



ALMA MATER STUDIORUM
UNIVERSITÀ DI BOLOGNA

ARCHIVIO ISTITUZIONALE DELLA RICERCA

Alma Mater Studiorum Università di Bologna Archivio istituzionale della ricerca

Early Alpine occupation backdates westward human migration in Late Glacial Europe

This is the final peer-reviewed author's accepted manuscript (postprint) of the following publication:

Published Version:

Early Alpine occupation backdates westward human migration in Late Glacial Europe / Bortolini, Eugenio; Pagani, Luca; Oxilia, Gregorio; Posth, Cosimo; Fontana, Federica; Badino, Federica; Saupe, Tina; Montinaro, Francesco; Margaritora, Davide; Romandini, Matteo; Lugli, Federico; Papini, Andrea; Boggioni, Marco; Perrini, Nicola; Oxilia, Antonio; Cigliano, Riccardo Aiese; Barcelona, Rosa; Visentin, Davide; Fasser, Nicolò; Arrighi, Simona; Figus, Carla; Marciani, Giulia; Silvestrini, Sara; Bernardini, Federico; Menghi Alessia; Lessica C.; Fiorenza, Luca; Cecchi, Jacopo Moggi; Tuniz, Claudio; Kivisild, Toomas; Gianfrancesco, Fernando; Peresani, Marco; Schell, Christiane; Talamo, Sahra; D'Esposito, Maurizio; Benazzi, Stefano. - In: CURRENT BIOLOGY. - ISSN 0960-9822. - ELETTRONICO. - 31:11(2021), pp. 2484-2493.e7. [10.1016/j.cub.2021.03.078]

DOI: <http://doi.org/10.1016/j.cub.2021.03.078>

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (<https://cris.unibo.it/>).
When citing, please refer to the published version.

(Article begins on next page)

This is the final peer-reviewed accepted manuscript of:

Bortolini, Eugenio, Luca Pagani, Gregorio Oxilia, Cosimo Posth, Federica Fontana, Federica Badino, Tina Saupe, Francesco Montinaro, Davide Margaritora, Matteo Romandini, Federico Lugli, Andrea Papini, Marco Boggioni, Nicola Perrini, Antonio Oxilia, Riccardo Aiese Cigliano, Rosa Barcelona, Davide Visentin, Nicolò Fasser, Simona Arrighi, Carla Figus, Giulia Marciani, Sara Silvestrini, Federico Bernardini, Jessica C. Menghi Sartorio, Luca Fiorenza, Jacopo Moggi Cecchi, Claudio Tuniz, Toomas Kivisild, Fernando Gianfrancesco, Marco Peresani, Christiana L. Scheib, Sahra Talamo, Maurizio D'Esposito, Stefano Benazzi et al. 2021. Early Alpine occupation backdates westward human migration in Late Glacial Europe, *Current Biology* 31(11):2484- 2493

The final published version is available online at:

<https://doi.org/10.1016/j.cub.2021.03.078>

© [2021]. This manuscript version is made available under the Creative Commons Attribution-NonCommercial-NoDerivs (CC BY-NC-ND) License 4.0 International

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>)

1 Early Alpine occupation backdates westward 2 human migration in Late Glacial Europe

3
4 Eugenio Bortolini^{1,2ab*}, Luca Pagani^{3,4a*}, Gregorio Oxilia^{1a*}, Cosimo Posth^{5,6}, Federica
5 Fontana⁷, Federica Badino^{1,8}, Tina Saube^{4,9}, Francesco Montinaro⁴, Davide Margaritora⁷,
6 Matteo Romandini¹, Federico Lugli¹, Andrea Papini¹⁰, Marco Boggioni¹¹, Nicola Perrini¹²,
7 Antonio Oxilia¹³, Riccardo Aiese Cigliano¹⁴, Rosa Barcelona^{14,15,16}, Davide Visentin¹⁷,
8 Nicolò Fasser⁷, Simona Arrighi¹, Carla Figus¹, Giulia Marciani¹, Sara Silvestrini¹, Federico
9 Bernardini^{18,19}, Jessica C. Menghi Sartorio⁷, Luca Fiorenza^{20,21}, Jacopo Moggi Cecchi²²,
10 Claudio Tuniz^{19,23,24}, Toomas Kivisild^{4,25}, Fernando Gianfrancesco¹⁵, Marco Peresani⁷,
11 Christiana L. Scheib⁴, Sahra Talamo^{26,27}, Maurizio D'Esposito^{15†}, Stefano Benazzi^{1,27}

12
13 ¹ Department of Cultural Heritage, University of Bologna, Via degli Ariani, 1 48121
14 Ravenna, Italy

15 ² CaSEs (Culture and Socio-Ecological Dynamics) Department of Humanities, Universitat
16 Pompeu Fabra Ramon Trias Fargas, 25-27, 08005 Barcelona, Spain

17 ³ Department of Biology, University of Padova, Viale G. Colombo 3 35131 Padova, Italy

18 ⁴ Estonian Biocentre, Institute of Genomics, University of Tartu, Riia 23 51010 Tartu,
19 Estonia

20 ⁵ Department of Archaeogenetics, Max Planck Institute for the Science of Human History,
21 Jena 07745, Germany

22 ⁶ Institute for Archaeological Sciences, Archaeo- and Palaeogenetics, University of
23 Tübingen, Rümelinstrasse 19-23, 72070 Tübingen, Germany.

24 ⁷ Department of Humanities – Section of Prehistoric and Anthropological Sciences,
25 University of Ferrara, Corso Ercole I d'Este 32, 44121 Ferrara, Italy

26 ⁸ Research Group on Vegetation, Climate and Human Stratigraphy, Lab. of Palynology and
27 Palaeoecology, CNR - Institute of Environmental Geology and Geoengineering (IGAG),
28 20126 Milano, Italy

29 ⁹ Department of Evolutionary Biology, Institute of Molecular and Cell Biology, University of
30 Tartu, Tartu, 51010, Estonia

31 ¹⁰ Dentist surgeon, via Walter Tobagi 35, 59100, Prato, Italy

32 ¹¹ Dentist surgeon, via D'Andrade 34/207, 16154, Genova Sestri Ponente, Italy

33 ¹² Dentist surgeon, Centro di Odontoiatria e Stomatologia, Via Luca Signorelli, 5, 51100
34 Pistoia PT

35 ¹³ General surgeon, via Marcantonio Della Torre, 7, 37131, Verona, Italy

36 ¹⁴ Sequentia Biotech, Calle Comte D'Urgell 240, 08036 Barcelona, Spain

37 ¹⁵ Institute of Genetics and Biophysics "Adriano Buzzati-Traverso", National Research
38 Council of Italy, Via P.Castellino 111, 80131 Naples, Italy.

39 ¹⁶ Departamento de Matemáticas, Escuela Técnica Superior de Ingeniería Industrial de
40 Barcelona (ETSEIB), Universitat Politècnica de Catalunya (UPC), Diagonal 647, 08028
41 Barcelona, Spain

42 ¹⁷ Archaeology of Social Dynamics, Institució Milà i Fontanals, Spanish National Research
43 Council (IMF-CSIC), C/Egipcíacques 15, 08001 Barcelona, Spain

44 ¹⁸ Department of Humanities, Università Ca' Foscari Venezia, Dorsoduro, 3484/D, 30123
45 Venezia, Italy.

46 ¹⁹ Multidisciplinary Laboratory, The "Abdus Salam" International Centre for Theoretical
47 Physics (ICTP), Strada Costiera, 11 - 34151 Trieste, Italy.

48 ²⁰ Monash Biomedicine Discovery Institute, Department of Anatomy and Developmental
49 Biology, Monash University, Melbourne VIC 3800, Australia

50 ²¹ Earth Sciences, University of New England, Armidale NSW 2351, Australia

51 ²² Department of Biology, University of Florence, Via del Proconsolo, 12, Firenze 50122,
52 Italy

53 ²³ Centre for Archaeological Science, University of Wollongong, Northfields Ave,
54 Wollongong NSW 2522, Australia.

