



## ADAPTATIONS AND CULTURES OF PLEISTOCENE HUMANS IN ITALY

Marco Peresani

Dipartimento di Studi Umanistici, Sezione di Scienze Preistoriche e Antropologiche, Univ. degli Studi di Ferrara, Ferrara, Italy.  
Istituto di Geologia Ambientale e Geoingegneria, Consiglio Nazionale delle Ricerche, Milano, Italy.

Corresponding author: Marco Peresani <psm@unife.it>

**ABSTRACT:** Italy preserves abundant biological and cultural fossil record, placed in peculiar geographical and ecological contexts that stimulate the study of population dynamics, adaptations, and cultural transitions during the whole Pleistocene. Such a variegated territory, bounded by the Alpine chain and longitudinally split by the Apennines, hosted distinct migration waves attributed to unidentified hominins, and to *Homo heidelbergensis*, *Homo neanderthalensis*, *Homo sapiens* in a heterogeneous scenario subjected to profound changes during extreme sea-level lowering. The first human colonization occurred around the Early to Middle Pleistocene transition, presumably driven by major faunal renewals which invested Southern Europe. These first proofs are documented in the oldest sites, Pirro Nord and Monte Poggiolo, with lithic industries based on core-and-flake technology. After a gap in the evidence of human settlements between MIS19 and MIS17, the earliest Acheulean makes its appearance in southern Italy starting from 661-614 ka. Large cutting tools typical of this complex remain however poorly represented throughout the early Middle Pleistocene, in favour of the tiny and medium-sized flakes which feature the lithic industries until the conventional end of the Lower Palaeolithic. Specifically, these small tools mark the Middle Pleistocene interaction between hominins and elephants, as documented in many sites in central Italy. As regards the Middle Palaeolithic, its archaeological and anthropological record looks more consistent and proves that Neanderthals inhabited southern Europe and continental Italy. The Neanderthal record refers to settlement patterns and mobility strategies in the geographic and environmental districts that feature most of the regions at the alpine fringe, along the Apennine chain and the rocky coasts. Settlements have complementarity character, with long-term occupations and other locations used for short time, particularly caves and sheltered sites, where the stratigraphic sequences record multi-occupations covering large time intervals and repeated environmental changes. As a matter of fact, some environmental changes are related to cultural turnovers like the appearance of the Mousterian Quina during MIS4 in the North of Italy. Hunting and dietary behaviour reconstructed from a number of sites stimulates debate around possible convergencies or divergencies between Neanderthals and the first *Homo sapiens* communities who started settling Italy since about 44-43 cal ka BP. Pieces of the Neanderthal-Sapiens biocultural transition with contested attributions have been unveiled in recent years at key archaeological sites, either in the North and in the South of Italy, producing an incontestable contribution for reconstructing these dynamics in Europe. This is specifically the case of the Uluzzian with its cultural package of lithic and bone technologies and ornamental beads, that follows in time the oldest known cultural expressions of *Homo sapiens* in other regions of Western Eurasia. The spread of early Sapiens is also related to the Aurignacian and marks another intriguing cultural dynamic of the Upper Palaeolithic, prolongating across the Last Glacial Maximum and the Late Glacial, two turning points for the bio-geographical, anthropological and cultural evolution marked by the loss of large continental plains and the rearrangement of all ecozones of human populations. As consequence of the Late Glacial interstadial warming, a large-scale Epigravettian colonization of the mountain ranges started and continued in the Mesolithic until the disappearance of those hunter-gatherer populations.

Keywords: Settlement, Human adaptation, Migration, Culture, Palaeolithic.

### 1. INTRODUCTION

Because of its strategic position between Africa and continental Europe, Italy with its variegated landscape is particularly suitable for palaeoecological, archaeological and palaeoanthropological studies. During the Pleistocene, distinct human migration waves occurred in western Eurasia, particularly in its southern area, leaving ephemeral and progressively more and more consistent traces framed in their ecological context. Continental Italy and, above all, peninsular Italy preserve abundant biological and cultural fossil record, placed in peculiar geographical and ecological contexts that stimulate the investigation of population dynamics, adaptations, and cultural transition across the whole Pleistocene. In the last two decades there have been a

number of new discoveries of sites, cultural items and human remains from across the country spanning from the Lower to the Upper Palaeolithic. In the meantime, many materials, specimens, chronologies have been reconsidered and re-evaluated to increase our knowledge of crucial findings attributed to *Homo heidelbergensis*, *Homo neanderthalensis* and *Homo sapiens* populations in the widest Western Eurasian scenario.

Italy is mostly a mountainous and coastal country. The Alpine chain, mainly E-W oriented, reaching elevations >4500 m in its western range, alongside with the Apennines, NW-SE oriented, with elevations >2500 m, acted as important ecological barriers, respectively towards continental Europe and splitting the peninsula in two sides. The western one is influenced by the Mediterranean climate, while the eastern side is more subjected

to continental conditions. Extensive and long-lasting tectonic activity, together with the major geomorphic processes attributable to glacial, fluvial and marine erosion, fluvial sedimentary aggradation, and volcanic activity contributed to produce a heterogeneous physiography, with considerable extension of the coasts during the extreme sea-level lowering. Furthermore, given its latitudinal extension from 38° to 47° N, Italy is featured by a strong climatic gradient, in turn favouring a marked biodiversity also enhanced by the extensive variety of bedrocks. The pattern of modern precipitation values ranges from >2000 mm/year in the prealpine belt of northern Italy to <500 mm/year in some areas especially of southern Italy and Sicily. During the Pleistocene global climatic turnovers, these values, alongside the average T° dramatically varied and impacted on the extension of the icesheets, landmass, biomass and ecological variability with maintenance of remarkable differences across the peninsula and especially between the western and eastern sides.

## 2. THE OLDEST LOWER PALAEOLITHIC SETTLEMENTS AND THE TRANSITION FROM THE EARLY TO MIDDLE PLEISTOCENE

When, where and in which conditions the first colonization of Western Mediterranean Europe by hominins occurred is one of the most debated topics in palaeoanthropology and prehistoric archaeology. Researchers agree on human's dispersal events towards W Europe during the late Early Pleistocene, probably occurred earlier than 1.2 Ma, as demonstrated by chronometrically dated finds in Spain (Huguet et al., 2017). Furthermore, models elucidate that this dispersal was likely part of the progressive faunal renewal, which also involved some large mammals of African origin during the Early Pleistocene (Manzi et al., 2011). Such a first distinct wave of humans is documented at Orce and Atapuerca - Sima del Elefante and has been referred to *Homo antecessor*, which remains were found associated with stone artefacts attributed to the so-called Mode 1. These industries are largely known in many sites of the Mediterranean and continental regions. Large discontinuities affect the archaeological record up to the early Middle Pleistocene for a range of taphonomic, visibility and research reasons, with no exclusion of ecological conditions. Human dispersal into Europe is thus attributable to morphologically derived hominins, well known from Atapuerca (Bermúdez de Castro et al., 2011) and to several sites where bone remains broadly included within the *Homo* sp. were found. This significant human presence has been related to the major faunal renewal that characterised the Early to Middle Pleistocene transition. This hypothesis is supported by evidence of a major episode in the reorganization of mammalian fauna since at least 1.3 Ma, with dispersals of taxa most of which persisted throughout the Middle Pleistocene and respective reconstruction of mammalian faunal complexes (Palombo, 2010).

