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A REAPPRAISAL OF LOWER TO MIDDLE PALAEOLITHIC BONE RETOUCHERS FROM SOUTHEASTERN FRANCE (MIS 11 TO 3)

Abstract

In southeastern France, many Final Acheulean/Early Middle Palaeolithic and Middle Palaeolithic assemblages have yielded bone retouchers. The oldest are dated to the Middle Pleistocene: from MIS 11 at Terra Amata; MIS 9 at Orgnac 3; and MIS 6-7 at Payre F, Sainte-Anne I and Le Lazaret. However, this early evidence of bone tool use only concerns a few dozen pieces among thousands of faunal and lithic remains. These retouchers indicate behavioural changes from MIS 11-9 onwards in southeastern France, associated with a mosaic of technological and subsistence changes that became more common during the Middle Palaeolithic. The frequency of these bone artefacts increases during MIS 7, becoming much more numerous after MIS 5, sometimes totaling more than a hundred items at one site, such as Saint-Marcel Cave. Bone retoucher frequency is still highly variable throughout the Middle Palaeolithic and seems to be determined by the type of occupation and activities rather than the associated lithic technologies. This broad, regional comparative analysis contributes to a better understanding of the technical behaviour developed by Neanderthals, as well as their Middle Pleistocene ancestors, and their ability to recover and use bones.

Keywords

Bone retouchers; Middle Palaeolithic; Southeastern France; Neanderthals; Pre-Neanderthals

Introduction

Bone retouchers were first discovered at the end of the 19th century (Leguay, 1877; Daleau, 1883). Discoveries continued into the beginning of the 20th century at the Middle Palaeolithic site of La Quina (Henri-Martin, 1906, 1907, 1907-1910), and retouchers are now well defined and described elements in a wide range of Palaeolithic faunal assemblages (Chase, 1990; Vincent, 1993; Patou-Mathis and Schwab, 2002). Retouchers are bone, dental

or other osseous fragments bearing diagnostic features resulting from their use in lithic tool making. These include “deep, short, sub-parallel, closely clustered grooves, V-shaped in cross section” (Chase, 1990:443). The presence of parallel micro-striations within the grooves, and sometimes on the surface of the use area (sliding striations), and small, embedded lithic fragments are two other criteria confirming their identification (Rigaud, 1977; Vincent,

1993; Malerba and Giacobini, 2002; Schwab, 2002; Mallye et al., 2012; Daujeard et al., 2014; Abrams et al., 2014; van Kolfschoten et al., 2015).

The oldest occurrences of the use of bone to modify lithic tools are dated from Marine Isotope Stage (MIS) 13 at Boxgrove, UK (Roberts and Parfitt, 1999; Smith, 2013). Other early sites yielding bone retouchers are Caune de l'Arago (MIS 12; Moigne, 1996), La Micoque (MIS 12-11; Langlois, 2004; Risco, 2011) and Terra Amata (MIS 11; Moigne et al., 2016) in France; Gran Dolina TD10 in Spain (MIS 10-9; Rosell et al., 2011, 2015); Orgnac 3 (MIS 9; Sam, 2009; Sam and Moigne, 2011, Moncel et al., 2012a) and Cagny-l'Épinette (MIS 9; Tuffreau et al., 1995) in France; Bolomor Cave in Spain (MIS 9; Blasco et al., 2013a); Schöningen in Germany (MIS 9; van Kolfschoten et al., 2015); and Qesem Cave in Israel (400-200 ka; Blasco et al., 2013a, 2014). Besides the large bone tools made on proboscidean remains recovered in many European sites since MIS 9 (Gaudzinski et al., 2005; Anzidel et al., 2012; Boschian and Saccà, 2015), these early bone retouchers, mostly dated between MIS 11 and 9 and variably related to the presence of bifacial technology, confirm that the behavioural changes observed in Europe between 400 and 300 kya included bone recovery and use as a technological raw material (Rosell et al., 2011; Moncel et al., 2012a; Blasco et al., 2013a; Moigne et al., 2016). This type of bone tool appears alongside other major behavioural changes, such as the regular use of fire (Roebroeks and Villa, 2011), standardized carcass processing (Stiner et al., 2009; Blasco et al., 2013b), the targeted hunting of large ungulates (Oakley et al., 1977; Thieme, 1997), a decrease in pachyderm scavenging sites (Valensi et al., 2011; Anzidel et al., 2012; Gaudzinski et al., 2005), and lithic core technologies based on predetermined flake production (Moncel et al., 2012a). After MIS 9, from the end of Middle Pleistocene to the beginning of the Upper Pleistocene, and coinciding with the development of Middle Palaeolithic technology, many more sites have yielded bone retoucher series (Blasco et al., 2013a). Examples in France dating to the end of the Middle Pleistocene include the assemblages of Biache-Saint-Vaast (MIS

7; Auguste, 2002) and Le Lazaret (MIS 6; Valensi et al. 2013; Moigne et al., 2016). During the Upper Pleistocene, this type of bone artefact occurs at many sites (see Daujeard et al., 2014, and references therein).

In order to enhance our understanding of the circumstances surrounding the emergence of this bone technology, we explore their occurrence at a regional scale and over a broad time scale, ranging from the Final Acheulean and Early Middle Palaeolithic to the Middle Palaeolithic. In this study, we focus on a comparison of bone retoucher series from various sites in southeastern France (**Figure 1**), dating from MIS 11 to MIS 3 (**Figure 2**). Most of the sites presented here were studied recently and yielded archaeological, geological and chronological data: Terra Amata (MIS 11) along the Mediterranean coast; Orgnac 3 (MIS 9) and Payre F (MIS 7) in the Rhône Valley; Sainte-Anne I (MIS 6) in the Massif Central; and the cave of Lazaret (MIS 6) near the Mediterranean. Most of the other sites are dated to the Upper Pleistocene, from the Last Interglacial (MIS 5e at Baume Flandin), to the Early and Middle Pleniglacial Periods until MIS 3. The earliest sites (MIS 11 to MIS 6), including Terra Amata, Orgnac 3, Payre, Sainte-Anne I and Le Lazaret, yielded Acheulean and Early Middle Palaeolithic lithic assemblages, with varying quantities of bifaces. From MIS 5 to MIS 3, all the lithic assemblages clearly belong to Middle Palaeolithic techno-complexes.

These numerous series of bone retouchers are variable in age and located in a circumscribed geographical area, enabling us to compare various features of these artefacts, including frequency, type of blank (species and anatomical element) and morphology of use traces. We are also able to place them in their discovery context according to hominin species, type of occupation, faunal spectrum, environment and lithic industries, which allows us to explore chronological and geographical differences in the selection of bone elements and their use as tools. Were there specific *chaînes opératoires* and management strategies for this type of bone tool? Or, conversely, was there merely an *a posteriori* selection of some bone elements from

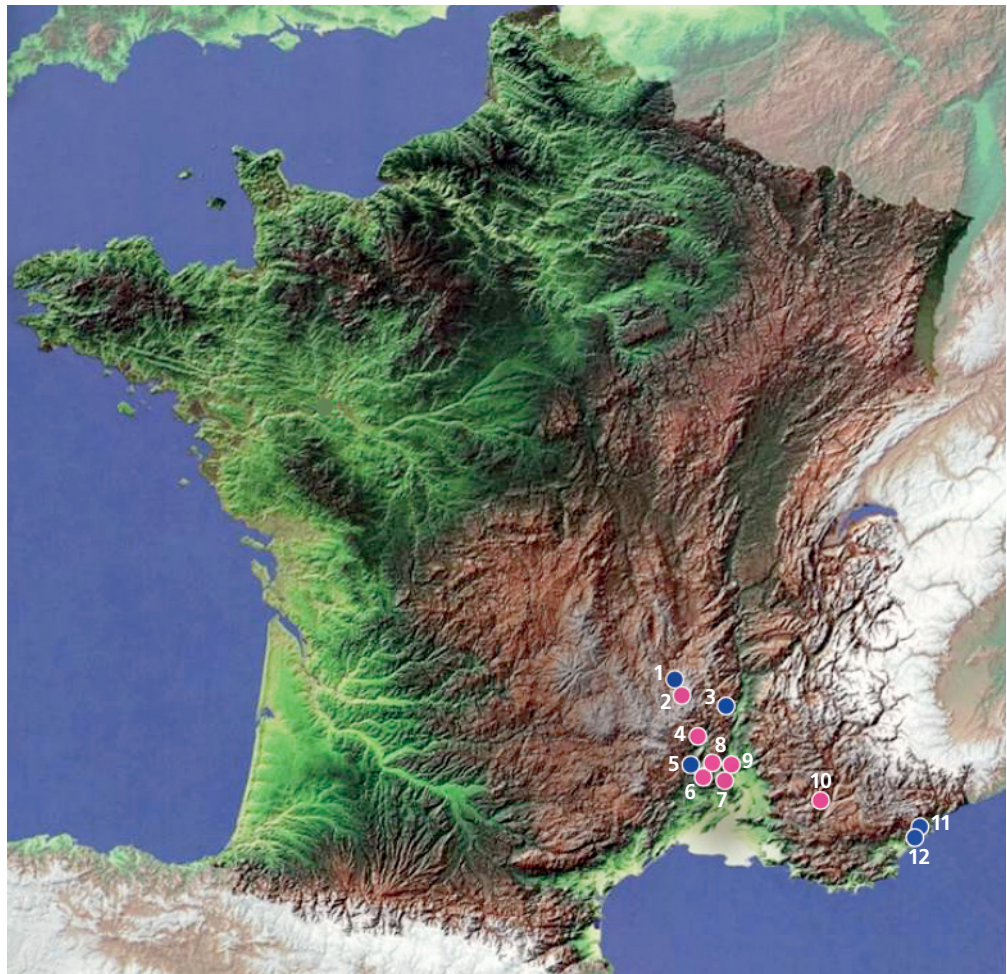


Figure 1 Location of the studied sites in southeastern France (Blue circles: Middle Pleistocene sites; Red circles: Upper Pleistocene sites). 1: Sainte-Anne I; 2: Baume-Vallée; 3: Payre; 4: Barasses II; 5: Orgnac 3; 6: Baume Flandin; 7: Le Figuier; 8: Saint-Marcel; 9: Abri du Maras; 10: Baume des Peyrards; 11: Le Lazaret; 12: Terra Amata.

among butchery remains shortly or some time after the accumulation of the deposits? Can we link the frequency, type, intensity and location of percussion marks (hash marks, grooves, cupules and striations) to any specific lithic technology (bifacial, discoid, Levallois, Quina), raw material (diverse flint types, quartzite, volcanic rocks, etc.), lithic tool management strategy and/or function (soft hammer, anvil, retoucher)? Finally, is there a relationship between the occurrence of these artefacts, activities and the type and duration of occupations?

Geographical, chronological and cultural contexts

Final Acheulean and Early Middle Palaeolithic sites

TERRA AMATA The site is an open-air locality in Nice, situated on the western slopes of Mount Boron. The archaeological deposits consist of a littoral marine formation at the base (stratigraphic unit C1a), composed of a beach of pebbles and silt (M unit), surmounted by a silt level (P4 unit), covered by a littoral barrier beach made of pebbles (CLs unit), and a large dune of sand at the top (stratigraphic unit C1b) (de Lumley et al., 1976; Pollet, 1990; de Lumley, 2013).

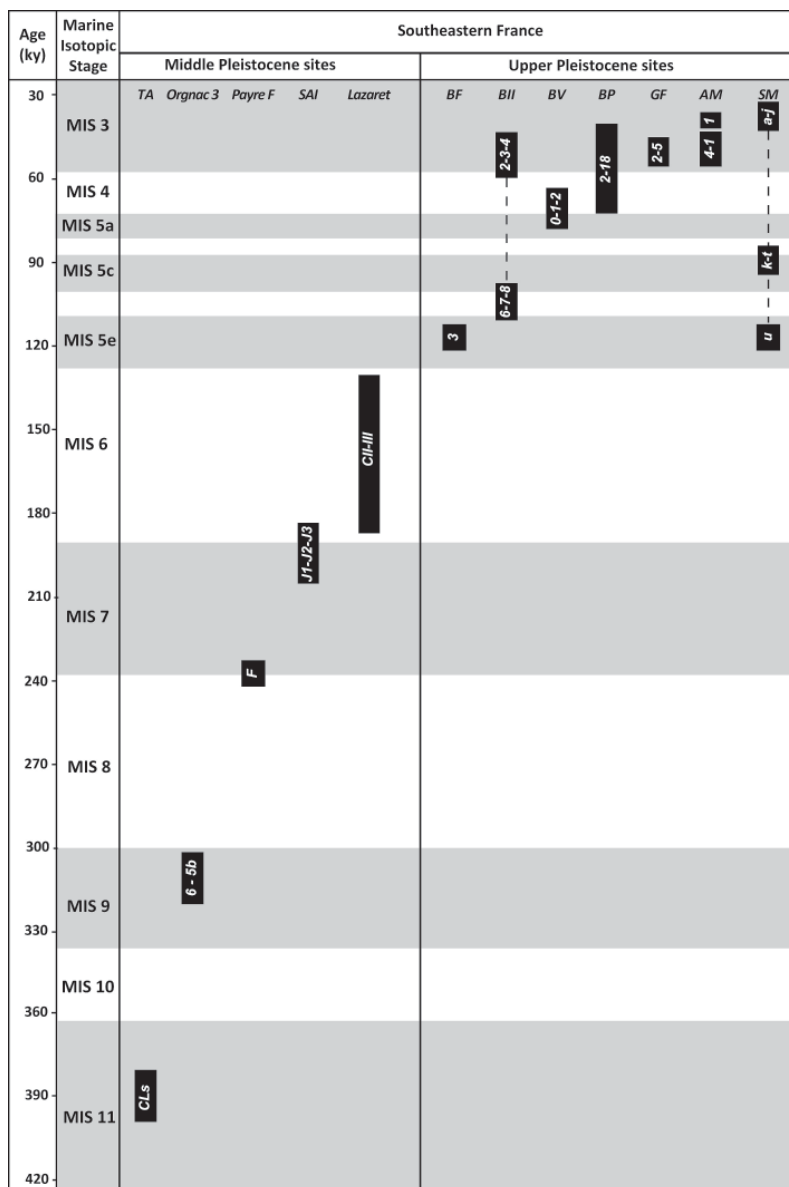


Figure 2 Chronological timespans of the various levels providing bone retouchers positioned according to the Marine Isotope Stages (MIS) (see references in text). TA: Terra Amata; Orgnac 3; Payre; SAI: Sainte-Anne I; Le Lazaret; BF: Baume Flandin; SM: Saint-Marcel; BII: Barasses II; BV: Baume Vallée; BP: Baume des Peyrards; AM: Abri du Maras; GF: Grotte du Figurier.

