., Arzarello, M., Arnaud, J., Berto, C., Cáceres, I., Caracausi, S., Colopi, F., Daffara, S., Canini, G. M., Huguet, R., Karambatsou, T., Sala, B., Zambaldi, M., Berruti, G. L. F., 2020. Correction to: Human behavior and *Homo*-mammal interactions at the first European peopling: new evidence from the Pirro Nord site (Apricena, Southern Italy). The Science of Nature 107, 33.

DE HEINZELIN, J., Clark, J. D., White, T., Hart, W., Renne, P., WoldeGabriel, G., Beyene, Y.,

Vrba, E., 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. Science 284, 625–629.

DE LUMLEY, H. (Ed.), 2009. Terra Amata Nice Alpes-Maritimes, France Tome I: Cadre géographique, historique, contexte géologique, stratigraphie, sedimentologie, datation. CNRS Éditions, Paris.

DE LUMLEY, H. (Ed.), 2011. Terra Amata Nice Alpes-Maritimes, France Tome II: Palynologie, anthracologie, faunes de vertébrés, mollusques, ecologie et biogéomorphologie, paléoanthropologie, empreinte de pied humain, coprolithes. CNRS Éditions, Paris.

DE LUMLEY, H. (Ed.), 2013. Terra Amata Nice Alpes-Maritimes, France Tome III: Individualisation del unités archéostratigraphique et description des sols d'occupation acheuléens du site de Terra Amata. CNRS Éditions, Paris.

DE LUMLEY, H. (Ed.), 2015. Terra Amata Nice Alpes-Maritimes, France Tome IV: Fascicule 1 Les industries acheuléennes du site de Terra Amata. CNRS Éditions, Paris.

DE LUMLEY, H. (Ed.), 2016. Terra Amata Nice Alpes-Maritimes, France Tome V: Comportement et mode de vie des chasseurs acheuléens de Terra Amata. CNRS Éditions, Paris.

DELAGNES, A., Lenoble, A., Harmand, S., Brugal, J. P., Prat, S., Tiercelin, J. J., Roche, H., 2006. Interpreting pachyderm single carcass sites in the African Lower and Early Middle Pleistocene record: A multidisciplinary approach to the site of Nadung'a 4 (Kenya). Journal of Anthropological Archaeology 25, 448–465.

DOMÍNGUEZ-RODRIGO, M., Pickering, T. R., Semaw, S., Rogers, M. J. 2005. Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. Journal of Human Evolution 48, 109–121.

DUVAL, M., Parés, J. M., Made, J. van der, Sahnouni, M., 2019. The earliest evidence of archaic human occupation in North Africa: chronological framework of Ain Boucherit site, Algeria. 20th

Congress of the International Union for Quaternary Research (INQUA), Dublin, p. 4276.

ESPIGARES, M. P., Martínez-Navarro, B., Palmqvist, P., Ros-Montoya, S., Toro, I., Agustí, J., Sala, R., 2013. *Homo* vs. *Pachycrocuta*: earliest evidence of competition for an elephant carcass between scavengers at Fuente Nueva-3 (Orce, Spain). Quaternary International 295, 113–125.

ESPIGARES, M. P., Palmqvist, P., Guerra-Merchán, A., Ros-Montoya, S., García-Aguilar, J. M., Rodríguez-Gómez, G., Serrano, F. J., Martínez-Navarro, B., 2019. The earliest cut marks of Europe: a discussion on archaic human subsistence patterns in the Orce sites (Baza basin, SE Spain). Scientific Reports 9, 1–13.

ESPIGARES, M. P., Martínez-Navarro, B., Ros-Montoya, S., García-Aguilar, J. M., Guerra-Merchán, A., Rodríguez-Gómez, G., Palmqvist, P., this volume. Hominins, mammoths, saber-tooths and giant hyenas in the Early Pleistocene of the Baza Basin (SE Spain).

EVANS, L. A., Adams, W. M., 2018. Elephants as actors in the political ecology of human-elephant conflict. Transactions of the Institute of British Geographers 43, 630–645.

FALGUÈRES, C., Bahain, J. J., Pérez-González, A., Mercier, N., Santonja, M., Dolo, J. M., 2006. The Lower Acheulian site of Ambrona, Soria (Spain): ages derived from a combined ESR/U-series model. Journal of Archaeological Science 33, 149–157.

FLADERER, F. A., Salcher-Jedrasiak, T. A., Händel, M., 2014. Hearth-side bone assemblages within the 27 ka BP Krems-Wachtberg settlement: fired ribs and the mammoth bone-grease hypothesis. Quaternary International 351, 115–133.

GERMONPRÉ, M., Udrescu, M., Fiers, E., 2014. Possible evidence of mammoth hunting at the Neanderthal site of Spy (Belgium). Quaternary International 337, 28–42.

GERMONPRÉ, M., Bocherens, H., Bessudnov, A., Lázničková-Galetová, M., Reynolds, N., Sablin, M., Wißing, C., this volume. Seasonality at Middle and Upper Palaeolithic sites based

on the presence and wear of deciduous premolars from nursing mammoth calves.

GHEERBRANT, E., 2009. Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. Proceedings of the National Academy of Sciences 106, 10717–10721.

HAMILTON, M. J., Milne, B. T., Walker, R. S., Burger, O., Brown, J. H., 2007. The complex structure of hunter-gatherer social networks. Proceedings of the Royal Society of London B: Biological Sciences 274, 2195–2203.

HAMMER, Ø., Harper, D. A. T., 2006. Paleontological data analysis. Blackwell Publishing, Oxford.

HAMMER, Ø., Harper, D. A., Ryan, P. D., 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 9.

HAYNES, G., Klimowicz, J., 2015. Recent elephant-carcass utilization as a basis for interpreting mammoth exploitation. Quaternary International 359, 19–37.

HOFFECKER, J. F., Kuz'mina, I. E., Syromyatnikova, E. V., Anikovich, M. V., Sinitsyn, A. A., Popov, V. V., Holliday, V. T., 2010. Evidence for kill-butchery events of early Upper Paleolithic age at Kostenki, Russia. Journal of Archaeological Science 37, 1073–1089.