55 ²⁴ Centro Fermi, Museo Storico della Fisica e Centro di Studi e Ricerche Enrico Fermi,
56 Piazza del Viminale 1, 00184, Roma, Italy

57 ²⁵ Department of Human Genetics, KU Leuven, Leuven, 3000, Belgium

58 ²⁶ Department of Chemistry “G. Ciamician”, University of Bologna, Via Selmi, 2, I-40126
59 Bologna, Italy

60 ²⁷ Max Planck Institute for Evolutionary Anthropology, Department of Human Evolution,
61 Deutscher Platz 6, D-04103 Leipzig, Germany

62

63

64 *a* These authors contributed equally to the present work

65 *b* Lead contact

66 * Correspondence and requests for materials should be addressed to
67 eugenio.bortolini2@unibo.it, luca.pagani@unipd.it, gregorio.oxilia3@unibo.it

68 twitter handle: @erc_success

69 **Keywords**

70 Paleogenomics; Population turnover; WHG; Upper Palaeolithic; Epigravettian; Late Glacial; Southern Europe

71

72 **Summary**

73 In Southern Europe a consistent change in lithic technology, material culture, settlement
74 pattern, and adaptive strategies is recorded at ~18-17 ka ago, before the end of the Last
75 Glacial Maximum (LGM, ~16.5 ka ago¹) set in motion major shifts in human culture and
76 population structure². In this time frame the landscape of Northeastern Italy changed
77 considerably, and the retreat of glaciers allowed hunter-gatherers to gradually recolonise
78 the Alps^{3, 4, 5, 6}. Change within this renewed cultural frame (i.e. during the Late
79 Epigravettian phase), is currently associated with migrations favoured by warmer climate
80 linked to the Bølling-Allerød onset (14.7 ka ago^{7, 8, 9, 10, 11}), that replaced earlier genetic
81 lineages with ancestry found in an individual lived ~14ka ago at Riparo Villabruna, Italy,
82 and shared among different contexts (Villabruna Cluster⁹). Nevertheless, these dynamics
83 and their chronology are still far from being disentangled due to fragmentary evidence for
84 long-distance interactions across Europe¹². Here we generate new genomic data from a
85 human mandible uncovered at Riparo Tagliente (Veneto, Italy), that we directly dated to
86 16,980-16,510 cal BP (2 σ). This individual, affected by focal osseous dysplasia, is
87 genetically affine to the Villabruna Cluster. Our results therefore backdate by at least 3,000
88 years the diffusion in Southern Europe of a genetic component linked to Balkan/Anatolian
89 refugia, previously believed to have spread during the later Bølling/Allerød event. In light of

90 the new genetic evidence, this population replacement chronologically coincides with the
91 very emergence of major cultural transitions in Southern and Western Europe.

92

93 **Results and discussion**

94 Riparo Tagliente represents the earliest available evidence of human occupation of the
95 southern Alpine slope¹¹ while the major glaciers in the area started withdrawing at 17.7-
96 17.3 cal BP (2σ)^{13,14}, and is therefore critical to address questions on the impact of human
97 movement in this time frame (Figure 1; STAR Methods). We performed anthropological
98 (STAR Methods, Method details) and genetic analyses to assess the biological
99 background of the sampled individual. The hemimandible, which is affected by focal
100 cemento-osseous dysplasia (Figure 2; Figure S1; STAR Methods, Method details), was
101 also directly dated to independently ascertain its chronology and the possible
102 contemporaneity with contextual, post-cranial human remains from a partially preserved
103 burial (Tagliente1¹⁵; STAR Methods). The root of the first molar (LM₁) from the
104 hemimandible of Tagliente2 was directly dated to 16,980-16,510 cal BP (95.4% probability
105 using IntCal20¹⁶ in OxCal v.4.3¹⁷; Data S1A) confirming the attribution to the Late
106 Epigravettian chronological range, i.e. the same cultural context as Tagliente1 (16,130–
107 15,560 cal BP (2σ range obtained using¹⁶); Data S1A; STAR Methods, Method details).

108 We extracted DNA from five samples taken from mandibular and tooth tissues and
109 screened for the presence of endogenous human DNA through a pooled whole genome
110 sequencing. One of the healthy mandibular samples yielded sufficient endogenous DNA
111 (5.06%) and was re-sequenced to achieve a total genome wide coverage of 0.28x, yielding
112 266K SNPs overlapping with the 1240K *Human Origins* SNP Array. We also provide a
113 number of non-reference sites found to overlap with genes known to be involved with
114 cementoma insurgence, which, given low coverage and ancient DNA degradation, are
115 reported with no further interpretation (Data S1B; STAR Methods, Method details). Overall
116 contamination estimated from mtDNA was 2.158% and 0.60 – 1.53% from the X
117 chromosome (Data S1C). The mtDNA haplogroup is a basal U2'3'4'7'8'9 (Data S1C and
118 S1D), consistent with a European Palaeolithic individual (Figure 3A), also shared by
119 Rigney1 (15.5ky cal BP⁹) and Paglicci Accesso Sala 2 Rim P (~13ka ago¹⁸). X/Autosome
120 coverage ratio in the order of 0.56 suggests the individual was male, in accordance with
121 results of morphological analysis (STAR Methods, Method details), and the chromosome Y
122 haplogroup was estimated to be I2, which captures the majority of diversity in Europe after
123 ~14ka ago (Figure 3B, Data S1E). Most samples dated to this period fall within a single

124 mtDNA (U5b¹⁰) and chrY (I2⁹) branch, flagging a putative expansion from a single founding
125 population.

126 From a population perspective, we performed a MDS analysis based on outgroup f3
127 distances (Figure 4A) and found the sample to fall within the broader European Western
128 Hunter Gatherer (WHG) genetic variation, pointing to an affinity to the previously described
129 Villabruna Cluster. This group has been defined on the basis of genetic affinity among
130 individuals known to have largely replaced previous European Hunter Gatherer
131 populations at least ~14 ka ago. Notably these individuals showed little or no trace of
132 genetic contributions from pre-existing European groups such as the ones genetically
133 close to the Dolní Věstonice or to Goyet-Q116-1 human remains and known to have
134 inhabited Europe until the LGM⁹. One of the defining features of the Villabruna Cluster is a
135 higher affinity with Near Eastern genetic components than that exhibited by pre-existing
136 palaeolithic West Eurasians. The significantly negative f4 test (Kostenki14, Tagliente2,
137 Druze, Mbuti: $f_4 = -0.0037$; standard error = 0.00063; $Z = -5.88$) further confirmed Tagliente2
138 to share genetic features with the Villabruna Cluster and to be in discontinuity with the
139 preceding European genetic background. We followed up this observation using a series
140 of f4 tests in the form (Tagliente2, X; Y, Mbuti), where Y is a population of interest and X is
141 either Villabruna (~14ka ago⁹), Bichon (~13.7ka ago⁹) or a Mesolithic Italian from Grotta
142 Continenza (~11.9ka ago¹⁹; Figure 4B). We chose three independent WHG samples to
143 control for potential biases introduced by the genotyping strategy, and indeed found small
144 discrepancies when we compared results obtained using capture (Villabruna) or shotgun
145 (Bichon and Continenza) data. To minimise this effect we chose to put more weight on the
146 interpretation of shotgun results, deemed to be more readily comparable with the shotgun
147 data generated for Tagliente2 in this study. We also show that the data available is
148 sufficient to achieve significance in a f4 test when the order of X and Y populations are
149 inverted, as for (Tagliente, Y, Grotta Continenza, Mbuti, Figure S2). The higher affinity of
150 Continenza and Bichon to later WHG (Loschbour, Iberia_HG and Continenza, Bichon, and
151 Villabruna themselves) when compared to Tagliente2 may be explained by the more
152 ancient age of Tagliente2 or with the former individuals being genetically closer to the
153 ancestry that reached central Europe at least by 14ka ago. Alternatively, the higher affinity
154 emerging among more recent WHG samples may also be ascribed to subsequent
155 admixtures between the newly arrived Tagliente2 individuals and pre-existing Dolní
156 Věstonice- or Goyet Q116-1-like (~35ka ago⁹) genetic substrates, as already reported for
157 Loschbour (~8.1ka ago^{9, 20}). We then modelled the position of Tagliente2 within the tree
158 proposed by Fu and colleagues⁹ (Figure S3A) and found that it may fit well within the

159 Villabruna branch confirming previous results (Figure S3B-D). To minimise the effects of
160 the mismatch between capture and shotgun data due to attraction, we also explore the
161 feasibility of the basic qpGraph (Figure S3B) using, where possible, shotgun samples
162 (Figure S4).