As expressed above, the Italian peninsula is an important benchmark for reconstructing the chronological and cultural data about the diffusion of genus *Homo* outside Africa. Archaeological sites (Fig. 1) testify to an

early occupation of Italy and corroborate models about the exit from Africa that could have spread from the Middle East. The oldest archaeological evidence comes from Pirro Nord in Apulia, S Italy, dated on biochronological base to 1.6-1.3 Ma. The site counts a large assemblage of fossil vertebrates (Pirro Nord Faunal Unit) and short reduction sequences deeply adapted to obtain flakes (Arzarello et al., 2012). However, this chronological interval has been criticized by Muttoni et al. (2018) because of the lack of magneto-stratigraphical and numerical dates. Thus, an age of >0.78 Ma has been proposed for Pirro Nord, instead, according to the biochronology of the mammal association, the correlation between bones and cut-marked bones, stone tools and the sedimentary infill of the karts structure. If the old chronology is confirmed, a long gap separates Pirro Nord from the open-air site of Cà Belvedere di Monte Poggio in the N Apennine, dated to about 0.9 Ma by ESR and palaeomagnetism (Muttoni et al., 2011). The site is characterized by core-on-flake technology and abundant refitting which allowed the reconstruction of complete reduction sequences (Peretto et al., 1998). Thanks to refits, it has been possible to understand that local raw materials only allowed the production of short reduction sequences (SSDA or centripetal) to obtain flakes which were rarely shaped through retouched edges. This first phase of occupation fits perfectly with the other European sites dated between 1.3 and 0.9 Ma. However, the oldest Italian sites do not present retouched lithic elements in their assemblages, although at Pirro Nord it might be observed a strong predetermination (Chelli Cheheb et al., 2019).

## 3. THE MIDDLE PLEISTOCENE, THE ACHEULEAN AND OTHER COMPLEXES

Ultimately, there are no archaeological sites between Marine Isotope Stage (MIS) 19 and MIS 17 and the sites recorded in an indisputable stratigraphic context between MIS 17 and MIS 12 are few and fragmented both temporally and spatially (Fig. 1). However, the timing and occurrence of the settlement in this timespan and the related technical behaviours are subjected to different interpretations (Muttillio et al., 2021).

The Middle Pleistocene human fossil record is represented by the partial femur shaft from Venosa Nartarchirico (Moncel et al., 2020), and the human deciduous incisor from Isernia La Pineta (Peretto et al., 2015). It is worth to mention Ceprano in southern Latium for human remains, as a calvarium in primary deposits was recovered and dated to 400 ka. It has no apomorphic Neanderthal trait, while shows similarities with specimens attributed to *Homo heidelbergensis* in E Africa (Manzi et al., 2001). It supports the phylogenetic significance of Ceprano as the best candidate to represent the ancestral morphology of this putative polymorphic species (Manzi, 2016). Nearby this site, the human teeth recovered at Fontana Ranuccio (K/Ar dated to 0.46, Muttoni et al., 2009) shows morphological traits supporting an evolutionary continuity between the Mid Pleistocene humanity and Neanderthals (Rubini et al., 2014; Zanolli et al., 2018). This affinity, alongside with the apparent contrast with Ceprano, hints at more archaic morpholo-



Fig. 1 - Most relevant Lower Palaeolithic sites in Italy: 1) Visogliano; 2) Quinzano; 3) Monte Poggiolo; 4) Ficoncella; 5) Castel di Guido; 6) Torre in Pietra; 7) Polledrara di Ceccanibbio; 8) Fontana Ranuccio; 9) Valle Giumentina; 10) Pirro Nord; 11) Isernia La Pineta; 12) Guado San Nicola; 13) Roccamonfina; 14) Notarchirico; 15) Atella (source <http://tinitaly.pi.ingv.it>; elab. by D.Delpiano).

gies retained by 400 ka populations in Italy, contrary to other populations in southern and central Europe (Manzi, 2016). These, instead, already showed varying grades of morphological progression towards the typical Neanderthal assemblage of traits, thus suggesting the occurrence of different sub-species of *Homo heidelbergensis* in the same timeframe.

Profound changes between the first appearance of human groups in southern Europe and the early use of hand axes occurred at the end of the Middle Pleistocene climatic revolution. Notarchirico is the earliest Acheulean assemblages in Italy, and it is dated to 661-614 ka

(Moncel et al., 2020). During this phase, large cutting tools are poorly or not represented in the Italian peninsula. The lithic assemblage of Isernia La Pineta (583-561 ka) reflects this situation. It is mainly composed of small and medium-sized flakes of local flint and limestone but no bifaces (Peretto et al., 2015). These sites share similar riverine contexts despite the differences observed in the archaeological assemblages (Muttullo et al., 2021).

One of the most intriguing pieces of evidence of Middle Pleistocene hominin behaviour in Italy is related to the interaction between hominins and elephants, as

testified from elephant bones with presence of anthropogenic surface modifications. Such evidence can be found to archaeological and taphonomic records in Africa, Europe, and Asia where remains of *Palaeoloxodon antiquus* and lithic tools coexist (Agam & Barkai, 2018; Panagopoulou et al., 2018 and references therein). Medium sized lithic tools with residues and use-wear related to animal tissues processing, found in association with carcasses and articulated bones, corroborate the involvement of these animals in the diet of Lower Palaeolithic hominins (Aranguren et al., 2019). Elephants were not exclusively exploited for meat, fat, and marrow: their bones were also used as raw material to produce flakes and various types of large bone tools among such as handaxes (Barkai, 2021; Villa et al., 2021). Given the paramount importance of these animals as sources of food and raw material it might be assumed that also affected hominins' behaviour and their landscape exploitation strategies (Lemorini et al., 2022). Under this light, a remarkable site of reference is La Polledrara di Ceanibbio where elephant carcass and lithic implements were found in fluvial and fluvio-palustrine fossiliferous deposits included in the Ponte Galeria Sequence 6 of the Aurelia Formation (MIS10 and MIS9; Santucci et al., 2016). The optimal quantity and degree of preservation of the faunal remains thanks to the contemporaneous re-sedimentation of a volcanic unit dated 325–310 ka (Pereira et al., 2017), allowed to unearth large mammals like *Palaeoloxodon antiquus* and *Bos primigenius*, together with lithic and bone artifacts but no bifaces. The interpretation of butchering activities going on the site is consequence of the over 500 stone flakes recovered around the carcass of a single elephant in anatomical connection. Data obtained from a recent study and compared to previous published papers (Cerilli & Fiore, 2018) shed light on a sequence of events occurring over a long-time span from a fresh carcass to a completely bare skeleton. The human interaction with the body of the elephant, entrapped in the mud, consisted in a series of butchering sessions occurring in a few days (Lemorini et al., 2022). These interactions probably followed the organization of a hunting session. Another hypothesis is that the elephant carcass, probably partly scavenged by other predators, was found during routine exploration and exploitation of the landscape and totally scavenged by hominins adapted with flexible dietary behavior and equipped with a toolkit suitable to these situations.

#### 4. NEANDERTHALS AND THE MIDDLE PALAEO-LITHIC

Due to the blurred chronology of the Middle Palaeolithic, especially of its earliest phase, the understanding of the variability and evolutionary patterns of the Late Acheulean and first Mousterian techno-complexes is quite limited. Nonetheless, a consistent archaeological record attests that Neanderthals inhabited S Europe and Italy throughout the entire Middle Palaeolithic (Fig. 2). Starting from the earliest attestations, one of the most spectacular pieces of evidence is reported at Foresta ichnosite in SW Italy, also known as 'Devil's Trails', impressed on top of the LS7 pyroclastic unit dated 345-

350 ka (MIS 10). At this site, a minimum number of three individuals left isolated footprints and trackways moving downslope but also in the opposite direction with respect to the others (Panarello et al., 2020; Mietto et al., 2022).