HULME, M. F., Sanderson, F. J., Vickery, J. A., 2020. Impacts of wildlife on tropical agro-forestry crops, and the implications for international conservation initiatives. International Journal of Pest Management 66, 89–98.

ICHIKAWA, M., this volume. Elephant hunting by the Mbuti hunter-gatherers in the eastern Congo Basin.

KAHLKE, R. D., 2015. The maximum geographic extension of Late Pleistocene *Mammuthus primigenius* (Proboscidea, Mammalia) and its limiting factors. Quaternary International 379, 147–154.

KITRATPORN, N., Takeuchi, W., 2020. Spatiotemporal distribution of human-elephant conflict in Eastern Thailand: A model-based assessment using news reports and remotely sensed data. Remote Sensing 12, 90.

VAN KOLFSCHOTEN, T., 2000. The Eemian mammal fauna of central Europe. Netherlands Journal of Geosciences 79, 269–281.

KONIDARIS, G. E., Tourloukis, V., this volume. Proboscidea-*Homo* interactions in open-air localities during the Early and Middle Pleistocene of western Eurasia: a palaeontological and archaeological perspective.

KONIDARIS, G. E., Athanassiou, A., Tourloukis, V., Thompson, N., Giusti, D., Panagopoulou, E., Harvati, K., 2018. The skeleton of a straight-tusked elephant (*Palaeoloxodon antiquus*) and other large mammals from the Middle Pleistocene butchering locality Marathousa 1 (Megalopolis Basin, Greece): preliminary results. Quaternary International 497, 65–84.

KUFEL-DIAKOWSKA, B., Wilczyński, J., Wojtal, P., Sobczyk, K., 2016. Mammoth hunting-impact traces on backed implements from a mammoth bone accumulation at Kraków Spadzista (southern Poland). Journal of Archaeological Science 65, 122–133.

LEWIS, J., this volume. BaYaka elephant hunting in Congo: the importance of ritual and technique.

LITT, T., 1990. Stratigraphie und Ökologie des eeminterglazialen Waldelefanten-Schlachtplatzes von Gröbern, Kreis Gräfenhainichen, in: Mania, D., Thomae, M., Litt, T., Weber, T. (Eds.), Neumark-Gröbern: Beiträge zur Jagd des mittelpaläolithischen Menschen. Veröffentlichungen des Landesmuseums für Vorgeschichte, Halle 43, 193–208.

MANZANO, I., Expósito, A., Pérez-González, A., Soto, E., Sesé, C., Yravedra, J., Ruiz-Zapata, B., Millan, A., Beneitez, P., Torres, T., Mondéjar, J. A., Zarco, E., Sanchez, H., Citores, A., Ramos, M., Rodríguez, A., 2011. El yacimiento arqueo-paleontológico de EDAR Culebro I (Estación Depuradora de Aguas Residuales en la Cuenca Baja del Arroyo Culebro. Ministerio de Medio Ambiente. Confederación Hidrográfica del Tajo). Comunidad de Madrid, Dirección General de Patrimonio Histórico, Alcala de Henares, Madrid, pp. 203–214.

MANZI, G., 2016. Humans of the Middle Pleistocene: The controversial calvarium from Ceprano (Italy) and its significance for the origin and variability of *Homo heidelbergensis*. Quaternary International 411, 254–261.

MARINELLI, F., Lemorini, C., Barkai, R., this volume. Lower Palaeolithic small flakes and megafauna: the contribution of experimental approach and use-wear analysis to reveal the link.

MARKS, L., Binka, K., Woronko, B., Majecka, A., Teodorski, A. 2019. Revision of the late Middle Pleistocene stratigraphy and palaeoclimate in Poland. Quaternary International 534, 5–17.

MCHENRY, L. J., Stanistreet, I. G., 2018. Tephrochronology of Bed II, Olduvai Gorge, Tanzania, and placement of the Oldowan–Acheulean transition. Journal of Human Evolution 120, 7–18.

MEIJER, H. J., van den Hoek Ostende, L. W., van den Bergh, G. D., de Vos, J., 2010. The fellowship of the hobbit: the fauna surrounding *Homo floresiensis*. Journal of Biogeography 37, 995–1006.

MELAMED, Y., Kislev, M. E., Geffen, E., Lev-Yadun, S., Goren-Inbar, N., 2016. The plant component of an Acheulian diet at Gesher Benot Ya'aqov, Israel. Proceedings of the National Academy of Sciences 113, 14674–14679.

MONCEL, M. H., Santagata, C., Pereira, A., Nomade, S., Bahain, J. J., Voinchet, P., Piperno, M., 2019. A biface production older than 600 ka ago at Notarchirico (Southern Italy) contribution to understanding early Acheulean cognition and skills in Europe. PLoS ONE 14, e0218591.

MORENO, D., Duval, M., Rubio-Jara, S., Panera, J., Bahain, J. J., Shao, Q., Pérez-González, A., Falguères, C., 2019. ESR dating of Middle Pleistocene archaeo-paleontological sites from the Manzanares and Jarama river valleys (Madrid basin, Spain). Quaternary International 520, 23–38.

MORIN, E., Meier, J., El Guennouni, K., Moigne, A. M., Lebreton, L., Rusch, L, Valensi, P., Conolly, J., Cochard, D., 2019. New evidence of broader diets for archaic *Homo* populations

in the northwestern Mediterranean. Science Advances 5, eaav9106.

Morwood, M. J., Brown, P., Jatmiko, Sutikna, T., Wahyu Saptomo, E., Westaway, K. E., Due, R. A., Roberts, R. G., Maeda, T., Wasisto, S., Djubiantonio, T., 2005. Further evidence for small-bodied archaic humans from the Late Pleistocene of Flores, Indonesia. Nature 437, 1012–1017.

Mosquera, M., Saladié, P., Ollé, A., Cáceres, I., Huguet, R., Villalaín, J. J., Carrancho, A.,Boulés, D., Braucher, R., Vallverdú, J. 2015. Barranc de la Boella (Catalonia, Spain): an Acheulean elephant butchering site from the European late Early Pleistocene. Journal of Quaternary Science 30, 651–666.