163 With our work we provide genomic, uniparental, and chronological evidence that
164 backdates the presence of the so called Villabruna component in Northern Italy to as early as
165 as 17 ka ago, when it chronologically overlaps with major cultural transitions involving the
166 region. The shift from Early to Late Epigravettian has not been abrupt, and despite the
167 emergence of regionalism and environmental/cultural differences between Adriatic and
168 Tyrrhenian contexts¹², change in the relative frequency of artefact types and reduction
169 sequences, as well as in raw material procurement and settlement patterns can be
170 recorded since ~17ky cal BP^{4, 5, 12, 21, 22, 23, 24, 25, 26, 27, 28}. After 14ky cal BP a more marked
171 discontinuity is attested by the greater reliance on geometric microlithic pieces, and a
172 stronger presence of engraved and painted bones and stones bearing linear, geometric,
173 zoomorphic or anthropomorphic motives^{21, 23, 28}.

174 The Early to Late Epigravettian transition is broadly coeval to a marked retreat of
175 Alpine glaciers (ca 18-17.5ka ago²⁹) after they had reached their maximum between 26-
176 24ka ago¹⁴, and to a rapid rise in sea levels since 16.5ka ago¹. These processes led to
177 considerable change in the geomorphology of the Alpine sectors and stabilised large
178 surfaces of the Great Adriatic/Po Region¹². A rapid forest recolonization of the Alpine
179 foothills started about 17ka cal BP, well before the major Bølling/Allerød warmup^{13, 30, 31}.
180 Alpine forelands became (open) pine forests with tree *Betula* and *Larix*³ (Figure 1c), while
181 open vegetations developed in the distal sector of the megafans^{12, 32}. At the end of LGM,
182 local faunal availability was limited and mostly consisted of species adapted to open
183 environments which had been able to find their climatic optimum by moving to higher
184 elevations in warmer interstadials (e.g. Alpine ibex and marmot) or taking refuge (e.g. Elk)
185 in areas with favourable microclimates. Most Central European, cold-adapted megafaunal
186 species had entered northern Italy before the onset of LGM through the central Slovenian
187 corridor - the same used by Gravettian hunter-gatherers to follow game and settle across
188 the Adriatic¹². During LGM both new arrivals and northward movements of these large
189 mammals were hampered, and they either locally disappeared or became extinct in
190 association with short LGM interstadials (as in the case of cave bears, between 24.2-
191 23.5ka ago³³). The reduction of the forest cover during colder phases is confirmed by the
192 presence of *Capra ibex*, *Rupicapra rupicapra* and *Marmota marmota*, both in the core of

193 the Po Plain and in caves and shelters of Berici Hills^{34, 35}. In the same area,
194 archaeological records show the presence of palaeoartic birds³⁶ currently only found in
195 high-latitude regions of the northern hemisphere.

196 Taken together, our results support two different - although not mutually exclusive -
197 scenarios. The first one involves a broad network of refugia connecting Mediterranean and
198 Eastern Europe during and immediately after the LGM. The network could have facilitated
199 long-distance transmission through a stepwise exchange of both cultural and genetic
200 information from the Black Sea all the way to the Iberian Peninsula. This scenario, which
201 cannot be tested with the available evidence, would predict a relationship between the age
202 of a sample, its geographic location, and the relative abundance of Villabruna genetic
203 components shared with present-day Near Easterners. From a cultural point of view, the
204 development of Early and Late Epigravettian material culture in Southern Europe would
205 not be directly driven by abrupt, millennial-scale climatic events, and could result from
206 convergence, local adaptation, and cultural diffusion without entailing population
207 movement. In this case, geographic distance between sites would also predict similarity in
208 lithic assemblages.

209 The second scenario implies instead population movement and replacement, a
210 more abrupt genetic turnover and a distribution of both genetic and cultural similarities that
211 is not well predicted by geographic clines. This population shift could have taken place
212 during the LGM, i.e. after ~27ka ago when Věstonice-like components were still visible at
213 Ostuni (Southern Italy), and before ~17ka ago. Groups bearing the Villabruna lineage may
214 have exploited the Slovenian corridor and lower Adriatic Sea levels to occupy Adriatic Italy
215 up to the Po plain, and recolonised pre-Alpine valleys only at a later stage. According to
216 this model, after ~27ka ago genetic lineages found in Italy, and only later in France and
217 Spain, should show either or both of i) genomic affinities with the Villabruna Cluster, and ii)
218 uniparental lineages belonging to U2'3'4'7'8'9 /U5b mtDNA and/or I2/R1a Y groups.
219 According to this model, cultural change recorded in Italy across the Epigravettian
220 sequence may have been at least in part triggered by demic processes linked to
221 population replacement.

222 From a cultural perspective, the biased spatial and temporal distribution of the
223 available archaeological record can hardly be used to directly discriminate between these
224 two models, and there is still considerable uncertainty on the temporal dynamics
225 underlying the beginning of the Late Epigravettian across the whole of Italy¹². Since ~18-
226 17cal kBP there is evidence of a shift from Solutrean to Magdalenian material culture in

227 Southwestern Europe, and from Early to Late Epigravettian material culture in a vast area
228 ranging from the Rhone river to the Southern Russian plain^{12, 23, 37, 38}. Environmental
229 pressure conditioned the movement of megafauna during the LGM and limited the
230 movement of human groups to corridors connecting Southern Europe, the Balkans, and
231 Eastern Europe. In this period, human groups inhabiting Southern Europe were exposed
232 to limited ecological risk compared to other regions of Central and Northern Europe^{2, 39, 40,}
233 ⁴¹. Variability in Sr isotope composition of individuals uncovered at Grotta Paglicci (Apulia,
234 Southern Italy) shows a conspicuous change in residential mobility patterns and adaptive
235 strategies between Gravettian and Early Epigravettian hunter-gatherers. Given the lack of
236 any contextual evidence for change in climate, these differences are imputed to cultural
237 factors and possibly linked to population replacement which may have taken place already
238 at an early stage of the Epigravettian sequence⁴².

239 Similarity in the distribution of artefact types between Italy and the Balkans, on the
240 other hand, supports the possible expansion of techno-complexes from Central Europe via
241 eastern/Slovenian routes and hint at long-distance mobility for Epigravettian hunter-
242 gatherers¹². The same pattern, however, has been used to challenge this view in favour of
243 a social network hypothesis²⁴. Similarity between Balkan and Italian contexts is
244 documented from the Gravettian to the Mesolithic, and contacts involved raw lithic
245 materials, marine molluscs, ornamental beads, clay figurines, decorative motives, and
246 lithic technology^{5, 23, 25, 43}. At the same time, the reliability of some cultural markers (such
247 as shouldered points) as proxies of human movement/interaction has been recently
248 questioned¹².