Human fossil specimens have been found all over Italy and bear a mixture of archaic features and more progressive (Neanderthal) traits, as attested by the skeleton from Altamura (S Italy) and skulls found at Saccopastore. Skulls, teeth and appendicular skeleton remains were found at Grotta Guattari also during recent excavations (Rolfo et al., in press). Isolated teeth come from several sites from northern to southern Italy, like Ciota Ciara, Riparo Broion, Riparo Tagliente, Grotta Fumane, Grotta De Nadale and Grotta Taddeo, Grotta Cavallo, Spinadesco, and Campoverde (Buzi et al., 2021). The Altamura skeleton is one of the most complete human specimens of late Middle Pleistocene in Europe. It was found in the karstic cave of Lamalunga in Puglia and apparently was not associated to any lithic artifact. It is covered of large calcite concretions, U/Th dated between  $172 \pm 15$  and  $130.1 \pm 1.9$  ka (Lari et al., 2015). Bones support the idea that the individual remained trapped in the karstic system and died right in the place of deposition, as any sign of transportation, modification or deformation was observed.

Neanderthals' settlement patterns and mobility strategies varied in the different Italian geographic and environmental areas, although adaptations to ecological contexts are still poorly known all across many districts. The settlements are characterised by a complementarity between long-term occupations and locations showing short-time, repeated occupations, particularly in caves and sheltered sites where stratigraphic sequences span wide time intervals and cover an ensemble of environmental changes (Romagnoli et al., 2022). The techno-economic variability might be explained by different mobility strategies, technological traditions and Neanderthal behaviour. The result is a complex mosaic between expediency and curation in the organization of production and maintenance of stone tools, with continuities and ruptures across time. Currently, this dynamic and kaleidoscopic scenario cannot be interpreted according to a universal model either of time or space (Romagnoli et al., 2018; Delpiano et al., 2019).

Italy was well-populated by Neanderthals all across the MP and especially at its end, as demonstrated by the density of sites. Human presence was recorded in caves and shelters, in the open-air on fluvial terraces, hill tops, karst surfaces, mountain ridges. Although Neanderthal population density cannot be estimated yet, studies on land-use patterns and mobility reveal that their settlements covered a wide biogeographic range, bounded from the North by the Pre-Alpine fringe and to the South by the marine coasts.

Unfortunately, due to alpine glaciers and periglacial processes, the archaeological record preserved only on mountain and hilly sectors on the Southern Alpine slope spared by these processes. The reconstruction of the settlement system can be inferred by sites located on those fluvial terraces situated at the edge of the mountain range, spared by destructive post-depositional processes. The same holds for the Apennine range, which hosts several sites also up to its inner ridge. In the Ital-



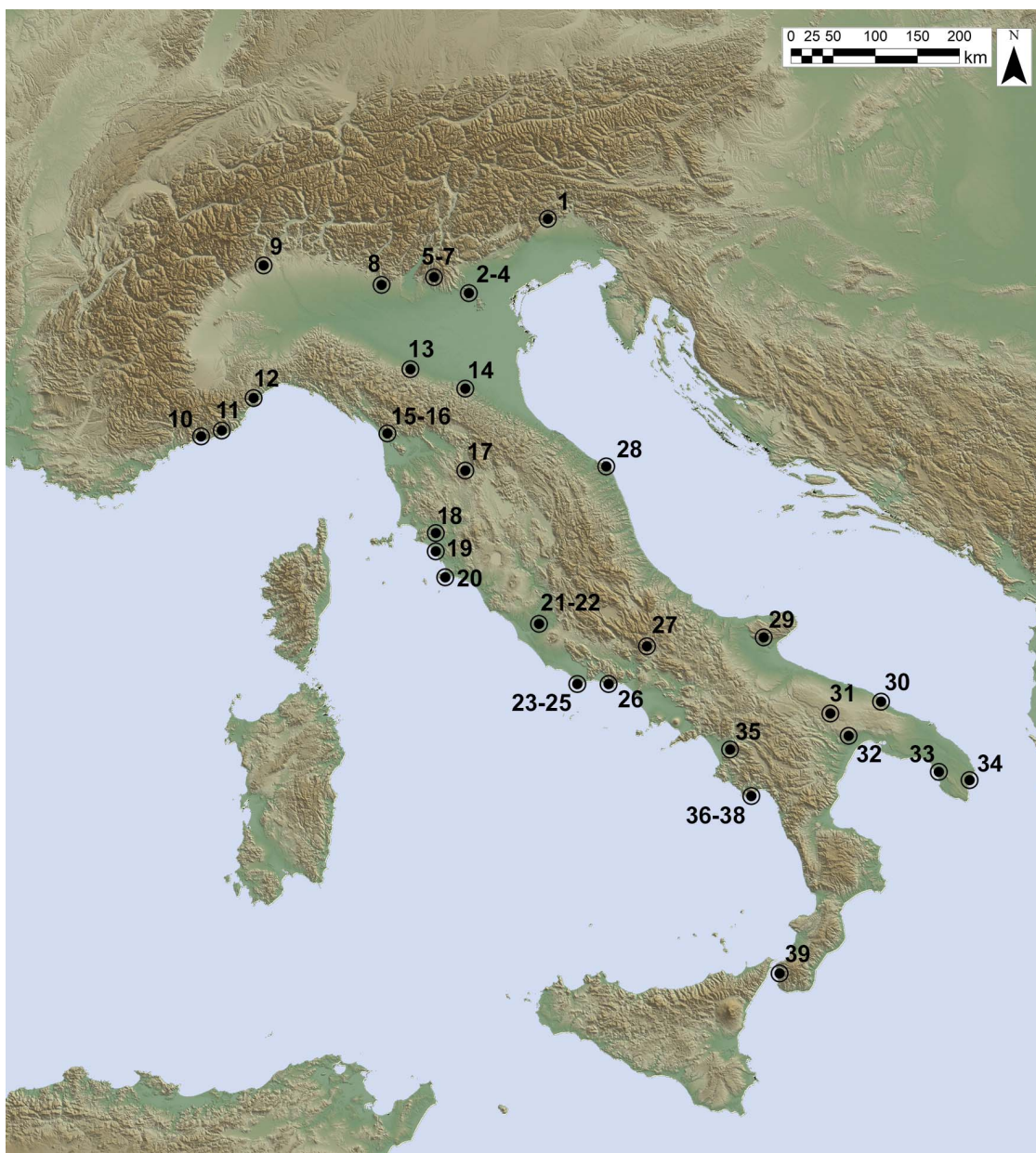


Fig. 2 - Selection of Middle Palaeolithic sites in Italy: 1) Grotta del Rio Secco; 2) Grotta Maggiore di San Bernardino; 3) Grotta e Riparo del Broion; 4) Covolo De Nadale; 5) Grotta di Fumane; 6) Riparo Tagliente; 7) Vajo Salsone; 8) Monte Netto; 9) Ciota Ciara; 10) Balzi Rossi; 11) San Francesco; 12) Arma delle Manie; 13) Ghiardo; 14) Podere due Pozzi 15) Grotta del Capriolo; 16) Grotta all'Onda; 17) Campitello; 18) Poggetti Vecchi; 19) Grotta la Fabbrica; 20) Grotta di Cala dei Santi; 21) Saccopastore; 22) Casal de Pazzi; 23) Grotta Guattari; 24) Grotta Breuil; 25) Grotta del Fossellone; 26) Grotta dei Moscerini; 27) Grotta Reali; 28) Monte Conero; 29) Grotta Paglicci e Riparo Esterno; 30) Grotta delle Mura; 31) Lamalunga; 32) Riparo dell'Oscurusciuto; 33) Grotta del Cavallo; 34) Grotta Romanelli; 35) Grotta di Castelcivita; 36) Grotta della Cala; 37) Grotta e Riparo del Poggio; 38) Riparo del Molare; 39) Archi (source <http://tinity.pi.ingv.it>; elab. by D.Delpiano).

ian Alps, mid-altitude caves like for instance the Caverna Generosa at 1,450 m of altitude in the Lombard Pre-Alps can be viewed as refugia-locations used in function of constrained factors influenced by altitude and ecoclimatic situations (Bona et al., 2007). These mountain sites scattered at 1300-1400 m a.s.l., peaking at 1600 m and bearing traces from ephemeral to consistent, might well be integrated within the seasonal movements of

humans all along the Pre-Alpine area (Margaritora et al., 2020). Settling this region was favoured by the geographical variability and dense spacing of biotopes which characterize the belt between the upper alluvial plain and the Pre-Alpine range. Presumably, Neanderthal groups developed different models of mobility and exploitation of resources across this territory and used the main caves for complex and intense human occupa-

tions. This was particularly the case of the Venetian and Carnic Pre-Alps, where differences in anthropogenic features, spatial patterning, stone knapping methods and bone industries likely reflect different adaptive responses at ecological factors.

