The late middle Palaeolithic occupation of Abri du Maras (Layer 1, Neronian, southeast France): integrating lithic analyses, ZooMS and radiocarbon dating to reconstruct Neanderthal hunting behaviour

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The Late Middle Palaeolithic Occupation of Abri du Maras (Layer 1, Neronian, Southeast France): Integrating Lithic Analyses, ZooMS and Radiocarbon Dating to Reconstruct Neanderthal Hunting Behaviour

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Abstract

The exact strategies and technologies underlying Neanderthal hunting events remain open for debate with lithic points being sparse across the European Middle Palaeolithic. An exception is the Neronian entity in southeast France, defined by ventrally retouched Soyons points. This study contextualises one of the largest Neronian assemblages, layer 1 at Abri du Maras. Our lithic analyses focussed on attributes described as indicative of projectile use or hafting to contextualise the morphometric and technological characteristics of the pointed implements at an assemblage level. We found that retouched points were made on a variety of blank types (including Levallois, laminar and discoidal flaking techniques) and ventral retouch is present across different artefact types (including points, scrapers and denticulates). Next, these lithic data were compared to similar typo-technological data recorded on a sample from the recently excavated and well-contextualised point-rich layer 4.1 of Abri du Maras (MIS-3). Zooarchaeology by Mass Spectrometry (ZooMS) was applied to 280 faunal remains from layer 1 and indicated significant proportions of equids, bovids, cervids and reindeer. Carnivore remains and carnivore modifications are absent, while human bone surface modifications are present across a variety of species. Five bones had sufficient collagen for radiocarbon dating but returned dates younger than expected (ca. 41–31 ka cal BP). Finally, we place Abri du Maras layer 1 in its broader regional context and discuss its relation to other Neronian assemblages and more general problematics inherent to studying material from old excavations.

Keywords Middle Palaeolithic · Neanderthal · Neronian · Zooarchaeology by Mass Spectrometry · Lithic technology · Radiocarbon dating

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Introduction

The exact mechanisms and dynamics of Neanderthal hunting behaviour, including prey acquisition methods and weapon technologies, remain difficult to reconstruct and continue to form a topic of debate (Gaudzinski-Windheuser, 2016; Smith et al., 2020). In addition to rare archaeological discoveries providing direct insights into hunting strategies (e.g., wooden spears at Schöningen; Thieme, 1997) or hunting lesions (e.g., Neumark-Nord; Gaudzinski-Windheuser et al., 2018), zooarchaeological studies (Daujeard et al., 2019; Gaudzinski, 1995; Gaudzinski & Roebroeks, 2000; Hardy et al., 2013; Marean & Kim, 1998; Rendu, 2010; Romandini et al., 2018; Smith, 2015; Villa & Lenoir, 2009) and isotope analyses (Bocherens, 2011; Bocherens et al., 2001, 2005; Britton et al., 2011; Jaouen et al., 2019; Richards & Trinkaus, 2009; Richards et al., 2001) continuously demonstrate that Neanderthals were skilled hunters. However, this effectiveness of Neanderthal hunting is not equally reflected in the associated stone tool technology, creating an enigmatic discrepancy between the common occurrence of faunal remains from hunting events and the sporadic occurrence of identifiable hunting weapons.

It has been suggested that stone-tipped hunting weapons are an important marker of the technical and cognitive capacities of Palaeolithic hominins and represent a crucial tipping point in human behavioural evolution, facilitating an important advancement in prey acquisition through more efficient distance hunting (Haidle et al., 2016; Iovita & Sano, 2016; Lombard & Haidle, 2012; Rhodes & Churchill, 2009; Wadley, 2010). The common presence of lithic points across the African Middle Stone Age (MSA) is seen as an important element in the rise of behaviourally modern humans and their eventual global success. The exact timing of the appearance and subsequent spread of hafted hunting weapons remains a point of contention, and their occurrence across the European Middle Palaeolithic remains an understudied topic (Villa et al., 2009).

Potential spear points are rare in many European Middle Palaeolithic assemblages, taxonomic entities (e.g. Quina Mousterian) and even geographic regions (e.g. Germany). Main exceptions are the larger number of point shapes in MIS-5 northern France (Goval et al., 2016) and the Neronian entity, which are characterised by points with ventral retouch (southeast France; Slimak, 2008). Inverse or ventral retouch only occurs sporadically in Middle Palaeolithic assemblages, does not define any other taxonomic entities and only forms a defining element of a few of Bordes’ Middle Palaeolithic tool types (e.g. scraper on interior face; Bordes, 1961). This Neronian entity further stands out due to its stratigraphic position at the site of Grotte du Mandrin, in between two Mousterian layers (Slimak, 2004), and its recently suggested link to the Initial Upper Palaeolithic (IUP; Slimak, 2019; Slimak et al., 2022). One of the largest Neronian assemblages was excavated in the rock shelter of Abri du Maras by René Gilles from 1946 to 1950 and by Jean Combier in 1958 and 1963. Here, the Neronian material (layers 1, 1’ and 1’’) was found at the top of a deep Mousterian sequence (Combier, 1967). Maras is one of the few sites in Europe containing various Mousterian layers with a focus on the production of points, providing a unique case study to assess the subsistence practices underlying these point-rich assemblages.

In this paper, we conduct new analyses on both the lithic and faunal material from Abri du Maras layer 1 to provide additional insights into Neanderthal hunting behaviour at the site. The focus of our lithic analyses was on contextualising the lithic points by assessing morphological and technological characteristics used to imply projectile use. This was done both at an intra-assemblage level (comparing pointed and non-pointed implements within Maras layer 1) and at an inter-assemblage level (comparing Maras layers 1 and 4.1). High bone fragmentation at Abri du Maras prevented the taxonomic identification of a large portion of remains based on morphology. Collagen peptide mass fingerprinting, also known as Zooarchaeology by Mass Spectrometry (ZooMS), is a minimally destructive proteomic method focusing on morphologically unidentifiable bone fragments (Buckley et al., 2009). Through the analysis of collagen protein type I, it provides a taxonomic identification based on amino acid sequence variation and allows for an increase in the number of identifiable specimens (NISP). Previous studies have emphasised the potential of this technique to provide additional information on hominin behaviour in relation to subsistence strategies (Welker et al., 2015), but also on site formation, especially when combined with bone surface modification analysis of the bone specimens (Bouchard et al., 2020; Sinet-Mathiot et al., 2019). The unidentifiable fraction of the faunal remains from layers 1, 1’ and 1″ was analysed through ZooMS coupled with a detailed study of the taphonomic patterns preserved on the surface of the bone fragments. Further, we obtained new radiometric dates for five bone fragments from Maras layers 1, 3 and 4 (Combier excavations). Finally, we place our results in the broader context of Neanderthal site use at Abri du Maras, discuss the Neronian as a spatio-temporal taxonomic entity and assess the potential of our integrated multi-methodological approach for studying museum collections.

Background

Abri du Maras (Saint-Martin-d’Ardèche, southeast France) is a large southeast-facing rock shelter located at the exit of the Ardèche gorges at an altitude of 170 m (Fig. 1). It contains a 3-m-deep sequence of Middle Palaeolithic layers. Archaeological discoveries at the site were already mentioned in the literature at the end of the nineteenth century (Chiron, 1896). The first systematic excavations took place from 1946 until 1950 and were led by René Gilles (Baudet et al., 1955). He focused on the eastern part of the rock shelter (Fig. 2) and distinguished four geological units (A–D, Table 1), including one archaeological horizon (layer C) positioned under two archaeologically sterile units (layer A, 30-cm thick, and layer B, 17-cm thick). Gilles, although he did not excavate by square metre, did screen the sediments. In total, he collected 227 bone fragments and 2808 lithics from ca. 17 m^2 (Fig. 2, Table 1). The fauna is very fragmented and the presence of bovids, equids and cervids (including reindeer) is mentioned (Baudet et al., 1955). The lithic assemblage is described as a Mousterian with artefacts of small dimensions, laminar elements, various tool types with ventral retouch and numerous Upper Palaeolithic tool types (Baudet et al., 1955).

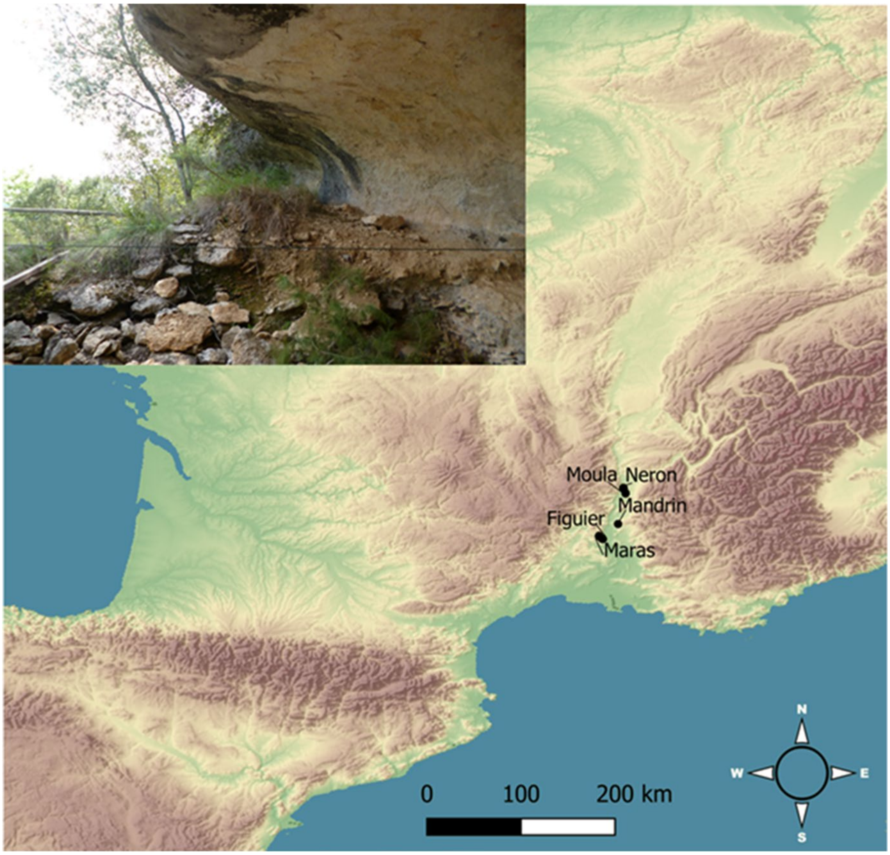


Fig. 1 Current view of the Abri du Maras rock shelter looking west and the location of Abri du Maras and other Neronian sites in the Rhone valley (southeast France). Photo by K. Ruebens and elevation map from the European Environment Agency

Jean Combier went back to the site in 1958 to verify whether the Gilles lithic assemblage might represent two distinct industries associated in the same thin layer. He excavated the central part of the rock shelter that year and then again in 1963 (Fig. 2). He also dug a trench that extended outside of the rock shelter and onto the slope in front of the rock shelter, and he identified a stratigraphic sequence of 18 geological layers with eight archaeological horizons (Combier, 1967; Table 1). These geological layers consist of deposits of loess and loam interspersed with gravels. On top of the bedrock, there is the ensemble inférieur (layers 6–8) which was only excavated over 4 m^2 (outside the rock shelter). From this, 238 lithics (Ferrassie Mousterian) and 929 faunal remains (dominated by red deer) were recovered (Combier, 1967). The overlying ensemble supérieur contains two laminar Mousterian (layers 2 and 3) and two Ferrassie Mousterian assemblages (layers 4 and 5). The fauna is marked by an increase in reindeer across the sequence (Combier, 1967).