The large faunal assemblage is composed of eight large mammal species, with straight-tusked elephant (*Palaeoloxodon antiquus*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) as the most abundant species. The other species are aurochs (*Bos primigenius*), which is well represented in the upper levels (dune), brown bear (*Ursus arctos*), tahr (*Hemitragus bonali*) and rhinoceros (*Dicerorhinus [Stephanorhinus] hemitoechus*). The mammals, similar across the different levels, characterize a temperate period of the Middle Pleistocene (MIS 11 or 9) (Valensi, 2009; Valensi et al., 2011). The geology and general site

context more precisely correlate Terra Amata with MIS 11 (de Lumley et al., 2001).

The taphonomic study shows that the bone assemblage from the beach levels (M, P4 and CLs units) is the best preserved. Zooarchaeological data (Valensi and El Guennouni, 2004; Valensi et al., 2011) indicate widespread red deer hunting with transportation of whole carcasses to the habitation, followed by intense processing for subsistence purposes. Deer remains show a significant number of intentional green bone fractures, cut marks and striations. Hominins also brought portions of au-

rocks and young elephant carcasses to the camp. Marks left by carnivores are almost nonexistent on the faunal material.

The lithic industry, described as Acheulean, is characterized by abundant products from cobble shaping (choppers, chopping-tools, bifaces and cleavers). The majority of flake tools are scrapers, with some denticulates and notches. There is no Levallois, but unipolar and centripetal core technologies are present. About twenty retouchers on soft pebbles have been recorded within the beach levels (de Lumley et al., 2008; de Lumley, 2015).

ORGNAC 3 The site of Orgnac 3 is located on a plateau near the Ardèche River. It was initially a cave site, but was transformed into a rock shelter and finally into an open-air site (Combié, 1967; Moncel et al., 2005). The sequence was divided into ten archaeological levels. The ESR-U/Th ages obtained from the lower levels (4a-8) vary within the transition between MIS 9 and MIS 8 (Shen, 1985; Falguères et al., 1988; Laurent, 1989; Masaoudi, 1995; Michel et al., 2011, 2013). The upper level 2 contains volcanic minerals from an eruption of the Mont-Dore volcano, which can be attributed to the beginning of MIS 8 (Debard and Pastre, 1988). This age is in agreement with the age obtained by Fission track dating on zircons (Khatib, 1994; Michel et al., 2013). The upper level 1 is indirectly attributed to MIS 8 due to the presence of tahr (*Hemitragus bonali*) and bear (*Ursus deningeri*), which suggests that this level cannot be more recent than MIS 8 (Moncel et al., 2012a). Levels 2 and 1 are mainly characterized by species typical of an open landscape and mark the replacement of *Equus mosbachensis* by *Equus steinheimensis* (Forsten and Moigne, 1988). Combined biostratigraphical studies of mammal remains, microfauna and fossil pollen suggest that the layers 4a to 8, including layers 5b and 6 with bone retouchers, were deposited in a temperate context, characteristic of a Middle Pleistocene interglacial period (Guérin, 1980; Jeannet, 1981; Gauthier, 1992; El Hazzazi, 1998; Aouraghe, 1999; Sam, 2009). In these lower layers, fauna is rich and well preserved, with an abundance of cervid bones. Horse repre-

sents the second most hunted species, followed by large bovinds. As the site was still a cave, carnivores were abundant, but marks on bones mainly indicate activities subsequent to those of hominins (Moncel et al., 2005, 2011, 2012a; Sam and Moigne, 2011). The lithic industry is related to the Acheulean Complex with centripetal core technology. These layers yielded eight hominin teeth with evidence of living children (de Lumley, 1981).

Recent studies of the complete lithic and faunal assemblages from the ten archaeological levels of Orgnac 3 (1959-1972 excavations) (Combié, 1967; Aouraghe, 1999; Sam, 2009; Moncel et al. 2011; 2012 a) provide an opportunity to observe the contextual evidence of some behavioural changes. The site contains records of Upper Acheulean occupations (Combié, 1967), with evidence of Middle Palaeolithic behaviour at the top of the sequence (Moncel, 1999).

PAYRE The Payre site was a small cave above the confluence of the Rhône and Payre Rivers, located at the crossroads of various biotopes (Moncel, 2008). The five metre thick stratigraphic sequence yielded eight occupation layers dated from MIS 8-7 (Valladas et al., 2008). The spectrum of ungulates throughout the sequence is mainly composed of red deer (*Cervus elaphus*), horse (*Equus mosbachensis*), bovines (*Bos primigenius* and *Bison priscus*) and rhinoceroses (*Dicerorhinus [Stephanorhinus] hemitoechus* and *D. kirchbergensis*). Carnivores are especially numerous in level F. Among them, the cave bear (*Ursus spelaeus*) is predominant and associated with other carnivores, including wolf (*Canis lupus*), hyena (*Crocuta spelaea*) and cave lion (*Panthera [leo] spelaea*). This faunal list reveals a mildly cold climate and different biotopes, including forests, wooded prairie, steep rocky slopes (Payre canyon), as well as open steppe environments. The microfaunal remains indicate cold and steppe environments in layers G and F (Moncel, 2008).

Carnivores inhabited the site in layer F, suggesting that hominin occupations alternated with carnivore denning (Daujeard, 2008; Daujeard et al., 2011). The study of ungulate tooth microwear patterns

attests to longer occupations for layer G. During the accumulation of layer F, the cave was smaller in size with reduced ceiling height, which is reflected in the small number of lithic artifacts and taphonomic features of the faunal remains. Layer F was mostly a carnivore den with shorter-term hominin occupations (Rivals et al., 2009).

In both layers, we recorded a diversity of anthropic impacts on horse, red deer and bovines, the three main hunted taxa at Payre. Ungulate bones were intensively cut marked, broken, and some were burned. The use of fire is attested in each layer, but clear hearth structures appear only in layer G. Lithic residue and use-wear analyses show evidence of fish processing in layers Fa and D, as well as the use of avian resources (Hardy and Moncel, 2011). The lithic material is attributed to the Early Middle Palaeolithic, with a discoidal and orthogonal core technology on flint and mainly scrapers and points (Moncel, 2008; Baena et al., 2017). Some heavy-duty tools, as well as bifaces and pebble tools, were made on-site or outside the site on local quartzite, limestone and basalt (Moncel, 2008). Flint was mainly collected within a radius of less than 25 km around the site, although some flint flakes came from an area 60 km south of the site, suggesting hominin mobility on the plateaus bordering the Rhône Valley (Fernandes et al., 2008).

Neanderthal remains, including teeth, a mandible and a fragment of parietal, were discovered within the sequence, with most grouped in a small area at the bottom of sub-layer Ga (Moncel, 2008). The hominin remains belong to children, sub-adults and adults, except for the mandible of one old individual. It seems that familial groups were present, unless these remains were brought to the cave by carnivores.

SAINTE-ANNE I The cave of Sainte-Anne I is a small, south-facing cavity (50 m²) at 737 m above sea level. The stratified deposit contains several Middle Palaeolithic assemblages with bifaces. The stratigraphy preserves three main units (J1, J2 and J3) biochronologically attributed to MIS 6; however, ESR dates are younger (Raynal, 2007). The three main

units contain the same ungulate species (Raynal et al. 2005, 2008; Raynal, 2007), dominated by reindeer (*Rangifer tarandus*), horse (*Equus caballus* cf. *piveteaui*) and ibex (*Capra ibex*). Woolly rhinoceros (*Coelodonta antiquitatis*), bovines and other cervids complete the faunal spectrum. From a palaeoenvironmental viewpoint, the most important elements of the spectrum represent open arctic and mountain fauna groups, suggesting harsh and severe climatic conditions prevalent during MIS 6. Carnivore remains are rare, but fox (*Vulpes vulpes*), wolf (*Canis lupus*), lynx (*Lynx lynx*) and extinct cave lion (*Panthera [leo] spelea*) are present. Cut marks are more frequent on bones than carnivore tooth marks. Reindeer were the focus of hominin butchery activities, such as skinning, dismembering, defleshing, scraping of the metapodials and marrow extraction. Hominins consumed carcasses in the cave, and carnivores scavenged from these kills. Traces of fire are scarce. The presence of reindeer and horse deciduous teeth indicates an autumnal kill season. Data associate this site with a regular hunting camp alternately visited by carnivores.

Here, quartz, volcanic rocks and certain types of local flint exhibit complete reduction sequences, indicating that these abundant local lithic materials were flaked at the site. However, bifaces and unifacial flake-tools were produced outside the site, then brought there and used before being broken (Santagata et al. 2002; Santagata 2006, 2012; Raynal, 2007). Levallois and discoidal flaking were applied to cores made of volcanic rocks, and the occasional production of quadrangular flakes was the result of orthogonal or other unipolar flaking activity. The dense nature of the available raw materials sometimes required core reduction using bipolar anvil percussion. For all the raw materials, traditional core reduction technologies were used alongside opportunistic flaking methods. This dual approach produced flakes with functional, unmodified edges for particular subsistence activities, which explains the small number of retouched tools found at the site. Typologically, the lithics resemble the series recovered from Payre, where raw materials were chosen for their proximity to the site rather than for qual-

ity (Moncel 2003; Raynal et al. 2005; Raynal, 2007; Fernandes et al. 2008).

LE LAZARET Lazaret Cave is a vast cavity some 40 m long and approximately 15 m wide, located in Nice on Mediterranean coast. Systematic excavations brought to light 29 archaeological units in the CIII stratigraphic complex (UA 1-UA 12) and in the underlying CII complex (UA 13-UA 29) (de Lumley et al., 2004). Paleontological data concur with radiometric dating (ESR/U-Th) that correlates the CIII and CII stratigraphic complexes to MIS 6, the last glacial period of the Middle Pleistocene (Valensi and Psathi, 2004; Michel et al., 2009, 2011; Valensi, 2009; Hanquet et al., 2010). An interdisciplinary study of the fauna (amphibians, reptiles, birds and mammals) suggests a variety of continental landscapes linked to a relatively cold climate, moderated by the southern position of the site. A relative decrease in temperature and a gradual opening of the landscape occurred between complexes CII sup. (UA 13-UA 25) and CIII (Valensi et al., 2007; Hanquet et al., 2010). The spectrum of ungulates is mainly composed of red deer (*Cervus elaphus*), ibex (*Capra ibex*), aurochs (*Bos primigenius*) and to a lesser extent, roe deer (*Capreolus capreolus*), alpine chamois (*Rupicapra rupicapra*) and straight-tusk elephant (*Paleoloxodon antiquus*). Among the carnivores, wolf (*Canis lupus*) is predominant relative to other species, such as cave bear (*Ursus spelaeus*), brown bear (*Ursus arctos*), cave lion (*Panthera [leo] spelaea*), cave lynx (*Lynx spelaeus*), wolverine (*Gulo gulo*) and other small carnivores.

The multidisciplinary analyses conducted at this site revealed successive occupations by groups of nomadic large herbivore hunters (mainly red deer and ibex in all the levels), who set up temporary camps and sometimes occupied the cave for more prolonged periods (M'Hamdi, 2012; Valensi et al., 2013). The CII complex contains an Acheulean lithic assemblage with numerous bifaces and some Levallois debitage (5-10%). Above this deposit, the CIII complex is attributed to an Epi-Acheulean culture (de Lumley et al., 2004; Cauche, 2012). During the various periods of site occupation, the heavy-duty tools,

as well as bifaces and pebble tools, were mostly shaped from limestone pebbles collected in the river near the cave. Light-duty tools, preferentially made on siliceous raw materials are mainly composed of scrapers, points and notches. In the Acheulean levels UA28 and UA29, retouched products represent 5% and 7.5% of the assemblage, respectively (Cauche, 2012). In the different hominin occupation levels, many retouchers on small and flat pebbles have been identified (de Lumley et al., 2004).

Twenty-five Pre-Neanderthal remains have been discovered at Lazaret Cave, some of which present a transitional morphology between *Homo heidelbergensis* and *Homo neanderthalensis* (de Lumley et al., 2006).

Middle Palaeolithic sites

BAUME FLANDIN The site is a small cave near Orgnac 3, located along a small valley on the Orgnac plateau. The first archaeological investigations carried out at Baume Flandin (Orgnac l'Aven) began in the early 1950s (Gagnière et al., 1957). The excavators considered the site as a specific case study for understanding Middle Palaeolithic laminar assemblages, comparable to the nearby Abri du Maras. Faunal remains were studied by S. Gagnière, who attributed one archaeological level to a temperate period, just before the last glacial. Combier (1967) studied the sequence again and described three levels, with the hominin occupation dating to the Würm I glaciation. All the cave sediments were removed during the early excavations. In 2005, a new trench was excavated on the terrace in front of the cave (Moncel et al., 2008). Four levels were observed. The hominin presence at Baume Flandin (*in situ* level 3 and disturbed level 2) corresponds to an occupation inside the cave and on the present-day open-air terrace.

The faunal spectrum is dominated by red deer (*Cervus elaphus*) and horse that can be linked to a transitional form, *Equus germanicus* (*Equus* cf. *taubachensis*). Carnivores are numerous, dominated by wolf (*Canis lupus*), cave hyena (*Crocuta spelaea*) and fox (*Vulpes vulpes*). The large bovid

remains are attributed to the forested type (*Bison priscus mediator*). Ibex belongs to the Alpine type, *Capra ibex cebennarum*, recognized at the Abri des Pêcheurs (Moncel et al., 2010; Crégut-Bonnoure et al., 2010). The ungulate group, especially the abundance of cervids, as well as the presence of lynx (*Lynx spelaeus*), panther (*Panthera pardus*), wild boar (*Sus scrofa*), *Bison priscus mediator* and the great wood grouse (*Tetrao urogallus*), points to forested environmental conditions. The equid remains attest to more open areas, and the presence of *Equus hydruntinus* suggests mild climatic conditions. Hominin-induced cut marks were only found on red deer and roe deer (*Capreolus capreolus*), whereas horse and bovid remains present numerous carnivore marks.

The lithic assemblage from level 3 (outside the cave) appears to be homogeneous. The flaking sequence is complete, except for cores, which are not present on site. Most flakes are made from local Cenozoic flint. The flake tools represent 8% of the series and are mainly composed of lateral scrapers. The largest tool (115 mm long) is bifacially-worked from a flint slab. The assemblage is not exactly the same as that from inside the cave, and there is little evidence of laminar flaking. The differences observed between the inside and outside assemblages may result from different activities/occupations, or from the small size of the excavated area (Moncel et al., 2010).

BARASSES II This site is a small cavity above the Ardèche River, opening into a steep and rocky, south-facing cliff. Combiér (1968) conducted the first excavations in 1967 and 1968 and recognized various Middle Palaeolithic layers. New investigations began in 2011 to gather more data on the lower part of the sequence, which was only reached in one square metre during the first excavations (Combiér, 1968; Daujeard, 2014). The sequence is divided into two main lithostratigraphic parts: the lower (units 6-8) belongs to MIS 5d and the upper (units 2-4) dates between the end of MIS 4 and the beginning of MIS 3 (Richard et al., 2015). Both yielded Middle Palaeolithic industries.

