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SUPPLEMENTARY MATERIALS

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ARCHAEOLOGY

The makers of the Protoaurignacian and implications for Neandertal extinction

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The Protoaurignacian culture is pivotal to the debate about the timing of the arrival of modern humans in western Europe and the demise of Neandertals. However, which group is responsible for this culture remains uncertain. We investigated dental remains associated with the Protoaurignacian. The lower deciduous incisor from Riparo Bombrini is modern human, based on its morphology. The upper deciduous incisor from Grotta di Fumane contains ancient mitochondrial DNA of a modern human type. These teeth are the oldest human remains in an Aurignacian-related archaeological context, confirming that by 41,000 calendar years before the present, modern humans bearing Protoaurignacian culture spread into southern Europe. Because the last Neandertals date to 41,030 to 39,260 calendar years before the present, we suggest that the Protoaurignacian triggered the demise of Neandertals in this area.

The timing and pattern of the biological and cultural shifts that occurred in Western Europe around 45,000 to 35,000 calendar years before the present (cal yr B.P.) fuel continuing debates among paleoanthropologists and prehistorians (1–3). During this period, Neandertals were replaced by anatomically

modern humans (AMHs) (4), and a variety of “transitional” and early Upper Paleolithic cultures emerged. Among them, the Protoaurignacian is

crucial to current interpretations regarding the timing of arrival of AMHs and their interaction with Neandertals (5–9).

The Protoaurignacian appeared around 42,000 cal yr B.P. (8, 10) in southwest and south-central Europe (fig. S1). In addition to the presence of personal ornaments, such as perforated shells and worked bones, the Protoaurignacian is characterized by a dominance of bladelets with typical retouched standardized implements such as Font-Yves points and Dufour bladelets produced from unipolar cores (5). This techno-complex has been tentatively linked to the Ahmarian industry of the Levant (6, 9). Because the Ahmarian has been attributed to modern humans (11), it has been suggested that the Protoaurignacian reflects a westward population movement of AMHs from the Near East (1, 7). However, because only three nondiagnostic human remains are associated with this culture, it is still uncertain who the makers of the Protoaurignacian were (9, 12). The fossil remains associated with the Protoaurignacian that are available for study consist of the undiagnostic skeletal fragments of a fetus retrieved from Le Piage rock shelter (France) (13), for which the stratigraphic integrity of the Châtelperronian/Aurignacian sequence has been questioned (5), and two deciduous incisors from two northern

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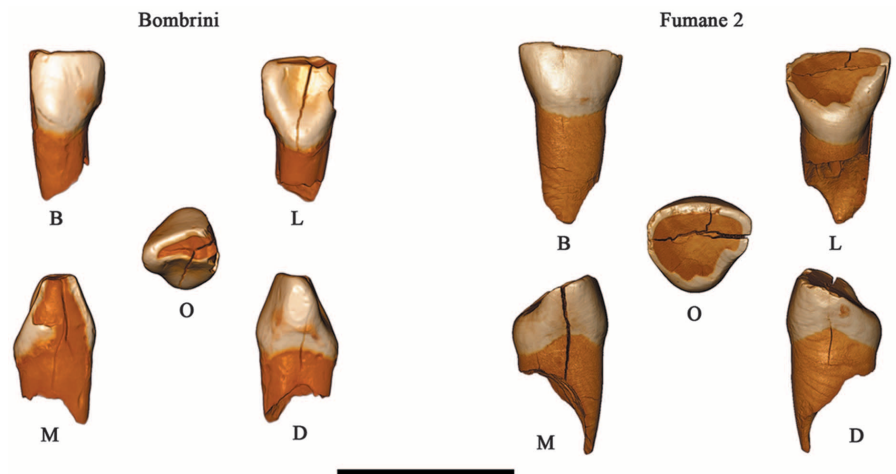


Fig. 1. Three-dimensional digital models of the Protoaurignacian human remains. The Bombrini tooth is a lower left lateral deciduous incisor (Ldi_2), whereas Fumane 2 is an upper right lateral deciduous incisor (Rdi_2). B, buccal; D, distal; L, lingual; M, mesial; O, occlusal. Scale bar, 1 cm.

Italian sites: Riparo Bombrini (western Ligurian Alps, Italy) and Grotta di Fumane (western Lessini Mountains, Italy). The lower left lateral deciduous incisor (Ldi₂; Fig. 1) found in 1976 in Riparo Bombrini (14, 15) (figs. S2 to S5) and the upper right lateral deciduous incisor (Rdi₂; Fig. 1) labeled Fumane 2, which was retrieved in 1992 from the Protoaurignacian deposit of Grotta di Fumane (15, 16) (figs. S6 and S7), have to date not been conclusively attributed to modern humans or Neandertals.