249 Uniparental genetic markers might be useful to disentangle the two proposed
250 scenarios. The majority of samples attributed to the Villabruna Cluster (Figure 3) on a solid
251 genetic and chronological basis share mtDNA and chrY belonging to a limited number of
252 lineages. Reduced diversity within the uniparental Villabruna landscape is consistent either
253 with a bottleneck interrupting the network or with a founder event in a broader scenario of
254 population shift¹⁰. This uniparental landscape, paired with evidence for seamless cultural
255 exchange across the Adriatic¹² and increased affinity with eastern genomic components,
256 make genetic replacement the most likely explanation for our results. The presence of
257 Paglicci71 (~18.5 ka ago¹⁰) within the Villabruna maternal lineage advocates for a founder
258 event in Southern Italy as early or even before ~18.5 ka ago, followed by a later expansion
259 in Northern Italy at the beginning of deglaciation. In this light, Tagliente2 may be seen as
260 an early settler of the Southern Alpine region, perhaps explaining the basal mtDNA lineage

261 of this sample. The possibility of an earlier connection between Eastern and Western
262 Europe through southern corridors, either in the form of an extended LGM network or as
263 an early arrival of Villabruna-like individuals in Western Europe, is also supported by El
264 Mirón, an Iberian sample dated to ~18.7ka ago^{9, 12, 20} presenting with an admixture of
265 Magdalenian, Goyet-2-like ancestry and ancestry related to the Villabruna cluster. The
266 most parsimonious interpretation of the emerging genetic scenario suggests that
267 cumulative cultural change observed in Southern Europe from the end of LGM to the end
268 of the Younger Dryas (~11.7 ka ago) was at least in part triggered by gene flow from
269 southeastern refugia into Italy. This process, in its early stage and to the south of the Alps,
270 was independent of the later Bølling-Allerød event, and contributed to the gradual
271 replacement of pre-LGM ancestry across the Italian peninsula⁴⁴ and beyond. Further
272 genetic evidence from Southern European contexts dated between ~27-19 ka ago, and
273 analyses of cultural similarity between Italy and putative sources of population movement,
274 however, will be needed in the future to test this hypothesis.

275 In conclusion, Tagliente2 provides evidence that the major migrations which
276 strongly affected the genetic background of all Europeans^{7, 8, 9, 10, 11} started considerably
277 earlier in Southern Europe than previously reported, and were already in place in this
278 region during the cold phase following the LGM peak, possibly favoured by stepwise
279 reductions of glacier extent and forest expansion preceding the Bølling-Allerød rapid
280 warming. At this stage, Southern Europe, the Balkans, and Eastern Europe/Western Asia
281 were already connected into the same network of potential LGM refugia, and exchanged
282 both genes and cultural information posing the basis for the observed population
283 replacement. This finding also backdates previous conclusions concerning a plausible
284 demic component to change over time in the coeval material culture of Southern Europe^{7,}
285 ^{8, 9, 10, 11}, and temporally locates this process at the transition between Early and Late
286 Epigravettian or even possibly at the very beginning of the Epigravettian sequence.

287

288 **Acknowledgements**

289 This work is dedicated to the memory of the late Maurizio D'Esposito. The research was
290 supported by the European Union through the European Research Council under the
291 European Union's Horizon 2020 Research and Innovation Programme (grant agreement
292 No 724046 – SUCCESS awarded to S.B. - www.erc-success.eu; grant agreement No.
293 803147 RESOLUTION awarded to S.T., <https://site.unibo.it/resolution-erc/en>) as well as
294 through the European Regional Development Fund (Project No. 2014–2020.4.01.16–0030

295 to C.L.S. and T.S.) and projects No. 2014-2020.4.01.16-0024, MOBTT53 (L.P.); by the
296 Estonian Research Council personal research grant [PRG243] (C.L.S); by UniPd PRID
297 2019 (L.P.). We thank the Ministry of Cultural Heritage and Activities of Italy, and Veneto
298 Archaeological Superintendency for granting access to the human remains of Tagliente2,
299 in particular the SABAP of Verona, Rovigo and Vicenza. We are grateful to Dr. Francesca
300 Rossi and Dr Nicoletta Martinelli for giving access to human remains from Riparo Tagliente
301 and for the support they provided during sampling. We also thank Dr. Elisabetta Cilli and
302 Mr. Andrea De Giovanni for assistance with the preliminary documentation of the
303 hemimandible Tagliente2.

304

305 **Author contribution**

306 Designed Study: E.B., L.P., G.O., S.B., Run Analyses: E.B., L.P., G.O., C.P., T.S., F.M.,
307 T.K., C.S., S.T., Wrote Manuscript: E.B., L.P., G.O., F.F., F.Ba., M.R., F.L., M.P., S.B.,
308 Provided Samples, Reagents or Sequences: F.F., R.A., C.S., S.T., M.D., S.B.,
309 Contributed Interpretation of Results: C.P., F.F., F.Ba., D.M., M.R., F.L., A.P., M.B., N.P.,
310 A.O., S.A., C.F., G.M., S.S., F.Be., J.Me., L.F., J.Mo., C.T., T.K., F.G., M.P., S.T., M.D.

311

312

313 **Declaration of Interests**

314 The authors declare no competing interests

315

316

317

318

319

320

321

322 **Figure Legends**

323

324 **Figure 1 Geographical, ecological, and cultural context of the study. a)**

325 Palaeogeographic map of Europe during Late Glacial, centered at 17 ka ago (see Method
326 details). Coloured areas refer to the distribution of Epigravettian and Magdalenian material
327 culture at 17ka ago, while white symbols indicate the geographic location of the main
328 sampling sites discussed in the text (~30-8ka ago); b) 3D lateral view of the hemimandible
329 Tagliente2 with roots, pulp chambers, dentine and enamel of the preserved teeth, as well
330 as the cementome (in red) between the distal side of P₃ root and the mesial root side of M₁
331 (Figure S1); c) Comparison between palaeoclimate, palaeoenvironmental and cultural
332 proxies over the 30-11 ka cal BP time span. Key to panels: (1) Reconstruction of Southern
333 Alpine past vegetation^{3, 6, 13, 45, 46}; (2) Eurasian major megafaunal transitions (regionwide
334 extirpations or global extinctions, or invasions, of species or major clades)^{33, 47}; (3) NGRIP

335 $\delta^{18}\text{O}$ record in 20 yrs means on the GICC05 time scale⁴⁸; (4) Material cultural sequence
336 for Eastern and Southern Europe. Chronology for Tagliente2 (2σ obtained using¹⁶; Data
337 S1A) is marked in blue.

338
339

340 **Figure 2 Tagliente2 virtual (left) and physical (right) section.** On the left, microCT
341 distal view of the premolar and its pathological cementum tissue. On the right, histological
342 section. Magnification (250X) of the cementum tissue colored by Hematoxylin/Eosin. B =
343 Buccal; L = Lingual; scalebar = 0.5mm (see Figure S1, Data S1B and STAR Methods).

344
345

346 **Figure 3 Uniparental haplogroups of Tagliente2.** A) mtDNA haplogroup of Tagliente2
347 (in gold, Data S1C, Data S1D, Figure S4) within a number of pre (Green) and post (blue)
348 Villabruna samples; B) chrY haplogroup of Tagliente2 (gold, Data S1C, Data S1E)
349 surrounded by post-Villabruna samples (including Bichon, BC). Y Haplogroup splits are
350 drawn according to the dater estimates based on high coverage modern sequences⁴⁹. The
351 ancient individuals are mapped on this tree considering the available haplogroup-
352 informative available SNP data and private mutations in the ancient samples have been
353 ignored.

354
355

356 **Figure 4 Demographic inference from Tagliente 2.** A) Mutidimensional Scaling based
357 on (Mbuti; X, Tagliente2) outgroup f3 statistics show Tagliente2 (golden star) to cluster
358 within the Villabruna Cluster (in blue) and away from the pre-existing South European
359 samples (in green). B) f4 tests (Tagliente2, X, Y, Mbuti +/- 3 s.e.) where X is either a
360 Mesolithic Italian, Villabruna or Bichon WHG sample and Y, shown along the y axis, is a
361 population of interest (Data S1C, Figure S2, Figure S3, Figure S4).

362
363

364 **STAR Methods**

365

366 **RESOURCE AVAILABILITY**

367 **Lead Contact**

368 Further information and requests for resources and reagents should be directed to and will
369 be

370 fulfilled by the Lead Contact, Eugenio Bortolini (eugenio.bortolini2@unibo.it)

371 **Materials Availability**

372 X-ray microCT scans and the digital model obtained after segmentation of the mandibular
373 section interested by cementoma are currently stored at the Virtual Anthropology section of
374 Bones Lab, University of Bologna, and can be accessed upon request (Gregorio Oxilia).

