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Background to Neanderthal presence in Western Mediterranean Europe

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ABSTRACT

This paper provides a background to Neanderthal presence in Western Mediterranean Europe. Habitual tool-use underpinned human survival in late Early Pleistocene western Mediterranean Europe. By the onset of the early Middle Pleistocene, early humans (descendants of *Homo antecessor* in all likelihood) were exploiting diverse biotopes, sometimes (perhaps often) attaining primary access to large game, and deploying a variety of stone artifacts and rock types, which implies not only manual dexterity but also technical competence and cognitive versatility. Late Early Pleistocene human behaviour foreshadowed that of Middle Pleistocene pre-Neanderthal humans whose background conceivably had deep regional roots. By the mid-Middle Pleistocene *Homo heidelbergensis*, some of whose anatomical features herald Neanderthal morphology, was exploiting a wide range of natural resources in western Mediterranean environments, including small game and plants. Neanderthal morphology began to emerge during the second half of the Middle Pleistocene, accompanied by increasing technological diversity and an expanding variety of small tools, conjecturally favoured by hafting, perhaps following development of wooden spears (or other tools) and adhesive and binding technologies, and generation and heat-control of fire (which undoubtedly was necessary for activities inside Bruniquel cave). By the onset of the last interglacial period, Neanderthal morphology and Mousterian artifacts are widespread, and there are indications of coordinated retrieval and treatment of body-parts of large ungulates.

1. Foreword

Western Mediterranean Europe here includes Mediterranean river basins in France and Spain as well as other parts of both countries and Italy lying within about 300 km from the Western Mediterranean. Sites further afield are mentioned mainly for comparative purposes, because a principal aim here is to draw attention to rugged terrain that forms much of the Western Mediterranean *spatial* background. That aspect, in our view, was particularly significant for shaping the *temporal* background in which were laid down the *roots* of Neanderthal behaviour in the region, for which reason our discourse is directed principally to sites dated to *before* 0.05 Ma (>50,000 BP) - thereby excluding, moreover, a possibility that contact with modern humans could have influenced the Neanderthal behaviours under consideration: by and large, a site with an assemblage dating from ~0.05 Ma (or less) is mentioned only if it also contains *older* dated assemblages. Our principal aim is to chronicle and briefly describe the spatio-temporal background to Neanderthals in Western Mediterranean, a region that is regrettably overlooked in many English-language accounts of human evolution in the Late (Upper) Pleistocene. Readers may draw their own conclusions from, or have reservations about, some of the published information to which we draw their attention. We stress that we do not strive to endow Neanderthals or their forebears with the same cognitive or technical competences as those of *Homo sapiens* in Europe after the disappearance of the Neanderthals, given their incommensurability in *time*. Nor do we seek to equate the competences of Neanderthals with those of *Homo sapiens* in Africa during the early Late Pleistocene, given their incommensurability in *space*. We are aware that some readers will hold views, based often on formal arguments, which colour their preferred methodological arguments about human evolution and heighten their reservations about contrary arguments that lay claim to empirical support. We therefore have tried to eschew interpretations that go much

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beyond a minimal reading of the literature that we have tried to summarize as succinctly as possible for the benefit of readers unfamiliar with it. We begin by giving pride of place to dated assemblages of the last ice age that are older than 0.05 Ma, particularly where they lie above assemblages adding from the last interglacial. We then turn our attention first to late Middle Pleistocene assemblages, then to mid- and early Middle Pleistocene ones, and finally to late Early Pleistocene sites. This temporal arrangement involves some to-ing and fro-ing between Mediterranean Spain, Mediterranean France, and Italy, which is why we provide a map to help readers. We do not think it appropriate, however, to attempt chronological synoptic tabulation of sites or assemblages, lest that induce a temptation to imbue change with either quasi-evolutionary (biological, "palaeoanthropological") or quasi-historical (historicist, "culture-history") significance.

2. Background and foreground

The foreground to Neanderthal presence in Western Mediterranean Europe is well represented after ~0.25 Ma by many "Middle" Palaeolithic assemblages with "Mousterian" artefacts and several skeletal remains of large-brained Neanderthals. Like skeletally-modern *Homo sapiens*, they seem to have become *obligatory* tool-users (Shea, 2017a). How that evolved from their earlier *habitual* use of tools requires consideration of their background.

Returning to the foreground, few assemblages disrupt broad Mousterian homogeneity until ~0.045 Ma, whether within Western Mediterranean Europe or further afield, notwithstanding well-known Mousterian subdivisions within it and equally well-known appearance in some Mousterian contexts beyond it of modern-looking human skeletons. Concern here is with neither of those, nor yet with the impingement from ~0.045 Ma of modern humans or "Upper" Palaeolithic technology.

Instead, attention will be paid to the local background, in both time and space, particularly before the MIS-5a/MIS-4 transition ~0.075 Ma. Sites with Neanderthal and Mousterian assemblages after ~0.05 Ma only receive attention if they contain well-dated earlier deposits or offer aspects relevant to comparison with older sites. Among matters that attract attention are noteworthy stratigraphical sequences at some sites and the rugged landscape near several of them. Particular attention will be paid to those, bypassing several hundred sites without secure chronostratigraphical referents. The aim is to offer a narrative, not to propose explanations. Even where deep stratigraphical sequences exist at sites, it is implausible to presume their continuous occupation (or exploitation of their surroundings) during scores of millennia. Nevertheless, their sporadical attraction to Neanderthals cannot pass unremarked, especially in western Mediterranean Europe. Perhaps not unsurprisingly, a Europe-wide study involving modelling suggests that Mediterranean coastal regions afforded suitable environments for Neanderthals during MIS-5 (Benito et al., 2017), which have been demonstrated clearly by pollen, charcoal, and macrofossil analyses (Carrión et al., 2008; Carrión and Leroy, 2010; González-Sampériz et al., 2010; Magri et al., 2017).

Local environments, especially in western Mediterranean Europe, can undergo rapid changes where relief is high and surface features of landscapes are affected by geomorphological processes responding to oscillations of sea-level or neotectonic activity, but where, nonetheless, local biogeographical refuges may exist. These can offer alternative natural resources for human ingenuity to exploit, both edible and inedible (the latter embrace stone, bone, caves, and fire). In the face of climatic and ecological upheavals, escape from adversity via inexorable dispersal - by traipsing in the footsteps of ungulates thriving on open landscapes and steppe - is not the only alternative to local human extinction (Hosfield, 2016). Whilst valuable insights into Pleistocene habitats have been attained by analyzing continent-wide environmental changes, reflected in biostratigraphical findings correlatable with changing obliquity-related Milanković insolation cycles, unfortunately the vagaries of preservation of delicate remains mean that quite often their sampling has been possible only at places that sometimes lie many kilometres away from Palaeolithic sites (Leroy et al., 2011). We therefore have chosen to give attention to early Palaeolithic sites in the hope of trying to achieve a less coarse-grained approach to interpreting plausible relationships between archaic humans and their surroundings in western Mediterranean Europe; that is to say, before the Upper Palaeolithic when a finer-grained spatio-temporal record can be studied sometimes at sites used by modern humans.

Human survival could ensue from awareness of the possibilities afforded by alternative natural resources perhaps <20 km away. Intermontane valleys and coastal areas sheltered ice-age vegetational refugia in Mediterranean Spain (Carrión, 2002; Carrión et al., 1999, 2003; 2008, 2011; González-Sampériz et al., 2010; Manzano et al., 2017). Local ecosystems are influenced differentially by changes in temperature (rising as altitude falls), sunlight (varying with slope-orientation, altitude, and woodland canopy), and rainfall (dependent on local slope-orientation as well as on widespread atmospheric fluctuations); all can cause local variation in altitudinal zonation of ecosystems. One side of a valley can differ from the opposite side. One side of a mountain can differ from the other side. When valleys in a drainage basin are constrained by geological faulting, tectonically-induced abrupt changes in drainage may lead to significant differences between exploitation territories around neighbouring cotemporaneous sites. Little more than that need be reflected by significant differences between materials excavated at nearby sites - providing that their erstwhile denizens had sufficient cognitive versatility and manual dexterity to vary their handiwork. A complication, however, is that communities undoubtedly vanished from some sites that subsequently were frequented by other human groups that left different material remains.

To the foregoing matters may be added changes in land-forms. These may be induced both by glacioeustatic effects on riverine base-levels, which sometimes may be correlated with climatic regularities in consequence of obliquity-related Milanković insolation cycles (and, within them, shorter climatic oscillations and fluctuations), but which also can be the outcome of sporadical impingements of neotectonic activity - after all, high relief is often the prominent result of tectonic activity and alerts us to its likelihood in the Pleistocene. Either of those processes can skew visibility of Pleistocene sites, whether by exposing caves and erosion surfaces, or by burying them under sediment eroded from the surrounding landscape. Radiometrical estimates from high-resolution analyses of later Pleistocene Palaeolithic sites are beginning to offer a possibility of correlating human behaviour with local palaeoenvironmental circumstances. The complex later Pleistocene palaeoclimatological record determined by high-resolution analysis of polar ice-cap cores, and the impingement of volcanic eruptions on local environments, warn against drawing facile inferences about relationships between environment and human behaviour at Middle Pleistocene sites, most of which lack high-resolution spatiotemporal analysis of archaeological and palaeoclimatological sequences.

3. The near background, 0.3–0.1 Ma

3.1. *Cova del Bolomor*

Praiseworthy efforts to redress the deficit are underway at Spanish sites. Sediments 10 m deep are under excavation at Cova del Bolomor (~5 km from and 100 m above the Spanish Mediterranean shore and the Valencian town of Tavernes de la Valldigna sheltered by hills 500–600 m high). Visited by geologists and archaeologists since the 19th century (Fernández et al., 2007; Vilanova y Piera, 1893), systematic methodical excavation began only in 1989. Phases 1 and 2 (levels XVII-XIII) date from ~0.35 to ~0.23 Ma (MIS-9,-8,-7). Phases 3 and 4 (levels XII-I) date from ~0.18 to ~0.12 Ma (MIS-6,-5e). Magnetic susceptibility corroborates the climatic sequence (Fernández-Peris, 2007; Sañudo et al., 2016). Mousterian assemblages are homogeneous throughout the sequence (Villaverde, 2007). There are neither hand-axes nor cleavers. Combustion features occur from levels XIII to II (Fernández-Peris et al., 2012). Bolomor human fossils are comparable to 0.43 Ma Neanderthal precursors from Atapuerca Sima de los Huesos (Arsuaga et al., 2012).

The Bolomor palimpsest of >25 occupation episodes between levels I and XII (~0.18 - ~0.12 Ma) has been scrutinized with good resolution (Sañudo et al., 2016). It would be unwise, nevertheless, to presume that the time span of sixty millennia can be broken down into ≥25 periods, each lasting 1000–3000 years (thereby permitting 50–150 human reproductive generations of 20 years each). Sixty-thousand years can embrace 3000 human generations; long enough for some kinds of behaviour to disappear, be supplanted by different kinds, and reappear again later on – all, plausibly, the handiwork of separate Neanderthal groups. An interesting finding is identification at the close of levels IV, XI and XII of impingements by carnivores, likely attracted by, and sometimes causing, dispersal of Neanderthals' rubbish. Nevertheless, refitting of bone and stone pieces shows only trivial vertical displacements. Sedimentological analysis implies a slow rate of accumulation, which raises the interpretative problem (Sañudo et al., 2016) that it may render invisible periods of abandonment by humans between possibly brief visits lasting barely a few days, occurring sporadically during decades (or perhaps centuries), too short for accumulation of enough rubbish to attract scavengers. Moreover, such behaviour would render misleading archaeological attempts to determine energetic costs to Palaeolithic humans of seeking, obtaining and preparing foodstuffs, based on notional expectations about nutrition gleaned from considering excavated remains mainly of ungulates; furthermore, it is not known how glacioeustatic oscillations of sea level might have influenced availability of terrestrial resources behind shorelines.

Red deer is common throughout the Bolomor sequence, and horse is well represented in deeper levels becoming displaced by aurochs in higher ones that also show a marked decline in rhinoceros and appearance of elephant, hippopotamus, boar and ass (Fernández-Peris, 2004, 2007). Fallow deer and tahr (cf. Martínez Valle, 2001a; *Hemitragus* aff. *cedrensis*: Rivals and Blasco, 2008) occur in several levels. Faunal analysis shows that deep level XVII (MIS-9) afforded significant incidence of red deer and lagomorphs among which are rabbit bones bearing cut-marks (Blasco et al., 2013a) - seen also in MIS-9 on some from Atapuerca Trinchera Dolina TD10-1. Analysis of level XI (~0.18 Ma) animal remains suggests cotemporaneous practice of different strategies for capture of wild horses vis-à-vis red deer, and also as regards rabbits and mute swans (Blasco et al., 2010, 2013a). Slightly before 0.12 Ma, level IV also offers a picture of diverse strategies for capturing horse, red deer, tahr, lagomorphs, birds and tortoise (Blasco, 2008; Blasco and Fernández-Peris, 2009, 2012a, b; Blasco et al., 2013a; Fernández-Peris et al., 2012, 2014). Ongoing pollen analyses support a mosaic-like, partially forested vegetational landscape coherent with this picture (Juan Ochando, pers. comm., Murcia University). Statistical analysis of impact points on bones broken open (probably to extract marrow), suggests "counter-intuitive" preferences in those of level IV, perhaps owing to a local behavioural practice, because the particular distribution of impact points is unparalleled in other levels or elsewhere (Blasco et al., 2013b).

The diversity of strategies used to obtain animal foodstuffs indicates cognitive versatility and organizational capability of getting primary access to large fast-moving ungulates, small fast-moving mammals and birds, and slow-moving tortoises. From MIS-9 onwards, lagomorphs in early levels include rabbit and hare (Sanchís and Fernández-Peris, 2008, 2011) that is even harder to catch or trap than are burrowing rabbits because it lives in the open and is swift. Cut-marks on bones of lagomorphs at this and other early sites call into question a widespread view that lagomorphs played a trivial part in Neanderthal diets (Fa et al., 2013). Capture at warrens of rabbits, particularly females, is a possible interpretation at Atapuerca TD10 and Bolomor (Blasco et al., 2013a), also proposed (Cochard et al., 2012) at Abri des Canalettes layer 4 (see below).

Large Bolomor carnivores are wolf, lion and lynx - albeit making but sparse appearances other than in levels with scant traces of human impingement (Blasco et al., 2010; Fernández-Peris, 2004) - among a score of mammalian taxa that include hippopotamus, rhinoceros, elephant, aurochs, giant deer, boar, ass, monkey, beaver, fox, and badger. Perhaps scarcity of large carnivores was unrelated to relative abundance of larger herbivores sometimes. Primary human access to game is implied by cut-marks overlaid by gnaw-marks on some animal bones (Blasco and Rosell, 2009). Several bones were modified for retouching stone artefacts (Blasco et al., 2013c).

Statistical univariate, bivariate, and multivariate analyses were undertaken on 35,000 chert (flint), quartzite and limestone pieces excavated in levels I–XVII (Cuartero-Monteagudo, 2007; Fernández-Peris, 2001; Fernández-Peris, 2007). Chert extractions by unipolar, bipolar, and particularly centripetal removal, tend towards an oblong shape, often <25 mm in size, followed in incidence by either triangular flakes or thicker wedge-shaped flakes often with a "knife"-like edge produced by semi-abrupt stepped and scalariform secondary ("Charentian Quina") knapping, whereas limestone extractions, with noteworthy incidence in level VI, tend to show less secondary knapping. Preparation of ("Levallois") facetted striking platforms is seen but infrequently on flakes until the end of the stratigraphical sequence. Secondary knapping of edges gave rise frequently to scrapers, denticulate, and notched pieces, small trihedral ("trifacial") artefacts, and less often to pointed ones, end-scrapers, beaked pieces ("*becs*"), and pointed perforators, awls or borers, in what is undoubtedly a Middle Palaeolithic assemblage, albeit with very few gravers and garden slugs ("*limaces*"). Its composition embraces technical "modes" A, B, C, D-1, and probably D-3, F, and G-1, that are definable by an exclusionary principle of differential diagnosis applied to lithic analysis by Shea (2013; 2017b) (Table 2).

Manual dexterity and cognitive versatility were required. No clear-cut trend is seen whether the temporal sequence is examined by univariate, bivariate, or single-link cluster analyses. Among interesting findings are that a few levels (e.g., II, III, VI) show noteworthy incidence of "Charentian" Mousterian knapping, and that whereas some levels have few lithic finds (VII, VIII, IX, X, XI) these are well-represented in deep levels XIII, XV and XVII; furthermore, levels II and XV show high incidence of very small (<20 mm) "microlithic" artefacts. Perhaps the variability might be a reflection of local Neanderthal populations vanishing and eventually being replaced by others with particular behavioural practices. More important, perhaps, is that, as at Orgnac 3 in France (see below), the Mousterian at Bolomor is traceable as far back in the Middle Pleistocene as ~0.35 Ma.

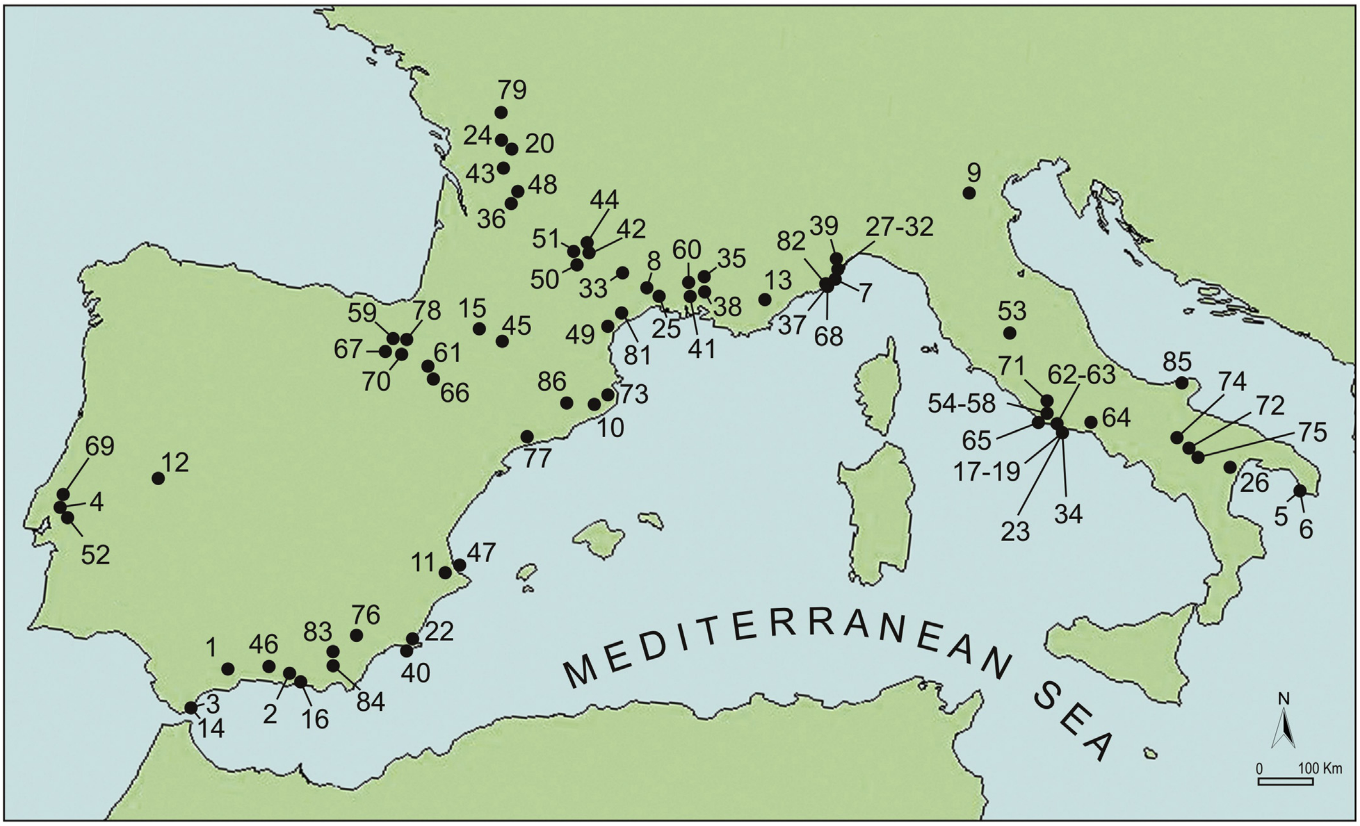

Fig. 1. Map of numbered sites in Table 1.

