

### 3. PROBOSCIDEA-HOMO INTERACTIONS IN OPEN-AIR LOCALITIES DURING THE EARLY AND MIDDLE PLEISTOCENE OF WESTERN EURASIA: A PALAEOANTHROPOLOGICAL AND ARCHAEOLOGICAL PERSPECTIVE

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#### ABSTRACT

In recent years, a significant number of Pleistocene localities with evidence of proboscidean exploitation by humans has been discovered, substantially enriching our knowledge on *Homo* subsistence strategies and megafauna acquisition. In this study, we provide a synthesis of the evidence for Proboscidea-*Homo* interactions in Early and Middle Pleistocene open-air sites of western Eurasia with direct (e.g., presence of cut marks, proboscidean bone artifacts, fractures for marrow extraction) and indirect (e.g., association and refitting of lithic artifacts, use-wear analysis) evidence of exploitation. Sex and ontogenetic age of butchered proboscideans are recorded, in order to assess possible human preferences. Furthermore, we investigate the role of large carnivores focusing on important renewals in the carnivore guilds, and their significance in terms of carrion availability for scavenging and human-carnivore competition for access to food resources. By applying an ecomorphological/be-

havioral approach, we examine the large carnivore community structure and dynamics, with emphasis in the hunting strategies of large predators. Additionally, we aim to infer their possible role in the changes of early human subsistence strategies focusing on proboscidean acquisition, and to explore the role of humans within the predatory guild. The ecological adaptations of the two common Middle Pleistocene proboscideans in Europe, the European straight-tusked elephant *Palaeoloxodon antiquus* and the steppe mammoth *Mammuthus trogontherii*, are also evaluated. Finally, we discuss various aspects of the *Homo* bio-cultural evolution during the period under study, including developments in material culture and relevant inferences about human social behavior.

#### 3.1 INTRODUCTION

The last decades, a significant number of sites with evidence of anthropogenic exploitation of



proboscideans has been discovered in western Eurasia, dating to the Early and Middle Pleistocene, considerably increasing our knowledge on *Homo* subsistence strategies. Proboscideans, the largest terrestrial animals during the Pleistocene, were widely distributed on all continents (apart from Antarctica and Australia). Although they constituted an ideal food package and therefore an attractive target for early humans (Ben-Dor et al., 2011; Reshef and Barkai, 2015; Agam and Barkai, 2016), their enormous size would have demanded the employment of special obtainment/exploitation methods and coordinated effort by a group of people, as well as investment of energy and time (Lupo and Schmitt, 2016). Assessing the human agency in proboscidean-bearing faunal assemblages is not always straightforward. First, the stratigraphic association of proboscidean and cultural remains does not in itself necessarily imply anthropogenic processing of carcasses and the verification of their functional relation requires taphonomic analysis (e.g., Giusti et al., 2018; Giusti, this volume). Second, hominin exploitation of carcasses can be difficult to demonstrate, because bone modifications can result from other (non-human) agents, human-induced cut marks are only rarely preserved, and possible subsequent weathering or other natural processes may delete direct evidence on bone surfaces (e.g., Haynes and Klimowicz, 2015). Despite these impediments, the Proboscidea-*Homo* interactions are relatively well recorded in the Pleistocene of western Eurasia. The objective of this study is to evaluate the Proboscidea-*Homo* record in open-air continental localities during the Early and Middle Pleistocene of western Eurasia, and to assess emerging patterns between ecological, ethological, environmental and cultural parameters.

### 3.2 METHODS

We included in our study 35 open-air sites from western Eurasia, dated from the Early until the Middle/Late Pleistocene boundary, and ranging

from ~1.3 Ma to ~120 ka (Eemian Interglacial), thus covering the Lower and the early Middle Palaeolithic periods. We selected proboscidean single- and multi-carcass localities, as well as key localities where proboscideans constitute an important faunal element of the large mammal assemblage, in which human presence is indicated by the occurrence of human fossils, lithic/wooden artifacts and/or anthropogenic bone modifications. Their geographic position and chronology are shown in Figures 3.1 and 3.2, and Appendix 3.1. For each locality the parameters that we recorded are: Marine Isotope Stage (MIS; glacial/interglacial); proboscidean taxon; direct evidence of processing (cut marks, breakage for brain/marrow extraction, proboscidean bone tools, weapons associated with proboscidean skeleton); cut-marked/fractured skeletal element and purpose of modification; indirect evidence (presence of lithic/wooden artifacts, refitting of lithics, use-wear analysis, human fossils); lithic technology; bone artifacts; gender and ontogenetic age of the proboscidean individual; presence of large carnivores; occurrence of carnivore gnawing and coprolites; and associated large mammals (Appendix 3.1). In examining the sites, we do not directly compare data on mortality patterns, body part representation, site taphonomy and lithic or bone assemblages, because of discrepancies and/or information shortage in the published datasets.

Several studies analyzing the ecomorphology and guild structure of carnivores have been conducted, mainly as a tool to infer palaeoenvironmental conditions (Morlo et al., 2010 and references therein), but also to investigate carnivore communities during the Plio-Pleistocene and/or correlate them with early human settlements in Europe (e.g., Turner, 1992; Croitor and Brugal, 2010; Palombo, 2016; Rodríguez-Gómez et al., 2017). Here, we introduce a modified version of the three-dimensional ecomorphological approach of Morlo et al. (2010) in order to: 1) examine the community structure and dynamics (with emphasis on hunting strategy) of the large predatory guild of Europe during the Early and



**Figure 3.1:** Map showing the location of the studied open-air Early–Middle Pleistocene sites of western Eurasia with Proboscidea-Homo interactions (made with Natural Earth, [naturalearthdata.com](http://naturalearthdata.com)).

Middle Pleistocene, 2) infer the possible role of large carnivores in the changes of early human subsistence strategies (passive/active scavenging and hunting), with emphasis on megafauna acquisition and in particular proboscideans, and 3) assess the position and role of humans within the predatory guild. We combine four ecomorphological/behavioral parameters of carnivores (body mass, diet type, hunting strategy, sociality), which are presented by three-dimensional guild structure diagrams (Fig. 3.3b). We used only large carnivores, >20 kg (Carbone et al., 2007), that practice hunting and/or scavenging on large prey, with only exception the large-sized mustelid *Gulo gulo* (wolverine), which although its average body mass is <20 kg (but >10 kg), it preys on mammals much

larger than its size (MacDonald, 2009). We excluded small-sized mustelids, felids (*Felis*) and canids (*Vulpes*), with a weight <10 kg, because their meat consumption relies mainly on small vertebrates and the processing time for each of their prey is short. We ruled out as well the cave bears *Ursus deningeri* and *U. spelaeus*, because they were predominantly herbivorous, with occasional but no systematic scavenging/hunting behavior (Bocherens et al., 2011; van Heteren, 2011). However, we included the omnivores Asian black bear (*U. thibetanus*) and brown bear (*U. arctos*), because their diet includes ungulates, and both species are reported to exhibit hunting and more commonly scavenging behavior (MacDonald, 2009; Saladié et al., 2013; Pappa et al., 2019 and references

therein). We separated carnivores into two chrono-faunas: 1.8–1.0 Ma (within Early Pleistocene) and 500–300 ka (within Middle Pleistocene); the former includes the carnivores that were present during the first human colonization of Europe, and the latter involves a time when human presence is well recorded in various localities almost throughout the continent. The estimated body mass (BM) of carnivores is taken from Meloro et al. (2007), Palmqvist et al. (2011), Hemmer et al. (2011), Van Valkenburgh et al. (2016) and Rodríguez-Gómez et al. (2017). Three BM classes were defined, keeping the large-sized classes of Morlo et al. (2010): 1. 10–30 kg, 2. 30–100 kg, and 3. >100 kg. Diet was classified into four categories based on Van Valkenburgh (1988) and Morlo et al. (2010): 1. hypocarnivorous (includes the omnivores, <50% meat with non-vertebrate material predominating), 2. carnivorous (50–70% meat supplemented with non-vertebrate material), 3. hypercarnivorous (>70% meat), and 4. bone/meat (>70% meat with the addition of bones). Diet data were modified from Palombo (2016). Four foraging behavior groups (carcass acquisition strategy) have been distinguished following Werdelin (1996): 1. pursuit carnivore, 2. “stalk-and-ambush”, 3. “ambush-and-slash”, and 4. scavenger. Hunting strategy data were modified from Palombo (2016). Sociality is distinguished into: 1. social (group/pack-hunting), and 2. solitary, acknowledging, however, the flexibility of fission/fusion sociality. Sociality data were acquired from Treves and Palmqvist (2007) and Palombo (2016). The dataset is given in Table 3.1.

### 3.3 THE RECORD OF PROBOSCIDEA-HOMO INTERACTIONS

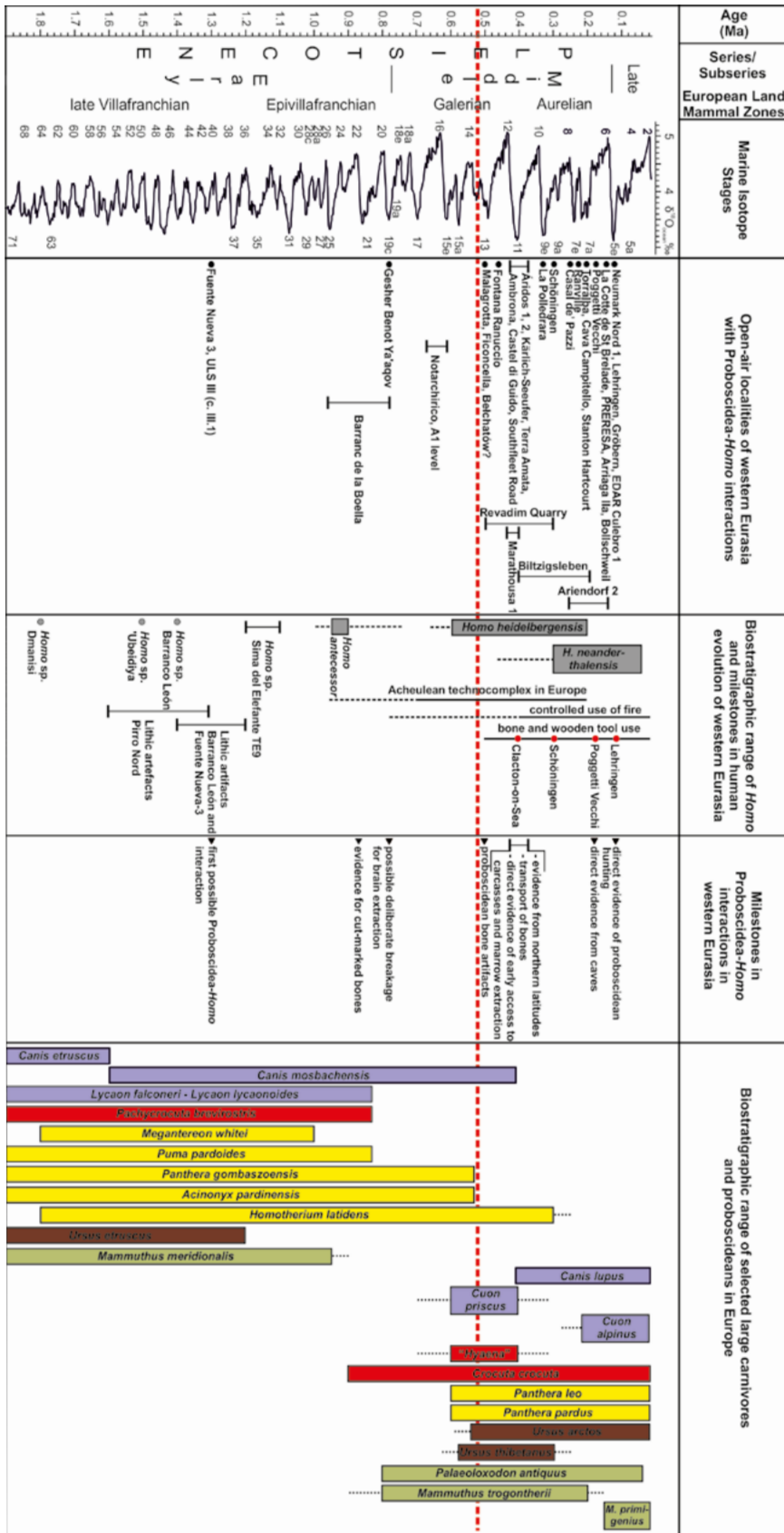
In this section we briefly present some key localities, where more systematic studies on Proboscidea-*Homo* interactions have been conducted, but the reader is referred to Appendix 3.1 and the references cited therein for more detailed accounts, as well as for the whole set of sites considered in this study.