375 **Data and Code Availability**

376 Whole genome sequences generated for this study are freely available for download at
377 www.ebc.ee/free_data/Bortolini_2020/

378

379 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

380 A new genomic sequence and direct dating were obtained for the hemimandible
381 Tagliente2, uncovered at Riparo Tagliente (Stallavena di Grezzana, Verona, Italy). The
382 anthropological materials found at Ripato Tagliente are currently stored at the Natural
383 History Museum of Verona. Permission to access the hemimandible was granted by the
384 SABAP of Verona, Rovigo and Vicenza (Veneto Archaeological Superintendency, Ministry
385 of Cultural Heritage and Activities of Italy) which is legally responsible for the conservation
386 and scientific study of the skeletal remains found at the site. The shelter is located on the
387 left slope of Valpantena, one of the main valley bottoms of the pre-Alpine massif of Monti
388 Lessini. The site lies under a rock-shelter and was discovered in 1958 by Mr. Francesco
389 Tagliente. It opens at the base of Monte Tregnago under a bank of oolitic limestones at an
390 altitude of 250 m a.s.l. Archaeological investigations were carried out by the Museo Civico
391 di Storia Naturale of Verona from 1962 to 1964 and resumed by the University of Ferrara
392 since 1967. The site preserves a stratigraphic series which reaches a thickness of over
393 4.50 m in the outer area of the rock-shelter. Such sequence is formed by two main
394 deposits separated by river erosion: the lower deposit contains evidence of Mousterian
395 and Aurignacian occupations and the upper one is characterized by rich record related to
396 several intense Late Epigravettian settlement occurrences⁵⁰. According to radiocarbon
397 dates which range from 17,219-16,687 cal BP (layer 13 alpha) to 14,572–13,430 cal BP
398 14535-13472 (levels 10–8), the Epigravettian series is one of the most complete in
399 northern Italy spanning from the first part of the Lateglacial to the the Bølling–Allerød
400 interstadial^{5, 51}.

401 The hemimandible Tagliente2 was found in 1963 during the first excavation campaigns in
402 the site within disturbed sediments located immediately outside the shelter⁵². According to
403 excavators such sediments could come from the inner area of the shelter and have been
404 removed during historical excavations in the uppermost deposits which had led to
405 destruction of part of the prehistoric stratigraphic sequence and dumping of sediments
406 outside the shelter entrance. An *in situ* burial was found ten years later (1973) at the

407 southern edge of the sheltered area⁵⁰. The burial had been partially destroyed by the same
408 historical excavations. Nonetheless the lowermost part of the skeleton - from the pelvis to
409 the feet - was well preserved in the grave while only a few ribs and vertebrae, the distal
410 fragments of the radius and ulna and some phalanxes were collected on the trampling
411 floor of the artificial chamber created by historical excavations. The skeleton was
412 contained in a 60 cm deep and 60 cm wide pit with a concave section. It had been laid in a
413 supine position with outstretched arms. The original composition of the grave goods
414 assemblage is unknown due to the incompleteness of the burial but a limestone pebble
415 covered with traces of ochre was found between the feet and a fragment of bovid horn
416 near the right femur. The intentional deposition of a pierced *Cyclope* collected near the left
417 knee is uncertain. The legs were covered with some limestones blocks of different
418 dimensions. A large stone located on the femurs was characterized by engravings of a lion
419 and the horn of an auroch⁵⁰. The skeleton belonged to a young adult male aged 20–29
420 years and about 163 cm tall⁵³. Carbon and nitrogen stable isotope analysis performed on
421 the bone collagen from the partial skeleton (from a rib) and 11 faunal remains from layers
422 consistent with the burial deposition, suggests that the human individual had a terrestrial
423 diet integrated by consumption of aquatic resources¹⁵. Radiocarbon dating of the
424 hemimandible, of the partial burial and the stratigraphic position of the burial pit, which
425 intersects the Mousterian deposits, shows consistency with the first phase of Late
426 Epigravettian occupation in the site. At Riparo Tagliente, layers referred to this period are
427 better known in the northern sector where they have been extensively explored in the area
428 protected by the rock-shelter over a surface of around 20 s.q.m.

429

430 **METHOD DETAILS**

431 **Palaeogeographic map of Europe at 17ka ago**

432 Coordinate system ETRS89 / UTM zone 32N (EPSG 25832); Digital Elevation Model
433 (base topography – Copernicus Land Monitoring Service 2019 (CLMS,
434 http://land.copernicus.eu/pan_european), and General Bathymetric Chart of the Oceans
435 (GEBCO 2019 grid, doi:10.5285/836f016a-33be-6ddc-e053-6c86abc0788e). Sea level
436 drop at – 110 m¹. Scandinavian and British Islands ice sheets, mountain glaciers Last
437 Glacial Maximum (LGM) extent (striped areas) and freshwater systems modified after
438 Badino et al.⁶. Scandinavian and British Islands ice sheets (pale blue) at 17 ka after
439 Hughes et al.⁵⁴. Alpine glaciers extent (dashed outline) modelled at 17 ka from Seguinot et
440 al.⁵⁵ (<https://doi.org/10.5446/35164>). Modelled extension is generally underestimated in the
441 northwestern Alps and overestimated in the eastern and south-western Alps⁵⁵.

442 The period ranging between the Last Glacial Maximum (LGM) and the onset of the
443 Holocene (ca. 30-11 ka cal BP) experienced large-scale climate changes that produced
444 distinctive local and regional ecological and bio-cultural responses (Fig. 1). This time
445 interval is characterised by large migratory events of modern human populations linked to
446 dramatic changes in demography, human behaviour, and the appearance of various
447 material culture complexes¹⁰ (Fig. 1). Glaciated Alps represented an effective
448 physiographic barrier for meridional moist advection^{56, 57} supporting tree growth and
449 boreal forests in the southern alpine foreland.

450 A phase of major forest contraction occurred between ca. 26 to 21 ka cal BP during the
451 GS-3 stadial (Fig. 1c). At this time, European mountain glaciers expanded^{14, 54} and large
452 piedmont glaciers advanced onto the Alpine foreland around 25 ky ago (e.g.^{14, 58}). A
453 continental shelf emerged as consequence of extreme sea level fall (i.e., ~120m^{59, 60})
454 connecting the Balkans to the Western Mediterranean regions with a major role in driving
455 large-scale migratory fluxes of Gravettian-Postgravettian hunter-gatherers. During the
456 LGM culmination there is at present no direct evidence of megafaunal extinction events
457 (Fig.1c). The extinction of Cave bears³³, is one of the most relevant issues of the Late
458 Quaternary⁴⁷ whose main causes are human hunting and interference^{61, 62} and climate
459 change^{63, 64, 65, 66, 67, 68}. On the other hand, major megafaunal (mainly steppe taxa)
460 extinction events rather appear to be associated with warming events towards the end of
461 the Pleistocene (~14 to 11 ka; Fig.1c). During the interval ranging between ca. 19-11.7 ka
462 yrs cal BP, the Epigravettian colonization of the Alps, Apennines, and the Dinarids started.
463 After ca. 18 ka, the deglaciation was characterised by dynamic glacial fluctuations⁵⁵ (Fig.
464 1a) through the two combined processes of down melting (in altitudes) and ice-retreat
465 controlled by slope-damming processes along the valley floors. Pine-birch groves and
466 open larch stands established in the South-Alpine foreland, while open woodland of
467 spruce, pine and larch with a juniper understorey colonized ice-free areas in the eastern
468 Pre-Alps^{3, 13}. During this period the first human occurrence at the foot of the Pre-Alps is
469 documented at Riparo Tagliente ⁵¹.

