

# Neanderthal Use of Fish, Mammals, Birds, Starchy Plants and Wood 125-250,000 Years Ago

Bruce L. Hardy<sup>1\*</sup>, Marie-Hélène Moncel<sup>2</sup>

**1** Department of Anthropology, Kenyon College, Gambier, Ohio, United States of America, **2** Département de Préhistoire, Muséum National d'Histoire Naturelle, Institut de Paléontologie Humaine, Paris, France

## Abstract

Neanderthals are most often portrayed as big game hunters who derived the vast majority of their diet from large terrestrial herbivores while birds, fish and plants are seen as relatively unimportant or beyond the capabilities of Neanderthals. Although evidence for exploitation of other resources (small mammals, birds, fish, shellfish, and plants) has been found at certain Neanderthal sites, these are typically dismissed as unusual exceptions. The general view suggests that Neanderthal diet may broaden with time, but that this only occurs sometime after 50,000 years ago. We present evidence, in the form of lithic residue and use-wear analyses, for an example of a broad-based subsistence for Neanderthals at the site of Payre, Ardèche, France (beginning of MIS 5/end of MIS 6 to beginning of MIS 7/end of MIS 8; approximately 125–250,000 years ago). In addition to large terrestrial herbivores, Neanderthals at Payre also exploited starchy plants, birds, and fish. These results demonstrate a varied subsistence already in place with early Neanderthals and suggest that our ideas of Neanderthal subsistence are biased by our dependence on the zooarchaeological record and a deep-seated intellectual emphasis on big game hunting.

**Citation:** Hardy BL, Moncel M-H (2011) Neanderthal Use of Fish, Mammals, Birds, Starchy Plants and Wood 125-250,000 Years Ago. *PLoS ONE* 6(8): e23768. doi:10.1371/journal.pone.0023768

**Editor:** Michael D. Petraglia, University of Oxford, United Kingdom

**Received:** June 22, 2011; **Accepted:** July 25, 2011; **Published:** August 24, 2011

**Copyright:** © 2011 Hardy, Moncel. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Funding:** Thanks to the French Ministry of Culture for support of the excavations at Payre and to the Kenyon College Labalme Fund. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors have declared that no competing interests exist.

\* E-mail: hardyb@kenyon.edu

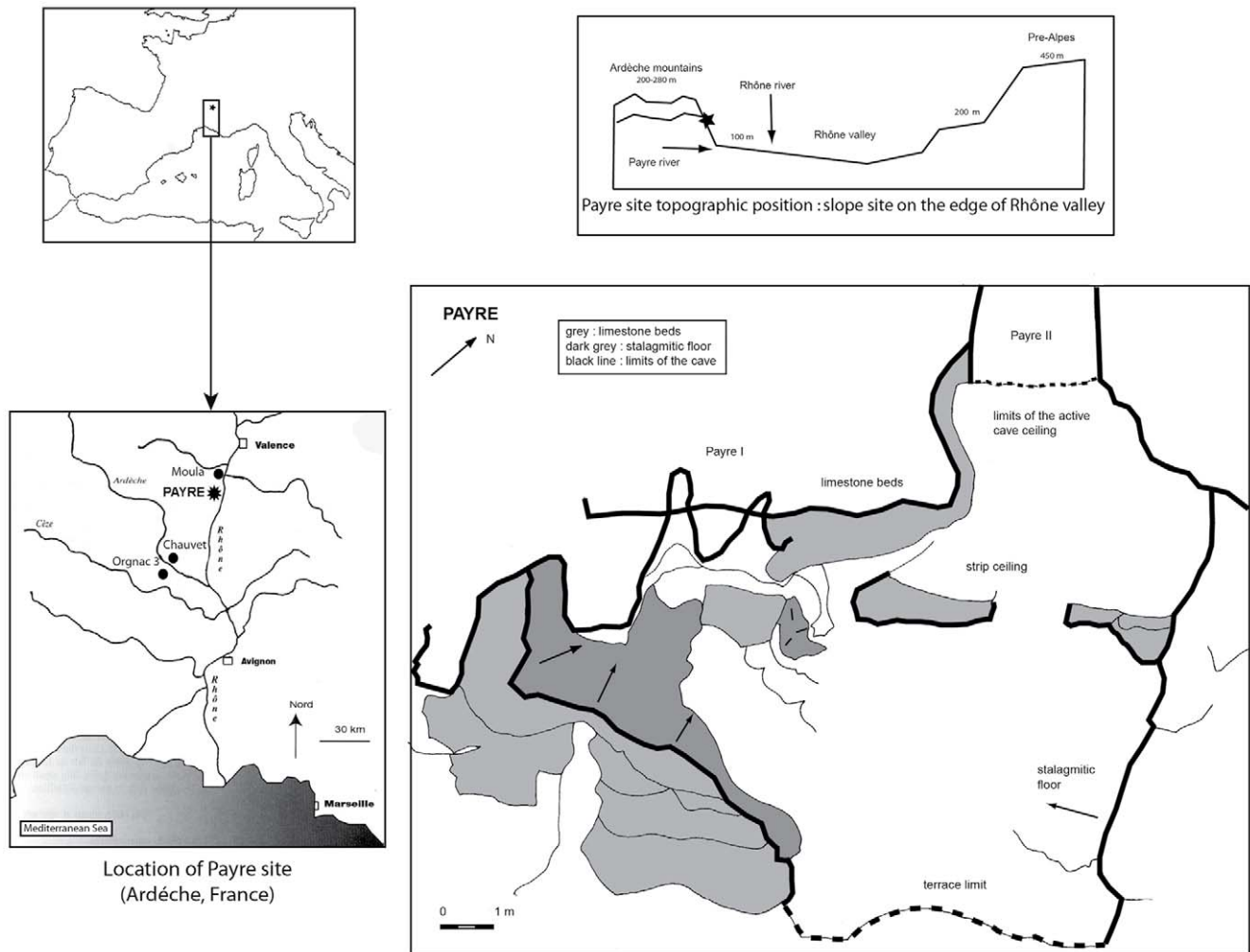
## Introduction

Meat, particularly in the form of hunting large game, has long been viewed as a vital component of human evolution as an energy rich food and valuable protein source [1]. Neanderthals, according to recent dietary reconstructions, have taken this adaptation to another level, deriving the vast majority of their calories from meat of large terrestrial herbivores [2]. Neanderthal sites certainly contain plenty of evidence of consumption of large herbivores, but there is increasing evidence that they also consumed small game, birds, fish, molluscs, and plants [3,4]. Despite this evidence, the Neanderthal diet is still seen as consisting predominately of large herbivore meat. Many have argued that a diet such as this would lead to problems with protein poisoning and that some other energy source would have been necessary [1,5]. The continued dominance of the Neanderthals as top carnivores hypothesis, even with the growing evidence that other types of game and plants were also consumed, speaks to the persistence and embedded nature of the big game hunting paradigm. Furthermore, it is unlikely that there was one Neanderthal diet, rather, diets likely varied according to the locally available resources [3,6]. Here, we report evidence for consumption of a broad range of plant and animal foods by Neanderthals in interglacial contexts at the site of Payre in southern France 125–250 ka.