#### 3.3.1. LATE EARLY PLEISTOCENE (~1.8–0.78 MA)

The oldest-known Proboscidea-*Homo* event in Europe is attested at the Upper Archaeological Level of Fuente Nueva-3 (Spain), with an estimated age of ~1.3 Ma ( $1.19 \pm 0.21$  based on U-series/ESR dating;  $1.50 \pm 0.31$  Ma from cosmogenic nuclides; Espigares et al., 2013; this volume and references therein). The discovery of a partial skeleton of the southern mammoth *Mammuthus meridionalis*, in association with lithic artifacts of “Mode 1” character and coprolites of the hyena *Pachycrocuta brevirostris* was interpreted as possible competition for scavenging between *Homo* and *Pachycrocuta* (Espigares et al., 2013; this volume). At Barranc de la Boella (Spain; 960–781 ka), the remains of a *M. meridionalis* skeleton, including two cut-marked ribs, were found together with lithic artifacts and were interpreted as representing a butchering event (Vallverdú et al., 2014; Mosquera et al., 2015).

#### 3.3.2. MIDDLE PLEISTOCENE (0.78–0.12 MA)

In Geshar Benot Ya’aqov (Israel; 780 ka, MIS 19) a cranium of *Palaeoloxodon antiquus* (or perhaps *P. recki*) was discovered in association with Acheulean lithic artifacts; a basalt core, a boulder and an oak log that were found below the cranium, were possibly used to invert it. The upside-down position of the cranium, the missing basicranial and palatal regions, and the damage below the nasal opening, were attributed to possible deliberate brain extraction and trunk removal (Goren-Inbar et al., 1994). A similar case may also be represented in Notarchirico (Italy; 670–610 ka, MIS 16). In this locality, a cranium of *P. antiquus* was lying in an overturned position, lacking the masticatory apparatus and the occipital, and the mandible was found some meters away, indicating possible anthropogenic utilization of the brain, the tongue and the trunk (Piperno and Tagliacozzo, 2001). The lithic assemblage includes bifaces, however,



**Figure 3.2:** Chronology of the studied localities, biostratigraphic range of *Homo*, carnivores and proboscideans, and milestones in human evolution and Proboscidea-*Homo* interactions in western Eurasia.

the association between lithic artifacts and bones is not clearly demonstrated (Moncel et al., 2019).

In Ficoncella (Italy; ~500 ka, MIS 13), the discovery of a *P. antiquus* partial skeleton bearing carnivore gnawing and a small-tool lithic assemblage (with refits), indicates human occupation and *in situ* knapping events, as well as carnivore access to the carcass (Aureli et al., 2015). In Marathousa-1 (Greece; 500–400 ka, probably close to MIS 12/11 transition; Panagopoulou et al., 2018 and references therein), a partial skeleton of *P. antiquus*, and isolated elephant and other vertebrate remains were found in spatial and stratigraphic association with a small-tool lithic assemblage and bone artifacts (Konidararis et al., 2018; Tourloukis et al., 2018). Cut marks on the tibia and astragalus of the elephant skeleton, as well as on isolated elephant ribs (accompanied with peeling) and on other mammal bones, indicate butchering activities (Konidararis et al., 2018). A bone percussor, most likely made from an elephant limb bone, is also documented at this site (Tourloukis et al., 2018).

In Áridos 2 (Spain; ~380 ka, MIS 11), there is a strong human exploitation signal on the elephant bones: here, remains of a *P. antiquus* were associated with lithic tools, and the presence of cut marks on the scapula and on one rib suggest butchering activities. Their location on the bones indicates defleshing and evisceration, the latter pointing to early access to the carcass by humans before carnivores accessed it, leaving tooth marks and furrowing on the bones (Yravedra et al., 2010). In Ambrona (Spain; >350 ka, MIS 11), large mammals, most notably *P. antiquus*, were identified in several stratigraphic units. Of particular interest is the AS3 unit, where several elephant specimens were discovered, including a partial elephant skeleton. Human modifications were not detected on the skeleton; however, a cut mark was identified on another cranium, and two femoral shafts show anthropogenic fractures (Villa et al., 2005). The taphonomic analysis indicated that Ambrona represents a combination of natural accumulations and activities of humans, who regularly visited the site for exploiting elephants and other mam-

mals (Villa et al., 2005). In Southfleet Road (England; ~425–375 Ma, MIS 11), a *P. antiquus* partial skeleton was found without direct evidence of anthropogenic activity. However, the tight spatial association between lithic artifacts and elephant bones, as well as the lithic refits and edge damage on some lithics, which probably resulted from on-site production and subsequent use as butchery tools, altogether indicate butchering activities (Wenban-Smith, 2013). In Castel di Guido (Italy; ~412 ka, MIS 11), abundant remains of *P. antiquus* and other mammals (notably the auroch *Bos primigenius*) were associated with Acheulean lithic artifacts; human bones were also discovered at the site. The locality represents a complex palimpsest formed by natural processes, human activities and minor carnivore involvement (Boschian and Saccà, 2010; Saccà, 2012). In addition to the exploitation of elephants for meat and marrow, elephant bones served as raw material for shaping tools, including bifaces. In the levels of Terra Amata (France; MIS 11), several *P. antiquus* remains were discovered in association with lithic artifacts; in addition to red deer hunting and carcass transport, young elephant remains were also transported to the site (Valensi et al., 2011).

In La Polledrara di Cecanibbio (Italy; ~325 ka, MIS 9), a great amount of *P. antiquus* remains were discovered, accompanied by a diverse mammal fauna rich in *Bos primigenius*; additionally, a deciduous premolar is attributed to *Homo heidelbergensis* (Anzidei et al., 2012). Of great interest are the remains of an elephant, which was possibly trapped in muddy sediments and exploited by humans (Santucci et al., 2016). A rich lithic industry was produced at the site (refitting, knapping debris) and the use-wear analysis indicates butchering activities. Human modifications on elephant bones include intentional fractures and removals, as well as production of bone tools (Anzidei et al., 2012; Santucci et al., 2016). In Revadim Quarry (Israel; ~500?–300? ka) several specimens of *P. antiquus* were found together with other faunal remains and a rich lithic assemblage. Among the elephant bones, one scapula and two ribs bear cut

marks indicative of filleting, and others have been shaped to tools (Rabinovich et al., 2012). The interpretation of butchering activities at Revadim is further supported by use-wear and fat residue analyses (Solodenko et al., 2015).

In Poggetti Vecchi (Italy; MIS 7/6), wooden (digging sticks), bone (including elephant ones) and lithic artifacts were found in association with vertebrate remains; several *P. antiquus* individuals possibly died due to a natural cause and were subsequently exploited by humans (Aranguren et al., 2019). The Layers 3 and 6.1 of La Cotte de St Brelade (England; MIS 6) preserve evidence for megafauna exploitation (wooly mammoths and rhinos). Some mammoth bones show cut marks, while there exist also indications for brain extraction (rib driven into the cranium) (Smith, 2015). In PRE-RESA (Spain; MIS 6), bones of an elephantid individual show, in addition to cut marks, green fractures and percussion damage indicative for marrow extraction (Yravedra et al., 2012, 2019). The earliest so far known evidence for the use of wooden weapons in proboscidean hunting dates close to the Middle/Late Pleistocene boundary and is attested at Lehringen (Germany; ~120 ka, MIS 5e), where a wooden lance was discovered within a *P. antiquus* skeleton, associated also with lithic artifacts (Weber, 2000).

### 3.4 DISCUSSION

#### 3.4.1. CARNIVORE GUILDS AND HOMININS

Shortly after the first “out of Africa” human dispersal, documented at Dmanisi (Georgia, ~1.8 Ma), and contemporaneous with the first appearance of humans in Europe (~1.3 Ma), the first association of a proboscidean skeleton with lithic artifacts in western Eurasia is documented at Fuente Nueva-3 (~1.3 Ma), where a possible competition between humans and *Pachycrocuta brevirostris* for scavenging a mammoth skeleton was suggested (Espigares et al., 2013). With a powerfully built body, mass nearly twice that of the spotted hyena *Crocuta crocuta*

and unique craniodental features, the giant hyena *P. brevirostris* was well adapted for dismembering carcasses and consuming bones, and was the most direct competitor of *Homo* for scavenging large mammal carcasses during the Early Pleistocene (Martínez-Navarro, 2010; Palmqvist et al., 2011). *Pachycrocuta* and *Homo* were highly dependent on flesh-eating predators, such as the saber-toothed cats *Megantereon whitei* and *Homotherium latidens*, which were well adapted to hunt, but possibly ate mainly the soft parts of their prey (especially of large carcasses like proboscideans), leaving behind food resources (leftovers) that could be afterwards scavenged (Turner, 1992; Martínez-Navarro, 2010; Palmqvist et al., 2011; see also Blumenschine, 1987 for large herbivores and for proboscideans in particular). In particular, *Homotherium* groups were able to hunt (having cursorial adaptations), disarticulate, transport and deflesh very large prey (~5,700 kg) compared to their own size, including juveniles, adult female and young adult male proboscideans (Rawn-Schatzinger, 1992; Marean and Ehrhardt, 1995; Hemmer, 2001; Palmqvist et al., 2003, 2011; Van Valkenburgh et al., 2016; Barnett et al., 2020). But the large carnivore guild of the European Early Pleistocene was much more diversified, and apart from *Pachycrocuta*, *Megantereon* and *Homotherium*, included wolves (*Canis etruscus*<sup>1</sup>-*C. mosbachensis*), wild dogs (*Lycaon falconeri*-*L. lycaonoides*), bears (*Ursus etruscus*), lynxes (*Lynx issiodorensis*), jaguars (*Panthera gombaszogensis*), giant cheetahs (*Acinonyx pardinensis*) and puma-like cats (*Puma pardoides*)<sup>2</sup>, each of them equipped with great hunting, killing or scavenging

1 In Dmanisi the recently described *Canis borjgali*.

2 The sympatry of these 10 large carnivores is recorded at Untermaßfeld (Germany; *Ursus* cf. *dolinensis* instead of *U. etruscus*) and these are present collectively in the various sedimentary units of Pirro Nord (Italy). Other localities rich in large carnivores (≥7 species) include Dmanisi (Georgia), Apollonia-1 (Greece), Venta Micena, Cueva Victoria, Vallparadís Estació (all Spain), Ceyssageut and Vallonnet (both France); Cueva Victoria, Vallparadís Estació and Vallonnet with *U. deningeri* instead of *U. etruscus*. All sites include *Pachycrocuta* and saber-toothed felids, and yielded also *Mammuthus meridionalis*; Pirro Nord includes lithic artifacts; Dmanisi both lithic artifacts and human remains.

capabilities, and dental specializations related to their diet preferences; some of them were also characterized by social foraging behavior (Fig. 3.3b, Table 3.1). Therefore, as a member of the predatory guild<sup>3</sup>, encompassing 10 large carnivores, early *Homo* (estimated BM: 40–65 kg, stature: 145–155 cm; based on Dmanisi specimens; Gallagher, 2013) would have been positioned below the median of body mass of the carnivores (Fig. 3.3a), much smaller or nearly equal to 5 felids and *Pachycrocuta*, and only larger than the lynx and the canids; the latter, however, are pack-hunters (allowing them to kill prey much larger than their own size and larger than what a single individual would succeed) and, like the other large carnivores, also faster-running than *Homo*. This means that early humans had to confront and compete constantly, if they were to regularly exploit animal resources. Although the carnivores of that period occurred at low densities in Southern Europe, based on the low number of prey species (moderate herbivore biomass; Rodríguez and Mateos, 2018), we can assume that prime and undefended carcasses would have been rather rare (in particular the small- to medium-sized ones; Blumenschine, 1987), considering also the high diversity of large carnivorous/hypercarnivorous/bone-cracking predators, particularly with *Pachycrocuta* (the most important agent of bone accumulations during the Early Pleistocene of Eurasia; Martínez-Navarro, 2010) being present at the kill sites soon after the event, as it happens with recent hyenas (Domínguez-Rodrigo, 2001; Van Valkenburgh, 2001). This would result in relatively high competition for carcass acquisition, both among carnivores, and between carnivores and humans. Therefore, although early *Homo* could have taken advantage of naturally died proboscideans before