The faunal list for the upper units 2-4, excavated from 2011 to 2013, shows a varied spectrum. Ibex (*Capra ibex*) largely dominate throughout the sequence, followed by cervids (*Cervus elaphus*, *Rangifer tarandus*), bovines, horse (*Equus* sp.) and chamois (*Rupicapra rupicapra*). Among the carnivores, which represent almost a third of the total number of identified specimens (NISP), we find mostly fox (*Vulpes vulpes*), cave bear (*Ursus spelaeus*), wolf (*Canis lupus*) and panther (*Panthera pardus*). In the newly investigated lower units 6-8, the faunal list does not change, apart from the absence of panther. However, carnivores are much less abundant, especially the large predators. Alterations to this mixed faunal assemblage resulted primarily from numerous carnivore visits to the small cave, which was regularly used for hibernation and denning. Throughout the sequence, about a third of the remains display carnivore marks. Cut marks increase from the bottom to the top of the sequence. Hominins preferentially processed secondary ungulates, such as cervids, bovines and equids. Evidence of fire is very scarce. Thus, this small cave may have provided a convenient shelter for various animals during harsh weather conditions, including recurrent and brief visits by small Neanderthal groups.

The lithic assemblages are diverse, composed of debitage products with long or short cutting edges. Most of them were brought to the cave, and were produced by various core technologies outside the site. Levallois technology predominates. Rare cores are on flint flakes, except for one in basalt. Some cores are retouched as flakes or used for the complementary debitage of small flakes. Flint flake-tools are rare. Some points are broken, probably accounting for their abandonment in the cave. Flint is the main raw material, brought in from a large perimeter around the site, but the lower unit indicates a broader use of volcanic stones available at the foot of the cave along the Ardèche River. In all units, volcanic stones provided pebbles for percussion (i.e., hammerstones), pebble-tools and perhaps a bifacial tool. These were also generally knapped outside the cave. In all the units, the flint *chaînes opératoires*, as well as many of the volcanic stone

chaînes opératoires, are partial, suggesting short-term occupations throughout the sequence. The more widespread use of volcanic stones in the lower unit may point to different types of occupations for the earliest uses of the cave.

BAUME VALLÉE The southeast-facing Baume-Vallée cliff with the Laborde rock-shelter is located at Solignac-sur-Loire in the Velay, 795 m above sea level. It lies on the left bank of the Ourzie River, which is a left bank tributary of the Loire. In its lower part, the shelter contains several stratigraphic units (0-2) belonging to the Ferrassie-type Charentian Mousterian. The stratigraphy shows that sedimentation was the result of primary and secondary frost action, particularly solifluction, which becomes increasingly evident towards the top of the Mousterian sequence and delineates a secondary strato-genesis. Dates achieved by TL and ESR give an age of around 80 kya (MIS 5a) (Raynal and Huxtable, 1989; Raynal et al. 2005).

Horse (*Equus caballus* cf. *germanicus*) is the dominant species, followed by cervids (*Cervus elaphus*, *Rangifer tarandus*), ibex (*Capra ibex*), bovines (*Bos* or *Bison* sp.) and other equids (*Equus hydruntinus*), while the remainder of the assemblage is composed of bird species and indeterminate carnivore fossils (Fiore et al., 2005; Gala et al., 2005; Raynal et al. 2005). In addition to a certain displacement of the faunal remains, periglacial taphonomic processes have also caused significant surface abrasion and fragmentation of the assemblage (Guadelli, 2008). In spite of the poor state of preservation, butchery processes, including marrow extraction and defleshing, have been identified. Carnivore modification to the bone assemblage is very rare and most of the fresh bone fractures can be attributed to hominin activity. Very few burnt bones were recorded. At Baume-Vallée, hunting focused mainly on cervids and equids during the first period of hominin occupation, while equids become the dominant hunted species during later times. Data support the hypothesis that the site was used regularly as a seasonal hunting camp (Fiore et al. 2005; Raynal et al. 2005).

Flint comprises 90% of the lithic assemblage recovered from unit 1 (Fernandes et al., 2006). Despite

the fact that most of the siliceous materials were gathered relatively close to the site, the geological knowledge of the inhabitants included an awareness of resources found up to 53 km from the site. Quina and Levallois knapping methods were used within both unique and composite reduction sequences, illustrating a concern for conserving lithic resources and a sophisticated technical understanding of the properties of different materials. Retouched products consist mainly of Levallois debitage or cortical Quina products and represent 20% of the assemblage in unit 1 and 35% in unit 2. Around 80% of the pre-determined Levallois flakes and 50% of the diverse cortical flakes were modified by continuous adjacent retouch. Notches represent 8% and 3% of the total in units 1 and 2, respectively, while denticulates are rare. Numerous retouchers on small and flat pebbles were identified in the different units (Raynal et al., 2005).

BAUME DES PEYRARDS The Baume des Peyrards, in Vaucluse, is a huge rock shelter situated in the east of the studied region, on the left bank of the Rhône. The site is located at 20 m above the right bank of the Aiguebrun River, facing southwest. It was first discovered by E. Arnaud in the second half of the 19th century and excavated at the beginning of the 20th century by M. Deydier and F. Lazard. In the 1950s, de Lumley (1969) excavated a large part of the terrace and recognized 29 levels distributed along 13 m of stratified deposits. Hominin occupations belonging to the upper units a to d are associated with the Würm I and II, which indicate alternating cold and temperate climates. These units yielded Middle Palaeolithic industries and rich faunal series.

In the upper part of the sequence (units a to d), ibex (*Capra ibex*) is dominant among ungulate species, followed by red deer (*Cervus elaphus*) and horse (*Equus caballus* cf. *germanicus*). Carnivores are scarce and include some forested species, such as brown bear (*Ursus arctos*), lynx (*Lynx pardinus*), fox (*Vulpes vulpes*) and dhole (*Cuon alpinus europaeus*). The faunal list in the upper units c and d is almost the same, except for an increase in cold indicators. The faunal accumulations are mostly due

to hominin activities. Cut marks are prevalent and indicate the exploitation of whole ungulate carcasses. The abundance of burnt bones and green bone breakage confirm the variety of subsistence activities carried out at the rock shelter. Data point toward the use of this huge rockshelter as a residential camp (Daujeard, 2008).

Raw materials are mostly local flint. In this Ferrassie assemblage, Levallois debitage is predominant, with abundant products modified by continuous retouch on convergent edges. A particular feature of this assemblage is the thinness of some of the Levallois flakes or scrapers (de Lumley, 1969; Porraz, 2002). De Lumley noted the homogeneity of the lithic industries throughout the sequence. Four Neanderthal teeth belonging to three young adults and one child (10-11 years old) were discovered in the Würm II layers (de Lumley, 1973).

LE FIGUIER Le Figuiier Cave opens above the Ardèche River, with the vast porch facing to the south. The cave is composed of three chambers, the largest being the closest to the entrance. A small corridor leads to the second and third chambers 20 m from the cave entrance. Initial excavations took place in the 1940s (Combier, 1967). Two Middle Palaeolithic layers were identified at the bottom of the sequence and have been attributed to the Quina facies (Moncel, 2001). Upper Palaeolithic levels (Aurignacian to Magdalenian) overlie the Middle Palaeolithic layers and yielded remains of a *Homo sapiens* child in the first chamber.

New fieldwork in all three chambers (Moncel et al., 2012b) led to the identification of a common infilling within the cave, consisting of six sedimentary units with one main Middle Palaeolithic layer at the bottom (units 2 to 5) (Moncel et al., 2012b). Sporadic disturbances due to cave bears and hyenas are observed within each layer in chambers 2 and 3. These disturbances do not affect the whole sequence, as each layer is clearly distinct from the others. Upper Palaeolithic artefacts are not *in situ*, while Middle Palaeolithic items from the bottom of the sequence resulted from hominin occupations within the chambers. Faunal and sedimentary data for this

main Middle Palaeolithic occupation indicate a cold phase of the Middle Pleniglacial (MIS 3) (Moncel et al., 2012b). A single ESR-U/Th age implies that the site was used at the end of MIS 4 and/or beginning of MIS 3 (Richard et al., 2015).

The ungulate spectrum is varied. Reindeer (*Rangifer tarandus*), horse (*Equus caballus*) and ibex (*Capra ibex*) are dominant, indicating a cold steppe environment. In the lower levels (unit 2), fallow deer (*Dama dama*), wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*) highlight warmer and more humid climatic conditions. Carnivores are abundant, mostly in the smaller chambers 2 and 3, including cave bear (*Ursus spelaeus*), cave hyena (*Crocota spelaea*), wolf (*Canis lupus*) and fox (*Vulpes vulpes*), among others. Taphonomic data indicate that carnivores frequently used the cave as dens and hibernating places, particularly the deep and narrow chambers 2 and 3. A few cut marked and broken bones with percussion marks attest to some Neanderthal incursions inside the karstic system, far from the entrance. Butchery and carnivore marks are found on the same species: reindeer, red deer and horse. Zooarchaeological data suggest regular short-term hominin camps alternating with carnivore occupations (Daujeard, 2008; Daujeard and Moncel, 2010; Moncel et al., 2012b).

Excavations in chamber 1 yielded two Middle Palaeolithic levels (2 and 4), including one Quina facies. This facies was not detected in chambers 2 and 3, which are further from the present entrance. In the three chambers, the debitage is mainly discoid on small flint core-flakes. Occupations in the dark chambers were different in nature, although they display the same technological behaviour. Flaking took place in the three chambers, producing elongated and thick flakes. Core-flakes were introduced into the site; some show Quina retouch in chamber 1 and smaller retouch in chambers 2 and 3 (scrapers, points).

ABRI DU MARAS The Abri du Maras site is a large rock-shelter located in a small valley near the Ardèche River. This site was first investigated by Gilles and Combier in the 1960s, followed by Moncel

since 2006 (Combiér, 1967; Moncel et al., 2015). This site is famous for Middle Palaeolithic deposits bearing a Levallois laminar debitage at the top of the sequence (level 1) (Combiér, 1967). The early excavations describe seven other distinct levels (levels 8-2) with Middle Palaeolithic assemblages (Combiér, 1967; Moncel, 1994, 1996). Since 2006, new excavations have focused on this lower part of the sequence. Rich lithic and faunal remains and hearths characterize level 4 of the new excavations, which comprises more than 40 m² and contains two phases of hominin occupations. The oldest layer, named layer 5 (levels 8-6 of earlier excavations), consists of an organic brown level with a sandy-silt matrix, covering the limestone substratum. The geological study demonstrates that the shelter's roof collapsed over time and that the most recent occupations took place below a small shelter (Debard, 1988). New ESR-U/Th ages obtained on layers 4.1 and 4.2 indicate that the site was still occupied at the beginning of MIS 3, thus extending the known chronology (Moncel et al., 1994; Moncel and Michel, 2000; Richard et al., 2015).

In order of abundance, the large faunal spectrum of layer 4 is composed of reindeer (*Rangifer tarandus*), horse (*Equus caballus* spp.), red deer (*Cervus elaphus*), bison (*Bison priscus*), ibex (*Capra ibex*) and giant deer (*Megaloceros giganteus*). Some lagomorphs, bird and fish remains attest to the occasional human consumption of small prey (Hardy et al., 2013). There are no carnivore remains, no carnivore gnawing marks, and no evidence of digestive corrosion. The broad faunal spectrum points to cold and open environments, which is consistent with sedimentary data and dating (Moncel et al., 1994, 2010; Daujeard and Moncel, 2010). Faunal remains are mainly related to Neanderthal activities. For reindeer, the most abundant prey, autumnal mortality is suggested by cementochronology and periods of tooth eruption; furthermore, the presence of mixed populations (all age classes) indicates far-sighted and organized slaughter during major autumnal migrations (Daujeard, 2008; Daujeard and Moncel, 2010). Systematic and intensive carcass processing occurred at the site. Data suggest the use of this rock shelter

as a place of large seasonal gatherings for Neanderthals.

Most of the artefacts are in flint from the nearby northern and southern plateaus. The assemblages are composed of elongated Levallois flakes, points, cores and small flakes produced on small Levallois core-flakes on site. The longest products were introduced into the site. Flake-tools, such as scrapers, denticulates and points, are very rare (Moncel et al., 2014). The first analyses of microwear traces and residues (Hardy et al., 2013) indicate a variety of activities, in addition to butchery, and some evidence for projectiles.

SAINT-MARCEL This site is a vast porch cave opening to the south, situated at an altitude of 53 m above the Ardèche River. Middle Palaeolithic layers were discovered under the porch during excavations conducted by R. Gilles in the 1950s (Gilles, 1976; Debard, 1988; Moncel, 1998). According to stratigraphic and sedimentological studies, about 40 layers were identified. Radiocarbon dates, first conventional (Évin et al., 1985) followed the AMS ¹⁴C method (Szmídt et al., 2010), were made in the upper layers of the sequence and yielded dates corresponding to the MIS 3 time range. Seven climatic sub-phases were identified throughout the sequence, with archaeological remains (levels u-c) and sedimentation gaps (Debard, 1988). Levels u-k, at the bottom of the upper layer, correspond to MIS 5e and the end of MIS 5. The rest of the sequence was deposited during a temperate and wet period during MIS 4/beginning of MIS 3. Levels f-c, at the top, belong to the Late Middle Palaeolithic. Hominin occupation is recurrent throughout the sequence and, except for level u, did not record behavioural change despite sedimentary breaks.

Throughout the sequence, the faunal spectra are largely dominated by cervids. Above level u, red deer (*Cervus elaphus*) is the most abundant taxon, followed by roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), ibex (*Capra ibex*), giant deer (*Megaloceros giganteus*), horse (*Equus caballus* cf. *germanicus*), aurochs (*Bos primigenius*), European ass (*Equus hydruntinus*) and wild boar (*Sus scrofa*).

Carnivore remains are absent. This association indicates temperate and humid climatic conditions with a mosaic of forested, open grassland and rocky environments. The faunal accumulation is mainly due to hominid activities. Cut marks are very frequent and carnivore tooth marks are almost absent. Seasonality indices show that the red deer assemblage, mainly made up of young animals and adults killed in herds, were hunted year round, with most slaughters occurring during the autumn (Moncel et al., 2004; Daujeard, 2008; Daujeard and Moncel, 2010). Carcasses were systematically brought back whole to the shelter and were then entirely eviscerated, skinned, dismembered, filleted and the bones broken for marrow and boiling. The levels yielded a huge number of bone retouchers and burnt elements. Data suggest a succession of long-term residential camps.

Lithic analyses reveal consistent technological behaviour through time based on a discoid core technology on flint flakes, and occasionally on nodules and pebbles. The flint was gathered on the northern and southern plateaus and along the Rhône Valley. Tools are rare, made up of side scrapers and points. Retouch is marginal and does not modify the shape of the products (Moncel, 1998; Moncel et al., 2004).