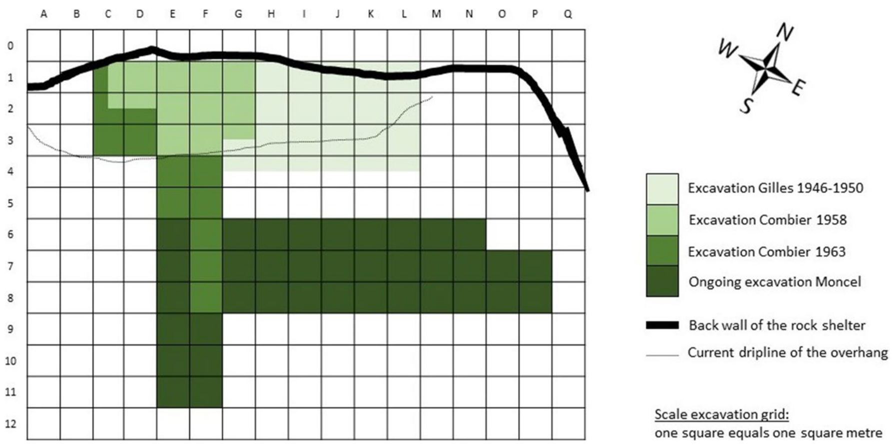


Fig. 2 Plan of the Abri du Maras rock shelter and the areas excavated by the various excavation campaigns (based on data from Baudet et al., 1955; Combier, 1967; Moncel et al., 2014, 2021). Gilles excavation area is approximate

Within the western part of the rock shelter, Combier subdivided the upper archaeological layer into units 1'' and 1'. Especially layer 1'' has an ashy grey colour and contains large amounts of small pieces of burnt bone. Outside of the current rock shelter (squares F4–F6, Fig. 2), the archaeological material of the upper layer becomes more sparse and more disturbed by roots and is labelled again as layer 1. He saw these three sublayers as part of the same occupations and recovered over 800 lithics and 800 faunal remains from them. Combier concluded that layer 1 did indeed contain a homogenous Mousterian assemblage with numerous Upper Palaeolithic tool types such as end scrapers, burins, piercers and a strong proportion of Levallois blades and bladelets (Combier, 1967). He describes the faunal remains from layer 1 as poorly preserved and different from the underlying layers with a larger proportion of bovids, a considerable amount of horse and a low presence of reindeer (Combier, 1967).

Both Gilles and Combier excavated the rock shelter to bedrock, and there are no sediments remaining in this part of the site. However, E. Debard went back to the remaining Combier section in the area in front of the rock shelter in 1981 (Debard, 1988) to conduct sedimentary analyses, and M.-H. Moncel did a small excavation campaign west of the section in 1993 (Moncel et al., 1994). Since 2006, Moncel has led a larger excavation campaign on the area in front of the current rock shelter (Daujeard et al., 2019; Moncel et al., 2010, 2014, 2021). In this area, Moncel only encountered rare artefacts in the upper layers (layers 1, 2 and 3), followed by a series of rich Mousterian levels (units 4.1, 4.2 and 5) (see Moncel et al., 1994, 2021) for a detailed stratigraphic sequence and spatial grid of the Moncel excavations). Layer 4.1 is characterised by a Levallois Mousterian with points (Moncel et al., 2021), and it has been argued that these were hafted as projectile points (Hardy et al., 2013). While Moncel has studied the layer 1 lithics in detail in the 1990s (Moncel, 1996)

Table 1 Overview of the various geological units with archaeological material recovered during the Gilles and Combier excavation campaigns at Abri du Maras (based on geological description from Combier, 1967; lithic data from Moncel, 1996, 2005; and faunal data from Daujeard, 2008)

Layer	Geology	Entity	Archaeology	Excavator		m2	cm	Lithics	Fauna	NISP
1		Sandy sediment with high proportion of rounded elements and unaltered rock fragments	Layer 1	Final Mousterian/Neronian	Gilles	33	7	2808	227	?
					Combier	ca. 10	?	249	138	?
1’	d	Yellowish loessy silt with plaquettes and fallen limestone blocks					10–30	376	696	
1’’	e	Greyish sediment with rounded gravels and a few plaquettes					15	262	5	
Total layer 1								**3695**	**1066**	**49**
2	h	Yellow silt with angular gravel partially conglomerated	Ensemble supérieur	Laminar Mousterian	Combier	12	5–15	209	741	181
3	j	Earthy beige-greenish silt with very scattered and altered gravels		Laminar Mousterian			15–40	1100		
4	k	Pebbles with earthy silt		Ferrassie Mousterian		38	15–35	440		
5	m	Yellow loam with pebbles		Ferrassie Mousterian		21	5–25	240		
Total Layers 2–5								**1989**	**741**	**181**
6	o	Clayey gravel with angular pebbles	Ensemble inférieur	Ferrassie Mousterian	Combier	4	15	132	929	50
7	p	Reddish gravel with subhorizontal plaquettes					10	72		
8	r	Light yellow angular gravel, infilling the fissures in the bedrock						34		
Total layers 6–8								**238**	**929**	**50**

and has extensively published on the layer 4.1 material (Moncel et al., 2021), no direct comparisons between layers 1 and 4.1 have been made so far.

Today, the Maras rock shelter is ca. 12-m long and 3-m wide, with an internal height of 2 m (Combier, 1967; Fig. 1). Various episodes of roof collapse mean that only a small rock shelter was remaining for the most recent occupations, while the older phases of occupations took place in a larger rock shelter in front of the currently remaining rock shelter (Debard, 1988). This could explain why the Moncel excavations did not encounter layer 1, which seems to have been restricted to the inner area of the current rock shelter. However, more detailed correlations between the old and new excavations remain difficult. The rich Mousterian layers 4.1 and 4.2 from the Moncel excavations probably relate to the lower part of the Combier sequence, but it is not possible to correlate individual layers (Moncel et al., 2021).

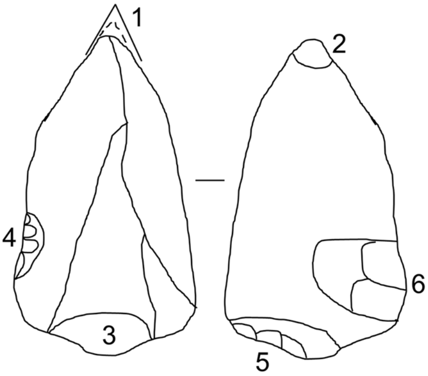
The chronological and biostratigraphic framework of the site has been refined several times, but, in general, the sequence indicates a climate becoming colder and drier over time interspersed with some more temperate and humid phases (Combier, 1967). The first set of radiometric dates was obtained from the 1993 Moncel excavation. Combier's layer 5 was dated by uranium series dating (U/Th) to late MIS-5 (ca. 90–70 ka BP). One AMS radiocarbon date gave an age of 37.700 ± 1.600 BP (GIF-A-97295), which at the time was interpreted as indicating an age > 40.000 BP, beyond the limit of the method (Moncel & Michel, 2000). More recent ESR/U-series dates on teeth placed Moncel's layer 4.1 between 46 ± 3 ka and 40 ± 3 ka BP (correlated with Heinrich Event 4 and DO Event 12; Richard et al., 2015, 2021). Layer 4.2 can also be positioned in MIS-3 (ages range from 42 ± 3 ka to 55 ± 2 ka BP), while the top of layer 5 was dated around 90 ka BP (MIS-5; Richard et al., 2015). Radiometric dates are not yet available for layer 1 and will be presented in this study.

Materials and Methods

The Abri du Maras lithic and faunal remains excavated by Gilles and Combier are currently stored at the Cité de la Préhistoire (Grand Site de France de l'Aven d'Orgnac). The lithic study focussed on the Gilles collection (layer 1) since this comprises the largest amount of lithics (ca. 3,000), including the Soyons points. Conversely, the ZooMS study considered the faunal remains recovered from layers 1, 1' and 1'' during both the Gilles and Combier excavation campaigns. Finally, besides layers 1, 1' and 1'', the dating programme also assessed bones recovered from layers 3 and 4 from the Combier excavations to provide additional chronological context.

Lithic Analysis

The focus of the lithic analysis was to contextualise the Neronian points from the R. Gilles collection (excavations 1946–1950) within its broader lithic assemblage. To this end, a series of typo-technological attributes were recorded on 542 flakes



Morphological feature	Interpretation
1. acute penetrating angle	to facilitate penetration
2. diagnostic impact fractures at the tip	impact damage
3. scarring at the base	impact damage
4. lateral edge scarring	damage from hafting
5. bulb removal	to facilitate hafting
6. proximal thinning or width reduction	to facilitate hafting
7. proximal notches (not illustrated)	to facilitate hafting

Fig. 3 Description, interpretation and illustration of the different morphological characteristics used to imply projectile use

(including tools, pointed and non-pointed blanks) using the program E4 developed by S. McPherron and H. Dibble (oldstoneage.com). A project-specific E4 configuration file was written to record attributes, including fragmentation, raw material type, flaking technique (including Levallois, discoidal, laminar), blank shape, platform type, cross section of the original blank, the estimated percentage of cortex remaining and metrics (maximum length, width, thickness, platform size and exterior platform angle, Supplementary Information 1). An additional focus was on recording attributes across all blank types that have been described as indicative of projectile use or hafting, such as macro-traces of use (e.g. breakage patterns at the tip and macroscopic edge damage) and modifications near the proximal end of the point that may be related to hafting (e.g. basal retouch and ventral thinning) (Fig. 3, Supplementary Information 1).

