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Inspecting human evolution from a cave. Late Neanderthals and early *sapiens* at Grotta di Fumane: present state and outlook

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Summary - *Of the many critical phases of human evolution, one of the most investigated is the transition from the Middle to the Upper Palaeolithic with the pivotal bio-cultural substitution of Neanderthals by* Homo sapiens *in Western Eurasia. The complexity of this over ten thousand years phase raises from the ensemble of evidence ascribed to the diverse adaptations expressed by Neanderthals and the first representatives of our species. In countless archaeological records Neanderthals left clear traces of a cultural variability dotted with innovations in the technology of stone and bone tools, alongside with manifestations in the range of the symbolic sphere. Together with other aspects of daily life, this evidence contributes shedding light on the cognitive aptitudes of those hominins and reassessing gaps in Pleistocene human diversities. Among archaeological contexts, the cave of Fumane in the Monti Lessini (Veneto Pre-Alps, northeastern Italy) is a key site. It is positioned along the potential trajectory of hominins moving into southern Europe from eastern and southeastern regions and includes a finely layered sedimentary sequence with cultural layers ascribed to the Mousterian, Uluzzian, Aurignacian and Gravettian. The ensemble constitutes one of the most complete, detailed and dated continental stratigraphic series from a segment of the late Pleistocene between 50 and 30 ka cal BP in a cave context of Southern Europe. Assessments based on sedimentological and palaeontological record provide indicators for framing Neanderthals in their respective ecological contexts since the late Middle Pleistocene until their demise during MIS3. On-going research is producing data ascribable to the human ecological relations and the interaction with specific natural resources, thus contributing to shed light on the complexity of Neanderthal behavior. Thanks to the high-resolution archaeological record of the earliest appearances of* Homo sapiens, *Fumane also provides clues to compare life, subsistence, and cultures between these Pleistocene hominins for comprehensive reasonings on our unicity.*

Keywords - *Palaeolithic, Human behavior, Cultural change, Pleistocene, Palaeoecology, Multidisciplinary research, Italy.*

Introduction

The pivotal phase of human evolution represented by the Middle to Upper Palaeolithic 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 heated debate and far from being clarified yet (Hublin 2015; Vaesen et al. 2021; Zilhão 2020). Collected data on the ecological, behavioral and cognitive spheres of these taxa, drive studies focused on the relations between these biological taxa and their respective ecological conditions and material cultures. Pieces of this intriguing puzzle with attributions, sometimes contested, of some specific expressions of past human diversity have been unveiled in recent years from multidisciplinary research at archaeological sites producing an incontestable contribution for reconstructing the bio-cultural dynamics also in Southern Europe (Benazzi et al. 2011; Hublin et al. 2020; Slimak et al. 2020). Of many archaeological and anthropological records in Eurasia, the Grotta di Fumane contains one of the most important records and is fruitfully producing evidence of direct implication for the history of humankind in this strategic area of the Mediterranean rim. The following manuscript resumes the last achievements in the comparation of life, subsistence, and cultures between these Pleistocene hominins.

The Fumane cave context

The Monti Lessini form a mountainous area in the Veneto Prealps where the Fumane cave (Grotta di Fumane) lies at 350 m a.s.l. in a narrow stream valley. It is a carbonatic pleateau tilted to south and dissected by deep gorges with scattered caves, shelters and different biotopes. Fumane cave is part of a fossil karst complex formed during the Neogene. It opens in micritic and calcarenitic limestones at the base of a carbonate cliff (Ooliti di San Vigilio Formation, Upper Lias), extensively dolomitized. It develops from a previous pit filled at the base of the present-day explored deposits with residual dolomitic sands. The pit walls and the sedimentary deposits preserved on it were partially eroded during the Pleistocene due to geomorphic processes along the stream valley. They were brought to light after road construction works in 1950. In this year, also the first explorations were carried out by the Natural History Museum of Verona (1964 and 1982) at the bottom of the sequence exposed by the road cutting (Cremaschi et al. 1986). A new series of investigations begun in 1988 (Bartolomei et al. 1992) under the patronage of the Superintendence for the Archaeological Heritage of Veneto and it is still going on year after year.

Three tunnels open at the upper levels of the karst complex. The main (B) and secondary (C) tunnels form the major rock-shelter, while a third western (A) tunnel connects with B forming a vault at the present-day cave entrance in the calcarenitic bank, still unstable, due to several fractures running roughly parallel along the overhung rock wall. These cracks are consequence of several collapse events also provoked by repeated frost actions occurred during the late Pleistocene, which caused the sealing of the cave entrance and the deposition of large blocks and slabs which were gradually removed during the past excavation campaigns (1988-1996). Hence, the cave entrance was originally positioned few meters south than the present. Today, the sheltered entrance is about 30 sqm large as result of the combined action of rock collapses.

The sedimentary sequence, brief cultural and chronological layout

The whole karst complex preserves a sedimentary component estimated to be approximately 220 m3 according to the geometry of the visible sections and 12m thick as measured from the present-day ground to the top above the cave entrance (Abu Zeid et al. 2020). Four macro-units, S, BR, A and D have been distinguished based on lithology and archaeological evidence (Bartolomei et al. 1992; Cremaschi et al. 2005). Traces of repeated human frequentations are recorded across macro-unit S, while in macro-unit BR – except the high density in cultural remains of BR11 – the anthropic evidence suggests short-term occupations characterized by dispersed lithic artefacts and faunal remains or hearths with scattered tools and bones. Traces of much more intense human occupation have been inferred from the macro-unit A record. Overall, the Paleolithic sequence includes a cultural record ascribed to the Mousterian, Uluzzian, Aurignacian and Gravettian cultural periods.

Above the residual yellow massive dolomite sandy plug, the macro-unit S groups layers of dolomite sand, angular stones, surface weathered boulders, and traces of Neanderthals' use of the cave from layers S10 to S1, for a total thickness of 1.4m. This differentiation is based on the grade of anthropization rather than on the lithological content. Macroscopic features, grain size, heavy minerals, micromorphology, and magnetic properties indicate that pedogenesis affected the

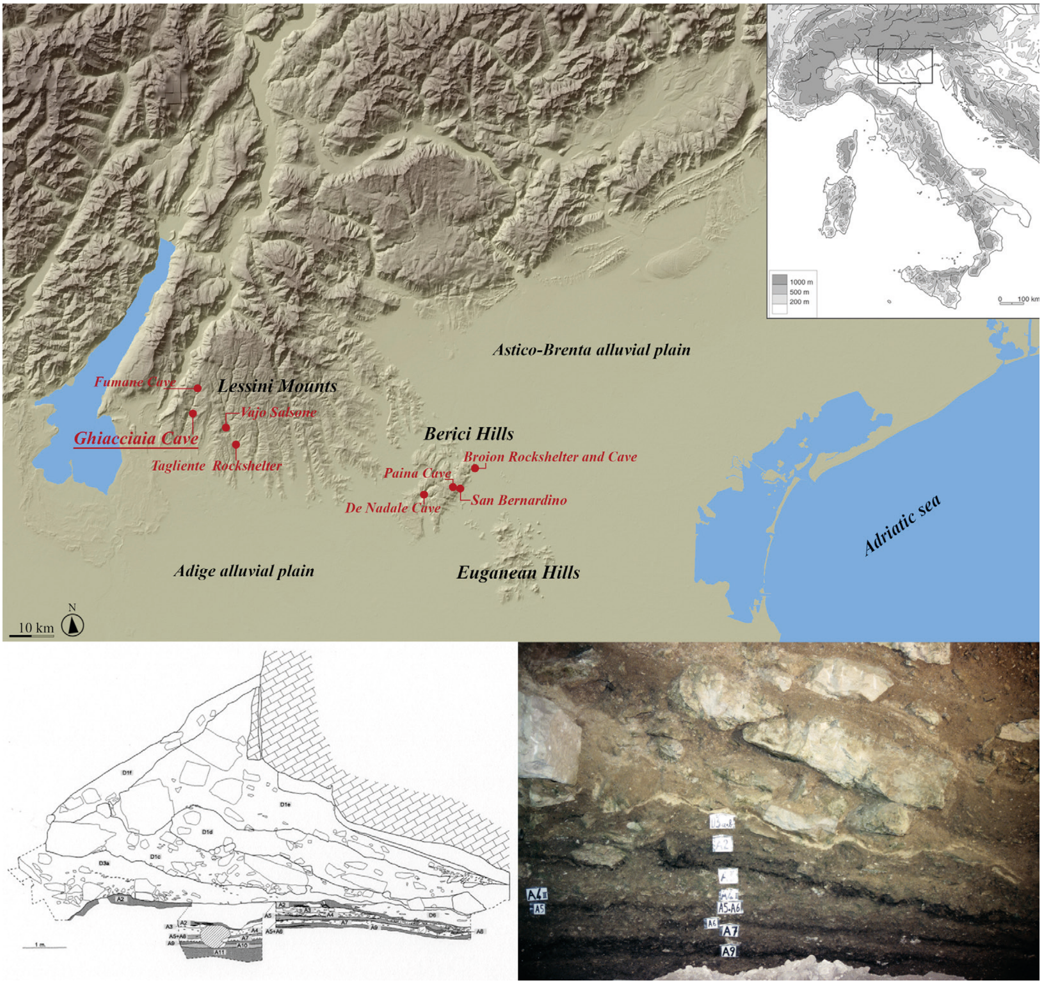

***Fig. 1** - Location and stratigraphy of Fumane cave: top, physical map of the North of Italy showing the geographical location of the cave and of the main Middle Palaeolithic sites; bottom left, the upper part of the stratigraphic series showing the late Middle Palaeolithic (units A11-A4), Uluzzian (A3), Protoaurignacians (A2), late Protoaurignacians (D3-D1c) and Gravettian (D1d) units; bottom right, the lower part of the stratigraphy visible on the main sagittal section removed after 1995.*

bedrock in conditions of climatic instability, followed by moderate roof degradation and hydrological redistribution of the dolomite sands. The overlying macro-unit BR is a massive sedimentary body made of stones and aeolian dust (Cremaschi et al. 2005). Layer BR11 is a 0.4m thick dense accumulation of cultural material, ungulate bones still articulated, knapped stones, charcoal and associated combustion features. A massive sedimentary body groups units from BR10 up to BR7a for a total thickness of 1.6m. Above, units from BR6 to BR4 lie in paraconcordance with BR7. These coarse open-work frost breccia seal scattered Mousterian fire-places and associated material evidence (Cremaschi et al. 2002). An increased content in the fine fraction characterizes layers from BR3 to BR1, covered by a clear paraconcordance by the macro-unit A (Fig. 1).

Macro-unit A is an aggradation of numerous thin to very thin parallel levels and lenses grouped into stratigraphic units labelled A13 to A1 from the bottom to the top. Apart from A13 and A12, composed of flat angular stones embedded in yellow residual dolomite sands and silts, the other units consist of angular fine-medium sized stone layers originated from frost-shattering. They are characterized by variable percentage of sand and aeolian dust becoming almost exclusive from the sheltered area to the exterior. Sediments are generally loose or densely packed, but never intensively cemented. Macro-unit A contains variable content of organic and cultural material related to traces of intense and repeated human uses of the cave. Mousterian living floors are documented in A11, A10, A9, A6-A5 and A4 (Peresani 2012), Uluzzians in A3 (Peresani et al. 2016) and proto-Aurignacians in A2 and A1 (Bertola et al. 2009; Broglio et al. 2006, 2009). All these have been extensively explored at the cave entrance until unit A9. Units A13, A12 and A7 are archaeologically sterile, although A12 contains portions of the overlying anthropogenic unit A11, displaced by post-depositional deformations. Unit A11 is composed of loamy dark-brown sediment, with stones associated with abundant lithic artefacts and faunal remains. Above this, unit A10 yielded anthropogenic lenses and levels embedded in various stone-lines and levels of stones resulting from frost-shattering. Unit A9 comprises several layers showing a succession of thin, dark, anthropogenic levels alternating with loose, stone-supported layers or thin sandy levels. Unit A7 is a stony layer between A9 and A6. The latter consists of dark sediment with high content of cultural anthropogenic remains. Units A5 and A4 yield less archaeological remains than A6 and are composed of frost-shattered slabs with variable sand content and aeolian dust, which becomes more prevalent towards the outermost part of the cave. The early Upper Palaeolithic sequence is recorded in units labelled from A3 to A1, plus D6 and D3, where A3 is composed of slabs, loose stones and loamy fine fraction, A2 and A1 are thin Aurignacian cultural layers alongside with D6 and D3, which are part of the Macro-unit D at the top of the sequence. The cave entrance and the main tunnels were sealed from this Macro-unit mostly composed of boulders resulted from rock falls and stones, sands and variable content of aeolian dust accumulated during MIS2. The thickness of the layers gradually decreases moving towards the cave-mouth where post-depositional deformations acted under the influence of periglacial conditions at the onset and during MIS2 (Cremaschi et al. 2005). Macro-unit D includes evidence of Aurignacian human presence in D3d, D3b and D3a, becoming very scarce in D1c and is replaced in the last anthropic level, D1d, by Gravettian cultural evidence (Falcucci and Peresani 2022).