Mosquera, M., Ollé, A., Saladie, P., Cáceres, I., Huguet, R., Rosas, A., Villalaín, J., Carrancho, A., Bourles, D., Braucher, R., Pineda, A., Vallverdú, J., 2016. The Early Acheulean technology of Barranc de la Boella (Catalonia, Spain). Quaternary International 393, 95–111.

Movius, H. L., 1950. A wooden spear of third interglacial age from Lower Saxony. Southwestern Journal of Anthropology 6, 139–142.

Mucina, L., 1997. Classification of vegetation: past, present and future. Journal of Vegetation. Science 8, 751–760.

Mussi, M., Villa, P., 2008. Single carcass of *Mammuthus primigenius* with lithic artifacts in the Upper Pleistocene of northern Italy. Journal of Archaeological Science 35, 2606–2613.

Nadachowski, A., Lipecki, G., Wojtal, P., Miękina, B., 2011. Radiocarbon chronology of woolly mammoth (*Mammuthus primigenius*) from Poland. Quaternary International 245, 186–192.

Palombo, M. R., 2009. Biochronology of terrestrial mammals and Quaternary subdivisions: a case study of large mammals from the Italian peninsula. Il Quaternario 22, 291–306.

Palombo, M. R., 2018. Faunal dynamics in SW Europe during the late Early Pleistocene: Palaeobiogeographical insights and biochronological issues. Comptes Rendus Palevol 17, 247–261.

Panera, J., Torres, T., Pérez-González, A., Ortiz, J. E., Rubio-Jara, S., Uribelarrea del Val, D., 2011. Geocronología de la Terraza Compleja de Arganda en el valle del río Jarama (Madrid, España). Estudios Geológicos 67, 495V504.

Panera, J., Rubio-Jara, S., Yravedra, J., Blain, H.A., Sesé, C., Pérez-González, A., 2014. Manzanares valley (Madrid, Spain): a good country for proboscideans and Neanderthals. Quaternary International 326, 329–343.

Panagopoulou, E., Tourloukis, V., Thompson, N., Athanassiou, A., Tsartsidou, G., Konidaris, G., Giusti, D., Karkanas, P., Harvati, K., 2015. Marathousa 1: a new Middle Pleistocene archaeological site from Greece. Antiquity Project Gallery 89, http://antiquity.ac.uk/projgall/panagopoulou343.

Panagopoulou, E., Tourloukis, V., Thompson, N., Konidaris, G., Athanassiou, A., Giusti, D., Tsartsidou, G., Karkanas, P., Harvati, K., 2018. The Lower Palaeolithic site of Marathousa 1, Megalopolis, Greece: overview of the evidence. Quaternary International 497, 33–46.

Pant, G., Dhakal, M., Pradhan, N. M. B., Leverington, F., Hockings, M., 2016. Nature and extent of human-elephant Elephas maximus conflict in central Nepal. Oryx 50, 724–731.

Pante, M. C., Njau, J. K., Hensley-Marschand, B., Keevil, T. L., Martín-Ramos, C., Peters, R F., de la Torre, I., 2018. The carnivorous feeding behavior of early *Homo* at HWK EE, Bed II, Olduvai Gorge, Tanzania. Journal of Human Evolution 120, 215–235.

Pawlowska, K., 2015. Elephantids from Pleistocene Poland: state of knowledge. Quaternary International 379, 89–105.

Pawlowska, K., 2017. Large mammals affected by archaic humans: Paleogeography of butchering for the European Early and Middle Pleistocene. Quaternary International 438, 104–115.

Pawlowska, K., Greenfield, H., Czubla, P., 2014. 'Steppe' mammoth (*Mammuthus trogontherii*) remains in their geological and cultural context from Bełchatów (Poland): A consideration

of human exploitation in the Middle Pleistocene. Quaternary International 326, 448–468.

PEREIRA, A., Nomade, S., Voinchet, P., Bahain, J. J., Falguères, C., Garon, H., Lefèvre, D., Raynal, J. P., Scao, V., Piperno, M., 2015. The earliest securely dated archaic human fossil in Italy and evidence of Acheulian occupation during glacial MIS 16 at Notarchirico (Venosa, Basilicata, Italy). Journal of Quaternary Science 30, 639–650.

PEREIRA, A., Nomade, S., Falguères, C., Bahain, J. J., Tombret, O., Garcia, T., Voinchet, P., Bulgarelli, G. M., Anzidei, A. P., 2017. 40Ar/39Ar and ESR/U-series data for the La Polledrara di Cecanibbio archaeological site (Lazio, Italy). Journal of Archaeological Science: Reports 15, 20–29.

PIPERNO, M. (Ed.), 1999. Notarchirico. Un sito del Pleistocene medio iniziale nel bacino di Venosa. Edizioni Osanna, Venosa.

PIPERNO, M., Tagliacozzo, A., 2001. The elephant butchery area at the Middle Pleistocene site of Notarchirico (Venosa, Basilicata, Italy), in: Cavarretta, G., Gioia, P., Mussi, M., Palombo, M. R. (Eds.), The World of Elephants - 1st International Congress. Consiglio Nazionale delle Ricerche, Rome, pp. 230–236.

PINEDA, A., Saladié, P. 2019. The Middle Pleistocene site of Torralba (Soria, Spain): a taphonomic view of the Marquis of Cerralbo and Howell faunal collections. Archaeological and Anthropological Sciences 11, 2539–2556.

PINEDA, A., Cáceres, I., Saladié, P., Huguet, R., Morales, J. I., Rosas, A., Vallverdú, J., 2019. Tumbling effects on bone surface modifications (BSM): An experimental application on archaeological deposits from the Barranc de la Boella site (Tarragona, Spain). Journal of Archaeological Science 102, 35–47.

POTTS, R., 1989. Olorgesailie: new excavations and findings in Early and Middle Pleistocene contexts, southern Kenya rift valley. Journal of Human Evolution 18, 477–484.