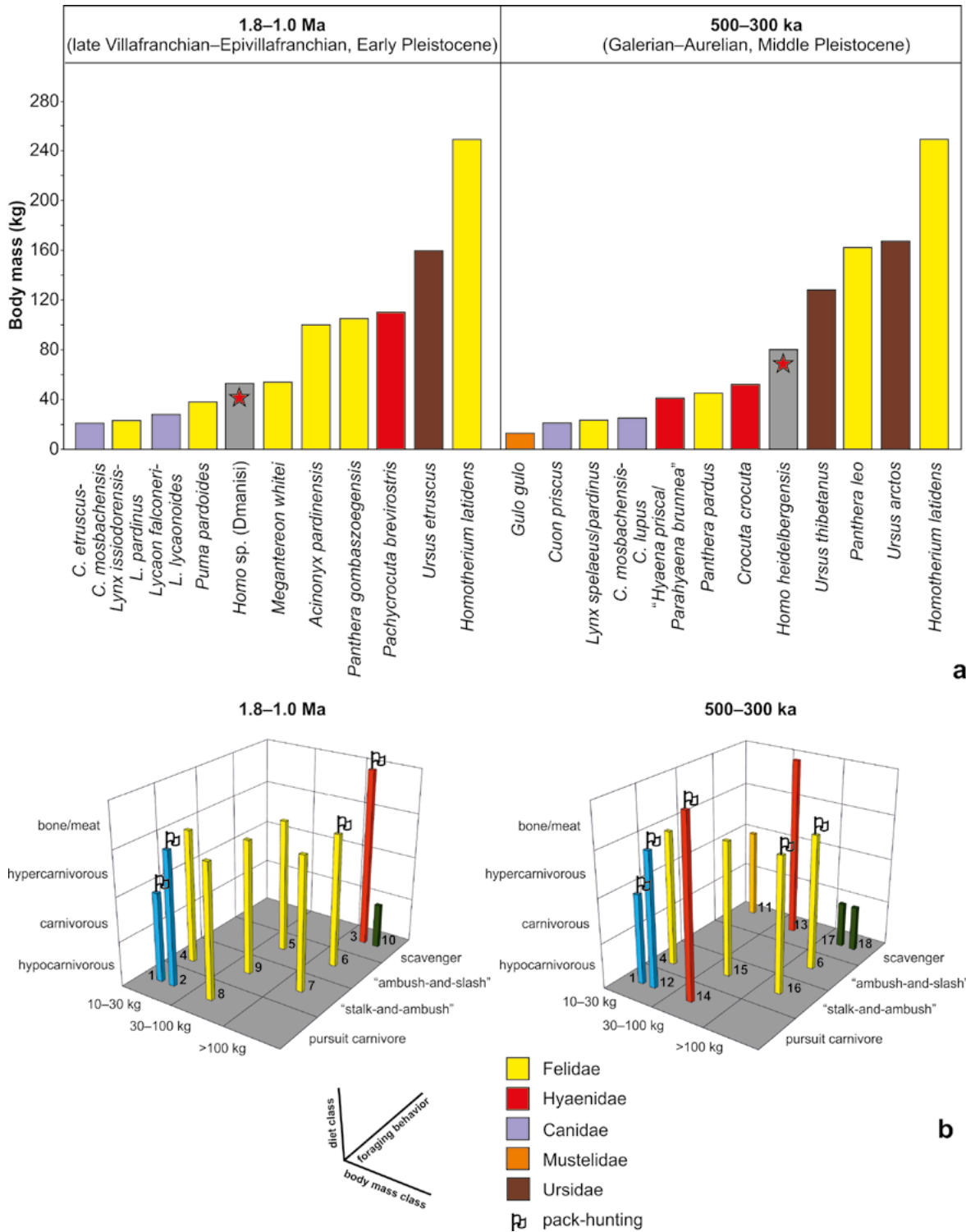
carnivores discovering them, and in lack of strong evidence for elaborate hunting weaponry or techniques, we can assume, in particular for megafauna carcasses, that: a) access of early *Homo* to carcasses would have been possible mainly through passive scavenging of an already consumed and abandoned carnivore kill, and perhaps more possibly through active (confrontational/kleptoparasitic) scavenging (Blumenschine, 1987; Espigares et al., 2013; Madurell-Malapeira et al., 2017), and b) food acquisition and exploitation, carcass- and self-defense especially in the shadow of the fierce scavenger *P. brevirostris* would have been impossible without a certain degree of cooperation, social intelligence, and use of “weapons”, even if these were still relatively simple (see also Agam and Barkai, 2018). Indeed, the scenario of stone-throwing for intimidating other carnivores was proposed for Dmanisi and Fuente Nueva-3, based on the abundant cobbles associated with mammal fossils (Espigares et al., 2013).

From the end of the Early Pleistocene/beginning of Middle Pleistocene and until ~0.6 Ma, an important faunal turnover took place, which involved the disappearance of several Villafranchian/Epivillafranchian taxa and the arrival of new immigrants (Galerian fauna), including also carnivores and proboscideans (Palombo, 2014). In proboscideans, the latest appearance of *Mammuthus meridionalis* is documented at ~900–800 ka, while around that time the steppe mammoth *M. trogontherii* and the European straight-tusked elephant *Palaeoloxodon antiquus* appear in Europe, increasing the number of proboscidean representatives.

In carnivores, the most prominent event is the extinction of *Pachycrocuta* and the arrival of *Crocuta crocuta* (“*Crocuta crocuta* event”). The last appearance of *P. brevirostris* is traced at ~800 ka, while the oldest European records of *C. crocuta* are documented at ~900–800 ka (Palombo, 2014). The extinction of *P. brevirostris* and the survival of *C. crocuta* are possibly attributed to ecological reasons: the super specialist scavenger *P. brevirostris* could not survive in the changing climatic conditions of the Middle Pleistocene, in which the more generalist and social hunting/scavenging *C. crocuta* could

<sup>3</sup> In the European Early Pleistocene, percussion and cut marks, although occasional, thus suggesting a more opportunistic behavior, prove that meat, fat and marrow were integral part of early human diet. Human modifications are recorded on bones from a wide range of animal body sizes, including both slow and fast prey, which indicates a generalist behavior. In the discussion that follows, our premise is that Early Pleistocene *Homo* can be considered as a member of the large predatory guild, to which we also refer as “carnivore guild”.





**Figure 3.3:** a, body mass distribution of large carnivores and *Homo* and, b, 3D guild structure diagrams of large carnivores, for 1.8–1.0 Ma and 500–300 ka in Europe. The numbering and the groups in (b) is according to Table 3.1.1, *Canis etruscus*-*C. mosbachensis*-*C. lupus*; 2, *Lycaon falconeri*-*L. lycaonoides*; 3, *Pachycrocuta brevirostris*; 4, *Lynx issiodorensis*-*L. pardinus*; 5, *Megantereon whitei*; 6, *Homotherium latidens*; 7, *Panthera gombaszoegensis*; 8, *Acinonyx pardinensis*; 9, *Puma pardoides*; 10, *Ursus etruscus*; 11, *Gulo gulo*; 12, *Cuon priscus*; 13, "*Hyaena prisca/Parahyaena brunnea*"; 14, *Crocota crocuta*; 15, *Panthera pardus*; 16, *Panthera leo*; 17, *Ursus thibetanus*; 18, *Ursus arctos*.

	FAMILY	SPECIES	BODY MASS (KG)	DIET CLASS	HUNTING BEHAVIOR	SOCIALITY
1.8–1.0 Ma (late Villafranchian–Epivillafranchian, Early Pleistocene)						
1.	Canidae	<i>Canis etruscus</i> - <i>C. mosbachensis</i>	10–30	carnivorous	pursuit carnivore	pack
2.	Canidae	<i>Lycaon falconeri</i> - <i>L. lycaonoides</i>	10–30	hypercarnivorous	pursuit carnivore	pack
3.	Hyaenidae	<i>Pachycrocuta brevirostris</i>	>100	bone/meat	scavenger	pack
4.	Felidae	<i>Lynx issiodorensis</i> - <i>L. pardinus</i>	10–30	hypercarnivorous	stalk-and-ambush	solitary
5.	Felidae	<i>Megantereon whitei</i>	30–100	hypercarnivorous	ambush-and-slash	solitary
6.	Felidae	<i>Homotherium latidens</i>	>100	hypercarnivorous	ambush-and-slash	pack
7.	Felidae	<i>Panthera gombaszoegensis</i>	>100	hypercarnivorous	stalk-and-ambush	solitary
8.	Felidae	<i>Acinonyx pardinensis</i>	30–100	hypercarnivorous	pursuit carnivore	solitary
9.	Felidae	<i>Puma pardoides</i>	30–100	hypercarnivorous	stalk-and-ambush	solitary
10.	Ursidae	<i>Ursus etruscus</i>	>100	hypocarnivorous	scavenger	solitary
500–300 ka (Galerian–Aurelian, Middle Pleistocene)						
11.	Mustelidae	<i>Gulo gulo</i>	10–30	carnivorous	scavenger	solitary
1.	Canidae	<i>C. mosbachensis</i> - <i>C. lupus</i>	10–30	carnivorous	pursuit carnivore	pack
12.	Canidae	<i>Cuon priscus</i>	10–30	hypercarnivorous	pursuit carnivore	pack
13.	Hyaenidae	" <i>Hyaena prisca</i> / <i>Parahyaena brunnea</i> "	30–100	bone/meat	scavenger	solitary
14.	Hyaenidae	<i>Crocuta crocuta</i>	30–100	bone/meat	pursuit carnivore	pack
4.	Felidae	<i>Lynx pardinus</i>	10–30	hypercarnivorous	stalk-and-ambush	solitary
6.	Felidae	<i>Homotherium latidens</i>	>100	hypercarnivorous	ambush-and-slash	pack
15.	Felidae	<i>Panthera pardus</i>	30–100	hypercarnivorous	stalk-and-ambush	solitary
16.	Felidae	<i>Panthera leo</i>	>100	hypercarnivorous	stalk-and-ambush	pack
17.	Ursidae	<i>Ursus thibetanus</i>	>100	hypocarnivorous	scavenger	solitary
18.	Ursidae	<i>Ursus arctos</i>	>100	hypocarnivorous	scavenger	solitary

**Table 3.1:** Large carnivores with their ecomorphological/behavioral parameters included in the guild structure analysis (see Figure 3.3b). Data were acquired from references cited in "3.2 Methods".

adapt (Martínez-Navarro, 2010). The extinction of *Pachycrocuta* might be additionally correlated with the disappearance of *Megantereon*, which resulted in a decrease of carrion available for scavengers. At ~600–500 ka *Panthera gombaszoegensis* and *Acinonyx pardinensis* also disappear, while the modern pantherine cats, *Panthera leo* and *Panthera pardus* occur in Europe (Fig. 3.2). The two latter species exploited carcasses more intensively than *Megantereon*, which possibly resulted in the decrease of the carrion that would be left available for both hye-

nas and hominins (Palmqvist et al., 2011). On the other hand, the disappearance of *Pachycrocuta* possibly offered the opportunity for larger amounts of available carrion, and for easier and early access to carcasses by hominins, who would have been most possibly outcompeted during the Early Pleistocene by the fierce giant hyena.

When we compare the Early and the Middle Pleistocene carnivore guilds (Fig. 3.3a, b, Table 3.1), we see that: 1) their structure and dynamics are different, and 2) the carnivore diversity

slightly increased to 11 species during the Middle Pleistocene. It should be noted, however, that in contrast to the Early Pleistocene, the sympatry of all (or most of) these predators is not recorded so far anywhere during the Middle Pleistocene; on the contrary, the number of both predator species<sup>4</sup> and predator specimens in the archaeo-palaeontological sites is rather low (see also Martínez-Navarro, 2018); this is the case also for the proboscidean localities examined here, for which the predator assemblage is poor in most of them (Appendix 3.1).