From Maras layer 4.1 (Moncel excavations), 2,041 lithic artefacts have been recovered (Moncel et al., 2021). For comparative purposes, the above-described typo-technology attributes (Fig. 3) were recorded in exactly the same manner on 311 flakes (including pointed and non-pointed blanks) from this layer.

Zooarchaeology by Mass Spectrometry (ZooMS)

A total of 280 morphologically unidentifiable bone fragments with a museum label assigning them to layer 1, 1’ or 1″ were selected for ZooMS analysis. Our sample selection excluded bone specimens smaller than two centimetres in length or bones exhibiting evidence of burning (Stiner et al., 1995). In total, we sampled 151 bone fragments from Gilles layers 1 and 129 from the Combier excavation campaign (layer 1: 40, layer 1’: 85, layer 1’’: 4).

ZooMS analysis followed protocols detailed elsewhere (Buckley et al., 2009; van Doorn et al., 2011; Welker et al., 2016). In short, all bone fragments were sampled destructively (10–30 mg), and soluble collagen was extracted a first time through a semi-destructive soluble collagen extraction technique using a 50-mM ammonium bicarbonate (NH_3CO_3, AmBic) buffer. Subsequently, because of low success rates with the AmBic buffer, all bone samples were demineralised in 120 µl of 0.6-M HCl at 4 °C for 21 h. After being rinsed thrice with AmBic, bone samples were then incubated for 1 h in 100 µl of AmBic solution at 65 °C. Then, 50 µl of the resulting supernatant was digested with trypsin (0.5 µg/µl, Promega) overnight at 37 °C, acidified using 1 µl of 10% TFA and cleaned on C18 Ziptips (Thermo Scientific). Eluted peptides were subsequently spotted in triplicates on a MALDI Bruker plate with the addition of matrix solution (α-cyano-4-hydroxycinnamic acid (CHCA)). MALDI-TOF MS analysis was conducted at the IZI Fraunhofer in Leipzig, and spectra were identified in comparison to a database containing peptide markers masses for all medium- to larger-sized mammalian genera in existence in Europe during the Pleistocene (Brown, Douka, et al., 2021; Welker et al., 2016).

In order to address protein degradation and collagen preservation, glutamine (Gln) deamidation ratios were measured on all samples for the peptide COL1α1 508–519 following existing protocols (Wilson et al., 2012). Such ratios obtained during ZooMS screening have been used for the detection of outliers permitting the possible identification of intrusive material or differential bone preservation (Sinet-Mathiot et al., 2019; van Doorn et al., 2012; Welker et al., 2017) although with varying success (Brown, Kozlikin, et al., 2021). The deamidation ratio ranges from %Gln = 1.0, indicating no deamidation from glutamine to glutamic acid, to %Gln = 0.0 indicating complete deamidation of glutamines to glutamic acid.

A series of taphonomic modifications to bone surfaces were recorded using the E4 software by one individual (VSM) to avoid any potential inter-individual variability. Similar to the lithic analysis, a project-specific configuration file was created to record bone surface readability, weathering stages, abrasion, corrosion, mineral staining, root etching, break morphology, non-anthropogenic modifications (carnivore tooth marks, bone breakage and digestion and rodent tooth traces) as well as butchery marks (cut marks, chop marks, marrow bone breakage and scraping traces) (Behrensmeyer, 1978; Binford, 1981; Fernandez-Jalvo & Andrews, 2016; Fisher, 1995; Lyman, 1994; Morin, 2012; Smith, 2015).

Radiocarbon Dating

Eleven cortical long bone fragments, where possible with human modifications, were selected for radiocarbon pretreatment (three from Gilles layer 1 and two from each of Combier's layers 1, 1'', 3 and 4). All bone samples were pretreated at the Department of Human Evolution at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA), Leipzig, Germany, using the method described in Talamo et al. (2021). The preservation of collagen was evaluated using the yield, C:N ratios, together with isotopic values (Talamo et al., 2021; van Klinken, 1999). The stable isotopic analysis was carried out at the MPI-EVA (Lab Code S-EVA) using a Thermo Finnigan FlashEA coupled to a Delta V isotope ratio mass

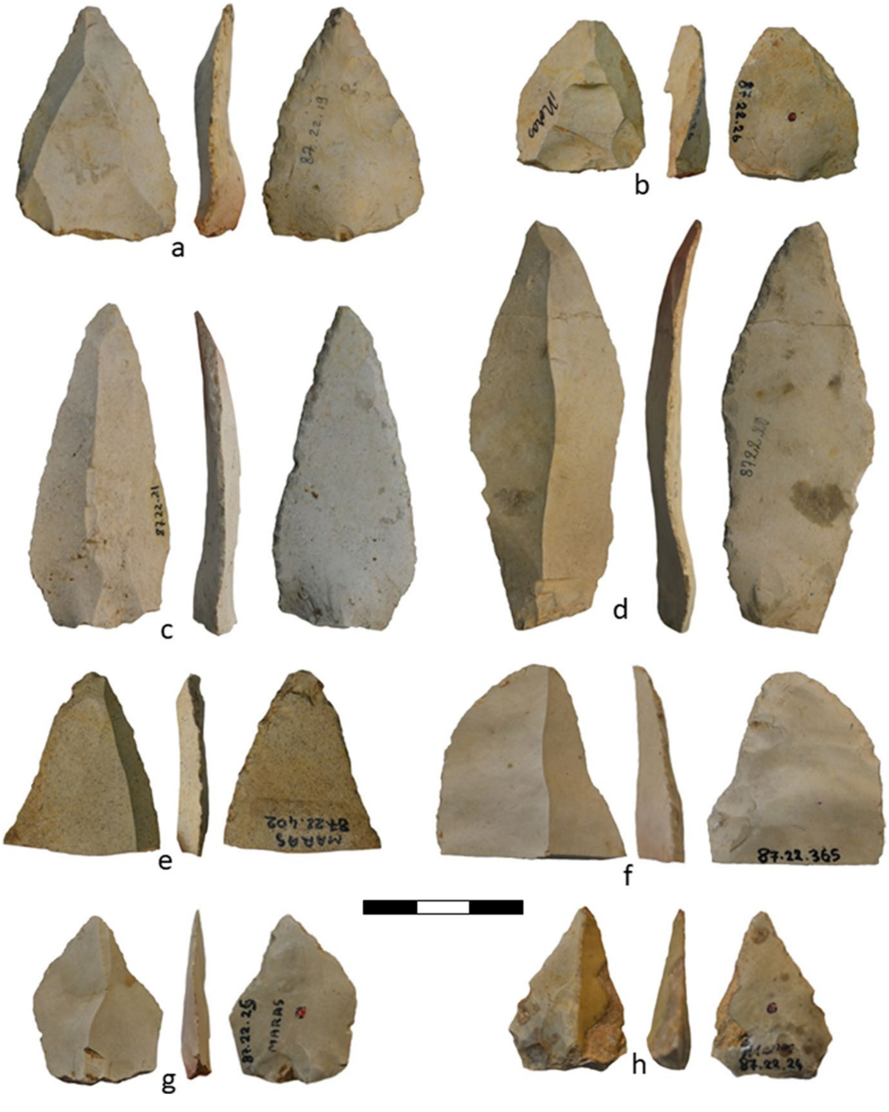


Fig. 4 **a**–**h** Points with ventral retouch (so-called Soyons points) from Abri du Maras layer 1 (collection R. Gilles)

spectrometer. The collagen extracted from each sample was transferred into precleaned tin capsules. These were sent to the Mannheim AMS laboratory (Lab Code MAMS), where they were graphitized and dated (Kromer et al., 2013).

Fig. 5 **a**–**g** Pointed blanks from Abri du Maras layer 4.1 (Moncel excavation)

Results

The role of pointed forms in the lithic collections of Maras layers 1 and 4.1

For Maras layer 1, 542 flakes from the Gilles collection were studied, containing 92 pointed forms (17%, Fig. 4). For Maras layer 4.1 (Moncel excavations), 311 flakes were studied, including 37 pointed blanks (12%, Fig. 5).

Artefact Condition

In both layers, fine-grained flints are the dominant raw material, and the artefacts have been altered by a series of physical processes. Across both collections, few artefacts are lightly patinated (Table 2), with the majority having a white or heavy patina, and around 10% are desilicified (mineral dissolution resulting in a porous, white appearance). Burning was recorded in higher proportions in

Table 2 Alteration due to burning and patination on the recorded artefacts from both Abri du Maras collections (for definitions of the various categories see supplementary information)

Alteration	Layer 1		Layer 4.1	
	n	%	*n*	%
Burned	33	6.09%	5	1.61%
Desilicified	70	12.92%	29	9.32%
White	97	17.90%	208	66.88%
Heavy	298	54.98%	68	21.86%
Light	11	2.03%	1	0.32%
Unpatinated	33	6.09%	0	0.00%
Total	542	100.00%	311	100.00%

Table 3 Remaining portions of the recorded artefacts following breakage (for definitions of the various categories see supplementary information)

Portion	Layer 1		Layer 4.1	
	n	%	*n*	%
Complete	277	51.11%	195	62.70%
Tip missing	91	16.79%	45	14.47%
Lateral break	55	10.15%	22	7.07%
Distal	19	3.51%	8	2.57%
Medial-distal	21	3.87%	9	2.89%
Medial	24	4.43%	7	2.25%
Medial-proximal	35	6.46%	17	5.47%
Proximal	17	3.14%	8	2.57%
NA	3	0.55%	0	0.00%
Total	542	100.00%	311	100.00%

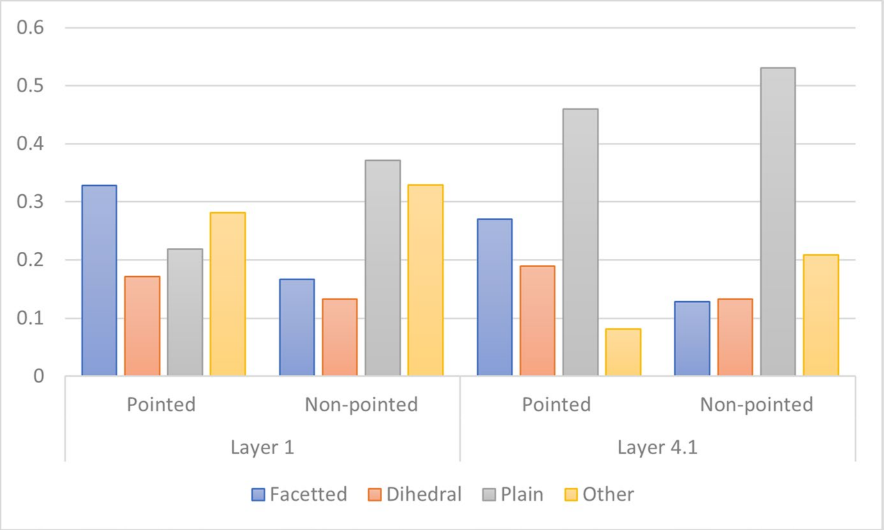


Fig. 6 Comparison of the main platform types recorded for pointed and non-pointed blanks across Maras layer 1 (Gilles collection) and layer 4.1 (Moncel excavation)

layer 1 (6.09%) compared to layer 4.1 (1.61%, Table 2) although heavy patination across both assemblages made it harder to identify traces of burning. 62.7% (layer 4.1) and 51.1% (layer 1) of recorded flakes are complete and the distribution of the remaining portions is similar across both sample sets (Table 3). These physical alterations restricted the recording of certain typo-technological attributes, but overall the preservation state of both collections is similar and allows for further comparisons to be made.