The crown diameters of deciduous incisors are undiagnostic for Neandertals and modern humans, as is also the case for other tooth classes (2). However, on the basis of the buccolingual crown diameter, the Bombrini specimen is close to the mean of Upper Paleolithic modern humans, whereas Fumane 2 is closer to the Neandertal mean (table S1). Other than that, the worn deciduous lower incisors do not provide any morphologically diagnostic information.

To establish the identity of the makers of the Protoaurignacian, we analyzed the three-dimensional enamel thickness components of the Bombrini Ldi₂ using a digital approach (17), and we were able to investigate DNA from the Fumane 2 specimen (15).

The relative enamel thickness (RET) index has been recognized as an effective taxonomic discriminator between Neandertals and modern humans. Neandertal deciduous and permanent teeth are characterized by significantly thinner enamel relative to dentine volume (18).

To facilitate comparisons with the Bombrini specimen, which is affected by wear stage 4, the Neandertal and recent modern human (RMH) di₂ samples were divided into subgroups based on their degree of wear (from wear stage 1/2 to wear stage 4) (15, 19) (Table 1 and table S2). The Neandertal di₂ RET indices are lower than those of RMHs at similar wear stages, and no overlap in the range of variation is observed between the two groups. The RET index of Bombrini is higher than any values obtained for Neandertals (table S2), despite the missing portion of the enamel cap, and its computed standard (*Z*) score is close to the modern human mean in wear stage 4 (Table 1).

To test how much the loss of enamel on the mesial side of the Bombrini tooth affects the computed RET value, two RMH specimens were digitally worn and damaged to simulate the condition observed in Bombrini (15) (fig. S8). The results confirm that tooth wear, at least up to wear stage 4, decreases the RET index by about 10%, whereas the mesial loss of enamel affects the index by less than 1.6% (much less than the values considered acceptable for intra- and interobserver error) (2). Therefore, the RET value for the unworn Bombrini Ldi₂ was certainly much higher (table S3), further supporting its attribution to modern humans.

DNA was extracted from the Fumane 2 tooth, which yielded few mitochondrial DNA (mtDNA) sequences (table S4). With respect to 63 “diagnostic” positions at which 10 Neandertal mitochondrial genomes differ from those of 311 present-day humans (20), these sequences were of modern human origin (table S5). To further explore this, we prepared a second DNA extract and two DNA

libraries from this specimen, which yielded a total of 335,628 unique mtDNA fragments (table S4).

The frequencies of cytosine (C) to thymine (T) substitutions at the ends of these fragments (34 to 37%, fig. S9), which reflect the deamination of cytosine residues typical of ancient DNA (21, 22), are consistent with results from other specimens of similar age (23–26). Among the fragments carrying terminal C-to-T substitutions, we estimated the residual present-day DNA contamination to be 3.8% (15).

Using these fragments, we reconstructed a mitochondrial genome of 157-fold coverage (fig. S10). This mtDNA sequence was aligned to the mtDNAs of 54 present-day humans, 10 ancient modern humans, 10 Neandertals, 2 Denisovans, a hominin from Sima de los Huesos (Spain), and a chimpanzee (*Pan troglodytes*). The Fumane 2 mitochondrial genome falls within the variation

of modern humans (Fig. 2) and basally in haplogroup R (table S6), as also observed for the ~45,000-year-old AMH specimen from Ust’-Ishim [in western Siberia (26)], a major group of related mtDNAs in Eurasia (27) into which most pre-agricultural mtDNAs in Europe fall (28).

As expected for an ancient specimen (23, 25), the Fumane 2 mtDNA has accumulated fewer nucleotide substitutions than present-day mtDNA (Fig. 2). Using 10 directly dated ancient modern humans (25, 26) as multiple calibration points, we estimated the age of the Fumane 2 terminal node to be 44,599 (95% highest posterior density: 19,755 to 72,070) yr B.P.

We thus conclude that the Fumane 2 individual carried a mitochondrial genome of a modern human type. This shows that this individual was a modern human or had at least some ancestors who were modern humans.

Table 1. 3D enamel thickness. Bombrini (Ldi₂) is standardized to *Z* scores (for RET index) of the Neandertal and recent modern human (RMH) di₂ sample in different wear stages. Standard deviations are indicated in parentheses. AET, average enamel thickness index; RET, relative enamel thickness index.