Aside the chronological uncertainty still affecting the middle-lower part of the sedimentary sequence due to controversial dates (U/Th on bone teeth and TL on burnt chert artefacts and sediments, see Gruppioni et al. 2005 and Martini et al. 2001, respectively), a large set of radiocarbon dates prove that the late Mousterian, the Uluzzian, the Aurignacian and the Gravettian fall in the MIS3 up to the onset of MIS2 (Douka et al. 2014; Higham et al. 2009; Martini et al. 2001; Peresani et al. 2008). The time range of unit A9 is bracketed by the minimum radiocarbon age at 47.6 ky cal BP (Higham et al. 2014; Peresani et al. 2008) and the lower chronological boundary of layer A5+A6 at 44.8ky cal BP, which is also the upper boundary of layers A6 and A7. A new set of radiocarbon dates is thus needed for providing chronological resolution from A6 down to A11. The final Mousterian from A5+A6 to A4 dates to between 44.8 and 42.2 ka cal BP (Higham et al. 2009) and is followed by the Uluzzian up to 40.4 ka cal BP and the Protoaurignacian in A2 and A1 to 41.2–40.4 ky cal BP (Douka et al. 2014; Higham et al. 2009). Layers D3, D6, D3+D6 record the late Protoaurignacian at 38.9–37.7 ky cal BP (Falcucci et al. 2020; Higham et al. 2009), and D1d the Gravettian to 35 ky cal BP as maximum age (see discussion in Falcucci and Peresani, 2019).

Palaeoenvironmental contexts of the late Middle – early Upper Palaeolithic sequence

The ensemble of macro-units A and D constitutes one of the most complete and detailed continental stratigraphic series from a segment of the late Pleistocene (ca. 50-30 ka BP) in cave context of the Adriatic region and the Italian Peninsula. Assessments based on sedimentological, pedological and palaeontological records have been reported elsewhere (Cassoli and Tagliacozzo 1994; Cremaschi et al. 2005; López-García et al. 2015) and will be resumed here. Ecological indicators are provided by small mammal, mammal and avifaunal associations, which are representatives of a rich and diversified ensemble of animals brought to the cave and exploited by humans, carnivores and birds of prey. Since pollen grains are not preserved, palynological analyses are precluded, so that direct palaeobotanical reconstructions rely on small vertebrate palaeontological associations and at a lower level by the anthracology of charred wood. This latter indicates progressive cooling from the basal units up to A9, defined by the gradual and regular decrease of *Pinus sylvestris/mugo* to the advantage of larch which progressively predominates over *Picea/Larix* and *Betula* sp., other than *Pinus sylvestris/mugo* (Maspero, 1998). More in-depth analysis on unit A9 shows the presence of typical mountain vegetation with Larch (*Larix decidua*) dominating the landscape on very steep or washed-out slopes in association with pine and birch species, whereas the presence of spruce, *Picea abies* L., seems to testify to a forest environment, denser along the valley floor (Basile et al. 2014). This trend is interrupted in A5-A6 where, despite the dominance of *Picea/Larix* (probably the common European larch), other taxa like willow (*Salix*), ash (principally *Fraxinus excelsior*, but also *Fraxinus ornus/angustifolia*), birch (*Betula* sp.), maple (*Acer* sp.,) make their appearance together with pine (Peresani et al. 2011a). From A3 onwards, a climatic deterioration starts and culminates in units D6-D3, as indicated by a marked increase in fir tree charcoal (Maspero, 1998).

Resolution from small mammals

In light of palaeoclimatic and palaeoenvironmental data obtained by the analysis of the small-mammal assemblages, various fluctuations were detected (López-García et al. 2015). The Mousterian units A11 to A9 show a high diversity index, high percentages of woodland formations, high values for MAT (7.6-9.1 °C), MTW (16.8-17.2 °C) and MTC (between -0.78 and 1.80 °C), and relatively high MAP (1348-1414 mm). This suggests a temperate and relatively moist period, with a landscape dominated by open-woodland formations. These levels might correspond to an interstadial before HE5. The large-mammals assemblage is consistent with these temperate humid conditions and forested habitats, as testified by the abundance of the ungulate species *Cervus elaphus* (red deer) and *Capreolus capreolus* (European roe deer) (Fiore et al. 2004; Romandini et al. 2014a).

The successive units A7 and A6 record the prevalence of *M. arvalis* and *M. agrestis* (respectively 50.3% and 37.1% of the association) over forest species, indicating a contraction of woodland formations, relatively high percentage of rocky environments and a sharp decrease in MTC (between -0.18 and -0.99 °C) and MAP (1305-1319 mm). These units are probably related with a cold and relatively dry period with a landscape dominated by open meadows and less abundant *Pinus* sp. (Fiore et al. 2004; Peresani et al. 2011a) which could correspond to Heinrich Event 5 (H5).

Units A5+A6 and A4 are characterized by high values in the diversity index (0.88-0.90), high percentages of woodland formations, high values in MAT (8.1 to 9.0 °C), MTW (16.4-17.2 °C) and MTC (0.9 to 2.1 °C), and a relatively high MAP (1408-1491 mm). Hence, these units are probably related with a temperate and moist period with a landscape dominated by open-woodland formations as suggested by the increase of species with forest environmental requirements such as *Apodemus* (*Sylvaemus*), together with *Muscardinus avellanarius*, *Dryomys nitedula*, *Glis glis* and *Eliomys quercinus*. These conditions likely correspond to the Greenland

Interstade 12 (IS12), in accordance to continental conditions recorded at large-scale.

The successive Uluzzian (A3), Aurignacian (A2 to D1c) and Gravettian (D1d) units show an alternation of two cold and one warm phases. The small-mammal assemblage indicates that units A3 to D3a+b relate to two cold periods (situated between IS12 and H3): the first one was observed in A3 until A1, as attested by the increase of remains of *M. arvalis* and *M. agrestis* and the presence of *M. oeconomus* and *C. nivalis,* hinting to a brief worsening of the climate a slower woodland formations, and lower values for MAT, MTC and MAP. This phase might be associated to the Heinrich Event 4 (H4), as suggested by the decrease in arboreal pollen detected along the Lake Fimon pollen core, located about 35 km to the east (Pini et al. 2010; Badino et al. 2020). The second phase corresponds to the formation of units D6 to D3a+b. It is characterized by a relative decrease in woodland formations, MAT, MTW and MTC but with an increase in MAP. Finally, a warm and dry phase recorded in units D1c and D1d is characterized by faster woodland formations, higher MTW but lower MAP, occurred probably during an interstade (GI8-5) between GS2 and H3. Finally, unit D1e (with no cultural remains) shows the lowest values of the entire sequence for the diversity index (0.75), the marked reduction of forest species such as *Apodemus* spp. and waterside species, as well as the highest percentage of rocky-habitat species, to advantage of *C. nivalis* and *M. arvalis*, MAT (6.5 ºC), MTW (15.4 ºC) MTC (-1.4 ºC) indicating that this unit is related with a cold and relatively dry period with landscape dominated by open meadows, probably existed during Heinrich Event 3 (H3).

Ecology of avifaunal assemblages

The ecological framework showed by the avifaunal assemblages reflects diverse environments, rock cliffs and alpine meadows, mountainous zones and ponds, woodlands of high mountains and subalpine forests (Cassoli and Tagliacozzo 1994b; Fiore et al. 2016; Gala and Tagliacozzo 2005; Peresani et al. 2011b). The bird species identified belong to extant Italian avifauna with the exception of two Boreal species: the willow grouse (*Lagopus lagopus*) and the snowy owl (*Bubo scandiacus*), both never observed in Italy in historical times. During the cold climatic phases of the Pleistocene, these species shifted southwards their distribution, seeking suitable climate conditions (Carrera et al. 2018a,b, 2022). Taxa linked to open and rocky environments are the most abundant. Bearded vulture (*Gypaetus barbatus*), golden eagle (*Aquila chrysaetos*), alpine chough (*Pyrrhocorax graculus*), red-billed chough (*P. pyrrhocorax*), common raven (*Corvus corax*), Eurasian crag martin (*Ptyonoprogne rupestris*) and white-winged snowfinch (*Montifringilla nivalis*) indicate the presence of rocky cliffs, while treeless terrains with rocky outcrops are inferred by rock partridge (*Alectoris graeca*), rock ptarmigan (*Lagopus muta*) and horned lark (*Eremophila alpestris*). Conversely, the presence of wooded areas in the surroundings of the cave is indicated by the black grouse (*Lyrurus tetrix*), woodcock (*Scolopax rusticola*), stock dove (*Columba oenas*), common woodpigeon (*Columba palumbus*), Boreal owl (*Aegolius funereus*), tawny owl (*Strix aluco*), white-backed woodpecker (*Dendrocopos leucotos*), Eurasian jay (*Garrulus glandarius*), and Eurasian bullfinch (*Pyrrula pyrrhula*). The presence of coniferous forests is pointed by the Northern nutcracker (*Nucifraga caryocatactes*) and the common and parrot crossbill (*Loxia curvirostra* and *L. pytyopsittacus*). Open grasslands are indicated by common quail (*Coturnix coturnix*), grey partridge (*Perdix perdix*) and Montagu's harrier (*Circus pygargus*), whereas corncrake (*Crex crex*) and Northern lapwing (*Vanellus vanellus*) point to the presence of wet meadows. Willow grouse (*L. lagopus*) and snowy owl (*B. scandiacus*) could indicate tundra-like open areas such as moors and peatlands. Wetlands or slow-flowing water courses are represented by ducks (*Anas platyrhynchos*, *Anas* cf. *crecca, Spatula querquedula, Aythya ferina*), waders (*Tringa glareola* and *Actitis hypoleucos*) and Rallidae (*Rallus aquaticus* and cf. *Gallinula chloropus*). Substantial evidence on the exploitation of this avifauna by Neanderthals is documented (Fiore et al. 2016; Peresani et al. 2011b; Tagliacozzo et al. 2013; Romandini et al. 2016).

As a whole, the bird assemblage points to an Alpine ecological setting with forests and open areas. Several identified bird species (rock ptarmigan, black grouse, golden eagle, bearded vulture, white-backed woodpecker, Alpine and red-billed chough, Northern nutcracker, white-winged snowfinch and common crossbill) currently live in Italy at considerably higher altitudes than Fumane. The presence of their remains at 350 m asl suggests the downward shifting of the vegetational zones during MIS 3 due to the lowered climate value parameters. As concerns unit A9, the avifauna suggests the presence of temperate conditions and woodland, open, rocky and water environments. Colder climate conditions affirm in layer unit A5-A6, as indicated by the willow grouse and by the increase in the bird taxa from open environments. These latter species underwent a sharp decline in layer A4 (attributed to the GI12 interstadial) balanced by an increase in layer A3, marking the beginning of Heinrich Event 4, which persisted in layers A1+A2. The presence in these layers of the parrot crossbill, a Boreal species which is currently rarely observed in Italy, supports the presence of cold climatic conditions. The bird taxa in A1+A2 and A3 also attest the persistence of open forests, despite the deterioration of the climatic conditions (Gala and Tagliacozzo 2005; Tagliacozzo et al. 2013). Lastly, the snowy owl in layer D1d-1e possibly indicates the onset of harsh climatic conditions of the Heinrich Event 3.