## The Site of Payre

The site of Payre is located in the Rhone Valley of France (Fig. 1). The site was first a cave, then a shelter before the collapse

of the limestone ceiling. In spite of the varied nature of the site, Neanderthals came back at several different periods, perhaps because of its location on a promontory above the Rhone and Payre Valleys providing access to diverse environments. The excavations took place between 1990 and 2002 and yielded a 5 m thick sequence of deposits and 8 occupation levels. According to ESR, U-Th series, TL and TIMS methods, the sequence is dated to the end of MIS 8 and beginning of MIS 7 (levels Gb to Fa) and the end of MIS 6 and beginning of MIS 5 (levels E and D, Fig. 2) [7,8]. Neanderthal remains were discovered throughout the sequence, but most of them are located in levels Gb and Ga. The lithic and faunal assemblages are related to the early Middle Paleolithic and Neanderthals came for short-term seasonal occupations [9–11]. These occupations took place under temperate conditions at the beginning of interglacial periods, as attested by the faunal, microfaunal and palynological studies [12–13]. Flint came from local and semi-local outcrops located on the southern plateau and geological surveys suggest that raw material gathering took place during other subsistence activities from various outcrops with some long distance transport of flint up to 60 km [14–15]. The core technology is mainly discoid on flint, secondarily on quartz and limestone. Discoid cores show one or two secant flaking surfaces (convex or pyramidal section of each surface) with centripetal or unidirectional removals. All stages of the lithic reduction sequence are present at the site for local and semi-local flint, and partial for local quartz. This kind of technology produces many diverse flakes (thin, thick, short, elongated, triangular or quadrangular). The main flake-tools are scrapers and points



**Figure 1. Location of the site of Payre.**  
doi:10.1371/journal.pone.0023768.g001

(around 10–15% for the whole series). Some large bifacial tools were worked outside the site on large quartzite and basalt pebbles found in the Rhone Valley bank.

Based on zooarchaeological analyses and skeletal part representation, three large herbivores were mainly hunted (cervids, equids and bovids). Whole carcasses of cervids were brought to the site. Rare remains of rhinoceros and elephants (limb and skull elements) suggest scavenging of these very large mammals. Bones are largely broken for marrow and cut-marks attest to human butchery activities. Fire is also in evidence through burned bones and flint and a small ash lens in level Ga. Hyenas and bear remains demonstrate that the cave was occasionally inhabited by carnivores, who came when Neanderthals left the cave, especially level F [7].

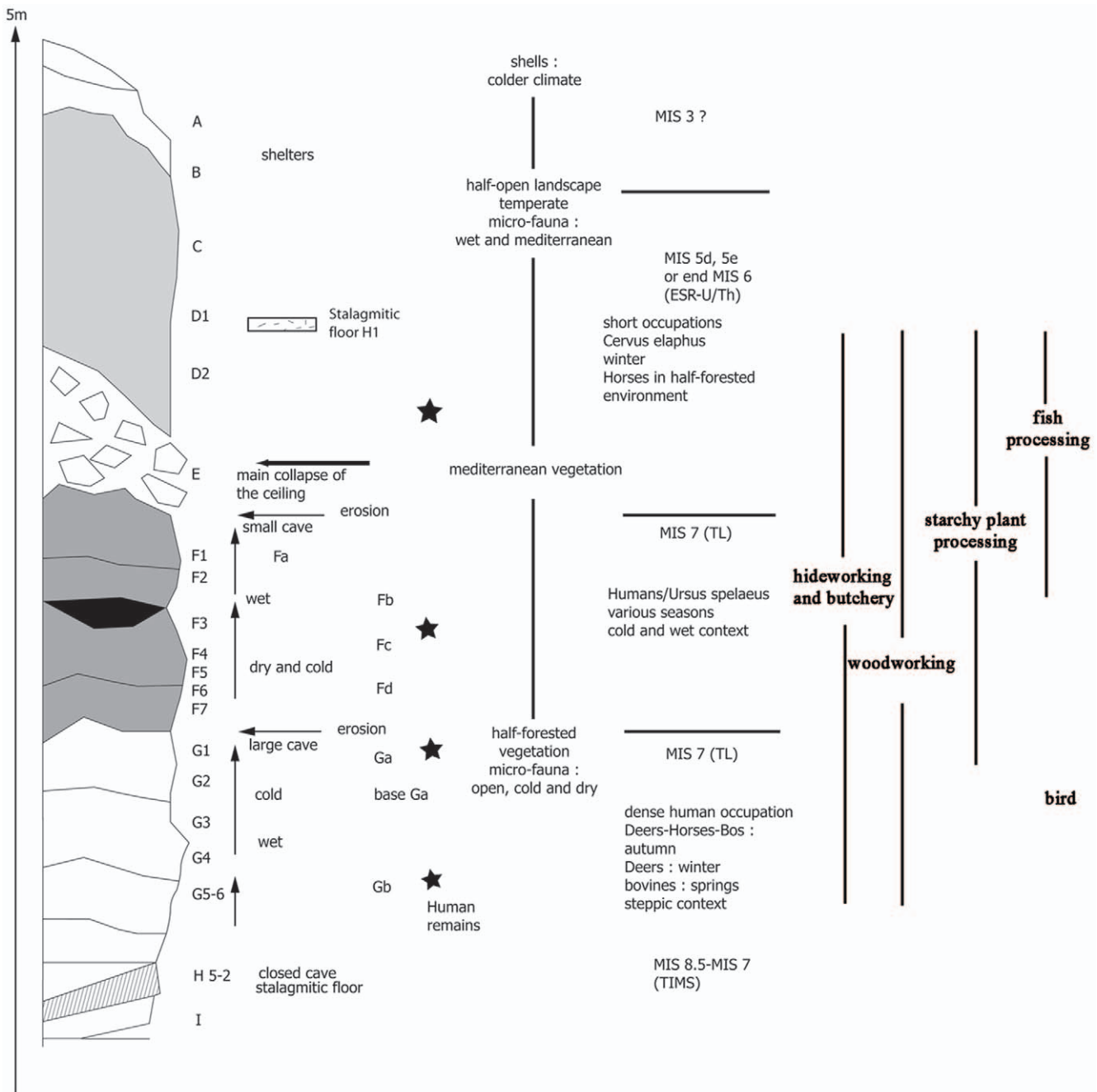
## Materials and Methods

### Lithic Use-wear and Residue Analysis

A sample of 182 minimally handled stone artifacts was examined under bright field incident light at magnifications ranging from 50–1000x using an Olympus BH30 microscope. Use-wear and adhering residues were photographed with a Nikon Coolpix 995 digital camera and their locations recorded on a line drawing of the artifact. Use-wear analysis included the identifica-

tion of striations, edge rounding and microflake scarring to help identify relative hardness of the use-material and the use-action [16–17]. Due to the potential overlap of polishes from different worked materials, polishes were identified as either “soft” or “hard/high silica” [18–21]. Soft polish derives from working soft materials such as animal skin or muscle while hard/high silica polish forms from processing bone, antler, wood, or soft plants with high silica content. One additional category is characterized by dull greasy polish in linear streaks with bright spots and may be associated with fish processing [22–23].