3.2. *Cueva del Ángel*

A comparable time-span is covered by a somewhat different sequence at Cueva del Ángel near Lucena in the Spanish province of Córdoba, 600 m asl and 80 km from the Mediterranean coast (Barroso Ruiz et al., 2011, 2014a,b; Botella et al., 2006). A U-ser determination of ~0.12 Ma comes from level VIII, about halfway down a 3.5 m-deep archaeological deposit (which attains 5 m at some parts of the site). Pollen analyses of sediment and coprolite samples by one of us (JS Carrión) were unsuccessful due to bad palynomorph preservation, or total absence of microfossils. The sequence presents a horse-dominated faunal assemblage, not unlike that of Bolomor in both composition and scarcity of large carnivores, and the incidence of both cut-marks and fire is likewise widespread in the sequence. Nevertheless, the Palaeolithic artefacts show a significant difference: whereas >5000 items resemble those from Bolomor (including bone retouchers: Moigne et al., 2016), a noteworthy difference is that 11 hand-axes were excavated between levels XV and III at Cueva del Ángel (and a further 35 in disturbed sediment), perhaps implying “that there is no clear boundary between the Lower and Middle Palaeolithic in the Iberian Peninsula” (Barroso Ruiz et al., 2011 and see below).

3.3. *Orgnac 3*

From a comparable late Middle Pleistocene time-span, Orgnac 3 is a site on a limestone plateau at ~250 m asl between the Rivers Cèze and Ardèche, western tributaries of the Rhône, ~100 km inland from the French Mediterranean coast. Excavation has provided numerous Palaeolithic artefacts spanning ≤0.35 - ≥0.28 Ma (Michel et al., 2011, 2013; Raynal et al., 2013) in a depth of ~7 m of sedimentary accumulation in a sink-hole or swallow-hole that developed after collapse of a karst cavity or aven (Combier, 1967). 7 human teeth come from deep levels dated to ~0.3 Ma. Lithic finds include a few bifacially-flaked artefacts (Moncel, 2010), and abundant small flint flakes, extracted often by repetitive knapping of flint slabs or cobbles (and occasionally other rock types). Most bifacial artefacts came from the deeper archaeological layers. Flakes removed by repetitive centripetal knapping of cores prevailed in the deeper archaeological layers but the higher layers provided evidence also of hierarchical knapping of prepared (“Levallois”) cores (~15% of cores) for repetitive extraction of standardized flakes, several of which show secondary knapping of edges, sometimes with abrupt retouch, producing side- and end-scrapers, points, denticulates, awls, piercers, notched pieces, beaks, and gravers, and plausible bone retouchers occur (Combier, 1976, 2005; Moigne et al., 2016; Moncel, 1993, 1999, 2011; Moncel and Combier, 1992; Moncel et al., 2005, 2011, 2012). The assemblage embraces Shea's modes A, B, C, D-1, D-3, E, and F (Table 2). Orgnac *Homo neanderthalensis* forebears had sufficient manual prowess (assuredly enabled by cognitive versatility) for responding with some behavioural autonomy to climatic oscillations and environmental fluctuations. Support comes from statistical breakdown of ~50,500 artefacts, considered from standpoints of (a) sources of raw materials, (b) taphonomical attention to site-formation processes, and (c) faunal analyses from a time when temperate MIS-9 environmental conditions gave way to MIS-8 (and *Equus mosbachensis* gave way to *E. steinheimensis*). Numbers of carnivore fossils identified in layers beneath the archaeological deposits decrease markedly in higher ones notwithstanding the greater volumes of sediment excavated in them. Human behaviour apparently changed between MIS-10 and MIS-8. Plausibly, the uppermost (level 1) assemblage reflects “farsighted logistical behavior based on a circular migration of human groups in territories with different

Table 1
Sites mentioned in text, ordered in terms of the *latest* Middle Palaeolithic material assemblage identified (the right-hand number in column 4). The sites *later* than the MIS 5a/MIS 4 transition are limited to those few that are mentioned for particular reasons in the text.

No. in Fig. 1	Sites	Ma	MIS	Location	Height (m asl)	Distance (Km)
1	Cueva de Ardales (Doña Trinidad)[b]	~0.65	4–1	Ardales, Málaga, Spain	450	60
2	Cueva de la Carihuela[b]	~0.11 7-<0.04	5–1	Píñar, Granada, Spain	1020	90
3	Gorham's Cave	0.05–0.03	3–2	Gibraltar	0	0
4	Gruta da Oliveira[a]	0.1–0.035	5–2	Almonda karst, Torres Novas, Portugal	115	450
5	Grotta di Uluzzo[b]	0.045–0.04	3–2	Porto Selvaggio, Nardò, Apulia, Italy	0	0
6	Grotta del Cavallo		3–2	Porto Selvaggio, Nardò, Apulia, Italy	0	0
7	Barma Grande[b]		3–2	Balzi Rossi, Grimaldi, Ventimiglia, Liguria, Italy	20	0
8	Grotte du Salpêtre	>0.03	3–2	Pompignan, Gard, France	380	35
9	Grotta di Fumane[b]	≥0.045–0.4	5–2	Fumane, Veneto, Italy	350	80
10	Abric Romaní[b]	~0.11–0.04	5–2	Capellades, Barcelona, Spain	280	35
11	Cova Negra de Bellús[b]	~0.117-<0.05	?6? 5-2	Xàtiva, Valencia, Spain	160	30
12	Cueva de Maltravieso[a] [b]	<0.18-<0.06	6–2	Cáceres, Cáceres, Spain	460	360
13	Baume Bonne[b]	≥0.27-≤0.125	10–2	Quinson, Alpes-de-Haute-Provence, France	400	75
14	Vanguard Cave	≥0.03	3	Gibraltar	0	0
15	Mauran		?3?	Mauran, Cazères, Haute-Garonne, France	500	150
16	Cueva del Boquete de Zafarraya	0.045	3	Zafarraya, Granada, Spain	1100	25
17	Grotta Breuil	~0.035	3	Monte Circeo, San Felice Circeo, Latium, Italy	0	0
18	Grotta Fossellone		3	Monte Circeo, San Felice Circeo, Latium, Italy	0	0
19	Grotta di San Agostino		3	Monte Circeo, San Felice Circeo, Latium, Italy	0	0
20	La Quina[a] [b]	0.05–0.04	3	Gardes-le-Pontaroux, Charente, France	150	360
21	Cueva de El Sidrón[a]	0.05	3	Cadanes, Asturias, Spain	250	475
22	Sima de las Palomas del Cabezo Gordo	~0.13–~0.04	5–3	Torre Pacheco, Murcia, Spain	125	5
23	Grotta Guattari	~0.08–~0.05	5–3	Monte Circeo, San Felice Circeo, Latium, Italy	0	0
24	Les Pradelles[a]		4/3	Marillac-Le-Franc, Charente, France	100	340
25	Grotte de l'Hortus		4/3	Valflaunès, Hérault, France	390	30
26	Riparo l'Oscurusciuto	~0.055	4/3	Ginosa, Taranto, Apulia, Italy	240	20
27	Santa Lucia Superiore		4	Toirano, Liguria, Italy	210	10
28	Via San Francesco		4	Sanremo, Liguria, Italy	0	0
29	Caverna Arma delle Manie		4	Finale Ligure, Liguria, Italy	250	2
30	Abri Lorenzi		?5/4?	Balzi Rossi, Grimaldi, Ventimiglia, Liguria,Italy	20	0
31	Barma dou Cavillou		?5/4?	Balzi Rossi,Grimaldi, Ventimiglia, Liguria,Italy	20	0
32	Grotta Madonna dell'Arma	~0.09–0.07	5–4	Sanremo, Liguria, Italy	0	0
33	Abri des Canalettes	~0.09–~0.065	5–4	Nant, Aveyron, France	700	80
34	Grotta dei Moscerini	0.12–0.07	5–4	Monte Circeo, San Felice Circeo, Latium, Italy	0	0
35	Baume Moula-Guercy	0.072	6–4	Valence, Drôme, France	80	150
36	Combe Grenal[a]	>0.11–0.045	6–4	Domme, Dordogne, France	80	240
37	Grotte du Lazaret	~0.17–~0.06	6–4	Nice, Alpes.Maritimes, France	10	1
38	Payre	≤0.34/~0.25 –0.16	8-6/5	Payré, Ardèche, France	60	140
39	Caverna delle Fate	0.08	5	Finale Ligure, Liguria, Italy	300	2
40	Cueva de los Aviones	0.115	5	Cartagena, Murcia, Spain	0	0
41	Abri.du Maras	~0.1–0.075	5	Saint-Martin-d'Ardèche, Ardèche, France	170	80
42	Grotte Rescoundudou[a]	0.125–0.115	5	Sébazac-Concourès, Rodez, Aveyron, France	600	150
43	Grottes de La Chaise[a]	≤0.25-≥0.1	6–5	*La Chaise*-de-Vouthon, Vouthon, Charente, France	100	360
44	Grotte de La Borde[a]		6–5	Livernon, Lot, France	320	200
45	Grotte Boule/La Terrasse/Coupe Gorge/La Niche[a]		7–5	Montmaurin, Haute-Garonne, France	350	230
46	Cueva del Ángel	?0.3?-~0.12	?8/7?-5	Lucena, Córdoba, Spain	600	80
47	Cova del Bolomor	~0.35–~0.12	?9?/8-5	Tavernes de la Valldigna, Valencia, Spain	100	5
48	Grotte Vaufrey[a]	~0.55–0.11	?14?/10-5	Cénac-et-Saint-Julien, Dordogne, France	200	240
49	Caune de l'Arago	≥0.55–~0.1	15–5	Tautavel, Pyrénées-Orientales, France	190	25
50	Grotte de Bruniquel	0.176	6	Bruniquel, Tarne-et-Garonne, France	300	150
51	Grotte de Coudoulous	~0.2–~0.1	6	Tour-de-Faure, Cahors, Lot, France	200	180
52	Vilas Ruivas[a]		6	Vila Velha de Ródão, Castelo Branco, Portugal	0	425
53	Campitello Quarry		7–6	Bucine, Tuscany, Italy	200	100
54	Saccopastore	~0.245–~0.22	8–7	Rome, Lazio, Italy	50	30
55–57	Rebibbia-Casal de' Pazzi/Ponte Mammolo/Sedia del Diavolo	~0.29–~0.22	8–7	Rome, Lazio, Italy	50	30
58	Castel di Guido	~0.325–~0.26	8–7	Rome, Lazio, Italy	25	15
59	Atapuerca Trinchera Galeria[a]	~0.4–~0.2	9–7	Atapuerca, Burgos, Spain	1080	400
60	Orgnac 3	≤0.35- ≥0.28	(9)-8/(7)	Orgnac-l'Aven, Ardèche, France	250	100
61	Loma de los Huesos[a]	?~0.25-~?0.2	?9–7?	Ambrona, Soria, Spain	1100	230
62	Malagrotta		?8?	Rome, Lazio, Italy	25	10
63	La Polledrara di Cecanibbio	~0.325	8	Rome, Lazio, Italy	50	30
64	Ceprano	0.35	?9–8?	Ceprano, Frosinone, Lazio, Italy	100	30
65	Torre in Pietra (Torrimpietra; Torre di Pagliaccetto)	0.354–0.334	9–8	Rome, Lazio, Italy	25	5
66	Loma del Sáuco[a]	~0.43–~0.3	12–8	Torralba del Moral, Soria, Spain	1100	225

(*continued on next page*)

Table 1 (*continued*)

No. in Fig. 1	Sites	Ma	MIS	Location	Height (m asl)	Distance (Km)
67	Atapuerca Trinchera Dolina TD10[a]	~0.34—~0.3	9	Atapuerca, Burgos, Spain	1080	400
68	Terra Amata	~0.4—~0.38	11—10	Nice, Alpes-Maritimes, France	10	2
69	Gruta da Aroeira[a]	~0.436—0.39	12—10	Almonda, Torres Novas, Santarém, Portugal	130	450
70	Atapuerca Sima de los Huesos[a]	0.43	?12?	Atapuerca, Burgos, Spain	1080	400
71	Fontana Ranuccio	~0.46	13—12	Anagni, Lazio, Italy	235	20
72	Loreto		?15—13?	Venosa, Basilicata, Italy	400	75
73	Parc de Vallparadís/Cal Guardiola	~1/~0.85—~0.6	?23/21? - ?15?	Terrassa, Barcelona, Spain	275	25
74	La Pineta	~0.7—~0.45	?17—13?	Isernia, Molise, Italy	455	65
75	Notarchirico	~0.67-~≤0.6	?16—14?	Venosa, Basilicata, Italy	400	75
67	Atapuerca Trinchera Dolina TD8[a]	~0.7—~0.6	?17—15?	Atapuerca, Burgos, Spain	1080	400
67	Atapuerca Trinchera Dolina TD7[a]	~0.78	19	Atapuerca, Burgos, Spain	1080	400
76	Cueva Negra del Estrecho del Río Quípar	<0.99->0.78	?21?	Caravaca de la Cruz, Mucia, Spain	740	75
67	Atapuerca Trinchera Dolina TD6[a]	~0.9—~0.8	21	Atapuerca, Burgos, Spain	1080	400
67	Atapuerca Trinchera Dolina TD5[a]	≥~0.93	?25—22?	Atapuerca,, Burgos, Spain	1080	400
77	El Forn, Barranc de la Boella	~1.07—~0.87	?23/22?	La Canonja, Tarragona, Spain	50	5
78	Atapuerca Sima del Elefante TE9[a]	~1.2—1.1	?35—33?	Atapuerca, Burgos, Spain	1080	400
79	Pont-de-Lavaud[a]	~1.1—1	?31—27?	Éguzon-Chantôme, Indre, France	260	400
80	Cà Belvedere di Monte Poggiolo[a]	1.06	?31—29?	Forlì, Forlì-Cesena, Emilia-Romagna, Italy	50	10
81	Bois-de-Riquet		?35—29?	Lézignan-La-Cèbe. Hérault, France	25	25
82	Grotte de Vallonnet	1.2—1	?35/33?	Roquebrune-Cap-Martin, Alpes-Maritimes, France	110	5
83	Fuente Nueva 3	~1.2—1.1	?35?	Orce, Granada, Spain	900	90
84	Barranco León/Fuente Nueva 3	~1.2	?35?	Orce, Granada, Spain	900	90
85	Pirro Nord P13		?37?	Cava dell'Erba, Apricena, Foggia, Italy	75	10
86	Cova de Les Teixoneres[b]	>0.1—0.3	5—3	Moià, Barcelona, Spain	760	40

Age (Ma) = million years ago, based on radiometrical estimates.
MIS = marine isotope stages, based on biochronological or stratigraphical indications that sometimes imply a time-span *greater* than that part occupied by published radiometrical determinations.
Height (m asl) = Height (metres above sea level).
Distance (Km) = Distance from Mediterranean coast (kilometres).

[a] Sites lying >200 km from the Mediterranean coast that are mentioned for particular (often comparative) reasons in the text.

[b] Presence of deposits more recent than Mousterian Middle Palaeolithic (e.g. Chatelperronian, Uluzzian, Upper Palaeolithic, Holocene).

durations of occupations” (Moncel et al., 2011), though it is hard to see how the conjecture might be transformed into a working hypothesis open to rigorous testing.

Reflexion on the Orgnac sequence raises the matter, which has both epistemological and ontological aspects, of how to interpret Middle Pleistocene human behaviour in western Mediterranean Europe from the standpoint of the wider spatiotemporal context of Early, Middle and early Late Pleistocene Palaeolithic assemblages from not only the rest of Europe but also Africa and western and southern Asia. In this context it is worth remembering that biacially-flaked (“Acheulian”) hand-axes or large cutting tools (Shea's mode E-1) coexist with repetitive hierarchical knapping on prepared cores (“Levallois”; Shea's mode F) in assemblages from ~0.385 Ma at Attirampakkan in India (Akhilesh et al., 2018), ~0.33 Ma at Nor Geghi in Armenia (Adler et al., 2014), ~0.5—0.4 Ma at Jaljulia in Israel (R. Barkai, pers. comm.), and ~0.3 Ma in the Kenyan Kapthurin Formation (Cornelissen, 1992; McBrearty et al., 1996; McBrearty and Brooks, 2000; Tallon, 1978).

3.4. *Grotte Vaufrey*

Returning to France, it is appropriate to mention that hand-axes present from MIS-10 to MIS-8 were succeded by assemblages dominated by “Typical Mousterian” secondarily-knapped flake artefacts from MIS-7 to MIS-5, according to OSL dates from Grotte Vaufrey in the Dordogne (Hernández et al., 2012). The sequence exemplifies a mid-Middle Pleistocene change in western Europe involving a trend (perhaps in response to hafting) away from bifacially-flaked hand-axes towards subsequent prevalence in the Mousterian of a range of secondarily-knapped flake artefacts. Undoubtedly the archaeological record reflects spatiotemporal mosaic change towards knapping cores in increasingly longer reduction sequences that favoured producing flakes of different shapes by hierarchical repetitive knapping of cores which prepared surfaces suitable for release of flakes, sometimes permitting their recurrent removal (Shea's “mode F-2”: Shea, 2013, 2017b) (Table 2). From level 1 many unretouched flakes 15—20 mm long are “microlithic”: “use of small products has been underestimated for a long time”

Table 2
Framework of nine major technological modes of stone tool technology, modes A—I according Shea (2013). Most subdivisions are not major changes in technological organization but accommodations to archaeological practices. Distinctions are based on primarily technological criteria.

Mode	Description and sub-modes
A	Stone percussors
B	Bipolar cores
C	Pebble cores/non-hierarchical cores
D	Retouched flakes
	D1. Retouched flake-tools
	D2. Backed/truncated flakes
	D3. Burins
	D4.Retouched microliths
E	Elongated core tools
	E1. Large cutting tools
	E2. Thinned bifaces
	E3. Bifacial core tools with retouched proximal concavities (BRPC)
	E4. Celts
F	Bifacial hierarchical cores (BHC)
	F1. BHC —Preferential
	F2. BHC -Recurrent
G	Unifacial hierarchical cores
	G1. Platform cores
	G2. Blade cores
H	Edge-ground tools
I	Groundstone tools

(Moncel et al., 2011). This recalls an inference from Isernia La Pineta (Longo, 1994; see below).