Flaking Technology

Few cortical flakes are represented in both sample sets with flakes with at least 40% cortex representing only 3.3% (layer 1) and 9.3% (layer 4.1). In both collections, three types of reduction methods can be identified: Levallois, discoidal and laminar flaking. For many individual artefacts, it is difficult to assign them to a specific flaking technology but recording technological attributes such as platform variables (including measurements, see supplementary information) and dorsal scar patterns allows to identify these flaking methods. The combination of facetted platforms with complex dorsal flake scar patterns is present in both layers and can be assigned to the Levallois method. A smaller proportion of flakes can be related to discoidal flaking, as indicated by dihedral platforms, debordant flakes and pseudo-Levallois points (Figs. 4 and 5).

While in both collections, the pointed blanks have facetted, dihedral and plain platforms, in layer 1 facetted platforms are dominant, while in layer 4.1 plain platforms are most numerous (Fig. 6). In both collections, facetted platforms are more dominant on the pointed blanks, a Levallois point production scheme (Fig. 6).

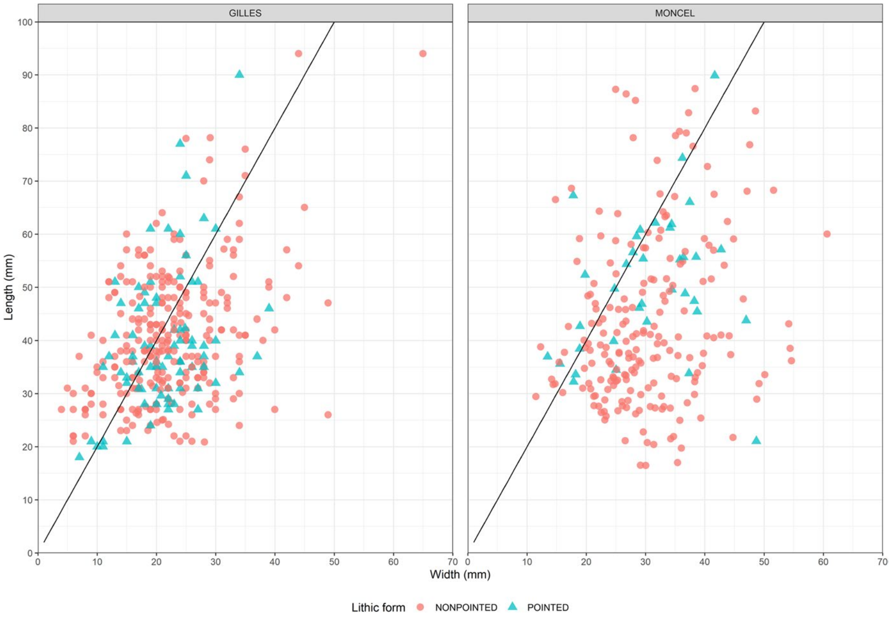


Fig. 7 Plot comparing length and width measurements of pointed (blue) and non-pointed (red) blanks across Abri du Maras layers 1 (Gilles collection, *n*: 368) and 4.1 (Moncel excavation, *n*: 240). The black diagonal line represents where length is twice the width, which corresponds to the metric definition of a blade

Blank Elongation

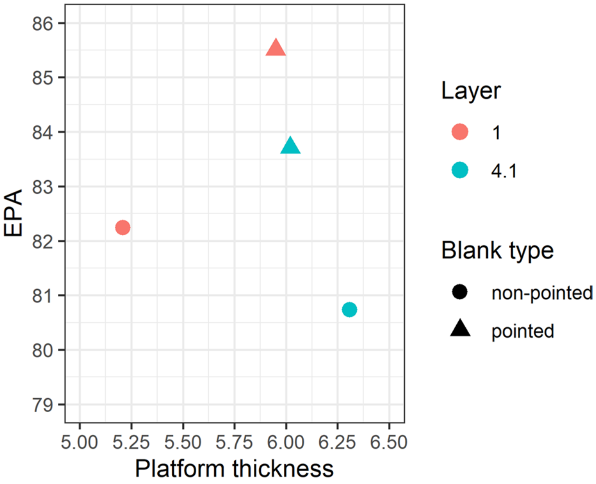
To assess the laminar component of the assemblage, the length and width of all unbroken pieces were plotted (Fig. 7). Artefacts above the black line are twice as long as wide and therefore laminar by definition. The plot shows that a larger proportion of the artefacts from layer 1 are laminar, and especially the smallest laminar artefacts (< 10-mm width) are not represented in layer 4.1. In both cases, the pointed blanks are spread across the plot but with a stronger presence of laminar pointed blanks in layer 1 (Fig. 7).

Exterior platform angle (EPA) and platform thickness are two key variables underlying blank size and shape (Dibble, 1997; Dibble & Rezek, 2009; Lin et al., 2013). An increase in EPA has been linked to the production of more elongated blanks (Dibble & Rezek, 2009). In both collections, the pointed blanks have a higher average EPA compared to the non-pointed blanks (Fig. 8). The lithics of layer 1 generally have smaller platforms and higher EPA values, indicating the more laminar aspect of this collection.

Blank Selection

Only a low proportion of artefacts from layer 4.1 have been retouched (also see Moncel et al., 2021). In the sample analysed here, there are 14 tools (4.5%),

Fig. 8 Mean values of EPA and platform thickness comparing pointed and non-pointed blanks across Abri du Maras layers 1 (Gilles collection, $n=120$) and 4.1 (Moncel excavation, $n=107$)



including denticulates, scrapers and retouched points. This contrasts with the layer 1 material where retouch is much more common with 140 tools (25.8%), dominated by denticulates. Furthermore, 40 of the layer 1 pointed blanks (43.5%) have been retouched. While the dimensions of the pointed and non-pointed blanks are similar, the pointed tools from layer 1 are made on the longest, widest and thickest blanks (Table 4).

Inverse Retouch

One of the most characteristic features of the layer 1 material is the presence of retouch on the ventral face of the artefacts, known as inverse retouch (Fig. 4). In layer 1, 18% of the analysed tools have inverse retouch (13 pointed and 13 non-pointed blanks), most often distally. There are eleven ventral scrapers and eight points with inverse retouch along both edges, the so-called Soyons points. These Soyons points are made on various types of blanks, including laminar and Levallois blanks (Fig. 4). Conversely, inverse retouch is very rare in the 4.1 sample and was only present on one tool, a denticulate.

Table 4 Comparison of the dimensions of the pointed and non-pointed flakes and tools from Abri du Maras layer 1 (Gilles collection)

		Length (mm)		Width (mm)		Thickness (mm)	
		Average	StdDev	Average	StdDev	Average	StdDev
Flake	Pointed	36.53	11.23	19.73	6.3	4.66	2.38
	Non-pointed	36.58	11.17	19.92	8.08	3.45	3.35
Tool	Pointed	43.71	13.91	24.06	6.96	5.82	2.4
	Non-pointed	42.69	13.18	22.59	7.31	3.23	3.68

Morphological Alterations Linked to Projectile Use

A series of attributes were recorded across both pointed and non-pointed blanks which have been suggested to relate to hafting or impact damage (Fig. 3). In layer 1, basal modifications (mainly width reduction) occur more commonly on pointed (*n*: 17, 21.8%) compared to non-pointed (*n*: 48, 14.1%) blanks. Basal retouch is also more common on pointed blanks. In general in layer 1, pointed blanks are more commonly retouched at the tip, while non-pointed blanks have more retouch in the medial zone.

Small breaks at the distal end of an artefact were recorded across both collections and across blank types in similar proportions (ranging from 11 to 18%, Table 5). In general, distal fractures seem common, and linking them to damage specifically relating to hunting remains a major methodological challenge (also see Rots & Plisson, 2014).

Edge Damage Distribution

The presence of edge damage (as represented by macroscopically visible small pits and chips) was recorded for the distal, medial and basal zones of all unbroken artefacts. Damage that had a clear recent origin was not recorded, nor were edges damaged due to desilicification. In general, edge damage is most common on the medial part of all artefacts, and pointed blanks are more damaged than non-pointed blanks (Fig. 9). Investigating links between edge angles and edge damage distribution (McPherron et al., 2014) was beyond the scope of this study and is required before functional inferences can be made.