POTTS, R., Behrensmeyer, A. K., Ditchfield, P., 1999. Paleolandscape variation and Early Pleistocene hominid activities: members 1 and 7, Olorgesailie Formation, Kenya. Journal of Human Evolution 37, 747–788.

POSTIGO-MIJARRA, J. M., Gómez-Manzaneque, F., Morla, C., 2017. Woody macroremains from the Acheulian site of Torralba: Occurrence and palaeoecology of Pinus cf. sylvestris in the Middle Pleistocene of the Iberian Peninsula. Comptes Rendus Palevol 16, 225–234.

RABINOVICH, R., Biton, R., 2011. The Early–Middle Pleistocene faunal assemblages of Gesher Benot Ya'aqov: Inter-site variability. Journal of Human Evolution 60, 357–374.

RABINOVICH, R., Ackermann, O., Aladjem, E., Barkai, R., Biton, R., Milevski, I., Solodenko, N., Marder, O., 2012. Elephants at the Middle Pleistocene Acheulian open-air site of Revadim Quarry, Israel. Quaternary International 276, 183–197.

RESHEF, H., Barkai, R., 2015. A taste of an elephant: The probable role of elephant meat in Paleolithic diet preferences. Quaternary International 379, 28–34.

RODRÍGUEZ-GÓMEZ, G., Palmqvist, P., Rodríguez, J., Mateos, A., Martín-González, J. A., Espigares, M. P., Ros-Montoya, S., Martínez-Navarro, B., 2016. On the ecological context of the earliest human settlements in Europe: Resource availability and competition intensity in the carnivore guild of Barranco León-D and Fuente Nueva-3 (Orce, Baza Basin, SE Spain). Quaternary Science Reviews 143, 69–83.

ROKSANDIC, M., Radović, P., Lindal, J., 2018. Revising the hypodigm of *Homo heidelbergensis*: A view from the Eastern Mediterranean. Quaternary International 466, 66–81.

ROKSANDIC, M., Radović, P., Wu, X, Bae, C., 2019. *Homo heidelbergensis*: What do we need to set the question of the validity of this taxon to rest. American Journal of Physical Anthropology 168, 207–207.

ROSELL, J., Blasco, R., this volume. Elephants and humans in Iberia: a zooarchaeological approach.

ROSELL, J., Blasco, R., Peris, J. F., Carbonell, E., Barkai, R., Gopher, A., 2015. Recycling bo-

nes in the Middle Pleistocene: some reflections from Gran Dolina TD10-1 (Spain), Bolomor Cave (Spain) and Qesem cave (Israel). Quaternary International 361, 297–312.

SAHNOUNI, M., Rosell, J., Made, J. van der, Vergès, J. M., Ollé, A., Kandi, N., Harichane, Z., Derradji, A., Medig, M., 2013. The first evidence of cut marks and usewear traces from the Plio-Pleistocene locality of El-Kherba (Ain Hanech), Algeria: implications for early archaic human subsistence activities circa 1.8 Ma. Journal of Human Evolution 64, 137–150.

SAHNOUNI, M., Parés, J. M., Duval, M., Cáceres, I., Harichane, Z., Made, J. van der, Pérez-González, A., Abdessadok, S., Kandi, N., Derradji, A., Medig, M., Boulaghraif, K., Semaw, S., 2018. 1.9-million-and 2.4-million-year-old artifacts and stone tool-cutmarked bones from Ain Boucherit, Algeria. Science 362, 1297–1301.

SAITOU, N., Nei, M., 1987. The neighbour-joining method: a new method for reconstructing phylogenetic trees. Molecular Biology and Evolution 4, 406–425.

SÁNCHEZ-ROMERO, L., Benito-Calvo, A., Pérez-González, A., Santonja, M., 2016. Assessment of accumulation processes at the Middle Pleistocene site of Ambrona (Soria, Spain). Density and orientation patterns in spatial datasets derived from excavations conducted from the 1960s to the present. PLoS ONE 11, e0167595.

SANTONJA, M., Pérez-González, A., Villa, P., Soto, E., Sesé, C., 2001. Elephants in the archaeological sites of Aridos (Jarama valley, Madrid, Spain), in: Cavarretta, G., Gioia, P., Mussi, M., Palombo, M. R. (Eds.), The World of Elephants - 1st International Congress. Consiglio Nazionale delle Ricerche, Rome, pp. 602–606.

SANTONJA, M., Pérez-González, A., Mora, R., Parcerisas, J., Sesé, C., 2005. New data from Ambrona: closing the hunting versus scavenging debate. Quaternary International 126, 223–250.

SANTONJA, M., Pérez-González, A., Panera, J., Rubio-Jara, S., Méndez-Quintas, E., 2016. The coexistence of Acheulean and Ancient Middle Palaeolithic techno-complexes in the Middle Pleistocene of the Iberian Peninsula. Quaternary International 411, 367–377.

SANTONJA, M., Rubio-Jara, S., Panera, J., Sánchez-Romero, L., Tarriño, A., Pérez-González, A., 2018. Ambrona revisited: the Acheulean lithic industry in the lower stratigraphic complex. Quaternary International 480, 95–117.

SAÑUDO, P., Blasco, R., Peris, J. F., 2016. Site formation dynamics and human occupations at Bolomor Cave (Valencia, Spain): An archaeostratigraphic analysis of levels I to XII (100–200 ka). Quaternary International 417, 94–104.

SANTUCCI, E., Marano, F., Cerilli, E., Fiore, I., Lemorini, C., Palombo, M. R., Anzidei, A. P., Bulgarelli, G. M., 2016. *Palaeoloxodon* exploitation at the Middle Pleistocene site of La Polledrara di Cecanibbio (Rome, Italy). Quaternary International 406, 169–182.

SCOTT, B., Bates, M., Bates, R., Conneller, C., Pope, M., Shaw, A., Smith, G., 2014. A new view from la Cotte de St Brelade, Jersey. Antiquity 88, 13–29.