470 This phase was followed by an abrupt shift to warmer conditions at ca. 14.7 ka cal BP
471 (onset of Bølling–Allerød interstadial period, GI-1e in the Greenland ice record) (Fig. 1c),
472 which promoted the displacement of alpine habitats to higher altitudes and an increase in
473 woodland density with dominance of pine, larch, spruce and birch³. The second part of this
474 Interstadial was marked by the expansion of mixed oak forests in the Po plain and
475 submountain belt. Such favourable climatic conditions promoted the increase in the
476 number of Epigravettian sites and also a gradual colonization of high altitudes (i.e., above

477 1000 m a.s.l.). Renewed cold conditions occurred at the beginning of the Younger Dryas
478 (YD, also regarded as event GS 1 in Greenland ice cores; ca. 12.9 -11.7 ka cal BP; e.g.⁶⁹;
479 Fig. 1c). It certainly had strong effects on stands of thermophilous trees formerly expanded
480 in the forelands of the Southern Alps. During the second half of this event, a renewed
481 glacial activity is recorded in the high valleys and extends well into the early Holocene⁵⁸.
482 ⁷⁰. This oscillation precedes the final transition to Holocene interglacial conditions at 11.7
483 ka cal BP. Palaeoecological data indicate a rapid transformation of forests composition in
484 the valley floors and lower slopes. Here, mixed forest with thermophilous trees such as
485 *Quercus*, *Ulmus*, and *Tilia* expanded³. Due to the increase of temperature, the timberline
486 rapidly reached an altitude of about 2100 m a.s.l. within few centuries⁷¹. During the
487 Mesolithic, an intense human colonization of the highlands as well as the valley floors and
488 the middle high landscapes of the Alps and the Italian Prealps is documented⁷². In this
489 context, larger residential sites surrounded by more ephemeral sites could be tied together
490 in seasonal vertical mobility along the treeline belt⁷³.

491

492 **Radiocarbon dating**

493 The tooth from the hemimandible (Tagliente2) was pretreated at the Department of Human
494 Evolution at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA), Leipzig,
495 Germany, using the method previously published⁷⁴. Circa 500 mg of the whole root of the
496 tooth is taken. The sample is then decalcified in 0.5M HCl at room temperature until no
497 CO₂ effervescence is observed. 0.1M NaOH is added for 30 minutes to remove humics.
498 The NaOH step is followed by a final 0.5M HCl step for 15 minutes. The resulting solid is
499 gelatinized following Longin (1971)⁷⁵ at pH3 in a heater block at 75°C for 20h. The gelatine
500 is then filtered in an Eeze-Filter™ (Elkay Laboratory Products (UK) Ltd.) to remove small
501 (<80µm) particles. The gelatine is then ultrafiltered⁷⁶ with Sartorius “VivaspinTurbo” 30
502 KDa ultrafilters. Prior to use, the filter is cleaned to remove carbon containing
503 humectants^{77, 78}. The samples are lyophilized for 48 hours. The date is corrected for a
504 residual preparation background estimated from ¹⁴C free bone samples. These bones
505 were kindly provided by D. Döppes (MAMS, Germany), and one was extracted along with
506 the batch from the tooth⁷⁹. To assess the preservation of the collagen yield, C:N ratios,
507 together with isotopic values must be evaluated. The C:N ratio should be between 2.9 and
508 3.6 and the collagen yield not less than 1% of the weight⁸⁰. For the tooth stable isotopic
509 analysis is evaluated at MPI-EVA, Leipzig (Lab Code R-EVA 1606) using a
510 ThermoFinnigan Flash EA coupled to a Delta V isotope ratio mass spectrometer. The
511 Tagliente tooth passed the collagen evaluation criteria and between 3 and 5 mg of

512 collagen inserted into pre-cleaned tin capsules. This was sent to the Mannheim AMS
513 laboratory (Lab Code MAMS-27188) where it was graphitized and dated⁸¹.
514 The age of Tagliente2 is 16980-16510 years cal BP (95.4% probability obtained using¹⁶). If
515 we compare this result to the one from Tagliente1 (16130-15570cal BP at 95.4%
516 probability, calibrated using the same curve) it appears that the two calibrated radiocarbon
517 ages differ beyond the 2 σ level. Therefore, we suggest that Tagliente1 and Tagliente2
518 specimens likely belonged to different individuals. Likewise, stable isotopes of collagen
519 indicate diverse dietary inputs for Tagliente1¹⁵ and 2, corroborating the hypothesis of a
520 different origin for these samples. Nevertheless, both age determinations are consistent
521 with an attribution of all the fossils to the first phase of Late Epigravettian occupation at
522 Riparo Tagliente.

523

524

525

526 **DNA Extraction and Sequencing**

527 The DNA extraction and sample library was prepared in the dedicated ancient DNA
528 laboratory at the Estonian Biocentre, Institute of Genomics, University of Tartu, Tartu,
529 Estonia. The library quantification and sequencing were performed at the Estonian
530 Biocentre Core Laboratory. The main steps of the laboratory work are detailed below.

531 ***DNA extraction***

532 Tooth/bone material was powdered at the aDNA clean lab of the Department of Cultural
533 Heritage, University of Bologna by G.O. and S.S. and sent to the University of Tartu. To
534 approximately 20 mg of powder 1000 μ l of 0.5M EDTA pH 8.0 and 25 μ l of Proteinase K
535 (18mg/ml) were added inside a class IIB hood. The sample was incubated for 24 h on a
536 slow shaker at room temperature. DNA extracts were concentrated to 250 μ l using
537 Vivaspin® Turbo 15 (Sartorius) concentrators and purified in large volume columns (High
538 Pure Viral Nucleic Acid Large Volume Kit, Roche) using 10X (2.5 ml) of PB buffer (Qiagen)
539 following the manufacturers' instructions with the only change being a 10 minute
540 incubation at 37 degrees prior to the final elution spin and eluted in 100 μ l of EB buffer
541 (QIAGEN). Samples were stored at -20 C.

542

543 ***Library preparation***

544 The extracts were built into double-stranded, single-indexed libraries using the NEBNext®
545 DNA Library Prep Master Mix Set for 454™ (E6070, New England Biolabs) and Illumina-
546 specific adaptors^{82, 83, 84}. DNA was not fragmented and

547 reactions were scaled to half volume, adaptors were made as described in⁸² and used in a
548 final concentration of 2.5uM each. DNA was purified on MinElute columns (Qiagen).
549 Libraries were amplified using the following PCR set up: 50µl DNA library, 1X PCR buffer,
550 2.5mM MgCl₂, 1 mg/ml BSA, 0.2µM inPE1.0, 0.2mM dNTP each, 0.1U/µl HGS Taq
551 Diamond and 0.2µM indexing primer. Cycling conditions were: 5' at 94C, followed by 18
552 cycles of 30 seconds each at 94C, 60C, and 68C, with a final extension of 7 minutes at
553 72C. Amplified products were purified using MinElute columns and eluted in 35 µl EB
554 (Qiagen). Three verification steps were implemented to make sure library preparation was
555 successful and to measure the concentration of dsDNA/sequencing libraries – fluorometric
556 quantitation (Qubit, Thermo Fisher Scientific), parallel capillary electrophoresis (Fragment
557 Analyser, Advanced Analytical) and qPCR.

558 Library quality and quantity have been assessed by using Agilent Bioanalyzer 2100 High
559 Sensitivity and Qubit DNA High Sensitivity (Invitrogen). The initial shotgun screening was
560 done on NextSeq500 using the High-Output 75 cycle single-end kit. The secondary,
561 paired-end sequencing was performed on the NovaSeq6000 (Illumina), flowcell S1,
562 without any other samples to ensure no index-hopping due to the single-indexing of the
563 sample, generating 150-bases paired-end reads. Whole genome sequencing with Illumina
564 paired-end (2x150 bp) led to 488 million high-quality reads. About 6.99% of the reads
565 could be successfully mapped on the human genome sequence with a duplication rate of
566 51%, leading to an average 0.28x genome coverage (Data S1C). The mapped reads
567 showed nucleotide misincorporation patterns which were indicative of post-mortem
568 damage.

569 ***Sequencing filtering, mapping and variant calling analysis***

570 Before mapping, the paired end reads were merged and corrected using FLASH⁸⁵. The
571 merged reads were trimmed of adapters, indexes and poly-G tails occurring due to the
572 specifics of the NextSeq500 and NovaSeq technology using cutadapt-1.11⁸⁶. Sequences
573 shorter than 30 bp were also removed with the same program to avoid random mapping of
574 sequences from other species (Figure S5). The sequences were aligned to the reference
575 sequence GRCh37 (hs37d5) using Burrows-Wheeler Aligner (BWA 0.7.12)⁸⁷ and the
576 command mem with seeding disabled. After alignment, the sequences were converted to
577 BAM format and only sequences that mapped to the human genome were kept with
578 samtools-1.3⁸⁸. Afterwards, the data from different flow cell lanes were merged and
579 duplicates were removed using picard 2.12
580 (<http://broadinstitute.github.io/picard/index.html>). Indels were realigned using GATK-3.5⁸⁹
581 and reads with a mapping quality less than 10 were filtered out using samtools-1.3. In

582 order to maximise the coverage of sites included in the 1240 Human Origin capture array,
583 a random read with mapping quality above 30 and phred score above 33 was chosen to
584 represent the pseudo-haploid genotype of our sample, and then merged with reference
585 data from ancient and modern European samples.