3.5. Payre and other sites in or close to the Rhône valley

Payre (Moncel, 2008) is a collapsed cave on the western flank of the middle Rhône valley, 60 m above the confluence of the small River Payre, 150 km north of the Mediterranean coast. It provided a depth of 5 m of sediments laid down after ~0.3 Ma (Moncel, 1993; Moncel and Debard, 2008; Raynal et al., 2013; Valladas et al., 2008a,b; possibly after ~0.23 Ma: Grün et al., 2008). There are Neanderthal teeth and a parietal fragment (Condemi and Moncel, 2008; Moncel and Condemi, 1996, 1997, 2007). Significant Middle Palaeolithic deposits date from late MIS-8 to early MIS-7 (units G, F) and also from late MIS-6 to early MIS-5 (unit D), according to ESR, U-ser/TIMS, and TL determinations (Moncel, 2011; Valladas et al., 2008a,b). Stable-isotope analysis of tooth enamel of large mammals implied that temperate woodland at the time of unit G gave way to more open conditions when units F and D formed (Bocherens and Rousseau, 2008). By contrast, rodent fauna, particularly *Microtus* (*Iberomys*) *brecciensis* and *Pliomys lenki*, points towards cold, dry conditions when unit G was laid down and cold, moist ones and a mosaic landscape when units D and A formed (Desclaux et al., 2008). Consideration of large mammals at Payre underlay a proposal that those from units G and F might reflect an increasingly temperate phase during MIS-6, whilst those from unit 5 might belong somewhere within MIS-5 (Patou-Mathis et al., 2008); the proposal seemed to be in accord with a chronology that excludes the MIS-8/MIS-7 estimates. It is interesting that in units G, F, and D, both *Stephanorhinus hemitoechus* and *S. kirchbergensis* were present as was the tahr *Hemitragus bonali* (Lacombat et al., 2008), and also that in unit F the presence of *Ursus spelaeus* remains is consistent with an interpretation that human activities likely took place when bears were absent (Auguste, 2008). Isotopic analyses of mammalian and Neanderthal dental enamel ascribe changes in both, from units G to F, to changing Neanderthal exploitation strategy from relatively greater interest in ungulates in moist contexts with gallery woodlands to those (red deer, tahr) on more open uplands, without marked palaeoenvironmental change in a cool but not very cold climate (Bocherens et al., 2016; Ecker et al., 2013).

Signs of combustion were observed in most of the units, and a particularly well-defined horizontal lens of burnt sediment was excavated in a high situation within unit G (Moncel et al., 2008b). In the several human occupation phases at Payre, the main core technology was discoidal reduction producing unstandardized flakes, together with a few instances of both “Levallois” (in unit F) and “Kombewa” reduction. Apart from a few large uni- and bifacial artefacts (fashioned on basalt, quartzite, quartz, limestone, and chert or flint) found particularly in deep levels of unit G (Daschek et al., 2008; Moncel, 2008), and a large quartzite artefact from unit Fa (Daschek et al., 2008; Moncel, 2011; Moncel et al., 2008a,b; Raynal et al., 2013), the assemblages from all units are characterized by an abundance of small items, mainly of chert (flint) and quartz, that rarely had undergone secondary knapping. Only 270 of 3697 artefacts from unit F were classifiable as tools, mainly with secondary edge knapping as scrapers, notched and denticulate pieces (Theodoropoulou et al., 2009), and “convergent tools” (Moncel et al., 2009) and 15 bone retouchers were identified (Daujeard et al., 2011). Microscopy suggests that some convergent stone artefacts might have been mounted (Borel, 2008; Moncel and Chacón Navarro, 2008) maybe in thrusting spears, but transverse cross-sectional areas of their tips imply unsuitability for throwing spears (Shea, 2009). Small numbers also occur of backed flakes and secondary “Quina-type” Mousterian knapping of edges. Whereas most raw materials (including limestone and basalt) come from nearby or local outcrops and gravels, a few hail from upto 60 km to the south (Moncel et al., 2002; Moncel and Fernandes, 2008; Raynal et al., 2013), though secondary knapping is no more marked on the latter than on the former. Lack of hafted points and importation of large flakes made from various local stone types, along with introduced flint flakes and nodules, may reflect seasonal occupation at the site, perhaps favoured by its environmental location. The flint reduction sequences are quite complete but those on local stones are often partial, maybe implying mobility of the occupants and off-site manufacture of stone artefacts. The eclecticism seems to reflect cognitive versatility and technical skilfulness. Microscopical analysis of 125 stone artefacts showed use-wear or residue evidence of use on starchy and other plants, wood, fish, bird, and bones and hides of mammals, implying that “Neanderthals had a broad-based diet that included starchy plants, large animals, fish, and possibly birds”, belying a notion that “acquisition of fast-moving small prey” depends on “a presumed cognitive superiority of modern humans” (Hardy and Moncel, 2011). Evidence of starch implies processing of underground storage organs, or perhaps seeds, and “that Neanderthal consumption of plants was routine as early as MIS 8/7” (Hardy and Moncel, 2011). A plausible conjecture is that Neanderthal extractive activities took place within a region of perhaps 5000 km^2, using a general purpose toolkit, and constrained in time and space by resource availability that likely demanded small human groups to be often on the move and roam in quasi-circulatory fashion within their microenvironmental habitat, perhaps seasonally and implying organizational competence and foresight (cf., Daujeard et al., 2011; Moncel, 1996, 2000, 2003, 2004, 2008, 2010, 2011; Moncel et al., 2007, 2011; cf., “dispersed hunting”, Boyle, 1998). Similar interpretations are inferred for Cova del Bolomor, and (see below) Cova Negra de Bellús and Abric Romaní in Spain. Several late Middle and early Upper Pleistocene sites in or close to the Rhône valley have been put forward as plausible participants in strategies of territorial exploitation around Orgnac 3 and Payre (Moncel, 2000, 2003; 2004, 2008; 2010, 2011; Moncel et al., 2008a; Moncel et al., 2010; Moncel et al., 2011, 2012; Raynal et al., 2013). Space precludes discussing detailed aspects of similarity and difference, regarding chronology or assemblage characteristics, between those sites. Nevertheless, among those deserving special mention is Baume Moula-Guercy, 80 m above the River Rhône, where twenty sedimentary layers span a period that began in MIS-6 and ended in MIS-4. The deep layer XV assigned to MIS-5 contained a “Ferrassie Mousterian” assemblage with “Levallois” core-reduction, and bones showing cut-marks and signs of defleshing (maybe for extracting marrow and brain) of both red deer and six Neanderthals, perhaps implying cannibalism (Defleur et al., 1993, 1998; 1999; Hlusko et al., 2013; Mersey et al., 2013).

3.6. Abri du Maras

Excavated in sediments dated to ~0.1–0.075 Ma (between MIS-5d and MIS-5a) at Abri du Maras (Moncel, 1996; Moncel and Michel, 2000; Moncel et al., 1994), 170 m asl and 70 m above the River Ardèche near where it flows into the Rhône, are “Levallois” flakes and flake-blades bearng microscopical residual traces of twisted fibres suggestive of twine, animal residues including rabbit hairs, fish scales and fragments of feather barbules of Accipitriformes and Anseriformes (Hardy et al., 2013; Rufá et al., 2016a,b), five stone points showing traces of use-wear and transverse cross-sectional areas appropriate for projectile point tips, stone flakes bearing residues containing mushroom spores, chub and perch fish bones, and cut-marked bones of rabbits and other animals showing cut-marks (Hardy et al., 2013).

3.7. Baume Bonne

An important site with sedimentary deposits and 64,000 Palaeolithic artefacts from MIS-10 to MIS-3 is the Baume Bonne rock-shelter in the River Verdon gorge near Quinson, about 400 m above and 75 km from the Mediterranean Sea (Bottet, 1956; Bottet and Bottet, 1947; de Lumley, 1969a, 1975; 1976a; Falguères et al., 1993; Gagnepain, 2007; Gagnepain and Gaillard, 2005, 2011; Gagnepain et al., 2004; Notter, 2007; Valensi et al., 2005). The site also contained Upper and post-Palaeolithic material. Stratigraphical revision combined with reassessment of the Palaeolithic sequence (Notter, 2007) shows that the oldest archaeological assemblages ("II-IVa") span MIS-10,-9,-8,-7 and -6, embracing U-ser and ESR determinations of ~0.27 and ~0.2–0.17 Ma, and include many traces of combustion and several bifacially-flaked artefacts, although secondarily-knapped "proto-Charentian" flake artefacts predominate, made mainly by non-hierarchical reduction sequences, though "Kombewa" reduction occurs also, and hierarchical "Levallois" reduction is present in the later stages (Notter, 2007). Assemblage "IV" characteristics persist in MIS-6, according to age determinations of ~0.17 Ma, with disappearance of bifaces (no longer found after "IVa"), appearance of trihedral flakes with secondary knapping on one surface ("Quinson points"), and flakes with edges showing "Quina"-type semi-abrupt stepped and scalariform knapping; the "IVc" assemblage merits the designation "Quina Mousterian" (Notter, 2007); sediments containing a putative assemblage "V" cannot be later than age determinations of ~0.13–0.125 Ma (MIS-5e) when calcrete formed, after which sparse Mousterian artefacts characterize deposits assigned to MIS-4/MIS-3 (assemblage "M") containing lynx, bear (possibly hibernating), and lemming (Paunescu, 2001). "Quina-type" artefacts occur sporadically in MIS-6 assemblages elsewhere (e.g., La Chaise: Debénath, 1992), though "Quina"-dominated Mousterian assemblages often are from MIS-3.

3.8. Hortus and La Quina

La Quina lies outside the geographical purview of this review. It lies 350 km north-west of the Grotte de l'Hortus which is an important Mousterian site near Valflaunès in Hérault, 390 m above and 31 km from the Mediterranean coast north of Montpellier, to which a detailed monograph was dedicated (de Lumley, 1972) before geochronological dating was readily available. Nevertheless, palynological, palaeontological, sedimentological, and other palaeoenvironmental indicators allow comparison with a part of the Combe-Grenal sequence in the Périgord (cf., Bordes et al., 1972) that is comparable to layers at La Quina with age determinations implying 0.055–0.045 Ma (Jelinek, 2013). A 7 m-deep sequence of five layers, containing Mousterian and palaeontological remains, with sterile sediments intercalated between each of the layers, suggests a climate changing from cold and dry to milder and damper conditions. Despite ascription to "Würm III Phases I-V", the sequence could well correspond to late MIS-4 when four milder episodes (GI-17,-16,-15,-14) intervened ~0.056 - ~0.052 Ma (plausibly the "Würm II-III" transition), followed by the marked MIS-3 cooling ("Würm III") that included the GS-13 Heinrich-5 event ~0.047 Ma. Only two reindeer bones were identified (Pillard, 1972a), perhaps reflecting an environment less suited to reindeer that the tundra around La Quina where the species dwindled in higher levels. Environmental indicators at Hortus imply cold winters and milder summers during which mesothermophilous species (cf. *Quercus pubescens, Q. ilex, Fraxinus, Phillyrea*) were able to survive notwithstanding their tendency to succumb to winter frost (Renault-Miskovsky, 1971, 1972; Vernet, 1972). Open graminoid communities with sparse *Betula* and *Pinus* domain the landscape during the colder episodes. Ibex predominated among the larger mammals and likely was hunted and perhaps dismembered or butchered at Hortus (Pillard, 1972a). Red deer and horse were more abundant than aurochs and bison. Rabbit also abounded, perhaps preyed on by the carnivorous mammals and avian raptors identified (Mourer-Chaviré, 1972; Pillard, 1972a), because 3000 rabbit bones lacked cut-marks (Pillard, 1972b). Remains of large carnivores were most frequent in the upper layers. Several bat taxa identified (Jullien, 1972) imply periods when humans were absent. "Levallois" reduction of chert, flint and quartz cores was practised (de Lumley and Licht, 1972) and a metrical analysis was performed (Rolland, 1972). Remains of a score of Neanderthals were published and defleshing of cadavers may have taken place (de Lumley et al., 1972; de Lumley, 1973). Intriguingly, both bear and leopard paws were excavated with bones in anatomical connexion, which was also the case for two leopard paws excavated beside articulated Neanderthal skeletons dating from ~0.055–0.05 Ma at the south-eastern Spanish Mediterranean Neanderthal site of Sima de las Palomas del Cabezo Gordo (see below). Hortus provided no fish remains, whereas 8 km to its north the Grotte du Salpêtre, near Pompignan in Gard, afforded remains of eel, trout, cyprinids pehaps roach, and maybe also whitefish (de Lumley et al., 1972) though because these are not mentioned in a study of the Mousterian sequence (Farbos-Texier et al., 1981) perhaps they came from the Upper Palaeolithic deposits at Salpêtre.

3.9. Monaguesque and Ligurian coastal sites

The Monaguesque and Ligurian coast has a score of Middle Palaeolithic sites, including the well-known Balzi Rossi (Baousse Rousse) rock-shelters in Mediterranean coastal cliffs at Grimaldi, between Menton and Ventimiglia (de Lumley, 1969a; Vicino, 1976; Vicino and de Lumley, 1976). Few have well-dated assemblages. Most are probably no earlier than MIS-5b. An exception is the seaside Grotta del Principe (Grotte du Prince) with MIS-7 deposits of ~0.22 Ma (Barral and Simone, 1987; Yokoyama, 1989). They provided a human "ante"-Neanderthal pelvic fragment (de Lumley, 1976b; de Lumley, 1972a,b; de Lumley, 1973) and both larger artefacts (flaked cobbles, chopping tools, and "Acheulian" hand-axes) and smaller ("pre-Mousterian") ones including flakes and elongated flake-blades removed (using hard hammerstones and softer knapping billets) by reduction procedures ranging from unipolar and bipolar to orthogonal, discoidal and recurrent and centripetal "Levallois" removals, with several instances of secondary knapping of flakes and flake-blades, with side- and end-scrapers, points, awls, garden slugs, beaks, notched and denticulate forms (Rossoni-Notter et al., 2016); the range embraces Shea's modes except H and I, and demonstrates both the knappers' skilfulness and their cognitive versatility. They were aware of the affordances for knapping offered by different raw materials and of outcrops where these were available. Petrological diversity implies that raw materials were obtained both locally and from ≥20 km eastwards and westwards along the coast (Rossoni-Notter and Simon, 2016; Rossoni-Notter et al., 2016). The fauna includes ibex, red deer, hippopotamus, bear, wolf, and micromammals typical of temperate woodland. In later deposits, assigned to MIS-6, the proportion rises of chopping tools and hand-axes, small flake artefacts are less frequent, and the petrological range is limited mainly to local raw materials.

Most western Ligurian Mousterian assemblages belong to MIS-5 or MIS-4. Exotic petrology sporadically recorded at Principe, Cavillou and Abri Lorenzi implies sources upto 150 km away (Rossoni-Notter and Simon, 2016). Barma dou Cavillou (Grotte du Cavillon) MIS-5/MIS-4 levels contained combustion deposits, Mousterian artefacts, including flake-blades produced by "Levallois" core-reduction, and a rich fauna with ibex, red and fallow deer, horse, Merck's rhinoceros and elephant (de Lumley, 2016). Caverna delle Fate, at Le Manie 300 m above and ~2 km from the sea at Finale Ligure, provided Neanderthal remains and Mousterian artefacts dated to ~0.08 Ma by U-ser and ESR, and a fauna of red deer, ibex, horse, aurochs, and large carnivores (Giacobini et al., 1982).

Palynology of the Madonna dell'Arma cave shows the Ligurian coastal vegetation between the end of the last interglacial period and the beginning of the pleniglacial. The sequence of transition shows a noticeable representation of arboreal cover and a persistence of thermophilous elements in this refugial area. The onset of the pleniglacial is characterized by *Pinus, Juniperus* and *Artemisia*. This palynological record suggests correlations between changing environments and Mousterian activities (Kaniewski et al., 2004a,b, 2005a,b). Marine regression at Madonna dell'Arma was followed by continental deposits of ~0.091–0.073 Ma (ESR on bone) containing Mousterian artefacts (on flakes removed by "Levallois" core-reduction), Neanderthal skeletal fragments, and a fauna, appropriate for the MIS-5a dates, of red deer, aurochs, boar, hyaena, Merck's rhinoceros, straight-tusked elephant, and hippopotamus. Similar Mousterian artefacts, Neanderthal skeletal remains, and a fauna with ibex, roe deer, and wolf were excavated at Santa Lucia Superiore and assigned to MIS-4. Principal component analyses of pollen spectra indicate a MIS-5a landscape corresponding to a dry Mediterranean temperate climate, albeit with humidity increasing with altitude. It gave way to growing aridity and corresponding retreat upwards of deciduous trees to where precipitation still fostered them, though evergreens predominated; the climate was cool, rainfall low, and river flow diminished. Later on, the climate became still colder, and in consequence aridity increased, with development of steppe landscape, sparse stands of trees, deciduous species confined to ephemeral gallery woodland, and rainfall to higher mountains. Statistical comparison of faunal remains from Lazaret, Grotta del Principe, Grotta Madonna dell'Arma, Caverna Arma delle Manie, the via San Francesco at Sanremo, Santa Lucia Superiore, and Caverna delle Fate implies that only at the last were carnivores mainly responsible for the accumulation (albeit contributing to it at others), and that Neanderthals were most likely unspecialized hunters of cervids and bovids in open woodland landscapes nearby, from MIS-6 to MIS-3, perhaps often during the second half of the year when young animals were available after the mating season, as well as older ones, though prime animals were prominent at Arma delle Manie (Valensi and Psathi, 2004).

3.10. Coastal Latium and the conjecture of cannibalism

The matter of how Mousterian behaviour and activities reacted to changing environments is impervious to research capable of fine-grained analysis. Nevertheless, Neanderthals appear to have coped somehow with changes in their surroundings. Lack of fine chronostratigraphical resolution hampers attempts to interpret several caves excavated decades ago (not to mention >2000 open sites and find-spots) in southern France and Italy. Accomodative conjectures about Neanderthal behavioural responses to landscape evolution across Mousterian phases at sites, or under particular environmental circumstances, frequently involve chains of inferential (quasi-ethnographical) reasoning with rather weak links. This can apply often to conjectures about relations between environmental circumstances or faunal abundances on the one hand, and, on the other, predominance in particular Middle Palaeolithic assemblages of some artefact forms over others. Some conjectures carry overtones of (quasi-biological) adaptation influenced by environmental determinism. A quasi-ethnographical conjecture no longer credible was that of cannibalism at Grotta Guattari on the central Italian Mediterranean coast of Latium south of Rome: a parsimonious interpretation is that scavengers (e.g., hyaenas) disturbed Neanderthal skeletal remains (Kuhn, 1995; Piperno and Giacobini, 1990–1991; Stiner, 1991, 1994). Following (probably MIS-5e) marine sediments, poorly-dated archaeological deposits (~0.08-~0.05 Ma) continuing into MIS-4 contained small flaked pebbles (available locally) and secondarily-knapped flakes of the regional "Pontinian" Mousterian, likened to "Charentian Quina" forms (Taschini, 1979), though perhaps better regarded as sui generis (Bietti et al., 1991) with minor differences between the coastal Latium rock-shelters around Monte Circeo of Grotta Guattari, Grotta di Sant'Agostino, Grotta dei Moscerini, Grotta del Fossellone and Grotta Breuil (Kuhn, 1995). After studying old faunal collections from the Monte Circeo sites Stiner (1994) inferred that opportunistic hunting and scavenging could suffice to interpret much Mousterian behaviour and that only later on (<0.04 Ma) is ambush hunting suggested by noteworthy presence of prime ungulate remains, though skewing of some samples might have occurred were early excavators to have disregarded diaphyseal fragments (Marean and Assefa, 1999). Phytolith research into Neanderthal dental calculus from Grotta Guattari and Grotta del Fossellone suggests a plant component in the diet (Power et al., 2018). Neanderthal dietary breadth is inferred also from analysis of occlusal wear on teeth from Saccopastore, Grotta Guattari, and Barma Grande (Fiorenza, 2015; Fiorenza et al., 2011). A noteworthy apect of Grotta dei Moscerini, where archaeological sediments including combustion features (Vitagliano, 1984) followed a probably MIS-5e marine deposit (10 ESR determinations span ~0.12-~0.07 Ma), is that percussion flaking similar to that on pebble cores was carried out on clam shells (*Callista chione*), and, although not seen in other coastal Latium assemblages, marine shell artefacts have been identified sporadically at other coastal sites (Barma Grande, Grotta del Cavallo, Grotta di Uluzzo: Kuhn, 1995; Romagnoli et al., 2014, 2015). Mussels, clams, and cockles abounded in some Moscerini levels, often showing signs of burning, particularly in levels with stone artefacts, suggesting that Neanderthals roasted shellfish (Stiner, 1994).