SEMAL, P., Rougier, H., Crevecoeur, I., Jungels, C., Flas, D., Hauzeur, A., Maureille, B., Germonpré, M., Bocherens, H., Pirso, S., Cammaert, L., De Clerck, N., Hambucken, A., Higham, T., Toussaint, M., van der Plicht, J., 2009. New data on the late Neandertals: direct dating of the Belgian Spy fossils. American Journal of Physical Anthropology 138, 421–428.

SEMAW, S., 2000. The world's oldest stone artefacts from Gona, Ethiopia: Their implications for understanding stone technology and patterns of human evolution between 2.6-1.5 million years ago. Journal of Archaeological Science 27, 1197–1214.

SEMAW, S., Renne, P., Harris, J. W., Feibel, C. S., Bernor, R. L., Fesseha, N., Mowbray, K., 1997. 2.5-million-year-old stone tools from Gona, Ethiopia. Nature 385, 333.

SHIPMAN, P., Rose, J., 1983. Evidence of butchery and hominid activities at Torralba and Ambrona; an evaluation using microscopic techniques. Journal of Archaeological Science 10, 465–474.

SILVA BARROSO, P. G., López Recio, M., Cuartero Monteagudo, F., Baena Preysler, J., Tapias, F., 2012. Contexto geomorfológico y principales rasgos tecnológicos de nuevos yacimientos del Pleistoceno Medio y Superior en el Valle Inferior del Manzanares (Madrid, España). Estudios Geológicos 68, 57–89.

SMITH, G. M., 2012. Middle Palaeolithic subsistence: the role of archaic humans at Lynford, Norfolk, UK. Quaternary International 252, 68–81.

SMITH, G. M., 2015. Neanderthal megafaunal exploitation in Western Europe and its dietary implications: a contextual reassessment of La Cotte de St Brelade (Jersey). Journal of Human Evolution 78, 181–201.

SOLODENKO, N., Zupancich, A., Cesaro, S. N., Marder, O., Lemorini, C., Barkai, R., 2015. Fat residue and use-wear found on Acheulian biface and scraper associated with butchered elephant remains at the site of Revadim, Israel. PLoS ONE 10, e0118572.

STRINGER, C., 2012. The status of *Homo heidelbergensis* (Schoetensack 1908). Evolutionary Anthropology: Issues, News, and Reviews 21, 101–107.

SVOBODA, J., Péan, S. Wojtal, P., 2005. Mammoth bone deposits and subsistence practices during Mid-Upper Palaeolithic in Central Europe: three cases from Moravia and Poland. Quaternary International 126, 209–221.

TOURLOUKIS, V., Thompson, N., Panagopoulou, E., Giusti, D., Konidaris, G. E., Karkanas, P., Harvati, K., 2018. Lithic artifacts and bone tools from the Lower Palaeolithic site Marathousa 1, Megalopolis, Greece: Preliminary results. Quaternary International 497, 47–64.

VALENSI, P., de Lumley, H., Beden, M., Jourdan, L., Serre, F., 2011. Les faunes de grands mammifères des formations du Pléistocène moyen du site acheuléen de Terra Amata, in: de Lumley, H. (Ed.), Terra Amata, Nice, Alpes-Maritimes, France, Tome II. CNRS Éditions, Paris, pp. 41–290.

VENDITTI, F., Cristiani, E., Nunziante-Cesaro, S., Agam, A., Lemorini, C., Barkai, R., 2019. Animal residues found on tiny Lower Paleolithic tools reveal their use in butchery. Scientific Reports 9, 1–14.

VALLVERDÚ, J., Saladié, P., Rosas, A., Huguet, R., Cáceres, I., Mosquera, M., Garcia-Tabernero, A., Estalrrich, A., Lozano-Fernández, I., Pineda-Alcalá, A., Carrancho, A., Villalaín, J. J., Bourlès, D., Braucher, R., Lebatard, A., Vilalta, J., Esteban-Nadal, M., Lluc Bennàsar, M., Bastir, M., López-Polín, L., Ollé, A., Vergés, J. M., Ros-Montoya, S., Martínez-Navarro, B., García, A., Martinell, J., Expósito, I., Burjachs, F., Jordi Agustí, J., Carbonell, E., 2014. Age and date for early arrival of the Acheulian in Europe (Barranc de la Boella, la Canonja, Spain). PLoS ONE 9, e103634.

VILLA, P., 1990. Torralba and Aridos: elephant exploitation in Middle Pleistocene Spain. Journal of Human Evolution 19, 299–309.

VILLA, P., 1996. Torralba et Aridos: Chasse, charognage et dépeçage d'éléphants au Pléistocène moyen en Espagne. Publications du CERP, 61–71.

WEBER, T., 2000. The Eemian Elephas antiquus finds with artefacts from Lehringen and Gröbern: are they really killing sites? Anthropologie et Préhistoire 111, 177–185.

WENBAN-SMITH, F., (Ed.), 2013. The Ebbsfleet elephant. Excavations at Southfleet Road, Swanscombe in advance of High Speed 1, 2003-4. Oxford Archaeology, Oxford.

WISSING, C., Rougier, H., Crevecoeur, I., Germonpré, M., Naito, Y. I., Semal, P., Bocherens, H., 2016. Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe. Quaternary International 411, 327–345.

WISSING, C., Rougier, H., Baumann, C., Comeyne, A., Crevecoeur, I., Drucker, D. G., Gaudzinski-Windheuser, S., Germonpré, M., Gómez-Olivencia, A., Krause, J., Matthies, T., Naito, Y. I., Posth, C., Semal, P., Street, M., Bocherens, H., 2019. Stable isotopes reveal patterns of diet and mobility in the last Neandertals and first modern humans in Europe. Scientific Reports 9, 4433.

WILCZYŃSKI, J., Wojtal, P., 2011. Jaksice II - a new Gravettian site in southern Poland. Přehled výzkumů 52, 37–41.

WILCZYŃSKI, J., Wojtal, P., Sobczyk, K., 2012. Spatial organization of the Gravettian mammoth hunters' site at Kraków Spadzista (southern Poland). Journal of Archaeological Science 39, 3627–3642.