Environmental indications from mammal assemblages

In the mammal assemblages, Cervids prevail from units A11 to A4, until their abrupt prevalence of Alpine ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*) which relate to cold and dry conditions with unit A3 and the Protoaurignacian in A2 (Cassoli and Tagliacozzo 1994; Fiore et al. 2004; Peresani et al. 2011a; Tagliacozzo et al. 2013). As concerns the ecological context, the faunal spectra are consistent with a picture of persistent afforestation with some temperate trees (Pini et al. 2010). However, due to chronometric incertitude, we cannot exclude the occurrence of DO events that supported moderate mixed conifer (*Pinus*, *Picea* and *Betula*) forest contraction with the expansion of steppic communities. Fumane cave could thus well be inserted in a context not far from open-spaced forests, in conditions of transitive to discontinuous Alpine grasslands or pioneer vegetation on carbonate rocks. Their faunal assemblages indicate that the prevalent associations of ungulates during the Middle Palaeolithic - mostly red deer and roe deer with fewer chamois and ibex, with limited exploitation of Bos/Bison, giant deer, elk and wild boar - fit the ecological conditions around the site and show shifts correlated with the most relevant climatic oscillations as shown by the predominance of the alpine ibex in the Upper Palaeolithic sequence (Fiore et al. 2004; Terlato et al. 2019).

The late Neanderthals at Fumane

Human remains

Late Neanderthals who settled at Grotta di Fumane left as huge as varied ensembles of traces related to their daily life, subsistence, economy, technology and symbolic behaviour. Direct evidence is provided by human remains. All of them are deciduous teeth: Fumane 1, a lower left second deciduous molar found in unit A11; Fumane 4, an upper right central deciduous incisor and Fumane 5, a lower right lateral deciduous incisor coming from layer A9I and layer A9 respectively. Fumane 4 and Fumane 5 probably belong to the same individual, approximately six years old, younger than the one to which Fumane 1 belongs (ca. 10 years old). Aside some difficulties due to heavy incisal wear on Fumane 4, Neandertal affinity is secured from metric data of crown and cervical outline, lateral enamel thickness and non-metric dental traits like the mid-trigonid crest (Benazzi et al. 2014). Spatially-resolved chemical/isotopic analyses and histomorphometry of these teeth, together with other Neanderthal specimens coming from sites placed in the same region of Fumane and compared to the *Homo sapiens* decidual tooth from the Protoaurignacian of Fumane revealed that these Neanderthals shared with modern humans a similar nursing strategy, with onset of weaning at 5-6 months (Nava et al. 2020). Metabolic constraints during early life were thus similar and supported excluding late weaning as a factor contributing to Neanderthals' demise. Biofilm preserved on these Fumane Neanderthal teeth, together with the *H. sapiens* tooth, has contributed to reconstruct oral metagenomes. These revealed similitudes between the microbial profiles of both Neanderthals and modern humans, thus implying the same functional adaptations in nutrient metabolism. These are related to an apparent *Homo*-specific acquisition of salivary amylase-binding capability by oral streptococci, suggesting microbial coadaptation with host diet (Fellow-Yates et al. 2021).

Palaeoliving floors and anthropogenic features

Anthropogenic features, fire-places and purported combustion features were discovered from unit A11 to A4 during extensive excavations (Peresani et al. 2011a). Their frequency decreased moving up towards the top of the sequence. The most common shape of the combustion features is circular or subcircular, with a diameter generally ranging from 20 to 50 cm, and between 4 to 10 cm deep. Some features preserved several sublayers that were also visible during the excavation. The outcomes of microcontextual analyses carried out by integrating micromorphology with organic petrology, found out that only a few of these features were primary, intact hearths (Marcazzan et al. 2022). Indeed, many of them appear to be the remnants of partially preserved occupation horizons and peripherally related to combustion. Of this vast majority of features originated by a single activity it is worth to mention structure A5_SIII for its peculiar traits: the considerable size (~100 cm of diameter), the presence of a half-circle of slabs delimiting it towards the exterior of the cave, and several sublayers suggests that this feature was re-used at the centre of the activities. The spatial distribution of these combustion features varies in each stratigraphic context and suggest the existence of distinct areas for manufacturing activities, prey exploitation, combustion, and wasting. In addition, the number of features seems to follow the same pattern outlined by artifacts and ecofacts, suggesting a human use of the cave shifting from intense and persistent (e.g., in A6) to more ephemeral (e.g., in A5 and A4). Furthermore, variable fuel sources, herbaceous tissues, woody tissues and a mix of wood, herbaceous and bones were identified in different features, implying a high degree of flexibility in the fuel-selection strategies of the Neanderthal occupants.

Cultural layouts and exploitation of faunal resources

Along the cultural sequence from the top of BR7 up to unit A4, a marked break in lithic technology caused by the replacement of the Levallois with Quina assemblages occurred in BR6, BR5 and BR4 (Peresani 2012). It culturally frames Fumane in the Quina techno-complex, and it turned the site in one of the most iconic examples in this part of central southern Europe (Delpiano et al. 2022). The appearance of the Quina coincides with a specific and targeted use of the dwelling space. Lithic and faunal remains scattered in proximity of hearths record a palimpsest originating from repeated events involving the activation of combustion structures, together with the consumption and discard of bones and lithics in BR6 (Cremaschi et al. 2002). The assemblage of BR5-BR4 is almost exclusively composed of Quina and demi-Quina cortical and uncortical large scrapers used to process an omogeneous category of materials through a limited range of activities, a few flakes and cores. This transect suggests that cultural-economic factors must be carefully examined in the light of further (functional and zooarchaeological) investigations.

The major indicator of cultural variability across the late Middle Palaeolithic sequence is the lithic production system, supported by the exploitation of local and semi-local chert and flint contained in the Upper Jurassic to middle Eocene carbonatic formations in the western Monti Lessini. These raw materials vary in macroscopic features and mechanical properties which affect their aptitudes to flaking. The most exploited raw materials are the ones from Maiolica (Biancone), Scaglia Rossa and Scaglia Variegata Alpina Jurassic and Cretaceous formations. These kinds of cherts displayed finer-textures than those from Tertiary calcarenites, and oolitic limestones of Tenno formations. Usually, their finding at Fumane reflects the lithological variability of the area, which is so rich in lithic sources easy to collect within a range of 5-10 km from the site, and where knappable rocks are also available loose in fluvial deposits, on the slopes and in soils. Moreover, Quina and Discoid (unit A9) technologically featured Neanderthals also picked up older and patinated artifacts, following a well-known practice even for the limited territory of Middle Palaeolithic north-eastern Italy and despite the technological background (Peresani et al. 2015).

A major discontinuity corresponds to the first massive anthropization of macro-unit A, providing new evidence of technological variability at different levels in the context of the lithic production systems. Considering the volumetric concept and its exploitation (Boëda 1994), Discoid complexes are in A9 and embed in A10 multilayered unit alternating throughout the sequence with Levallois assemblages in A11, A10V, A10, A5-A6 and A4, where Levallois recurrent modalities make the reduction sequences comparable. Indeed, closer similarities emerge amongst A11, A10V, A10, A5-A6 than in A4. The cultural sequence ends with the replacement of the Levallois technology by other volumetric concepts and flaking modalities in the Uluzzian unit A3.

Units A11 and A10

These Units record variable density of artefacts and ecofacts. Lithic industry in Unit A11 is largely based on Levallois production, as clearly visible from the first decortication phases and the obtention of Levallois flakes through uni-bidirectional modality (Peresani 2012). In A10, lithics are present in the form of flakes, cores, retouched tools and fragments ascribed to Levallois and Discoid procedures, either alternating or coexisting with no relation with the type of flint. A10 is articulated in several subunits from A10V to A10I (Peresani et al. 2017). Starting from the lowermost, a loose breccia below A10V records a dearth of artifacts that can be ascribed to the phase of full production of Levallois. In some instances, they were retouched into simple scrapers. The uni-directional recurring Levallois dominates the A10IV and A10IV/AIII. In these layers, lithic blanks are more reduced and transformed into lateral, transversal and convergent scrapers. Also A10III is rich of Levallois artifacts. These blanks were obtained with uni-bidirectional and centripetal modalities as well. This level records a slight increase of cores on flakes. Along the same line, in the lithic assemblage of A10IBRII the uni-bidirectional Levallois is the main reduction strategy. The rare cores and the abundance of cortical blanks pinpoint to the spatial fragmentation of the operational chains. In A10I, to the dominant Levallois is associated the Discoid as well. This latter is attested by cores, pseudo-Levallois points, centripetal and dejeté flakes, and the exploitation of core-flakes (Fig. 2).

The faunal assemblage consists of abundant ungulate and few caprine, as mainly the red deer (*Cervus elaphus*) and the roe deer (*Capreolus capreolus*), as showed by bone remains of the limbs. Also, elk (*Alces alces*) and giant deer (*Megaloceros giganteus*) were hunted. Less abundant are big (*Bison priscus* e *Bos primigenius*) and medium (*Capra ibex* e *Rupicapra rupicapra*) size bovids (Fiore et al. 2004; Peresani et al. 2017). In addition, in this layer was found the only remain of horse of Fumane. Units A11 and A10 also yielded a rich avifaunal assemblage, however still undetermined at taxonomical and taphonomical levels. Ongoing analysis will shed light on the nature of these materials and aim to confirm the exploitation of birds documented by residues on lithic tools (Cnuts et al. 2022) and to reinforce the previous finding of a cut-marked claw of golden eagle showing the deliberate removal of the claw from the toe (Fiore et al. 2004).

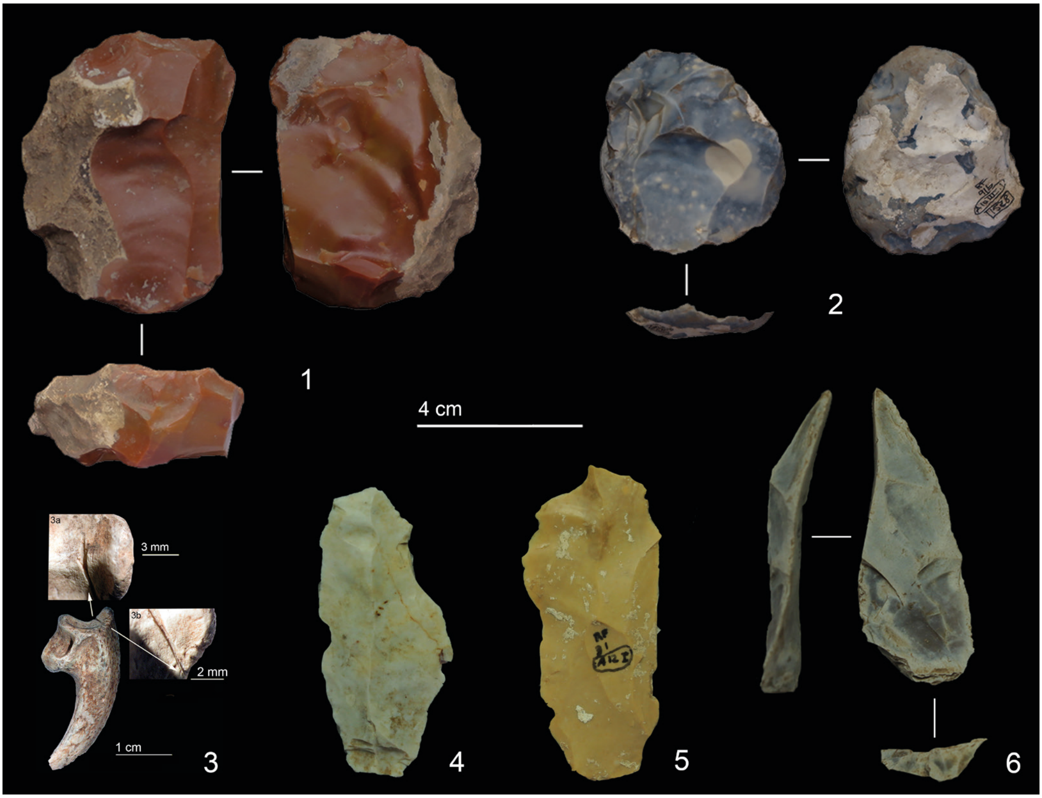

***Fig. 2** – Lithic artifacts from units A11-A10: 1-2) unidirectional recurrent Levallois cores; 3-5) Levallois blades; 6) side scraper on core-edge cortical Levallois blade (pictures by J.Gennai); 7) cut-marked ungual phalanx of Golden Eagle* (Aquila chrysaetos) *from Unit A12 (after Fiore et al. 2004; Peresani et al. 2017; Gennai 2021, modified).*

Unit A9

The cultural relevance of this unit was highlighted on several occasions, both for the lithic production technology and for different aspect of Neanderthals' innovative behavior, diet and subsistence. A9 records an almost exclusive application of the Discoid technology embedded between two Levallois cultural units - A10 below and A6 above. Results from a techno-economic analysis carried out on this large lithic assemblage produced consistent data for the reconstruction of the spatial distribution of the reduction sequences and its relation to local, semilocal and allochtonous geological sources of knappable cherts. Alongside with the complete and ordinary reduction sequences - mostly developed using materials collected within a radius of 5km - semi-local cherts were reduced in accordance with their different physical aptitudes and exploited to perform specific tasks. Thus, the organization of subsistence economy combined both daily residential exploitations embedded within the local territory and logistical planning due to the quality and distance of available raw materials sources (Delpiano et al. 2018). Furthermore, several lithotypes and gastropod fossil shells found in A9 were collected from longer distances. Old patinated recycled artifacts were recognized in this context as well (Peresani et al. 2015).