3.11. Marine resources and birds: Bajondillo and Gibraltar caves

Burnt mussel and other marine shells are known also from Spain where the Bajondillo rock-shelter, 250 m from the Andalusian Mediterranean shore at Torremolinos, afforded a sequence of deposits beginning ~0.15 Ma with Middle Palaeolithic flake artefacts, and remains of aurochs, red deer, ibex, and rabbit (Cortés-Sánchez et al., 2011). Late Mousterian collection of marine resources is recorded also at the Gibraltarian Vanguard and Gorham's Caves (Stringer et al., 2008). However, across the Gibraltar Strait, marine molluscs were present in an early Middle Palaeolithic assemblage of ~0.25 Ma at the Benzú cave at Ceuta (Ramos et al., 2008).

The Gibraltar caves offer convincing instances of late Mousterian use not only of marine resources but also birds (Finlayson, 2008; Finlayson et al., 2006, 2012), albeit from contexts that seem to be later than the 0.05 Ma time-limit of this review (see Foreword), which is also the case of the feathers and avian remains from ~0.044 Ma at Grotta di Fumane (Fiore et al., 2016; Peresani and Blasco, 2016; Peresani et al., 2011), which is 350 m above sea level at Fumane, north-west of Verona in Italy, and provided a Late Pleistocene fauna (Fiore et al., 2004; Tagliacozzo et al., 2013). Nevertheless, Neanderthal activities with feathers and bird bones are reported from as early as ~0.1-0-075 Ma at Abri du Maras in the Rhône valley (Hardy et al., 2013), and similar evidence comes from some other French Mousterian MIS-4 and MIS-3 assemblages (Laroulandie et al., 2016) lying slightly outside our geographical purview (see Foreword), not to mention sites further afield such as Krapina in Croatia (Radovčić et al., 2015).

3.12. Boquete de Zafarraya

Slightly later than our main chronological purview (see Foreword) is the cave at Boquete de Zafarraya, at 1100 m above and 25 km from the Andalusian Mediterranean coast at Málaga, which provided a Neanderthal mandible and a Mousterian assemblage (Barroso Ruiz, 2003), dated to ~0.046 Ma (Barroso Ruiz and Caparrós, 2015). It is suggested from a statistical path analysis of faunal remains that Neanderthals likely hunted large herbivores in the nearby polje whereas ibex and chamois were preyed on by large carnivores presumably when humans were not at the cave (Caparrós et al., 2015a,b). Pollen analysis depicts xerophytism in the surrounding landscape, although with sparse pines and junipers (Lebreton et al., 2006).

3.13. Cueva de la Carihuela

Also in Andalusia, the Cueva de la Carihuela near Piñar in Granada, at 1020 m above and 90 km from the Mediterranean Sea, has provided numerous U-ser, TL and radiocarbon determinations spanning MIS-5, MIS-4, MIS-3, MIS-2 and the Holocene, and an extensive palynological record (Carrión, 1992; Carrión et al., 1998; Fernández et al., 2007; Vega Toscano, 1993). A U-ser determination of ~0.117 ± 0.04 Ma suggests that deep sediments could well belong to MIS-5, and the Late Pleistocene pollen sequence certainly resembles that both in the cave (Carrión, 1992) and in the nearby Padul lake sediments in the Sierra Nevada in Granada (Pons and Reille, 1988). Micromammals accord with the climatological findings (Ruiz Bustos and García Sánchez, 1977). With sharp alternation of forests and steppes, and the occurrence of mesothermophytes, pollen sequences from MIS-3 and MIS-2 sediments are comparable to findings at other Spanish Mediterranean sites (Carrión et al., 1995, 1999). Further inland there is a shortage of long, well-dated, palaeobotanical records for the Early and Middle Pleistocene (Carrión et al., 2009). It is frustrating that investigation of possible correlations between palaeoenvironmental oscillations and Neanderthal behaviours at Carihuela is hindered by difficulties concerning the stratigraphical provenance of several TL determinations (Fremlin, 1974; Göksu et al., 1974; Vega Toscano, 1988) from some of the Mousterian deposits (Almagro Basch et al., 1970; Spahni, 1955a,b; Vega Toscano, 1983, 1987, 1988, 1993; Vega Toscano et al., 1988). "Charentian" analogies were proposed for the lithic assemblage (de Lumley, 1969b). Neanderthal cranial and other remains were excavated in various levels (de Lumley and García Sánchez, 1971; de Lumley, 1973; Fusté Ara, 1956; García Sánchez, 1957, 1960; García Sánchez et al., 1994; Garralda, 1970; Spahni, 1955b); however, prudence counsels against regarding any of the Mousterian and Neanderthal finds as incontrovertibly older than 0.05 Ma (cf., Fernández et al., 2007). As at several sites in western Europe, Mousterian deposits were followed by dated levels with Upper Palaeolithic and post-Palaeolithic assemblages and modern human skeletal remains.

3.14. Canalettes

Returning to southern France, the Abri des Canalettes, at 700 m asl on the Causse du Larzac, 80 km north-west of Montpellier and the Mediterranean coast, provides late MIS-5/earlyMIS-4 evidence (Meignen, 1993) from all layers of Neanderthal predation on deer, horse, and other ungulates, with only slight incidence of carnivores. Horse and aurochs are somewhat more abundant in higher layers though red deer abounded. Exploitation of game perhaps took place between late spring and early autumn, with repeated seasonal utilization of the site. Mares and foals may have been taken preferentially and killed away from the site, back to which dismembered body parts were carried, whereas perhaps entire lighter deer carcasses were brought back. Rabbit bones abound; in layer 3 presence of broken and burnt rabbit bones suggested human activity (Patou-Mathis, 1993), confirmed by identification of cut-marks on rabbit bones from layer 4 (Cochard et al., 2012), though intact bones in all layers perhaps imply that other rabbits died naturally, maybe in a warren (Patou-Mathis, 1993) which could underlie a high incidence found of mature females (Cochard et al., 2012). Arboreal anthracology (Vernet, 1993) and rodent biostratigraphy support attributing the sequence to MIS-5b or perhaps MIS-5a/early MIS-4, supported by three layer-2 TL determinations ~0.079–0.067 Ma (Valladas and Joron, 1993). The environment evolved from drier open parkland to damper mesophilous woodland as layer 3 gave way to layer 2, though presence of squirrel in layer 3 and walnut in layers 3 and 2 (unless it is intrusive, as Vernet wondered) could hint at a mosaic landscape with various biotopes around and below the site, including vegetational refuges (such an interpretation has been proposed for walnut from Late Pleistocene sediments at the eastern Andalusian Carihuela cave: Carrión and Sánchez-Gómez, 1992; Carrión et al., 1998, 1999).

The Canalettes 1.5 m sedimentary fill likely spans 0.09–0.75 Ma, a period marked by brief Dansgaard-Oeschger fluctuations including episodes of marked cooling at ~0.086 Ma and ~0.075 Ma (Dahl-Jensen et al., 2013; Johnsen et al., 1997; Mogensen, 2009; Rasmussen et al., 2014). Climatic swings probably induced environmental responses in the Causses, oscillating between harsher and less harsh landscapes. Hearth stones around a fire place were excavated in layer 3 (Meignen, 1993). Mousterian stone artefacts (Meignen, 1993) include flakes and (as at Baume Bonne) elongated flake-blades removed by hierarchical, "Levallois" (Shea's mode F), reduction of chert cores, with widespread secondary knapping of points, side-scrapers, denticulates, and a few end-scrapers and gravers. A possible slicker, or burnisher, for working hides or leather was proposed on the grounds of polish observed at one end of 125 mm-long fragment of a deer rib (Patou-Mathis, 1993); bone slickers (*lissoirs*) occurred in Mousterian assemblages from the Dordogne sites of Pech de l'Azé and Abri Peyrony (Soressi et al., 2013), dating respectively from ~0.051 to ~0.047 Ma (McPherron et al., 2013).

3.15. Bruniquel, Le Rescoundudou, La Borde, Coudoulous, Mauran, Les Pradelles

To the west of Canalettes, Bruniquel cave lies in the Aveyron valley, 150 km from the Mediterranean. Inside, 336 m from the entrance, large stalagmite fragments seem to have been arranged intentionally, with associated combustion features, at a time during MIS-6 dated by U-ser to ~0.176 Ma (Jaubert et al., 2016), indicating Neanderthal ability to undertake activities in the dark zone of caves. The variable composition of predominant large game at sites from MIS-6 to MIS-4 sites in southern France has attracted notice (Patou-Mathis, 1989). Plausibly, at several sites advantage was taken of ungulate herds on steppe, or sometimes taiga. Fallow deer and horse are dated to ~0.125–0.115 Ma (Guibert et al., 2008) at Le Rescoundudou on the Causse Comtal near Rodez (Jaubert, 1988, 1993a; Jaubert and Maureille, 2008; Jaubert and Mourre, 1996; Jaubert et al., 1992). Further north, aurochs were prominent at La Borde on the Causse de Gramat near Livernon (Jaubert et al., 1990). At Coudoulous, near Cahors, bison prevailed during MIS-6 (with deposits dated to between ~0.2 and ~0.1 Ma: Guibert et al., 2008). Bison abounded at the large open site of Mauran (probably belonging to MIS-5a or MIS-4), near Cazères in the Garonne headwaters, with Mousterian denticulate and other artefacts (Farizy et al., 1994; Jaubert, 1993b) Many broken long bones suggest marrow extraction and removal of attached bison meat, distal limb segments receiving less atttention (Rendu et al., 2012). Organized hunting is proposed, perhaps late in the warm season, maybe with removal and storage of body parts for winter consumption. Les Pradelles in Charente, where reindeer predominated, is interpreted similarly (Rendu et al., 2012). Social organization of activities scheduled on annual basis implies cognitive and probably also communicative skills. Plausibly, hunting at Mauran and La Borde involved ambushing groups of large animals that were slaughtered indiscriminately (White et al., 2016).

3.16. *Lazaret*

At Grotte du Lazaret, beside the French Mediterranean coast at Nice, MIS-7 transgressive marine sedimentary complexes A and B were followed by 26 archaeostratigraphical layers in complexes C-F. U-ser and ESR estimates (Michel et al., 1997) of ~0.17 and ~0.13 Ma imply MIS-6 for complexes C-I,-II and -III, followed by concretions in complexes D and E and vestigial upper deposits (ravaged by old excavations) from MIS-5e ~0.1 Ma and MIS-4 ~0.61 Ma (complex F). Early MIS-6 archaeological layers contained bifacially-flaked artefacts, chopping tools and flaked cobbles (Darlas, 1994; de Lumley, 1975, 1976a,b; de Lumley et al., 1976a; Octobon, 1956), fragments of "*antenéandertalien*" child and adult skulls, teeth and bones (de Lumley, 1973). Tiny sea-shells excavated around combustion features could have been present in sea-weed, perhaps used as bedding though other explanations are possible (de Lumley, 2004; Gall, 1983; Laafar et al., 1995). Reindeer decreased as C-III developed over time (Valensi, 2000) and artefact assemblages became dominated by flakes removed from cores by discoidal and hierarchical "Levallois" reduction, with several flakes secondarily-knapped into denticulate, notched and pointed forms, or given retouched edges (scrapers), showing more in common with Middle Palaeolithic assemblages elsewhere than with Middle Pleistocene assemblages dominated by (Shea's mode E-1) (Table 2) bifacially-flaked "Acheulian" large cutting tools (confined to the deeper layers at Lazaret). Raw materials include fine-grained limestone, quartzite, rhyolite and cherts (flint and jasper), mostly obtainable within 15 km from Lazaret, though some flint may have come from 30 km away, and fine-grained quartzite from 60 km away in Italy.

Humans were responsible for retrieving large game, especially red deer, ibex, and body parts of horse, aurochs, bison, fallow deer, roe deer, giant deer, woolly rhinoceros, steppe rhinoceros, and straight-tusked elephant, and small game including rabbits (Boyle, 1998; Valensi, 1996, 2000). Primary access by carnivores may have been infrequent given that few ungulate bones show signs of carnivore impingement, whereas cut-marks occur on some carnivore bones. Carnivores include leopard, hyaena, lion, bear, wolf, lynx, and fox, and coprolites testify to visits. Statistical analyses suggest intensive springtime slaughter of hunted red deer and ibex, with dismemberment of carcasses at kill sites or perhaps the cave (Boyle, 1998). Inspection of percussive and cut-marks implies efficient reduction of carcasses for meat, marrow, and grease. Perhaps a strategy was employed involving indiscriminate slaughter of a group of animals in an ambush followed by selective processing of carcasses (cf., White et al., 2016).

Skinning of hung carcasses could have taken place. In complex C, a line of stones was interpreted as packing-stones for poles of a possibly skin-covered structure (de Lumley, 1969c, 2005; de Lumley and Boone, 1976; Villa, 2004). Stone arrangements perhaps implying flimsy structures were described at both late MIS-6 Vilas Ruivas beside the Portuguese coast near Ródão (GEP, 1983) and the MIS-3 (~0.055 Ma) Riparo l'Oscurusciuoto rock-shelter at Ginosa near Taranto in Italy (Ronchitelli et al., 2014; Villa et al., 2009) where hearths separated a possible sleeping area within from an outer area where knapping and carcass processing took place (Spagnolo et al., 2018).

3.17. *Abric Romaní and adaptability of Neanderthal behaviour*

Curing skins is a conjectural use of possible tripods represented by wood pseudomorphs excavated in level 1 (~0.05 Ma) at Abric Romaní which lies 300 m asl, overlooking the River Anoia near Capellades, 35 km from the Catalan Mediterranean coast (Carbonell and Castro-Curel, 1992, 1995; Carbonell et al., 1996; Castro-Curel and Carbonell, 1995). At Romaní 16 m-deep sediments are divided into 20 archaeological levels (the uppermost [A] containing Upper Palaeolithic material). Occupation probably was discontinuous (Vallverdú et al., 2005). Deep levels date from 0.11 Ma (Sharp et al., 2016). As mentioned in the Foreword, most assemblages later than 0.045 Ma are outside the scope of this article unless preceded, as at Romaní, by older ones. Particular recognition must be granted to the spatiotemporal resolution achieved at Romaní (Carbonell, 2012; Sañudo et al., 2012; Vallverdú-Poch and Courty, 2012). Levels dated to 0.06–0.04 Ma by U-ser and ^{14}C (Bischoff et al., 1988, 1994; Carbonell et al., 1994; Vallverdú-Poch et al., 2012) permit correlation with palaeoclimatic oscillations recorded in Greenland ice-cap cores (Vallverdú et al., 2014a) and continental palaeopalynological records (Burjachs and Julià, 1994, 1996). A stratigraphical sequence of combustion features suggests recurring preferences for circumscribed locations of hearths ~0.055–0.045 Ma (according to U-ser dating of levels N, M, K, J, I), implying cognitive appreciation of structured spaces (Allué et al., 2012a; Carbonell et al., 2007; Romagnoli and Vaquero, 2016; Vaquero et al., 2001, 2004). Whilst pollen and palaeoenvironmental analyses (Allué et al., 2012b; Burjachs and Julià, 1994, 1996) indicate *Pinus* dominance throughout, thermophilous woodland persisted between ~0.070 and ~0.066 Ma interrupted by episodes of steppe vegetation, followed by a cold, moist environment with abrupt changes ~0.066 - ~0.057 Ma that gave way to climatic oscillations including milder, humid episodes from ~0.057 to ~0.050 Ma, followed by cold, dry conditions ~0.050 - ~0.046 Ma, ending in a milder episode ~0.046 - ~0.040 Ma with thermophilous and Mediterranean trees or shrubs (*Quercus, Rhamnus, Pinus, Juniperus, Acer,* Oleaceae): the ~0.070 - ~0.040 Ma Romaní environmental findings mirror palaeoclimatological oscillations recorded in Greenland ice during MIS-4 and MIS-3 (cf., Mogensen, 2009; Rasmussen et al., 2014). There are analyses of faunal and Palaeolithic remains (Cáceres et al., 2012; Rosell et al., 2012; Vaquero et al., 2012). Abundant red deer, horse, and goat remains suggest procurement strategies different from those for retrieving less abundant bulky parts of rhinoceros and aurochs carcasses (Marín et al., 2016; Rosell et al., 2012). Occasionally carnivores were taken (Gabucio et al., 2014). Animal bone was modified into denticulated artefacts sporadically.

Chert (flint) artefacts were knapped by different reduction sequences, and both spatial and vertical differentiation of their forms have been analyzed combined with refitting, use-wear, and comparative experimental studies. Denticulated chert artefacts abound in level J, used probably for processing carcasses and hide. Several were made by discoidal reduction, often away from the excavated area according to spatial analysis of refitting studies. Characterization of chert artefacts and geometrical morphometric indicators of the varying incidences of hierarchical recurrent centripetal ("Levallois") and discoidal centripetal reduction sequences between levels O and M imply changing frequencies of visits to bring chert from outcrops >25 km from Romaní vis-à-vis nearer ones (Chacón et al., 2013; Fernández-Laso et al., 2011; Picin and Carbonell, 2016; Picin and Vaquero, 2016; Picin and Weniger, 2013; Picin et al., 2014; Vaquero et al., 2012). Knapped limestone and quartz occur (Chacón et al., 2013; Vaquero et al., 2012) albeit with uneven representation in the sequence.

Foresight and competent organization undoubtedly enabled exploitation of natural resources ~30 km around Romaní, a neighbourhood adequate for human activity during various periods; changing environmental and climatic circumstances imply that Neanderthal behaviour was adaptable enough to cope sometimes with harsh conditions rather than succumbing to them. Suggestive circumstantial evidence of Neanderthal versatility with regard to local resources comes from the site with layers from MIS-5, MIS-4 and MIS-3 which is the Gruta da Oliveira in the Almonda karst near Torres Novas in Portugal (outside our geographical purview: see Foreword) where analysis of strontium in Neanderthal dental enamel implies six different strontium-isotope catchments in the surrounding landscape (Pike et al., 2016). As with several Late Pleistocene Middle Palaeolithic sites in western Europe, suitability of Abric Romaní was recognized later on by early Upper Palaeolithic hunter-gatherers. Many cognitive aspects of land-use were common to Neanderthals and their skeletally-“modern” successors; it therefore is unsurprising that Neanderthals came and went, and came again perhaps after several generations of absence.