Taxon	Wear stage*	<i>n</i>	AET (mm)		RET (scale free)		<i>Z</i> scores for RET index
			Mean	Range	Mean	Range	
Bombrini	4		0.29		9.22		
Neandertals	1/2	3	0.29 (0.01)	0.28–0.30	7.88 (0.33)	7.54–8.20	4.06
Neandertals	3	2	0.26 (0.007)	0.26–0.27	6.95 (0.55)	6.56–7.34	4.13
RMH	2	3	0.35 (0.006)	0.35–0.36	11.41 (0.41)	10.97–11.77	–5.34
RMH	3	11	0.31 (0.04)	0.24–0.35	9.98 (1.17)	8.01–11.85	–0.65
RMH	4	4	0.26 (0.04)	0.22–0.32	8.67 (1.4)	6.98–10.40	0.39

*Based on (19).

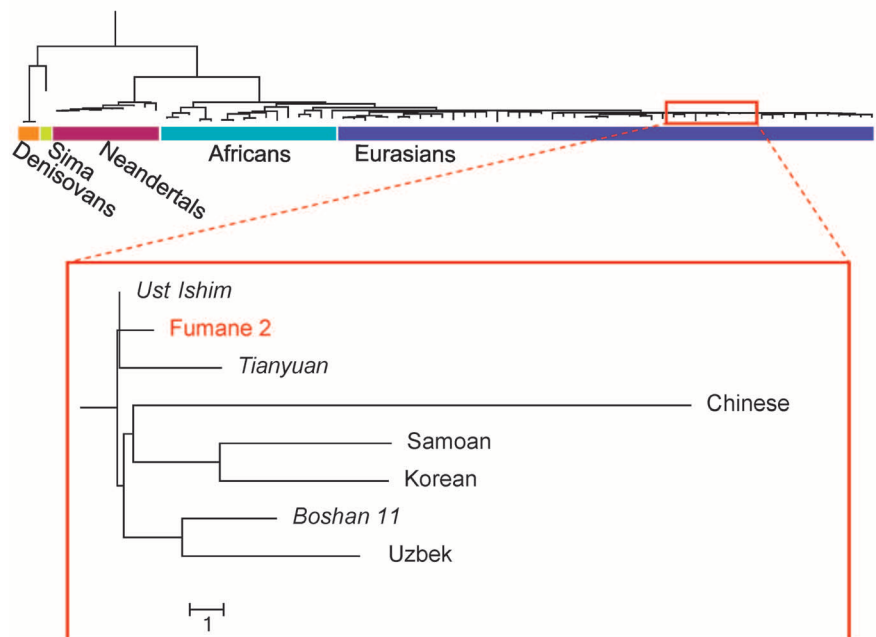


Fig. 2. Phylogenetic analysis of the Fumane 2 mtDNA genome, inferred using the neighbor-joining method. The Fumane 2 mitochondrial genome falls within the variation of modern humans and outside the variation of Neandertals, Denisovans, and a hominin from Sima de los Huesos. The insert shows the branches closest to Fumane 2. Other ancient modern humans are noted in italics. Branch lengths represent the evolutionary distance between individuals, reflected by the number of inferred substitutions per sequence.

Based on recent chronometric data for the Protoaurignacian deposit of Grotta di Fumane, the Fumane 2 specimen is dated to 41,110 to 38,500 cal yr B.P. (10), as recalibrated with IntCal13 (29). Among modern humans in western Europe, it is currently predated only by the contested Kent's Cavern maxilla (30, 31) and by the 45,000 to 43,000 cal yr B.P. AMH specimens from the Uluzzian levels of Grotta del Cavallo (2), about which a recent taxonomic reassessment is stimulating intense debate (32, 33).

Radiocarbon dates of the Protoaurignacian layers of Riparo Bombrini were obtained from faunal bones recovered during the G. Vicino excavation (five samples) and the more recent 2002–2005 excavations (three charcoal specimens and eight animal bones) (15) (tables S7 to S10). These dates confirm the integrity of the cemented deposit explored in 1976 by Vicino (which yielded the Ldi₂ tooth) but suggest that some stratigraphic disturbance affected a restricted area explored during the 2002–2005 excavations (15) (table S7 and

fig. S11). The ¹⁴C dates of the Vicino 1976 excavation (table S7) were incorporated into a Bayesian model for the distribution of ages (34) (Fig. 3). The Protoaurignacian levels (level III to level II) are dated between 40,710 and 35,640 cal yr B.P. (68.2% probability), corresponding to a cold phase that marks the onset of Heinrich Stadial 4 (35).