In canids, the only difference involves the “replacement” of *Lycan lycaonoides* by the slightly smaller *Cuon priscus* (still within the same BM group), but with the same diet type and hunting strategy. The number of the hypocarnivorous ursids increased with the “more omnivorous” *Ursus arctos* and the “more herbivorous” *U. thibetanus* (van Heteren, 2011; Pappa et al., 2019). There are two main changes in the Middle Pleistocene carnivore guild, compared to that of the Early Pleistocene (Fig. 3.3b): 1) the decline of taxa with a hypercarnivorous diet (the bulk of carrion providers) and an ambush hunting strategy, and 2) the increase in the number of taxa with a bone/meat diet, as well as in the representation of pack-hunting and scavenging behavior. With the disappearance of the solitary species *Megantereon whitei*, *Acinonyx pardinensis*, *Puma pardoides* (all from the middle-sized group 30–100 kg) and *Panthera gombaszoegensis*, the number of felids significantly decreased (overall from six to four), along with the demise of “ambush-and-slash” hunters. Most importantly, all these carnivores were hypercarnivorous and carcass providers (hunters), having primary access to and control of carcasses; consequently, their disappearance resulted in a decrease of available carrion for scavengers. For hominins, this change would have a dual effect: on one hand,

there were less hypercarnivorous predators to compete with, and, on the other hand, less available carrion; the latter would have resulted in fewer scavenging opportunities and thereby could have offered an ecological incentive towards more regular hunting. In contrast, the number of the bone/meat eating (bone-cracking) hyenas increased to two (however, both of them were smaller than *Pachycrocuta*); as this was accompanied with the inclusion of the wolverine *Gulo gulo* and the increase of the mostly scavenging ursids (although their diet relied only little on meat), the scavenging behavior is altogether reinforced. The so far rare “*Hyaena priscal Parahyaena brunnea*” (or *Pliocrocuta perrieri*; the taxonomy of this taxon is debated; see Palombo, 2014) takes over the scavenging niche previously occupied by *Pachycrocuta*. *Crocuta crocuta* employs cooperative strategies, and considering also the inclusion of *Panthera leo* (as well as of *Homo*; see below), cooperative foraging is in general reinforced during the Middle Pleistocene (see also Croitor and Brugal, 2010).

Notwithstanding the complexities surrounding the Middle Pleistocene hominin phylogeny and nomenclature (e.g., Roksandic et al., 2018), for the sake of our discussion we use *H. heidelbergensis* (*sensu lato*) as the (more or less) “representative” taxon of early-middle Middle Pleistocene hominins. When comparing body mass values in the two carnivore guilds (Fig. 3.3a), the increased BM and stature of *Homo heidelbergensis* (estimated BM of males: 70–90 kg, stature of males: 170–180 cm; Gallagher, 2013) places humans at a higher rank than that in the Early Pleistocene: besides the hypocarnivorous ursids, only *Panthera leo* and *Homotherium latidens* lie above *Homo* (Fig. 3.3a). The potential for successful confrontational scavenging, early access to and defense of carcasses against predators, would have been much higher than in the Early Pleistocene, considering also some shifts in hominin technology and subsistence strategies (including regular hunting from ~400–300 ka onwards) and an inferred increase in human social cooperation (see below). Therefore, within the carnivore guild, an overall more privileged position

4 Among the richest localities of this period in terms of large predators are Lunel-Viel (France) with 7 species, Taubach (Germany) with 6 species, and Arago III and Orgnac 3 (both France) with 5 species, all with human presence, and Taubach and Arago III additionally with *Palaeloxodon* and *Mammuthus* remains, respectively.

can be assumed for hominins in the Middle as opposed to the Early Pleistocene.

Large predators (skeletal remains, carnivore bone modifications or carnivore coprolites, the latter in most cases attributable to hyenas) are present in 29 of the herein studied sites (83%), and 12 out of those (41%) preserve also carnivore modifications on proboscidean bones (34% of all the 35 sites). Moreover, 7 out of these 12 sites (58%) preserve also direct evidence (or possible direct evidence) of human exploitation (Appendix 3.1), indicating a certain degree of carnivore-human competition for early access to proboscidean carcasses, and highlighting the important interference and crucial role of carnivores in the human-proboscidean interactions. At least in two cases, humans acquired early access: at Áridos 2, where cut marks on the ventral side of a rib was attributed to evisceration (which takes place at the early stages of carcass consumption; see e.g., Blumenschine; 1986 and Potts, 1988), and at Marathousa 1, where cut and scrape marks on the ventral side of a rib are accompanied by classical peeling (fresh breakage). The vertebral column and the rib cage seem to be the proboscidean skeletal locations, which are mostly gnawed by carnivores (Appendix 3.1). Carnivore marks in the thorax region in particular are related to its opening for the consumption of intestines and inner organs, which happens at the initial feeding stages of recent and extinct lions and spotted hyenas (Haynes, 2005; Diedrich, 2014).

Recent lions (*Panthera leo*), and presumably also *Homotherium*, prey on proboscideans, but preferentially on young individuals (MacDonald, 2009; Power and Compion, 2009; van Valkenburgh et al., 2016). Considering the much larger size of *Palaeoloxodon antiquus* and *Mammuthus trogontherii* compared to recent *Loxodonta africana*, *Homotherium* would selectively target young individuals in the Middle Pleistocene. However, during this period, the Proboscidea-*Homo* record is dominated by adult proboscidean individuals (see below); it can be safely assumed that felids would have managed to kill such large adult prey only occasionally and with great difficulties, with

the exception perhaps of weakened individuals. It follows that humans would not regularly acquire access to proboscidean carcasses from felid kills. Rather, they would likely take advantage of individuals already dead or caught in natural traps, in which case they would exercise either passive or active scavenging, according to the degree of carnivore interference. Alternatively, humans acquired carcasses by hunting, employing tactics such as ambush hunting, hunting with traps or confrontational encounters. However, we should note that humans take a high risk when approaching and try killing an elephant, which renders proboscidean hunting a challenging and dangerous procedure (Lewis, this volume).

In this light, we suggest the following, as a working hypothesis. In the Early Pleistocene predatory guild (Fig. 3.3b), humans would occupy the ecological space that was “available” for a predator with a 30–100 kg BM and a (mostly?) scavenging behavior, perhaps with a carnivorous or hypocarnivorous diet according to ecological circumstances and geographic setting. In the Middle Pleistocene guild, humans would occupy the niche that was previously held by the saber-toothed cat *Megantereon* (see also Werdelin and Lewis, 2013 and Egeland, 2014 for African examples) in the group of predators with 30–100 kg BM. Similar to *Megantereon*, humans could have a carnivorous to hypercarnivorous diet, but unlike the large solitary felid, the biological, technological, cultural and social developments would have allowed humans to employ not only the “ambush-and-slash” hunting strategy, for instance modified into a cooperative “ambush-and-spear” strategy (in accordance with the evidence for use of hunting spears during this period), but also a number of other hunting tactics, including for example prey stalking or prey impediment by driving animals into natural or anthropogenic traps. *The seizing of a niche previously occupied by a large felid such as Megantereon and the incorporation of such hunting behavior made humans fairly independent of erratic food sources from scavenging carnivore kills and allowed the provisioning of animal resources on a more regular basis.*

### 3.4.2. PROBOSCIDEAN EXPLOITATION AND HOMININ BEHAVIOR

Rather than regular hunting of proboscideans, a more opportunistic subsistence behavior of Early Pleistocene European *Homo* is suggested also by recent studies, based on estimates of carrying capacity, resource availability, the competition intensity within the carnivore guild and the network analysis of food webs (Rodríguez-Gómez et al., 2016; Lozano et al., 2016; Rodríguez and Mateos, 2018; see also Palombo and Cerilli, this volume; Rosell and Blasco, this volume). Human presence together with *Mammuthus meridionalis* is documented at a number of localities during this period, such as Dmanisi, Pirro Nord, Barranco León and Sima del Elefante (Spain). The latter sites lack so far evidence of proboscidean processing and it is not clear whether this is a real lack of human exploitation, absence of cut marks due to the thickness of periosteal connective tissue and cartilage of the bones, or a result of low archaeological resolution (e.g., due to taphonomy and preservation). Thus, on the basis of the evidence at hand, during the Early Pleistocene, the acquisition of megafauna in general, and of proboscideans in particular, appears to have been mainly occasional and sporadic. Aside from issues of differential preservation and research intensity, which undoubtedly mask our archaeological visibility, we identify two main reasons to explain the low archaeological signal for Proboscidea-*Homo* interactions in the Early Pleistocene: 1) The large carnivore guild remained stable during 1.8–0.8 Ma and all these powerful carnivores (especially *P. brevisrostris*), constituted a prohibiting factor for human access to large carcasses, including proboscideans, until -0.8 Ma, when most of them became extinct (Martínez-Navarro, 2010; Madurell-Malapeira et al., 2017). 2) The social structure of human groups, their technological means and the behavioral solutions that they employed to mitigate the risks from competition with other members of the predatory guild, were not converging towards the inclusion of proboscidean exploitation as a regular and systematic component of their subsistence strategies. Yet,

one could counter-argue that an annual catch rate of “only” one or two proboscideans, such as that observed for the Mbuti hunter-gatherers [Ichikawa (this volume); of the African forest elephant *Loxodonta cyclotis*, which is much smaller than *Palaeoloxodon*; see also Lewis (this volume) and Yasuoka (this volume) for similar catch rates among the BaYaka and Baka) provides an ethnographic example of a “regular and systematic” foraging of proboscideans, and then the question is whether a comparable rate (in the Early Pleistocene) would still create a signal that is archaeologically detectable today. Factors related to the structure of the carnivore community (e.g., the ratio of flesh-eaters to carcass-destroyers, which largely determines carcass availability; Turner, 1992), habitat traits, and climatic parameters such as seasonality, would have altogether conditioned the scale to which hominins would employ any of the strategies included within their range of capabilities: from opportunistic, non-confrontational scavenging as an effective, low-risk and low-cost means of food gathering, to more active scavenging, hunting, and any combination of tactics within this spectrum of foraging options.

Whatever the means of procurement in the Early Pleistocene, carcasses were processed by use of apparently non-specialized, core-and-flake tool-kits with few retouched blanks and an overall expedient character. Nevertheless, at Barranc de la Boella, an Acheulean-like pick that was probably shaped off-site and transported to the mammoth-butchery locality, points to some degree of tool curation and foresight. Notably, at Fuente Nueva-3, one of the main aims of the debitage was the production of small flakes (flakes >30 mm are rare). The association of proboscidean carcasses with small-sized, simple flakes is observed also in the Middle Pleistocene (see below) and the evidence from Fuente Nueva-3 may be reflecting the roots of a long-lasting trend, which remains largely unexplored and unexplained. Barranc de la Boella (Pit 1 level 2) is so far the oldest locality, where possibly cut-marked proboscidean bones are reported, as well as the oldest locality with possible

human modifications on proboscidean remains outside of Africa.

In the Middle Pleistocene, lithic technology associated with proboscidean carcass processing mainly involved possible heavy-duty (core-)tools, such as choppers, chopping tools and bifacial implements (including handaxes and other Large Cutting Tools), as well as flake-based retouched tools, but also minimally modified blanks (usually flakes) and cores (Appendix 3.1). However, the artifact class most commonly found together with proboscidean remains is simple, unretouched flakes of variable sizes and morphologies, together with flake fragments and debris. Use-wear and residue data show that both large(r) tools, such as bifaces or core-tools, and retouched or unretouched flakes, often of small size (<30 mm), were used in carcass processing activities such as butchering (Barkai et al., 2010; Yravedra et al., 2010; Mosquera et al., 2015; Solodenko et al., 2015; Aureli et al., 2016; Santucci et al., 2016; Lemorini, 2018; Venditti et al., 2019; Marinelli et al., this volume). Nevertheless, the traceological evidence is overall limited and obscured by preservation and excavation biases, hence it is not possible to discern inter-assembly trends in associations between specific artifact types, typological characteristics or techno-functional traits, with distinct activities such as defleshing, evisceration, filleting, skinning or disarticulation. At the moment, it is probably safe to assume that different tool types and artifact size fractions, such as bifaces and small retouched or unretouched flakes, were used in various and possibly (but not necessarily) different tasks. Use-wear data and cut marks support such a case, for instance at Áridos 2 (Yravedra et al., 2010) and Revadim (Solodenko et al., 2015; Venditti et al., 2019). This hypothesis agrees well also with results from experimental studies, which have shown that, while handaxes may be more efficient at specific tasks such as defleshing, simple or retouched flakes can be equally efficient at other tasks, such as disarticulation (Galán and Domínguez-Rodrigo, 2014; see also Jones, 1980). Moreover, both unmodified flakes and bifaces have been reported as efficient

tools in proboscidean butchery experiments (e.g., Schick and Toth, 1993; Gingerich and Stanford, 2018). In carcass processing activities, simple and/or small flakes appear to entail two main advantages over bifaces: 1) they allow for better precision (e.g., Venditti et al., 2019) and 2) they yield higher return rates when raw material economics are considered, mainly because a smaller mass of raw material is needed for their production; as they also provide more cutting edge per unit of mass, tool-kits based on small-sized blanks offer economic advantages, especially to groups that are highly mobile (Galán and Domínguez-Rodrigo, 2014; Pargeter and Shea, 2019). Taphonomic biases aside, those advantages alone could partly explain the higher frequency of small flake blanks, as opposed to large(r) flakes and bifaces, at the sites included in this study, notwithstanding the broader complexities surrounding the variability in Middle Pleistocene lithic industries and questions that remain open regardless of whether we are looking at proboscidean-exploitation sites or not.