This issue is sometimes related to technological innovation. Kahlke et al. (2011) argue that unstable environmental conditions would have facilitated the development of subsistence strategies. Innovation would have been prompted by the highest rates of environmental change, which may be seen both in Neanderthals and our species. In more recent periods, this pattern is visible. After examining the distribution of Middle to Upper Palaeolithic transitional industries across Europe from 45 to 30 ka, Finlayson and Carrión (2006, 2007) correlated the archaeological location with the presence of sharp physiographical boundaries, suggesting that these industries, made by both Neanderthals and AMHs, were independent responses to rapid climatic changes.

3.18. *Cova de les Teixoneres*

The Cova de les Teixoneres near Moià, at 760 m asl and 40 km inland from Barcelona, is a part of the Coves del Toll cave system from which Mousterian artefacts and a few Neanderthal remains come from sediments dating from MIS-5 to MIS-3 (Rosell et al., 2014). Early excavations at Toll produced finds of bear, hyaena, horse, deer and aurochs in sediments dating from ~0.07–0.06 Ma, though deep levels may be as old as MIS-5. At Teixoneres unit III dates from ~0.051 to ~0.04 Ma, whilst later (unit II) deposits may be as late as 0.03 Ma (Talamo et al., 2016); unit III lies above calcrete dating from ~0.1–0.09 Ma. Faunal, environmental, and archaeological analyses at Teixoneres point to cold conditions in MIS-3 when predation on ruminants and small game by carnivores with dens inside the cave was interrupted by sporadic Neanderthal presence at the front of the cave (Rosell et al., 2010, 2017; Rufà et al., 2014, 2016a,b; Sánchez-Hernández et al., 2014). The carnivores are bear, hyaena, porcupine, wolf, lynx, cat, fox, and badger; among the larger herbivores are rhinoceros, horse, aurochs, red and roe deer, wild goat, and boar.

3.19. *Sima de las Palomas*

During at least two different times Neanderthals were present at Sima de las Palomas del Cabezo Gordo, discovered in 1991 near Torre Pacheco in Murcia, Spain, 125 m asl and 6 km from the Mediterranean Mar Menor lagoon (Trinkaus and Walker, 2017; Walker et al., 2012). Burnt bone abounds, especially of rhinoceros, ruminants, herbivores, lagomorphs, and tortoise, in levels dated by OSL to 0.13–0.1 Ma (Walker et al., 2017) that provided Mousterian artefacts and Neanderthal teeth and a mandibular ramus. Carnivores are infrequent and include hyaena, wolf and porcupine. Those levels were sealed by a solid conglomerate band dated by U-ser to 0.068–0.065 Ma (Walker et al., 2017). Above it, there lay three articulated Neanderthal skeletons dated to ~0.055–0.05 Ma by U-ser and OSL (Trinkaus and Walker, 2017). A woman and child had flexed elbows with hands at their faces (for which Mousterian analogies exist from France to Israel: Defleur, 1993), a post mortem situation before rigor mortis developed; two articulated leopard paws, horse astragali, and chert artefacts lay beside them. All became covered by large stones (intentionally, for deterring scavenging animals?) partly cemented by $CaCO_3$ and surrounded by a combustion feature and higher sediments (that accumulated probably ~0.045–0.04 Ma) containing skeletal fragments of other Neanderthals (Walker et al., 2008, 2010a) and Mousterian artefacts. There is a minimum number of 15 Neanderthal individuals represented by bones and teeth from Sima de las Palomas. Small adult stature (Trinkaus and Walker, 2017; Walker et al., 2011a,b) may imply local genetic drift. Carious lesions (Walker et al., 2010b) and phytoliths extracted from dental calculus suggest a Neanderthal dietary plant component (Power et al., 2018). Artefacts were knapped on chert, marble, limestone, quartz and quartzite. Raw materials are mostly local although one outcrop of chert knapped lies 30 km away. Smooth subspherical river cobbles, the size of tennis balls, were carried up to the site from alluvia in the plain below (nowadays concealed by extensive orchards). This littoral platform joined to the adjacent mountains is outstanding palaeobotanically and may well have been one of the most important woody angiosperm nuclei of the European Pleistocene refugia (Jalut et al., 2006). The pollen record from Sima de las Palomas includes an extraordinary diversity of trees (*Quercus, Pinus, Corylus, Betula, Fraxinus, Arbutus, Salix, Olea*) and shrubs (*Hedera, Buxus, Erica, Rhamnus, Pistacia, Phillyrea*), together with North African hyperthermophilous relics (*Periploca, Withania, Maytenus, Myrtus*) (Carrión, 2002; Carrión et al., 2003; González-Sampériz et al., 2010; Yll and Carrión 2003).

3.20. *Pigments and engravings: Cueva de los Aviones, Cueva Antón, Grotta Fumane and Gorham's Cave*

Barely 30 km from Sima de las Palomas the sea-side Cueva de los Aviones at Cartagena afforded a Mousterian assemblage below flowstone dated by U-ser determinations to ~0.117–0.115 Ma (Hoffmann et al., 2018b). It contained perforated valves of *Acanthocardia* and *Glycymeris* (Montes Bernárdez, 1989), to one of which red haematite residues adhered, and also to the inside of a *Spondylus* shell fragment there adhered ground hamaetite and pyrite in a red lepidocrocite base (Zilhão et al., 2010). 100 km inland, at Cueva de Antón near Mula, traces of pigment were identified on the inside of a perforated *Pecten* shell fragment from the Mousterian assemblage (Zilhão et al., 2010). A fossil sea-shell with adherent pigment was identified in the ~ 0.044 Ma Mousterian assemblage at Grotta Fumane in northern Italy (Peresani et al., 2013). Dates of ~0.065–0.067 Ma have been obtained from carbonate crusts covering pigment at the Spanish caves of Ardales in Málaga, Maltravieso in Extremadura and La Pasiega in Cantabria (Hoffmann et al., 2018a), though further dating research on them may be in order (Pearce and Bonneau, 2018). An engraving ascribed to the Mousterian at Gorham's Cave, Gibraltar, seems to be older than 0.039 Ma (Rodríguez-Vidal et al., 2014) but as it has not been shown definitely to be older than 0.05 Ma, it falls outside the scope of this review.

3.21. *El Salt*

Somewhat further north, the El Salt rock shelter, at Alcoi in Alicante, 600 m above and 35 km from the Spanish Mediterranean shore, contained a series of 54 combustion features, with burnt pine wood, which is later than ~0.08 Ma and spans ~0.067, ~0.052,

~0.047 and ~0.045 Ma according to U-ser, TL and OSL determinations (Galván et al., 2014). Excavation has provided Neanderthal remains and a fauna of horse, ass, ibex, red deer, aurochs, tortoise and rabbit. Use-wear study of Mousterian artefacts implies a range of activities from working on animal materials to plants or wood (Rodríguez Rodríguez et al., 2002).

3.22. *Cova Negra de Bellús*

Slightly further north still, known since 1866 (Vilanova y Piera, 1893) Cova Negra de Bellús lies beside the River Albaida near Xàtiva, 30 km from the Valencian coastline in Spain. Excavations in the 1920's (Viñes Masip, 1929, 1930; Viñes et al., 1942, 1947) and 1940's (Jordá Cerdá, 1946, 1953) have necessitated revision following later research (Villaverde, 1984, 2001; Villaverde et al., 1996, 2014). This implies 6 phases, from phase A (level XV) dated by TL to ~0.117 Ma (MIS-5) through Middle Palaeolithic levels followed in phase F by Upper Palaeolithic deposits. After roof-collapse in phase A, sediments with human impingement and late Middle Pleistocene micromammals imply phase B climatic cooling (levels XIV-XIII) persisting with seasonal humidity in phase C dated by TL to ~0.107 and ~0.096 Ma. Phase D was a cold period with oscillating humidity and temperature, perhaps MIS-4 (if 3 TL estimates be discounted of 0.25–0.2 Ma on burnt chert from levels XI-V). Phase E (level IV) has TL determinations ~0.05 Ma. Phase F has typically MIS-3 and MIS-2 micromammals in levels III-I that contained a palimpsest of combustion features. Riverine gallery woodland existed even when open landscape prevailed where horses thrived, judging from their abundance in level VI. In levels IV-V cervids are common and in III-II tahr and ibex are significant. Red, fallow and roe deer occurred during several phases; other species include aurochs, boar, steppe rhino, elephant, macaque, lion, leopard, hyaena, bear, wolf, and dhole (Martínez Valle, 2001b; Pérez Ripoll, 1977), significant occurrence of rabbit, hare and beaver, 15 bat species (suggesting sporadical rather than continuous human presence), and 33 bird species (Martínez Valle et al., 2016). Tortoise (*Testudo hermanni*) is common (Morales and Sanchis, 2009). There are 26 human cranial and postcranial remains from early as well as late phases (Arsuaga et al., 1989, 2001a,b,c; Fusté Ara, 1953). Chert (flint), quartz and limestone were knapped variably. Discoidal reduction and "Quina" secondary knapping are present in phases A, C, and D; hierarchical ("Levallois") preparation is conspicuous in phases B, late D, E, and early F.

3.23. *La Niche and Coupe-Gorge*

On the French side of the Pyrenees, the La Niche fissure (diaclase) descending beside the Coupe-Gorge cave, together comprising a karst erosive system overlooking the Seygouade tributary of the River Save, 330–350 m asl, near Montmaurin in the Pyrenean Garonne basin, 75 km southwest of Toulouse, human fossils (Baylac et al., 1950; Billy, 1982, 1985; Billy and Vallois, 1977; Cammas and Tavoso, 1986; Méroc, 1963, 1969; Mounier et al., 2009; Vallois, 1955, 1956; Vialet et al., 2017, 2018) of the *Homo heidelbergensis-Homo neanderthalensis* lineage accompanied MIS-7 fauna with appropriate palynology (Cammas and Tavoso, 1986; Crégut-Bonnoure et al., 2010; Girard and Renault-Miskovsky, 1983; Renault-Miskovsky and Girard, 1998) and Palaeolithic artefacts. At La Niche, calcrete flowstone covered 2 m of (probably MIS-6) sediment containing reindeer, steppe rhinoceros, giant, red and fallow deer, chamois, bison, aurochs, horse and ass. The lowest 4.5 m of (perhaps late MIS-7) sediments afforded rhinoceros and other herbivores (including 3 cut-marked horse and aurochs bones), carnivores (bear, lion, leopard, wild cat, wolf, dhole, badger and fox), marmot, and human and Palaeolithic remains.

Coupe-Gorge bed 3 contained an MIS-7/MIS-6 fauna (including tahr *Hemitragus bonali*: Guadelli, 1990), and from its lower part 463 secondarily-knapped artefacts ("pre-Mousterian" side-scrapers, denticulate and notched pieces, and "Levallois", "pseudo-Levallois" and other points) were classified by Gaillard (1982) among 3000 flakes (~2% produced by hierarchical "Levallois" reduction) including numerous "micro-flakes", of chert (flint), lydite, quartz and schist (Gaillard, 1983). Upper bed 3 provided a score of pebble tools and small, bifacially-flaked, quartzite hand-axes (Gaillard, 1982, 1983) lacking the tapered shape of "Micoquian" bifaces to which Méroc (1963, 1969) compared them. Bed 3 pollen implies late MIS-6 and perhaps early MIS-5 (Girard and Renault-Miskovsky, 1983; Renault-Miskovsky and Girard, 1998). Higher beds contained Upper Palaeolithic (Aurignacian) artefacts and last ice-age fauna. Palynology (Renault-Miskovsky and Girard, 1998) assigns the La Niche and Coupe-Gorge "Mousteroid" ("*moustéroïde*") deposits, respectively, to a late "Riss" open environment and "Riss-Würm" wooded landscapes, and Coupe-Gorge "Micoquian" ("*micoquien*") deposits to "Würm I" woodland conditions ("Würm I" implies MIS-5d,-5c,-5b,-5a, spanning ~0.114 - ~>0.0755 Ma: cf., Dahl-Jensen et al., 2013; Mogensen, 2009; Rasmussen et al., 2014).

3.24. *Grotte Boule and La Terrasse*

Immediately above Coupe-Gorge lie the Grotte Boule (Grotte Montmaurin) fossiliferous breccia and La Terrasse sediments. Grotte Boule pollen demonstrates mild environmental circumstances with Scots and maritime pines, *Picea* (spruce), *Larix* (larch), several species of deciduous trees and shrubs, including *Ligustrum* (privet), *Rhamnus* (buckthorn) and *Vitis* (vine), though a decline in spruce and increase in grasses and ferns suggests late MIS-7 (Renault-Miskovsky and Girard, 1998). Mammals include horse, bovines, cervines, hyaena, a homotherine ("*Machairodus latidens*"), lion, leopard, bear (Boule, 1902; de Saint-Perier, 1922; Méroc, 1948) and steppe rhinoceros (Guérin, 1980, who demolished claims for Merck's rhinoceros). Made from quartzite (>75%), lydite and chert or flint (5–15%), and quartz (<2%), 6500 small artefacts lack signs of hierarchical ("Levallois") flake-removal. They included 81 side-scrapers, numerous denticulate and notched pieces, a few "Tayac" points, slugs and awls, a graver and a push-plane (Serra-Joulin, 2002). Apart from being mainly of quartzite La Terrasse small artefacts otherwise resemble Coupe-Gorge bed 3 (Serra-Joulin, 2002; Tavoso, 1976). Sediment with hyaenid coprolites was followed by upper La Terrasse deposits containing quartzite cleavers and hand-axes larger than Coupe-Gorge bifaces (Serra-Joulin, 2002). La Terrasse sediments belong either to MIS-7 or an MIS-6 interstadial (Serra-Joulin, 2002). Whereas Méroc believed collapse of some La Terrasse deposits filled La Niche below it, taphonomical and sedimentological considerations imply La Niche was a carnivore den visited sometimes by humans (Crégut-Bonnoure et al., 2010; Tavoso et al., 1990).

4. The distant background, 0.9–0.3 Ma

4.1. *Caune de l'Arago and remarks on the ecology and technology of pre-Neanderthals*

The Caune de l'Arago rock-shelter, overlooks the River Verdouble at the exit of the Gouleyrous Gorges near Tautavel 20 km north of Perpignan, 190 m above the level of the Mediterranean Sea 25 km away, and 50 km north of the Pyrenees. It contains sediments 16 m deep. Radiometrical dating (de Lumley, 2014, 2015a) indicates that high deposits of ~0.1–~0.35 Ma overlay remarkable palaeoanthropological, palaeontological and Palaeolithic assemblages in sediments that accumulated above a 0.69 Ma stalagmitic formation

(Falguères et al., 2004). The highest sediments contained carnivore and herbivore assemblages implying a sequence of temperate MIS-5,-7,-9 and -11 deposits (Moigne et al., 2006), with stratigraphical hiatuses, and sparse palaeontological (or other) testimony, corresponding to MIS-6,-8 and -10 cold stadia; palynology suggests alternating cold dry and temperate moist conditions (Renault-Miskovsky, 1976). MIS-12, -13,-14, and −15 (levels D-Q) are well represented. A human incisor comes from level Q dated by ^{26}Al/^{10}Be to ~0.565–0.525 Ma (Chevalier et al., 2015), and impressive pre-Neanderthal (*Homo heidelbergensis*) cranial, mandibular and post-cranial remains come from MIS-13 - MIS-12 (especially level G, early in MIS-12) sediments dating from ~0.52 to ~0.4 Ma (de Lumley, 1971a, 1975; de Lumley and de Lumley, 1974, 1982; de Lumley et al., 1976b; de Lumley, 1976a).

Spanning ~0.2/0.25 - ~0.4/0.45 Ma, levels D-G provided >5000 secondarily-knapped artefacts, 18,000 flakes, ~600 pebble tools, and 21 bifacial items conspicuously absent from uppermost D (late MIS-12) where small quartz and chert (flint) artefacts predominated (Barsky, 2013). Caune de l'Arago has yielded up > 100,000 artefacts. There are 75 bifacially-flaked large cutting tools or hand-axes, distributed unequally in levels D-Q, some containing none or only one. Level P (MIS-14) provided 31, as well as 420 secondarily-knapped small artefacts, including keeled pieces, and 4500 flakes of various sizes (Barsky, 2013; Barsky and de Lumley, 2010). Much knapping took place on site. Initially, terms such as “Tayacian”, “proto-Charentian”, and “proto-Quina” were applied (de Lumley, 1971b). “Tayacian” is a concept viewed askance nowadays (Chase et al., 2009; Dibble et al., 2006), and anyhow was applied usually to asemblages without bifaces. Nevertheless, it has long been mooted that the roots of French Mousterian tool-kits lie in the Middle Pleistocene (Bordes, 1953, 1961, 1973; Bordes and Bourgon, 1951; Bourgon, 1957; de Lumley, 1969a, 1971b, 1975, 1976c), and terms such as “proto-Levalloisian”, “proto-Mousterian”, “pre-Mousterian” and “Mousteroid” recur in French (and European) articles. Caune de l'Arago provides evidence of hierarchical recurrent removal of flakes by centripetal knapping of discoidal cores, including instances from level F (MIS-12) of prepared striking platforms “comparable to recurrent Levallois conception” (Barsky, 2013). Knappers worked on chert (flint), quartz, quartzite, limestone, quartzose sandstone, and hornfels; one source of flint lies 30 km away from the site (Grégoire et al., 2007).

Middle Pleistocene fauna prevailed at Caune de l'Arago (Crégut, 1979, 1980; de Lumley, 1976b; Hanquet and Desclaux, 2011; Montuire and Desclaux, 1997a,b; Pernaud, 1990). During the intensely cold MIS-12 (~0.475–0.425 Ma) steppe rhinoceros (*Stephanorhinus hemitoechus*), horse (*Equus ferus mosbachensis*), bison (*Bison schoetensacki*), and tahr (*Hemitragus bonali*) were accompanied (in contrast to peninsular Italy or Mediterranean Spain) by musk ox (*Praeovibos priscus*), argali (*Ovis ammon antiqua*), reindeer (*Rangifer tarandus*), chamois (*Rupicapra* aff. *pyrenaica*), and steppe pika (*Ochotona pusilla*) (Moigne et al., 2006). In deep levels H-J red and fallow deer (*Cervus elaphus*, *Dama clactoniana*) reflect MIS-13 temperate conditions, following levels K-Q when humans and canids impinged sporadically on lairs of felid carnivores and hibernating bears, vying with them for prey - reindeer and argali - in a cool, open landscape interspersed with gallery woodland during MIS-14 (~0.56–0.535 Ma) which probably was less extreme than MIS-16 (~0.675–0.625 Ma) when severe cooling worldwide, inferred from marine cores (Lisiecki and Raymo, 2005), impelled biogeographical fluctuations. Nevertheless, carnivores and several taxa of large herbivores underwent less change during MIS-14,-13,-12 at the site. Maybe some, perhaps reindeer, had greater environmental tolerance than later on (Lister, 1990; cf., Van der Made, 2015); alternatively, reindeer body parts could either have been brought from afar within a wide exploitation territory or reflect migratory herds (Lister, 1990).

Was *Homo heidelbergensis* a generalist? Undoubtedly the cave was used differently at different times (a putative erstwhile structure within it was claimed: de Lumley and Boone, 1976), sometimes inhabited seasonally, and at others visited sporadically, according to inferences drawn from the Palaeolithic remains and differential palaeontological and taphonomical aspects of the abundant fauna on which both humans and carnivores preyed. Noteworthy remains in levels F, G, J, and L of large herbivores with signs of human impingement imply indiscriminate opportunistic capture undertaken in diverse biotopes, perhaps seasonally (Moigne, 1983; Moigne et al., 2005; Rivals, 2002; Rivals et al., 2003, 2004, 2006, 2009), though some cotemporaneous large ungulates are poorly represented or lacking (e.g. hippopotamus).