However, due to the bias in the preservation of the archaeological record, not all the finds share the same informative potentiality. For instance, open-air sites, strongly affected by post-depositional disturbance which caused the impoverishment of past human activity traces with substantial loss of information. At any rate, some information can be acquired also by their location features furnishing details about territoriality and site catchment. As a consequence, aspects of the settlement system inferred from site exploitation territory, site function and raw material circulation are accessible only in a limited range of evidence, the more detailed of which are often provided by the stratified archives (i.e., Delpiano et al., 2019). Thanks to the layout of these contexts human behavior can be explored in relation to the environmental context: current data on systems in coastal, hill and mountain landscapes can enrich our knowledge on the seasonal nomadism practiced by Neanderthals.

Caves presumably had a main role thanks to their strategic position, being favourable for catchment in different environments through short-range movements. The variety of hunted animal species confirms opportunities to diversify the exploitation of animal resources. If we add the possibility for the human groups to easily access the primary exposures and secondary deposits of chert, we can argue that Neanderthal hunter-gatherers' ecological adaptations were deeply influenced from the not homogenous distribution of resources, so typical of the Italian landscape.

This plethora of evidence allowed the reconstruction of Neanderthal hunting behaviour. Hunting was shaped by game availability in the surroundings, particularly at hilly and mountain landscape - lowlands junction rather than specialization or selection of selected taxa, as confirmed by zooarchaeological data. Not surprisingly, caves in the pre-Alpine and sub-Alpine area, located in proximity of a range of ecological contexts, reveal that ungulates were hunted conformably to the respective specific ecological conditions at each site (Romandini et al., 2020; Terlato et al. 2021). The location and the ecological context of caves placed at low-mid altitude in landscapes dissected by deep valleys with cliffs and steep slopes in proximity to the alluvial plain and the mountain grassland belt, favoured the exploitation of different prey, despite the efforts required to cover the distance from and to the site. Although for some context we only have preliminary data, it seems that these sites were used as place where to finalize the processing of carcasses after having begun at the kill site and especially for red-deer and roe-deer. As a matter of fact, as indicated by the pattern of preservation of skeletal elements, selected anatomical parts with high nutritional value, such as limbs, especially hind, and to a lesser extent the cranium, were brought to the site. Thus, it can be envisaged well-established and cost-effectiveness patterns in the selection of specific skeletal portions, as a function of factors like the weight of the red-deer and roe-deer carcass portions and the distance between the

kill site and the home base (Romandini et al., 2014a; Terlato et al., 2021). On the other hand, some sites at the edge of the Murge karst plateau in southern Italy showed hunting adaptation behaviours, where skeletal parts from *Bos* and other ungulates were selected in relation to the exploitation of long bones for the extraction of marrow and the probable use of epiphysis and articular bones as fuel (Bosco et al., 2011).

Further signatures of uncommon hunting and dietary behaviour produced at Fumane stimulate debate around possible convergencies or divergencies between Neanderthal groups and also with modern human communities. As a matter of fact, the hunting of bears and cave bears by Neanderthals marks a particular signature, together with the ones of carnivores and rodents exploited for fur, like fox, which are animals commonly targeted during the Upper Palaeolithic (Romandini et al., 2018a; 2018b). During different periods and Mousterian cultures, it can be inferred also the role that birds played in the complexity of Neanderthal subsistence, especially when evidence of avifaunal resource exploitation was found at different sites, as shown at Fumane (Peresani et al., 2011; Fiore et al., 2016). Birds were likely not an elusive resource, possibly favoured by the ecological conditions and the presence of cliffs in proximity of the sites and their contribution in the dietary balance is far from the amount of protein provided by herbivore prey. These conditions stimulate future investigations to deep our knowledge about the acquisition of birds, the butchering process and the successive consumption.

One further point of interest is marked by the variability of technocomplexes all across the late Middle Palaeolithic, as shown by certain key sites like Grotta De Nadale, Fumane, Riparo Tagliente, Grotta Rio Secco, Grotta Madonna dell'Arma, Grotta Guattari, Grotta Castelcivita, Riparo Paglicci, Riparo Oscurusciuto and others. It stimulates debating about Neanderthals' cultural variability, ecology and economy of subsistence related to different methods of chert knapping and the design of a range of lithic tool types. These variables are under the focus of ongoing research when advanced evidence might be achieved following the same approach and protocol of investigation for identifying similarities or divergencies in the exploitation patterns of specific prey. Particularly in cases where the zooarchaeological record produces signatures of standardized actions on both soft and hard tissues, systematic practices in the sequence of faunal processing have been assessed. Further evaluation whether each range of game available at the site surroundings was exploited following standardized processes but by different cultural groups using distinct lithic technologies and related stone tools, is an intriguing issue (Romandini et al., 2020). It is undeniable that this requires in-depth inspections across Mousterian sequences, where Levallois alternates with Discoid, which were the most common technologies used by Neanderthals in Italy.

Levallois was the dominant knapping method at most of MP sites, despite of their function, geomorphological and ecological context, raw materials and hunting behaviours of their inhabitants (Palma di Cesnola, 1996; Marciari et al., 2020). Currently, early MP technology including Levallois and prepared-core technolo-

gy, branching and a large variety of retouched items, is attested since MIS 9-8 at Cave dall'Olio in Emilia-Romagna (Fontana et al., 2013), and in Latium (Villa et al., 2016). However, in multi-layered sites is attested the alternation or co-presence with other lithic exploitation strategies following the Discoid method (e.g., Fumane and Rio Secco, Bombrini and Riparo Mochi and Grotta Principe, Grotta Cavallo and Riparo Bernardini). Lamina production is also known in the Italian MP. Blades were produced both within Levallois modalities and as unipolar volumetric debitage (Marciani et al., 2020). Bladelets are sporadically attested, and the assemblages are never characterised by a sole production method. Furthermore, in the assemblages, expeditive productions are usually associated with more formal technologies. As a matter of fact, it seems plausible that the production with Discoid knapping methods by certain groups of Neanderthals supported them to adopt an opportunistic exploitation of cherts (Delpiano et al., 2018).

Neanderthal behavioural variability is also expressed by the Mousterian Quina techno-complex, as attested by lithic assemblages found at Fumane and De Nadale, both chronologically framed in a cold phase of the Upper Pleistocene between 70 and 60 ka, coincident with MIS4. The assemblages consist of cores, large flakes with thin transverse edge or short and thick flakes, and scrapers shaped by three or more orders of stepped-scaled (Quina-type) retouch. Overall, they share similarities with the Quina reduction methods and techno-functional lay-outs identified in W Europe, providing opportunities to compare evidence at the large scale in the same chronological interval (Delpiano et al., 2022).