The technological Discoid industry is typically represented by cores, thick flakes, pseudo-Levallois points, backed flakes with sharp opposing edges, polygonal and triangular flakes. The production system was structured around two reduction sequences: the first was the main and complex one, while the second was simpler and less productive. Both shared the same goal of producing short, strong, and sometimes pointed artefacts, as attested by pseudo-Levallois points, backed flakes, and subcircular, quadrangular, or triangular flakes (Peresani 1998; Delpiano et al. 2018; Lemorini et al. 2003). The main reduction sequence exploited blocks and nodules, whereas the secondary one used flake-cores either originated from by-products (i.e., cortical flakes) or directly introduced onto the site. Cores yielded usable blanks right from the initial steps, with the core outlines gradually changing from unidirectional to Discoid pattern with simple schemes to obtain parallel or convergent detachments. Simple schemes were then replaced by centripetal ones. This process also involved morphological and functional arrangements as the management of the convexities of the cores. The results of these operations were cores with polyhedral shape. Core reduction patterns were also virtually inspected after the discovery of structure A9II_SXLII, a concentration of a dozen flakes with their core, giving us a precise view of what the Neanderthal knapper had in hand both initially and throughout the reduction of the core (Delpiano and Peresani 2017; Delpiano et al. 2017). Thanks to the volumes caught by the 3D recording of these artefacts and with a virtual support, it was possible to conduct an accurate and complete analysis, allowing to explore the informative potential of this multiple refitting. It was noticed how the core exploitation was planned in advance and intended to rectify the core volumetrics and convexities in order to maximize the production. This evidence provided relevant information about the Neanderthal's theoretical and practical concepts, knapping gestures and choices the knapper had to face during lithic production. Moreover, 3D models allowed to achieve reliable information on sizes, angles, convexities, and exploited volumes of the core with its products, included the missing ones (Delpiano et al. 2019a).

Retouched tools are few in number, represented by scrapers, points, and denticulates. They were shaped using bone retouchers which, however, do not reveal an intense and continued use (Martellotta et al. 2020). The morphology of the bone blanks seems to play a major role, and influenced the selection and use of these tools. Previous functional analyses based on macroscopic use-wear have shown that retouched tools were used for different purposes, on soft, medium-hard, and hard materials (Lemorini et al. 2003). A particular class of tools is represented by several artifacts purposedly modified creating a back via retouch or through the modification and adjustment of an already existing back (Delpiano et al. 2019b). It was shown that some of these modifications were aimed to adjust the shapes of these knives and/or scrapers for manual handling, although traces consistent with hafting cannot be ruled out (Delpiano et al. 2019b). Furthermore, these adjustments involved mainly tools used in precision activities, implying different levels of expertise and technical skills and thus raising the backing of the blanks to be considered a typical feature in the technological repertoires of late Neanderthals. Although during the Middle Paleolithic backing is still not systematic or standardized, it is recognized as an important step in the design of stone tools for manual activities and the development of tool ergonomics. Backed artifacts are generally associated with systematic hafting, mostly because they are widespread within Middle Stone Age (MSA) or since Early Upper Paleolithic (EUP) assemblages attributed to *Homo sapiens*. However, in Europe these tools were firstly manufactured by Neanderthals belonging to other lithic technologies than the Discoid one and their investigation unravels various aspects about the behavioral complexity of Paleolithic humans (Fig. 3).

The fauna exploited in A9 is dominated by cervids like red deer, giant deer and roe deer, with smaller amounts of bovids and caprids like ibex and chamois and other mammal species, as well as birds. Actions that can be attributed to different stages of the butchery process of

***Fig. 3** – The Mousterian "package" of unit A9: 1-4) selection of artifacts – pseudo-Levallois points (1-2), quadrangular core-edge-removal-flake (2) fractured scraper (3) – showing modification of the back; 5) refitted flakes and core from the structure A9II_SXLII; 6) the* Aspa marginata *shell with location of the micrographs (a–c), a) palimpsest of striations present on the inner lip, b-c) outer surface covered with micropits and networks of grooves produced by bioeroders and filled of pure red iron oxide; 7) different views of the cut-marked carpometacarpus of Eurasian black vulture (*Aegypius monachus*); 8) proximal carpometacarpal fragment of Merlin (*Falco columbarius*) with detail of the peeling traces (8a) and detail of the cut-mark (8b); 9) distal radius of Greater spotted eagle (*Clanga clanga*) with breakthrough of the surface. Scales = 100 µm unless indicated otherwise (after Delpiano et al. 2017, 2019b; Peresani et al. 2011b, 2013a; Romandini et al. 2016, modified).*

mammals, such as skinning, dismembering, and filleting, were identified as well (Romandini et al. 2014a). The composition of skeletal elements allowed to infer that selected anatomical parts with high nutritional value (both marrow and meat), such as limbs, especially hind, and to a lesser extent the cranium, were transported to the site in respect to well-established cost-effective patterns. These patterns reflect the selection of specific skeletal portions, as a function of several factors like the weight of the red-deer and roe-deer carcass portions and the distance between the kill/butchering site and the home base. Aside the efforts required to cover this distance to the cave in a landscape so dissected by deep valleys with cliffs and steep slopes, the location and the ecological context of Fumane supported differentiation in game exploitation.

Other than these mammals, the exploitation of birds has also been confirmed by the presence of traces like cut-marks and gnawing scores on Black grouse (slaughtering) vertebrae and other bird bones (Fiore et al. 2016). Neanderthals had an interest in the Alpine chough as food too. In the archaeological context, a differentiated distribution pattern of the avifaunal remains indicates the way how the activities were organized around the exploitation of these prey. A clear picture is provided by the remnants of the Alpine cough. These birds were dismembered and cooked in the exterior central area of the cave rather than along the eastern wall. On the contrary, the distal wing portions underwent a different treatment, not linked to consumption but to the careful extraction of other anatomical elements such as sheaths, feathers, and tendons. Indeed, interests towards birds lay also in the collection of feathers, wings and bones of four raptor, the Cinereous vulture, Bearded vulture, Greater spotted eagle, and falcons (Peresani et al. 2011; Romandini et al. 2016).

To reinforce this view that Neandertal material culture conceived the use of adorments and symbolic items, unit A9 yielded a fragmentary Miocene-Pliocene marine shell: the *Aspa marginata*, was collected at a fossil exposure probably located more than 100 km southern to the site and deliberately transported and painted. The outer surface of the shell was smeared of ocher, as testified by residues of pigment trapped inside micropits produced by bioeroders (Peresani et al. 2013a). Furthermore, clusters of striations identified on its inner lip support the hypothesis that this object was modified and suspended by a rope for visual display as a pendant.

Unit A5-A6

Unit A5-A6 is known for the prevailing reappearance of the Levallois technology in the lithic industry, while the production of bladelets and artefacts obtained by Discoidal volumetric cores is anecdotical (Peresani 2012). The Levallois expresses a range of variability consisting in the production of blades and flakes as a consequence of the application of different recurrent flaking modalities which generally follow one another until the conclusion of the core exploitation. This sequence does not outweigh a dominant focus towards the extraction of elongated Levallois flakes, blades and their related by-products. After the core shifts from uni or bidirectional to centripetal modality, flakes less constrained in shape and dimensional rates are obtained until the last steps of the reduction sequence. These Levallois artefacts - together with other cortical products issued from core shaping - are retouched in simple, double and convergent scrapers in addition to rare points. Bone retouchers are also associated with this assemblage (Jéquier et al. 2012, 2018). These were selected from long bones and metapodial diaphyseal fragments belonging to Cervids and less frequently to Caprids, except for one antler object found in layer A6. Among these bone tools there is the exceptional presence of a side scraper made on the diaphysis of a large ungulate (Romandini et al. 2014b).

The faunal assemblage includes a rich association of ungulates, carnivores, and birds from diverse environments and climates in the cave surroundings, here characterized by open and rocky habitats, alpine forest habitats and humid zones. This assemblage is thus ecologically comparable to Unit A9, notably for the most abundant species like red deer, ibex, and roe deer, whereas chamois, bison, and giant deer are less frequent (Peresani et al. 2011a; Terlato et al. 2019). Moose, horse, and wild boar are rare. All ungulate species, with the exception of horse and wild boar, bear consistent traces of human exploitation like cut-marks, percussion cones and notches as well as impact scars, supporting the anthropic nature of bone accumulation. The same holds for the few carnivores like fox,

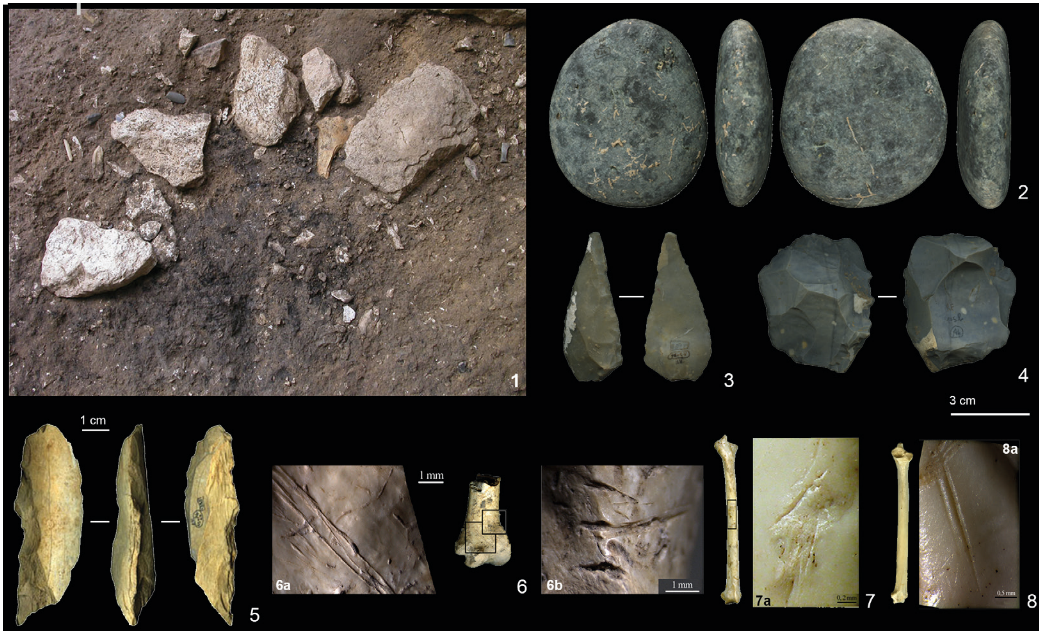

*Fig. 4 – The Mousterian "package" of unit A5-A6: 1) view from the inner cave of fireplace A5_SIII; 2) serpentinite pebble from layer A6; 3) side scraper on Levallois blade; 4) Levallois core; 5) bone scraper from layer A5+A6; 6) cut-marked distal end of right ulna of lammergeier (***Gypaetus barbatus***) with close-ups (6a, 6b); 7-8) cut-marked right (7) and left (8) ulnae of Alpine chough (***Pyrrocorax graculus***) with close-ups (after Peresani et al. 2011a,b, 2021; Romandini et al. 2014b, modified).*

brown bear and cave bear with the exception of wolf, butchered for fur recovery and defleshing. Cave bear and brown bear were potential Neanderthals' competitors for environmental resources. Evidence proving the predation of varied age classes of these mammals during or near the end of hibernation has also been reinforced with data from Rio Secco Cave to 49-42 ky cal BP, despite it remains sporadic in Europe (Romandini et al. 2018a).