Apart from cut marks, which comprise the most straightforward proof of proboscidean meat/fat exploitation and they are present in 12 (34%) of the studied sites, breakages for brain and marrow extraction, and proboscidean bone artifacts are also regarded as direct evidence of its utilization. In Geshert Benot Ya'aqov, Notarchirico and La Cotte de St Brelade the exploitation of the brain and/or other edible parts of the head is documented. The elephant's head is of high nutritional value, and constitutes a high-quality source of protein and calories, which can be found in the brain, the tongue, the trunk and the mandible (Agam and Barkai, 2016). Bearing in mind that the head of the recent African elephant *Loxodonta africana* weighs >400 kg and an even higher weight is expected for *P. antiquus*, its full exploitation should have required from the Lower Palaeolithic humans the investment of a significant amount of time and energy (Reshef and Barkai, 2015), knowledge of its edible components, as well as social skills and constructive cooperation among the group members. Geshert Benot Ya'aqov is the oldest known

locality with possible intentional breakage of a proboscidean cranium.

Intentional bone fracturing for marrow extraction is reported much later, during MIS 11, although older assemblages with proboscidean bones should be reassessed for this kind of exploitation. A recent study on *P. antiquus* limb bones from Castel di Guido, showed that, although marrow cavities are proportionally small compared to the bones' size, they do exist, and the fracturing of proboscidean bones at this site involved not only bone tool fashioning, but also consumption of marrow for nutritional purposes (Boschian et al., 2019; see also Anzidei et al., 2012: fig. 16e). Bone fracturing for marrow extraction usually takes place at a second stage of carcass exploitation, after the stripping of meat and the removal of fat, and possibly when bones are still fresh, producing thus green bone fractures (e.g., EDAR Culebro 1, PRERESSA); however, the time interval between these stages is not easy to define archaeologically and would depend on the environmental conditions (for the preservation of fresh bone and of edible marrow) and on food availability (seasonality) (see also Boschian et al., 2019). Some localities evidence a third processing stage, namely the bone tool production, which experimentally has proved to be feasible on both fresh and drier bones (Stanford et al., 1981; Backwell and d'Errico, 2004); again, the time interval from the previous stage is difficult to ascertain. Taken together, brain exploitation and fracturing of bones are evident in 8 sites (23%), indicating that proboscidean carcasses were important sources not only for meat and fat.

Full exploitation of carcasses becomes evident with the manufacturing of proboscidean bone artifacts. Indeed, proboscidean bone artifacts (or possibly attributed to proboscideans) are present in 11 sites (31%) —many of which yield also bone artifacts made from other mammal bones (e.g., equids, bovids). The use of proboscidean bones as raw material for the production of cultural objects suggests that the exploitation of carcasses involved behavioral aspects beyond those related to subsistence. In lack of micro-wear investigations, we can-

not discuss any possible functional use of blanks and tools made on bone fragments: depending on ecological and cultural contexts, some of them, such as percussors, scrapers or unmodified flakes, could have been produced to serve functional goals, while others were possibly manufactured for non-utilitarian purposes. Zutovski and Barkai (2016) proposed that proboscidean bone artifacts might additionally hint to cosmological, cultural and symbolic relations between proboscideans and humans. Fontana Ranuccio and Malagrotta (Italy; both MIS 13) currently represent the oldest sites with evidence of bone tools made on proboscidean bones in western Eurasia (Fig. 3.2); other younger localities include Castel di Guido, La Polledrara, Revadim, Casal de' Pazzi, and perhaps Marathoussa-1, Biltzigsleben and Vértesszölös (Hungary; but see Fluck, 2011) (Appendix 3.1).

Overall, considering the limitations of preservation of human-induced modifications in proboscidean bones, as already stated in the introduction, the presence in 22 (63%) of the studied localities of direct evidence of human exploitation can be considered a relatively high number, almost double than that of direct carnivore gnawing in proboscidean bones (34%; higher also than 41%, the percentage in sites with carnivore presence; see above), indicating the significant contribution of humans in the accumulation and modification of the bones, and overall in the formation and taphonomic history of the localities.

### 3.4.3. REMARKS ON PROBOSCIDEAN PALAEOECOLOGY

The Middle Pleistocene Proboscidea-*Homo* records are far from being equally divided between *P. antiquus* and *Mammuthus* (in particular *M. trogontherii*, the widely distributed mammoth during the Middle Pleistocene), and there is a clear dominance of *P. antiquus* (26 sites in total<sup>5</sup>; 81% of the Middle

<sup>5</sup> In Stanton Harcourt the mammoth accounts for more than half of the faunal assemblage and therefore the locality is included here in the *Mammuthus*-bearing sites.

Pleistocene ones with identification at genus level), as well as of localities correlated with interglacial stages (Appendix 3.1). The latter correlation can be attributed to the different ecological adaptations of these proboscideans, the environmental preferences or tolerances of hominins, as well as preservation biases. *Mammuthus trogontherii* is generally considered a steppe dweller and was a common faunal element of the glacial stages in Central Europe, adapted to open landscapes and aridity, being less abundant in the more temperate conditions of Mediterranean Europe (Athanasios, 2012). Recent dental micro- and macrowear studies indicate grass-dominated mixed-feeding preferences (Rivals et al., 2019 and references therein). Although European sites with skeletons of *M. trogontherii* do exist during the Middle Pleistocene, there is hardly any evidence of human presence, which can be attributed to preservation biases, local extinctions of (small) human populations, lack of adequate procurement strategies, or to the less favorable habitats. On the other hand, *P. antiquus* had wide and flexible ecological adaptations, as it was an inhabitant of mild humid, warm to warm-temperate and moderately wooded to wooded environments, but also of wooded grasslands or even rather arid grasslands (Palombo et al., 2010). Palaeodietary studies indicate a dietary plasticity, which included browsing, grazing and mixed feeding (Rivals et al., 2019 and references therein). In Northern and Central Europe, it occurred during interglacial phases and apart from some exceptions, it was generally absent from the intervening cold stages of open habitats, when it was contracted to Southern Europe, which acted as a refugium (Lister, 2004). In particular, most of the Proboscidea-*Homo* localities have yielded a diversified fauna rich in medium- to large-sized herbivores, offering a wide prey spectrum for large carnivores and humans (Appendix 3.1). A lot of them include *Castor* (beaver) and *Hippopotamus*, as well as a diversity of cervids and some also the rarer primate *Macaca* (macaque), indicating the presence of permanent freshwater bodies (river or lake settings) and substantial woodland com-

ponents under (at least relatively) temperate conditions. Importantly, climatic conditions in these settings would never, or only rarely, reach freezing temperatures, as indicated by the presence of beavers and hippos in the faunal lists. Thus, it seems that the environments that *P. antiquus* inhabited were also favorable settings for human occupation and subsistence (hunting/scavenging). Almost all of the sites examined here occur in fluvial or lacustrine environments; these are known to be nutritionally advantageous locations, but also depositional regimes that foster archaeological preservation.

#### 3.4.4. EXPLORING ASPECTS OF PROBOSCIDEAN ETHOLOGY AS INTERPRETATIVE TOOLS

*Mammuthus meridionalis*, *M. trogontherii* and *P. antiquus* with mean BMs >9 tones (Larramendi, 2016) were by far the largest terrestrial animals of the Pleistocene terrestrial ecosystems of Europe, clearly surpassing other megaherbivores, such as *Hippopotamus* and the rhino *Stephanorhinus*. However, direct evidence (in the form of cut marks) for the exploitation of these latter taxa in Europe is so far limited (Appendix 3.2), while although 22 (63%) of the studied proboscidean localities yielded also hippos and/or rhinos, only 2 of them (9%) preserve also cut marks on these megaherbivores. Moreover, in contrast to the 12 localities bearing cut marks on proboscidean bones, cut marks in hippo bones exist so far only in 4 localities and in rhino bones in 8 (including both open-air and cave ones). For *H. antiquus* this could be possibly attributed to its strongly aquatic life habits going usually only sporadically outside of water bodies and feeding mainly on aquatic vegetation (Palmqvist et al., 2003; Martínez-Navarro, 2010). Even if we consider an occasional nocturnal feeding activity on land, like the recent *H. amphibius*, its tracking down and hunting in the dark would be particularly difficult and challenging for humans, especially considering that *H. amphibius*



is a dangerous animal, responsible for numerous human deaths annually (Eltringham in Hutchins et al., 2004). Similarly, rhinos show aggressive behavior and can be frightening animals to encounter, often chasing human intruders (especially the black rhino *Diceros bicornis*); rhinos have also an acute sense of smell, detecting human scent even at a distance of ~800 m, alarming them to run away (Owen-Smith in Hutchins et al., 2004).

In contrast to the scanty evidence for hippo and rhino exploitation, the proboscidean exploitation record is rather abundant (Appendix 3.1), even though the enormous size of elephants and the fact that they live in flocks constituted probably a prohibiting factor for the direct confrontation and hunting by both large carnivores and humans. Firstly, it seems possible that human exploitation involved individuals that were already killed by other predators or died by natural causes, or individuals that were vulnerable and/or weakened by e.g., diseases, injuries or malnutrition; the latter would usually stay close to water sources, abandoned from their flock (Cannell, 2014). Secondly, certain aspects in the behavior of proboscideans and the way they modify the landscape would have served to the advantage of human foraging tactics (Haynes, 2006, 2012). For example, elephants repeatedly use known paths leading to water sources; this habit would have allowed hominins to practice particular hunting strategies, including the use of natural traps, ambushes, use of spears and inflicting injuries, especially on their vulnerable cushioned feet (Haynes, 2006, 2012; Cannell, 2014; Agam and Barkai, 2018; Lewis, this volume). Thirdly, male individuals acquire a more solitary life after puberty (see below), which makes them more vulnerable and perhaps an easier target, while specifically during the musth period (when testosterone levels are increased) combats between males (accompanied by loud vocalizations and thus easy to be located by humans) can potentially end with the death of one of the individuals (Lister in Hutchins et al., 2004). Lastly, elephants are not territorial, they do not defend their range, which overlaps with that

of other animals, and they are not aggressive except when males are in musth (Lister in Hutchins et al., 2004).

In light of the above, there are two additionally interesting outcomes from the assessment of the Proboscidea-*Homo* open-air Early-Middle Pleistocene localities in western Eurasia: 1) males prevail in the record, and 2) most of the sites involve subadult/adult proboscidean individuals<sup>6</sup> (Appendix 3.1), corresponding to the Type C (“selective mortality”) of Haynes (2017). Despite the fact that adult males had markedly more robust body size and more powerful tusks compared to females and juveniles, and thus were more deterring, there are some possible explanations of their higher percentage in butchering sites, related mainly to the elephants’ social organization: 1) The fact that elephants live in flocks is a prohibiting factor for predators (both carnivores and humans), which would have to face the protection and defensive behavior of adults (MacDonald, 2009). Indeed, young elephants stay closely dependent on their mother in the first ten years, being additionally protected by the whole female-dominant group (MacDonald, 2009). 2) In contrast to females, males on puberty leave or are forced out of the family; fully-grown adult males acquire a more nomadic and solitary life, roaming either alone or in loose groupings (Moss, 1988; Lister in Hutchins et al., 2004; MacDonald, 2009). Consequently, it becomes more possible for males to enter an unfamiliar landscape, get into more difficult or dangerous situations and take higher risks when roaming a more adventurous terrain, increasing also the proneness to be caught, injured or die in natural traps (Moss, 1988; see also Lister and Agenbroad, 1994; Álvarez-Lao et al., 2009; Haynes, 2017; Pečnerová et al., 2017 for mammoth analogies). Studies on extant African elephants show that particularly during dry seasons, adult males frequent more types of habitats than

<sup>6</sup> When the approximate ontogenetic age is known, we infer that these individuals did not die due to advanced age, considering that *P. antiquus* lifespan was ~75 years.

family units do, which stay closer to permanent water spots; and that bulls roam widely away from drinking water sources in order to exploit scattered feeding “hotspots” and avoid conflict with bulls in musth (Stokke and du Toit, 2002; see also below). 3) Another reason is based on the frequency of injuries. Observations on African elephants show that injuries (67% human-caused) are by far more common (84.3%) in adult individuals (older than 8 years according to the study) than juveniles, and that males are the dominant sex injured (84%), indicating that adult males are the most susceptible group (Obanda et al., 2008). Moreover, during the musth period, starting on average at ~29 years old, male elephants present highly aggressive behavior towards other males. During this periodic condition, agonistic interactions are more intense, involving threat displays, chasing and minor combat using tusks, possibly causing injuries, while these fights can even result in the death of one of the males (MacDonald, 2009). Under all the above more venturous circumstances, the vulnerability potential of the male individual is increased. Particularly in the case of natural traps, apart from the higher preservation ratio (Pečnerová et al., 2017), it would be also easier for early humans to take advantage of trapped, weakened, injured or even dead individuals. Skeletons of subadult/adult male individuals dominate also in the non-anthropogenic record of Middle Pleistocene open-air localities, which further supports the observation that adult males are more prone to die from predation, injuries from intra-specific combats and other causes (e.g., natural traps) not related to senility (e.g., Lister, 1996; Lister and Stuart, 2010; Tsoukala et al., 2011; Athanassiou, 2012; Lister et al., 2012; Kevrekidis and Mol, 2016; Titov and Golovachev, 2017). Late Middle Palaeolithic hominins were practicing both selective (i.e., targeting prime adults; see e.g., Gaudzinski and Roebroeks, 2000) and non-selective (e.g., Marín et al., 2017) large mammal hunting strategies. The aforementioned adult-biased pattern in our proboscidean dataset may be foreshadowing a similar situation, indi-

rectly reflecting the process of hominin establishment in the hunting niche.