The Bombrini Ldi₂ and potentially the Fumane 2 Rdi₂ thus represent the oldest AMH remains in an Aurignacian-related (i.e., Protoaurignacian or Early Aurignacian) archaeological context, confirming that by around 41,000 cal yr B.P. (68.2% probability), AMH populations bearing Protoaurignacian culture had spread into Europe along the Mediterranean coast. They are similar in age to, or slightly older than, the modern human remains from Peștera cu Oase (Romania, ~40,000 cal yr B.P.), which lack archaeological context; Kostenki 14, Layer III (Russia, ~38,000 cal yr B.P.), which is possibly Aurignacian; Kostenki 1, Layer III (~38,000 cal yr B.P.), which is associated with diagnostic Aurignacian artifacts; Kostenki 14, Layer IVb, and Kostenki 17, Layer II, which underlie the Campanian Ignimbrite tephra and are of comparable age to the Protoaurignacian in Italy, are tentatively assigned to AMHs, and also associated with an assemblage that includes bladelets; and La Quina-Aval and Brassempouy (France), which are Early Aurignacian and more recent than 40,000 cal yr B.P. [for a review, see (9)].

The Protoaurignacian dispersal overlaps in time with late Neandertal populations, as indicated by the 41,030 to 39,260 cal yr B.P. age of the last Mousterian sites (4) and the ~45,000 to 40,000 cal yr B.P. age of the Châtelperronian culture (3), which is currently attributed to Neandertals (36). The Protoaurignacian dispersal may therefore have been a cause (either directly or indirectly) of the extinction of the Neandertals, at least in northern Italy.

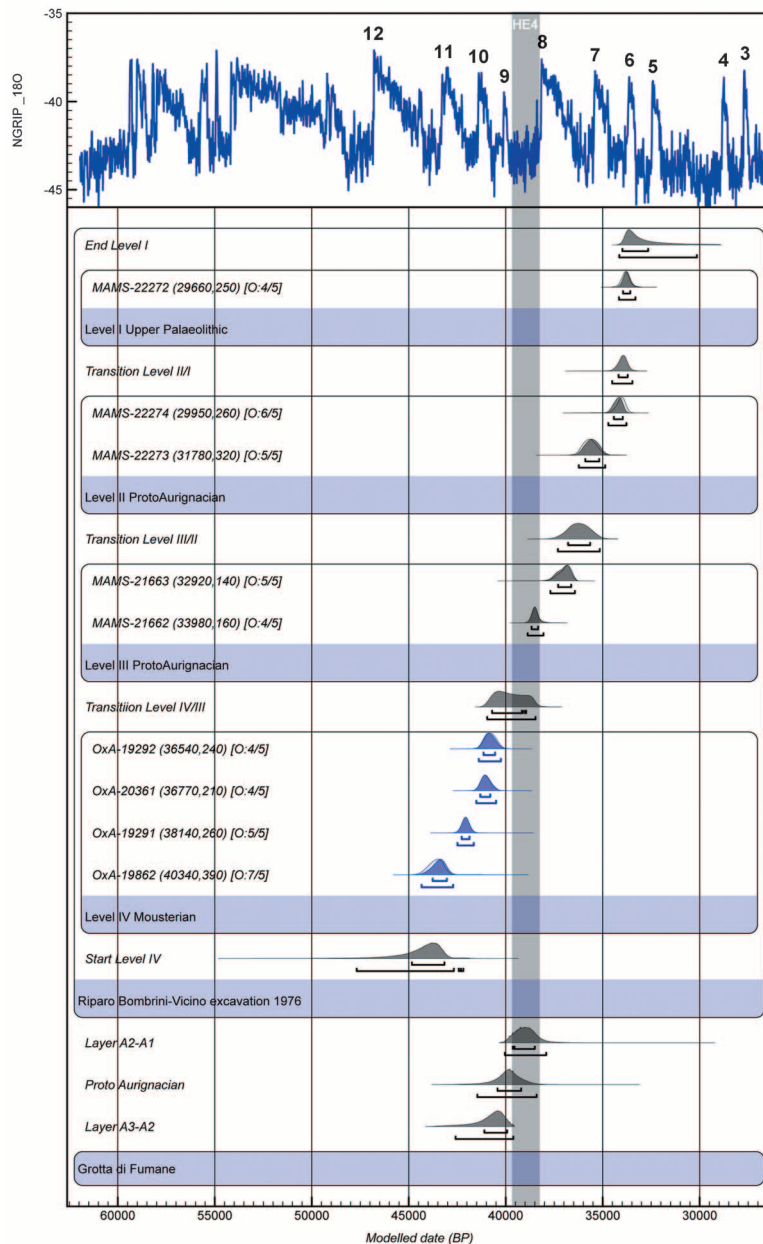


Fig. 3. Bayesian model of dates from the 1976 excavation by Vicino at Riparo Bombrini. Bombrini accelerator mass spectrometry results are compared with Grotta di Fumane boundaries created in (4). Bone samples treated with ultrafiltration are in gray; shell samples from the Mousterian level (4) are in blue. Radiocarbon dates were calibrated in IntCal13 (29) and Marine13 (29) for shell samples. The model and boundaries were calculated using OxCal 4.2 (34), including the performance of the General t-type Outlier Model (34). The results are linked with the North Greenland Ice Core Project $\delta^{18}\text{O}$ climate record (15). The gray-shaded bar denotes Heinrich event 4 (HE4) (35).