Aside the Quina tools, sidescrapers in the Italian Mousterian industries are the most frequent retouched tools, followed by denticulates, notched tools and rare points. The intensity of retouch and resharpening varies from site to site, as the ratio between retouched and unretouched items. The fact that knappable stones and finished tools were introduced to a given site have been related to multiple factors like the duration of human occupation, site function and cultural patterns, including recycling. Chert is the mainly exploited material in the Middle Palaeolithic sites, and it was generally collected locally and regionally (within 30 km of the site). Nevertheless, the presence of very homogeneous resources related to supply areas located more than 100 km away has occasionally been identified and is always present in low percentages in most of the assemblages (Negrino & Starnini, 2003; Porraz & Peresani, 2006; Spinapolice, 2012). Raw material collected from far away sites usually arrived at the site as finished tools as part of a personal toolkit. Resources other than chert, like quartzite, jasper, silcrete, limestone, are also attested, although their frequency varies from layer to layer and from site to site, suggesting adaptation of these communities to the local landscape. Furthermore, several examples demonstrate that a variable part of the tool-kit was made and maintained not only on exogenous materials, but also on old patinated artefacts, collected, exploited or resharpened and used after their first phase of life and the new functional cycle. At Fumane, San Bernardino and Broion caves it seems that the recycling of previously abandoned and patinated flakes was not focused on specific

blanks (Peresani et al., 2015) but it was related to both expedient and curated behaviours in different moments across the stratigraphic sequences, probably due to changes in mobility strategies and toolkit provisioning in accordance with site function and the duration of occupation. Although its documentation in the archaeological record is still partial, this behaviour might also be correlated to the use of a site as a storage location over time (Peresani et al., 2015). Amongst the sites showing adaptation to the distribution of resources, it is worth mentioning the Pontinian Mousterian in coastal Latium. This ensemble of industries was based on the exploitation of small pebbles chipped also by bipolar percussion on anvil and further reduced by free-hand percussion or retouched to obtain cortical tools (Kuhn, 1990). Although dates are uncertain, the Pontinian should have been a local technological tradition from MIS 5-3. A further example of specific Neanderthal adaptation to local resources is attested by the exploitation of *Callista chione*'s marine shells to shape retouched tools (Douka & Spinapolice, 2012). This behaviour is recognized in several sites along the Tyrrhenian and Ionian coasts, although their chronological framework is still uncertain (Romagnoli et al., 2016).

In continuity with the abovementioned dynamic material culture of Neanderthals, Fumane Cave has provided clues on the evolution of human behaviour refusing the view that Neanderthals did not make use of symbolic items. Rather, they gave attention to the aesthetic or uniqueness of certain materials of biological nature. Although direct and indirect evidence are still scanty if compared to the Upper Palaeolithic, the Middle Palaeolithic groups a varied ensemble of materials also of inorganic nature like raptor claws, remix feathers, ochre, marine shells, green colour pebbles (Peresani et al., 2011; 2021, Romandini et al., 2014b).

## 5. TRANSITION FROM THE MIDDLE TO THE UPPER PALAEOOLITHIC

The pivotal phase of human evolution represented by the Middle to Upper Palaeolithic transition in western Eurasia had a definitive impact on humankind. When and how the native population of *Homo neanderthalensis* lived and was definitely replaced by *Homo sapiens* is a subject of heat debate and it is far from being clarified yet. Studies focused on the relations between them and their respective ecological conditions and material cultures were carried on based on ecological, behavioural and cognitive spheres of these humans. Recently, a multidisciplinary research conducted at key archaeological sites in Italy produced an incontestable contribution for reconstructing the bio-cultural dynamics southern Europe jigsaws of such an intriguing puzzle with contested attributions of some specific expressions of past human diversity. Amongst many archaeological and anthropological records, Grotta Fumane, Riparo Broion, Riparo Bombrini, Grotta Cavallo, Grotta Castelcivita, Grotta Roccia San Sebastiano and others contain the most important record and are successfully producing evidence of direct implication for the history of humankind in this strategic area of the Mediterranean rim (Fig. 3). The last achievements in the reconstruction

of life, subsistence, and cultures of these hominins are resumed in the following sections.

## 6. HOMO SAPIENS AND THE UPPER PALAEO-LITHIC

### 6.1. Uluzzian

An important role to unveil these dovels of the MP-UP transition puzzle is played by the Uluzzian cultural complex, which spread across the central Mediterranean rim in Italy and the South of the Balkans (Moroni et al., 2018; Peresani, 2014). Traditionally, it is characterized as a lithic and bone technocomplex that produces flakes and blades with pieces that are splintered or backed, crescent-shaped microliths, as well as end-scrapers, bone tools and ornamental beads. At the present state of research, the Uluzzian follows in time the presumably oldest known cultural expressions associated to *Homo sapiens* in Western Eurasia, namely the Neronian (Slimak et al., 2022) and the Initial Upper Palaeolithic (Hublin et al., 2020). The Uluzzian, in fact, is attributed to modern humans on an anatomical base of two deciduous teeth discovered in the 60ies in Cavallo Cave (Benazzi et al., 2011). Along the Italian peninsula, the Uluzzian is currently best known by its stratigraphic position placed above the Mousterian in cave sedimentary sequences, as in northern Italian sites. As a matter of fact, the discovery of assemblages at Grotta Fumane (Peresani et al., 2016) and Riparo Broion (Peresani et al., 2019) proved an expansion of its cultural borders further north from what was thought to be exclusively a southern extension. Unfortunately, the stratified sites along the Ligurian arch (Riel-Salvatore & Negrino, 2018) and along the southern and eastern margins of the Po Plain (Peresani, 2011; Karavanić et al., 2018) are lacking of comparable diagnostic evidence. This geographical space constrained from the Apennine, the Southern Alps, the Dinarids and the shallow Adriatic reach of MIS3, features high ecological diversity, and raises its pivotal importance in influencing human migratory routes. Furthermore, interactions between different bi-cultural worlds are relevant evidence for further increasing the frame of the on-going debate regarding the makers of the Uluzzian (Zilhão et al., 2015; Moroni et al., 2018; Peresani et al., 2019), and the biological taxonomy of the settlers recognized at Fumane (Peresani et al., 2022). Additional cultural and taphonomic data from the transitional sequence in question are needed. Indeed, serious doubts have been cast on the reliability of the stratigraphic position of the teeth found at Grotta Cavallo (Zilhão et al., 2015), based on the lack of data available to ascertain the consistency of the Uluzzian sequence from layers EIII to DI. Cavallo B and Cavallo C teeth were discovered in association with anthropically modified faunal remains, knapped stones, bone tools and marine shells which form the foundation for this technocomplex. Due to their state of preservation, uniqueness, tiny size and lack of dentine, the teeth cannot be directly radiocarbon dated. However, Moroni and colleagues (2018), based on a recent detailed re-examination from the field notes of Arturo Palma di Cesnola, confirmed that they were recovered from undisturbed deposits. To reinforce their finding context, the

analysis of two tephra layers, the Y6 and Campanian Ignimbrite, sandwiching the Uluzzian at the base (layer Fa) and at the top (layer CII) respectively, dispels doubts on the solidity of the Uluzzian at Grotta Cavallo, and sets its duration not earlier than  $45.5 \pm 1.0$  ka BP and not later than  $39.85 \pm 0.14$  ka BP (Zanchetta et al., 2018). This date range does not contradict the previous chronometry based on marine shells, charcoal and a probability distribution function for layer EIII (Douka et al., 2014) which has now been directly dated to between 44 and 43 cal ka BP (Higham et al., 2022), close to the age ranges at Broion and Fumane. Current research focuses on improvements for this resolution to confirm results with greater certainty. However, in accordance with the cultural marked affinities between the southern site and Broion mentioned above, it can be asserted that these uluzzians were the first *Homo sapiens* settling Italy. Despite the lack of any reliable evidence, the provenance of this population is presumably trackable from the Near East, notably from its coastal belt. This corridor was traditionally considered to have been well-used by early sapiens population waves since 170 ka (Hershowicz et al., 2018).