Examination of residues on stone tool surfaces allows the identification of hair, feathers, animal tissue, bone/antler, starch grains, plant tissue, raphides, phytoliths, wood and resin [19,24,25]. Residues were identified based on comparison with modern experimental samples and published materials [26–41]. Fish processing experiments and comparison with histology of fish tissues [42] allowed the characterization of fish residues (nerve tissue, bone, skeletal muscle, epithelial tissue, iridophores, scales, etc.) [43]. Starch grains can potentially be mistaken for fungal spores [44]. In order to confirm starch identification, putative starch grains were extracted and observed under transmitted light [45]. Patterning and distribution of residues as well as the co-occurrence of use-wear helped establish that residues were related to use [17,24,46–47].



**Figure 2. Stratigraphy, dating, climate, season, and activities at Payre.**  
doi:10.1371/journal.pone.0023768.g002

**Results**

Of the 182 artifacts examined, 125 (68.7%) preserved some type of functional evidence. The results show processing of plants, wood, fish, bird, starchy plants, bone, butchery and hideworking. Some artifacts showed evidence for processing of multiple residue types. See Table 1 for a breakdown of activities by level.

**Plants**

Woodworking activities (23/182 artifacts, 12.6%) were identified through diagnostic wood anatomy (tracheids, pitting, perforation plates, etc.) [30] and associated hard/high silica

polish, striae and sometimes edge rounding. Woodworking is present in all levels except Ga; however, this level does have artifacts with undiagnostic plant tissue and hard/high silica polish. This evidence most likely represents woodworking. In two cases, diagnostic anatomy allowed more specific identification. Bordered pits on a flake from Level Fc indicates gymnosperm processing while a scalariform perforation plate on a sidescraper from Level Ga likely derives from birch (Fig. 3) [30]. An additional 23 artifacts showed plant processing but more specific identification of the type of plant was not possible.

Starchy plant processing (18/182 artifacts, 9.9%) was identified by the presence of starch grains exhibiting an extinction cross

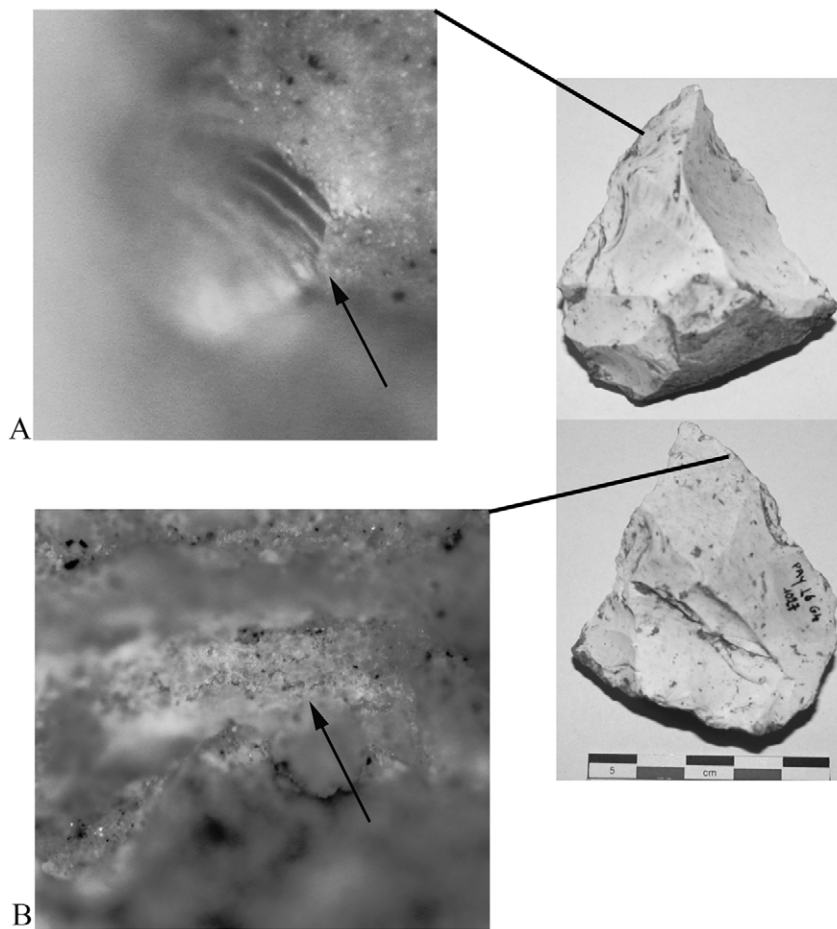
**Table 1.** Frequency of worked materials by level.\*

Level	Bone	Bird	Hide/Animal	Wood	HHS Plant	Soft Plant	Starchy Plant	Fish	Hard	Soft	Unknown
Gb n = 15	6.7%	---	33.3%	13.3%	20%	---	---	---	6.7%	---	33.3%
Ga n = 16	---	6.3%	18.8%	25%	---	6.3%	18.8%	---	---	---	25%
Fd n = 20	---	---	25%	---	25%	5%	5%	---	---	---	45%
Fc n = 14	---	---	21.4%	35.7%	7.1%	---	14.3%	---	7.1%	---	64.2%
Fb n = 26	4%	---	11.5%	7.7%	4%	---	4%	11.5%	11.5%	---	50%
Fa n = 51	---	---	31.8%	9.8%	3.9%	3.9%	11.8%	9.8%	15.7%	---	29.4%
D n = 40	---	---	12.5%	10%	15%	2.5%	15%	2.5%	22.5%	---	22.5%

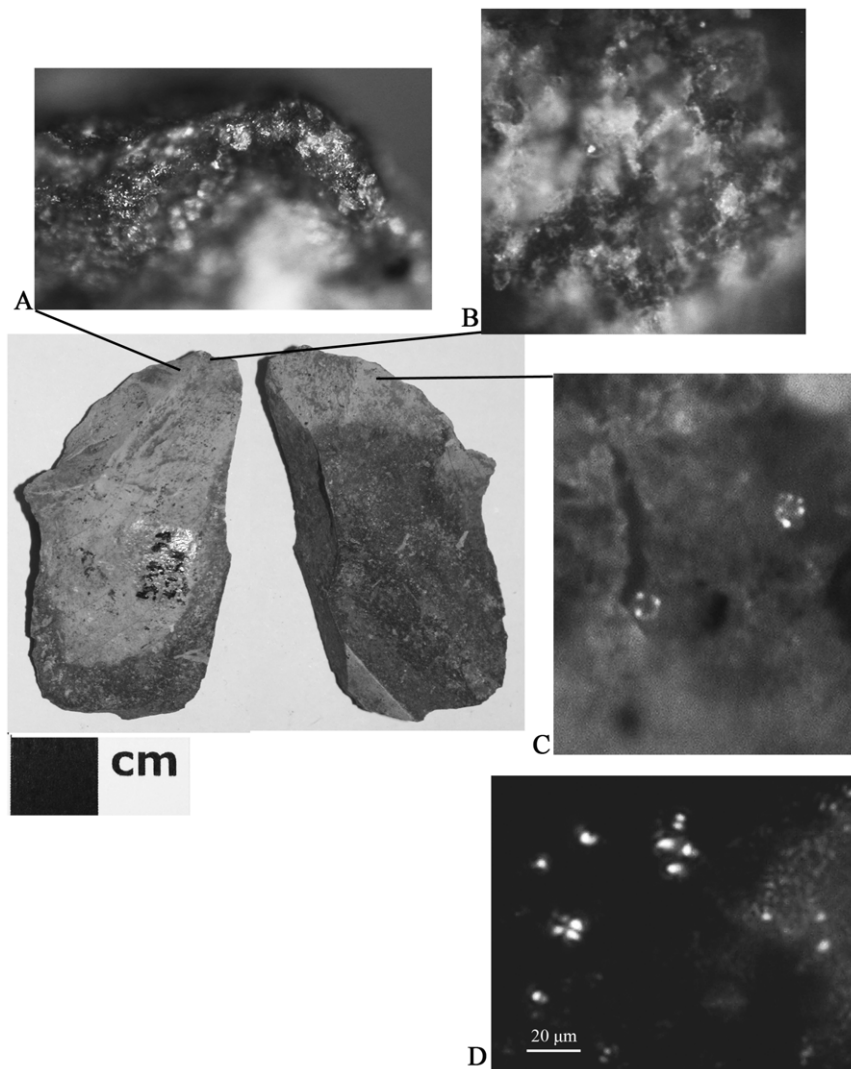
\*categories are not mutually exclusive and some artifacts are used on more than one material; therefore, rows may not total 100%.  
doi:10.1371/journal.pone.0023768.t001