586

587 ***aDNA authentication***

588 As a result of degrading over time, aDNA can be distinguished from modern DNA by
589 certain characteristics: short fragments and a high frequency of C=>T substitutions at the
590 5' ends of sequences due to cytosine deamination. The program mapDamage2.0⁹⁰ was
591 used to estimate the frequency of 5' C=>T transitions. Rates of contamination were
592 estimated on mitochondrial DNA by calculating the percentage of non-consensus bases at
593 haplogroup-defining positions as detailed in ⁹¹. Each sample was mapped against the
594 RSRS downloaded from phylotree.org and checked against haplogroup-defining sites for
595 the sample-specific haplogroup.

596 Samtools 1.9⁸⁸ option stats was used to determine the number of final reads, average read
597 length, average coverage etc. (Data S1C).

598

599 ***Calculating genetic sex estimation***

600 Genetic sex was calculated using the methods described in⁹², estimating the fraction of
601 reads mapping to Y chromosome out of all reads mapping to either X or Y chromosome.
602 Additionally, sex was determined using a method described in⁹³, calculating the X and Y
603 ratio by the division of the coverage by the autosomal coverage.

604

605 ***Determining mtDNA and Y chromosome haplogroups***

606 Mitochondrial DNA haplogroups were determined using Haplogrep2 on the command
607 line⁹⁴. For the determination, the reads were re-aligned to the reference sequence RSRS
608 and the parameter --rsrs were given to estimate the haplogroups using Haplogrep2.
609 Subsequently, the identical results between the individuals were checked visually by
610 aligning mapped reads to the reference sequence using samtools 0.1.19⁸⁸ command tview
611 and confirming the haplogroup assignment in PhyloTree. A total of 5703 Y chromosome
612 haplogroup informative variants^{49, 95} from regions that uniquely map to Y chromosome
613 were covered by at least one read in the sample and these were called as haploid from the
614 BAM file using the --doHaploCall function in ANGSD⁹⁶. Derived and ancestral allele and
615 haplogroup annotations for each of the called variants were added using BEDTools
616 2.19.0⁹⁷ intersect option. Haplogroup assignments of each individual sample were made

617 by determining the haplogroup with the highest proportion of informative positions called in
618 the derived state in the given sample.

619

620 **Anthropological and virtual analysis of Tagliente2**

621 The left hemimandible Tagliente2 is mesially broken to the alveolus of the first premolar
622 (P_3), while the ramus is mostly complete, except for the condyle and coronoid process.
623 Four permanent teeth (P_4 - M_3) are still in place into their respective alveoli, but only a tiny
624 apical portion of the LP_3 root is preserved (Fig. S1). The presence of wear pattern on the
625 third molar (wear stage 2⁹⁸) and its eruption suggest that the mandible can be ascribed to
626 a young adult, while the robusticity index (42.59, this study) and the gonial angle (110°) fall
627 within the range of male variability⁵². X-ray microCT scans and digital segmentation of
628 Tagliente2 (Fig.2) identified the presence of a rounded alteration close to the buccodistal
629 aspect of the P_4 root. The identified lesion shows homogeneous radiopacity surrounded by
630 a radiotransparent thin area (Fig.3) and consists of an irregular (Volume = 10.71 mm^3 ;
631 bucco-lingual diameter = 2.48cm; mesio-distal diameter = 2.90cm; see Fig.2) and compact
632 dental tissue which was mechanically removed and physically analysed through
633 histological examination (see following section). The latter suggests the presence of
634 stratified and acellular cementum material (Fig.2), which together with anatomical position
635 and morphology (Fig.1b) provides evidence ascribable to focal cemento-osseous
636 dysplasia (FCOD; STAR Methods, Method details), a benign lesion of the bone in which
637 normal bone is replaced by fibrous tissue, followed by calcification with osseous and
638 cementum tissue⁹⁹.

639

640 **Histopathological examination**

641 A thin section of 0.005 mm was sampled for histological analysis. The cross-section has
642 been performed following mesiodistal direction based on the best location for core
643 sampling. The core was fixed in buffered neutral formalin 10% in order to protect the
644 fibrous elements of cementum from damage caused by the acids used as decalcifying
645 agent performed with Trichloroacetic acid for 7 days. Finally, the section was coloured by
646 Hematoxylin / Eosin. The sample was mounted on frosted glass slides and thin-sectioned
647 using a Struers Accutom-50. The preparation of the histological section was carried out at
648 the Centro Odontoiatria e Stomatologia F. Perrini, Pistoia, Italy (STAR Methods, Method
649 details). The section was studied using a Nikon E200 microscope. Photomicrographs were
650 captured using NIS D 3.0 Software and edited in Adobe Photoshop CC.

651

652 **Removal of Cementoma**

653 ***Equipment***

- 654 • 24 volt dental micro-motor
- 655 • 24 volt power supply with a reduction possibility to 18 and 12 volts
- 656 • Single cell charger
- 657 • 5x dental red ring contra angle handpiece
- 658 • 1/1 dental blue ring contra angle handpiece
- 659 • Dental straight handpiece
- 660 • Slotted diamond bur 25mm long and 0.5mm tip diameter
- 661 • Tungsten carbide bur 31mm long and 0.8mm tip diameter
- 662 • Tungsten carbide rosette bur 31mm long and 0.8mm diameter
- 663 • Diamond disc for ceramic 0.35mm thick and 20mm diameter
- 664 • Blade n°12 surgical scalpel
- 665 • Buck 5/6 periodontal scalpel
- 666 • The rotation speed of the 1/1 dental blue ring contra angle handpiece is 40.000
- 667 rpm, i.e. the motor speed
- 668 • The rotation speed of the 5x dental red ring multiplier contra angle handpiece is
- 669 200.000 rpm. This speed is reduced to about 150.000 rpm when switching to 18
- 670 volts, and to 100.000 rpm when switching to 12 volts
- 671 • The rotation speed of the 1/1 dental straight handpiece is 35.000 rpm

672

673 ***Procedure***

674 The procedure consisted of creating an area around the specimen in which a possible
675 introduction of external biological material linked to the extraction procedure was
676 minimized; previously, the specimen had already been widely contaminated and even
677 likely protected with a vinyl glue thin layer. Each operator wore sterile gown, mask, cap
678 and sterile gloves. All the instruments used, including the handpieces, were sterile; the
679 micro-motors have been sanitized and protected by disposable antiseptic sheaths. The
680 specimen was placed on a sterile sheet. The procedure was carried out entirely by working
681 with the aid of a Zeiss 6x binocular microscope.

682 The aim of the project was the extraction of a bone piece containing a pathological
683 alteration (a probable cementoma) located under the buccal vestibulum, slightly distal to
684 half the root height of the lower left second premolar. The other priority of the procedure
685 was the need to minimize the corruption of the specimen by reducing the operational

686 invasiveness, trying to keep the lingual surface intact, which is the side displayed to
687 museum visitors. Therefore, the difficulty was the extraction of a bone piece limited to the
688 vestibular surface including the lesion and the root portion connected to it without
689 damaging or removing the bone portion and the dental crown above it, also avoiding
690 damaging areas visible to the public.