In this extensive debate surrounding the modifications in human societies that occurred in concomitance with the spread of Sapiens in Europe, a key role is covered by the shell assemblages largely used as ornamental and symbolic objects (Vanhaeren & d'Errico, 2006). Although Neanderthals were not unaware of their use at Fumane (Peresani et al., 2013), the frequency of marine and freshwater shells increases considerably across Early Upper Palaeolithic sites and in inland farther areas located great distances (Taborin, 2003; White, 2004). In these sites, the lack of seashells was compensated by freshwater taxa. For instance, the open-air site of Kostenki 14 yielded tens of specimens of *Theodoxus fluviatilis* (Sinitsyn, 2003). Similarity in the use of marine shells has been observed during the Uluzzian at both northern and southern sites, as reported at Cavallo, La Cala and Castelcivita. At Klissoura Cave in Greece, where intentionally perforated and/or fractured shells (*Cyclope neritea*, *Columbella rustica*, *Pecten* sp., *Glycimeris*, *Antalis*) were discovered throughout all the Uluzzian phases (Arrighi et al., 2020a). Specifically, *Antalis* from Cavallo Cave marks similitudes with the very few specimens found at Broion associated also to one *Theodoxus danubialis* specimen (Arrighi et al., 2020b).

Hence, the discovery of the Uluzzian at Fumane and Broion confirms that the northern cultural frontier of this complex is an archaeological reality, which dispels doubts of its existence outside the "core" area in southern peninsula, now nullified by the discovery of Colle Rotondo (Villa et al., 2018). Furthermore, this revelation stresses the importance of the northern Adriatic area as a corridor for attracting the movements of faunal and human groups from the East during the extension of landmass as a consequence of the sea-level MIS3 fall. Given the co-existence of Neanderthals and *Homo sapiens* for around 2,600-5,400 years in Europe (Higham et al., 2014) or even more (Slimak et al., 2022), genetic exchange has been claimed for this period (Fu et al., 2016), together with the fact that a possible transmission



of cultural and symbolic behaviours might have occurred between these distinctively acculturated human groups. This being the case, the Neanderthal population still remained active during the onset of the Uluzzian, not only in western Europe with the Chatelperronian technocomplex (Ruebens et al., 2015), or in some Eurasian confined areas like Murcia in southern Spain (Hoffman et al., 2018), but also in corridors like the Ligurian Arch up to 40.5 cal ka BP (Higham et al., 2014). Crucially, this is an area where the Uluzzian has not been recorded yet. Under the light of this evidence, the Uluzzian, as a behavioural system developed in southern Europe, displaces an intriguing potential for investigating stimulus diffusion and other processes of knowledge transfer in this scenario of coexistence with different humans. This ignites the need to move away from the traditional dichotomy, commonly used to explain the significant cultural phenomena of this phase exclusively as products of one hominin taxon or another.

## 6.2. Protoaurignacian

In the kaleidoscopic scenario of the spread of early *Homo sapiens* into Western Eurasia, the appearance of the Aurignacian corresponds to one amongst the most intriguing cultural dynamics of the Upper Palaeolithic. Thus far, research has focused on the origin and chronological expansion of this technocomplex and its arrival to different regions, regardless of the climate and ecological conditions faced by the new incomers (Nigst et al., 2014; Shao et al., 2021). The *Homo sapiens* populations progressively settled following eastern-northern Mediterranean and central-European trajectories (Hublin, 2015; Mihailović, 2020), bringing with them the diffusion of the new cultural traits represented by portable and cave art, musical instruments (not in Italy, yet) and evidence of use of specific categories of symbolic objects for personal purpose, even peculiar of Italy (Martini, 2007; Arrighi et al., 2020; Sigari, 2022). For instances, marine shells, collected and modified for making ornaments are one further evidence in support of past human communication behaviour and cultural exchange during this early Upper Palaeolithic phase (Vanhaeren & d'Errico, 2006). Despite the paucity of marine and freshwater shell assemblages of similar age and composition in southern Europe, shells from Fumane, Bombrini, Mochi, Castelcivita, partly smeared with red ochre, confirm similarities in the taxonomic composition (Peresani et al., 2019; Arrighi et al., 2020a). Among these elements, shells of *Homalopoma sanguineum* probably played a fundamental role in maintaining a communication system over a large geographic area. They might have represented group consciousness or even longstanding ethnic identities between the Rhone basin and the eastern Mediterranean regions (Vanhaeren & d'Errico, 2006; Nitu et al., 2019).

Early modern humans' subsistence strategies were successful for their dispersal throughout Italy despite the MIS3 abrupt climatic oscillations and the uneven topographic and ecological conditions. In northern Italy one of the first European regions where Aurignacians settled (Frouin et al., 2022), archaeozoological data indicate seasonal site occupations during late spring/summer. The exploitation was mostly oriented on ibex and cham-

ois, hunted in the site surroundings in a mostly open and patchy woodland landscape under cold climatic conditions. A recent estimation of Net Primary Productivity (NPP) reflects how its fluctuations in the Prealpine area, where Fumane cave is located, affected the biotic resources in contrast to known Mediterranean sites. Nonetheless, Protoaurignacians' resilience was successful in a mosaic of environments that were affected by significant climate changes and supported rapid dispersal of human groups (Marin-Arroyo et al., 2023).

About the lithic industry, recent studies carried out on the Fumane lithic assemblages have contributed to a more precise definition of the Protoaurignacian through a high-resolution inspection of the production of blades and bladelets (Falcucci & Peresani, 2022). This re-evaluation revealed that dissociate reduction sequences were addressed to obtain bladelets within a single and continuous knapping from the same core as the result of its progressive reduction. The first goal of production was thus bladelets which did not originate from a broad range of independent core reduction strategies. An additional analysis focusing on carinated core technology furnished further evidence to the theory about a common technological background shared by the Protoaurignacian and the Early Aurignacian (Falcucci et al., 2017). In fact, the major difference with the Protoaurignacian is the frequency of retouched bladelets, which are much more common in this complex. This emerging view challenges the traditional focus paid on the northern Aquitaine Basin and raises once again the importance of the Mediterranean Basin as a region worthy of consideration (Gennai, 2021). Furthermore, the dense stratigraphic sequence of Fumane is stimulating investigations on cultural diachronic variability across the time interval framed by these cultural units. The goal is to test if the Early Aurignacian with its new organic artifacts followed the Protoaurignacian. Data have shown that the Protoaurignacian techno-typological features do not switch throughout the stratigraphic sequence and across the Heinrich Event 4, thus challenging the debated view that environmental deteriorations at the onset of this event explain remarkable differences detected in technologies and human adaptive systems in the Early Aurignacian by respect to the Protoaurignacian (Falcucci et al., 2020). By the other hand, the appearance of split-based points in the youngest phase of the sequence at Fumane is once again an expression of extensive networks that allowed this technological innovation to spread in Italy (Tejero & Grimaldi 2015) and across different Aurignacian regions.