under cross-polarized light [45] and the co-occurrence of a suite of other plant tissues and parts (Fig. 4) [44]. The starch grains observed ranged in size from 3–16  $\mu\text{m}$ . Given their small size

(many under 5  $\mu\text{m}$ ), putative starches were extracted from a sample of 10 artifacts for observation under transmitted light (500x) in order to confirm that they were not starch look-alikes



**Figure 3. Wood processing tool.** Payre L6 G4 1027, Layer Ga; A) scalariform perforation plate characteristic of birch (*Betula* sp.), original magnification 500x; B) wood tissue, original magnification 100x.  
doi:10.1371/journal.pone.0023768.g003



**Figure 4. Starchy plant processing tool.** Payre L7 F4 6451, Layer Fa; A) hard/high silica polish and edge rounding, original magnification 100x; B) macerated plant tissue, original magnification 100x; C) starch grains in situ, cross-polarized reflected light, original magnification 500x; D) starch grains extracted from tool, transmitted cross-polarized light, original magnification 500x.  
doi:10.1371/journal.pone.0023768.g004

such as conidia [44,45]. Starch was confirmed on all ten artifacts. Many of the grains are 3–6  $\mu\text{m}$ , spherical with a centric hilum, and lack lamellae. A smaller number are elliptical with an eccentric hilum and also lack lamellae. In addition, rectangular phytoliths were observed in extractions from two artifacts.

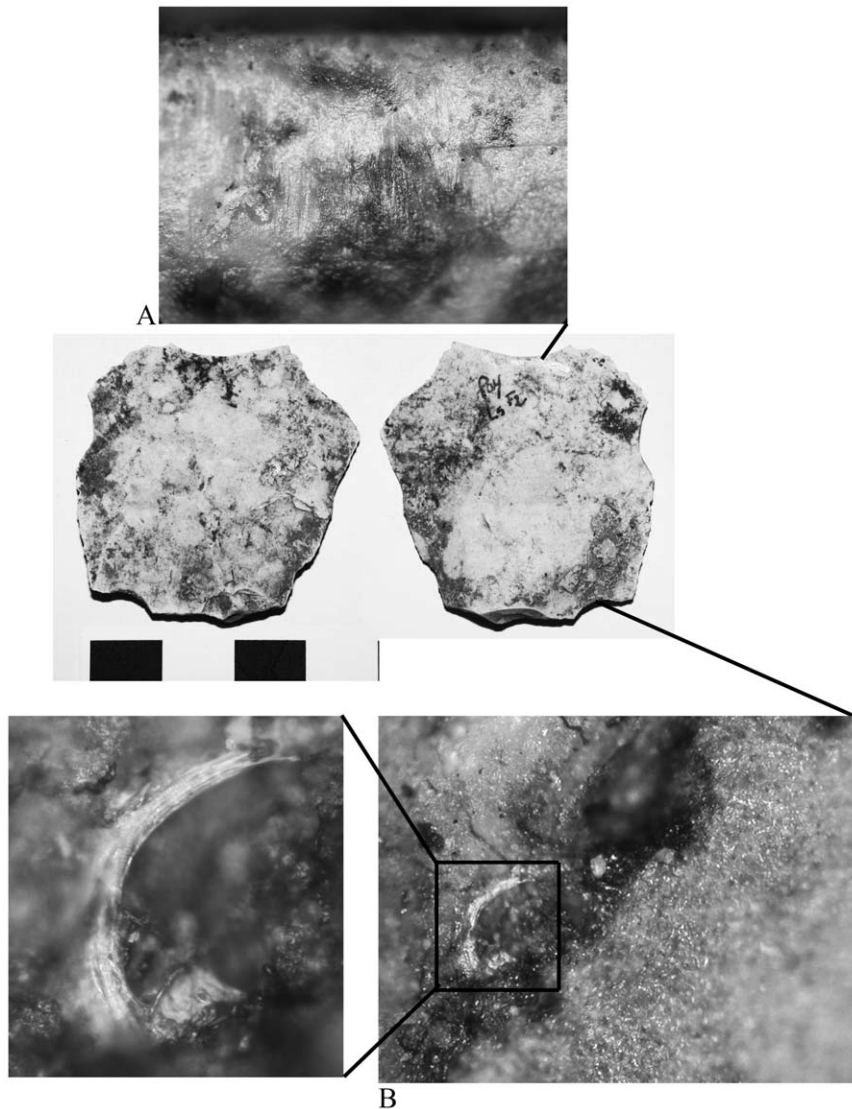
### Animals

As with plant processing, the identification of animal processing is most secure when supported by multiple lines of evidence [19,46]. Evidence of mammal processing (31/182 artifacts, 17.6%) in the sample includes hair, skin, bone, muscle tissue and accompanying wear patterns (soft polish and striae). Skin and hair fragments on scrapers demonstrate hidescraping while hair, bone, and skin on unmodified flakes suggest animal butchery. Animal processing is present throughout the sequence at Payre indicating that this was a routine activity.

Recent experiments involving scaling and butchering fish with stone tools [43] as well as clarification of use-wear patterns associated with fish processing [22] have provided new criteria for

recognizing fish exploitation in the archaeological record. Use-wear patterns associated with fish include scalar edge scarring and randomly oriented streaks of dull, greasy polish. These traces, however, have often been viewed as ambiguous [23]. Högberg et al. [22] have recently used protein analysis to confirm that this use-wear pattern is indeed evidence of fish processing. At Payre, identification of fish processing was only made if characteristic wear patterns were accompanied by fish residues (Fig. 5). Fish residues identified included scale fragments, bone fragments, iridophores (pigment cells of the epidermis), and skeletal muscle. Fish processing first appears in Layer Fb (beginning of OIS 7) and continues through Fa and D (end of MIS 6/beginning of MIS 5). A total of 10 artifacts show evidence of fish processing. The lack of fish bones at Payre could be due to taphonomic bias or could suggest that fish processing took place off site while some fish processing tools were curated and returned to the site.