The focus of this lithic analysis was on placing the typo-technological attributes of the pointed forms in the context of the non-pointed component of the assemblages. While there are clear differences between the lithic collections from Abri du Maras layers 1 and 4.1 (e.g. presence of retouch, elongation of the artefacts), in both collections there is a lot of typo-technological variability within the pointed and non-pointed blanks. Both blank types are produced with various flaking techniques, resulting in the presence of various platform types and dorsal scar patterns. Distal breaks occur on both blank types although pointed blanks do more commonly have edge damage on their distal parts. To be

Table 5 Small breaks at the distal end of the artefacts (recorded in the tip missing category) across pointed and non-pointed blanks and across tools and flakes, from across the Abri du Maras layer 1 and layer 4.1 lithic collections

Tip missing	Layer 1		Layer 4.1	
	n	%	*n*	%
Pointed blanks	14	15.22%	5	13.51%
Non-pointed blanks	77	17.07%	40	14.60%
Tools	16	11.35%	2	14.29%
Flakes	75	18.66%	43	14.48%

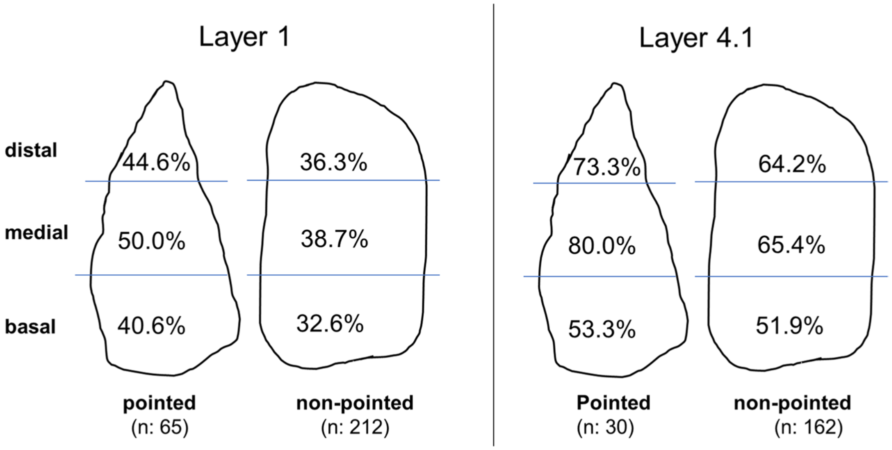


Fig. 9 Percentage of unbroken pointed and non-pointed blanks with edge damage in their distal, medial and basal zones from Abri du Maras layer 1 (Gilles collection) and layer 4.1 (Moncel excavation)

able to link the observed patterns to Neanderthal behaviour, further contextualization of the data is required, both at an intra- and inter-site level.

Zooarchaeology by Mass Spectrometry (ZooMS)

The analysis of faunal material from archaeological sites provides essential insights into subsistence practices as well as site formation. The vast majority of the bone remains recovered from layer 1 (both by R. Gilles and J. Combier) are highly fragmented and hence morphologically unidentifiable (Combier, 1967; Daujeard, 2008). Out of the 280 unidentifiable bone fragments sampled for ZooMS analysis within the framework of this study, 226 could be assigned to a taxon, providing an identification rate of 80.7%. As with previous research of this type, proteomic identification success rates are well above that possible using morphological criteria only.

Taxonomic Identification

The 226 identified ZooMS fragments complement the existing zooarchaeological data (NISP: 49; Daujeard, 2008) and indicate a varied faunal spectrum (Table 6, Fig. 10). Peptide marker series can be similar for some closely related species, which is the case for *Bos/Bison*, Cervid/Saiga, Equidae and Suidae. Thus, Cervid/Saiga can be attributed to either *Cervus elaphus* (red deer), *Megaloceros giganteus* (giant deer), *Alces alces* (elk) or *Dama* sp. (fallow deer); an attribution to *Saiga* sp. can be excluded based on our knowledge of the fauna in this region for this period. Equidae and Suidae include, respectively, species from the genera *Equus* and *Sus*, most likely *Equus ferus* and *Sus scrofa* based on available faunal records from the region. The combined NISP (*n*: 275) obtained from the faunal and ZooMS analysis

Table 6 Overview of the different species identified from layers 1, 1' and 1'' at Abri du Maras (zooarchaeological data from Daujeard, 2008)

	Zooarchaeology		ZooMS		Total NISP	
	n	%	*n*	%	*n*	%
Cervus elaphus	5	10.20%			5	1.82%
Cervid/Saiga			51	22.57%	51	18.55%
Cervid/Saiga/Capreolus			20	8.85%	20	7.27%
Cervus/Rangifer	1	2.04%			1	0.36%
Capreolus capreolus	1	2.04%	3	1.33%	4	1.45%
Rangifer tarandus	23	46.94%	25	11.06%	48	17.45%
Total Cervidae	**30**	61.22%	**99**	43.81%	**129**	46.91%
Bison priscus	9	18.37%			9	3.27%
Bos/Bison			68	30.09%	68	24.73%
Caprinae			3	1.33%	3	1.09%
Capra sp.			9	3.98%	9	3.27%
Total Bovidae	**9**	18.37%	**80**	35.40%	**89**	32.36%
Equus cf. *germanicus*	9	18.37%			9	3.27%
Equus hydruntinus	1	2.04%			1	0.36%
Equidae			32	14.16%	32	11.64%
Total Equidae	**10**	20.41%	**32**	14.16%	**42**	15.27%
Total Suidae			**1**	0.44%	**1**	0.36%
Bovidae/Cervidae			8	3.54%	8	2.91%
Bovidae/reindeer			5	2.21%	5	1.82%
Capra sp./reindeer			1	0.44%	1	0.36%
Total	**49**	100.00%	**226**	100.00%	**275**	100.00%

Values in bold relate to the family totals

of layer 1 (both R. Gilles and J. Combier collections) show that Cervidae (*n*: 129) are most frequent, followed by Bovidae (*n*: 89) and Equidae (*n*: 42). Within the Cervidae, the Cervid/Saiga grouping (which includes red deer) is most numerous, followed by reindeer (*Rangifer tarandus*) and roe deer (*Capreolus capreolus*). The addition of Caprinae and Suidae to the faunal spectrum was possible through the use of ZooMS. Based on the local setting, the specimens assigned to *Capra* sp. (*n*: 9) most likely relate to *Capra ibex*. The grouping 'Caprinae' (*n*: 3) indicates that the peptide marker that allows to distinguish *Ovis* and *Rupicapra* from *Capra* sp. could not be observed.

While low sample size (especially for layer 1'') makes it difficult to compare the taxonomic distribution across layers, overall the species representation and richness seems similar (Fig. 10).

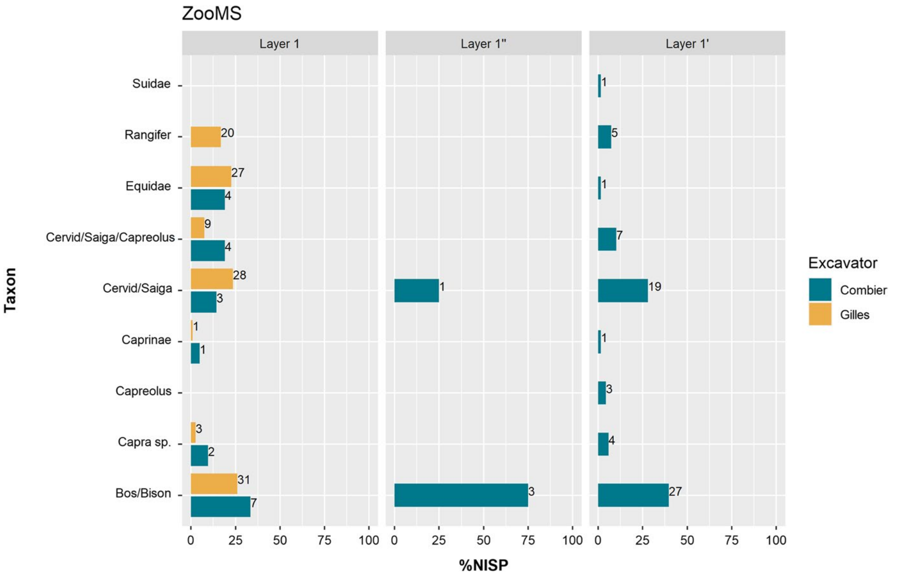


Fig. 10 Taxonomic distribution across archaeological units (Gilles (in yellow) layer 1 ($n=151$), Combier (in blue) layer 1 ($n=40$), Combier layer 1' ($n=85$) and Combier layer 1'' ($n=4$)). This figure only includes taxonomic identities obtained through the ZooMS analysis of the faunal material from layer 1 at Abri du Maras. Numbers associated with the bars indicate the total number of specimens (NISP)

Molecular Diagenesis

The level of glutamine deamidation is linked to the preservation state of collagen in bone. It is studied here to assess the presence of differential preservation patterns that could provide additional insights into the association between the lithic and faunal material recovered from layer 1. When looking at slow-deamidating peptides such as COL1α1 508–519, the Gln deamidation values from the analysed Abri du Maras material cluster between 0.15 and 0.45 with values closer to 0 showing a higher proportion of deamidated glutamines (Fig. 11a). The comparison between extraction methods shows slightly higher values obtained after acid demineralisation of the bone samples (Fig. 11d). No outliers could be identified, and the values for molecular diagenesis overlap for the two excavator collections (Combier, Gilles) when compared to bone specimen length (Fig. 11a), taxonomic identity (Fig. 11c) and archaeological layer (Fig. 11b). Overall, the glutamine values did not provide clear indications of intrusive material or differential preservation although it does also not allow excluding these. The molecular diagenesis could be similar across the stratigraphy and can only be fully assessed through the sampling of other layers at the site, which was beyond the scope of this study.

Zooarchaeological Analysis

The assessment of bone surface modifications allows for the characterisation of accumulation agents at the site. The ZooMS analysis of the bone material from layers 1, 1’ and 1″ highlights the absence of carnivore remains. Our taphonomic study of these ZooMS fragments identified no non-anthropogenic modifications, which would be related to the activity of carnivores and rodents on site. Conversely, human modifications such as butchery marks were identified across all taxa within the ZooMS assemblage (Fig. 12), suggesting that the accumulation of these remains was a result of human activity. When addressing the bone preservation related to weathering in order to identify any potential differential depositional processes between layers 1, 1’ and 1″, we note that all bone specimens from Gilles and Combier’s collections show low weathering stages (stages 0–2) with highly weathered bones (stages 3–5) being very rare (layer 1: $n=1$, layer 1’’: $n=0$, layer 1’: $n=1$) suggesting similar depositional conditions for these three layers.

Radiocarbon Dating

The collagen yield from the eleven selected cortical bone fragments was very variable, ranging from 0.29 to 7.32% (Table 7). The three bone fragments from the Gilles excavation could not be dated due to low collagen yields (Table 7). A similar low value was obtained for one of the Combier bones from layer 1’’ (Table 7). In total, five bones were dated in Mannheim.