## 6.3. Gravettian, Early Epigravettian and the Last Glacial Maximum peopling of Italy

Despite their biological and cultural success compared to the previous European "native" populations, Upper Palaeolithic *Homo sapiens* hunter-gatherers experienced dramatic biological turnovers during the Late Pleistocene glacial cycle, as attested by discontinuous archaeological record (Djindjian et al., 1999; Bocquet-Appel et al., 2005). Nonetheless, these Last Glacial Maximum (hereafter LGM) human groups reacted by increasing their resilience at some middle latitudes, but also through migrating at large scale along the corridors

connecting European regions. Demography and behaviour were thus deeply affected, resulting in the synchronic and diachronic development of a variety of archaeological cultures in different regions and at different times. For this reason, the timing and pattern of multiscalar shifts that occurred from the LGM to the onset of the Late Glacial (hereafter LG) interstadial (14.7 cal ka BP) are considered among the most important events, also in Italy. Before 30 ka BP in the Alps, glaciers were already growing and reached their maximum extent around  $25.0 \pm 1.7$  cal ka BP (Monegato et al., 2017). Despite these geographic and climate changes (Antonlioli & Vai, 2004), in Southern Europe several regions experienced the development of open boreal forests and highly productive wetlands thanks to more favourable conditions supporting (Badino et al., in press) which also helped the survival of several mammal species (Svenning et al., 2008): here they could thrive while large part of their former distribution areal, in Central and Northern Europe, was covered by ice sheets. In turn, hunters-gatherers groups' subsistence was favoured by the presence of a rich mammal fauna in these southern refugial areas in turn gave subsistence to hunters-gatherers groups enhancing their capability to maintain large-scale networks (Soffer & Gamble, 1990; Djindjian et al., 1999; Moreau, 2009) as attested also by large scale distribution of *Homalopoma sanguineum* shells in the Balkans (Nitu et al., 2019). As a matter of fact, south of the Alpine chain, more favourable conditions allowed the survival and delayed extinction of important consumers like cave bears (Terlato et al., 2019a).

Nonetheless, a full understanding of the way Upper Palaeolithic groups modulated their biological, cultural and social adaptation to the Late Pleistocene climate change is still far from being achieved, especially in regions of strategic importance for their geographic position, geomorphological setting and biodiversity. The reason is also due to the low number of archaeological sites that have been radiocarbon-dated to the LGM: these are in western Liguria, in the northern and north-eastern fringes of the Po valley, along the Tyrrhenian coast and, to the East, in Apulia (Palma di Cesnola, 2001; Mussi, 2001) (Fig. 3). All of them are either caves or rockshelters, since only one open-air settlement has been excavated so far (Mussi & Peresani, 2004): these are the Piovesello and Bilancino sites on the Apennine range. At Piovesello, a site situated on the watershed of the northern Apennine (Peresani et al., 2018), unexpected archaeological evidence dated to GS-5 was recovered proving that open, extreme landscapes were the edge of elevational logistical movements of human groups along mountain ecozones. Bilancino is a specialized site excavated on a fluvial terrace of the western slope of Central Apennine (Aranguren & Revedin, 2008). Acquisition strategies of lithic raw materials hint for a well-established territory extended from the central Tyrrhenian coasts to across the mountainous chain towards Umbria or Marche regions, where chert outcrops provided a relevant amount of knappable stone (Aranguren et al., 2015). Overall, this patchy Gravettian archaeological record in Italy is to some extent the result of a lack of scientific investigation (Palma di Cesnola,

2001). Site size is also different in the two better investigated areas. Some substantial or even large sites are known at sea level in Liguria at the Balzi Rossi. Grotta Arene Candide, further East, is possibly another major site. In southern Italy, evidences of human occupation are very scarce in number indeed. Grotta Paglicci witnessed traces of repeated frequentations and human burials across its long-stratified deposits, thus becoming a reference cultural complex site (Palma di Cesnola, 2004). Following the Aurignacian, the Gravettian technological signatures spread in a rather short time interval across Europe (Reynolds & Green, 2019) and also Italy. Here, the earliest known Gravettian assemblages at the edge of the Great Po Plain are dated at Fumane to ca. 35-34 cal ka BP and slightly later at Paglicci Cave in the southern Adriatic region (Palma di Cesnola, 2004; Talamo et al., 2014; Falcucci & Peresani, 2019). The early Gravettian appears in Italy to be more homogeneous than the later stages of this technocomplex, being characterized by the presence of backed points and the absence of other typical tool types. After this phase, the Adriatic and Tyrrhenian records took different cultural trajectories: Noailles burins were designed, manufactured and used in western Italy as a result of cultural contacts between adjacent regions (Santaniello & Grimaldi, 2019), but they are missing in the archaeological record of Adriatic Italy and the Balkans (Mihailovic & Mihailovic, 2007).

A key region for human and animal migrations was the Great Adriatic-Po Plain (GAPR). This vast continental shelf emerged as consequence of the LGM sea level low stand, extending from the Western Balkan Peninsula to peninsular Italy (Peresani et al., 2021). This area is a paradigmatic case, thanks to its peculiar geographic setting and climatic and ecological variability, which supported refugia for temperate species and witnessed vast movements of populations. The human adaptive flexibility expressed by the Gravettian-Epigravettian material culture, human mobility, subsistence and symbolic thinking from this region has been the focus of multidisciplinary investigations. In the last decade new paleo-geographic, ecological and anthropogenetic data were obtained from a large set of sources circumscribing the GAPR, including the Italian Prealps, to boost our understanding of the settlement dynamics. Summarizing, cultural and petroarchaeometric evidence of chert tools reveal the existence of large-scale circulation patterns across the GAPR of finished or semifinished early Epigravettian artefacts made of chert coming from the formations of the Umbria-Marche Apennines in the sub-alpine zone, Istria and Dalmatia, thus pointing to the GAPR as a suitable land for Gravettian and Epigravettian hunter-gatherers. This point of view was questioned several times since the end of the 80's of the 20th century. Some contrasting positions supported at times the view of a plain seasonally crossed by large migratory herbivores, thus rich in game, water and a variety of resources, especially along water courses, across ecotones, around lakes and on the coastal and estuarine environments. Under this light the plain has become more attractive for human populations than the karstic inland, sporadically settled on a strictly seasonal basis and careful planning (Peresani et al., 2021, and refer-



Fig. 3 - Key Upper Palaeolithic sites in Italy: 1) Grotte di Pradis; 2) Altopiano del Cansiglio; 3) Riparo Villabruna; 4) Riparo Dalmeri; 5) Riparo del Broion; 6) Covolo di Trene e Grotta di Paina; 7) Grotta di Fumane; 8) Riparo Tagliente; 9) Balzi Rossi; 10) Grotta della Basura; 11) Arene Candide; 12) Piovesello; 13) Bilancino; 14) Grotta la Fabbrica; 15) Fosso Mergaoni e Grotta della Ferrovia; 16) Fonte delle Mattinate; 17) Grotta Polesini; 18) Colle Rotondo; 19) Grotta Paglicci; 20) Serino; 21) Grotta di Castelcivita; 22) Grotta della Cala; 23) Grotta della Serratura; 24) Grotta del Romito; 25) Grotta di Santa Maria di Agnano; 26) Grotta del Cavallo e Grotte della Baia di Uluzzo; 27) Grotta delle Veneri; 28) Grotta Romanelli; 29) Grotta San Teodoro; 30) Grotta dell'Addaura (source <http://tinitaly.pi.ingv.it>; elab. by D.Delpiano)..

ence therein). Connections between sites located over 250 km apart from another do not contradict the scenario drawn in the innermost continental Europe, when hunter-gatherers inhabited with variable continuity cold, cold-temperate and often moister biomes. At the edge of the GAPR, stable terraces along the Apennine belt were potential areas to settle on a seasonal base or maintain a network of exchanges between different groups.

Although data about human mobility during the

middle Gravettian are too sparse in the GAPR to reconstruct the settlement dynamics in this landscape, a marked trend in the design and circulation of chert artefacts has been highlighted starting with the Late Gravettian-early Epigravettian and up to the early Late Epigravettian (Peresani et al., 2021). This event coincided with a renewal in hunting weaponry around 24 cal ka BP, mainly consisting in the introduction of shouldered points rather than other backed implements. The long-

range circulation of these points encompasses several macro-regions of Europe and could be related to new mobility strategies or changes in human groups and their way of exploiting resources in this territory. Around 24 cal ka BP, the early Epigravettian replaced the former technocomplex in coincidence of the GI-2, a climatic threshold marking major cultural changes in western Eurasia (Ruiz-Redondo et al., 2022). Extensive renewals in the variety of marine species used as ornaments are recorded only during the Late Epigravettian, hence leaving uncertainty on a wide chronological range (Martini et al., 2007).