One artifact from layer Gb shows evidence of use of avian resources. This artifact has soft use-wear polish accompanied by feather barbules (Fig. 6). While this single example does not



**Figure 5. Fish processing tool.** Payre L5 F2, Layer Fa; A) polishing with linear streaks characteristic of processing fish, original magnification 100x; B) fragment of a ctenoid fish scale, original magnification 100x.  
doi:10.1371/journal.pone.0023768.g005

provide information about the frequency of use of avian resources, it does attest to their use [48].

## Discussion

### Patterns of Tool Use

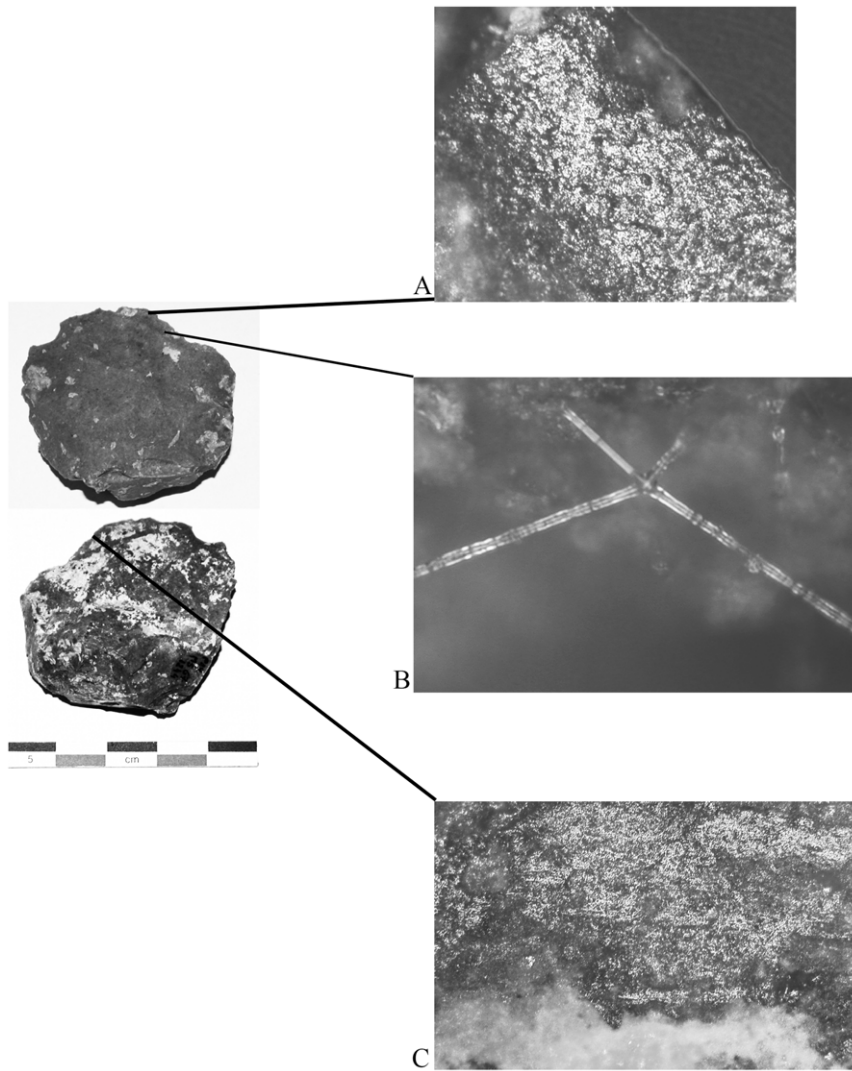
The stone tools examined from Payre show a diversity of action and use-materials and suggest broad-based economic and subsistence activities. The discoid flaking method typical at Payre provides many useful cutting edges that appear to have been used whatever the size and shape of the artifacts. As has been observed elsewhere in the Middle Paleolithic (La Quina, Starosele, and Hohle Fels), there is no specific use associated with different tool types [19–21]. This corroborates earlier findings on convergent tools from Payre analyzed through macro-traces [49]. Furthermore, shape, presence of cortex, and size do not correlate with specific uses. At Payre, the artifacts are primarily made from local flint, but some is imported from as far as 60 km away, arriving as broken nodules or large flakes [15]. No specific technical behavior

is observed on this rare or the local flint. The selection of stone tools for different activities thus appears to have been utilitarian and opportunistic. Tools are used for one part of their edges and not for their general form or location of retouch. Both retouched and unmodified edges are used frequently. The tools from Payre show a great variety of forms because retouch is not invasive and does not modify the general shape of tools. Resharpener is rare; therefore, individual sections of artifacts are functionally important, not the entire piece.

### Economic and subsistence activities

Woodworking is common in all levels at the site. Levels Gb/Ga (MIS 8/7) and D (MIS 6/5) formed in a temperate context when wood have been available in great quantities around the site [50–51]. Level F would have formed in a cooler context, but wood was still available near the site. It is impossible to predict precisely the types of wooden tools or objects that were being shaped through this activity, but the almost complete lack of evidence for hafting (with the exception of one scraper from Level Fa) suggests the





**Figure 6. Bird processing tool.** Payre M5 G7 1244, Layer Ga; A and C) soft polish, original magnification 100x; B) feather barbule fragment, original magnification 500x.  
doi:10.1371/journal.pone.0023768.g006

manufacture of other types of wooden technology. Both microscopic and macroscopic analyses of convergent tools from Payre do not show any indication of hafted projectile points. Nevertheless, hunting is clearly attested by residue and use-wear evidence and faunal remains. One likely woodworking activity may therefore have been the construction of spears similar to those recovered from Schöningen [52].

The diet at Payre was quite diverse, including plants, large and small animals, fish, and possibly birds. Starchy plant processing first appears in level Ga and continues through the rest of the sequence. Given the large number of potentially edible species that would have been available to Neanderthals [5] and the lack of a sufficiently detailed comparative collection, we do not provide a more specific identification. The morphology of the stone tools used for starchy plant processing, unmodified flakes and scrapers, along with the use-wear patterns suggests a scraping or cutting motion. Since the two major categories of wild edible plant foods with significant quantities of starch are underground storage organs (USOs) and seeds, the most likely use was in the removal of the woody and unpalatable exterior of USOs. This evidence

suggests that starchy USOs were a regular part of the Neanderthal diet at Payre from MIS 8/7 onwards. These results corroborate the recent evidence of starch grains in Neanderthal dental calculus at Spy and Shanidar [4] and demonstrate that Neanderthal consumption of plants was routine as early as MIS 8/7.

Animal processing at Payre includes both butchery and hideworking activities. Hair and skin fragments are found on a variety of retouched and unretouched tools. In addition to large animals attested to by skeletal remains (including *Cervus elaphus*, *Bos primigenius*, and *Equus ferus*, among others), fish and birds were also processed. Fishing and fowling are often used as markers of modern human behavior [53], despite their remains having been reported from numerous early hominin (as far back as 1.95 Ma) [54] and Neanderthal sites (see below). In fact, fishing is difficult to detect in the archaeological record for several reasons: 1) many coastal sites are lost due to rise in sea level; 2) fish bones are fragile and may be lost due to taphonomic processes; 3) many fish bones are small and may require specialized recovery techniques; and 4) the widespread assumption that fishing is a modern human behavior may lead investigators not to look for evidence in the first

place [55]. The argument that Neanderthals did not fish has recently been bolstered by stable isotope research [56–57] that suggests that Neanderthal  $\delta C^{13}$  values do not match those of fish. This evidence must be treated with caution, however, as  $\delta C^{13}$  for fish can vary greatly, particularly from freshwater fish [58–59].