### 3.5 CONCLUSIONS

It is relatively shortly after the first “out of Africa” dispersal and contemporaneously with the first appearance of humans in Europe, at ~1.3–1.2 Ma, when the first possible Proboscidea-*Homo* event is attested (Fuente Nueva-3). During the Early Pleistocene and the early part of the Middle Pleistocene, sites with evidence of proboscidean (and, generally, megafauna) exploitation are geographically confined to southern, temperate regions. Proboscidean exploitation likely involved individuals that died naturally, caught in natural traps, injured or died because of combat with conspecifics; alternatively, it involved juveniles, adult female and young adult male individuals that were injured and/or killed by formidable predators, with the saber-toothed cat *Homotherium* probably being the most capable attacker. However, access to these carcasses by humans, especially in the presence of the largest ever hyena *Pachycrocuta brevirostris*, would have been particularly challenging, if not usually impossible. Considering the scantiness of the evidence (Fig. 3.2, Appendix 3.1), proboscidean exploitation during the Early Pleistocene seems to have been only occasional and sporadic; carcass acquisition possibly relied on passive and —perhaps more possibly— active scavenging, and carcasses were processed with expedient lithic tool-kits. Proboscidean hunting cannot be excluded, but, along with the arguments presented here, e.g., with regard to carnivore guild dynamics, the archaeological evidence does not support the case for regular, systematic hunting in the Early Pleistocene, although we acknowledge the pitfalls of such an inferential, qualitative assessment: future studies should address the issue of how many proboscideans should a group hunt in order to “qualify” for hunting that is “regular and systematic” enough to leave a traceable signal in the archaeological record or

the isotopic data and/or also be comparable with ethnographic accounts.

Between ~900 ka and ~600–500 ka (late Early and early Middle Pleistocene), there is a general scarcity of Palaeolithic sites in Europe and a gap (absence of human presence) is observed at sites with long sequences (e.g., Atapuerca). Therefore, the scarcity of proboscidean-processing sites in this time-block likely reflects a broader picture of a scattered, low-density and discontinuous human presence. Similarly, the remarkable increase of sites with proboscidean exploitation after ~500 ka onwards is certainly related to an overall increase of archaeological sites in western Eurasia, signaling a more continuous hominin occupation.

The more extensive utilization of proboscidean carcasses in the Middle Pleistocene is supported by direct evidence, such as cut marks, breakages for brain and marrow extraction, bone artifacts and impact flakes, as well as by early access to carcasses and transport of bones to occupational locations (Fig. 3.2, Appendix 3.1). Overall, there exist indications for some sort of “niche incursion” by humans as highly carnivorous omnivores, acquiring a higher rank within the predator guild. The firm archaeological signal for proboscidean and other megafauna exploitation (Fig. 3.2, Appendices 3.1, 3.2) indicates that megafauna procurement and carcass processing was “more-than-a-marginal” strategy (Yravedra et al., 2010) and included not only scavenging but also hunting; in either case, the main targets appear to have been subadult/adult males, which were roaming solitary in the landscape.

Unsurprisingly, there is no specific reduction method, type of tool-kit, or techno-complex associated with proboscidean exploitation sites. In various combinations, bifaces co-occur with core-tools of “Mode 1” morphologies as well as with small-sized tools and simple flakes, diachronically (see e.g., the Italian sites), synchronically, and even within the same lithic assemblage (e.g., Notarchirico). As a broad-brush pattern, we are dealing with usually small lithic assemblages, characterized by an *ad hoc* production of mostly flake blanks made

on local raw materials. However, a more or less expedient character is not mutually exclusive to the presence of curated and imported tools, as well as to the evidence for on-site tool maintenance, which can be seen as structural elements in the technical systems, in turn suggesting planned activities. A fuller exploitation of proboscidean carcasses, i.e., including bone fracturing for marrow and the manufacturing of bone implements, chronologically matches the main spread of the Acheulean after ~600–500 ka, but it remains unclear exactly how developments in lithic technology influenced the ways and the extent to which proboscidean carcasses were being exploited. Reporting on an elephant-butchery experiment, Gingerich and Stanford (2018: p. 272) note that “hafting style was the most important determinant of a tool’s functionality” and that “efficiency and preference for a particular tool was based more on the haft than any other factor”. The hafting of stone-tools on shafts would have increased leverage and efficiency in certain processing tasks, but, besides Cava Campitello (Italy; ~200 ka) there is hardly any evidence for hafting before MIS 7 in general and at the sites examined here in particular (but see Alpersen-Afil and Goren-Inbar, 2016). After ~200 ka, we see the appearance of more complex technological procedures, such as hafting, and more curated, “mobile industries” (e.g., Levallois), which increase core productivity and allow for the production of standardized blanks with multiple cutting edges. However, the ways in which such shifts in lithic technical systems influenced (viz. improved) proboscidean *procurement strategies* (e.g., hunting) and/or *processing* activities, remain largely unexplored. Wooden implements, which are essentially invisible in the record, would have almost certainly been utilized for both procurement and processing tasks; it is of note that some (if not all) of the most important wooden artifacts ever found, have been recovered from sites where megafaunal remains (including proboscideans) are also present: Clacton-on-Sea, Schöningen, Lehringen and Poggetti Vecchi. It appears that *from ~600–500 ka and perhaps especially after ~200 ka onwards, hominins had*

resolved most of the behavioral or logistical limitations associated with rendering proboscidean exploitation an ecologically viable, nutritionally gainful, socially beneficial and energetically efficient component of their subsistence strategies. This change is chronologically correlated and largely associated causally with the following parameters and processes:

1. The disappearance of most of the late Villafanchian–Epivillafranchian (Early Pleistocene) components of the large carnivore guild, which was dominated by large-sized, hypercarnivorous and mostly ambush-hunting felids, and by the large-sized, bone-cracking (possibly pack-hunting) scavenger *Pachyrocata*. These taxa were replaced during the Middle Pleistocene by the Galerian to modern hyenas and felids (Fig. 3.2); as a whole, the large carnivore guild is marked by a decrease in carrion providers, and by a higher representation of species with scavenging, bone-cracking and pack-hunting behavior. Moreover, even though the carnivore diversity slightly increased during this period, carnivore representation in the archaeo-palaeontological localities is rather low in both species and specimens number. Decline of large carnivore representation is possibly an anthropogenic effect on the ecosystem: first, due to the firmer establishment of the hominin niche, including anti-predator strategies and expulsion of large carnivores from the region of human influence; and second, due to the reduction of food quantity through human confrontational scavenging or decrease in prey availability through human hunting (see also Lewis and Werdelin, 2007; Faurby et al., 2020). This effect was probably initiated in the Early Pleistocene, but it is essentially in the Middle Pleistocene, when humans appear to successfully outcompete large carnivores.
2. Human brain size and body size/mass increased to modern levels, with implications that include cognitive developments and behavioral plasticity (e.g., Galway-Witham et al., 2019 and references therein).
3. A more continuous occupation of Europe is observed, which is probably related to a demographic growth and included also the peopling of higher latitudes (Roebroeks, 2001). This is reflected in the appearance of Proboscidea-*Homo* localities in the more continental climates of central and northern Europe (Figs. 3.1, 3.2; see also Wenban-Smith, this volume).
4. A number of other biocultural changes can be inferred from the hominin fossil and archaeological record. Some of the most important include: a potential increase in group sizes; (expansion of) cooperative breeding and foraging, possibly accompanied with more regular food sharing practices; habitual use of fire and possible emergence of pyrotechnology; and the standardizing of hunting as foraging strategy. An overall increase in foraging efficacy is thereby inferred, and there is some consensus that, under favorable social and ecological conditions, cooperative hunting was well-embedded in the suite of hominin subsistence strategies already from ~500–400 ka.

In sum, alongside the changes in large carnivore dynamics, rather than technological developments *per se* (spread of the “biface phenomenon” a.k.a. the Acheulean, and prepared-core techniques, e.g., Levallois), it was biologically, socially and culturally negotiated behaviors that enabled or encouraged in the middle–late Middle Pleistocene the exploitation of proboscideans, to an extent that was broader and probably more systematic than that of the preceding periods but still conditioned by a presumably narrow range of ecological and social circumstances. Consequently, even if it can be inferred that middle–late Middle Pleistocene hominins hunted proboscideans more regularly and successfully than in preceding periods, this does not necessarily mean that proboscidean hunting became a fixed and omnipresent subsistence behavior from a particular point in time onwards. In our interpretation of the data, and following the argumentation of Byers and Ugan (2005), there is no strong evidence for hominin specialization

in proboscidean exploitation, at least not in the sense of exploiting proboscideans preferentially over other smaller-sized taxa, or in the sense of a very specific hunting target, as in the case of Neanderthal hunting of certain middle-sized ungulates (e.g., monospecific hunting of bovids, cervids or equids; see e.g., Gaudzinski and Roebroeks, 2000; Dusseldorp, 2012, 2013 and references therein).

Several behavioral aspects, such as strategic hunting using relief, decoys or wooden traps, are hardly detectable (if at all) in the material culture or on the fossil remains, and the challenge is to develop analytical tools that will address their role and provide nuanced interpretative frameworks. Along with research on hominin social systems, observations from proboscidean ethology and ethnographical accounts need to be more extensively incorporated, not only in large-scale studies, but also in the interpretations of individual sites. Finally, the proboscidean *versus* hominin palaeoecology, and in particular their position and role in trophic dynamics, as well as home range expansions and contractions, also require further investigation.

Proboscidean procurement and processing must have posed significant, and in many ways unique, challenges to hominins; in that sense, the trajectory and possible evolutionary implications of proboscidean exploitation offers valuable insights to human evolution. Elephants are nowadays among the animals known to use tools, and they exhibit mirror self-recognition, which indicates some degree of self-awareness and a high level of cognition. They are also well-known for mourning their dead and for having strong individual personalities, high intelligence and memory skills, a complex social organization and large social networks (MacDonald, 2009). Provided that some of these properties can be projected to the Pleistocene taxa, proboscideans were to hominins more than a source of food (Speth, 2010; Barkai, 2019). Exploring the non-nutritional, non-functional aspects of hominin-proboscidean interactions is a major challenge for future research.