WIŚNIEWSKI, A., Adamiec, G., Badura, J., Bluszcz, A., Kowalska, A., Kufel-Diakowska, B., Mikołajczyk, A., Murczkiewicz, M., Musil, R., Przybylski, B., Skrzypek, G., Stefaniak, K., Zych, J., 2013. Occupation dynamics north of the Carpathians and Sudetes during the Weichselian (MIS5d-3): The Lower Silesia (SW Poland) case study. Quaternary International 294, 20–40.

WILCZYŃSKI, J., Wojtal, P., Łanczont, M., Mroczek, P., Sobieraj, D., Fedorowicz, S., 2015. Loess, flints and bones: Multidisciplinary research at Jaksice II Gravettian site (southern Poland). Quaternary International 359, 114–130.

WILCZYŃSKI, J., Wojtal, P., Oliva, M., Sobczyk, K., Haynes, G., Klimowicz, J., Lengyel, G., 2019. Mammoth hunting strategies during the Late Gravettian in Central Europe as determined from case studies of Milovice I (Czech Republic) and Kraków Spadzista (Poland). Quaternary Science Reviews 223, 105919.

WOJTAL, P., 2001. The woolly mammoth (*Mammuthus primigenius*) remains from the Upper Palaeolithic site Kraków Spadzista Street (B), in: Cavarretta, G., Gioia, P., Mussi, M., Palombo, M. R. (Eds.), The World of Elephants - 1st International Congress. Consiglio Nazionale delle Ricerche, Rome, pp. 367–372.

WOJTAL, P., Wilczyński, J., 2015. Hunters of the giants: Woolly mammoth hunting during the Gravettian in Central Europe. Quaternary International 379, 71–81.

XU, Z., Wei, Z., Jin, M., 2020. Causes of domestic livestock–wild herbivore conflicts in the alpine ecosystem of the Chang Tang Plateau. Environmental Development, 100495.

YASUOKA, H., this volume. Sharing elephant meat and the ontology of hunting among the Baka hunter-gatherers in the Congo Basin rainforest.

YRAVEDRA, J., Domínguez-Rodrigo, M., Santonja, M., Pérez-González, A., Panera, J., Rubio-Jara, S., Baquedano, E., 2010. Cut marks on the Middle Pleistocene elephant carcass of Áridos 2 (Madrid, Spain). Journal of Archaeological Science 37, 2469–2476.

YRAVEDRA, J., Panera, J., Rubio-Jara, S., Manzano, I., Expósito, A., Pérez-González, A., Soto, E., López-Recio, M., 2014. Neanderthal and *Mammuthus* interactions at EDAR Culebro 1 (Madrid, Spain). Journal of Archaeological Science 42, 500–508.

YRAVEDRA, J., Rubio-Jara, S., Panera, J., Martos, J. A., 2019a. Hominins and proboscideans in the Lower and Middle Palaeolithic in the Central Iberian Peninsula. Quaternary International 520, 140–156.

YRAVEDRA, J., Rubio-Jara, S., Panera, J., Made, J. van der, Pérez-González, A., 2019b. Neanderthals diet in open air sites in the central of iberian Peninsula at the end of middle Pleistocene/begining of the late Pleistocene: PRERESA site in the Manzanares valley (Madrid, Spain). Quaternary International 520, 72–83.

ZHOU, W. X., Sornette, D., Hill, R. A., Dunbar, R. I., 2005. Discrete hierarchical organization of social group sizes. Proceedings of the Royal Society of London B: Biological Sciences 272, 439–444.

	GEOGRAPHICAL LOCATION		LOCALITY	LATITUDE N	LONGITUDE W
1	Africa	Republic of Djibouti	Barogali	11.09141389	42.0976
2		Kenya	Olorgesailie basin member 1, Site 15	-1.58	36.45
3			Nadung'a 4	4.251111111	35.83361111
4	SW Asia (Levant)	Israel	Gesher Benot Ya'akov	33.008	35.629
5			Revadim Quarry	31.784	34.818
6	NW Europe	United Kingdom	Southfleet Road unit 3	51.440	0.323
7			La Cotte de St Brelade	49.1756167	-2.1881444
8			Lynford	52.520	0.687
9	W Europe	Germany	Lehringen	52.87	9.38
10			Gröbern	51.68	12.44
11		Belgium	Spy	50.478	4.674
12		Austria	Krems-Wachtberg	48.415	15.604
13			Krems-Hundssteig	47.413	15.587
14	S Europe	Spain	Fuente Nueva 3, layer c.III.1	37.71	-2.40
15			Barranc de la Boella, level 2 at Pit 1	41.13	1.16
16			Ambrona, AS3	41.16	-2.498
17			Tafesa	40.35	-3.68
18			Áridos 2	40.29	-3.51
19			Áridos 1	40.29	-3.51
20			Torralba	41.16	-2.498
21			Bolomor Cave level XII	39.0722	-0.2658
22			Arriaga II	40.30	-3.56
23			EDAR Culebro 1	40.30	-3.60
24			PRERESA	40.30	-3.59
25		France	Terra Amata C1	43.698	7.289
26		Italy	Notarchirico, A1 level	40.967937	15.826531
27			La Polledrara di Cecanibbio	41.935	12.302
28			Castel di Guido	41.89	12.28
29			Poggetti Vecchi	42.819140	11.072058
30			Asolo	45.4757	11.5454
31		Greece	Marathousa 1	37.41	22.08
32	E Europe	Poland	Bełchatów	51.3	19.3
33			Oporów in Wroclaw Site A1	51.10	17.02
34			Kraków Spadzista Street (B)	50.053	19.924
35			Jaksice II	50.1436111	20.5038333
36		Russia	Kostenki 1	51.66	39.16
37			Kostenki 12	51.66	39.16
38			Kostenki 14	51.66	39.16
39			Kostenki 15	51.66	39.16