Kahlke et al. (2011) combine a large spatial scale with a community-level approach to present an impressive mammal record of 221 key sites and provide a chronicle of the changes recorded in western Palaearctic habitat diversity between 2.6 and 0.4 Ma. The time span between 0.9 and 0.4 Ma shows long climatic cycles (100 ka periodicity) and the cyclic replacement of forested landscapes by open landscapes. In contrast, the period from 1.2 to 0.9 Ma is one of increased climatic and habitat instability. Mammal communities responded to these environmental changes, and humans were not an exception.

How should we regard the presence of bifacially-flaked large cutting tools among small secondarily-knapped artefacts at Caune de l'Arago, Cueva del Ángel, or Orgnac 3? Those assemblages differ significantly in composition from those of Saint-Acheul, Abbeville, Swanscombe or Boxgrove, not to mention Olduvai where Mary Leakey (1975) took note that Kleindienst (1962) had favoured reserving “Acheulian” for assemblages where >50% of artefacts are bifacially-flaked hand-axes or cleavers. A different approach gives pride of place to technical and cognitive aspects of bifacially-flaked large cutting tools (Manrique and Walker, 2017; Nicoud, 2013; Shea, 2013, 2017a; Wynn, 1989, 1995, 2002). Nicoud (2013) considers that whereas tools with a wide angle (≥60°) along the edge between the opposing flake-scars of a large biface were fashioned mostly by flaking along the edges of thinnish cobbles of appropriate shape for reduction to almond-shape hand-axes or tranchet-ended cleavers, many tools with a narrowly angled edge (≤50°) had required a longer manual procedure in order to reduce stone blocks or large flakes and then rough them out prior to flaking the opposing surfaces alternately in order to prepare a “techno-functional unit”. The latter group implies cognitive awareness of the conceptual possibilities of a range of raw materials, suggesting a pre-planned strategy requiring tactically-differentiated manual procedures (cf., Boëda, 1991a). Conceivably, the limitations of the first group stimulated development of the second. However, just as pebble tools and chopping tools occur in assemblages throughout the Middle Pleistocene (and later), it is no less plausible that the first group includes expedient artefacts quickly made by people who knapped the second group. In line with this conjecture is a well-fashioned, thin, quartzite hand-axe with signs of soft-hammer treatment of its edges (Barsky, 2013), excavated in level P (below which, early MIS-14 level Q is dated by ^{26}Al/^{10}Be to ~0.565–0.525 Ma: Chevalier et al., 2015). Therefore it seems that skilfully executed hand-axes made with care and attention were being made by 0.5 Ma in Europe (just as they were in Africa). Several Caune de l'Arago bifaces fashioned on small river pebbles have wide-angled edges, perhaps because unpromising blanks were not flaked intensively. Availability of raw materials capable of being flaked or knapped undoubtedly influenced Palaeolithic assemblage composition throughout Western Mediterranean Europe and perhaps underlies the widespread presence of small artefacts and their predominance at many sites.

4.2. Atapuerca: Sima de los Huesos, and Trincheras Dolina and Galería

South of the Pyrenees, Sima de los Huesos, in the Sierra de Atapuerca at ~1100 m above sea level in northern Spain, near the upper reaches of the Ebro which feeds the Mediterranean, has provided impressive remains of >30 individuals, dated to 0.43 Ma (Arnold et al., 2014), belonging to a *Homo heidelbergensis* "pre-Neanderthal" clade, probably a sister group to subsequent Neanderthals (Arsuaga et al., 2014) if not an early form of *Homo neanderthalensis* (Stringer, 2012). Indeed, Neanderthal nuclear DNA is present at Sima de los Huesos (Meyer et al., 2016), but it is somewhat puzzling that a "Denisovan" form of mitochondrial DNA is present (Meyer et al., 2013) which may have disappeared by chance during subsequent evolution of the Neanderthal lineage which left it with only the modern human variant or into which the latter introgressed (cf. Posth et al., 2017). Genetic analysis of a Neanderthal bone from the Siberian Denisova Cave (Prüfer et al., 2014) imples an evolutionary trajectory for mitochondrial DNA in *Homo* characterized by a split ~0.8 Ma between a lineage shared by humans alive today and a lineage at first common to "Denisovans" and pre-Neanderthals that itself underwent a split before ~0.5 Ma. Another possibility is that positive natural selection might have led to fixation of genes in the modern human lineage *after* the "Denisovan" and Neanderthal lineages had separated (Peyrégne et al., 2017), and their possible incorporation into Neanderthals by hybrid introgression. The matter is complicated by both the paucity of fossil specimens available for analysis and their diverse spatiotemporal contexts.

Morphological considerations suggest that the Atapuerca Trinchera Dolina *Homo antecessor* from ~0.9–0.8 Ma in layer TD6 (see below) is phylogenetically close to common ancestors of Neanderthals and modern humans (Arsuaga et al., 1999, 2001d; Bermúdez de Castro and Martinón-Torres, 2013; Bermúdez de Castro et al., 1997, 2013; 2017; Dennell et al., 2011). Latitudinal genetic influences on dental morphology in Pleistocene Europe could have been at least as significant as those from African early *Homo* (Martinón-Torres et al., 2007); moreover, Eurasian large mammals played a larger part than African ones in the European Mid-Pleistocene transitional faunal turnover (Van der Made, 2011). Empirical findings that early *Homo* skulls underwent morphological change at a different evolutionary rate from that of their teeth carry an implication that the Sima de los Huesos lineage had begun $\geq$0.7 Ma (Gómez-Robles, 2017; cf., Gómez-Robles et al., 2013, 2015, 2017). That is in line with wider considerations based on human population genetics implying that Neanderthal lineages extend back to ~0.75 Ma (Rogers et al., 2017). An accretionary process likely underpinned "mosaic" evolution in western Eurasian Neanderthals which is favoured by the Atapuerca researchers.

The foregoing matters impinge on competing opinions about relationships conjectured to exist between early Neanderthals in mid-Middle Pleistocene Western Europe and African sources of such Palaeolithic artefacts (cf., Foley and Lahr, 1997; Villa et al., 2009, 2016; White et al., 2016) as bifacially-flaked large "Acheulian" cutting tools or secondarily-knapped small artefacts removed by hierarchical "Levallois" preparation of cores, and putative African immigrants (e.g. *Homo rhodesiensis*: Hublin, 2009; *Homo helmei*: Foley and Lahr, 1997). Were pre-Neanderthals, few in number ~0.75 Ma, to have burgeoned later on and spawned dispersed breeding isolates, then genomic diversity could have developed (Rogers et al., 2017). They would dispense with a need to conjure up African immigrants arriving by ~0.27 Ma in order to interpret the noteworthy diversity of Neanderthal mitochondrial DNA implied by analysis of a ~0.124 Ma femur from Germany (Posth et al., 2017). The background to Neanderthal presence in western Europe requires meticulous attention be paid to evidence from the long time-span that began with the palaeoecological and palaeoclimatological transition from the Early to the Middle Pleistocene straddling the palaeomagnetic change ~0.78 Ma from the Matuyama reverse polarity chron to the Brunhes normal polarity chron.

A lone quartzite hand-axe found with the Sima de los Huesos human remains inspired conjectural ascription to it of a "symbolic" rôle (Carbonell and Mosquera, 2006). Young men predominated, maybe hinting at a calamity following adverse change in environmental circumstances (Bocquet-Appel and Arsuaga, 1999), perhaps implying a local demographical crisis (for an alternative interpretation, see Rabadà I Vives, 2017). At the nearby Trinchera Galería site a few *H. heidelbergensis* fossils, some bifacially-flaked large cutting tools on quartzite and chert, and many small secondarily-knapped artefacts come from deep levels of ~0.4 - ~0.2 Ma (Falguères et al., 2001), resembling assemblages from the deepest part of high level 10 at the adjacent Trinchera Dolina. 35,000 artefacts from level 10 (~0.4 - ~0.3 Ma) include instances of hierarchical knapping of prepared "Levallois" cores for repetitive removal of flakes and secondarily-knapped "pre-Mousterian" artefacts (scrapers, denticulates and points). The deep parts of level TD10 and Galería seem to be contemporary with Sima de los Huesos. The deep Galería IIa deposits of ~0.5 Ma contain Acheulian bifacial artefacts (García-Medrano et al., 2014). A bifacial hand-axe was excavated in Sima de los Huesos. Galería and TD10 have abundant faunal remains. A higher part of TD10 has a noteworthy presence of bison and chert (flint) artefacts. Faunal and taphonomical analyses of the highest part (TD10-1, ~0.34–0.3 Ma, MIS-9) demonstrate a wide range of taxa, especially horse, red deer, bison, and Leporids, including cut-marked lagomorph bones (Blasco et al., 2013a). It is argued that human groups can "select those resources that they consider suitable from a range of resources available in the landscape" (Blasco et al., 2013a) implying "high plasticity in their methods and techniques to obtain resources and in the use of a wide spectrum of prey" (Blasco et al., 2013a), bearing in mind that they "can develop different subsistence strategies in the same environment depending on behavioural variables, which are difficult to control archaeologically" (Blasco et al., 2013a).

The pre-Neanderthal background before the 0.43 Ma Sima de los Huesos assemblage is somewhat unclear. Atapuerca Trinchera Dolina TD10 lacks the relict Arctotertiary plants (Araliaceae, *Cathaya, Elaeagnus, Engelhardia, Eucommia, Liquidambar, Keteleeria, Nyssa, Sciadopitys, Symplocos, Parrotia, Parthenocissus, Pterocarya* and *Tsuga*) (Postigo et al., 2009) which had lingered on in TD8 of ~0.7 - ~0.6 Ma (below TD8 the ~0.78 Ma Matuyama-Brunhes palaeomagnetic boundary exists in TD7). Later, between 0.8 and 0.6 Ma, others like Mimosaceae, *Carya* and *Ostrya* became extinct (Rodríguez Gómez et al., 2013), involving changes in the ecomorphology of the Iberian forests (Carrión et al., 2013). Clearly, in the Iberian context the Mid-Pleistocene Transition (MPT) period from 1.4 to 0.7 Ma, is within the last 65 Ma, the period with the highest rates of phytodiversity-loss, even higher than rates measured for the Oligocene and Miocene biodiversity crises (Carrión and Fernández, 2009). The relationships between the human fossil record in Atapuerca and the chronology and environmental changes associated with the extinction of plants in western Palaearctic, is an issue that deserves future research.

TD8 lacks traces of human activity but has early Middle Pleistocene herbivores *Equus altidens*, *Stephanorhinus* aff. *etruscus*, *Hippopotamus* sp. (cf. *tiberinus/georgicus*), *Bison voigtstedtensis*, *Eucladoceros* aff. *giulii*, *Megaceroides solilhacus*, *Dama vallonnetensis*, and *Cervus elaphus. Hyaena* now took its place alongside *Crocuta* and *Pachycrocuta*, (and at 0.43 Ma lion, wolf and dhole appeared at Sima de los Huesos), maybe in response to growing biodiversity during the prolonged faunal turnover ("Mid-Pleistocene Transition") between ~1.2 and ~0.5 Ma when 10 faunal stages involved appearance of 36 taxa by dispersal, 10 by continuous evolution, and 22 extinctions (Van der Made et al., 2017). By ~0.6 Ma Atapuerca faunal unit FU6 has a Middle Pleistocene profile that could imply an evolutionary outcome within a fairly stable environment (Rodríguez-Gómez et al., 2013). The TD8 fauna reflects both open country and (particularly small mammals, amphibians and squamate reptiles) woodlands (Rodríguez-Gómez et al., 2013). Climates both cold and mild permitted faunal change; thus Van der Made et al. (2017): "Either the cold stages before stage 16 did not lead to the spread into mid-latitude Europe of species that we recognize as "glacial", or these periods are poorly represented in the fossil record … While the first dispersals of cold adapted species can be explained by colder or longer cold periods, it is less clear, why new species adapted to temperate or warm climates did not survive in the refugia in southern Europe (e.g. *Stephanorhinus etruscus*), or why new species adapted to such climates appeared (e.g. *Cervus elaphus*)."

Some taxa in temperate landscapes may have adapted later on to cold ones; perhaps musk oxen, given *Praeovibos* remains in TD7 (Rodríguez Gómez et al., 2013; Van der Made et al., 2017). Palombo (2010) considered that "during the Middle Pleistocene, increasingly different habitats supported increasingly varied faunas … with new dynamic interspecific relationships. Accordingly, across the northwestern Mediterranean region a new scenario developed, which allowed, at around 600 ka, fully documented, human settlements"; extinction of some taxa was followed by dispersal of others from central or eastern Europe, southwards first, and then gradually westwards (Palombo and Valli, 2005). Carnivore responsibility for the TD8 deposits could reflect erstwhile physical restrictions on bipedal entry to the cave though also an increase in predatory taxa responding to growing faunal biodiversity could have detracted from human exploitation of landscapes where those taxa flourished (Rodríguez-Gómez et al., 2013, 2016b).

4.3. Final Early Pleistocene in Mediterranean Spain

The former matter is interesting because of noteworthy human (*Homo antecessor*) presence in the deeper TD6 level ~0.9–0.8 Ma. From that late Early Pleistocene time bifacially-flaked artefacts (Shea's mode E) (Table 2) are known in Mediterranean Spain. They are a cleaver on schist from El Forn unit II in the Barranc de la Boella at La Canonja near the Mediterranean sea-port of Tarragona, dated by ^{26}Al/^{10}Be to 1.07–0.87 Ma, in line with magnetostratigraphy and palaeontological findings (Vallverdú et al., 2014b), and a hand-axe on limestone from Cueva Negra del Estrecho del Río Quípar in the River Segura basin, at 740 m asl (75 km north of the Mediterranean coast) near Caravaca de la Cruz in Murcia, dated to <0.99 - >0.78 Ma by magnetostratigraphy and biochronology (especially Arvicoline rodents), plausibly MIS-21, 0.865–0.815 Ma (Scott and Gibert, 2009; Walker et al., 2013, 2016a). Small secondarily-knapped artefacts from Cueva Negra resemble those (Barsky et al., 2013; Martínez et al., 2010, 2014) from the 20 m-deep Parc de Vallparadís and Cal Guardiola fluviatile aggradation, at Terrassa near Barcelona (see below), most of which belong to a time between ~1 and ~0.85 Ma (Duval et al., 2011, 2012, 2015), though palaeontological considerations may imply some subsequent accumulation (García et al., 2011, 2012; Madurell-Malapeira et al., 2010, 2012, 2017).

4.4. La Pineta

Small artefacts from both those sites, and also Caune de l'Arago, resemble many of the >10,000 artefacts (mainly chert or flint, others of limestone) from the La Pineta fluviolacustrine sediments of the River Cavaliere in the Volturno basin, 455 above sea level at Isernia in Mosile, Italy. There are no bifacially-flaked hand-axes or cleavers. A deciduous human tooth is dated to ~0.58 Ma by ^{40}Ar/^{39}Ar (Lugli et al., 2017; Peretto et al., 2015). Over 1250 artefacts, palaeontological remains and pollen (Peretto, 1994a, 1996) come from unit 3 bed "t.3a" of ~0.7 - ~0.45 Ma (Accorsi et al., 1996; Peretto, 1994b; Peretto and Terzani, 1994); ^{40}Ar/^{39}Ar dating of sanidine crystals indicates ~0.6 Ma (Coltorti et al., 2000, 2005 and refs. therein) and elephant, rhinoceros and bison teeth gave ESR estimates ~0.55 Ma (previous K/Ar analyses implied $\geq$0.6 Ma). Bed t.3a pollen indicates grassland with stands of trees, followed (perhaps ~0.5 - ~45 Ma) by an open landscape where large ungulates grazed. Below t.3a, >4500 artefacts come from unit 3 bed t.3c. La Pineta has an early Middle Pleistocene fauna of Middle Galerian mammals and the Early Toringian rodent *Arvicola mosbachensis* (Abbazzi and Masini, 1997; Masini and Sala, 2007, 2011; Sala, 1996; Sala and Masini, 2007). Detailed faunal research shows human and carnivore impingement (Anconetani, 1996; Anconetani and Peretto, 1996; Anconetani et al., 1996; Peretto et al., 1996; Thun Hohenstein et al., 2004).

Research highlighted relationships between Palaeolithic knapping techniques and the natural structure of the raw material, backed up by experimental knapping and use-wear detection (Crovetto, 1994 Crovetto et al., 1994a,b,c; Longo, 1994; Minelli et al., 2004; Peretto, 1994a, 1996; Peretto et al., 2004). The studies pointed towards a counter-intuitive inference that some seemingly fashioned cores and keeled slug-like artefacts without use-wear traces, could well have been cores from which micro-flakes (e.g., 0.5–2 cm in size) were removed, and then used, without secondary knapping or retouch. The inference belies widely held notions that early humans habitually used only chunky tools, and that microliths came into use barely 15,000 years ago (though artefacts of "microlithic" size occur also at Orgnac, Coupe Gorge, Bolomor, Fontana Ranuccio, and Cueva Negra del Estrecho del Quípar). Flake-removal was not restricted to blanks with serviceable striking angles. Biconvex or discoidal blanks were the object of longer reduction procedures than those effected unifacially or unidirectionally on other blanks (Minelli et al., 2004). Early studies foussed on bed t.3a artefacts. Core-reduction analysis of 679 bed t.3c artefacts (Gallotti and Peretto, 2015) determined that 350 showed knapping, including 43 secondarily-knapped flakes; flake-removal was by both simple unifacial unidirectional extraction and in longer reduction sequences, by repetitive knapping of small discoidal cores, albeit with scanty platform preparation, though sometimes with secondary knapping of flake edges, particularly on flakes struck from discoidal cores.

La Pineta knappers could select cores of different shapes in relation to anticipated outcomes (e.g., removal of short or long flakes), make technical choices, and control their percussion according to the properties and volumetrical implications of raw materials chosen. It is of great interest from the standpoints of habitual skilfullness and cognitive versatility ~0.6 Ma (in the distant pre-Neanderthal background), that (a) Shea's knapping modes A, B, C, D, and F (Table 2) were practised; (b) flakes struck repetitively from discoidal cores were secondarily knapped often; (c) removal took place of longish flakes from elongated cores; and (d) diminutive flakes sometimes were used that had been struck from steeply-keeled cores.

4.5. Notarchirico

Fluviolacustrine sediments 7 m deep at Notarchirico (Piperno, 1996, 1999a) ~400 m asl in the Venosa basin in Basilicata, 75 km from the Italian Mediterranean coast, afford eleven MIS-16 layers (some separated by sterile sediment) from ~0.67 to ~0.61 Ma, with abundant faunal remains, Palaeolithic artefacts including bifacially-flaked hand-axes, and in high unit 1.4 a *Homo heidelbergensis* femur dated by $^{40}Ar/^{39}Ar$-ESR to ~0.66–0.61 Ma (Pereira et al., 2015). The dates accord with correlation of a unit 2.4 tephra layer 0.2 m-thick with one dated by $^{40}Ar/^{39}Ar$ to ~0.65–0.63 in the Rionero in Vulture subsynthem (Lefèvre et al., 2010; Villa and Buettner, 2009). Nearby Monte Vulture volcanic eruptions deposited ignimbrite in the Venosa basin ~0.86–0.83, ~0.67–0.66, and ~0.5–0.43 Ma according to K/Ar estimates (Cortini, 1975), and $^{40}Ar/^{39}Ar$ analyses of sanidine and phlogopite suggest activity ~0.8 - ~0.73 Ma (Buettner et al., 2003). Volcanic activity has complicated the stratigraphical analysis of Notarchirico (Lefèvre et al., 1994, 2010; Piperno et al., 1998; Raynal et al., 1998), where previously U-ser, TL, and AAR (amino acid racemization) gave estimates of ~0.75, ~0.64, ~0.5, ~0.36, ~0.3 and ~0.23 Ma, and, despite one of ~0.64 Ma (TL) low down in unit 2, those from higher units implied a later time; nor did the fauna look older than at La Pineta (Sala, 1991, 1999), whilst palynology only indicated an open landscape and stands of pine (Sala, 1991), equally appropriate for MIS-14 and MIS-16. It is worth remarking that hand-axes outside our geographical purview (see Foreword) date from ~0.665 Ma at La Noira in the Cher valley of the Loire basin (Moncel et al., 2013).