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	LOCALITY	AGE (KA)	MIS	SETTING	TAXON	MNI	GENDER	ONTOGENETIC AGE
1.	Fuente Nueva-3, ULS III (c. III.1)	~1300		fluvio-lacustrine	<i>M. meridionalis</i>	1	female	adult (60)
2.	Barranc de la Boella, Pit 1, level 2	960–780		fluvio-deltaic	<i>M. meridionalis</i>	2		1 adult (30), 1 juvenile
3.	Gesher Benot Ya'aqov, Layer II-6 L1	780	19	lacustrine	<i>P. antiquus</i>	1	female?	at least subadult
4.	Notarchirico, levels A-A1-B	670–610	16	fluvial	<i>P. antiquus</i>	1	male	subadult
5.	Ficoncella	~500	13	fluvial	<i>P. antiquus</i>	1	male	adult
6.	Malagrotta	~516	13		<i>P. antiquus</i>			
7.	Bełchatów	~500		fluvial	<i>M. trogontherii</i>	1		
8.	Marathousa 1	~500–400	12/11	lacustrine	<i>P. antiquus</i>	2	male	adult (~60)
9.	Ebbsfleet, Phase 6	~425–375	11	lacustrine	<i>P. antiquus</i>	1	male	adult (43–49)
10.	Castel di Guido	412	11	fluvio-lacustrine	<i>P. antiquus</i>	11		10 adults, 1 juvenile
11.	Fontana Ranuccio	~400	11	fluvio-lacustrine	<i>P. antiquus</i>			
12.	Kärlich-Seeufer	396±20	11	lacustrine	<i>P. antiquus</i>	8		juvenile to adult (subadults/adults prevail)
13.	Aridos 1	380±45	11	fluvial	<i>P. antiquus</i>	1	female	adult
14.	Aridos 2	~380	11	fluvial	<i>P. antiquus</i>	1	male	adult
15.	Ambrona, AS3	>350	11	fluvio-lacustrine	<i>P. antiquus</i>	3	male	adult
16.	Terra Amata (all levels)		11	coastal	<i>P. antiquus</i>	13		juvenile to adult (juveniles prevail)
17.	La Polledrara	325	9	fluvio-palustrine	<i>P. antiquus</i>	>25	males prevail	adults prevail
18.	Schöningen	~300	9	lacustrine	<i>P. antiquus</i>	>10		
19.	Biltzigsleben		11 or 9 or 7	fluvial	<i>P. antiquus</i>			
20.	Revadim Quarry	500–300		fluvial	<i>P. antiquus</i>	6		
21.	Ranville	230–205	7	karstic (secondary)	<i>P. antiquus</i>	1		subadult
22.	Torralba	~200	7	fluvial	<i>P. antiquus</i>			
23.	Stanton Harcourt	~200	7	fluvial	<i>M. trogontherii?</i> , <i>P. antiquus</i>			
24.	Casal de' Pazzi	270–250	7	fluvial	<i>P. antiquus</i>			
25.	Poggetti Vecchi	~171	7/6	lacustrine	<i>P. antiquus</i>	7	female and male	juvenile (1–8), subadults-adults (14–>40)
26.	Ariendorf 2		8 or 6	aeolian loess	<i>Mammuthus</i> sp.	2		subadult (15–18)
27.	Cava Campitello	206–201?	7?	fluvial	<i>P. antiquus</i>	1	female	subadult (18–20)
28.	La Cotte de St Brelade, Layers 3 & 6.1		6	fissure	<i>M. primigenius</i>	7/11 (3/6.1)		adult
29.	PRERESA	270–169	6	fluvial	Elephantidae indet.	1		
30.	Bollschweil	198–131	6	loess	<i>M. primigenius</i>	6		juvenile to adult
31.	Arriaga Ila		6–5	fluvial	<i>P. antiquus</i>	1	female	adult
32.	Neumark Nord 1	~120	5e	lacustrine	<i>P. antiquus</i>	~70	males prevail	adults prevail
33.	EDAR Culebro 1	~120	5e	fluvial	<i>Mammuthus</i> sp.	1	male	subadult
34.	Lehringen	~120	5e	lacustrine	<i>P. antiquus</i>	1		adult (45)
35.	Gröbern	~120	5e	lacustrine	<i>P. antiquus</i>	1	male	adult (35–40)



	<b>SKELETAL ELEMENTS (ELEPHANTIDAE)</b>	<b>DIRECT EVIDENCE</b>	<b>CUT-MARKED ELEMENT</b>	<b>CUTMARK PURPOSE</b>	<b>INDIRECT EVIDENCE</b>
1.	1 partial skeleton				LA
2.	1 partial skeleton, 1 neonatal tooth	CM	ribs	defleshing	LA, RF, UWA
3.	cranium, tusk, molar fragments	BE			LA, WA
4.	1 partial skeleton	BE?, HF? (long bone)			LA, HR
5.	1 partial skeleton				LA, RF, UWA
6.	bone fragments, molar	PBA			LA, BA
7.	rib	CM	rib	filleting	
8.	1 partial skeleton and other bones/teeth	CM, PBA	tibia and astragalus (skeleton), rib	disarticulation, defles- hing, peeling	LA, BA, RF
9.	1 partial skeleton				LA, RF
10.	1 partial skeleton and other elements	CM, HF, PBA	ribs and long bone diaphyses		LA, BA
11.	several elements	PBA			LA, HR, BA
12.	several bones/teeth				LA, RF
13.	1 partial skeleton				LA, RF, UWA
14.	1 partial skeleton	CM	ribs, scapula	evisceration (ribs), filleting (scapula)	LA, UWA
15.	1 partial skeleton and other elements	CM, HF (femur)	cranium (premaxilla)		LA
16.	500 elements				LA, BA
17.	3 partial skeletons and other bones/teeth	HF, PBA			LA, RF, UWA, BA, HR
18.	1 partial skeleton and other bones/teeth	PBA?			LA, BA, UWA, WA
19.	several bones	CM, PBA			LA, HR, BA
20.	155 bones and teeth	CM, PBA	ribs, scapula	filleting	LA, BA
21.	1 partial skeleton				LA
22.	several bones	CM, PBA	fragment		LA
23.	several bones/teeth				LA
24.	tusks/bones	PBA			LA
25.	292 bones and teeth	PBA			LA, WA, BA
26.	several bones/teeth				LA, RF
27.	1 partial skeleton				LA
28.	241 (Layer 3) and 168 (Layer 6.1) elements	CM, BE	including scapula, femur		LA
29.	1 partial skeleton	CM, HF	6 diaphyses fragments		LA, RF
30.	229 bones and teeth				LA
31.	1 partial skeleton	CM?	rib		LA
32.	>1500 elements, several partial skeletons				LA
33.	1 partial skeleton	HF (humerus)			LA
34.	1 partial skeleton	WW			LA, RF
35.	1 partial skeleton				LA, UWA

	<b>LARGE CARNIVORES</b>	<b>CARNIVORE GNAWING (ON ELEPHANT BONES)</b>	<b>CARNIVORE COPROLITES</b>	<b>OTHER LARGE MAMMALS</b>
1.	<i>Lynx cf. pardinus, Pachycrocuta brevirostris, Canis mosbachensis, Lycaon lycaonoides, Ursus etruscus</i>		yes ( <i>Pachycrocuta</i> )	Can, Mu, Rh, Eq, Hi, Bo, Ce
2.	+ (tooth marks from a medium-large carnivore on a cervid's antler)			Ce, Eq
3.	+ (carnivore modifications on 2 mammal bones)			Can, Hi, Ce, Bo
4.				Su, Ce, Bo
5.	Hyaenidae indet.? (based on coprolite)	vertebrae, pelvis	yes ( <i>Crocuta</i> ?)	Eq, ?Hi, Ce, Bo
6.	<i>Canis sp.</i>			Eq, Rh, Su, Hi, Ce, Bo, Cas
7.				Ce
8.	<i>Canis sp.</i>	vertebra, not of the skeleton		Cer, Fe, Can, Mu, Hi, Ce, Bo, Cas
9.				Mu, Rh, Su, Ce, Bo, Cas
10.	<i>Panthera leo, Canis lupus</i>			Eq, Rh, Su, Hi, Ce, Bo
11.	<i>Panthera leo, Crocuta crocuta, Canis mosbachensis, Ursus deningeri</i>			Cer, Eq, Rh, Su, Hi, Ce, Bo, Cas
12.	<i>Panthera leo</i> , Hyaenidae indet. (based on tooth marks)	vertebrae		Eq, Su, Ce, Bo
13.	Canidae indet.			Su, Hi, Ce, Bo, Cas
14.	Hyaenidae indet. (based on tooth marks)	humerus		
15.	<i>Panthera leo</i>			Eq, Ce, Bo
16.	<i>Ursus arctos</i>			Rh, Su, Ce, Bo
17.	<i>Canis lupus</i>			Cer, Can, Eq, Rh, Su, Ce, Bo
18.	<i>Homotherium latidens, Panthera leo?, Canis lupus, Ursus thibetanus, Ursus deningeri-spelaeus</i>	yes		Can, Mus, Eq, Rh, Su, Ce, Bo, Cas
19.	<i>Panthera leo, Crocuta crocuta, Canis lupus, Ursus deningeri-spelaeus</i>			Cer, Fe, Can, Mu, Eq, Rh, Su, Ce, Bo, Cas
20.	Hyaenidae indet.	rib, pelvis, mandible		Fe, Eq, Su, Ce, Bo
21.	<i>Canis lupus</i>			Can, Eq, Rh, Ce, Bo
22.	+ (carnivore modifications on several mammal bones)	rib, phalanx		Eq, Rh, Hi, Bo, Ce
23.	<i>Panthera leo, Ursus arctos</i> , Canidae indet., Hyaenidae indet.			Eq, Bo, Ce
24.	<i>Crocuta crocuta, Canis lupus</i>			Eq, Rh, Su, Hi, Ce, Bo
25.	<i>Crocuta crocuta, Ursus deningeri-spelaeus</i>	juvenile mandible, vertebrae, rib, ulna, humerus, femur	yes	Ce, Bo
26.	<i>Canis lupus</i>	ribs		Eq, Rh, Ce, Bo
27.				
28.	<i>Canis lupus, Ursus sp.</i>	yes		Can, Eq, Rh, Ce, Bo
29.	<i>Lynx pardinus, Canis lupus</i>			Can, Mu, Eq, Ce, Bo
30.	<i>Ursus sp.</i>			Eq, Rh, Ce, Bo
31.				Eq, Rh, Ce, Bo
32.	<i>Panthera leo, Crocuta crocuta, Canis lupus, Ursus spelaeus</i>	vertebrae, ribs, several limb bones	yes ( <i>Crocuta</i> )	Can, Mu, Rh, Ce, Bo
33.				Eq, Ce
34.	<i>Canis lupus, Ursus cf. arctos</i>			Fe, Eq, Rh, Ce, Bo, Cas
35.	+	yes		Rh, Ce

	NUMBER OF LITHICS	TECHNO-COMPLEX/CULTURAL PERIOD	LITHIC RAW MATERIALS
1.	17	core-and-flake	limestone; flint; local procurement
2.	125	core-and-flake; 1 LCT	chert; schist; quartz; sandstone; granite; quartzite; local procurement
3.	62935 (2228 >20mm)	Acheulean (Large-Flake-Acheulian)	flint; basalt; limestone; probably local procurement
4.	42	core-and-flake & Acheulean	limestone; flint; quartzite; local procurement
5.	409 (129 >5mm)	„small-tool“ production	flint; chalcedony; quartz; limestone; probably local procurement
6.	601	core-and-flake (incl. pebble-tools)	limestone; flint
7.			
8.	1876 (390 >15mm)	core-and-flake; „small-tool“ production	radiolarite; flint; limestone; quartz; local procurement
9.	77 (65 >20mm)	core-and-flake („Clactonian“)	flint; local procurement
10.	292	Acheulean; pebble-tools & small flake-tools	flint; limestone; lava; calcareous silt; sandstone; quartz; pumice
11.	>150	5 LCTs & „small-tool“ production	flint; lava; limestone
12.	146	core-and-flake & Acheulean	quartzite; quartz; siliceous slate; chert
13.	331	Acheulean	flint; quartzite; local procurement
14.	34	Acheulean	flint; chert; quartzite; local
15.	72	Acheulean	flint; limestone; quartzite; quartz; local & distant procurement
16.	>68000	Acheulean	flint; limestone
17.	~600	„small-tool“ production	limestone; flint
18.	~2000	core-and-flake	flint
19.		„small-tool“ production	flint; chert; local procurement
20.	984 (Locality 21); „few“ (Locality 31)	Acheulean	flint
21.	>300	early Middle Palaeolithic	flint, sandstone, quartz; local procurement
22.	887	Acheulean	flint; quartzite; quartz; limestone
23.	9	n/d	flint, quartzite
24.	~1700	Acheulean	flint; limestone
25.	Unit 2: 827	early Middle Palaeolithic	chert; radiolarite; quartzite; local procurement
26.	37	early Middle Palaeolithic	quartz; quartzite; siliceous slate
27.	3	n/d	flint
28.	1185 (Layer 3); 95 (Layer 6.1)	Middle Palaeolithic	flint
29.	754	n/d	flint; quartz
30.	12	n/d (Middle or Lower Palaeolithic?)	chert, quartz, quartzite, amphibolite, siliceous slate
31.	43	Acheulean/early Middle Palaeolithic?	flint; local procurement
32.		Middle Palaeolithic	flint; local procurement
33.	243	n/d	flint; local procurement
34.	27	Middle Palaeolithic	flint
35.	26	Middle Palaeolithic	flint