Materials and methods

This comparative study includes all the bone retoucher series from the 11 studied sites presented above. The number of bone artefacts is highly variable, depending on the layers (**Table 1**). All the studied material comes from recent (after 1950s) or ongoing excavations, with the exceptions of Le Figuier (Gilles and Combier), the upper units of Abri du Maras (Gilles and Combier) and Barasses II (Combier), and Baume Flandin (Gauthier), which include the former collections present at the Orgnac Museum (Orgnac-l'Aven, Ardèche). Thus, except for the early collections from Le Figuier and Baume Flandin, our study takes into account all the faunal remains, including sieving residues. Most of the lithic and faunal data result from our own analysis

and are first-hand or revised data (Fiore et al., 2005; Daujeard et al., 2014; Moigne et al., 2016). Detailed taphonomic data from the studied sites have been published in previous papers (Valensi, 2000; Fiore et al., 2005; Raynal, 2007; Daujeard, 2008; Daujeard and Moncel, 2010; Valensi et al., 2011, 2013; Moncel et al., 2012a,b; Daujeard et al., 2014).

In order to appreciate the bone retoucher frequency for each series, we present the number of bone retouchers (Nr) relative to the total number of anatomically identified specimens for ungulates (see **Table 1**). We could not provide total percentages, given that every author has a different way of calculating the total number of observed specimens (various minimum dimensions, which may or may not include illegible remains or teeth, etc.). We recorded anatomical, taxonomic, and modification data for each bone retoucher. For indeterminate fragments, we established three main size categories adapted to the ungulates in our sample: small-sized ungulates (SU) weighing less than 100 kg (chamois, roe deer, wild boar); middle-sized ungulates (MU) weighing between 100 and 300 kg (red deer, fallow deer, reindeer, ibex, European ass); and large-sized ungulates (LU) weighing between 300 and 1,000 kg (large bovines, horse and giant deer). Bone surfaces were studied with the naked eye and with a stereomicroscope (up to 80x) when necessary. For each specimen we recorded the type and location of the relevant modifications observed on legible surfaces, including those made by rodents, carnivores or hominins, as well as climatic and edaphic modifications (e.g., Behrensmeyer, 1978; Binford, 1981; Lyman, 1994; Fisher, 1995). The identification of breakage type (ancient green or dry bone fracture or recent fracture) was based on fracture colour, shape, features, angle and associated marks (Blumenschine and Selvaggio, 1991; Villa and Mahieu, 1991).

To identify the modifications resulting from hominid activity on bone retouchers, we used the criteria detailed in Patou-Mathis and Schwab (2002), Mallye et al. (2012), Daujeard et al. (2014) and Moigne et al. (2016). We noted the taxon and anatomical element for each bone artefact relative to the total

Table 1 Number and frequencies of bone retouchers and lithic tool types by site and layer. MIS = Marine Isotope Stage; Nr. = number of retouchers (%Nr. calculated on total number of ungulate remains), (+) = retouchers on pebbles; NI. = number of total lithic remains; NI.t. = number of lithic tools (%NI.t. calculated on NI); Nb. = number of bifaces (%Nb. calculated on NI); Ns. = number of scrapers (%Ns. calculated on NI.t.). no av. = no available data. Site abbreviations and excavations: Gauthier in 1950s at Baume Flandin (BF); Gilles and Combiér in 1950s-60s at Abri du Maras (AM: levels 1 and 2-5); Combiér in 1960s at Orgnac 3 and Barasses II (BII: levels 2-4); de Lumley from 1967 to 2014 at Le Lazaret, and in 1960s at Baume des Peyrards (BP) and Terra Amata (TA); Gilles in 1970s at Saint-Marcel (SM); Moncel in 1990s at Payre and since 2005 at Baume Flandin (BF), Abri du Maras (AM 4-1), Abri des Pêcheurs and Le Figuier (GF); Daujeard from 2011 to 2013 at Barasses II (BII) and Raynal in 1990s-2000s at Sainte-Anne I (SAI) and Baume Vallée (BV).

Site	Units	MIS	Nr.	%Nr.	NI.	NI.t.	%NI.t.	Nb.	%Nb.	Ns.	%Ns.
SM	a to j	3	274	7.3	3753	184	3.7-6.4	0	0.0	177	96.2
SM	k to t	5 s.l.	12	4.6	924	26	0-7	0	0.0	13	50.0
SM	u	5e	17	2.9	215	21	9.8	0	0.0	18	85.7
GF	2 to 5	3	3	1.1	304	33	10.9	0	0.0	17	51.5
AM	1	3	2	2.4	3695	45	1.2	0	0.0	26	57.8
AM	2 to 5	3	7	5.1	1989	144	7.2	0	0.0	82	56.9
AM	4-1	3	1	0.03	1864	50	2.7	0	0.0	15	30.0
BP	Upper	4-3	102	1.8	no av.	no av.	no av.	no av.	no av.	no av.	no av.
BV	0	5 s.l.	2 (+1)	0.8	89	3	3.4	0	0.0	2	66.7
BV	1	5 s.l.	11 (+4)	2.6	1602	320	20.0	0	0.0	285	89.1
BV	2	5/4	7 (+10)	1.7	956	335	35.0	0	0.0	295	88.1
BV	sup	3	0 (+22)	0.0	2977*	153	5.1	0	0.0	146	95.4
BII	2 to 4	3	4	1.1	173	10	5.8	0	0.0	7	70.0
BII	6 to 8	5 s.l.	5	1.2	618	8	1.3	0	0.0	3	37.5
BF	3	5e	5	4.0	136	11	8.1	1	0.7	7	63.6
SAI	J1-E1	6	37	2.1	4368	141	3.2	8	0.2	90	63.8
SAI	J2-E2	6	29	1.6	6734	93	1.4	0	0.0	64	68.8
SAI	J3-E3	6	7	2.5	680	19	2.8	0	0.0	12	63.2
SAI	Ind.	6	13	1.2	no av.	no av.	no av.	no av.	no av.	no av.	no av.
Lazaret	CIII	6	4	0.1	24916	1189	4.8	19	0.08	521	43.8
Lazaret	CII	6	14	0.2	56089	2366	4.2	311	0.6	1332	56.3
Payre	F	7	15	0.4	3700	422	11.6-30.6	6	0.2	193	45.7
Orgnac 3	5b	9	3	0.3	4174	447	10.7	28	0.7	209	46.8
Orgnac 3	6	9	5	0.4	2288	337	14.7	5	0.2	136	40.4
TA	CLs	11	1	no av.	6811	1263	18.5	8	0.1	52	4.1

*NI for the upper levels of BV including the fine fraction

NISP present in the faunal assemblages. For the dimensions, we recorded the length (L), width (W) and thickness (T) of the artefacts in millimetres (mm) and give L/W ratios when available.

For the use marks, we listed the number of use areas by artefact and classified the type of use marks as follows (nomenclature adapted from Malloy et al., 2012; Daujeard et al., 2014; Moigne et al., 2016): hash marks or grooves and scores (hatched

areas); cupules or pits (pitted areas) and sliding striations (comet striations) (Daujeard et al., 2014). One of the main criteria for identifying percussion marks is the presence of perpendicular micro-striations inside the retouching marks, which are similar to the sliding marks on surfaces (Vincent, 1993; Daujeard, 2014; van Kolfschoten et al., 2015). We measured the maximum length of the use areas and categorized them into three classes: < 10 mm, 10-20 mm,

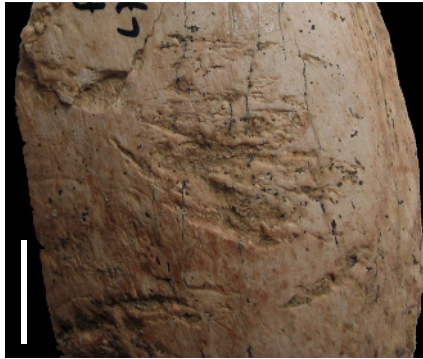


Figure 3 Bone retoucher on an indeterminate long bone shaft fragment from a large-sized ungulate (Payre/Fc-d, L7-990). The magnified use area is longer than 20 mm and presents deep scores (i2, i3) perpendicular to the long axis and situated on the extremity of the blank, on its lateral right side (scale = 1 cm).



> 20 mm. According to Mallye et al. (2012:1133), for the orientation of the retoucher and the localization of the marks, “the long axis of the retoucher is defined as its greatest length, and its apical part that on which the traces are located. When a retoucher has several areas with traces, it is reoriented for the analysis of each of them.” We thus localized the use marks on two axes. Relative to length, the use marks were identified as apical (extremity of the piece) or centred. In relation to width, use marks were categorized as centred, covering or lateral (right or left). The orientations of the marks relative to the long bone axis were recorded as perpendicular and/or oblique when possible. We used three categories to describe the distribution and depth of use marks within the use areas: dispersed (i1); concentrated (i2); or superimposed (i3). Finally, we noted all existing or directly associated marks, including scraping marks, cutmarks, cortical notches or heating marks.

Results

Frequency of bone retouchers in the context of lithic technology

For the early series of Final Acheulean and Early Middle Palaeolithic industries dated to MIS 11, 9 and 7, from Terra Amata, Orgnac 3 and Payre, we observe similar low rates of bone artefacts in relation to the number of ungulate remains (see **Table 1**). At Terra Amata, the only identified bone retoucher comes from a pebble layer or barrier beach (CLs), in which shaping and knapping activities took place. At Orgnac 3, bone artefacts are present at the bottom of the sequence, in layers 6 and 5b with bifaces and no Levallois cores. At Payre, the 19 bone retouchers come from a layer containing large, heavy-duty lithic tools. The technology is based on discoidal and orthogonal flint cores, with mainly scrapers

and points. In sites with Early Middle Palaeolithic industries dated to MIS 6, bone retoucher series occasionally become much more abundant, such as at Sainte-Anne I, where 87 bone artefacts are distributed throughout the three main units. There are some rare introduced bifaces at Sainte-Anne I, where Levallois and discoidal flaking were applied to cores made of volcanic rocks. There are many bifaces in the lower units at Le Lazaret (unit CII), which has provided more bone retouchers than the upper units (CIII) where bifaces become scarcer. Sequences containing Middle Palaeolithic industries dating from MIS 5 to 3, bone retouchers become more widespread, with marked variability in frequencies, regardless of core technology.

Types and dimensions of bone retoucher raw materials

At Terra Amata, the sole bone artefact is made on a red deer femur shaft, which is the main hunted species at the site. At Orgnac 3, distribution of retouchers by taxa is closely correlated to the overall faunal spectrum, with red deer, bovine and equid bone fragments (see **Supplementary data**). At Payre, we observed more selective behaviour with the predominant use of large or very large-sized ungulate remains (**Figure 3**). This differs from the relative pro-

portions of the total spectrum, where red deer is dominant. Except for one distal epiphysis of a horse humerus at Payre, all the bone artefacts are various types of long bone shaft fragments. For those three sites, all the bone retouchers are made on very large fragments, with a mean length of about 100 mm (**Table 2, Figure 4**). At Payre, one bone retoucher made on a proboscidean ulna shaft is 285 mm long. For Sainte-Anne I and Le Lazaret, species distribution follows that of the total faunal spectrum (see **Supplementary data**). Reindeer and horse are the most represented taxa at Sainte-Anne I, and red deer was mostly used at Le Lazaret. Elongated long bone shaft fragments are also preferred, especially tibias and metapodials (see **Table 2**). A few rib fragments were used at Sainte-Anne I, where the dimensions of the bone artefacts are among the smallest observed. Some of the small fragments may have been longer during use, given that frost action impacted the faunal assemblages from this mid-mountain site. Nonetheless, some small elements without truncated retouching areas or post-depositional fractures have been documented.

For the Upper Pleistocene series, bone artefacts generally follow the overall ungulate spectrum distribution (see **Supplementary data**). At Baume Flandin and Barasses II, red deer remains, mostly accumulated by hominins, were widely used for bone

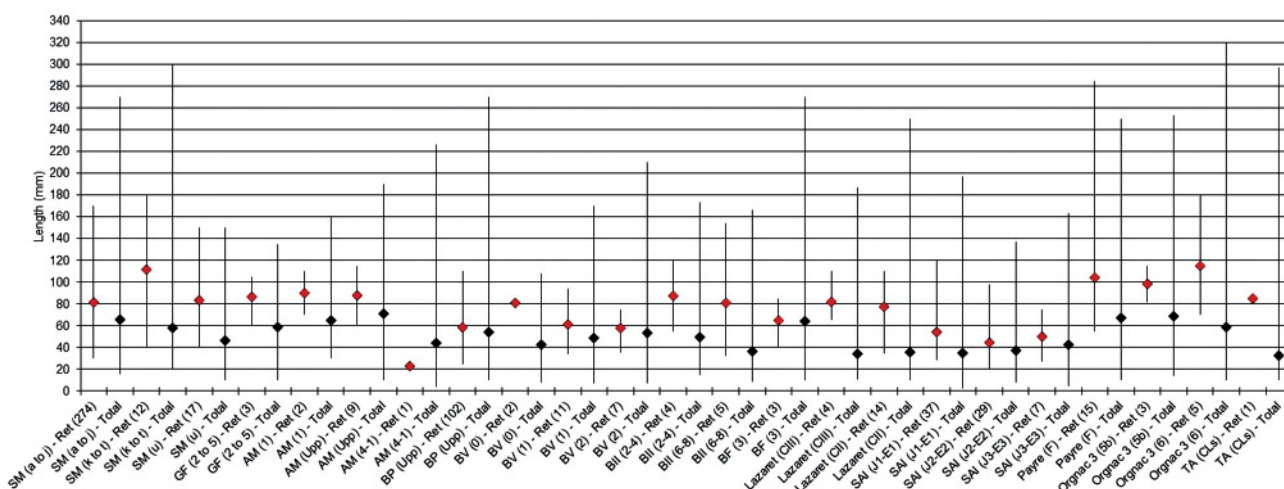


Figure 4 Minimum, maximum and mean lengths of the bone artefacts (red) compared to the lengths of the total bone remains for each series (black). See **Table 1** for site abbreviations.

Table 2 Description of the studied bone retouchers. Anatomical element data shown as % and (Nr) (Hum: humerus; Rau: radio-ulna; Rad: radius; Metc: metacarpal; Fem: femur; Tib: tibia; Mett: metatarsal; Metp: metapodial; Mand: mandible; LB: indeterminate long bone); Portion (SF: shaft fragment; EP: epiphysis); Breakage (GBB: green bone breakage); Nr burnt (number of burnt bone retouchers); Nr cut (number of cut marked bone retouchers); Dimensions (L: Length; W: Width; T: Thickness). no av. = no available data. See Table 1 for site abbreviations.