	Absolute Chronology	Marine Isotopic Stage	Elephant species
1	1.6–1.3 Ma (ESR)	between MIS 54 and MIS 39	*Palaeoloxodon recki*
2	0.992±0.039 – 0.974±0.01 Ma	MIS 28/MIS 27	*Palaeoloxodon recki*
3	~0.780 Ma	MIS 19	*Palaeoloxodon recki*
4	~0.780 Ma	MIS 19	*Palaeoloxodon antiquus*
5	younger than 780 ka and older than 500-300 ka	between MIS 19 and MIS 9	*Palaeoloxodon antiquus*
6	400 ka (AAR MIS 11)	MIS 11	*Palaeoloxodon antiquus*
7	238–240 ka; 238±35 ka	MIS 7	*Mammuthus primigenius*
8	67±5 ka; 64±5 ka (OSL); 53.7±3.1 ka; >49.7 ka (AMS ^{14}C)	MIS 4 to MIS 3 transition	*Mammuthus primigenius*
9	~125 ka	MIS 5e	*Palaeoloxodon antiquus*
10	120 ka	MIS 5e	*Palaeoloxodon antiquus*
11	from ~42.75 ka to 25.67 ka (1)	MIS 3-MIS 2	*Mammuthus primigenius*
12	~28.3–26.8 ka (^{14}C)	MIS 2	*Mammuthus primigenius*
13	28 ka	MIS 2	*Mammuthus primigenius*
14	1.19±0.21 Ma (upper archaeological level); cosmogenic nuclide burial age 1.50±0.31 Ma	?	*Mammuthus meridionalis*
15	between 0.96 Ma and 0.78 Ma	between MIS 27 and MIS 19	*Mammuthus meridionalis*
16	~470–430 ka (2)	MIS 12	*Palaeoloxodon antiquus*
17	---	MIS 12-MIS 11	*Palaeoloxodon antiquus*
18	---	late MIS 11	*Palaeoloxodon antiquus*
19	---	MIS 11, ?MIS 9	*Palaeoloxodon antiquus*
20	200 ka	MIS 7	*Palaeoloxodon antiquus*
21	152±23 ka (AAR-TL)	MIS 6	*Palaeoloxodon antiquus*
22	>133 ka, 134±50 ka (TL)	MIS 6	*Palaeoloxodon antiquus*
23	105±10 ka, 133±28 ka (AAR); 121±7 ka (OSL)	(?MIS 6) MIS 5	*Mammuthus sp.*
24	---	early MIS 6 to MIS 5	*Palaeoloxodon vel Mammuthus*
25	C1a level: 380±80 ka (ESR)	MIS 11	*Palaeoloxodon antiquus*
26	from 663±3 ka to 660±3 ka (^{40}Ar/^{39}Ar)	MIS 16	*Palaeoloxodon antiquus*
27	325±2 ka (^{40}Ar/^{39}Ar)	MIS 9	*Palaeoloxodon antiquus*
28	327–260 ka (U/Th-ESR)	MIS 9	*Palaeoloxodon antiquus*
29	171±3 ka (U-series); 170±13 ka (ESR/U-series)	MIS 6	*Palaeoloxodon antiquus*
30	(3)	MIS 4 or MIS 3	*Mammuthus primigenius*
31	500-450 ka (ESR); 450-400 ka (post-IR ISRL)	MIS 12	*Palaeoloxodon antiquus*
32	bout	MIS 11	*Mammuthus trogontherii*
33	66–41 ka (TL-ESR)	MIS 4	*Mammuthus primigenius*
34	between 24.0±0.3 ka and 19.45±0.12 ka (AMS-conventional ^{14}C)	MIS 2	*Mammuthus primigenius*
35	between 40.6±5.7 ka and 30.4±4.6 Ka (TL); between 24.14±0.18 ka and 21.19±0.14 ka (AMS ^{14}C)	MIS 2	*Mammuthus primigenius*
36	between 38.08±5.46 ka and 20.9±1.6 ka (AMS-conventional ^{14}C); between 30.67±2.75 and 30.58±2.74 ka (OSL)	MIS 3 or MIS 2	*Mammuthus primigenius*
37	between 36.28±0.36 and 28.5±0.14 ka (AMS-conventional ^{14}C); between 52.44±3.85 ka and 19.89±1.73 ka (OSL)	MIS 3 or MIS 2	*Mammuthus primigenius*
38	between 37.24±0.43 ka and 26.7±0.19 ka (AMS-conventional ^{14}C); between 47.78±3.48 ka and 26.34±1.92 ka (OSL)	MIS 3 or MIS 2	*Mammuthus primigenius*
39	~30 ka (^{14}C)	MIS 3/ MIS 2 boundary	*Mammuthus primigenius*