Notwithstanding a suggestion of butchery, inferred from excavation at the 1.4/1.5 unit interface of an *Elephas* (*Palaeoloxodon*) *antiquus* skull (Cassoli et al., 1993; Piperno, 1999b; Piperno and Tagliacozzo, 2001; Tagliacozzo et al., 1999), open to question is its stratigraphical relationship to maybe slightly earlier finds, made a few metres away, of artefacts from between units 1.1 and underlying 2.10, following which units 1.2 and 1.3 gravels and volcanic components seem to have preceded unit 1.4 (Lefèvre et al., 2010; cf., Nicoud, 2013). Limestone pebble tools, a flint hand-axe, and small retouched notched artefacts (Cassoli et al., 1993; Piperno, 1999b; Piperno and Tagliacozzo, 2001) could support the suggestion of butchery. Some artefacts were “clearly embedded in layer B” (Piperno and Tagliacozzo, 2001) implying unit 2.10. Depositional uncertainty renders “butchery” an insoluble albeit intriguing conjecture (cf., Lefèvre et al., 1994; Raynal et al., 1998). Bifacially-flaked, limestone, quartzite, and chert (or flint) hand-axes (23 in all) occurred throughout, from deep layer F in unit 2.1 to high layer A above unit 1.1 (Pereira et al., 2015; Piperno, 1999a,b). All have widely-angled edges (Nicoud, 2013) though near the elephant skull one flint hand-axe reveals skilful workmanship (Nicoud, 2013), recalling the careful preparation (~0.5 Ma) of a Caune de l’Arago hand-axe mentioned above, perhaps contrastable with the widely-accepted view of a mid-Middle Pleistocene transition (~0.4 - ~0.3 Ma) in Europe from clumsy “early Acheulian” bifaces to elegant “late” ones (sometimes attributed to conjectural African influence). Traces of knapping mark ~1500 of 2450 artefacts from Notarchirico unit 1 and the upper part of unit 2; struck flakes numbering <400 (including a few push-planes) with little secondary knapping (Piperno, 1999a,b). At the nearby Loreto site, archaeological layer A (with early Middle Pleistocene fauna including cut-marked bones, perhaps MIS-15: Mussi, 1995; if not MIS-13: Barral et al., 1978; Baïssas, 1980) provided a hand-axe and many small, secondarily-knapped, chert artefacts (mostly notched and denticulate pieces, with some scrapers and awls), flakes with dihedral or facetted striking platforms, and limestone chopping tools and fractured cobbles (Crovetto, 1991, 1993).

4.6. Fontana Ranuccio

The Palaeolithic and Middle Pleistocene finds from Fontana Ranuccio (Biddittu, 1993; Bidditto and Segre, 1984; Muttoni et al., 2009; Segre and Ascenzi, 1984), in the Sacco-Liri valley system at Anagni near Frosinone, ~235 m asl and 20 km from the Tyrrhenian coast of central Italy, come from layer 6, dated to ~0.46 Ma by K/Ar determination on inclusions of volcanic ejecta from the Vulcano Laziale (Colli Albani) 28 km away. 60 m^2 of layer 6 were uncovered and >6000 m^3 of sediment sieved. Middle Pleistocene fauna appropriate for an landscape with woodlsnand wetlands included *Elephas* (*Palaeoloxodon*) *antiquus*, *Stephanorhinus hemitoechus*, *Hippopotamus amphibius*, *Equus* cf. *mosbachensis*, *Dama clactoniana*, *Megaloceros* cf. *verticornis*, *Cervus elaphus*, *Capreolus capreolus*, *Panthera leo*, *Ursus deningeri*, *Cuon* cf. *alpinus*, *Bos primigenius*, *Bison* sp., *Sus scrofa*, *Macaca florentinus*, *Lepus capensis*, *Anser fabalis*, *Anas penelope*, and *Anas acuta* (Cassoli and Segre Naldini, 1993a,b; Segre and Ascenzi, 1984). Wood fragments were found (Cassoli and Segre Naldini, 1993a). There are 4 *Homo heidelbergensis* teeth (Ascenzi, 1993; Ascenzi and Segre, 1996; Segre and Ascenzi, 1984; Rubini et al., 2014). Chert (flint) artefacts include 5 hand-axes, a chopping tool, centripetally-flaked core, and 75 small (1–4 cm in size) secondarily-knapped discoidal, slug-like, notched, denticulate, and “scraper” artefacts, including one piece with secondary knapping on two surfaces (Biddittu, 1993; Segre and Ascenzi, 1984) that correspond to Shea's modes A, B, C, D, E and F. Lava artefacts were reported. Bifacially-flaked elephant and aurochs bone artefacts (Biddittu, 1993) have analogies from Torre in Pietra, Malagrotta, Castel di Guido, Ceprano, and Bilzingsleben (Segre and Ascenzi, 1984), as well as La Polledrara di Cecanibbio and Rebibbia-Casal de’ Pazzi (Anzidei, 2001; Anzidei et al., 2004; Villa et al., 1999).

4.7. Ceprano, Petralona, and Aroeira

Barely 30 km south-east from Fontana Ranuccio and 30 from the Tyrrhenian Sea, the robust Ceprano calvaria, formerly compared to *Homo erectus* and regarded as a late Early or initial Middle Pleistocene fossil, came from sediment dated to ~0.353 Ma by $^{40}Ar/^{39}Ar$ (Nomade et al., 2011) which also gave a 0.45 Ma K/Ar estimate (Muttoni et al., 2009); the calvaria probably belonged to a robust *H. heidelbergensis*. Near Ceprano human footprints were left in sediments dated to 0.345 Ma by $^{40}Ar/^{39}Ar$ analysis of Roccamonfina volcanic ejecta (Scaillet et al., 2008). Ceprano cranial robusticity has parallels in the robust Bilzingsleben cranial fragments from ~0.37 Ma, the robust Petralona skull of perhaps broadly similar age, and the fragmentary Gruta da Aroeira cranium in the Portuguese Almonda karst near Torres Novas dating from ~0.436–0.39 Ma accompanied by a Middle Pleistocene fauna and both bifacially-flaked quartzite and chert artefacts (including hand-axes) and small secondarily-knapped ones (Daura et al., 2017). The 0.6 Ma robust mandible from Mauer near Heidelberg typifies the Middle Pleistocene variability of European *Homo heidelbergensis*.

Palaeoecologically, the Italian scenario for early humans parallels the Iberian developments (Manzi et al., 2011). Again the so-called Mid-Pleistocene Revolution involved faunal turnover, decrease in frequency of carnivorous competitor species, landscape fragmentation, and a major change in the vegetation composition of interglacials, with forests becoming dominated by *Quercus* and *Carpinus*.

4.8. Ambrona

From MIS-11 to MIS-9 ~0.43–0.3 Ma (Falguères et al., 2006; Parès et al., 2005) are the finds from fluviolacustrine sediments at Loma de los Huesos at Ambrona, at 1100 m asl in the upper River Jalón (a tributary of the Ebro) near the watershed, in Spain, of the Rivers Ebro, Tagus and Duero (Pérez-González et al., 1999; Pérez-González and Santonja, 2005). Perhaps comparable to the Orgnac and Caune de l’Arago sequences, the Ambrona sequence (Panera, 1996; Rubio Jara, 1996; Santonja et al., 2005a,b,c) begins with bifacially-flaked forms alongside flake artefacts which higher up prevail exclusively, produced sometimes by “Levallois” core-reduction (Santonja et al., 2014). 3 km away, excavation began a century ago at Loma del Saúco near Torralba del Moral (de Aguilera y Gamboa, 1909, 1913a,b; Obermaier, 1924). Excavation at the sites recommenced in 1960 (Butzer, 1965; Freeman and Butzer, 1966; Freeman, 1978; Howell, 1966; Howell et al., 1963), and has continued for fifty years, expanding the well-studied Middle Pleistocene faunal assemblage and >6000 artefacts. Wood finds included pieces claimed as showing bevelled points and cut-marks.

Possible human modification of some bone and ivory pieces (Aguirre and Hoyos, 1977; Biberson and Aguirre, 1965) has been criticized (Villa and d’Errico, 2005). Putative ochre from Ambrona (Howell, 1966) was in fact siltstone (Butzer, 1980). Chronostratigraphical considerations imply a later date for hand-axes and cleavers at Torralba than for the Ambrona bifaces, undermining the actualistic conjecture of contemporaneous complementarity between the sites in Palaeolithic strategies for capturing big game along its annual migration route (Butzer, 1982), which once gained some favour (Binford, 1987; Klein, 1987). The sites offer tantalizing glimpses into scavenging behaviour and sporadical hunting during a 200,000-year time-span (cf., Villa, 1990; Villa et al., 2005). Both sites have typically Middle Pleistocene faunas (Aguirre, 2005; Aguirre and Fuentes, 1972; Baltanás et al., 2005; Fuentes Vidarte, 1994; Martínez Solano and Sanchiz, 2005; Perea and Doadrio, 2005; Pérez-González et al., 1999; Sánchez Marco, 2005; Sesé and Sevilla, 1996; Sesé and Soto, 2005), and palynological and palaeobotanical findings indicate a steppe landscape containing stands of pine woodland and probably also some wetland fringed by deciduous trees (Florschütz and Menéndez Amor, 1962; Menéndez-Amor and Florschütz, 1961, 1963; Ruiz Zapata et al., 2005).

4.9. *River Aniene and Torre in Pietra*

In Italy ^{40}Ar/^{39}Ar dating to 0.29–0.22 Ma (Marra et al., 2015, 2017) of fluviolacustrine sediments and gravels in the valley of the River Aniene (a tributary of the Tiber, in northern Rome) sheds new light on the Rebibbia-Casal de’Pazzi, Ponte Mammolo, Sedia del Diavolo and Saccopastore sites, and their palaeontological, Palaeolithic and palaeoanthropological remains, particularly the Saccopastore 1 and 2 early or pre-Neanderthal skulls, dated to 0.245 and 0.22 Ma respectively (Marra et al., 2017); Saccopastore 1 recalls aspects of Atapuerca Sima de los Huesos craniology (Bruner and Manzi, 2006). By 0.29 Ma (early MIS-8) at the Roman sites small artefacts prevailed which sometimes involved preparation by hierarchical (“Levallois”) knapping (Marra et al., 2017), whereas large bifacially-flaked cutting tools were scarce (perhaps intrusive from older sediments), contrasting their with noteworthy presence in Latium during MIS-10 and MIS-9. Geochronological accuracy is achievable by ^{40}Ar/^{39}Ar dating of ignimbrites ejected from Monte Sabatini and the Colli Albani. It implies ages of between 0.354 and 0.334 Ma for the hand-axes from layer 11*m* of the Aurelia Formation of the erstwhile Tiber delta at Torre in Pietra (Torre di Pagliaccetto), near the coast 26 km north-west of Rome, and, nearby, of ~0.325 Ma for those from La Polledrara di Cecanibbio (Villa et al., 2016) and U-ser/ESR indicates ~0.325–0.26 Ma for the artefacts from Castel di Guido (Michel et al., 2009). Subsequently, albeit lying quite deeply (layer *d*) in the 9 m Torre in Pietra sequence, small (“Mousterian”) artefacts probably belong to MIS-8/MIS-7 according to User-ESR estimates of ~0.27–0.24 Ma (Villa et al., 2016).

Revision of Torre in Pietra artefacts available for inspection from old excavations embraced 33 of 51 bifacially-flaked hand-axes from layer 11*m* (mostly of limestone; 3 of lfint) and 64 small artefacts (Villa et al., 2016). Only some bifaces have edges that form “techno-functional units” (cf., Nicoud, 2013), hierarchical flake-removal and resharpening being mainly absent. Small artefacts include knapped pebbles and secondarily-knapped flakes, including denticulate, notched and pointed forms, “scrapers”, and a few pieces knapped on two surfaces (“bifacially”), though “Levallois” cores were absent. Several aspects appear in the later Castel di Guido assemblage, which, however, may correspond to a depositional palimpsest (Villa et al., 2016). “Levallois” core-reduction characterizes numerous artefacts from Torre in Pietra level *d* where flakes tend to be thinner than in level *m*, though artefacts knapped on pebbles are present also.

An intriguing conjecture is that increasing production of small, thin artefacts was favoured by ability to haft these, which is supported by impact fractures on Mousterian stone points dating from ~0.055 Ma at the Riparo l’Oscurusciuto rock-shelter at Ginosa near Taranto in Italy (Villa et al., 2009, 2016). This is hardly astonishing, gven the cognitive versatility and technical ability involved in making long wooden spears in Middle Pleistocene Europe (Haidle, 2009). Two stone flakes with adherent birch-bark tar were excavated in Tuscany, at the Campitello Quarry clay pit, near Bucine in the upper Arno valley (Mazza et al., 2006); they were found together with straight-tusked elephant remains below a bed containing ≥0.2 Ma fauna (*Arvicola cantianus, Clethrionomys* cf. *glareolus*, *Microtus arvalis*, *Microtus* [*Terricola*] *multiplex-subterraneus*), which implies that pre-Neanderthals were hafting stone tools during MIS-7. That is no later, and probably earlier, than African Middle Stone Age use of adhesives (cf., Wadley, 2010; Wadley et al., 2009; Wragg Sykes, 2015). Later on, adhesive substances including bitumen come from Middle Palaeolithic assemblages between 0.12 and 0.04 Ma in Germany, Syria, and Spain (Boëda et al., 1996, 1998, 2008a,b; Grünberg, 2002; Grünberg et al., 1999; Hardy and Buckley, 2017; Koller et al., 2001a,b; Mania and Töpfer, 1973; Pawlik and Thissen, 2011). Neanderthal cognitive ability and technical skill involved an appreciation of both the properties of birch bark and the heat control needed for its destructive distillation in a reducing atmosphere (Kozowyk and Langejans, 2015). Perhaps a demographical increase, inferred from analytical considerations of population genetics (Rogers et al., 2017), favoured technical experimentation and diversification, such that habitual tool-use tended to become an *obligatory* aspect of the behaviour of large-brained Neanderthals (cf., Shea, 2017a).

4.10. *Terra Amata*

Terra Amata lies near where the River Paillon flowed into the Mediterranean at Nice, France. Research is published in a series of monographs (de Lumley, 2009, 2011, 2013, 2015b, 2016c, d). A human tooth and foot-print were found (de Lumley et al., 2016a,b). Pebble and chopping tools and hammer-stones abounded, together with a few (mainly limestone) hand-axes and cleavers, and many secondarily-knapped (mainly chert or flint) flakes and fragments (Villa, 1983, 1990; de Lumley, 1976b; de Lumley et al., 2009a). Small artefacts resemble those at Torre in Pietra, Isernia La Pineta, Caune de l’Arago, Vallparadís, and Cueva Negra del Estrecho del Río Quípar. Although its numerous large pebble and chopping tools set Terra Amata apart, that could reflect merely the abundance of pebbles visibly to hand and limitations they imposed on knappers whose handiwork was perforce expedient. A few elongated blades and rare instances of flake preparation by “Levallois” core-reduction are mentioned (de Lumley, 1975). Terra Amata affords instances of Shea's modes A, B, C, D, E, F1 and G1 (Table 2). Modified bones were detected (de Lumley, 1975, 1976b). Statistical breakdown of artefacts offered in early publications (de Lumley, 1976b; Villa, 1983) has been expanded (de Lumley, 2015b). Detailed stratigraphical analysis (de Lumley, 2013; de Lumley et al., 2009a) shows that artefacts mostly come from layers or lenses of argillaceous silt and a relict shingle bank of pebbles embedded in silty sand, embracing altogether a depth of barely 2 m, lying above ~1 m of sediments with sparse artefacts, and below 5–7 m of sands, silts, palaeosols and recent colluvia. Different layers reflect marine transgressive-regressive fluctuations as well as the lateral balance between a shingle bank, dune sands, and nearby silts and clays. Refitting studies imply some vertical displacement (Villa, 1977, 1983). Reflecting successive episodes of occupation, 26 archaeological layers are dated by ESR to ~0.4–0.38 Ma, when MIS-11 of stratigraphical complex C1a was followed by MIS-10 (=MIS 11.24) of complex C1b (de Lumley et al., 2009b), corroborating earlier proposals (de Lumley, 1975; Shackleton, 1975). This dating barely admits an African source for "Levallois" core-reduction at Terra Amata, without special pleading. Two TL determinations on burnt flint of ~0.23 Ma (Wintle and Aitken, 1977) had seemed unduly recent for the sequence of sterile sediments below and above the archaeological layers.) Possible post-holes and disposition of stone blocks hint at Palaeolithic structures (de Lumley, 1969d, 1975; de Lumley and Boone, 1976; Villa, 1983).

The archaeological layers contained combustion features and charcoal (de Lumley et al., 2016c), as well as 77 small (<20 mm) pieces of yellow (goethite) and red (haematite) ochre (de Lumley, 1966; de Lumley and Boone, 1976; de Lumley, et al., 2016c), some showing thermal alteration and others microscopical traces of use (de Lumley et al., 2016c; pace Wreschner, 1985; Middle Pleistocene ochre ~0.25–0.22 Ma occurred also at the Dutch Maastricht-Belvédère Mousterian site: Roebroeks et al., 2012). The excavated assemblages reflect human activities, including camping on the Terra Amata shingle, undertaken during short visits that likely involved scavenging or hunting. The fauna includes boar and straight-tusked elephant with lesser participation of steppe rhinoceros, aurochs, tahr, red and fallow deer, and rabbit, as well as several species of rodents, birds, small reptiles, and terrestrial and marine mulluscs. Together with pollen and charcoal anthracology they indicate a landscape of Mediterranean scrub and gallery woodland with deciduous trees and conifers (including larch, nowadays present only at high altitude), and temperate humid conditions with a warm sea are inferred (Beaulieu, 1967; de Lumley et al., 1976a, 2009a; 2011, 2016c; Miskovsky, 1971, 1975; Mourer-Chauviré and Renault-Miskovsky, 1980; Renault-Miskovsky et al., 2011), appropriate to MIS-11 interglacial conditions.

Whereas ~0.43 Ma large carnivores roamed the Atapuerca hills (see above), bear was the only large carnivore found at Terra Amata. Perhaps flourishing early Middle Pleistocene herbivore taxa (see above) allowed humans and large carnivores to side-step each another, as it were; parcelling out different exploitation territories, so to speak (cf., Rodríguez-Gómez et al., 2016a), with humans undertaking versatile provisioning strategies (cf., Blasco et al., 2013a).