In addition to the butchery marks on herbivore and carnivore species, cut-marks were also found on bird bones. They are linked to disarticulation of some wing elements of black-feathered birds like bearded vulture and Alpine chough, and also other raptors (red-footed falcon) and Passeriformes (common wood pigeon) (Peresani et al. 2011b). Specifically, some groups of scrape marks located around the sites of feather attachment produced from a lithic implement suggest the cut of the skin and the removal of the remiges. The most representative cases are observed on two right ulnae of Alpine chough. All these modified wing bones indicate deliberate action of recovering part of the wing or retrieving long feathers for adorning heads, bodies and clothes as the most parsimonious explanation.

The unearthing of green serpentinite smooth and flat pebbles with use modifications from this context points to the collecting of unusual, sometimes colorful mineral materials by Neanderthals at Fumane only from ca. 44 ka cal BP, despite the large availability of green serpentine pebbles in the alluvial beds few kms far from the cave. The selection and use of these unique pebbles relates to cognitive and functional criteria that influenced the Neanderthals' attraction for green materials, which remains exceptional for the Middle Palaeolithic (Peresani et al. 2021) (Fig. 4).

Unit A4

Unit A4 records a cultural continuity in the final Mousterian context with unit A5-A6, although some features hinting to the appearance of the Uluzzian in unit A3 are observed. The lithic assemblage is tied to the industry of A5-A6, A10 and A11 in the use of the Levallois technology following both unipolar and centripetal modalities. Thus, typical retouched tools like simple, double and converging scrapers are present, along with evidence of bladelets production although ephemeral (Peresani et al. 2016). The use of bipolar flaking of flakes is recorded as well, with limited splintering from both poles of a variety of flakes. Another novelty in A4 is represented by a handful of flakes, corticated, typical Levallois or other types, modified with an abruptly straight or convex back on one side, while the other edge is left thin and unretouched. After a former attribution of this assemblage to an initial phase of the Uluzzian, its position was re-assessed after few improvements in the definition of the technocomplex raised from elsewhere studies. Definitely, the assemblage from A4 effectively roots in the regional Middle Palaeolithic (Peresani et al. 2019).

Hunted game is still largely dominated by red deer, over ibex and roe deer. The bone assemblage indicates that red deer was first dismembered at the kill site, and that the highly nutritional portions were selected to be consumed inside the cave. Bird bones were also disarticulated and defleshed, as attested from traces on golden eagle, Alpine chough and other species (Tagliacozzo et al. 2013).

The Uluzzian and the first *Homo sapiens* at Fumane

The Uluzzian and the related arrival of the first *Homo sapiens* at Fumane is represented by an ensemble of evidence consisting in anthropogenic features, lithic industry and bone tools, other than faunal bones (Peresani et al. 2016). A very peculiar structure, not comparable with those found in the Middle Palaeolithic, is a concentration of a few hundred of flakes and bladelets, cores, backed knives, bones and charcoal discarded in a shallow pit. In addition to this, a hearth associates to flakes and bone shafts scattered around, pointing to reduced intensity in the human presence prior to the Aurignacian. The Uluzzian chronology is constrained between 44.7 and 40.4 ka cal BP although it partly overlaps with the Protoaurignacian unit A2 (Douka et al. 2014). Lithic knapping in A3 records radical changes due to the appearance of a series of operative sequences in the production of predetermined flakes, with the counterpart of the dramatic decrease in the number of Levallois items: flakes issued from centripetal cores, thin and wide flakes extracted from roughly prepared flat cores, flakes with a cortical back and an opposite cutting edge issued from plates, and sturdy flakes with thick edges related to bifacial cores with rhomboidal structure. Splintered pieces were made on a wide range of flakes, including Levallois ones. Backed pieces shows straight or convex back. Their number, however, remains low compared to other Uluzzian sites (Peresani et al. 2016). This might suggest a specific use of the cave albeit it is still to be assessed. Bone tools are one awl, two fragments of worked rib and few retouchers (Tagliacozzo et al. 2013; Romandini et al. 2020).

Compared to A4, A3 records a decrease of red deer in favor of ibex and chamois with the appearance of bison and woolly rhinoceros. Although evidence of exploitation is attested for most of these species, red deer dominates the assemblage over ibex and roe deer. Carnivores like wolverine, lynx, and ermine are also present in the assemblage, with uncontestable evidence of skinning of fox, wolf, and brown bear (Fig. 5).

The Protoaurignacian in unit A2

After extensive excavations, Unit A2 has produced one amongst the most complete evidence of an early Upper Palaeolithic cave settlement in Europe. It records changes within *Homo sapiens* cultures occurred 41.2 – 40.4 cal BP,

[Fig. 5](#) – The Uluzzian "package" of unit A3: 1) shallow pit filled of discarded material A3_SIV; 2) dense agglomeration of charcoals A3_SII; 3) unipolar core (with refitted maintenance flakes) exploited for producing squared flakes with natural back opposed to cutting edge; 4) large single flake core with refitting of unipolar flake and maintenance flake; 5) centripetal flake core; 6) unipolar short bladelet core with refitted bladelets and platform preparation flakes; 7) end-scraper on cortical flake with thinned lower face; 8) refitted splintered piece; 9) splintered flake; 10-11) splintered pieces; 12-15) backed knives with complete back; 16) awl made from a rib of mammal and close-ups of technological modifications (rounding, polish, longitudinal and transversal striae, depressions - 1,3,5), modifications produced while creating the awl blank through splitting (1), striations produced for regularizing the lower surface and the distal end of the awl by flint scraping (2,3), functional modifications (rounding, polish, striae and depressions - 4,5) and use-wear traces (6) (after [Peresani et al. 2016](#), modified).

represented by dwelling structures, lithic industries, bone and antler tools, painted stones, and ornamental objects. The structures are mostly located at the entrance of the present-day cave and just outside it. They include hearths and toss-zones with heaps of burnt remains, sometimes delimited by limestone slabs emerging from the ground. Other hearths are more superficial and some of them were featured from a peripheral belt of long charred wood branches and ash in the central zone (Broglio et al. 2003, 2006; Peretto et al. 2004). These features are remarkably different than the Middle Palaeolithic ones for their multi-layering and clear definition hinting for a change in the organization of human activities at the site (Marcazzan et al. 2022). Within this Proto-Aurignacian context was found a decidual *Homo sapiens* tooth (Benazzi et al. 2015).

The lithic industry is characterized by blades and bladelets and marks a rupture with the Uluzzian in A3. Platform, multidirectional, and parallel core reduction methods have different incidence: the first is the most represented, used to obtain blades and bladelets by direct organic percussion from carenoid-type, pyramidal, and prismatic unipolar cores. Multidirectional and parallel methods, instead, were aimed to produce flakes of various morphologies. The goals of stone knapping are regular and straight blades than twisted bladelets and microbladelets (Falcucci and Peresani 2018; Falcucci et al. 2017, 2022; Caricola et al. 2018). Together with some by-products, regular blades were also modified into endscrapers, the iconic tool of the Upper Paleolithic. At Fumane, both in A2 and late Protoaurignacian units D, the fabrication and maintenance technology of endscrapers led these tools to assume a consistent functional pattern with high levels of specialization in hide (Aleo et al. 2021) rather than bone and antler working, despite their morphological variability due to the use of laminar products and flakes. Endscrapers were also hafted. Comparison with endscrapers from transitional technocomplexes in Europe, exclude any direct relation between these Aurignacian tools and previous traditions. Straight bladelets were shaped into points and Dufour bladelets by means of marginal abrupt retouch (Falcucci et al. 2018; Falcucci and Peresani 2022). Bone industry is mostly made of cervid (red deer and giant deer) bone and antler (Bertola et al. 2013). In unit D it is composed of bone points, also split at the base, awls, borers, smoothers and tiny fragmentary points (Bertola et al. 2013) (Fig. 6).

Processing and use of mineral pigments at the cave is attested in the sedimentary sequence, as well as by red ochre stains still visible on stone and bone industry, portable art and ornamental marine shells. Concentrations of red pigments were exposed on the A3 layer substrate. These are two thin large ochre levels, that discontinuously sandwich layer A2. The smallest layer (S21) extends over about one half square meter in the cave-mouth, while the largest one (A2R) covers about 20sqm in the rear of the cave (Broglio et al. 2009; Cavallo et al. 2017). Hematite was also treated by heating (Cavallo et al. 2018). Red and dark red-purplish coats of pigment applied on stones portray graphic units with figurative themes in units A2, D3, and D5. They are considered among the main cultural symbolic features of earliest *Homo sapiens* portable art: a frontally depicted anthropomorphic figure wearing a headgear, handling an object and featured of two bilateral appendixes at the middle portion of the body; a zoomorphic shape interpreted as a mustelid; a circle with appendixes; possible scalariform geometric signs, and other more uncertain depictions of vivid red colour traces covering the whole surfaces, including the fractured edges of some stones (Broglio et al. 2009; Sigari et al. 2022) (Fig. 7).

Fumane further contributes to deep our knowledge on the ethno-cultural diversity of the Aurignacian across Europe and the Mediterranean rim as expressed through differences in the use of a range of categories of personal ornaments. The large assemblage of marine shells retrieved from the Protoaurignacian and late Protoaurignacian contexts is composed of over 800 perforated and unperforated shells representing 68 different taxa, including 56 gastropods, 11 bivalves and one scaphopod, all collected from MIS3 seashores. Use-wear traces and

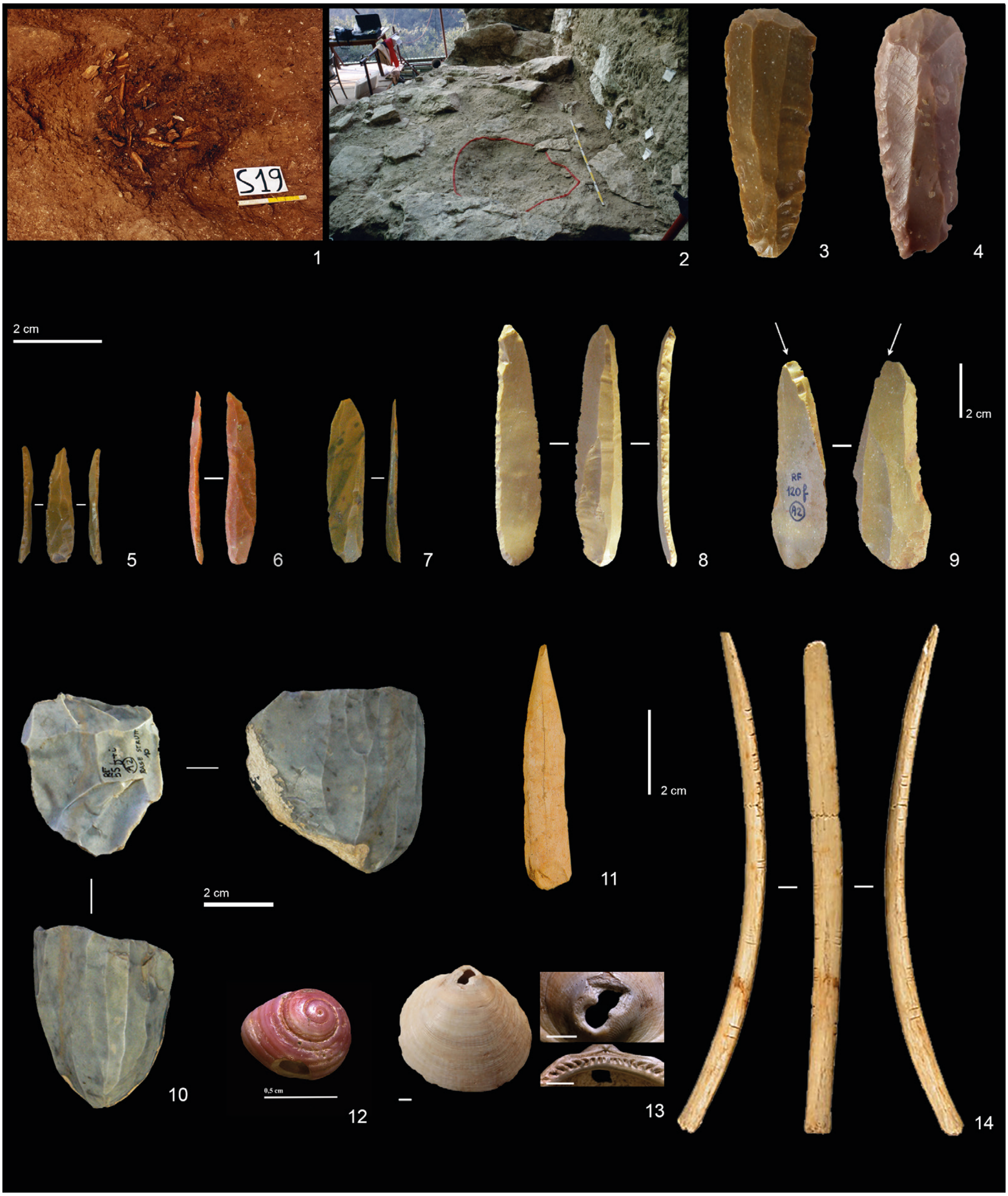

Fig. 6 - ***The Protoaurignacian "package" of unit A2: 1) structure A2_S19, a toss zone isolated at the present-day entrance of the cave; 2) a sector of the dwelling area outside the present-day entrance of the cave limited by stones and with the large fireplace A2_S10 surrounded by slabs emerging from the ground; 3-4) endscrapers made on blade; 5-8) dorsal, sagittal and ventral views of retouched bladelets; 9) burin; 10) bladelet core; 11) awl made on an undeterminable fragmentary shaft; 12-13)*** **Homalopoma sanguineum** ***(12) and*** **Glycymeris nummaria** ***(13) perforated shells; 14) undeterminable herbivore rib modified with spaced notches on the sides (after Aleo et al. 2021; Bertola et al. 2013; Falcucci et al. 2017; Falcucci and Peresani 2022; Peresani et al. 2019, modified).***