	SPATIAL DISTRIBUTION OF ELEPHANT BONES	HOMO SPECIES IDENTIFIED ON SKELETAL REMAINS	HOMO SPECIES INFERRED ACCORDING ARTIFACTS AND AGE	SELECTED REFERENCES
1	a skeleton partially disarticulated	*H. erectus* vel *H. ergaster*		1
2	a skeleton partially disarticulated	*H. erectus* (?)		2, 3
3	a skeleton partially preserved, bones mainly dispersed		*H. erectus* (?)	4
4	skull with tusks		*H. erectus*	5, 6
5	bones mainly dispersed, some element conjoined		*H. erectus* (?)	7, 8, 9
6	partial skeleton of an adult with bones mainly dispersed bones		*H. heidelbergensis* (?)	10
7	bones mainly dispersed	*H. neandethalensis*		11
8	bones mainly dispersed		*H. neandethalensis*	12
9	bones mainly dispersed		*H. neandethalensis* (?)	13, 14
10	partially articulated		*H. neandethalensis* (?)	14
11	bones mainly dispersed	*H. neandethalensis /* AMH-*H. sapiens*		15
12	bones partially dispersed, some each other articulated		*H. sapiens*	16
13	bones partially dispersed, some each other articulated		*H. sapiens*	17
14	a skeleton partially disarticulated		*H. heidelbergensis* (?)	18, 19, 20, 21
15	disarticulated axial elements of an adult individual		*H. heidelbergensis* (?)	22, 23
16	partial skeleton of a fully adult/ old male		*H. heidelbergensis*	24, 25, 26, 27
17	bones mainly dispersed		*H. heidelbergensis*	28
18	a skeleton partially disarticulated		*H. heidelbergensis*	29, 30, 31
19	a skeleton partially disarticulated		*H. heidelbergensis*	28, 29, 31, 32, 33
20	complete skeletal remains		*H. heidelbergensis / H. neandethalensis*	26, 29, 32, 34, 35, 36
21	partially represented		*H. neandethalensis* (?)	35, 37, 38, 39
22	bones mainly dispersed		*H. neandethalensis* (?)	28, 35, 40, 41
23	bones mainly dispersed		*H. neandethalensis*	28, 35, 41, 42, 43
24	bones mainly dispersed		*H. neandethalensis*	28, 35, 41, 42, 44
25	bones mainly dispersed		*H. heidelbergensis*	45, 46, 47, 48, 49, 50
26	skull with both tusks still in situ		*H. heidelbergensis*	51, 52, 53
27	bones mainly dispersed	*H. heidelbergensis*		54, 55, 56, 57
28	bones mainly dispersed	*H. heidelbergensis*		58
29	bones mainly dispersed		*H. neandethalensis*	59, 60, 61
30	bones mainly dispersed		*H. neandethalensis*	62
31	a skeleton partially disarticulated		*H. heidelbergensis* (?)	63, 64, 65, 66
32	bones mainly dispersed		*H. heidelbergensis* (?)	67, 68, 69
33	bones mainly dispersed		*H. neandethalensis* (?)	70, 71
34	bones mainly dispersed		*H. sapiens*	71, 72, 73, 74, 75, 76, 77, 78
35	bones mainly dispersed		*H. neandethalensis /* AMH-*H. sapiens*	79, 80, 81, 82
36	bones mainly dispersed		AMH-*H. sapiens*	83
37	bones mainly dispersed		AMH-*H. sapiens*	83
38	bones mainly dispersed		AMH-*H. sapiens*	83
39	bones mainly dispersed		AMH-*H. sapiens*	83

Appendix 4.1: List of elephant butchery sites selected for this study, including some geographical, chronological, palaeontological and palaeoanthropological information, and selected references.

(1) Lower level 42.75 +0.80 -0.65 ka; Intermediate level 29.04 + 0.18 -0.16 ka / 34.58 +0.33 -0.29 ka / 36.92 +0.40 -0.35 ka; Upper level 25.67 +0.13 -0.12 ka (AMS ^{14}C).

(2) An age contemporary of MIS 9 or the end of MIS 11 has been suggested by Falguères et al. (2006), based on combined ESR/U-series dates.

(3) The radiocarbon date of 27.8 ka obtained for the mammoth remains has to be rejected because the bones were consolidated using fish glue.

ESR, Electron Spin Resonance; AAR, Amino Acid Racemisation; OSL, Optically-Stimulated Luminescence; TL, Thermoluminescence; AMS, Accelerator Mass Spectrometry; post-IR, post-infrared Infrared Stimulated Luminescence.

References: 1, Berthelet, 2002; 2, Potts, 1989; 3, Potts et al., 1999; 4, Delagnes et al., 2006; 5, Rabinovich and Biton, 2011; 6, Melamed et al., 2016; 7, Rabinovich et al., 2012; 8, Agam and Barkai, 2016; 9, Solodenko et al., 2015; 10, Wenban-Smith (Ed.), 2013, 11; Smith, 2015; 12, Smith, 2012; 13, Movius, 1950; 14, Weber, 2000; 15, Germonpré et al., 2014; 16, Fladerer et al., 2014; 17, Bosch, 2012; 18, Duval et al., 2012; 19, Espigares et al, 2019; 20, Blain et al., 2016; 21, Duval et al., 2019; 22, Mosquera et al., 2015; 23, Pineda et al., 2019; 24, Shipman and Rose, 1983; 25, Falguères et al., 2006; 26, Santonja et al., 2016; 27, Sánchez-Romero et al., 2016; 28, Yravedra et al., 2019a, 29; Villa, 1990; 30, Santonja et al., 2001; 31, Yravedra et al., 2010; 32, Villa, 1996; 33, Santonja et al., 2005; 34, Shipman and Rose 1983; 35, Santonja et al., 2016; 36, Postigo-Mijarra et al., 2017; 37, Blasco and Fernández Peris, 2012; 38, Blasco et al., 2013; 39, Rosell et al., 2015; 40, Silva-Barroso et al., 2012; 41, Panera et al., 2014; 42, Moreno et al., 2019; 43, Yravedra et al., 2014; 44, Yravedra et al., 2019b; 45, Valensi, 2001, 46–50; de Lumley (Ed.), 2009, 2011, 2013, 2015, 2016; 51, Piperno, 1999; 52, Piperno and Tagliacozzo 2001; 53, Pereira et al., 2015; 54, Anzidei et al., 2012; 55, Santucci et al., 2016; 56, Pereira et al., 2017; 57, Cerilli and Fiore, 2018; 58, Boschian et al., 2019; 59, Capalbo et al., 2018; 60–61, Aranguren et al., 2018, 2019; 62, Mussi and Villa, 2008; 63, Konidaris et al. 2018; 64, Tourloukis et al., 2018; 65–66, Panagopoulou et al., 2015, 2018; 67, Pawlowska et al., 2014; 68, Pawlowska, 2017; 69, Marks et al., 2019; 70, Burdukiewicz and Wiśniewski, 2004; 71, Wiśniewski et al., 2013; 72, Wojtal, 2001; 73, Svoboda et al., 2005; 74, Nadachowski et al., 2011; 75, Bosch, 2012; 76, Wilczyński et al., 2012; 77, Pawlowska, 2015; 78, Kufel-Diakowska et al., 2016; 79, Wilczyński et al., 2019; 80, Wilczyński and Wojtal, 2011; 81, Wilczyński et al., 2015; 82, Wojtal and Wilczyński, 2015; 83, Hoffecker et al., 2010.