Site	Units	Anatomical element	Portion	Breakage	Nr. burnt	Nr. cut	Dimensions			
							L (mm)	W (mm)	T (mm)	L/W
SM	a to j	Tib: 19.3 (53), Rau: 11.3 (31), Metc: 11 (30), Hum: 11 (30), Fem: 7.3 (20), Mett: 6.6 (18), Metp: 5.5 (15), LB: 28.1 (77)	SF	Mostly GBB	17	40	81.6 (30-170)	no av.	no av.	no av.
SM	k to t	Tib: 6, Rau: 2, Fem: 2, Metc: 1, Hum: 1	SF	Mostly GBB	4	10	111.7 (40-180)	no av.	no av.	no av.
SM	u	Tib: 7, Metc: 3, Rau: 2, Hum: 2, Fem: 1, Mett: 1, LB: 1	SF	GBB	1	12	83.5 (40-150)	no av.	no av.	no av.
GF	2 to 5	Tib: 1, LB: 2	SF	GBB	1	1	86.7 (60-105)	no av.	no av.	no av.
AM	1	Rad: 1, LB: 1	SF	GBB	2	2	90 (70-110)	no av.	no av.	no av.
AM	2 to 5	Hum: 2, Fem: 1, Tib: 1, LB: 3	SF	GBB	2	2	87.9 (60-115)	no av.	no av.	no av.
AM	4-1	LB	SF	Ind.	1	1	23	8	no av.	2.9
BP	Upper	Tib: 21.6 (22), Fem: 20.6 (21), Hum: 15.7 (16), Rau: 4.9 (5), Metc: 3.9 (4), Mett: 1.9 (2), LB: 31.4 (32)	SF (1 EP)	Mostly GBB	2	85	58.6 (25-110)	no av.	no av.	no av.
BV	0	Tib: 1, Metc: 1	SF	GBB	2	2	81 (79-83)	28-29	7-7	2.8-2.9
BV	1	Hum: 3, Tib: 1, LB: 7	SF	GBB, frost	3	3	61.3 (34-94)	29.8 (20-44)	8.5 (2-14)	2.1 (1.3-3.4)
BV	2	Fem: 2, Tib: 1, LB: 4	SF	GBB, frost	5	5	57.9 (36-75)	31.9 (20-46)	11.4 (7-16)	1.8 (1.6-2.2)
BlI	2 to 4	Fem: 1, Rad: 1, LB: 2	SF	GBB	1	1	87.5 (55-120)			
BlI	6 to 8	Rib: 2, Tib: 1, Hum: 1, LB: 1	SF	Mostly GBB	1	1	81 (33-154)	23.8 (14-33)	6.8 (6-8)	3.5 (2.4-6.7)
BF	3	Tib: 2, Metc: 2, LB: 1	SF	GBB	4	4	65 (40-85)			
Lazaret	CIII	Metc: 3, LB: 1	SF: 3, EP: 1	Mostly GBB	1	1	82 (66-110)	25.5 (20-30)	19.5 (12-30)	3.3 (2.3-3.8)
Lazaret	CI	Tib: 5, Fem: 3, Hum: 1, Metc: 1, LB: 4	SF	Mostly GBB	7	2	77.5 (35-110)	23.9 (16-40)	14.6 (5-40)	3.2 (2.2-4.4)
SAI	J1-E1	Tib: 5, Mett: 4, Rib: 3, Rau: 3, Fem: 1, Metc: 1, Mand: 1, Ind. LB: 19	SF	GBB, frost	31	31	54.3 (29-120)	19.9 (9-42)	7.3 (2-21.1)	2.9 (1.3-8.6)
SAI	J2-E2	Tib: 2, Mett: 2, Rib: 2, Hum: 2, Metc: 2, Ind. LB: 19	SF	GBB, frost	23	23	44.7 (20-98)	17.7 (10-26)	5.4 (3-12)	2.6 (1.4-4.9)
SAI	J3-E3	Hum: 1, Metc: 1, Metp: 1, Ind. LB: 4	SF	GBB, frost	5	5	50.1 (27-75)	22.6 (12-41)	no av.	2.5 (1.6-5)
SAI	Ind.	Tib: 3, Hum: 3, Ind. LB: 7	SF	GBB, frost	10	10	65.2 (30-90)	27 (11-47)	9.1 (4-14)	2.5 (1.7-3.5)
Payre	F	Hum: 4, Ulna: 2, Tib: 1, Mett: 1, Metp: 1, LB: 7	SF: 15, EP: 1	Mostly GBB	8	8	104.3 (55-285)			
Orgnac 3	5b	Tib: 1, Metc: 1; Rad: 1	SF	GBB	1	1	98.5 (82-115)	26.5 (23-30)	21.5 (16-27)	3.7 (3.6-3.8)
Orgnac 3	6	Tib: 3, Mett: 1, Fem: 1	SF	GBB	1	1	115 (70-180)	32 (25-39)	21 (10-32)	5.1 (3.1-7.2)
TA	CLs	Fem	SF	GBB	85	27	85	27	20	3.1

retouchers. Conversely, the remains of other species that occur frequently in the assemblages but which were accumulated by carnivores or natural deaths, such as bovines or ibex, were not used. At Baume des Peyrards, ibex and red deer remains were preferentially selected. At Abri du Maras, horse and reindeer remains, the two dominant species, were also both selected. At Baume Vallée, bone artefacts are mainly on medium and large ungulate remains, following the same distribution as the faunal spectrum, with a majority of horse and cervids. Likewise, at Saint-Marcel, most of the bone retouchers are made of cervid remains (fallow deer, red deer, roe deer and giant deer, depending on the layers), which are far from the most important taxa in the sequence. Finally, in these youngest sites (MIS 5-3),

almost all the retouchers are made on elongated long bone shaft fragments (see **Table 2**). We only noted the exceptional presence of a utilized ibex femoral head at Baume des Peyrards. Tibias or femurs are the most represented long bones. Apart from the assemblage of Baume-Vallée, which was impacted by frost, Baume des Peyrards and Baume Flandin are the only sites where bone retouchers have a mean length lower than 80 mm.

Nearly all of the bone artefacts present green bone fractures and various types of carcass processing cut marks (**Figure 5**, see also **Table 2**), and thus probably selected from butchery waste. For example, one bone artefact at Baume des Peyrards presents some use marks overlapping the fracture edge, indicating that this bone artefact was used



Figure 5 Bone retoucher on a red deer tibia shaft fragment bearing cut marks and green bone fractures (Baume Flandin, n. 45, coll. Gauthier). The use area presents concentrated deep scores (i2; 10-20 mm) oriented perpendicular to the long axis, situated on the extremity of the blank on its lateral left side, and appears to have been broken during use (truncated area) (scale = 1 cm).



Figure 6 Bone retoucher on an indeterminate shaft fragment of a medium-sized ungulate (Sainte-Anne I, R26-727). The use area presents widespread deep scores (i2) on the small bone surface (> 20 mm) and was probably truncated by a green bone fracture during use. Numerous associated scraping marks are also present (scale = 1 cm).



Figure 7 Bone retoucher on a burnt metacarpal shaft fragment of a red deer (Le Lazaret, Laz10-Q12-4567). The use marks are dispersed scores within a large area (i1; > 20 mm), perpendicular to the long axis and situated on the extremity of the blank (scale = 1 cm).

after the bone fracturing process (Daujeard et al., 2014). In a few cases, broken modified areas show that use may have caused the break (Figure 6, see also Figure 3). However, in the absence of systematic refitting, it remains difficult to discern the intentionality of bone fracturing and/or shaping for the use of bone remains as retouchers.

In the lower Acheulean unit CII at Le Lazaret, half of the bone retouchers are burnt (Figure 7, see also Table 2), either as a result of being thrown in the fire after use or prior to heating, accidentally or intentionally. The presence of some scaled zones on these artefacts seems to indicate a loss of freshness, which lends support to the latter hypothesis. Compared to Le Lazaret, the Upper Pleistocene samples contain very few burnt artefacts, and it is difficult to establish the precise sequence of events.

Number, position and description of the use areas and associated retouching marks

Pitted or hatched areas are visible on the oldest series of Terra Amata and Orgnac 3 retouchers (Table 3), with marks mostly perpendicular to the bone axis and on the extremities of the blanks, characteristic of retouching/resharpening the lithic edges by percussion. At Orgnac 3, only two bone retouchers present two use areas; all others have a single retouching zone. This is also the case at Payre, where most of the artefacts bear a single use area. Two have use marks at both ends of the blank and one has four use areas. Payre provides the most robust and longest artefacts, with the deepest and most extensive use marks. Some retouchers have associated cortical notches, demonstrating a powerful striking action (Figure 8, see also Table 3). More than a third of the use areas on the Payre retouchers bear circumscribed scraping marks indicating that the surface was cleaned before use. At Le Lazaret, the 18 bone retouchers have one or two use areas with shallow hash marks and pits on their edges, perpendicular or slightly oblique to the bone axis. Unlike at Payre, the widespread presence of scraping marks on the blanks from Le Lazaret unit CII suggests a link to butchery activities (fracture process) rather than the cleaning of the areas used for retouching. At Sainte-Anne I, which provided the smallest blanks, the retouch marks are among the shallowest observed. In this sample, we recorded a particularly high number of pitted areas associated with sliding striations, or what we call comet striations (cf. Daujeard et al., 2014). Many of these are situated on the mesial part of the blanks (centred), which is quite rare for the hatched areas, and may be related to a specific action still unknown.

Finally, among the Upper Pleistocene series, most of the marks are shallow hash marks present on blank extremities perpendicular to the long axis (see Table 3). A few examples from Baume Vallée (unit 1), Saint-Marcel (k-t) and Abri du Maras (upper units) bear numerous use areas with deep hash marks (i3). Some others, including Baume des Pey-

Table 3 Description of the use areas. Na (number of use areas); Na/blank (number of use areas per blank: 1, 2 or > 2); Type of marks (sc: scores; pit: pitted areas; stri: sliding striations); Lmax (maximum length of the use area); Orientation of marks (perp: perpendicular; obl: oblique; no: no orientation for cupules); Distribution and depth of marks (i1: dispersed; i2: concentrated; i3: superimposed); Location on blank (ap: apical; cent: centered; cov: covering); Position on the width (cent: centered; cov: covering; lat: lateral; R: right; L: left); Associated marks (Scr: scraping marks; Perc: notches or green bone fractures; Tr: truncated). no av. = no available data. See Table 1 for site abbreviations.

Sites	Units	Na	Na/blank	Type of marks	Lmax (mm)	Orientation of marks	Distribution and depth of marks	Location on blank	Position on width	Associated marks		
										Scr	Perc	Tr
SM	a to j	188	1:115, 2:27, >2:6	sc:154, pit:30, stri:4	<10:65, 10-20:88, >20:35	perp:114, obl:40, no:34	i2:74, i1:65, i3:49	ap:178, cent:10	no av.	12	7	
SM	k to t	20	1:5, 2:6, >2:1	sc:14, sc-pit:6	<10:4, 10-20:7, >20:9	perp:10, obl:1, perp-obl:9	i2:10, i3:6, i1:4	ap:20	no av.		8	
SM	u	23	1:13, 2:2, >2:2	sc:19, sc-pit:2, pit-stri:1, sc-stri:1	<10:9, 10-20:13, >20:1	perp:16, obl:4, perp-obl:2, no:1	i1:12, i2:10, i3:1	ap:23	no av.	5	1	1
GF	2 to 5	4	1:2; 2:1	sc:3, pit:1	10-20:4	perp:1, obl:2, no:1	i1:2, i2:1, i3:1	ap	cent:2, no av.:2	2	1	1
AM	1	3	1:1; 2:1	sc-pit:2, sc:1	10-20:2, >20:1	perp:3	i1:2, i2:1	ap:3	cent:2, lat R:1	2	1	1
AM	2 to 5	12	1:5; >2:2	sc:10, sc-pit:2	10-20:8, >20:4	perp:7, obl:3, perp-obl:2	i3:7, i2:3, i1:2	ap:10, cent:1, ap-cent:1	cent:9, cov:1, lat R:1, lat L:1	2		3
AM	4-1	1	1:1	sc-pit-stri	<10	perp	i1	ap	no av.			
BP	Upper	118	1:102, 2:14, >2:2	sc:111, pit:5, stri:2	<10:15, 10-20:87, >20:16	perp:90, obl:23, no:5	i2:58, i1:46, i3:14	ap:99, cent:19	no av.	29	3	
BV	0	3	1:1; 2:1	sc:1, sc-pit:1	10-20:1:>20:2	obl:2; perp-obl:1	i1:1, i2:1, i3:1	ap:3	cent:1, lat L:2			1
BV	1	12	1:10; 2:1	sc:8, sc-pit:4	10-20:9:>20:3	perp:6, obl:5; perp-obl:1	i3:7, i1:3, i2:2	ap:12	cent:6, lat L:2, lat R:4	4	5	
BV	2	7	1:7	sc:5, sc-pit:1, pit:1	10-20:7	perp:3, obl:3; perp-obl:1	i1:4, i3:2, i2:1	ap:7	cent:5, lat L:2	1	4	
Bll	2 to 4	5	1:3; 2:1	sc:5	<10:1, 10-20:2, >20:2	perp:3, obl:1, perp-obl:1	i2:3, i1:2	ap:3, cent:2	cent:5	1	1	
Bll	6 to 8	6	1:4; 2:1	pit-stri:3, sc:2, sc-pit:1	<10:3, 10-20:2, >20:1	perp:1, obl:3, no:2	i1:5, i2:1	ap:3, cent:3	no av.	2	1	
BF	3	8	1:3; 2:1; >2:1	sc:6, sc-pit:2	10-20:4, >20:4	perp:6, perp-obl:2	i2:5, i1:2, i3:1	ap:8	lat L:5, cent:2, lat R:1	7	3	5
Lazaret	CIII	5	1:3; 2:1	sc:3, sc-pit:2	10-20:4, >20:1	perp:2, perp-obl:3	i1:4, i2:1	ap:5	lat L:3, cent:1, cov:1	1	1	1
Lazaret	CII	18	1:10; 2:4	sc:12, sc-pit:5, sc-pit-stri:1	<10:3, 10-20:8, >20:7	perp:7, obl:5, perp-obl:1, no:5	i1:9, i2:5, i3:4	ap:13, cent:4, ap-cent:1	cent:13, lat R:3, cov:2	5	4	1
SAI	J1-E1	43	1:30, 2:4, >2:3	stri:14, sc:10, pit:6, sc-pit:5, sc-stri:5, sc pit-stri:3	<10:4, 10-20:22, >20:17	perp:25, obl:1, perp-obl:2, no:15	i1:30, i2:8, i3:5	cent:18, ap:15, cov:9, Ind:1	no av.	2	3	
SAI	J2-E2	29	1:29	sc:8, pit:5, sc-pit:7, stri:5, sc-stri:1, sc-pit-stri:3	<10:4, 10-20:11, >20:14	perp:17, obl:1, perp-obl:2, no:9	i1:19, i2:8, i3:2	cent:10, ap:10, cov:9	no av.	4	2	
SAI	J3-E3	7	17	sc:5, sc-pit:2	10-20:6, >20:1	perp:7	i1:4, i2:2, i3:1	ap:4, cent:2, cov:1	no av.		1	
SAI	Ind.	20	1:11, 2:3, >2:1	sc:7, sc-pit:6, sc-stri:2, stri:3, pit:1, sc-pit-stri:1	<10:2, 10-20:12, >20:6	perp:16, perp-obl:2, no:2	i1:7, i2:7, i3:6	ap:12, cent:5, cov:2, Ind:1	no av.		2	
Payre	F	20	1:13, 2:1, >2:1	sc:13, sc-pit:4, pit:3	<10:1; 10-20:9, >20:10	perp:17, perp-obl:1, no:2	i3:9, i2:7, i1:4	ap:11, cent:8, cov:1		6	7	5
Orgnac 3	5b	4	1:3; 2:1	sc-pit:3, sc:1	>20:4	perp:4	i2:3, i1:1	ap:2, cent:1	cent:3, lat R:1		3	
Orgnac 3	6	6	1:5; 2:1	sc-pit:6	10-20:3, >20:3	perp:4, perp-obl:2	i2:5; i3:1	ap:4, cent:2	cent:6		5	1
TA	CLs	1	1:1	sc:1		perp:1	i3:1	ap:1	lat L:1			1