Sites with possible evidence of Neanderthal consumption of fish include Milan, Almada and Abreda Caves, Spain [60–61], Grotte XVI, France [62], Devil's Tower and Vanguard Cave, Gibraltar [63], Raj Cave, Poland [64], Grotta Maggiore, Italy [65], Ust-Kanskaya Cave, Siberia [66], and Figueira Brava Cave, Portugal [67]. Evidence at these sites includes the recovery of osteological remains, fish bones in association with hearths, and cut-marks on fish bones. At Payre, residues and use-wear indicative of fish are found in the absence of osteological remains. Fish may have been processed off-site (at local streams or rivers), and the tools returned to the site or fish may have been processed on site but the bones did not preserve. In Level Fa, all of the artifacts with fish residues are located in one square meter near the wall, a possible indicator of a specialized intrasite activity area. These results highlight the difficulty in recognizing fish consumption archaeologically and suggest that fish consumption by Neanderthals may be underrepresented. The growing list of sites with fish remains as well as the detection of fish processing in the absence of fish bones at a site further suggests that fish consumption should not be seen as exclusively in the domain of modern humans.

The evidence of bird exploitation at Payre is less clear, but still present. As with fish, the exploitation of birds is commonly portrayed as part of a larger broadening of the dietary niche associated with modern humans which gave them an advantage over Neanderthals [68–69]. Recent finds at Bolomor Cave, Spain, showing butchery and consumption of birds (*Aythya* sp., diving ducks) demonstrate that at least some Neanderthals hunted and ate birds [70]. At Bolomor, the evidence of consumption is straightforward and includes cut-marks, burning and human toothmarks. Bird remains are found at several other Neanderthal sites but their interpretation is seen as ambiguous. Depending on the size of the bird and the method of processing and cooking, evidence of human activity (cutmarks, human toothmarks) may be lacking. Furthermore, birds may represent more than just food. For example, at Fumane Cave in Italy, cutmarks and scraping on wing elements of birds of prey have been interpreted as evidence of the removal of feathers for ornamentation [71].

Osteological bird remains at Payre include *Tetrao tetrix* (black grouse), *Pyrhacorax graculus* (alpine chough), *Corvus monedula* (jackdaw), and *Corvus corone* (carrion crow), but none of the bones display cutmarks. Previous research has suggested that the remains would have been brought into the cave by carnivores [13]. However, an endscraper from Level Ga exhibits soft polish and fragments of feather barbules indicating that it was used in processing bird tissue and feathers. While it is possible to potentially identify feather barbules to the Order level [34], isolated fragments may not preserve sufficient anatomical characteristics to do so [19] and therefore the taxon for the feather residues remains unknown. Two of the species of birds at Payre (black grouse and alpine chough) are also represented in the Fumane sample that may have been exploited for feathers. All four species at Payre are of low food value and, if they were introduced by humans, may have been of more interest for their feathers. At this point, however, this suggestion remains speculative.

The occupants of Payre were exploiting a wide range of materials. This fits with results of dental wear analysis of fauna that indicate a series of short-term occupation (level F) and longer-term occupations (level G and D) [12]. Faunal analysis on a regional scale (MIS 7 to MIS 3) indicates a far-sighted circulating model

with occupations of various durations [72]. Payre would have been primarily served as a short-term seasonal occupation site over time.

The occupations at Payre all occur at the beginning of interglacial cycles. The climate was therefore temperate through the entire archaeological sequence. The location of the site on a promontory above the Rhone and Payre valleys would have provided easy access to a diverse range of resources. The topography of the area would have allowed access to multiple ecological zones, including plateau, slope terraces, valley floor, streams and rivers. While there is some variation in the range of resources exploited (starchy plants first appear in level Gb and fish in level Fb, bird confined to level Ga), all activities attested to by the functional analysis of stone tools at Payre appear in end of MIS 8/beginning of MIS 7. Occupations in both MIS 8/7 and MIS 6/5 show a similar pattern of use of a broad range of resources. However, it is unclear from the present data whether this pattern of resource exploitation was characteristic of all Neanderthal populations or whether it is unique to Payre. Some have suggested that a broader resource base could be tied to temperate conditions and that during colder conditions resources may have been more limited and subsistence more focused on large herbivores [6]. However, even during colder conditions, some plant foods remain available [5] and it is likely that Neanderthal diet varied according to what was available [73]. Nonetheless, the broad range of resources exploited at Payre certainly demonstrates that Neanderthals had the ability to access them.

## Conclusions

Neanderthals are often portrayed as specialized large game hunters who derived the vast majority of their diet from meat [74]. They are seen as having little interest in, or being incapable of acquiring, small game, fish, birds, or plants [75]. This view remains dominant in the field despite growing evidence to the contrary [4,50,60–61,63,70]. For example, it has been commonly accepted that Neanderthals could not hunt birds. New data from Bolomor Cave [70], Fumane [71] and now from Payre suggest that this view is not accurate. Furthermore, results from Payre now provide evidence that Neanderthals could acquire fish, an activity that is often seen as too advanced for Neanderthals [59]. Functional analysis of stone tools at Payre further bolster the case that Neanderthals had a broad-based diet that included starchy plants, large animals, fish, and possibly birds. The acquisition of fast-moving small prey items such as fish and birds are often seen as exclusively the domain of modern humans and their capture is often linked to a presumed cognitive superiority of modern humans [3]. The remains of birds and fish are fragile and often do not preserve as well as those of larger animals. This introduces a potential bias into the archaeological record in favor of large terrestrial game. Furthermore, as seen at Payre, the processing of these prey items may leave no archaeologically detectable trace on bone. As the results from Payre demonstrate, zooarchaeological analyses do not provide a perfect record of the activities at a site. In this case, the application of residue and use-wear analyses revealed activities that were otherwise not visible. The exploitation of plants, birds, and fish were all undetected by more traditional forms of analysis.

Neanderthals are often defined by their extinction. Because they went extinct, they must have been doing something wrong. However, as evidence continues to mount that shows that Neanderthals practiced what has been considered exclusively modern human behavior (plant consumption, fishing and fowling, ornamentation, etc.), it is important to remember that Neanderthals prospered for over 200,000 years. Our evidence suggests that



they did this, in part, with a broad-based diet and economy that was already in place 125–250,000 years ago.

## Acknowledgments

Thanks to the French Ministry of Culture for support of the excavations at Payre and to the Kenyon College Labalme Fund. We also thank two anonymous reviewers for their helpful comments.