The three bone fragments from Combier layers 1 and 1’’ were dated to between 34.7 and 31.7 ka cal BP (calibrated using IntCal20; Reimer et al., 2020). The single date obtained for layer 3 indicated an age of 41–40 ka cal BP and for layer 4 of around 35 ka cal BP (Table 7). These ages are younger than expected, and the ^{14}C dates do not

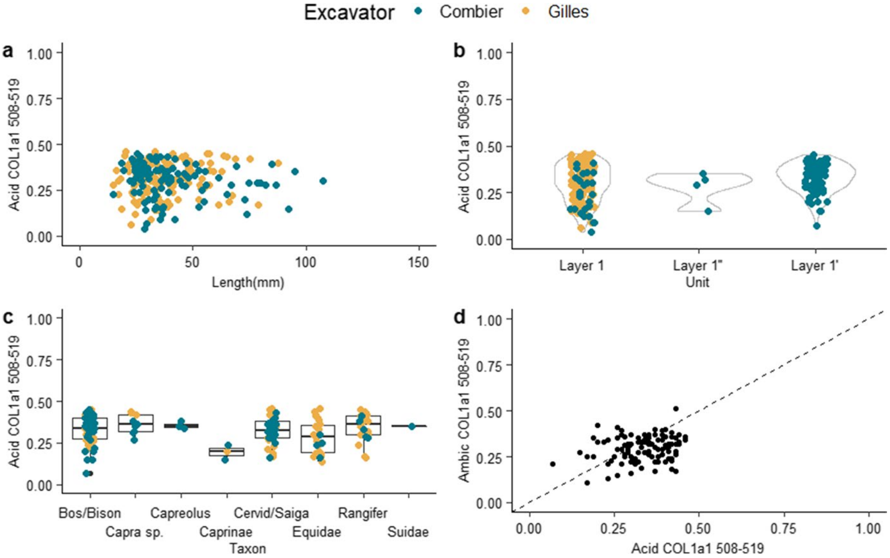


Fig. 11 Glutamine deamidation ratios of the peptide marker COL1α1 508–519 obtained for the Abri du Maras bone fragments from the Gilles and Combier excavations (layers 1, 1’ and 1’’), compared with **a** fragment length, **b** layer, **c** taxonomic identities and **d** extraction methods (dotted line is 1:1). R. Gilles’ collection is in yellow and J. Combier’s collection is in blue

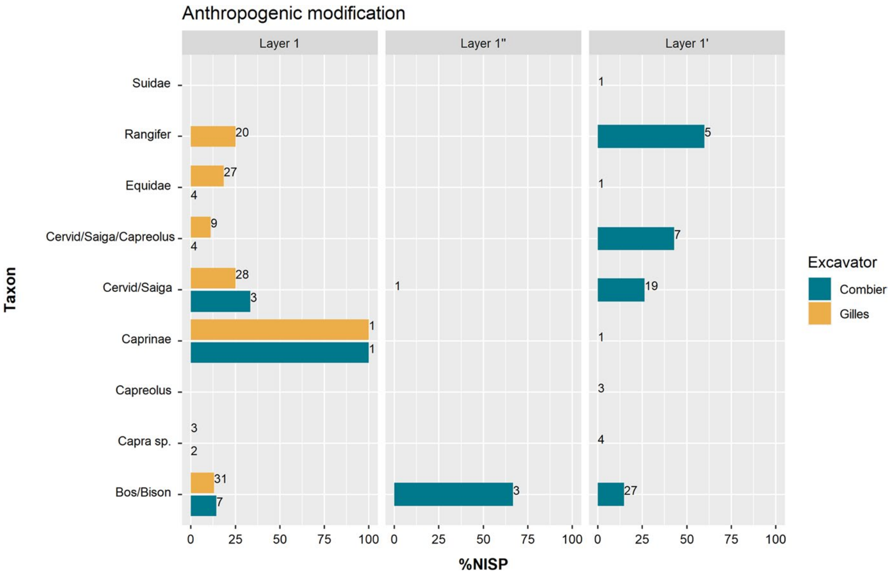


Fig. 12 Anthropogenic modifications across dominant taxon identified through ZooMS organised by sub-layer and excavation campaign. Numbers associated with the bars indicate the total number of specimens (NISP)

agree with the stratigraphic information. This situation does not allow us to produce a Bayesian model.

It is important to stress that all isotopic values obtained from the bones returned good results with C:N ratios of 3.3 and collagen yields generally larger than 1% of the weight (Table 7; Talamo et al., 2021; van Klinken, 1999). Further, two background bones were processed along with the five archaeological bones and returned values in the expected range, indicating that no modern contamination was introduced during the dating protocol. Moreover, the obtained dates are consistent, including the three from layer 1/1'', and in close range to each other.

On the other hand, problems are often encountered with dating bones from old excavations or from old museum collections, with results obtained often younger than expected due to inconsistencies in excavation and curation procedures (Benazzi et al., 2014; Hoffmann et al., 2011; Talamo et al., 2016, 2018). At Abri du Maras, the obtained dates for layer 1 fall within the range of the local Aurignacian and Gravettian (Quiles et al., 2016). However, none of the excavation campaigns (Gilles, Combier or Moncel) recovered diagnostic Aurignacian or Gravettian archaeological material. The original excavation reports mention that animal bones were only recovered from layer C (Baudet et al., 1955) and there are no traces of human occupation in the overlying layers. Moreover, the stratigraphic sections indicate that layer 1 is covered by ca. 47 cm of two archaeologically sterile layers.

Table 7 Radiocarbon dating results for Abri du Maras Gilles and Combier collections, including isotopic data, %Collagen, %C and %N and C:N for the samples. The ^{14}C ages were calibrated using IntCal20 (Reimer et al., 2020) and OxCal 4.4 (Bronk Ramsey, 2009)

Find ID	Layer	Species identification	Modifications	Final mass (mg)	Collagen (%)	δ^{13}C	$\delta 1^{5}$N	%C	%N	C:N	AMS Code	^{14}C Age	1 s Err	Cal BP 68,3% From–to	Cal BP 95,4% From–to
Gilles collection															
87.22.2059	1	Cervid/Saiga/ Capreolus	Yes	1.7	0.29										
87.22.2104	1	Cervid/Saiga	Yes	2.9	0.56										
87.22.2242	1	Tibia Bovidae sp.	No	2	0.34										
Combier collection															
87.22.3135	1	x	Yes	6.8	1.13	− 19.6	5.7	33.7	12.0	3.3	MAMS-38407	28,100	120	32,190–31,770	32,860–31,680
87.22.3134–2	1	x	No	16	3.05	− 19.9	5.7	37.5	13.1	3.3	MAMS-38408	28,450	120	32,980–32,210	33,130–32,060
87.22.3102	1"	Cervid/Saiga	No	4.7	0.91	− 19.7	4.4	37.6	13.1	3.3	MAMS-38409	30,050	140	34,600–34,360	34,730–34,210
87.22.3096	1"	Bos/Bison	No	2.7	0.41										
87.22.3234	3	Reindeer metapodial	No	25.1	4.42	− 19.2	4.1	41.9	14.9	3.3	MAMS-38410	35,600	250	41,030–40,540	41,230–40,170
87.22.3215–1	3	Cervid metapodial	No	38.6	5.74	− 19.9	5.6	42.0	14.9	3.3					
87.22.3276	4	Large ungulate tibia	Retouched	21.1	3.17	− 20.3	3.6	40.2	14.1	3.3	MAMS-38411	31,140	160	35,720–35,300	36,040–35,190
87.22.3271	4	Bovid humerus	Retouched	45.1	7.32	− 19.6	5.4	41.5	14.9	3.2					

Overall, a refined chronology for the Neronian occupation at Abri du Maras is, currently, not possible, and we can merely attribute an MIS 3 age. While we consider it unlikely due to the nature of the assemblages, we cannot exclude that the bones we selected from the assemblage represent an ephemeral Upper Palaeolithic visit that occurred at the top of the Middle Palaeolithic sequence. A refined radiocarbon chronology for the upper layers from the Moncel excavations is the best option to obtain a better understanding of the chronology of the Neanderthal occupation at this site.

Discussion

Neanderthal Subsistence in the Point-Rich Levels of Abri du Maras

Abri du Maras provides a unique case study to assess the subsistence practices underlying two different types of Mousterian with points (layers 1 and 4.1). Similar volumes were excavated from both layers (layers 1/1'/1'': ca. 40 m^2 with a layer thickness of ca. 7–30 cm, layer 4.1: 38 m^2 with a layer thickness of 30 cm, Table 8). While layer 1 seems to have a higher lithic density (layer 1: 123/m^2, layer 4.1: 54/m^2), a much smaller number of animal bones ($n = 1{,}066$, 27/m^2) was recovered from this layer compared to layer 4.1 ($n = > 11{,}000$, ca 290/m^2). Currently, it is difficult to assess if these differences in lithic and faunal density are related to excavation methods, collector bias, preservation conditions or Neanderthal behaviour. However,

Table 8 Comparison of Neanderthal technological and subsistence behaviour at Abri du Maras (Layers 1 and 4.1). (Based on data from this study as well as from Combier, 1967; Daujeard et al., 2019; Moncel, 1996; Moncel et al., 2014, 2021)

	Layer 1	Layer 4.1
Site type	Small rockshelter	Large rockshelter
Excavation campaigns	Gilles 1946–1959, Combier 1958 & 1963	Moncel 2006–ongoing
Excavation area	40m2	38m2
Layer thickness	7–30 cm	ca. 30 cm
Age	MIS-3	MIS-3
Lithic assemblage	3695	2041
Raw material	Flint	Local and semi-local flint (20–30 km)
Lithic technology	Levallois, laminar	Levallois
Tool types	Denticulates and scrapers	Few retouched tools
Point types	Ventrally retouched points	Unretouched points
Faunal assemblage	1066	> 11,000
NISP	275 (25.8%)	1,170 (10.5%)
Faunal spectrum	Bovids, cervids, equids, reindeer	Reindeer dominated
Carnivores	No	No
Butchery marks	Yes	Yes

we think it is important to integrate both lithic and faunal datasets to improve our understanding of these layers (Ruebens et al., 2020).

Lithic Data

Both lithic assemblages are characterised by the production of Levallois points, but there are also striking differences, with a higher proportion of elongated blanks in layer 1 and a very low occurrence of retouched tools in layer 4.1. While for layer 4.1, it has been demonstrated that large Levallois blades and points were produced elsewhere and imported to the site (Moncel et al., 2021), layer 1 seems to have a stronger focus on in situ knapping, as indicated by the presence of a series of small highly reduced cores ($n = 59$). In both layers, flint nodules and tabular pieces were collected, with low proportions of other raw materials (Combier, 1967; Moncel et al., 2014).