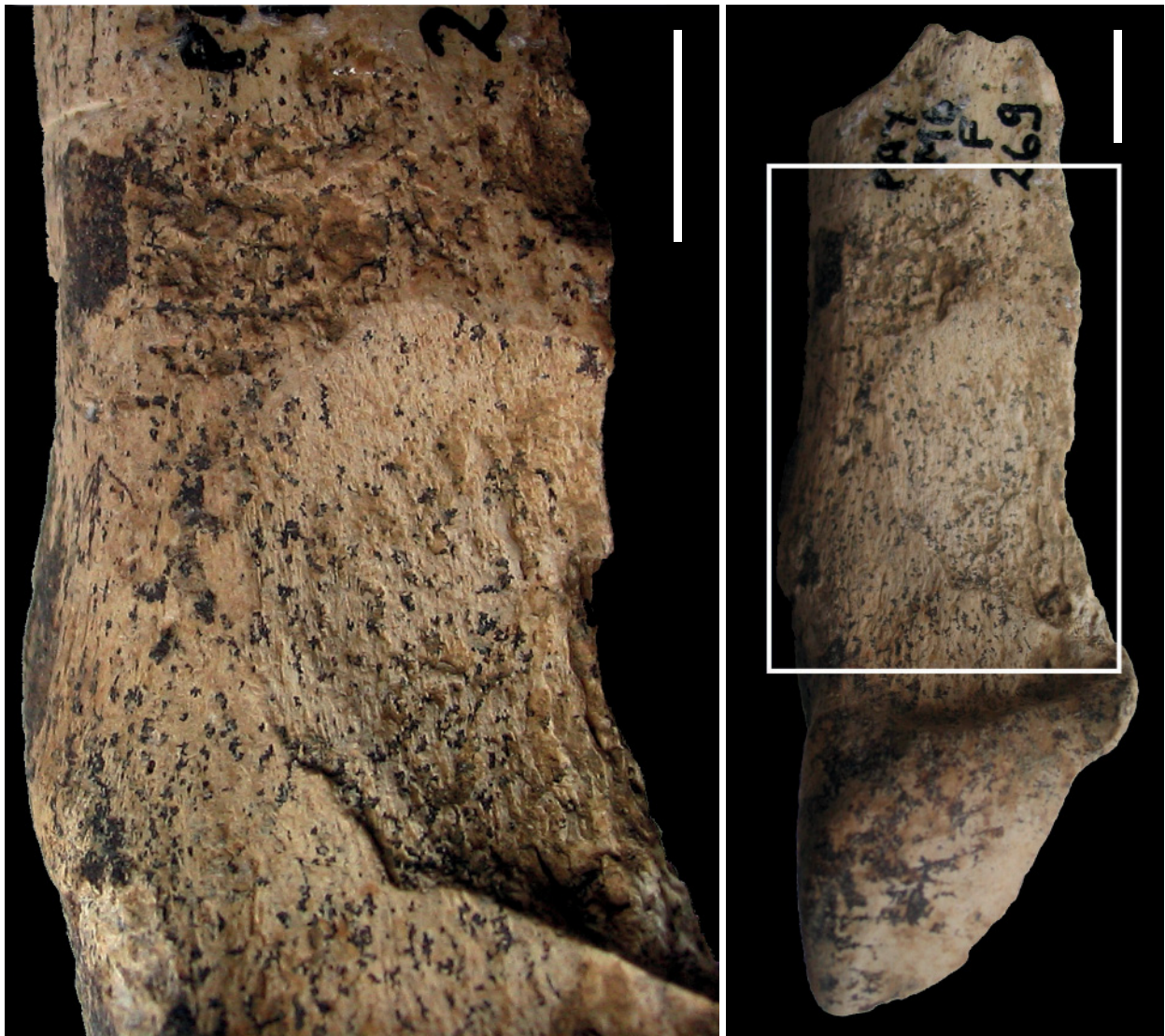


Figure 8 Bone retoucher on the distal part of a horse metapodial shaft fragment (Payre/Fc-d, M6-269). The use area present deep scores (i3) perpendicular to the long axis and concentrated on the extremity of the blank in its central part. The retouching area is associated with a percussion notch (scale = 1 cm).

rards, Saint-Marcel and Les Barasses II, show cupules (pits) associated with sliding striations (comet striations). With the exception of Baume Flandin, Baume Vallée (unit 1) and Saint-Marcel (k-t), where the majority of the use areas were “cleaned” beforehand, associated scraping marks are generally poorly represented (Figure 9; see also Daujeard et al., 2014). Finally, most of the recent series display some rare elements with deep grooves associated with notches or green bone fractures resulting from violent percussion (Daujeard et al., 2014).

Discussion

The main focus of this study was to analyze bone retoucher variability in relation to the faunal and cultural remains found in late Lower and Middle Palaeolithic sites in southeastern France, on both sides of the Middle Rhône valley. The large sample of bone retouchers studied here allows for a regional analysis of variability among these tools. Beyond that, we are able to extend our comparative approach to a wider European scale.



Figure 9 Bone retoucher on a tibia shaft fragment of a large-sized ungulate (Baume Vallée, unit 1, H6_811). The used area presents deep and concentrated scores on the extremity of the blank, associated with anterior scraping marks (see also Fiore et al., 2005 for the use mark description) (scale = 1 cm).

Variations in bone retoucher frequency

The main difficulty involved in comparative analyses concerns differences in counting faunal remains, which depend on the researcher (see Materials and methods). To overcome this, we compare the number of bone retouchers with the NISP of ungulates, which is a stable count in our faunal analyses (Figure 10, see also Table 1). The identification of retouching marks represents another difficulty. We listed in the method section the various criteria used

to distinguish the marks caused by the use of bone to shape lithic tools, but sometimes doubts persist. This is the case for incipient percussion marks concentrated on circumscribed surfaces that could be mistaken with intentional retouching marks. Another important point relates to the observation process itself. We only recognize the marks we expect to find, so it is likely that such use marks for earlier sites went unnoticed.

Nonetheless, based on current data, the oldest bone retouchers we studied are dated to MIS 11.

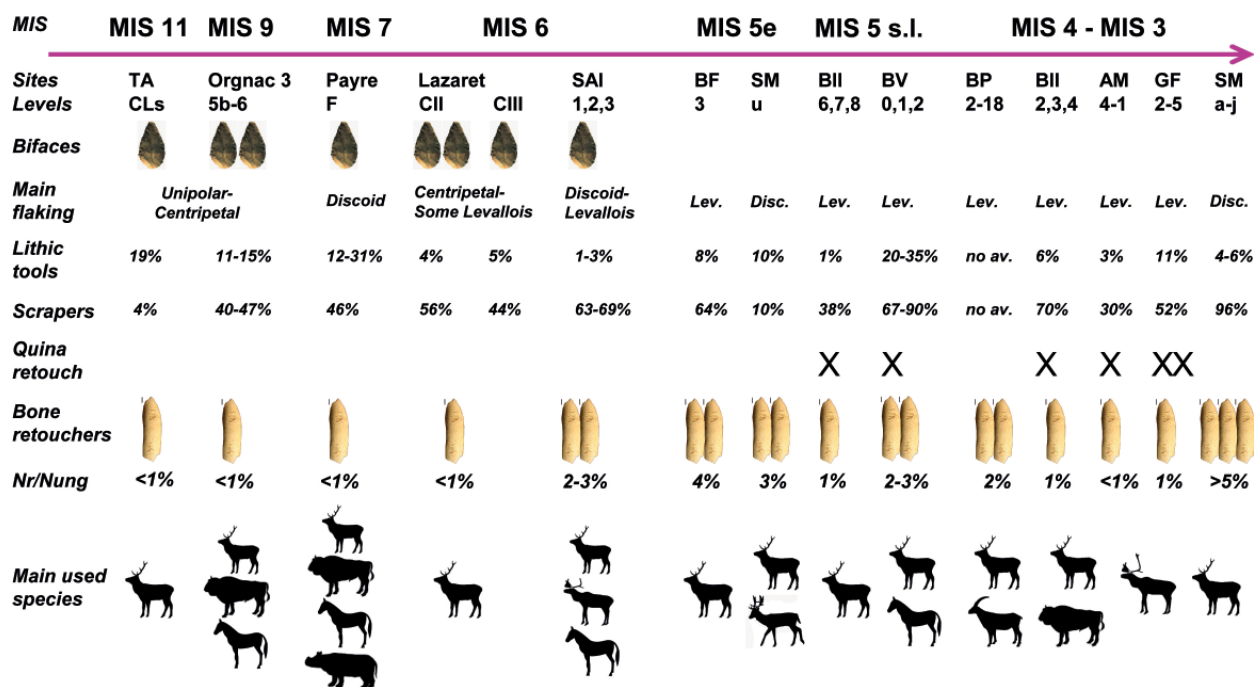


Figure 10 Contextual data for sites with bone retouchers in southeastern France: presence of bifaces; main flaking technology; percentages of lithic tools relative to the overall lithic assemblages; percentages of scrapers relative to overall number of tools; presence of Quina or semi-Quina retouch; frequency of bone artefacts; equivalence or non-equivalence with total ungulate spectra; and main used species. TA: Terra Amata; Orgnac 3; Payre; SAI: Sainte-Anne I; Le Lazaret; BF: Baume Flandin; SM: Saint-Marcel; BII: Barasses II; BV: Baume Vallée; BP: Baume des Peyrards; AM: Abri du Maras; GF: Grotte du Figuier.

From MIS 11-7, bone retouchers remain rare in the Final Acheulean and Early Middle Palaeolithic assemblages (see references in the Introduction). The number of these bone artefacts increases with the onset of Middle Palaeolithic technology, from the end of MIS 7 to MIS 5, for example at Sainte-Anne I in south-central France or Biache-Saint-Vaast in northern France (Auguste, 2002). Then, when the Middle Palaeolithic becomes widespread, with distinct regional traditions after MIS 5, these bone artefacts become ubiquitous. The sites with the highest numbers of bone artefacts, sometimes totaling several hundred pieces, are contemporaneous with the Late Middle Palaeolithic, such as the upper levels of Saint-Marcel (Nr = 274), level 22 at Jonzac (Nr = 202; Beauval, 2004) or Les Pradelles Facies 4a (Nr = 497; Costamagno et al., 2018) in France, Axlor (Nr = 492; Mozota, 2009, personal communication) in Spain or Kůlna in the Czech Republic (Nr = 248; Vincent, 1993; Auguste, 2002). Blasco et al. (2013a) also

underline this link between the emergence of bone retouchers and the development of post-Acheulean, Middle Palaeolithic technology, and further suggest that the latter technology required more retouching than the Acheulean (new or different lithic management strategy).

Nevertheless, from MIS 7 onwards, we observe great variations in the number of bone retouchers in each occupation layer throughout southeastern France, and Europe as a whole, and the reasons for this variability remain unknown.

Looking at the Orgnac 3 and Le Lazaret series, we could question the relationship between the presence of bone retouchers and bifacial technology, given that the bone artefacts are more numerous in the lower units. Yet, the frequencies of bone retouchers remain very low in these layers, and numerous bone retouchers series at other sites are associated with lithic industries devoid of or comprising very few bifaces, for example at Sainte-Anne I or

in all the youngest Middle Palaeolithic assemblages (see **Figure 10**). At the beginning of MIS 3 at Abri du Maras, which presents Levallois core technology, bone retouchers are rare. In contrast, many bone retouchers are associated with the mainly Levallois core technology at Baume-Vallée and Baume des Peyrards (MIS 5-3), as well as at Biache-Saint-Vaast (MIS 7). The site of Saint-Marcel (MIS 3), with discoid lithic technology, yielded abundant bone retouchers, as did the site of Le Rozel in northern France (Sévêque and Auguste, 2018). Finally, the sites of Les Pradelles and Qesem Cave in Israel, both with Quina technology and numerous Quina scrapers, also contain many bone retouchers (Blasco et al. 2013a; Rosell et al., 2015; Costamagno et al., 2018). Given that the presence of a high number of bone artefacts is associated with various types of lithic technology, bone retouchers cannot be linked to specific debitage modes.

The number of bone retouchers is also not related to the tool ratios and the type of lithic tools recovered in the assemblages. At Saint-Marcel, we observed some of the lowest ratios of stone tools and the highest ratios of bone retouchers. These very low ratios of tools compared to the richness of the bone retouchers cannot solely be explained by the export of some tool kits or by the unexcavated parts of the site (Daujeard et al., 2014). Regarding scraper production and re-sharpening, some series contain a very small number of retouched tools (Saint-Marcel and Sainte Anne I), while others, like Baume-Vallée, contain a high number of retouched tools that are essentially scrapers; nevertheless, both have the richest series of bones retouchers. In the rare sites with Quina or semi-Quina retouch (Le Figuiier, Abri du Maras, Barasses II and Baume-Vallée; see **Figure 9**), bone retouchers are not proportionally more abundant and there is no clear difference in their surface modifications.

Overall, we observe similar rates of bone retouchers for different sorts of raw material, for example the volcanic rocks at Sainte-Anne I and Baume Vallée compared to the various types of flint at the Middle Palaeolithic sites of Ardèche. Abri des Pêcheurs, which yielded mainly quartz artefacts, may be one

exception regarding the absence of bone retouchers in the Middle Palaeolithic.

Finally, could the frequency of bone retouchers be related to the type of hominin occupation and activities? For example, at Saint-Marcel, associated with long-term hominin occupations, we observe the most numerous retoucher series. In contrast, in the contemporaneous bivouac occupations of Les Barasses II or Les Pêcheurs, bone retouchers are rare or absent.

To conclude on the varying frequencies of bone retouchers studied on regional and temporal scales, it remains difficult to find a suitable explanation for their presence/absence or abundance/scarcity based on a single factor. Scraper production and re-use, the mobility strategy of the artefacts, the type of activities performed in and immediately surrounding the sites, or even the occupation duration, may all be taken into account in a multi-factorial attempt to explain patterns. Therefore, this question requires further investigation through more extensive data sets at a larger geographical and chronological scale (up to the Upper Palaeolithic); or, on the contrary, at a reduced scale with more information about very local subsistence strategies.

What about variations in the type of bone elements?