## References

- Speth JD (2010) The paleoanthropology and archaeology of big game hunting: Protein, fat, or politics. New York: Springer. 325 p.
- Bocherens H (2011) Diet and ecology of Neanderthals: Implications from C and N isotopes. In: Conard NJ, Richter J, eds. Neanderthal lifeways: subsistence and technology. Tübingen: Springer. pp 73–85.
- Brown K, Fa DA, Finlayson G, Finlayson C (2011) Small game and marine resource exploitation by Neanderthals: The evidence from Gibraltar. In: Bicho NF, ed. Trekking the shores: changing coastlines and the antiquity of coastal settlement Interdisciplinary Contributions to Archaeology DOI 10.1007/978-1-4419-8219-3\_10, Springer Science.
- Henry AG, Brooks AS, Piperno DR (2011) Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proc Natl Acad Sci USA* 108: 486–491.
- Hardy BL (2010) Climatic variability and plant food distribution in Pleistocene Europe: Implications for Neanderthal diet and subsistence. *Quat Sci Rev* 29: 662–679.
- Finlayson C (2004) Neanderthals and modern humans: an ecological and evolutionary perspective. Cambridge: University of Cambridge. 255 p.
- Moncel M-H, Débard E, Desclaux E, Buboïs J-M, Lamarque F, et al. (2002) Le cadre de vie des hommes du Paléolithique moyen (stades isotopiques 6 et 5) dans le site de Payre (Rompon, Ardèche): d'une grotte à un abri sous roche effondré. *Bull Soc Préhist Fr* 99: 249–273.
- Valladas H, Mercier N, Ayliffe LK, Falguères C, Bahain JJ, et al. (2008) Radiometric dates for the Middle Palaeolithic sequence of Payre (Ardèche, France). *Quat Geochron* 3: 377–389.
- Moncel M-H, Condemni S (1996) Découverte de dents humaines dans le site Paléolithique moyen de Payre (Ardèche, France). *Comptes Rendus Acad Sci* 322: 251–257.
- Moncel M-H, Condemni S (1997) Des restes humains dans le site Paléolithique moyen ancien de Payre (Ardèche): dents et pariétal. Nouvelles découvertes de 1996. *Bull Soc Préhist Fr* 94: 168–171.
- Moncel M-H, Condemni S (2007) Les restes humains du site de Payre (Sud-Est de la France, MIS 7-5). Remarques sur la position stratigraphique et l'intérêt. *Anthropologie* 45: 19–29.
- Rivals F, Moncel M-H, Patou-Mathis M (2009) Seasonality and intra-site variation of Neanderthal occupations in the Middle Palaeolithic locality of Payre (Ardèche, France) using dental wear analyses. *J Archaeol Sci* 36: 1070–1078.
- Moncel M-H, Auguste P, Ayliffe L, Bahain J-J, Bocherens H, et al. (2008) Le site de Payre. Occupations humaines dans la vallée du Rhône à la fin du Pléistocène moyen et au début du Pléistocène supérieur. Paris: Mémoire de la Société Préhistorique Française XLVI. pp 336.
- Daujeard C, Moncel M-H (2010) On Neanderthal subsistence strategies and land use: A regional focus on the Rhone Valley area in southeastern France *J Anth Archaeol* 29: 368–391.
- Fernandes P, Raynal J-P, Moncel M-H (2008) Middle Palaeolithic raw material gathering territories and human mobility in the southern Massif Central, France: first results from a petro-archaeological study on flint *J Archaeol Sci* 35: 2357–2370.
- Odell G, Odell-Verecken F (1980) Verifying the reliability of lithic use-wear assessments by blind tests: the low-power approach *J Field Archaeol* 7: 87–120.
- Mansur-Francomme ME (1986) Microscopie du matériel lithique préhistorique: Traces d'utilisation, altération naturelles, accidentelles, et technologiques. Paris: CNRS. 286 p.
- Fullagar R (1991) The role of silica in polish formation. *J Archaeol Sci* 18: 1–24.
- Hardy BL, Kay M, Marks AE, Monigal K (2001) Stone tool function at the Palaeolithic sites of Starosele and Buran Kaya III, Crimea: Behavioral implications. *Proc Natl Acad Sci USA* 98: 10972–10977.
- Hardy BL (2004) Neanderthal behaviour and stone tool function at the Middle Palaeolithic site of La Quina, France. *Antiq* 78: 547–565.
- Hardy BL, Bolus M, Conard NJ (2008) Hammer or crescent wrench? Stone-tool form and function in the Aurignacian of southwest Germany. *J Hum Evol* 54: 648–662.
- Högberg A, Puseman K, Yost C (2009) Integration of use-wear with protein residue analysis—a study of tool use and function in the south Scandinavian Early Neolithic. *J Archaeol Sci* 26: 1725–1737.
- Van Gijn AL (1989) The wear and tear of flint. Principles of functional analysis applied to Dutch Neolithic assemblages. *Analecta Praehistorica Leidensia* 22. Leiden: University of Leiden. 182 p.
- Lombard M (2004) Distribution patterns of organic residues on Middle Stone Age points from Sibudu Cave, KwaZulu-Natal, South Africa *S Afr Archaeol Bull* 59: 37–44.
- Wadley L, Lombard M, Williamson B (2004) The first residue analysis blind tests: results and lessons learnt. *J Archaeol Sci* 31: 1491–1501.
- Brunner H, Coman BJ (1974) The identification of mammalian hair. Melbourne: Inkata. 176 p.
- Catling D, Grayson J (1982) Identification of vegetable fibres. New York: Chapman and Hall. 106 p.
- Beyries S (1988) Functional variability of lithic sets in the Middle Paleolithic. In: Dibble H, Montet-White A, eds. Philadelphia: University Museum Press. pp 213–224.
- Anderson-Gerfaud P (1990) Aspects of behavior in the Middle Paleolithic: Functional analysis of stone tools from southwest France. In: Mellars P, ed. The emergence of modern humans. Ithaca: Cornell University Press. pp 389–418.
- Hoedley B (1990) Identifying wood. NewtonConnecticut: Taunton Press. 223 p.
- Teerink BJ (1990) Hair of west European mammals: Atlas and identification key. Cambridge: Cambridge University Press. 224 p.
- Hather J. Europe and southwest Asia. Oxford: Oxbow Books. 154 p.
- Hardy BL (1994) Investigations of stone tool function through use-wear, residue and DNA analyses at the Middle Paleolithic site of La Quina, France. Ph.D. Dissertation, Indiana University. 231 p.
- Hardy BL (1986) Microscopic identification of feathers and feather fragments of Palearctic birds *Bijdragen Dierkunde* 56: 181–204.
- Kardulias N, Yerkes R (1996) Microwear and metric analysis of threshing sledge flints from Greece and Cyprus. *J Archaeol Sci* 23: 657–666.
- Williamson B (1996) Preliminary stone tool residue analysis from Rose Cottage Cave. *S Afr J Field Archaeol* 5: 36–44.
- Hardy BL, Garufi GT (1998) Identification of woodworking on stone tools through residue and use-wear analyses: experimental results. *J Archaeol Sci* 25: 177–184.
- Pearsall D (2000) Paleoethnobotany: A handbook of procedures, 2nd ed. New York: Academic Press. 700 p.
- Haslam M (2004) The decomposition of starch grains in soils: implications for archaeological residue analyses. *J Archaeol Sci* 31: 1715–1734.
- Dove CJ, Hare PG, Heacker M (2005) Identification of ancient feather fragments found in melting alpine ice patches in southern Yukon. *Arctic* 58: 38–43.
- Fullagar R (2006) Starch on Artifacts. In: Torrence R, Barton H, eds. Ancient starch research. Walnut Creek: Left Coast Press. pp 177–204.
- Genten F, Terwinghe E, Danguy A (2009) Atlas of fish histology. Enfieldnew Hampshire: Science Publishers. 223 p.
- Warren R (2009) The potential role of fish in the diet of Neanderthals. Sr. Honors Thesis. Kenyon College, Gambier, Ohio. 117 p.
- Haslam M (2006) Potential misidentification of in situ archaeological tool-residues: starch and conidia. *J Archaeol Sci* 33: 114–121.
- Barton H, Fullagar R (2006) Microscopy. In: Torrence R, Barton H, eds. Ancient starch research. Walnut Creek: Left Coast Press. pp 47–52.
- Lombard M, Wadley L (2007) The morphological identification of micro-residues on stone tools using light microscopy: progress and difficulties based on blind tests. *J Archaeol Sci* 34: 155–165.
- Rots V, Williamson BS (2004) Microwear and residue analysis in perspective: the contribution of ethnographical evidence. *J Archaeol Sci* 31: 1287–1299.
- Haslam M (2006) An archaeology of the instant? Action and narrative in archaeological residue analyses. *J Soc Archaeol* 6: 402–424.
- Moncel M-H, Chacon-Navarro MG, Coudeneau A, Fernandes P (2009) Points and convergent tools in the European Early Middle Palaeolithic site of Payre (SE, France). *J Archaeol Sci* 36: 1892–1909.
- Kalai C (1998) Reconstitution du paléoenvironnement végétal et du paléoclimat de la fin du Pléistocène moyen et du Pléistocène supérieur d'après les analyses polliniques de la Baume Moula-Quercy, du site de Payre et de l'abri des Pêcheurs (Ardèche, France). Thèse de doctorat. Paris: Muséum National d'Histoire Naturelle. 170 p.
- Kalai C, Moncel M-H, Renault-Miskovsky J (2001) Le paléoenvironnement végétal des occupations humaines de la Grotte de Payre à la fin du Pléistocène moyen et au début du Pléistocène supérieur (Ardèche, France). *Trabajos de Prehistoria* 58: 143–151.
- Thieme H (1999) Lower Paleolithic hunting spears from Germany. *Nature* 385: 807–810.
- Henshilwood CS, Marean CW (2003) The origin of modern human behavior. *Curr Anthropol* 44: 627–651.
- Braun DR, Harris JWK, Levin NE, McCoy JT, Herries AIR, et al. (2010) Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proc Natl Acad Sci USA* 107: 10002–10007.