Paleogenetic studies focusing on Gravettian and post-Gravettian hunter-gatherer individuals, combined with fine resolution radiocarbon chronologies and cultural data allow a better comprehension of the population dynamics that accompanied modern human re-expansion towards the end of the LGM. Specifically, biomolecular data reveal that several population transformations took place across Europe, with reduced diversity in mtDNA during the LGM, but also survival of European maternal gene pool (Fu et al., 2016; Posth et al., 2016). In this scenario, a population turnover took place around 18 cal ka and well before the LG interstadial, as revealed from genetic discontinuity due to the spread of individuals of the Villabruna cluster (an individual retrieved in Riparo Villabruna, dated to 14.2-13.8 cal ka BP; Aymar et al., 1992), sharing distinctive affinity to present-day populations from the Near East. Additional genome-wide data have been achieved from the analysis of the individual from Riparo Tagliente, so essential to understand the distribution of such ancestry through time in southern European climatic refugia (Bortolini et al., 2021). This incoming genetic component largely replaced the ancestry identified also in older Magdalenian-related individuals from central Europe (Fu et al., 2016) and supports the hypothesis that, from at least 19-18 cal ka BP, European populations were broadly interconnected across the GAPR and beyond.

#### 6.4. Late-glacial, the submersion of the GAPR and the spread of Epigravettian hunter-gatherers

After the Last Glacial Maximum, the changes of vegetation and animal distribution viewed the peopling of Italy as a gradual process marked by the progressive colonization of new territories following (Naudinot et al., 2014; Vescovi et al., 2017) and coinciding with the spread of the Epigravettian. This cultural complex consists in an ensemble of industries following the Gravettian until the end of the Pleistocene. As stated above, the reaction of human groups to the LGM physical and ecological turnovers deeply contributed to the shaping of our present genetic ancestry.

In the GAPR, the end of the LGM witnessed, also in lowlands, quick geomorphological changes due to the corresponding collapse after 18 cal ka BP of the Alpine glaciers, starting their final withdrawal. The effects of these modifications on human occupation along river terraces in the plain are not yet detectable. Conversely, at the northern edge of the GAPR in the Prealpine foothills, Riparo Tagliente was a location persistently settled by human groups for the exploitation of local biotic and abiotic resources which marks one of

the first steps of the pioneering colonization of the inner mountain belt on relatively stable areas (Fontana et al., 2009). Evidence of this phase is however scanty. Such scarcity of data hampers the reconstruction of the peopling of the Italian Eastern Alps and Dinarides triggered by the climatic amelioration of the LG interstadial starting at 14.7/14.5 cal ka BP. In the LG interstadial, the progressive rise of the Adriatic coastline combined to the expansion of the treeline up to 1700-1800 m a.s.l. in the SE-Alps (Vescovi et al., 2007) are among the key factors leading human groups to intensely occupy the interior mountain ranges along new routes and to expand their settlements (Bertola et al., 2007; Naudinot et al., 2014) (Fig. 3). Late Epigravettian penetration, firstly limited to valley floors and high plateaus around 500 m above modern sea level (amsl), reached mid-altitude territories during the second part of the LG interstadial with the full development of a logistical occupation network at the ecotone between coniferous woods and alpine prairies (Bertola et al., 2007). This organisation corresponds to a seasonal mobility strategy based on sites that are functionally complementary to each other and located at different altitudes. Regarding the faunal target, the most exploited game was ibex, which is the dominant species in Dalmeri rock shelter and other mid-altitude sites (Tagliacozzo and Fiore, 2000), alongside with marmots, systematically exploited in the Pradis plateau (Romandini et al., 2012; Nannini et al., 2022). Lithic industries evolved towards a progressive simplification of the production systems, associated with the persistence of standardized lithic backed tools used as projectile implements in response to specific functional requirements and constraints (Duches et al., 2018; Montoya et al., 2018).

Other than the alpine slope, the general increase of evidence and radiocarbon dataset at the beginning of the Greenland Interstade 1 (GI-1), has been interpreted as the result of a major change in the socio-economic system of Epigravettian groups. Changes in lithic technology occurred during this period are likely to be associated with some major modifications of the mobility patterns with clear increase of task-oriented sites and a global multiplication of the sites. Evidence is sparse all over Italy, but more frequent in the Ligurian Arch, eastern Alps, northern and central Apennine, Sicily and patches along the Tyrrhenian and Adriatic coasts. In Liguria, an exceptional ichnosite is the Cave of B asura near Toirano, where about thirty footprints dated to 14 cal ka BP are referred to a small group of visitors (Avanzini et al., 2021).

The Pleistocene-Holocene transition also marked a major turnover in the history of the environment and prehistoric peopling of high latitude regions as much as mountain territories. After the GI-1, the progressive decrease in temperatures in coincidence of the Greenland Stage 1 (GS-1: 12.9-11.7 cal ka BP), gave rise to a set of modifications with which the hunter-gatherers related. The spread of hunter-gatherers is recorded with variable details in the Alps, the eastern sector, and the central Apennine, which were the scenarios of extensive research on human occupation since the 1970's. The archaeological record shows a relative scarcity of sites with evidence of GS-1 occupation, contrasting with the

major record available for both the GI-1 and the Greenlandian in the same region. Although GS-1 climatic cooling had an impact on vegetation (Vescovi et al., 2007), apparently it had only a limited effect on the exploitation of the middle altitude mountain landscape. Compared to GI-1 sites, GS-1 valley floor sites are characterized by the increase of roe deer in the spectrum of hunted faunas, while at higher elevations they document the prevalent predation of ibex and to a lesser extent deer (Fiore & Tagliacozzo, 2006). Evidence of smaller newly-established human settlements has been interpreted as resources stress in the human adaptation to mountain environment (Mussi & Peresani, 2011), and as reflecting shorter visits to this area, within a continuous but distinct use of resources, also through adoption of caching behaviour related to a higher mobility pattern (Peresani, 2006).

In continuity with the Epigravettian, the Early Mesolithic colonization covered the central-eastern Italian Alpine region, as attested by archaeological evidence richer than in any other mountain district of Europe (Montoya et al., 2018 and references therein). The Sauveterrian settlement system model was in accordance with a seasonal nomadism between highland and lowland camps located on the main valley bottoms, next to small lakes and/or sheltered under erratic boulders, attesting a varied functionality from residential camps to ephemeral short-term foraging task sites, intended to be exploited as different proximal ecological niches. Site variability thus reflects human mobility within a given system of gathering food or exploiting resources seasonally, mostly based on the hunting of ungulates (red deer, roe deer, wild boar, ibex and chamois), complemented with other smaller prey like pikes and cyprinids, sweet water molluscs, and marsh turtles in the valley bottoms (Wierer & Boscato, 2006; Bazzanella et al., 2007).

## 7. CONCLUSIONS

The Pleistocene human peopling of Italy was a complex process developed under the influence of different geographic and climatic contexts since the end of the Early Pleistocene. Their impact on the biology and culture of pre-Heidelbergensis, Heidelbergensis, Neanderthal and Sapiens scavengers and hunter-gatherers has been reconstructed through an ensemble of proxies, with more and more increasing detail for the Late Pleistocene latest attestations. Human biological turnovers do not support exclusive explanation of the variability of behavioural, economic and cultural aspects, which are expressed sometimes across chronologically constrained sequences and claim for a wider approach to disentangle the origin of cultural change and innovative behaviours. Italy is a potential context for providing clues for an in-depth inspection of the relations between different hominin groups and taxa.

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