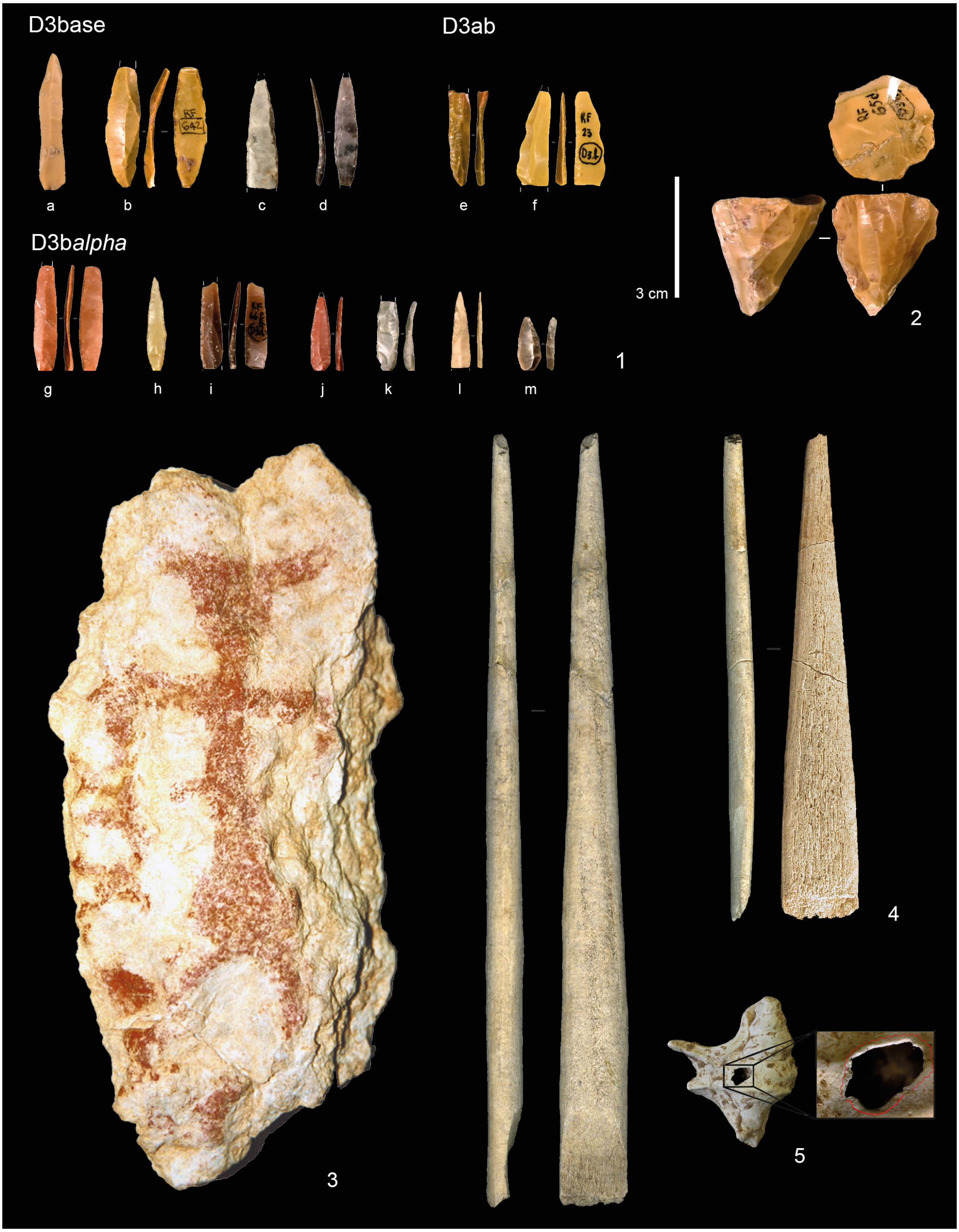

Fig. 7 - The Protoaurignacian "package" of unit D: 1) dorsal, sagittal and ventral views of retouched bladelets from units D3base (a-d), D3ab (e-f), D3balpha (g-m); 2) bladelet core; 3) painted stone; 4-5) bone points; 6) Aporrhais pespelecani *perforated shell (after Bertola et al. 2013; Broglio et al. 2009; Falcucci et al. 2020; Peresani et al. 2019, modified).*

ochre residues observed on well-preserved perforation edges pinpoint to the fact that shells were systematically manufactured and used like personal ornaments (Peresani et al. 2019). Although no clear differences have been observed between the two assemblages, comparisons within the techno-complex confirm that the Aurignacian of Fumane Cave was under the influence of the Southern European ethno-linguistic group (Vanhaeren and d'Errico 2006). In addition to these shells, the group of ornaments includes three pendants made on red-deer teeth engraved at the apex of the root and a rib of a middle size ungulate modified by equally spaced notches on both sides.

Discussion and conclusions

A comparison between Neanderthal and H. sapiens *cave settlement and subsistence patterns*

The late and final Middle Palaeolithic settlements in the North of Italy are recorded by a handful of sheltered and open-air sites repeatedly used or visited for short-term occupations aimed to exploit materials of mineral and organic nature, and to procure and process food (Peresani 2011). The settlement of this region was favoured by high geographical variability and the 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 occupations (Margaritora et al. 2021). 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 reflected adaptive strategies and responses at ecological and cultural levels. As a matter of fact, it is agreed that the use of the Discoid knapping methods by certain groups of Neanderthals made them dependent on an opportunistic exploitation of cherts (Delpiano et al. 2018). At any rate, precise data for most of these settlement contexts are largely unavailable yet and Fumane is no exception, although recent improvements resumed in the sections above are likely to contribute to shed light on the organization of the dwelling spaces.

The remarkable results achieved at Fumane from the spatial analysis and microcontextual analyses through integration of micromorphology with organic petrology of the purported combustion features exposed in the Middle Paleolithic contexts compared to the Upper Palaeolithic ones, have shown that only a few of these features represent primary, intact hearths (Marcazzan et al. 2022). As a matter of fact, some of them record repeated anthropogenic reworking phases, either through trampling or sweeping and dumping. Indeed, an ensemble of remnants of horizons of occupation were detected only partially preserved and peripherally related to combustion. Variable fuel sources were identified within several of the intact hearths, implying a degree of flexibility in the selection strategies of fuel consisting in the preferential use of plant material over bones for fire-making like wood and humified wood, herbaceous tissues and a mix of wood, herbaceous and bones. Coupled with other strategies, this provisioning pattern was part of a highly mobile settlement system. Although human activities did not change diachronically within the different frequentation phases, several features reflect a complex formation history of activities related to combustion and the maintenance of site. The study revealed diachronic patterns in the frequency and intensity of site occupation and the spatial distribution of activities with a decrease in the number of hearths throughout the Mousterian which continues into the Uluzzian, hinting that in these periods human groups frequented the site less and less or more sporadically (Marcazzan et al. 2022). This evidence encourages further investigation on the density of archaeological remains combined with age models and sedimentation rates, given its correspondence with the disappearance of the Neanderthals. With its 'simpler' features contrasting with the occupation horizon, the Middle Palaeolithic appears characterised by short-term but frequent occupation of the cave in the lower units, from A11.

This trend sees a reversal with the Protoaurignacian, where multi-layered and well-defined features contrast with largely most of the Mousterian and imply changes in the settlement dynamics and mobility strategies in coincidence with the arrival of *Homo sapiens*. Given this variation in the complexity of features from the Middle to the Upper Palaeolithic, it is likely to support the hypothesis that modern humans used Fumane more intensively and for longer spans of time in comparison with the Neanderthals (Marcazzan et al. 2022). Similar evidence stimulates to deep estimations on the accumulation rates of hearths, stone tools and bones, aside the influence of a range of local environmental, economic and social factors, to infer variations in occupation intensities of a site and, on a larger scale, its related territory (see French 2016 for review). Since the use of caves, shelters, open-air sites and territories could range from dense to ephemeral, estimates of the density of a specific class of cultural material or the dietary value of any faunal remains should reveal a positive correlation with the occupational intensity of a site. This correlation could support models thus based on an ensemble of proxies pointing for a disappearance of Neanderthals related to shrinking of their population densities, which caused them to cross a critical biological threshold for persistence (Vaesen et al. 2019; Kolodny and Feldman 2017; Skov et al. 2022), in contrast with demographic dynamics of *H. sapiens* Aurignacians leading to increase their densities (Mellars and French 2011; Conard et al. 2012).

For Neanderthals and modern humans hunter-gatherers, demographic dynamics were intimately related to dietary behavior and hunting strategies. At Fumane, zooarchaeological data confirm that hunting was not specialized to target one or several selected taxa but that was rather shaped by the game availability in the surroundings at the Monti Lessini – fluvial plain junction. Not surprisingly, Fumane is similar to the several Late Middle Palaeolithic settlements in the pre-Alpine fringe and sub-Alpine area, where sites like Riparo Tagliente and Riparo Mezzena in the Lessini, and Grotta San Bernardino and Grotta Rio Secco, locate in a range of ecological contexts and produced data revealing that the species of ungulates hunted conform to the respective specific ecological conditions at each site (Romandini et al. 2020; Terlato et al. 2021).

Data from Fumane demonstrate that this site was used as a habitat place where the processing of carcasses and especially red-deer and roe-deer was finalized after having begun at the kill site. This is clearly indicated by the pattern of preservation of skeletal elements, from which it is possible to infer that groups of humans transported to the site selected anatomical parts with high nutritional value, such as limbs, especially hind, and to a lesser extent the cranium. Well-established, cost-effective patterns were thus envisaged 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). The location and the ecological context of this cave placed at low-mid altitude in a landscape dissected by deep valleys with cliffs and steep slopes in proximity to the alluvial plain and the mountain grassland belt, supported the exploitation of different prey, despite the efforts required to cover the distance from and to the site.

One further point of interest at Fumane is marked by the variability of technocomplexes across the Middle Palaeolithic, stimulating debates about the Neanderthals' ecology and economy of subsistence bearing different methods of chert knapping and conceiving different lithic tools. These variables are under the focus of ongoing research when advanced evidence from units above and below A9, together from other sites, will be achieved using the same approach and protocol of investigation to identify similarities or divergencies in the patterns of exploitation of specific prey and the sharing of part of them between the members of the human group. Systematic practices in the sequence of faunal processing should be assessed under the light of social and cultural factors, especially in cases when it became identifiable where the zooarchaeological record produces signatures of standardized actions on both soft and hard tissues (Blasco et al. 2013; Yellen 1977). To evaluate if each limb bone was treated following a standardized process and determine if this process took different forms depending on the cultural group, is an intriguing issue if it will be related to the exclusive use of the Discoid lithic technology in A9. It is undeniable that this requires a combination of 3D spatial and taphonomical data from A9 compared to other units across the late Mousterian sequence of Fumane, where the Discoid alternates to other technologies.