## Author Contributions

Analyzed the data: BLH M-HM. Wrote the paper: BLH M-HM. Designed the analysis: BLH M-HM. Performed the microscopy: BLH. Contributed analytical tools: BLH.

55. Erlandson JM (2001) The archaeology of aquatic adaptations: paradigms for a new millennium. *J Archaeol Res* 9: 87–350.
56. Bocherens H (2009) Neanderthal dietary habits: review of the isotopic evidence. In: Hublin J-J, Richards MP, eds. *The evolution of hominin diets: Integrating approaches to the study of paleolithic subsistence*. New York: Springer. pp 241–250.
57. Richards MP, Schmitz RW (2008) Isotope evidence for the diet of the Neanderthal type specimen. *Antiq* 82: 553–557.
58. Katzenberg MA (2000) Stable isotope analysis: A tool for studying past diet, demography, and life history. In: Katzenberg MA, Saunders SR, eds. *Biological anthropology of the human skeleton*. New York: Wiley. pp 305–328.
59. Pearson JA (2007) Hunters, fishers and scavengers: A review of the isotope evidence for Neanderthal diet. *Before Farming* 2: 1–15.
60. Izquierdo R, Mumiz M (2005) Ictiofaunas Musterienses de la Peninsula Iberica: ¿Evidencias de Pesca Neandertal? *Munibe* 57: 183–195.
61. Adán GE, Álvarez-Lao D, Turmero P, Arbizu M, García-Vázquez E (2009) Fish as Diet Resource in North Spain During the Upper Palaeolithic. *J Archaeol Sci* 3: 895–899.
62. Rigaud J-P, Simek J, Thierry G (1995) Mousterian Fires from Grotte XVI (Dordogne, France). *Antiq* 69: 902–912.
63. Stringer CB, Finlayson JC, Barton R, Fernandez-Jalvo Y, Caceres I, et al. (2008) Neanderthal exploitation of marine mammals in Gibraltar. *Proc Natl Acad Sci USA* 105: 14319–14324.
64. Patou-Mathis M (2004) Subsistence behaviours in a Middle Palaeolithic site in Poland: the Raj Cave. *Intl J Osteoarch* 14: 244–255.
65. Fiore I, Gala M, Tagliacozzo A (2004) Ecology and Subsistence Strategies in the Eastern Italian Alps During the Middle Palaeolithic. *Intl J Osteoarch* 1: 273–286.
66. Derevianko AP, Postnov AV, Rybin EP, Kuzmin YV, Keates SG (2005) The Pleistocene Peopling of Siberia: A Review of Environmental and Behavioral Aspects. *Indo-Pacific Prehist Assoc Bull* 3: 57–68.
67. Bicho N, Haws J (2008) At the Land's End: Marine Resources and the Importance of Fluctuations in the Coastline in the Prehistoric Hunter-Gatherer Economy of Portugal. *Quat Sci Rev* 27: 2166–2175.
68. Stiner MC, Munro ND, Surovell TA, Tchernov E, Bar-Yosef O (1999) Paleolithic Population Growth Pulses Evidenced by Small Animal Exploitation. *Sci* 28: 190–194.
69. Cassoli PF, Tagliacozzo A (1997) Butchering and cooking of birds in the Palaeolithic site of Grotta Romanelli (Italy). *Intl J Osteoarch* 7: 303–320.
70. Blasco R, Fernández Peris J (2009) Middle Pleistocene bird consumption at Level XI of Bolomor Cave (Valencia, Spain). *J Archaeol Sci* 36: 2213–2223.
71. Peresani M, Fiore I, Gala M, Romandini M, Tagliacozzo A (2011) Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. *Proc Natl Acad Sci USA* 108: 3888–3893.
72. Daujeard C, Fernandes P, Guadelli J-L, Moncel M-H, Santagata C, et al. (2011) Neanderthal subsistence strategies in Southeastern France between the plains of the Rhone Valley and the mid-mountains of the Massif Central (MIS 7 to MIS 3). *Quat Int*;doi:10.1016/j.quaint.2011.01.047.
73. Bar-Yosef O (2004) Eat what there is: hunting and gathering in the world of Neanderthals and their neighbours. *Intl J Osteoarch* 14: 333–342.
74. Bocherens H, Drucker DG, Billiou D, Patou-Mathis M, Vandermeersch B (2005) Isotopic evidence for diet and subsistence pattern of the Saint-Césaire I Neanderthal: review and use of a multi-source mixing model. *J Hum Evol* 49: 71–87.
75. Kuhn SL, Stiner MC (2006) What's a Mother to Do? The Division of Labor among Neandertals and Modern Humans in Eurasia. *Curr Anth* 47: 953–981.