4.11. Vallonnet

Long before, large carnivores certainly abounded near Terra Amata, notably 10 km to the east, at Roquebrune-Cap Martin, where the late Early Pleistocene Vallonnet cave (dated to 1.2–1 Ma: Michel et al., 2017; cf., de Lumley, 1976b, 1988; Gagnepain et al., 1999; Yokoyama et al., 1992), at 110 m asl overlooking the Mediterranean near Roquebrune-Cap-Martin, contained remains of *Panthera gombaszoegensis*, *P. pardus*, *Acinonyx pardinensis*, *Homotherium crenatidens*, *Pachycrocuta brevisrostris*, *Ursus denigeri*, *Xenocyon lycaonoides*, *Canis mosbachensis*, *Lynx spelaeus*, *Felis silvestris*, *Alopex praeglacialis*, *Meles meles*, *Hippopotamus* cf. *antiquus*, *Stephanorrhinus hunsheimensis*, *Mammuthus meridionalis*, *Ammotragus europaeus*, *Hemitragus bonali*, *Dama nestii vallonnetensis*, *Praemegaceros* cf. *verticornis*, *Equus stenonis*, *Bison schoetensacki*, *Sus* sp., *Macaca sylvanus*, *Monachus monachus*, *Balaena* sp., *Diodon* sp., *Carcharias taurus*, *Testudo hermanni*, *Hystrix major*, *Eliomys* cf. *quercinus*, *Glis minor*, *Ungaromys nanus*, *Allophaiomys nutiensis*, *Pliomys lenki*, *Mimomys* cf. *savini*, *Arvicola terrestris cantiana*, *Apodemos mystacinus* (Chaline, 1971, 1988; de Lumley, 1976a; de Lumley et al., 1988; Echassoux, 2004; Granier, 1988; Moullé et al., 2006; Paunescu, 2001). The taxa are specified because they include species that require warm conditions and others implying cool ones; pollen findings suggest that an initially dry cool environment gave way to damp temperate conditions interrupted by a cool interlude (Renault-Miskovsky and Girard, 1976, 1978, 1988). There are 70 putative artefacts (limestone pebble tools, flakes and hammer-stones; bone and antler knapping billets) and animal bones possibly fractured by stone tools or bearing cut-marks (de Lumley, 1975, 1976a; de Lumley et al., 1976a, 1988), though perhaps none of those components need be attributed to human agency (Roebroeks and Van Kolfschoten, 1995). A cautious approach is understandable given so many carnivore taxa.

4.12. Vallparadís and Cal Guardiola

The ~20 m-deep Parc de Vallparadís and Cal Guardiola fluviolacustrine sediments at Terrassa, 25 km from the Mediterranean at Barcelona, provides abundant faunal remains from ~1.07 to – ~0.6 Ma, including *Elephas* (*Palaeoloxodon*) *antiquus* following the Jaramillo subchron, (Madurell-Malapeira et al., 2010). An "entire area (781 m^2) of layer 10 was excavated. The archeological material consists of more than 57,600 elements (24,854 faunal remains, the remainder being stone tools and debris) and is distributed along the horizontal plane without forming any significant concentrations" (Martínez et al., 2010). Small artefacts of chert (flint) and quartz reveal knapping procedures that include orthogonal flake-removal, bipolar core-reduction and centripetal flaking of cores; secondary knapping produced small denticulate and notched artefacts, including pointed or beaked pieces, and small trihedral keeled artefacts (small trihedral forms occur at various Spanish and French Middle and early Late Pleistocene sites, cf., Boëda, 1991b, "trifacial"). There are also chopping tools on cobbles of metamorphous petrology.

U-ser/ESR estimates of ~0.85 Ma provide a minimum age for the principal archaeological deposit (Duval et al., 2011, 2012, 2015) though biostratigraphical considerations implying a time soon after the Jaramillo subchron (Martínez et al., 2010, 2014) have been questioned (Madurell-Malapeira et al., 2012). Some bones bear cut-marks, likely reflecting extraction of animal fat or grease by early humans from carcass remains of large herbivores left by the European jaguar *Panthera gombaszoegensis* and the hyaenid *Pachycrocuta brevirostris* beside a swampy lake around which considerable biodiversity thrived (cf., Madurell-Malapeira et al., 2017). Cal Guardiola and Vallparadís pollen indicates a late Early Pleistocene open landscape retaining Tertiary survivals that disappeared with the onset of final Early Pleistocene cool, moist conditions when coniferous and deciduous trees increased and cold steppe taxa began coexisting with thermophytes. Meso-hygrothermophilous and river forest species abound including some taxa rarely recorded for the Pleistocene, such as the mesocratic group of species represented by *Juglans, Carya*, and *Platanus*. The occurrence of fossil wood of *Aesculus* and Taxodiaceae pollen are worth stressing, as these are the first Pleistocene references for both taxa in Iberia (Postigo et al., 2007). Artefacts from different levels imply several visits between the Jaramillo subchron and the Matuyama-Brunhes boundary (Barsky et al., 2013; Garcia et al., 2011, 2012; Martínez et al., 2010).

4.13. Whodunnit?

Perhaps one visitor was *Homo antecessor*, present in Atapuerca

Trinchera Dolina level TD6-2 ~0.85 Ma (according to thermally-transferred OSL dating: Arnold et al., 2014) in the late Early Pleistocene, morphologically close to common ancestors of Neanderthals and modern humans (though not necessarily implying existence of an impermeable barrier to genetic exchange with *Homo erectus*, cf., Rightmire, 2001). Adaptation for human endurance in Eurasian middle latitudes does not imply unbroken human presence, and the Atapuerca sites show little trace of human activity in the early Middle Pleistocene. Human appearances, disappearances, and reapparances are recorded at later Early and early Middle Pleistocene sites in western Mediterranean Europe (cf., Bermúdez de Castro and Martinón, 2013; Bermúdez de Castro et al., 2013; Dennell et al., 2011; MacDonald et al., 2012). Nevertheless, sometimes resilience, adaptability or resourcefulness (cf., Barsky et al., 2013; Carbonell et al., 2010b) likely thwarted or delayed local human extinction as an inevitable outcome of climatic forcing, or evaded it by spatial relocation or dietary variation (cf., Blasco et al., 2013a) and, indeed, several western Mediterranean early Palaeolithic sites have provided biological assemblages with biodiversity reflecting a variety of biotopes nearby.

Human resilience and cognitive versatility (cf., Manrique and Walker, 2017) likely underpinned the bifacial flaking of ("Acheulian") large cutting tools (Shea's mode E) during the late Early Pleistocene in western Mediterranean Europe, where their appearance need not imply outside influence (cf., Nicoud, 2013; Walker et al., 2013, 2016a). The same applies to repeated hierarchical (cf. "Levallois") release of flakes from bifacially-fashioned discoidal cores ~1.3 Ma at Pirro Nord P13 at Apricena beside the Italian Adriatic coast (Arzarello and Peretto, 2010; Arzarello et al., 2012, 2015). In Africa, ~1.6–1.4 Ma (presumably the handiwork of *Homo erectus*) both bifacially-flaked cutting tools and small artefacts struck from small prepared (often discoidal) cores, sometimes bearing stigmata indicative of possibly hierarchical flake-release (cf. "Levallois", but see Díez-Martín et al., 2012, 2015) were present at sites such as Peninj ST in Tanzania (de la Torre et al., 2003; cf., de la Torre and Mora, 2008). A parsimonious working hypothesis is that human evolution of technical skilfulness requiring manual dexterity and cognitive versatility sufficed to permit archaic humans in southern Europe from the late Early Pleistocene onwards to make different kinds of stone artefacts and manipulate aspects of their environment in ways that were already common in the genus *Homo*. There is no overwhelming substantive archaeological or palaeoanthropological evidence from Europe that negates a likely ascription to any hominin lineage *other than that which gave rise to Neanderthal humans* of any late Early and early Middle Pleistocene assemblages containing bifacially-flaked handaxes (and/or cleavers) together with abundant small artefacts struck from small prepared cores by repetitive flaking, occasionally showing signs compatible with hierarchical flake-release.

4.14. *Cueva Negra del Estrecho del Río Quípar*

As already mentioned, near the Catalan Mediterranean coast, a bifacially-flaked ("Acheulian") schist cleaver comes from El Forn unit II in the Barranc de la Boella (where small chert flakes and denticulate pieces were excavated also), dated by ^{26}Al/^{10}Be to 1.07–0.87 Ma, in line with magnetostratigraphy and palaeontological findings (Vallverdú et al., 2014b). Slightly later, plausibly MIS-21 (0.865–0.815 Ma) is a bifacially-flaked ("Acheulian") limestone hand-axe excavated at Cueva Negra del Estrecho del Río Quípar, a site lying at 740 m asl, 75 km north of the southeastern Spanish Mediterranean coast, near Caravaca de la Cruz in the Segura River basin. The cave lies on the active Quípar Fault and probably neoetctonic uplift in the Early Middle Pleistocene saved its erstwhile fluviolacustrine sedimentary fill from erosion. Palaeolithic and palaeontological remains come from Matuyama chron sediments (Scott and Gibert, 2009) with abundant teeth of arvicoline rodents from between 0.99 and 0.78 Ma (*Victoriamys chalinei*, *Mimomys savini*, *Iberomys huescarensis*, *Stenocranius gregaloides*, *Pliomys episcopalis*, *Terricola arvalidens*: López Jiménez et al., 2018) and archaic megacerine (*Megaloceros novocarthaginiensis*) antlers (Walker et al., 2013, 2016a). Rhinoceros, elephantids, horse, bison and other ungulates are more conspicuous than larger carnivores, which are limited to scanty remains of bear and *Crocuta*. Carrión et al. (2003) performed pollen analyses in the site and found a great diversity of Mediterranean forest taxa (evergreen and deciduous *Quercus, Pinus pinaster, Olea, Pistacia, Phillyrea, Arbutus*), and broad-leaf trees (*Corylus, Fraxinus*) including some likely riparian (*Ulmus, Salix*). A deep level contained evidence of combustion, including thermally-altered chert and bone (Walker et al., 2016b). Shea's modes A, B, C, D, E, F and G (Table 2) are present in an assemblage predominantly of small chert artefacts, including a few instances of repetitive knapping on cores and hierarchical (cf., "Levallois") preparation for flake-release (Walker et al., 2013, 2016a). A few knapped artefacts are "microlithic" in size. Striking locally-available subparallelepiped blocks or nodules of tabular Jurassic chert tends more often to split them into smaller ones rather than to produce conchoidal fracturing. Trace-element analyses imply that some chert came from upto 30 km away though most came from nearby (Zack et al., 2013).

4.15. *Early Pleistocene and Palaeolithic in Western Mediterranean Europe*

The Palaeolithic assemblages from Vallparadís, La Boella and Cueva Negra seem to have at least as much in common with each other as they do with those Early Pleistocene assemblages in Africa or the Near East that often contain a far larger proportion of bifacially-flaked large cutting tools. Local availability of mineral and biological resources in Western Mediterranean Europe may have wielded a strong influence over human behaviour and activities. If so, it is unsurprising that these differed in some respects from those of the African forebears of those late Early Pleistocene humans in Western Mediterranean Europe represented by fossils of *Homo* sp. from Atapuerca Sima del Elefante layer TE9 of ~1.2–1.1 Ma (Bermúdez de Castro et al., 2011; Carbonell et al., 2008) and the ~1.4 - ~1.2 Ma Barranco León BL5 bed at Orce in Granada (Gibert et al., 1999a; Ribot et al., 2015; Toro-Moyano et al., 2013). The aforementioned Palaeolithic assemblages attest to their cognitive versatility and manual dexterity, whilst drawing our attention to just how much the late Early Pleistocene human behaviour had in common with the behaviour of those Middle Pleistocene pre-Neanderthal humans whose background very likely had deep regional roots in Western Mediterranean Europe. As remarked earlier, morphological considerations suggest that the Atapuerca Trinchera Dolina *Homo antecessor* from ~0.9–0.8 Ma in layer TD6 is phylogenetically close to common ancestors of Neanderthals and modern humans. A thousand artefacts from Atapuerca Trinchera Dolina TD6 are mainly of chert or flint and quartz, with some of quartzite, limestone or sandstone; all raw materials outcrop <2 km away. Refitting studies imply that stone was worked on site (Carbonell et al., 1995, 1999, 2001; Terradillos-Bernal, 2010; Terradillos-Bernal and Rodríguez-Álvarez, 2014). Artefacts fall within Shea's modes A, B, C, and D (Table 2), and appear to be neither markedly different from small artefacts at Vallparadís and Cueva Negra on the one hand, nor, on the other, from the older late Early Pleistocene assemblages from BL5 and Fuente Nueva FN3 at Orce (cf., Barsky et al., 2010, 2013, 2015, 2016, 2018; Fajardo, 2008, 2010; Toro-Moyano et al., 2003, 2009, 2010, 2011; see also Walker, 2017). Indeed, revision of Fuente Nueva 3 limestone artefacts

(Barsky et al., 2015) may imply that modified stones >5 cm in size were no less abundant at Orce than at TD6 (cf., Terradillos-Bernal and Rodríguez-Álvarez, 2014). Probably too much weight has been given to notional distinctions between "light-duty" artefacts and "heavy-duty" modified cobbles and chopping-tools (not to mention flaked hand-axes and cleavers) such as those from Middle Pleistocene Terra Amata and Torre in Pietra, or the late Early Pleistocene assemblages from Cà Belvedere di Monte Poggiolo on the edge of the Po plain near Forlì and the Adriatic Sea, Pont-de-Lavaud in the Creuse valley of the Loire basin, the Grotte de Vallonnet at Roquebrune-Cap-Martin in the Alpes Maritimes, and Bois-de-Riquet at Lézignan-La-Cèbe near the Mediterranean port of Sète (cf., Walker, 2017). Palaeolithic activities must have been constrained often by local availability of petrological resources.

5. Epilogue or prologue? First footfall

These remarks will be confined to a possible contrast between the beginnings of primary access to animal carcasses by *Homo antecessor*, foreshadowing subsequent pre-Neanderthal behaviour in the western Mediterranean Europe, and previous Early Pleistocene behaviour in which scavenging may well have played a larger part. At TD6, primary human access to animal carcasses is suggested by an animal bone with a cut-mark interrupted by a later tooth-mark attributed to gnawing by a scavenging animal (Blasco and Rosell, 2009). The size of most TD6 gnaw-marks implies teeth of small carnivores such as foxes; moreover, cut-marks and other traces of human intervention are similar on skeletal parts of both very large and smaller animals, which would not have been expected were large carnivores to have gained prior access (Carbonell and Rosell, 2004). A significant part played by early humans is not unthinkable (Díez and Rosell, 1998; Díez et al., 1999) and given credence by a range of impingements on carcasses that implicates human agency (Saladié et al., 2011, 2014). Large carnivores in TD6-2 are *Ursus dolinensis* and *Crocuta crocuta* (Rodríguez Gómez et al., 2013). Carnivores and humans could have been sustained together by primary access to herbivore carcasses at Atapuerca according to a possibility, allowed by mathematical modelling, that environmental carrying capacity could have supported large predators and humans together in a landscape commensurable with that of some modern hunter-gatherers (Rodríguez-Gómez et al., 2013). Quite likely carcasses <100 kg in weight were butchered at Trinchera Dolina (Rodríguez-Gómez et al., 2013). A fascinating inference supported by taphonomical findings is that primary access to herbivore carcasses perhaps permitted unbroken early human existence in the Sierra de Atapuerca between ~1.3 and 0.78 Ma (Garcia et al., 2011; Huguet et al., 2013, 2015). Taphonomical analysis of TD6-2 animal and human bones suggests that early humans engaged in different activities there, perhaps at different times (Saladié et al., 2014). Cut-marks and signs of defleshing on *Homo antecessor* bones have inspired a conjecture of cannibalism (Carbonell et al., 2010a; Fernández-Jalvo et al., 1996, 1999; Rodríguez Gómez et al., 2013; Saladié et al., 2011, 2014), though it seems unlikely that alimentary necessity was the cause; no further evidence of comparable interference appears at western Mediterranean sites until MIS-5 at Moula-Guercy (see above).

In contrast to TD6, at Orce excavation at BL5 and FN3 (~1.4 - ~1.2 Ma) uncovered remains of both large ungulates and important carnivores (*Homotherium latidens*, *Megantereon whitei*, a pack-hunting canid *Lycaon lycaonides*, bear, a scavenging hyaenid *Pachycrocuta brevirostris*, the jackal-like *Canis mosbachensis*, and *Lynx* cf. *pardinus*). The relationship between the early humans and herbivorous game is uncertain. The Palaeolithic artefacts could have been used during scavenging on ungulate carcasses abandoned by large carnivorous predators, as well as for preparing food from lesser edible creatures and plants both of which perhaps accounted for about half of the Pleistocene human dietary needs. The other half could have been met by scavenging on ungulates, according to a plausible model (Rodríguez-Gómez et al., 2016b) of the likely biomass of large game and carrying capacity of the Orce basin. Mathematical modelling implies that scavenging was capable of sustaining - throughout the year in an area of ~100 km^2 - a human group of ~12 people with greater stability than were they to have relied on a mixture of scavenging and hunting ungulates. Taken into account, in this reconstruction, is the likely carrying capacity for large herbivores, carnivorous predators, and large mammalian scavengers. It implies that *Homo* could have been an effective scavenger, plausibly able to gain preferential secondary access to carcasses, thwarting competition from other scavengers (cf., Espigares et al., 2013). An inference derived from the model is that exclusive reliance on hunting seems unlikely, even were humans to have had primary access to small ungulates. Perhaps the model could be appropriate for Atapuerca Sima del Elefante layer TE9 of ~1.2—1.1 Ma, which provided a human mandibular fragment and a phalangeal bone (Bermúdez de Castro et al., 2011; Carbonell et al., 2008), though also dental calculus analysis shows plants were eaten raw (Hardy et al., 2016). TE9 provided 71 small artefacts of chert, limestone and quartz, of which 33 came from the same sub-level as the human remains (de Lombera-Hermida et al., 2015; Parés et al., 2006). Tortoise and doubtless other small game contributed to the human diet (Blasco et al., 2010). Ungulate bones with impact and cut-marks suggest that skinning, dismembering, and defleshing of carcasses may have taken place near the mouth of the karst shaft, possibly following primary access to prey, though it is likely that scavenging took place of carcasses of animals killed by the European jaguar (*Panthera gombaszoegensis*) and other carnivores.

6. Concluding remarks

Habitual tool-use underpinned human survival in late Early Pleistocene western Mediterranean Europe. By the onset of the early Middle Pleistocene, early humans (descendants of *Homo antecessor* in all likelihood) were exploiting diverse biotopes, sometimes (perhaps often) attaining primary access to large game, and deploying a variety of stone artefacts and rock types, which implies not only manual dexterity but also technical competence and cognitive versatility. By the mid-Middle Pleistocene *Homo heidelbergensis*, some of whose anatomical features foreshadow Neanderthal morphology, was exploiting a wide range of natural resources in western Mediterranean environments, including small game and plants. Neanderthal morphology began to emerge during the second half of the Middle Pleistocene, accompanied by increasing technological diversity and an expanding variety of small tools, conjecturally favoured by hafting, perhaps following development of wooden spears (or other tools) and adhesive and binding technologies, and generation and heat-control of fire (which undoubtedly was necessary for activities inside Bruniquel cave). By the onset of the last interglacial period, Neanderthal morphology and Mousterian artefacts are widespread, and there are indications of coordinated retrieval and treatment of body-parts of large ungulates.

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Appendix A. Supplementary data

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