Further signatures of uncommon hunting and dietary behavior produced at Fumane stimulate debate around the possible convergencies or divergencies between Neanderthal groups and also with modern humans 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,b). Once again, also the role of birds has been raised in the last decade for assessing the complexity of Neanderthal subsistence, especially when the evidence of avifaunal resource exploitation occurs in different periods and Mousterian cultures (Blasco and Peresani 2016). Although their contribution in the diet balance is far from the amount of protein provided by herbivore prey, birds eaten at Fumane might be not an elusive resource, possibly favored by the ecological conditions and the presence of long and high cliffs along the Fumane valley. These conditions are not unique in the pre-alpine belt and, once again, stimulate future investigations to deep our knowledge about the acquisition of birds, the butchering process and the successive consumption.

Differently from Neanderthals and similarly to Uluzzians, Protoaurignacians mainly exploited late spring/summer prime-age ibex and chamois, followed by red deer as recorded in both units A2 and D3, although a reduction in red deer individuals in D3 is likely related to the reduction of tree densities (Broglio et al. 2006; Fiore et al. 2004). However, environmental proxies show that this trend in the progressive opening of landscape results to be consistent with the sedimentation of unit A3 (López-García et al. 2015) and the related spectra of the hunted fauna (Tagliacozzo et al. 2013). Aside ibexes which were completely transported to the site, wolf and fox together with lynx were exploited as well for fur. A recent assessment addressed to estimate the Net Primary Productivity, a correlate with the whole mammalian biodiversity in these extinct ecosystems, has reflected fluctuations in the Prealpine area, capable to affect biotic resources and, as a consequence, the subsistence strategies adopted by these resilient Protoaurignacian groups dispersed in different environments subjected to the climate change across the Heinrich Event 4 (Marín-Arroyo et al. 2022).

Neanderthal cultural dynamics

During their long-lasting presence in Western Eurasia, Neanderthals expressed complex, flexible and innovative behavioral strategies. The variability of stone tool technology through time and space does not make exception at Fumane neither. The recent progress made on the study of cultural items along the late Middle Palaeolithic sequence has produced the ensemble of evidence resumed above, showing that diverse manufacturing strategies fulfilled the same functional needs despite the morphological and technological differences of the lithic tools. Indeed, the design, production, recycling, and discard of artefacts may reflect constraints imposed by the ecological and environmental conditions, human mobility patterns, food procurement strategies and, above all, tradition. As a matter of fact, in these archaeological contexts, cultural legacy is expressed by those concepts, methods and techniques used in the design of the knapped stone tools. At Fumane, although the lithic production is largely based on the application of Levallois technology, similarly to the vast majority of Mousterian sites in Europe, new details are expressed (Peresani 2012). Considering the North-Adriatic area of Southern Europe, this flaking method is common in northern Italy, the Italian peninsula and in western Balkans where it forms the substrate of traditionally labelled complexes in the Mousterian, such as the Pontinian and other different facies (Romagnoli et al. 2022).

Similarities observed at Fumane and elsewhere amongst reduction sequences concerning the Levallois recurrent uni-directional modalities, their variants and the recurrent centripetal methods at the final reduction steps, reveal a legacy in the production of blades and elongated flakes with thin converging margins common to various sites. The goals and significance of such a behaviour could be explained in terms of economic usefulness or functional efficiency, if we assume that this systematic strategy was designed for obtaining elongated blanks with regular cutting edges. This procedure became dominant in the Levallois system between 60 and 45 ky, despite the alternance with the Discoid technology and other methods (Delpiano et al. 2019c; Peresani 2011). Common tools like scrapers and points were mostly made on Levallois blades.

Embedded between Levallois contexts at Fumane, the Discoid technology appears in unit A9 and gradually disappears downward the sublevels of A10, irrespectively of the different chert aptitudes, to attest abrupt variation of the morphological arrangements of the cores in accordance with the main technical goals. The re-appearance of the Levallois in A5-A6 marks a further abrupt technological replacement, and at the same time indicates a continuity in the use of this volumetric conception until the end of the Middle Palaeolithic in unit A4, despite the variable size and shape normally assumed by the blanks within their recurrent predetermination. In addition, retouched tool kit does not differ from units A10 and A12, since it is composed of side-scrapers. Alongside with the manufacture of these Levallois flakes, Fumane does not make exception with respect to other sites for the existence of a blade volumetric concept aimed to obtain bladelets (Peresani et al. 2013b).

This technological dichotomy between Discoid and Levallois reduction methods at Fumane may help to better assess Neanderthals' behavioral complexity in most of southern and western Europe, where Levallois and Discoid industries characterize the last technological expressions pointing to coexistence or shift and replacement (Peresani 2003). Discoid and Levallois techno-complexes have been repeatedly compared, after being considered in relation to their functional and potential objectives, to fuel the debated topic of these technological shifts. Current models view the Discoid technology like an expression of cyclical and seasonal mobility of human groups or an adaptation to local conditions (Delpiano et al. 2018). In other words, this technology makes it possible to maintain highly productive technical systems together with the potential for flexibility in the operational sequence. Experimental and assemblage-based investigations on the productivity of the two knapping systems have demonstrated that in the Discoid system flakes are versatile and multi-functional, although characterized by a short life and therefore apparently unconceivable for being designed to be part of transportable tool-kits (Delpiano et al. 2018). The Discoid thus turns out to be more productive than Levallois in relation to technical gestures and management of the knapping system. It is characterized by a higher ratio of usable flakes and, among these, many products with natural or knapped backs. Moreover, the intention to produce new flakes with fresh edges, rather than renew the functional equipment is also confirmed by the low incidence of retouched tools. The Levallois method, on the other hand, records large quantities of cutting-edges in relation to a given volume of matter. The volumetric control of the method requires more preparation and greater quantity of wastes, though allowing for maximizing production. This is possible thanks to the regularity of the produced blanks, the extension of the cutting-edges, and their limited thickness. Among the possible reasons supporting this Levallois-Discoid shift, strategies of resource exploitation and territorial mobility, as well as the rates of productivity and effectiveness between the two methods were claimed support of these differences, although they cannot always justify a sharp change in the production choices. For instance, the use of diverse raw material types does not change, following the assumption that the Levallois method needs higher technical control. This was not the case, given that the alternating or coeval use of these methods cannot be related to different aptitudes of chert available in the Fumane cave surroundings, where optimal and excellent knappable rocks were largely available (Delpiano et al. 2018). Furthermore, given that the faunal and paleoenvironmental data broadly record similar conditions between A10-A11 and A9 units, alternation between Levallois and Discoid methods could thus represent differentiated responses to similar ecological conditions aimed to fulfill distinct technological and productive objectives.

Neanderthals' tool-making was complex at time: it underwent to an evolutionary path dotted with successful innovations and their consequent spread, with improvement of maintenance technologies. One further contribution to elucidate this shift among Neanderthals' cultures was provided from that poorly known class of tools represented by the purposedly backed artefacts found in unit A9, here interpreted like innovative, specific, relatively elaborate tools that also formed part of the mobile tool-kits modified during daily or seasonal movements before being discarded (Delpiano et al. 2019). Since backed tools part of the Neanderthal repertoire, found in diverse periods and associated with different forms of lithic technology, these implements can be viewed like potential proxies of cultural traditions and conditioning technological systems. Hence, the production of these prepared backed artifacts among a Discoid technologically based assemblage marks an important step in the design of MP tools in terms of manual activities and ergonomics, up to consider backing as a typical feature in the technological repertoires of late Neanderthals. The effectiveness of back thinning associated with different types of handles was observed after experimental trials and also on a comparative base with late Mousterian sequences of south France (Delpiano et al. 2018). Indeed, the production process of these implements does not seem to have been planned around a fixed conceptual scheme. This latter also involved blank pre-shaping useful for direct prehension and hafting. At Fumane A9, this last feature is considered further evidence of elaborate tools. The probable presence of two different hafting schemes, adapted to the size and shape of the blank, as well as intended function, may suggest a wider basis of knowledge, since hafting and composite tools have been generically considered in the literature as markers of modern behavior. However, concerning the Discoid method, the planning and design are not so visible in the shapes of individual implements. This means that functional requirements of handling and use, rather than cultural definitions of preferred shapes, were fundamental in determining their design. This enabled a detailed investigation of a pattern of cultural innovation, in the European Late Middle Paleolithic, which is backing to accommodate manual prehension as well as hafting. Systematic evidence from across Europe during MIS 3 supports the independent appearance of this innovation in different regions. The technical competence and behavioral flexibility of late Neanderthal populations are well illustrated by these tools, which are related both to ecological factors and functional needs.

An assessment on the productive differences between Levallois and Discoid backed artefacts reveals that, aside distinct choices based on the functional objectives, they share a low common potential for renewal and resharpening, which is rarely exploited (Delpiano et al. 2021). Levallois backed items have a conformation featured with high cutting effectiveness relative to size of the tools, and the regularity of the bevel. The techno-functional schemes record limited variability and preference for elongated supports with parallel margins, and regular thickness making them efficient for manual grip or adaptable being hafted. On the other hand, morphological variability of the Discoid backed artefacts is greater than Levallos, as suggested by a wide range of flakes with a later functional aptitude for manual handling (convex back) or hafting, sometimes achieved with the use of particular parts of the edge (Delpiano et al. 2021).

Finally, at Fumane unit A5-A6 has no backed tools. However, they reappear in different forms in A4, associated with centripetal Levallois and premises of novel lithic production systems and tools. Furthermore, it is worth noting that at the end of regional Mousterian sequences at Fumane and in the other Discoid or Levallois assemblages, there is no standardization of backing techniques and of the overall form of backed implements. This contrasts with the Uluzzian (Moroni et al. 2018) and the Chatelperronian (Roussel et al. 2015), or the Howiesons Poort and Post-Howiesons Poort complexes in South Africa (Villa et al. 2010), where standardized tools are considered proxies of modern behavioral expressions.

Neanderthals' use of symbolic items

In continuity with the abovementioned dynamic material culture of Neanderthals, Fumane provides clues on the evolution of human behaviour refusing the view that these hominins did not make use of symbolic items. Rather, they gave attention to the aesthetic or uniqueness of certain materials of biological nature (Frayer et al. 2021; Leder et al. 2021). Evidence remains still scanty if compared to the Upper Palaeolithic, but it groups a varied ensemble of materials also of inorganic nature. Among organic items, increasing findings pinpoint to the interaction between hominins and raptors from a vast area of Southern Europe, notably on black-feathered birds and birds of prey of different sizes, suggesting a probable special meaning that these birds had for hominin populations (Finlayson et al. 2019). As to this day, on-going research shows correlations across the Palearctic and Nearctic regions attesting that raptors and corvids were regular or seasonal scavengers in Neanderthals' home range. The specific selection of raptors pedal phalanges suggests the symbolic use of these parts of the body, despite the ephemeral occurrence with which they are discovered in the archaeological deposits. The most well-known findings are isolated, cut-marked bony cores of claws of golden eagle, white-tailed eagle, cinereous vulture, other birds of prey, as well as swan found in France (Pech de l'Azé I and IV, Baume de Gigny, Combe-Grenal and Les Fieux), Italy (Grotta del Rio Secco other than Fumane) and Croatia (Krapina) (see references in Jaubert et al. 2022; Radovčić et al. 2015, 2020; Romandini et al. 2014c), covering a time span between 100 and 45 ka BP. All these posterior phalanges bear disarticulation striations showing the successful removal of the claw from the toe using lithic tools to cut into the thick skin, the stratum corneum and severing the strong ligaments and tendons. Furthermore, the presence of diagnostic wear, in addition to the remnants of a string and traces of ochre was observed on the Krapina items. Because claws are not directly compatible with human consumption or use, an attractive hypothesis points for an ornamental use thanks to their length and curvature, and possibly their suspension in different ways. This use is observed in the present-day ethnographic records like tinkling pendants, suspended in isolation or still connected to the entire foot. This interpretation has also been supported from the over-representation of raptor feet bones bearing comparable traces ascribable to their deliberate removal, recorded for more recent periods of the Upper Palaeolithic in Europe and the Near-East (Laroulandie et al. 2020). As a striking case, the recent discovery of notched or unnotched eagle pedal phalanges in early Upper Palaeolithic contexts, Grotte Mandrin (Romandini et al. 2014c) and Cueva Foradada (Rodríguez-Hidalgo et al. 2019), and Aurignacian caves in South Western France (Laroulandie et al. 2020), very close or even chronologically embedded with the latest Middle Palaeolithic cultural expression, sheds light and fuels discussion on the certain convergence of such selections. It also supports the occurrence of shared traditional practices between the late Pleistocene Neanderthals and early modern humans in Southern Europe and the Mediterranean rim.