The same types of bone elements were used from MIS 11 to MIS 3: mainly long bone shaft fragments, usually on medium- or large-sized ungulate remains. They are sometimes, but not always, proportionate to the total faunal spectra and the long bone elements present in the faunal assemblages (see **Supplementary data**). Red deer is by far the most frequently used taxon (see **Figure 10**), but small- and other medium-sized ungulates such as roe deer, chamois, fallow deer, reindeer or ibex are frequent and were used for retouchers at Saint-Marcel, Abri du Maras and Baume des Peyrards. Large and even very large ungulates, such as bovines, horse, giant deer and rhinoceros offered suitable raw material for retouchers at Orgnac 3, Payre-F, Sainte-Anne I and Baume-Vallée. The only bone retouchers pro-

duced on an articular portion of the skeleton were recorded at Baume des Peyrards (on the femoral head of an ibex) and at Payre (on a distal end of a horse humerus). Except at Le Lazaret, no retouchers on antlers or animal teeth were discovered among our assemblages, nor did we observe any retouchers made on rare elements, such as human or carnivore remains. Generally, in southeastern France, no specific *chaîne opératoire* for the production of bone retouchers was recorded. They appear to have been selected *a posteriori* from discarded butchery remains, depending on how they fit in the hand, their physical properties and their surface characteristics, as well as cultural or individual preferences. In our earliest series, we observed the most robust bone artefacts, which may be related to specific needs, such as the manufacturing of heavy-duty tools at Payre or Orgnac 3 (pebble-tools and bifacial tools). In addition to these bone artefacts, some Middle Palaeolithic assemblages from the Iberian Peninsula (Cuartero, 2014), the site of Arma dell Manie in Italy (Cauche, 2007), Terra Amata (de Lumley, 2015), Le Lazaret (Darlas, 1994; de Lumley et al., 2004), Baume-Vallée (Raynal et al., 2005) and Champ Grand (Nicoud, 2008; Roux, 2008) in southeastern France, contain many small and flat pebbles used as retouchers. These are sometimes as frequent as bone retouchers and bear similar striations and hash marks. All these sites are distinct, both in terms of raw lithic materials and lithic industries. Furthermore the use of stone pebbles, as well as the use of bone, teeth, antlers or eventually wood for the same purposes, may indicate human preferences rather than functional requirements. Similarly, the use of cervid antlers is rarely observed during the Middle Palaeolithic, in contrast to the Acheulean or Early Middle Palaeolithic and Upper Palaeolithic periods. Is the use of antler also related to cultural aspects, or linked to functional purposes, perhaps handaxe shaping?

As for the morphology and size of the used blanks, they are usually elongated, with a mean length ranging from 50 to 120 mm – always greater than that of the total bone assemblages (see **Figure 4**). The oldest series include the largest bone artefacts. At Sainte-Anne I, Baume Vallée and Baume

des Peyrards, we recorded the smallest retouchers. Yet, it is difficult to determine if used blanks were fractured before, during or after use. For example, at the two mid-mountain sites of Sainte-Anne I and Baume-Vallée, post-depositional frost action may have caused fractures, reducing the dimensions of some pieces. Nonetheless, in some cases the small dimensions of the blanks can be considered as intentional, based on the position and completeness of the use marks on the piece. This is the case for Qesem Cave, where Rosell et al. (2015; see also Blasco et al., 2013a, 2014) observed very small bone retouchers mainly made on cervid remains and associated with Quina technology. Another example is the site of La Quina itself, which has yielded many reindeer first phalanges used as retouchers (Valensi, 2002). This introduces the question of dedicated *chaînes opératoires* for the production of bone retouchers, as we now know that bones are sometimes considered as a raw material for debitage. Some specific items, such as refitted bones, may allow us to study the manufacture and/or use histories of retouchers in the same way as lithic production. Such specific bone artefacts do exist in the Middle Palaeolithic, but are scarce; for example the bone retouchers on refitted cave bear elements from Scladina (Abrams et al., 2014) and from Fate Cave (Valensi and Psathi, 2004) or on brown bear remains at Biache-Saint-Vaast (Auguste, 2002) and Fumane Cave (Jéquier et al., 2012). There are also a few examples of bone retouchers made on Neanderthal remains: a parietal fragment at La Quina (Verna and d'Errico, 2011), femur shaft fragments at Krapina (Patou-Mathis, 1997) and Les Pradelles (Mussini, 2011), and on femur and tibia fragments at Goyet (Rougier et al., 2016). Indeed, the majority of Middle Palaeolithic bone retouchers seem to have been selected *ad hoc* from discarded butchery remains (i.e., recycling). However, this is only a cautious assumption, as systematic refits are usually not available.

In the same way, some authors observed splinters/flakes at the extremity of the bone retouchers, indicating the possible use of the bone as an intermediate tool or shaping to obtain flakes better adapted

for handling (Abrams et al., 2014; Costamagno et al., 2018; Toniato et al., 2018). Therefore, it appears necessary to study or revise bone retouchers series accordingly, by considering bone blanks as part of a complete *chaîne opératoire* (cf. Abrams et al., 2014) and not as “unmodified bone tools used for a particular purpose” (Rosell et al., 2011:125).

What about variations of the type and location of the percussion and associated marks?

The type of marks observed on bone artefacts may depend on either the use (e.g., anvil, hammer, retouching Quina or non-Quina scrapers, resharpening primary non-retouched lithic edges, etc.), intensity of use or the type of worked stone.

We mainly observed circumscribed use areas including slight hash marks with a V-shaped section situated on one extremity of the blank. Following the work of many authors who conducted experiments (Vincent, 1993; Armand and Delagnes, 1998; Tartar, 2002, 2009, 2012; Mozota, 2009, 2013; Mallye et al., 2012; among others and our unpublished data), these marks are characteristic of the short, once-off use of bone to resharpen or retouch lithic edges, producing marginal micro-retouch or to shape and re-shape semi-Quina or Quina scrapers. Some rare artefacts were used for vigorous percussion, scraping or pressure, or used as an anvil. Associated notches and green bone fractures, like at the sites of Payre-F, Baume Vallée or Saint-Marcel, may be the result of such use. The abundance of the use marks known as “comet striations” at Sainte-Anne I may possibly be linked to a particular function.

The depth and dispersal of retouching marks, as well as the number of use areas by blank (sometimes up to four), indicate the intensity and longevity of the utilization of some bone artefacts. The great majority of single and dispersed use areas indicate that bone artefacts generally have a short lifecycle. Nevertheless, in some cases, probably influenced more by the choice of the knapper than by the availability of faunal raw materials, bone artefacts seem to have been recycled, either by scraping the use area or by interchanging the used extremity.

Some experimental studies successfully differentiated the lithic raw materials struck by the retouchers based on retouching marks (e.g., Rosell et al., 2011; Mallye et al., 2012). The bone retouchers from Payre are robust and bear deep crushing marks, perhaps as a result of the particular resilience of the flint on which they were used; yet, the production of heavy-duty tools cannot be ruled out. At Sainte-Anne I, the widespread use of basalt and phonolite may also partly explain why the bone retouchers bear numerous pitted areas and sliding striations (comet striations).

The presence of circumscribed areas with associated retouching and scraping marks are indicative of periosteum removal before use and therefore of the fresh state of the blanks (Tartar, 2009). Except for the cleaning of the bone surfaces, which is recurrent among the series, no particular modifications were made after breakage, which may have been intentionally produced or a result of marrow recovery.

What type of nomenclature?

What type of nomenclature can we use for these ubiquitous bone artefacts? Should we opt for nomenclature based on function? Can we identify blank utilization through the experimental use of bone hammers, pressure flakers, anvils (use marks located on the mesial parts of the element), etc.?

The broad category of “soft knapping tools” (van Kolfshoten et al., 2015) could represent a good compromise, as it takes into account the similarity of these bone tools throughout time and the difficulty involved in clearly associating them with a specific function. However, the term “knapping” appears to be too simplistic.

It may be more appropriate to use a broader categorization, based more on the morphology of the observed marks than on function, as proposed by Patou-Mathis (2002). In that work, which includes the analyses of bone artefact series dating from various periods of the Palaeolithic, the main distinction is based on the type of anatomical support: long bone fragments, cervid antlers, articular portions, teeth, etc., rather than on the type of use marks,

grouped under the term *impressions et éraillures*. In most cases, bone artefacts were active tools used to strike lithic products in order to thin, retouch or resharpen flake/tool edges. In such cases, they can be called “retouchers” or “hammers”. It is only appropriate to use the terms “compressors” or “pressure flakers” in a few cases, particularly for Upper Palaeolithic periods.

Conclusion

In southeastern France, as well as elsewhere in Europe, the use of bone to retouch or shape lithic products can be related to the emergence of the Middle Palaeolithic and to new behaviours between MIS 11 and MIS 9. Their frequency increases after MIS 7 and becomes almost omnipresent after MIS 5, but is still highly variable throughout the Middle Palaeolithic. This variability in southeastern France seems to depend more on the type of occupations than on the associated lithic technologies. A regional study of these bone artefacts should be developed in the future to elucidate this point, taking into account occupation durations as well as the activities occurring in and around the sites.

This comparative work is still exploratory and should be completed and further developed by adding more archaeological as well as experimental data. Nevertheless, it highlights the widespread use of this bone tool and the similarity of these artefacts across Late Acheulean/Early Middle Palaeolithic to Middle Palaeolithic assemblages.

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Supplementary data

Number of identified specimens of ungulates (NISPU) and indeterminate ungulate remains (NRu) (LU: large ungulates; MU: middle-sized ungulates; SU: small ungulates), number of bone retouchers (Nr), number of identified specimens per ungulate taxa relative to all identified ungulate remains (%NISPU), and rates of bone retouchers based on the NISP of each ungulate taxon (1) and on the total number of ungulates (2). Standard errors and (Confidence Intervals with lower and upper confidence bounds) shown for percentage values.

Sites (1)	Saint-Marcel (a to j)			Saint-Marcel (k to t)			Saint-Marcel (u)						
	NISPU	Nr	%NISPU	%Nr(1)	%Nr(2)	NISPU	Nr	%NISPU	%Nr(1)	NISPU	Nr	%NISPU	%Nr (1)
Proboscideans													
Suids													
Rhinocerotids													
Equids	17	1	0.4 (0.5-1.4)	11.2 (-5.3-17.1)	0.7 (-0.3-1.1)	18	4.7 (6.1-15.6)	10.8	4.7 (6.1-15.6)	2	0.6 (-0.2-1.1)	0.5	0.6 (-0.2-1.1)
Megaloceros	4	1	0.2 (0-0.4)	42.4 (-17.4-67.4)	0.7 (-0.3-1.1)	3	2 (-0.2-3.8)	1.8	53.3 (13.3-120)	2	0.6 (-0.2-1.1)	0.5	0.6 (-0.2-1.1)
Reindeer	1624	158	9.6 (8.9-10.3)	9.7 (8.3-11.2)	5.9 (5.1-6.3)	99	7.5 (5.2-6.7)	59.6	7.1 (2-12.1)	84	9	3.7 (15.5-22.9)	10.7
Red deer	3	0.2 (0-0.4)	0.2 (0-0.4)	0.2 (0-0.4)	0.2 (0-0.4)	18	3	4.7 (6.1-15.6)	10.8	272	7	4.5 (57.6-66.6)	2.6
Fallow deer	108	8	1.1 (4.9-7.1)	4.9 (2.5-12.3)	2 (0.9-4.9)	23	5.3 (8.6-19.1)	13.9	15.3	67	3.4 (11.9-18.7)	15.3	15.3
Roe deer	10	0.6 (0.2-0.9)	0.6 (0.2-0.9)	0.6 (0.2-0.9)	0.6 (0.2-0.9)	1	0.4 (-0.2-0.7)	0.2	0.2	1	0.4 (-0.2-0.7)	0.2	0.2
Bovines	27	0.6 (0.9-2.1)	1.5 (0.9-2.1)	0.6 (0.9-2.1)	1.5 (0.9-2.1)	5	2.6 (0.4-5.6)	3.0	2.6 (0.4-5.6)	7	1.2 (0.4-2.8)	1.6	1.2 (0.4-2.8)
Rupicaprines													
LU	73	7	0.8 (2.9-4.5)	6.8 (2.8-16.3)	1.9 (0.7-4.4)	4	4 (0.2-8.1)	4.1	4 (0.2-8.1)	2	1.9 (-0.5-3.3)	1.4	1.9 (-0.5-3.3)
MU	1823	99	1.2 (91.2-93.6)	1.0 (4.4-6.5)	5.7 (30.4-41.8)	93	4 (91.9-99.8)	95.9	4 (91.9-99.8)	143	1	1.9 (96.7-100.5)	0.7
SU	77	0.9 (3-4.8)	0.9 (3-4.8)	0.9 (3-4.8)	0.9 (3-4.8)	7	1.2 (0.4-2.8)	1.6	1.2 (0.4-2.8)	7	1.2 (0.4-2.8)	1.6	1.2 (0.4-2.8)
Total NISPU	1793	168	9.4 (8-10.7)	1.3 (8-10.7)	5.8 (55.5-67.1)	166	12	61.3	3.9 (3.3-11.2)	438	16	3.7 (15.5-22.9)	3.7
Total NRu	1973	106	5.4 (4.4-6.4)	1 (4.4-6.4)	5.8 (32.9-44.5)	97	97	38.7	3.9 (3.3-11.2)	145	1	1.3 (-0.7-2)	0.7
Total UNG	3766	274	7.3 (6.4-8.1)	0.8 (6.4-8.1)	100.0	263	12	4.6	2.5 (2-7.1)	583	17	1.4 (1.6-4.3)	2.9

Sites (2)	Abri du Maras (1)			Abri du Maras (2 to 5)			Abri du Maras (4-1)					
	NISPu	Nr	%NISPu	%Nr(1)	NISPu	Nr	%NISPu	%Nr(1)	NISPu	Nr	%NISPu	%Nr (1)
Proboscideans												
Suids												
Rhinocerotids												
Equids	9	12.7	22 (9.3-34.6)		30	3	6.9 (14.9-28.6)	10.7 (-0.7-20.7)	75		6.6 (5.1-8)	
Megaloceros									20		1.7 (1-2.5)	
Reindeer	19	15.3	46.3 (31.1-61.6)	5.3 (4.8-15.3)	87	1	8.1 (55-71.1)	2.2 (-1.1-3.4)	1030		1.7 (88.3-91.8)	
Red deer	5	10	12.2 (2.2-22.2)		7		3.7 (1.4-8.7)		6		0.5 (0.1-0.9)	
Fallow deer												
Roe deer												
Bovines	8	19.5	12.1 (7.4-31.6)		6	1	4.3 (0.9-7.8)	16.7 (-13.2-46.5)	8		0.7 (0.2-1.2)	
Caprines					8		5.8 (1.9-9.7)		5		0.4 (0.1-0.8)	
Rupicaprines												
LU	6	14.6	10.8 (3.8-25.5)	16.7 (-13.2-46.5)	4	2	9.3 (0.7-19.3)	49 (1-99)	215		8.6 (7.5-9.7)	
MU	35	85.4	10.8 (74.5-96.2)		36	2	9.3 (80.7-99.3)	7.5 (-1.9-13)	2247	1	90.2 (89-91.3)	0.04 (0-0.1)
SU					7				30		1.2 (0.8-1.6)	
Total NISPu	41			2.4 (-2.3-7.2)	138	5		3.1 (0.5-6.7)	1144			0.04 (0-0.1)
Total NRu	41			2.4 (-2.3-7.2)	40	4		9.3 (0.7-19.3)	2492	1		0.03 (0-0.1)
Total UNG	82			2.4 (-2.3-7.2)	178	9		3.2 (1.8-8.3)	3636	1		0.1 (0-0.1)