The layer 1 lithic material has been studied by various scholars, and differences in description and interpretations indicate how difficult it is to taxonomically classify this assemblage (a problem noted for other Middle Palaeolithic assemblages as well; Dibble, 1995). On the one hand, affinities with the Upper Palaeolithic, and more specifically with the proto-Aurignacian (Baudet et al., 1955) or the Initial Upper Palaeolithic (Slimak, 2019; Slimak et al. 2022), have been suggested. On the other hand, scholars have stressed links with Mousterian entities such as the Mousterian of Acheulean Tradition (MTA, Combier, 1967) and the Charentian Mousterian (Moncel, 1996; Slimak, 2004, 2008). A complete typo-technological reassessment of this assemblage was beyond the scope of this paper. Rather, our focussed attribute analysis demonstrated how across both Abri du Maras layers differences between the pointed and non-pointed blanks are limited and the low incidence of clear lithic weapon tips in the Middle Palaeolithic record remains remarkable. Tip fractures occur both on pointed and non-pointed blanks, and interpreting how the tip of an individual artefact broke and if it was related to impact from hunting remains challenging (Rots & Plisson, 2014). While it is possible that some of the points from Abri du Maras were used for killing animals, previous interpretations of impact damage (Hardy et al., 2013) have more recently been challenged for some of the artefacts (Claud et al., 2019).

Faunal Data

Although bone preservation at Abri du Maras is overall rather poor, especially in relation to fragmentation and bone surface readability, it is clear that both layers 1 and 4.1 reflect a predominant human accumulation. This is indicated by the lack of carnivore modifications (< 1%) and carnivore remains (0%) and the high incidences of butchery marks (layer 1: 20%, layer 4.1: 21.8% of the legible remains). In both layers, burnt flint and burnt bones also indicate the presence of fire at the site (Combier, 1967; Daujeard et al., 2019). Due to high fragmentation rates, only 4.6% of the layer 1 faunal remains were taxonomically identifiable based on morphology alone (NISP = 49; Daujeard, 2008). For layer 4.1, the identification rate is slightly higher with 10.5% assigned to a taxon (NISP = 1170) and of this NISP 88% were identified as reindeer (MNI = 16, Daujeard et al., 2019) indicating a limited taxonomic diversity. These reindeer seem to relate to autumnal hunting episodes followed by the selective transport to the rock shelter of limb elements which were then intensively processed at the site as witnessed by various types of cut and scrape marks across species (Daujeard et al., 2019).

The smaller and highly fragmented faunal collection from layer 1 does not allow an assessment of body part representation or seasonality. However, the ZooMS analysis of the fragmented and unidentifiable bone specimens increased the identification rate, indicating a more diverse faunal spectrum with significant amounts of cervids, bovids, equids and reindeer (Table 6). Combined with the occurrence of human modifications across these species, predominantly cut marks associated with a low occurrence of percussion traces, this highlights the exploitation of different types of biotopes during a more temperate climatic phase. A more varied faunal spectrum, characterised by the occurrence of bison, horse, red deer, reindeer and giant deer, has also been identified in layer 4.2 underlying layer 4 (Daujeard et al., 2019), although both for layers 4.1 and 4.2 no ZooMS studies have yet been conducted.

Overall, layer 1 reflects the use of a small rock shelter by Neanderthals to process a range of medium and large herbivores. Because of the lack of detailed provenience data, it is difficult to assess and disentangle possible palimpsests captured in this layer. Conversely, the morphologically identifiable fauna from layer 4.1, coming from modern excavation techniques, seems to suggest a more specialised focus on hunting reindeer during a cold climatic phase with lithic artefacts brought in from elsewhere and used unretouched (Daujeard et al., 2019).

The Neronian: Mousterian Lithic Variability or Initial Upper Palaeolithic?

Lithic Data

At several sites in southeast France, lithic assemblages were recovered in the 1950s which were difficult to classify into the binary system of Middle Palaeolithic (Mousterian) Neanderthal and Upper Palaeolithic (Aurignacian) modern human lithic entities (Slimak, 2004). The Neronian assemblages contain both Middle Palaeolithic technologies (Levallois, discoidal) and tool types (e.g. scrapers and denticulates) as well as Upper Palaeolithic elements (blades, bladelets, end scrapers, burins and piercers). Another shared feature of five of these assemblages is the production of points, including ventrally retouched elongated Levallois points (Soyons points) (Combier, 1955, 1967, 1990; Veyrier et al., 1951). This led them to be classified as a newly defined entity, the Neronian (Table 9).

More recent discussions of the Neronian describe additional characteristics such as the lack of a dedicated flake production system; the presence of microliths, including points smaller than 3 cm; and the use of imported high-quality raw materials (Slimak, 2004, 2008, 2019). The cornerstone of these descriptions is the rock shelter site of Grotte du Mandrin where recent excavations (1990–ongoing) revealed

Table 9 Overview of all lithic assemblages that have been assigned to the Neronian taxonomic entity

	Néron	Moula	Figuier	Mandrin	Abri du Maras		
	Layer 1	Layer IV	Layer 1’	Layer E	Layer 1	Layer 1’	Layer 1’’
Main reference	Slimak, 2004	Defleur, 2015	Moncel, 2001	Slimak, 2004	Moncel, 1996		
Excavation	Combier 1950–1951	Defleur 1993–1999	Huchard-Gilles 1950s	Slimak, 1990–ongoing	Gilles 1946–1950	Combier 1958 & 1963	
Date	Undated (low collagen)	End MIS 3 /4	Undated	> 49,000	Undated	31–35 Cal BP	
Cores	23	9	6	28	49	9	1
Discoidal	*8*			*2*	*34*		*1*
Levallois	*1*	*2*			*3*	*6*	
Laminar	*3*				*4*	*1*	
Flakes	255	173	111	505	405	74	60
Levallois products		*23*			*636*	*43*	*18*
Blades	*10*		*7*		*366*		
Points		*17*					
Tools	50	63		57	242	20	25
Soyons points	*6*			*7*	*9*	*0*	*0*
Flakes < 2.5 cm	9	225	3	806	479	235	171
Debris	4	22	5	62	1032		12
Other	5	37	6		90	15	
Total nr of artefacts	**346**	**552**	**140**	**562**	**3057**	**376**	**262**

a 2-m-deep stratigraphic sequence containing several Mousterian layers encapsulating a Neronian assemblage (layer 6 or E) (Vandevelde et al., 2017). While the lithic and faunal data from Mandrin has been described in general terms in several publications, in-depth studies are still awaiting publication (e.g. Metz, 2015; Slimak et al., in press), making it difficult to fully assess the nature of this key Neronian assemblage. The recovery at the edge of the Neronian layer of a worn deciduous tooth, which has been assigned to *Homo sapiens*, has led to further comparisons of the Mandrin Neronian with the Initial Upper Palaeolithic stone tool technologies at Ksar Akil (Slimak et al., 2022). Further data and data-driven analyses are needed to contextualise and substantiate this claim and to fully understand its consequences for the other assemblages that have been assigned to the Neronian.

The other four Neronian sites have small lithic assemblages (e.g. Néron, Moula and Figuier) or were excavated early on (e.g. Maras) (Table 9). In general, the lithic characteristics of these assemblages are varied, and questions can be raised concerning assemblage integrity and collector bias. For example, at the eponymous site of Grotte de Néron 346 lithics were collected from layer 1 by Combier in the 1950s, and this layer was not described in subsequent excavations in the 1990s. The number of artefacts is rather low ($n = 346$), and discoidal, Levallois and laminar cores are present alongside six Soyons points and a very low proportion of small debitage (Table 9).

The main shared feature of these Neronian assemblages is the production of Levallois points alongside the use of ventral retouch, resulting in the presence of Soyons points. Ventral scrapers occur sporadically at other Middle Palaeolithic sites both in the Rhône valley (e.g. Baume Flandin; Moncel, 2005) and elsewhere and were a separate category in Bordes typological list (nr 25: scraper on interior face; Bordes, 1961). However, to our knowledge, no other Middle Palaeolithic or early Upper Palaeolithic assemblages show such a high frequency of inverse retouch. It also remains unclear what the functional advantage was of using a ventrally retouched artefact over an unretouched or dorsally retouched tool.

At both Néron (layer 3 to 1) and Maras (layer 3 to 1), a gradual increase in the production of blades and points across the sequence has been used to argue for a local Mousterian origin for the Neronian (Combier, 1990; Slimak, 2008). However, more recently the Neronian at Mandrin has been linked to the Initial Upper Palaeolithic based on comparisons with Ksar Akil (Lebanon; Slimak, 2019; Slimak et al., 2022) suggesting a modern human influence. Links between Maras and the Middle Palaeolithic record of Western Asia were also already made by Combier (1967).

Overall, based on the currently available data, it remains difficult to assess the homogeneity of the Neronian, both at a site and regional level. It seems preliminary to talk about a spatio-temporal entity with a modern human influence, rather it seems that the typo-technological affinities and chronostratigraphic context of the assemblages will need to be assessed on a site-by-site basis, and the outcome will most likely be different for different assemblages.