	<b>NOTES ON LITHIC ASSEMBLAGE</b>
1.	uni-, bi- or poly-facially reduced; bipolar; flakes >30mm rare; aim of debitage: production of small flakes
2.	simple flakes; few retouched tools; 1 LCT: pick; 3 hammerstones, 7 cobbles as percussors, 3 cores
3.	several red. methods, incl. Levallois, discoidal, cores-on-flakes; high freq. of small retouched tools on flint
4.	freehand & bipolar; diversified but poorly standardized artifacts; bifaces; pebbles; core-and-flake tools
5.	2 different reduction sequences for flint & limestone; high number of retouch & confection flakes
6.	multi- and bi-directional cores; 1 handaxe?
7.	
8.	freehand & bipolar, expedient knapping; tool manufacture, use, maintenance; diverse tool-kit; backing
9.	ad hoc reduction; multi- and alternate platform cores; flake-tools; on-site knapping
10.	mono- and bi-facial core-tools; few flake-tools
11.	high number of retouched tools (mostly scrapers); bifaces, cores, choppers, small flakes
12.	cores: uni- and bi-facial, 1 bipolar; very few retouched pieces; bifaces
13.	Levallois cores & flakes; 2 biface tip-resharpening flakes; on-site knapping of 16 cores and 3 choppers
14.	quartzite biface & cleaver maybe imported
15.	small-tools on flakes; 2 bifaces
16.	bifaces; choppers/chopping tools; diverse toolkit; „complete“ reduction sequences
17.	cores on pebbles & flakes: unidirectional, centripetal; bipolar; core-tools, fragmented & atypical retouched tools, composite tools frequent
18.	imported tools & retouching; unstandardized flakes; opportunistic use of natural spalls as blanks; hard+soft hammer; no cores
19.	cores: unifacial, uni-&bi-directional, alternate flaking, „discoidal“; backed & pointed tools, notches, bifacially-retouched points
20.	LCTs together with small-sized tools; 1-, 2 or multi-platform cores, „prepared“ cores with hierarchical surfaces; flaked-flakes (recycled)
21.	ad hoc working of imported cores (1 Levallois); handaxe reduction and subsequent export
22.	discoidal cores
23.	5 handaxes, 1 core-on-flake; rolled, weathered; artifacts may be non-contemporaneous
24.	scrapers, notches, denticulates, core-tools, 1 handaxe
25.	cores on flakes & pebbles, unidirectional; scrapers, notches, choppers; on-site retouching; low standardization; no prepared cores
26.	unmodified flakes, cores, core frag.; no prepared cores
27.	unretouched flakes with adhesives indicating hafting; centripetal flaking
28.	Layer 3: small discoidal cores, little Levallois flaking; on-site tool resharpening and recycling
29.	mostly unretouched flakes; tools: retouched flakes, denticulates, composite tools
30.	1 handaxe
31.	cores; bifaces; choppers; flakes; scrapers
32.	prepared cores (incl. discoidal, Levallois), flaked-flakes; elongated flake-tools, notches, denticulates, pointed, scrapers
33.	cores: discoidal, bifacial, polyhedral; high percentage of knapping debris and simple flakes (incl. resharpening flakes)
34.	refits; flakes produced from prepared cores
35.	lithics not produced on the spot; mostly large unretouched flakes, probably from prepared cores (discoid?)

	<b>BONE ARTIFACTS</b>	<b>INTERPRETATION</b>
1.		competition between humans and hyenas for mammoth exploitation
2.		butchering event of a mammoth carcass
3.		butchery site; inversion of the cranium and deliberate breakage for brain extraction
4.		butchering event including possible utilization of soft parts of the cranium; association between lithic artefacts and bones not clearly demonstrated
5.		the carcass was possibly partially trapped in floodplain sediments; alternating human and carnivores exploitation
6.	mainly on megafauna; 1 biface, 4 scrapers, 1 end-scrapers	lithic (and faunal?) material most likely in secondary context (fluvial): causal association between lithics and fossils is equivocal
7.		secondary context, fluvial bone transport
8.	flakes, flake-tools, mimicking lithics (size, form); percussor	knapping events in the vicinity of a lake shore and exploitation of large mammals including elephants
9.		on-the-spot manufacture of stone tools to butcher the elephant
10.	on diaphyses of bovids, equids, elephants; total N=366–372: bifaces (99), specimens with wear traces (142), various flake-tools & scrapers (125)	complex palimpsest with natural transport of bones, frequent human activities for exploitation of meat, marrow and tool production
11.	mainly on elephant bones, but also horse, bovid, deer; great variety in form, shape and size of bone tools, incl. handaxes	
12.		complex site formation processes; palimpsest involving human activities in the vicinity of a lake
13.		exploitation of elephant carcass
14.		exploitation of elephant carcass
15.		natural deposition with regular exploitation by humans
16.	retoucher	short-term visits and more sustained human occupation; red deer hunting and carcasses transportation, young elephants transported (hunted?)
17.	minimum 8: scrapers, denticulates, specimens with uni- & bifacial flaking	elephants were trapped in muddy sediments and exploited by humans
18.	~100: retouchers, percussors, anvils, used/smoothened-tip tools	hunting and local exploitation of a wide range of herbivores, most notably horses; carnivore modifications also present
19.	minimum 1 handaxe; minimally to heavily flaked specimens	association of fauna and lithics most likely fortuitous due to reworking by various site formation processes
20.	elephant bones: a wedge-like tool with smoothed edge; tools shaped on flakes, possible bifacial flaking	exploitation of elephant carcass(es?) (Loc. 21, 31?); causal association with anthropogenic material unconfirmed (e.g., Loc. 2, 3, 30, 25?, 31?)
21.		exploitation of elephant carcass, whose meat-bearing elements are missing and transported elsewhere; collapse of the primary context into the karstic fissure
22.	2 bifacially flaked elephant bones	alternating of human activity and natural events
23.		secondary, fluvial context: no causal association of artifacts and fauna
24.	1 specimen with truncated end & unidirectional scars	possibly natural accumulation with no causal association between lithics and fauna
25.	~15 flakes; retouched fragments; specimens with signs of abrasion	the elephants died by a natural cause and were butchered soon after their death
26.		humans killed a weakened animal or exploited an already died individual
27.		elephant exploitation cannot be demonstrated
28.		long-term Neanderthal occupation site used strategically, commanding a hunting locale, periodically being abandoned; original game drive locality/kill-site interpretation questioned
29.		exploitation of proboscidean carcass for meat and marrow
30.		humans contributed to the faunal accumulation, but not definitive causal association between lithic artifacts and fauna (reworked sediments)
31.		possible human exploitation of the carcass
32.		several partly articulated skeletons of a wide range of animals, occasionally associated with lithic artefacts; carnivore and human exploitation of herbivores
33.		exploitation of a mammoth carcass including acquisition of bone marrow
34.		hunting and butchery site
35.		humans either killed an already weakened by disease individual or took advantage of an already deceased individual

**Appendix 3.1:** Summary table with all studied Proboscidea-*Homo* localities of western Eurasia and the examined parameters.

Direct and indirect evidence: BA, (non-proboscidean) bone artifact; BE, brain extraction; CM cut marks; HF, human-made fracture; HR, human remains; LA, lithic artifacts; PBA, proboscidean bone artifact; RF, refitting of lithic artifacts; UWA, use-wear analysis; WA, wooden artifacts; WW, wooden weapons.

Fauna: Bo, Bovidae; Can, Canidae (*Vulpes*); Ce, Cervidae, Cer, Cercopithecidae (*Macaca*); Eq, Equidae; Fe, Felidae (*Felis*); Hi, Hippopotamidae; Mu, Mustelidae (except of *Gulo*); Rh, Rhinocerotidae; Su, Suidae; megafauna is marked with bold letters.

Techno-complex and lithic raw material: nd, not defined; limestone refers to siliceous and non-siliceous limestone.

Selected references for localities (see also references therein): 1, Barsky et al., 2010; Espigares et al., 2013; 2, Vallverdú et al., 2014; Mosquera et al., 2015; 3, Goren-Inbar et al., 1994, 2017; Rabinovich and Biton, 2011; 4, Piperno and Tagliacozzo, 2001; Moncel et al., 2019; 5, Aureli et al., 2015, 2016; 6, Cassoli et al., 1982; Marra et al., 2018; Ceruleo et al., 2019; 7, Pawłowska et al., 2014; 8, Konidaris et al., 2018; Panagopoulou et al., 2018; Tourloukis et al., 2018; 9, Wenban-Smith, 2013; 10, Boschian and Saccà, 2010, 2015; Saccà, 2012; Marra et al., 2018; 11, Segre and Ascenzi, 1984; Mussi, 2002; 12, Gaudzinski et al., 1996; Gaudzinski, 1998; 13, Villa, 1990; Santonja and Villa, 1990; Yravedra et al., 2010, 2019; 14, Santonja and Villa, 1990; Yravedra et al., 2010; 15, Santonja and Villa, 1990; Villa et al., 2005; Santonja et al., 2014; 16, Valensi et al., 2011; Moigne et al., 2016; 17, Anzidei et al., 2012; Santucci et al., 2016; 18, Julien et al., 2015; Serangeli et al., 2018, 2021; 19, Mania et al., 1997; Brühl, 2003; Müller and Pasda, 2011; Brasser, 2017; 20, Marder et al., 2011; Rabinovich et al., 2012; Solodenko et al., 2015; Zupancich et al., 2018; 21, Cliquet, 2008; 22, Santonja and Villa, 1990; Villa et al., 2005; Santonja et al., 2014; Pineda and Saladié, 2019; 23, Scott, 2001; 24, Anzidei, 2001; Mussi, 2002; Marra et al., 2018; 25, Aranguren et al., 2019; 26, Turner, 1997; 27, Mazza et al., 2006; 28, Scott et al., 2014; Smith, 2015; 29, Yravedra et al., 2012; Yravedra et al., 2019; 30, Conard and Niven, 2001; 31, Panera et al., 2014; Yravedra et al., 2019; 32, Brühl and Laurat, 2010; Palombo et al., 2010; Diedrich, 2014; 33, Panera et al., 2014; Yravedra et al., 2014; 34 and 35, Weber, 2000; Gaudzinski, 2004.

	LOCALITY	COUNTRY	AGE (KA)	MIS	SPECIES
1.	Barranco León, Level D	Spain	ca. 1400		<i>Hippopotamus antiquus</i>
2.	Vallparadís?	Spain	ca. 1000		<i>Hippopotamus antiquus</i>
3.	Vallparadís?	Spain	ca. 1000		<i>Stephanorhinus hundsheimensis</i>
4.	Boxgrove	England	ca. 500	13	<i>Stephanorhinus</i> sp.
5.	Marathousa-2	Greece	500–400?		<i>Hippopotamus antiquus</i>
6.	Caune de l'Arago, Level F	France	392±43	12	<i>Stephanorhinus hemitoechus</i>
7.	Guado San Nicola	Italy	ca. 360	11/10	<i>Stephanorhinus kirchbergensis</i>
8.	Biltzigsleben	Germany		11 or 9 or 7	<i>Stephanorhinus hemitoechus/S. kirchbergensis</i>
9.	Biache-Saint-Vaast	France		7	<i>Stephanorhinus hemitoechus/S. kirchbergensis</i>
10.	La Cotte de St Brelade	England		7–6	<i>Coelodonta antiquitatis</i>
11.	Taubach	Germany	ca. 120	5e	<i>Stephanorhinus kirchbergensis</i>
12.	Bolomor Cave, level IV	Spain	ca. 120		<i>Hippopotamus amphibius</i>

**Appendix 3.2:** European Early–Middle Pleistocene localities (both open-air and cave ones) with reported cut marks on rhinoceroses and hippopotamuses. References: 1, Espigares et al., 2019; 2 and 3, Martínez et al., 2010, but see Madurell-Malapeira et al., 2012; 4, Roberts and Parfitt, 1999; 5, Konidaris et al., 2019; 6, Chen and Moigne, 2018; 7, Sala et al., 2014; 8, 9, Brasser, 2017; Auguste, 1995; 10, Smith, 2015; 11, Bratlund, 2000; 12, Blasco and Fernández Peris, 2012.