Sites (3)	Grotte du Figuier (2 to 5)			Baume des Peyrards (Upper)				
	NISPU	Nr	%NISPU %Nr(1)	NISPU	Nr	%NISPU %Nr(1)	%Nr(2)	
Proboscideans								
Suids								
Rhinocerotids								
Equids	20		11.3 4.7 (6.6-16)	182	1	3.9 0.6 (3.4-4.5)	0.5 1.1 (-0.5-1.6)	1 1.9 (-0.9-2.9)
Megaloceros								
Reindeer	96	1	54.2 7.3 (46.9-61.6)					
Red deer	8		4.5 3.1 (1.5-7.6)	492	14	10.6 0.9 (9.7-11.5)	2.8 1.5 (1.4-4.3)	13.7 6.7 (7-20.4)
Fallow deer	3		1.7 1.9 (-0.2-3.6)					
Roe deer				135		2.9 0.5 (2.4-3.4)		
Bovines	7		4 2.9 (1.1-6.8)	23		0.5 0.2 (0.3-0.7)		
Caprines	41		23.2 6.2 (16.9-29.4)	3752	54	80.7 1.1 (79.5-81.8)	1.4 0.4 (1.1-1.8)	52.9 9.7 (43.3-62.6)
Rupicaprines	2		1.1 1.6 (-0.4-2.7)	68	1	1.5 0.3 (1.1-1.8)	1.5 2.9 (-1.4-4.3)	1 1.9 (-0.9-2.9)
LU	24	1	24.5 8.5 (16-33)	55	1	6.3 1.6 (4.7-7.9)	1.8 3.5 (-1.7-5.3)	1 1.9 (-0.9-2.9)
MU	74	1	75.5 8.5 (67-84)	796	31	90.8 1.9 (88.8-92.7)	3.9 1.3 (2.6-5.2)	30.4 8.9 (21.5-39.3)
SU				26		3 1.1 (1.8-4.1)		
Total NISPU	177	1	0.6 1.1 (-0.5-1.7)	4652	70		1.5 0.3 (1.2-1.9)	68.6 9 (59.6-77.6)
Total NRu	98	2	2 2.8 (-0.8-4.8)	877	32		3.6 1.2 (2.4-4.9)	31.4 9 (22.4-40.4)
Total UNG	275	3	1.1 1.2 (-0.1-2.3)	5529	102		1.8 0.4 (1.5-2.2)	100

Sites (4)	Baume Vallée (0)			Baume Vallée (1)			Baume Vallée (2)		
	NISPu	Nr	%NISPu	NISPu	Nr	%NISPu	NISPu	Nr	%NISPu
Proboscideans									
Suids									
Rhinocerotids									
Equids	18	1	13.1 (22.2-48.4)	55	1	10.2 (55.3-75.6)	116	1	83.5 (77.3-89.6)
Megaloceros									
Reindeer									
Red deer	25	1	13.7 (35.3-62.7)	9	1	10.7 (4.1-17.3)	9	1	6.5 (2.4-10.6)
Fallow deer									
Roe deer									
Bovines	2	2	5.3 (-1.4-9.2)	5	2	5.1 (0.9-11)	3	2	2.2 (-0.3-4.6)
Caprines	6	6	8.8 (2.9-20.6)	15	11	8.2 (9.7-26)	11	11	4.5 (3.4-12.4)
Rupicaprines									
LU	80	80	6.5 (31.2-44.3)	166	6	5.3 (42.6-53.1)	178	3	63.3 (57.7-69)
MU	128	1	6.6 (53.8-67)	174	4	5.3 (44.9-55.4)	102	4	36.3 (30.7-41.9)
SU	4	4	1.8 (0.1-3.7)	7	2	1.5 (0.5-3.5)	1	1	0.4 (-0.3-1.1)
Total NISPu	51	1	3.8 (-1.8-5.8)	84	1	2.3 (-1.1-3.5)	139	1	1.2 (0.2-2.7)
Total NRu	212	1	0.9 (-0.5-1.4)	347	10	1.8 (1.1-4.6)	281	7	2.5 (0.7-4.3)
Total UNG	263	2	1 (-0.3-1.8)	431	11	1.5 (1.1-4)	420	7	1.7 (0.4-2.9)

Sites (5)	Barasses II (2-4)			Barasses II (6-8)			Baume Flandin (3)					
	NISPu	Nr	%NISPu	%Nr(1)	NISPu	Nr	%NISPu	%Nr(1)	NISPu	Nr	%NISPu	%Nr (1)
Proboscideans												
Suids												
Rhinocerotids												
Equids	4		2.5 (0.1-5.1)		5		3.2 (0.4-6)		11		12.4 (5.5-19.2)	
Megaloceros												
Reindeer	7		3.3 (1.3-7.9)						1		2.2 (-1.1-3.3)	1.1
Red deer	12	1	4.3 (3.6-12.1)	8.3 (15.6 (-7.3-24))	31	2	20.1 (13.8-26.5)	6.5 (8.6 (-2.2-15.1))	57	4	10 (54.1-74)	6.6 (0.4-13.6)
Fallow deer												
Roe deer									2		3.1 (-0.8-5.3)	2.2
Bovines	7	1	3.3 (1.3-7.9)	14.3 (25.9 (-11.6-40.2))	5		3.2 (2.8 (0.4-6))		13		7.3 (7.3-21.9)	14.6
Caprines	123		6.3 (74.1-86.7)		100		7.5 (57.4-72.5)		5		4.8 (0.8-10.4)	5.6
Rupicaprines												
LU	11	2	3.2 (2.4-8.9)	18.2 (22.8 (-4.6-41))	16	1	6.2 (3 (3.9-2))	6.3 (11.9 (-5.6-18.1))	2		7.3 (-1.9-12.7)	5.4
MU	182		3.5 (89.8-96.8)		201	2	78.2 (5 (73.2-83.3))	1.4 (-0.4-2.4)	35	1	7.3 (87.3-101.9)	94.6
SU	2		1.4 (-0.4-2.4)		40		15.6 (4.4 (11.1-20))					2.9
Total NISPu	153	2		1.3 (1.8 (-0.5-3.1))	154	2		1.3 (1.8 (-0.5-3.1))	89	4		4.5 (4.3 (0.2-8.8))
Total NRu	195	2		1.4 (-0.4-2.4)	257	3		1.2 (1.3 (-0.1-2.5))	37	1		2.7 (5.2 (-2.5-7.9))
Total UNG	348	4		1.1 (1.1 (0-2.3))	411	5		1.1 (1.1 (0.2-2.3))	126	5		3.4 (0.6-7.4)

Sites (6)	Sainte-Anne I (J1-E1)			Sainte-Anne I (J2-E2)			Sainte-Anne I (J3-E3)		
	NISPu Nr	%NISPu	%Nr(1)	NISPu Nr	%NISPu	%Nr(1)	NISPu Nr	%NISPu	%Nr(1)
Proboscideans	2	0.7 (-0.3-1.7)		2	0.5 (-0.2-1.2)		14	10.1 (5.1-15.1)	
Suids									
Rhinocerotids	1	0.4 (-0.3-1)		12	1.7 (1.3-4.7)		22	15.8 (9.8-21.9)	
Equids	113	40.1 (34.4-45.8)	3.5 (0.1-6.9)	145	36.2 (31.5-40.9)	1.4 (-0.5-3.3)	52	37.4 (29.4-45.5)	1.9 (-1.8-5.7)
Megaloceros									
Reindeer	140	49.6 (43.8-55.5)	4.3 (0.9-7.6)	190	47.4 (42.5-52.3)	2.1 (0.1-4.1)	34	24.5 (17.3-31.6)	
Red deer	5	1.8 (0.2-3.3)	20 (-15.1-55.1)	12	2.7 (-2.5-7.9)	8.3 (-7.3-24)	7	5 (1.4-8.7)	14.3 (-11.6-40.2)
Fallow deer									
Roe deer									
Bovines	1	0.4 (-0.3-1)		37	9.2 (6.4-12.1)		8	5.8 (1.9-9.6)	
Caprines	18	6.4 (3.5-9.2)	5.6 (-5-16.1)	3	0.7 (-0.1-1.6)		2	1.4 (-0.5-3.4)	
Rupicaprines	2	0.7 (-0.3-1.7)		188	35.1 (19.8-50.5)	2.1 (0.1-4.2)	48	33.8 (26-41.6)	4.2 (-1.5-9.8)
LU	145	10 (8.5-11.6)	9 (4.3-13.6)	1251	86.6 (84.8-88.3)	1.4 (0.8-2.1)	92	64.8 (56.9-72.6)	3.3 (-0.4-6.9)
MU	1286	89 (87.4-90.6)	0.9 (0.4-1.5)	6	0.4 (0.1-0.7)		2	1.4 (-0.5-3.3)	
SU	14	1 (0.5-1.5)		401	32.4 (17.3-47.5)	1.7 (0.5-3)	139	24.1 (8.6-39.7)	1.4 (-0.5-3.4)
Total NISPu	282	2.4 (1.9-6.6)	4.3 (-1.9-6.6)	7	32.4 (17.3-47.5)	1.3 (0.5-3)	2	15.6 (8.6-39.7)	2 (-0.5-3.4)
Total NRu	1445	1.7 (1.1-2.4)	0.7 (1.1-2.4)	22	67.6 (52.5-82.7)	1.5 (0.9-2.2)	5	75.9 (60.3-91.4)	3.5 (0.5-6.6)
Total UNG	1727	2.1 (1.5-2.8)	0.7 (1.5-2.8)	29	100.0	1.6 (1-2.1)	7	100.0	2.5 (1.8-4.3)

Sites (7)	Lazaret (CIII)			Lazaret (CII)			Payre (F)					
	NISPU	Nr	%NISPU	NISPU	Nr	%NISPU	NISPU	Nr	%NISPU	NISPU	Nr	%NISPU
Proboscideans	2	0.04 (-0.01-0.08)	0.03	5	0.1 (0-0.2)	0.1	12	1	0.4 (0.3-1)	0.7	8.3	15.6 (-7.3-24)
Suids							12		0.4 (0.3-1)	0.7		
Rhinocerotids	15	0.1 (0.1-0.4)	0.2	2	0.05 (0-0.1)	0.03	225	2	1.5 (10.8-13.8)	12.3	0.9	1.2 (-0.3-2.1)
Equids	67	0.3 (0.8-1.3)	1.1	13	0.1 (0.1-0.3)	0.2	302	2	1.7 (14.8-18.2)	16.5	0.7	0.9 (-0.3-1.6)
Megaloceros	7	0.1 (0-0.2)	0.1	5	0.1 (0-0.2)	0.1	4		0.2 (0-0.4)	0.2		
Reindeer	15	0.1 (0.1-0.4)	0.2									
Red deer	4877	1 (76.7-78.8)	77.8	4899	8	1 (79-81)	80	2	2.3 (39.4-43.9)	41.7	0.3	0.4 (-0.1-0.6)
Fallow deer			0.04	1	0.03 (-0.02-0.05)	0.02	26		0.5 (0.9-2)	1.4		
Roe deer	22	0.1 (0.2-0.5)	0.4	66	0.3 (0.8-1.3)	1.1	87		1 (3.8-5.7)	4.8		
Bovines	91	0.3 (1.2-1.7)	1.5	293	1	0.5 (4.2-5.3)	4.8	2	1.7 (14.5-17.9)	16.2	0.7	0.9 (-0.3-1.6)
Caprines	1161	1 (17.6-19.5)	18.5	755	1	0.8 (11.5-13.2)	12.3		1 (4.1-6.2)	5.1		
Rupicaprines	14	0.1 (0.1-0.4)	0.2	85	0.3 (1.1-1.7)	1.4	7		0.3 (0.1-0.7)	0.4		
LU	2	0.6 (0.1-1.3)	0.7	3	0.7 (0.2-1.7)	1	704	5	2.5 (43-48)	45.5	0.7	0.6 (0.1-1.3)
MU	276	0.9 (97.7-99.5)	98.6	273	4	2.5 (85.3-90.2)	87.8	1	2.5 (52-57)	54.5	0.1	0.2 (-0.1-0.4)
SU	2	0.6 (0.1-1.3)	0.7	35	2.4 (8.9-13.6)	11.3	844	1				
Total NISPU	6271	3	0.05 (-0.01-0.1)	6124	10	0.2	1826	9	0.1 (0.1-0.3)	0.2	0.5	0.3 (0.2-0.8)
Total NRu	280	1	0.4	311	4	1.3	1548	6	1.3 (0.2-5)	1.3	0.4	0.3 (0.1-0.7)
Total UNG	6551	4	0.1	6435	14	0.2	3374	15	0.1 (0.1-0.3)	0.2	0.4	0.2 (0.2-0.7)

Sites (8)	Orgnac 3 (5b)			Orgnac 3 (6)			Terra Amata	
	NISpu	Nr	%NISpu	%Nr(1)	NISpu	Nr	%NISpu	%Nr(1)
Proboscideans								13
Suids	18	3.5 1.6 (1.9-5.1)			28	5.1 1.8 (3.2-6.9)		3
Rhinocerotids	13	2.5 1.4 (1.2-3.9)			17	3.1 1.4 (1.6-4.5)		1
Equids	152	29.5 3.9 (25.5-33.4)	0.7 1.3 (-0.6-1.9)		134	24.2 3.6 (20.6-27.8)	1.5 2.1 (-0.6-3.5)	
Megaloceros	1	0.2 0.4 (-0.2-0.6)			2	0.4 0.5 (-0.1-0.9)		
Reindeer					1	0.2 0.4 (-0.2-0.5)		
Red deer	157	30.4 4 (26.5-34.4)	1.3 1.8 (-0.5-3)		215	38.8 4.1 (34.8-42.9)		32
Fallow deer	73	14.1 3 (11.1-17.2)			66	11.9 2.7 (9.2-14.6)		1
Roe deer	10	1.9 1.2 (0.7-3.1)			8	1.4 1 (0.5-2.4)		
Bovines	84	16.3 3.2 (13.1-19.5)			70	12.6 2.8 (9.9-15.4)	4.3 4.7 (-0.5-9)	2
Caprines	8	1.6 1.1 (0.5-2.6)			8	1.4 1 (0.5-2.4)		2
Rupicaprines					5	0.9 0.8 (0.1-1.7)		
LU	212	48 4.7 (43.3-52.6)			278	36.4 3.4 (33-39.8)		
MU	210	47.5 4.7 (42.9-52.2)			414	54.2 3.5 (50.7-57.7)		3
SU	20	4.5 1.9 (2.6-6.5)			72	9.4 2.1 (7.4-11.5)		
Total NISPu	516	3	0.6 0.7 (-0.1-1.2)		554	5	0.9 0.8 (0.1-1.7)	54
Total NRu	442				764			3
Total UNG	958	3	0.3 0.4 (0-0.7)		1318	5	0.4 0.3 (0-0.7)	57