Table 10 Overview of the faunal material recovered in association with the Neronian lithic assemblages (data for Maras from this ZooMS study and Daujeard, 2008; Moula from Defleur et al., 2001; Figuier from Daujeard, 2008; Néron and Mandrin from Slimak, 2004; Mandrin ZooMS data from Chowdhury et al., 2019). Where no absolute numbers were available, the species are indicated by plus signs ranging from most abundant (+++) to present (+). To be able to facilitate comparisons across assemblages and identification methods, some of the species have been grouped (e.g. *Equus Germanicus* and *Equus hydruntinus* are grouped under Equidae and *Capra* sp. under Caprinae)

Species		Maras layer 1		Figuier layer 1		Mandrin level E		Neron layer 1	Moula layer IV
		NISP	%NISP	NISP	%NISP	Zooarch	ZooMS		
Cervus elaphus	Red deer	5	1.82%	9	6.77%	++	11	+	+
	Cervid/Saiga	51	18.55%						
	Cervid/Saiga/Capreolus	20	7.27%						
	Cervus/reindeer	1	0.36%						
Capreolus capreolus	Roe deer	4	1.45%					+	
Rangifer tarandus	Reindeer	48	17.45%	46	34.59%	+	2	+	+
	Bos/Bison	77	28.00%	6	4.51%	+	4		+
	Caprinae	12	4.36%	19	14.29%	+	5		+
	Equidae	42	15.27%	21	15.79%	+++	11	+	+
Sus sp.	Pig	1	0.36%	2	1.50%				
Rhinoceros sp.	Rhino					+			+
	Bovidae/Cervidae	8	2.91%						
	Bovidae/reindeer	5	1.82%						
	Capra sp./reindeer	1	0.36%						
Vulpes vulpes	Fox			1	0.75%				+
Canis lupus	Wolf			1	0.75%				+
Panthera pardus	Leopard								+
Ursus spelaeus	Cave bear			27	20.30%			+	+
Crocuta spelaea	Cave hyena			1	0.75%				+
Total		275	100.00%	133	100.00%		33		

Faunal Data

At all five Neronian sites, faunal remains have been preserved (Table 10), although detailed zooarchaeological studies have not been published for all sites. At several sites, faunal identifications are hindered by high fragmentation rates (e.g. Mandrin (Giraud et al., 1998) and Maras (Daujeard, 2008)). Aside from the study presented here, ZooMS has been applied only to a small sample from Grotte Mandrin ($n=43$; Chowdhury et al. 2019). In terms of herbivores, all of the faunal assemblages contain bovids, equids, cervids and caprinae (Table 10). However, based on the limited available faunal data and the overall small NISPs, it is difficult to compare the exact taxonomic proportions. It seems that in some assemblages, reindeer is dominant (e.g. Figuier and Neron) indicating a cold open environment, while other sites, such as Abri du Maras, have a more diverse temperate faunal spectrum with a broader variety of deer species. In the absence of good chronological data (see below), normally these data would indicate that the duration of the Neronian exceeded a single climatic phase and was not tied to a particular hunting strategy.

Chronological Data

The chronology of the Neanderthal and early *Homo sapiens* occupation of southeast France relies on a limited number of recent radiometric dates (Barshay-Szmidt et al., 2020; Higham et al., 2014; Richard et al., 2015, 2021; Slimak et al., 2022; Szmidt et al., 2010; Talamo et al., 2020). While there are numerous Middle Palaeolithic find spots, only few of them have radiometric dates placing them towards the end of the Mousterian phase (Table 11). For example, the late Mousterian occupation at Grotte Saint Marcel indicates a Neanderthal presence in southeast France around 49–38 ka cal BP (Szmidt et al., 2010; Talamo et al., 2020). Conversely, proto-Aurignacian and Aurignacian assemblages, associated with early *Homo sapiens*, are less common in the area (e.g. Pêcheurs, Figuier, Mandrin, Chauvet (Szmidt, 2009)). Radiometric dates for the proto-Aurignacian cluster around 42–38 ka cal BP, for example, at Esquicho-Grapaou (Barshay-Szmidt et al., 2020) and Mandrin (Higham et al., 2014; Slimak et al., 2022).

Recent attempts to radiometrically date the Neronian layers of Néron (layer 1), Moula (layer IV) and Grotte Mandrin (level E) have had varying success. The bones from Néron did not provide sufficient collagen for AMS dating (Higham et al., 2014), and the bones from Grotte Mandrin (Higham et al., 2014) and Moula (Willmes et al., 2016) produced infinite determinations, indicating an age older than 50,000 BP. At Mandrin, OSL dates suggest that the Neronian occupation took place sometime between 51,000 and 57,000 BP (Slimak et al., 2022). At Moula, ESR dating has placed the assemblage between 72 and 50 ka BP, at the end of MIS-4 or the beginning of MIS-3 (Willmes et al., 2016). Together with the young dates obtained for layer 1 from Abri du Maras in this study, this indicates that the chronological unity of these assemblages with Soyons points remains unclear and could, potentially, be of different ages.

Table 11 Main radiometric dates available for Neronian and late Mousterian assemblages from southeast France

Site	Layer	Material	Method	Non cal BP radiocarbon date	Lab number	Reference
Grotte Mandrin	C, Mousterian	Bone	AMS	45,300 ± 2200	OxA-21691	Higham et al., 2014
		Bone	AMS	42,800 ± 1800	OxA-X-2286–14	
		Bone	AMS	43,200 ± 2000	OxA-X-2286–13	
		Multi-grain	OSL	48,300 ± 3500	X 6718	Slimak et al., 2022
		Single-grain	OSL	52,000 ± 2900	MAN19-3	
	D, Mousterian	Bone	AMS	47,000 ± 2700	OxA-21698	Higham et al., 2014
		Bone	AMS	> 47,100	OxA-21694	
		Multi-grain	OSL	51,600 ± 3900	X 6719	Slimak et al., 2022
	E, Neronian	Bone	AMS	33,300 ± 230	Lyon 2755	Slimak, 2008
		Bone	AMS	> 49,000	OxA-X-2286–15	Higham et al., 2014
		Bone	AMS	> 47,300	OxA-21692	
		Bone	AMS	> 48,600	OxA-21693	
		Single-grain	OSL	54,900 ± 3100	MAN19-4	Slimak et al., 2022
	E(/F)	Multi-grain	OSL	54,600 ± 2900	X 6720	Slimak et al., 2022
	F, Mousterian	Bone	AMS	> 48,200	OxA-21695	Higham et al., 2014
		Bone	AMS	> 49,900	OxA-21696	
		Multi-grain	OSL	56,700 ± 6900	X 6721	Slimak et al., 2022
		Single-grain	OSL	60,600 ± 3500	MAN19-5	
		Single-grain	OSL	61,900 ± 3700	MAN19-6	
Moula	IV, Neronian	Bone	AMS	> 50,000	OxA-28093–96	Willmes et al., 2016
		Teeth	U-series	Between 6 and 9 ka		
		Teeth	CSUS/ESR	52 ± 2 ka–69 ± 3 ka		
Néron	1, Neronian	Bone	AMS	Low collagen yield		Higham et al., 2014
	2, Mousterian	Bone	AMS	Low collagen yield		

Table 11 (continued)

Site	Layer	Material	Method	Non cal BP radiocarbon date	Lab number	Reference
Maras	1, Neronian (Gilles)	Bone	AMS	Low collagen yield		This study
	1, Neronian (Combier)	Bone	AMS	28,100 ± 120	R-EVA-2927	
	1’’, Neronian (Combier)	Bone	AMS	28,450 ± 120	R-EVA-2928	
	1’’, Neronian (Combier)	Bone	AMS	30,050 ± 140	R-EVA-2929	
	3, Mousterian (Combier)	Bone	AMS	35,600 ± 250	R-EVA-2931	
	4, Mousterian (Combier)	Bone	AMS	31,140 ± 160	R-EVA-2933	
	4.1, Mousterian (Moncel)	Teeth	ESR/U-series	40 ± 3 to 46 ± 3 ka		Richard et al., 2015, 2021
		Teeth	U-Th	57 ± 1 ka		
		Bone	U-Th	3 ± 7 ka		
	4.2, Mousterian (Moncel)	Teeth	ESR/U-series	42 ± 3 to 55 ± 2 ka		
		Teeth	ESR/U-series	80 ± 2 ka		
		Teeth	ESR/U-series	67 ± 1 ka		
	5bis, Mousterian (Moncel)	Teeth	ESR/U-series	90 ± 9 ka		
Figuier	4, Mousterian	Tooth	ESR/U-series	52 ± 9 ka		Richard et al., 2015, 2021
		Tooth	ESR/U-series	29 ± 4 ka		
		Tooth	ESR/U-series	40 ± 4 ka		
Saint-Marcel Cave	f, Mousterian	Bone	AMS	37,850 ± 550	OxA-19623	Szmidt et al., 2010
				37,850 ± 600	OxA-19625	
				41,300 ± 1700	OxA-19624	

Overall, the lithic, faunal and chronological data currently available for the five archaeological assemblages assigned to the Neronian (Table 9) is too limited to assess if it concerns a distinct spatio-temporal Neanderthal lithic entity in line with other patterns of Neanderthal regionalised behaviour (Ruebens, 2013; Ruebens and Wragg Sykes 2016). As the analyses throughout this paper have indicated, caution is needed when making behavioural interpretations based on collections coming from old excavation campaigns.

Conclusion

Our combined lithic, faunal and chronological analyses demonstrate the potential of such an integrated multi-methodological approach to maximise the behavioural information that can still be recovered from existing museum collections. While we managed to obtain additional behavioural data from the Maras layer 1 collections, we also identified contextual issues that require caution when making interpretations of Neanderthal behaviour within these Abri du Maras upper layers. While the obtained radiocarbon dates question the integrity of the layer 1 material, the glutamine deamidation ratios were not able to confirm or reject this. The ZooMS analyses allowed us to increase the NISP and demonstrate a diverse faunal spectrum that can be related to the exploitation of various biotopes during a temperate phase. Finally, the comparative lithic analyses of layers 1 and 4.1 indicate different strategies for obtaining and retouching lithic points and elongated blanks, and overall the relation between technology, tool type and faunal diversity is still poorly understood, both at site scale and at a regional level. This was also the conclusion of the broader assessment of the Neronian for which more in-depth studies, incorporating lithic, faunal and chronological data, are needed before its position as a taxonomic entity can be confirmed.

Overall this study is only a first step into gaining a better understanding of the lithic variability, faunal diversity, subsistence strategies and chronological resolution of the key late Mousterian site of Abri du Maras. There is still scope for further analyses of the layer 1 museum collections. In terms of lithic analyses, usewear and refitting analyses can further help clarify technological behaviour at the site. Further, it would be very interesting to apply additional ZooMS analyses to the other Maras layers, both from the Combier and Moncel excavations. This would allow further insights into species representation, site taphonomy and carcass processing behaviour. Finally, NIR screening could be applied, for example, to the ZooMS identified bones from the Gilles collection, to find bones that have sufficient collagen preserved for radiocarbon dating. Dating the Gilles layer 1 bones as well as obtaining an overall larger number of radiocarbon dates is key in gaining a better understanding of the homogeneity and integrity of the assemblage. Finally, it needs to be stressed that ongoing fieldwork at Abri du Maras and Grotte Mandrin, and for the latter detailed lithic and faunal data publications, will be key in further illuminating patterns of Neanderthal subsistence behaviour in southeast France, the homogeneity of the Neronian as a spatio-temporal entity and the role of pointed forms in the Neanderthal toolkit.

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Data availability The datasets generated during this study are available from the corresponding author on request.

Code Availability Not applicable.

Declarations

Conflict of Interest The authors declare no competing interests.

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