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SUPPLEMENTARY MATERIALS

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HUMAN BEHAVIOR

Sex equality can explain the unique social structure of hunter-gatherer bands

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The social organization of mobile hunter-gatherers has several derived features, including low within-camp relatedness and fluid meta-groups. Although these features have been proposed to have provided the selective context for the evolution of human hypercooperation and cumulative culture, how such a distinctive social system may have emerged remains unclear. We present an agent-based model suggesting that, even if all individuals in a community seek to live with as many kin as possible, within-camp relatedness is reduced if men and women have equal influence in selecting camp members. Our model closely approximates observed patterns of co-residence among Agta and Mbendjele BaYaka hunter-gatherers. Our results suggest that pair-bonding and increased sex egalitarianism in human evolutionary history may have had a transformative effect on human social organization.

Contemporary mobile hunter-gatherers cooperate extensively with unrelated individuals across multiple social and economic domains. Many communities of mobile hunter-gatherers (hereafter hunter-gatherers) share food extensively within camp and hunt, gather, and fish cooperatively (1). Alloparenting is also commonplace (2, 3). The importance of cooperative activities is reflected in many hunter-gatherer societies by a pervasive ethic of egalitarianism (4, 5). Like a number of nonhuman primate species, humans live in multimale, multifemale groups (6). However, we maintain enduring pair bonds, resulting in what have been described as “multifamily” groups (7). In addition, in contrast to the bounded and territorial groups of chimpanzees (8, 9), bonobos (10), and gorillas (11), contemporary hunter-gatherers have fluid social networks where family units are relatively autonomous, with couples and their children moving often between bands (12), living with kin of either the husband or the wife. This residence pattern has been described as either “bilocal” or “multilocal” (13).

As well as being highly mobile, contemporary hunter-gatherer camps include a significant proportion of unrelated individuals (14) and are less closely related than groups of non-foraging small-scale societies (15). Given the inclusive fitness benefits of living with kin, why hunter-gatherers live with unrelated individuals is a puzzle, even more so if one considers that hunter-gatherers show a preference for living with siblings (13) and preferentially include kin in their campmate choices and social networks (16). Therefore, the mechanisms by which contemporary hunter-gatherers attempt to maximize co-residence and cooperation with kin, but nonetheless end up residing mostly with unrelated individuals, remain unclear.

Here, we offer a solution for this apparent paradox by demonstrating that, even where all individuals are actively assorting with kin, within-group relatedness is reduced if both sexes have influence over camp composition, as is the case among egalitarian, multilocal hunter-gatherers. We present a simulation of camp assortment where individuals attempt to reside with as many kin as possible under two conditions. In the egalitarian condition, men and women have equal influence on camp composition, whereas in the non-egalitarian condition, only one sex has influence. We compared the results with previously unpublished data from two hunter-gatherer groups, the Palanan Agta ($N = 4055$ dyads) and Mbendjele BaYaka (5) ($N = 1863$ dyads), as well as one farming population, the Paranan ($N = 1049$ dyads). We demonstrate that low within-camp relatedness emerges naturally from men and women seeking to maximize the presence of related kin. In contrast, in societies where decision-making on co-residence rests on one sex only, as in the case of patrilocal farmers, low relatedness does not emerge. Our model offers a mechanism that reconciles individual-level preferences for kin with reduced camp-level relatedness. Assuming that extant hunter-gatherers live in social structures resembling the ones existing in past hominins, our model explains how the shift from an ancestral hierarchical, female-dispersal system to a multilocal, egalitarian one would provide the selective context for expanded social networks, cumulative culture, and cooperation among unrelated individuals.

Among the Agta, we collected data from 191 adults across 11 camps, coding a total of 4055 dyadic relationships. Among the Mbendjele, we collected data from 103 adults across nine camps, totaling 1863 dyadic relationships. Mean experienced camp size was 18.09 adults ($SD = 8.62$) for the Mbendjele and 21.23 adults ($SD = 8.61$) for the Agta. Both populations were multilocal, with

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