In addition to this evidence of claws use, the incidence of raptor and corvid wing bones at Fumane, Vanguard Cave and Gorham's Cave in Gibraltar, suggests that Neanderthals exploited black-feathered birds to partition their wings or take off their feathers. Cutmarked humeri, radii and ulnae bones demonstrate that Neanderthals exploited the greater spotted eagle (*Clanga clanga*), the lammergeier or bearded vulture (*Gypaetus barbatus*), the Eurasian black vulture

(*Aegypius monachus*), the griffon vulture (*Gyps fulvus*), the red-footed falcon (*Falco vespertinus*), the merlin (*Falco colombarius*) and the red kite (*Milvus milvus*), as well as the Alpine chough (*Pyrrhocorax graculus*) and common wood pigeon (*Columba palumbus*) (Peresani et al. 2011b; Finlayson et al. 2012; Romandini et al. 2016). Two right ulnae of Alpine chough found in A5-A6 preserve the most striking modifications. Nevertheless, cutmarks linked to disarticulation are not the only class of traces observed on these specimens. Groups of scrape marks on the medial surfaces, located around the point of feather attachment (*Papillae remigiales*) indicate that the skin covering the ulna was cut and that remiges were removed (Peresani et al. 2011b).

The most parsimonious explanation for these modified wing bones from large raptors, choughs and other birds indicates that deliberate action was addressed to recover part of the wing or retrieve long feathers for use in adorning heads, bodies and clothes (Peresani et al. 2011b; Finlayson et al. 2019). An alternative hypothesis envisages the employ of feathers as stabilizing elements for hunting spears, or for arrows fired from a bow, although this latter was not used by Neanderthals yet. These hominins also eat raptors and corvids in northern Iberia (Gómez-Olivencia et al. 2018), which is an unsual practice reported by ethnographic literature. Feathers are inedible and also inadequate for bedding on Pleistocene cave floors. Therefore, the unquestionable zooarchaeological evidence from Fumane and the other sites in the Mediterranean rim prove that Neanderthals caught and exploited this range of birds for long time and that this practice continued after their disappearance during all the Upper Paleolithic, precluding any arguments of acculturation (Finlayson et al. 2019). The acquisition of valuable avian plumage long before the arrival of *Homo sapiens* in Eurasia, is thus pushed further back in the history of humankind and strengthens the argument for behavioural complexity among these Eurasian populations.

Neanderthals were also aesthetically sensitive to specific visual properties of certain stones, as the green serpentinite pebbles from Fumane unit A5-A6 suggest. Their selection, collecting and use reflects an autochthonous behavior of a group of Neanderthals, distinct from those who settled at Fumane before and just after 45-44 ka BP. Furthermore, their absence in the Uluzzian and Protoaurignacian marks out the unicity of these materials selected for purposes different than those recorded throughout the whole Upper Paleolithic in Eurasia. Neanderthals thus expressed aesthetic perceptions and attraction to roundness, brightness, and colorful objects, revealing how our tendency to symmetry, roundness, and interest in specific colors and/or bright shiny objects could be traced back to the earliest stages of humankind's history (Peresani et al. 2021). Colors constantly surrounded humans, and we might expect colors to be charged with different meanings and importance through time, suggesting an interesting preference for pigment use.

Neanderthals settled at Fumane chronologically close to their demise elsewhere in Western Eurasia (Higham et al. 2014) when *Homo sapiens* arrived in Southern and Central-Eastern Europe. In this scenario, the possible occurrence of acculturation has repeatedly been invoked to explain changes in technology and social behavior among the latest native communities. As a result, there is an interminable debate about the consistency of the local bio-cultural substratum and the impact of the newcomers (Gravina et al. 2018; Majkić et al. 2017; Nielsen et al. 2020; Villa and Roebroecks 2014; among others). For the evidence discussed above, Fumane points for an independent raising of symbolically mediated behavior among the autochtonous communities, in coherence with a wider scenario which attests marked changes in human behavior both in Europe and Africa at least from ca. 200 ka ago, as reported from an ensemble of archeologically visible innovations in dietary behavior, the use of heating sources to pretreat knappable rocks or produce glues, the design and maintenance of composite tools, and the use of colorants, objects and signs for visual display (D'Errico and Stringer 2011; McBrearty and Brooks 2000; Tartar 2015; Zilhão 2013, 2020).

Mousterian, Uluzzian and the first *Homo sapiens*

The Mousterian-Uluzzian transition at Fumane is relatively short and remains partially indistinguishable from the final Mousterian complex at 46–44ky cal BP from a chronological point of view (Douka et al. 2014). The sequence does not record major breaks neither in sedimentary pattern nor in micromammal associations, since the only changes regard the percentage representation of the taxa. At least from palaeoclimatic and palaeoenvironmental sides, evidence does not support major change in climate and ecological patterns that might have affected the Neanderthal communities and driven their replacement by *Homo sapiens*. Rather, the variability of the faunal assemblages is representative of the different environments surrounding the site, with ungulates being targeted for hunting and consumption. Furthermore, the way in which this ungulate fauna, in addition to carnivores, was exploited does not mark any detectable change in coincidence with the appearance of the Uluzzian in A3 (Romandini et al. 2018b; Tagliacozzo et al. 2013).

In A3, the cultural changes observed at the level of volumetric concepts of flake-making and tool-designing in coincidence with the appearance of this *H. sapiens*-related techno complex pinpoint the northern coastal belt of the Mediterranean Sea as being one of the key areas for setting the boundary between the Middle and the Upper Palaeolithic. It develops in a patchy scenario that documents the flourishing of behavioural shifts (Hublin 2015). Once again at Fumane, the revision of the previous attribution of the A4 context to the early Uluzzian (now to the final Mousterian) challenges the model of the emergence of the Uluzzian from a Mousterian substrate in the north of Italy. It further highlights the existence of an independent cultural change here and in neighbouring regions around the northern Mediterranean rim, where the first *H. sapiens* introgression with Uluzzian culture is recorded not earlier than 46-45 ka BP in the southern Italy (Zanchetta et al. 2018). Indeed, the Mousterian influence in A4 remains remarkable and is consistent with the end of the European Middle Palaeolithic. However, some novelties in flake making and stone tools might support the tracking of a cultural influence related to the Uluzzian and to other complexes disseminated by the earliest incomers since 47-48 ka (Muller 2011; Hublin et al. 2020) or even earlier from 54 ka (Slimak et al. 2022).

However, it has also been noted - still at a preliminary scale – how the A3 Uluzzian at Fumane diverges from the traditional Uluzzian profile. This is supported by the recent evidence found at Riparo Broion (layers 1f-1g), a coeval shelter in the Berici hills, or further South to Roccia san Sebastiano Cave (Collina et al. 2020) and to Cavallo Cave (layer EIII) and in the Uluzzo Bay area (Moroni et al. 2018). At Riparo Broion, the lithic assemblage records a largely prevalent use of the bipolar knapping technique leading to a high fragmentation rate and a large variety of splintered pieces and associated chips. Backed pieces, lunates and end-scrapers feature this industry, despite the fragmentation they underwent through bipolar knapping after use. Bone tools as well as marine and freshwater beads echo the cultural layout of the Uluzzian in the South of Italy, confirming the geographic spread of this technocomplex also in the North-Adriatic region (Peresani et al. 2019; Arrighi et al. 2020a, 2020b). At Fumane however, the marginal role of bipolar reduction and of laminar volumetric exploitation, the atypical morphometric characteristics of the backed pieces, the delineation of the back and the technology of flake manufacture, alongside with the appearance of manufactured bone tools, lightly deviate from the Uluzzian "package", although they undeniably proof how innovations in the variability of the technical aims and tool design definitely mark the cultural gap from the Mousterian traditions. Furthermore, differences between these Uluzzian people and the former users of the cave are expressed also from combustion features and the deliberate spatial patterning of materials, such as in the structure A3_SIV.

Given the current knowledge on the way the Uluzzians exploited the ecological contexts and organized their activities in sheltered sites, we cannot exclude that some divergences between Fumane A3, the southern Italian sites, and Riparo Broion might be ascribed to the diverse use of caves and shelters. This may have determined the incidence of different technological procedures and designed the composition of their tool-kits. A consequence of this factor is the structural deviation from the classic profile, which could raise the need to enlargen the spectrum of diagnostic traits for distinguishing the Uluzzian lithic form. Once the chronological factor is excluded for the broad contemporaneity between Fumane and Riparo Broion, one further possibility to explain these divergences grounds on cultural dynamics, also considering that the deviated character of the Uluzzian at Fumane might derive from contamination with the local cultural environment or the assimilation of know-how in technology, social communication, and hunting behavior, at least when the taxonomy of Fumane occupants will be disclosed.

Definitely sapiens

In the kaleidoscopic scenario of the spread of the early *Homo sapiens* into Western Eurasia, the appearance of the Aurignacian is related to one amongst the most intriguing cultural dynamics of the Upper Paleolithic. At this point, studies have focused on the origin and chronological expansion of this technocomplex and the arrival to different continental areas, stimulated by the climate and ecological conditions faced by the new incomers (Nigst et al. 2014; Shao et al. 2021). The Hs populations progressively settled in different regions following the eastern-northern Mediterranean and Centro-European trajectories (Hublin 2015; Mihailović 2020), promoting the diffusion of new cultural traits archaeologically represented by cave art, portable art and musical instruments. In addition, certain categories of symbolic objects used for personal purpose were renewed (Conard 2003, 2009). Thanks to the analysis of the lithic industry, Fumane has contributed to a more precise definition of the Protoaurignacian through the high-resolution inspection of the production of blades and bladelets (Falcucci et al. 2022). The re-evaluation of this and other assemblages reveals that dissociate reduction sequences were addressed to obtain bladelets within a single and continuous stone knapping from the same core as the result of its progressive reduction. Bladelets were thus the first goal of production and did not originate from a broad range of independent core reduction strategies. Additional data achieved from the analysis of carinated core technology reveal that the Protoaurignacian shares a common technological background with 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 and, notably, its extreme poles as a region worthy of consideration (Cortés-Sánchez et al. 2019; Gennai 2021). Fumane Cave is a pivotal site for tackling this issue because it bore evidence of repeated human occupations during the European Aurignacian. Thanks to its dense stratigraphic sequence, Fumane is stimulating investigations on the cultural diachronic variability across the time interval framed by the cultural units, with the aim to test if the Early Aurignacian with its new organic artifacts followed the Protoaurignacian. Results show 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 adaptative systems in the Early Aurignacian by respect to the Protoaurignacian (Banks et al. 2013; Bataille and Conard 2018; Falcucci et al. 2020; Higham et al. 2013; Nigst et al. 2014). By the other hand, the appearance of split-based points in the youngest phase of the sequence at Fumane reveals once again the existence of extensive networks that allowed this technological innovation to spread across different Aurignacian regions. One further evidence of past human communication strategies and cultural exchange during this early Upper Palaeolithic phase is also expressed by the number and variety of marine shells used like ornaments, which however is one further aspect of continuity between the two phases. Despite the paucity of marine and freshwater shell assemblages of similar age and composition in Southern Europe and part of central Europe, shells from Fumane confirm similarities in the taxonomic composition and taphonomic traces across different sites (Vanhaeren and d´Errico 2006), This supports the idea that early AMHs communicated through aesthetic elements in portable objects. Among these elements, the shells of *H. sanguineum* probably played a fundamental role in maintaining a communication system over a large geographic area and may have represented group consciousness or even longstanding ethnic identities between the Rhone basin and eastern Mediterranean. Shells were smeared with red ochre produced at Fumane also after heating of mineral pigments as the oldest evidence so far documented in the European Palaeolithic.

Following the Aurignacian at Fumane, the cultural trajectory led to an old appearance of the Gravettian in unit D1d preceding the Heinrich Event 3, associated with an unusual charcoal feature in course of analysis (Falcucci and Peresani 2019). The techno-typological study of the lithic assemblage confirmed a previous assignment to the Gravettian and provides reference for other minor sites in the rim of the Great Adriatic Po Region, where human settlement was sparse and discontinuos (Peresani et al. 2022).

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