691 After a careful tomographic examinations analysis of the exhibit to fully identify
692 the spatial location of the lesion and its relationship with the surrounding bone and dental
693 structures, we moved on to the extraction of the bone piece. The operational phase began
694 with the delimitation of the bone piece by cutting the cortex with a 20mm diameter and
695 0.35mm thickness diamond disc mounted on a red ring contra angle handpiece and micro-
696 motor set at 18 volts (150.000 rpm). We pick this thickness because a larger one (0.5)
697 would have been too destructive for the exhibit, while a smaller one (0.2) would have
698 made the bone piece subsequent mobilization more difficult. The slag and debris produced
699 in this surface cutting phase were collected in a sterile tube and labeled as “contaminated
700 external slag”. Once the area of about 1cm² was delimited, the grooves were deepened
701 with a 25mm long and 0.5mm diameter conical slotted diamond bur up to a depth of about
702 two thirds of the jaw thickness corresponding to the cortical-spongy bone limit. The
703 pressure exerted with the bur has always been gentle in order to avoid overheating of the
704 bone matrix and loss of diamond crystals. Exploiting the free alveolus of the lower left first
705 molar, as this had been used for previous studies and therefore made removable, it was
706 possible to perform a cut parallel to the lingual surface, orthogonal to the previous
707 perimetral cuts, using a 31mm long and 0.8mm diameter tungsten carbide bur. The slag
708 recovered at this stage has been collected in a sterile tube, and since it had not been
709 contaminated labeled as “useful for microbiological examination”. Given the impossibility to
710 proceed entirely with the diamond tip due to the risk of excessively corrupting the bone
711 matrix, the cuts were defined with a blade n°12 surgical scalpel and a Buck 5/6 periodontal
712 scalpel until complete detachment of the bone piece.

713 During some separation stages of the internal trabeculation, especially in the
714 periradicular areas, the scalpel blade was gently moved with the aid of small percussions
715 on the handle back, in order to get over the localized resistances that a continuous
716 pressure could not have overcome without significantly increasing strength and
717 dangerously decreasing control. Once all the release incisions were carried out, the bone
718 piece was easily mobilized and extracted with tweezers.
719 The lesion was therefore exposed by bone matrix abrasion with a 0.8mm tungsten carbide
720 rosette bur mounted on a straight handpiece with a 35.000 rpm micro-motor. This

721 progressive controlled abrasion allowed us to reach the exposure of a lesion portion large
722 enough to be easily accessible for histological and DNA examination.

723 The entire procedure was documented with a Nikon camera with a 105mm Micro-Nikkor
724 lens equipped with annular flash.

725

726 **Genetic analysis of cementoma**

727 We generated 0.28x coverage genome and searched for putatively pathogenic variants in
728 candidate genes (ALPL, ZNF687, CDC73, H3F3A, FOS, H3F3B, FOSB) known to be
729 involved in similar pathological conditions to Focal Osseous Dysplasia insurgence or
730 used to perform differential diagnoses^{100, 101, 102, 103, 104}, and found a number of non-
731 reference SNPs which, given the low coverage and ancient DNA degradation are reported
732 here with no further interpretation (Table S4).

733

734 **QUANTIFICATION AND STATISTICAL ANALYSIS**

735 MDS, f3, f4 and qpGraph Reference samples were downloaded from

736 [https://reich.hms.harvard.edu/downloadable-genotypes-present-day-and-ancient-dna-data-](https://reich.hms.harvard.edu/downloadable-genotypes-present-day-and-ancient-dna-data-compiled-published-papers)
737 [compiled-published-papers](https://reich.hms.harvard.edu/downloadable-genotypes-present-day-and-ancient-dna-data-compiled-published-papers) and merged with the newly generated Tagliente2 data. A set of

738 Outgroup f3¹⁰⁵ in the form (X, Y, Mbuti) was run on samples listed in Figure 4A, and the
739 resulting pairwise distance matrix (distance=1-f3) was used to compute a Multi-

740 Dimensional Scaling (MDS). The f4 test¹⁰⁵ was run using the popstats.py script¹⁰⁶.

741 qpGraphs were generated using Admixtools¹⁰⁵, starting from the backbone described in Fu
742 et al. 2016 and investigating putative positions for Tagliente2 as informed by the f4 results
743 described in Figure 4B. As far as mtDNA analysis is concerned, evolutionary history was
744 inferred by using the Maximum Likelihood method and General Time Reversible model¹⁰⁷.

745 The tree with the highest log likelihood (-24501.19) is shown. The percentage of trees in
746 which the associated taxa clustered together is shown next to the branches. Initial tree(s)

747 for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ
748 algorithms to a matrix of pairwise distances estimated using the Maximum Composite

749 Likelihood (MCL) approach, and then selecting the topology with superior log likelihood
750 value. A discrete Gamma distribution was used to model evolutionary rate differences

751 among sites (5 categories (+G, parameter = 0.0500)). The rate variation model allowed for
752 some sites to be evolutionarily invariable ([+], 49.11% sites). The tree is drawn to scale,

753 with branch lengths measured in the number of substitutions per site. This analysis

754 involved 39 nucleotide sequences. There were a total of 16578 positions in the final
755 dataset. Evolutionary analyses were conducted in MEGA X^{108, 109}.

756

757 **KEY RESOURCES TABLE (SEPARATE FILE FROM TEMPLATE)**

758

759

760

761 **Supplemental Information titles and legends**

762

763 **Data S1. Results of ¹⁴C and genetic analysis on Tagliente2. Related to STAR**

764 **Methods and Figures 1, 2, 3 and 4**

765

766 **A)** Dating of Tagliente2 and previous date obtained for Tagliente1. **B)** List of variants found
767 to have missense or stop gain consequences on eight genes (ALPL, CDC73, COL1A1,
768 FOS, FOSB, H3F3B, TP53, ZNF687) reported to be involved in predisposition or
769 insurgence of cementoma. Sequencing reads and qualities are reported as is from the
770 bam files and the consensus. Alternative allele has been queried on the VEP Ensembl
771 database on July 2020. Coordinates are in hg19. **C)** Summary statistics from the whole
772 genome sequencing of Tagliente2. **D)** List of Tagliente2 non reference mtDNA site. **E)** List
773 of ancestral and derived chromosome Y haplogroup I defining sites found in Tagliente2

774

775

776 **References**

777

- 778 1. Lambeck, K., Rouby, H., Purcell, A., Sun, Y. & Sambridge, M. Sea level and global ice
779 volumes from the Last Glacial Maximum to the Holocene. *Proc. Natl. Acad. Sci.* **111**,
780 15296–15303 (2014)
- 781 2. Wren, C. D. & Burke, A. Habitat suitability and the genetic structure of human
782 populations during the Last Glacial Maximum (LGM) in Western Europe. *PLOS ONE*
783 **14**, e0217996 (2019).
- 784 3. Vescovi, E. *et al.* Interactions between climate and vegetation during the Lateglacial
785 period as recorded by lake and mire sediment archives in Northern Italy and Southern
786 Switzerland. *Quat. Sci. Rev.* **26**, 1650–1669 (2007).
- 787 4. Naudinot, N., Tomasso, A., Tozzi, C. & Peresani, M. Changes in mobility patterns as a
788 factor of ¹⁴C date density variation in the Late Epigravettian of Northern Italy and
789 Southeastern France. *J. Archaeol. Sci.* **52**, 578 – 590 (2014).
- 790 5. Fontana, F. *et al.* Re-colonising the Southern Alpine fringe: diachronic data on the use
791 of sheltered space in the late Epigravettian site of Riparo Tagliente. in *Palaeolithic*

- 792 *Italy. Advanced studies on early human adaptation in the Apennine Peninsula* 287–310
793 (Sidestone Press, 2018).
- 794 6. Badino, F. *et al.* The fast-acting “pulse” of Heinrich Stadial 3 in a mid-latitude boreal
795 ecosystem. *Sci Rep* **10**, 18031 (2020).
- 796 7. Pala, M. *et al.* Mitochondrial DNA Signals of Late Glacial Recolonization of Europe
797 from Near Eastern Refugia. *Am. J. Hum. Genet.* **90**, 915–924 (2012).
- 798 8. Brewster, C., Meiklejohn, C., von Cramon-Taubadel, N. & Pinhasi, R. Craniometric
799 analysis of European Upper Palaeolithic and Mesolithic samples supports discontinuity
800 at the Last Glacial Maximum. *Nat. Commun.* **5**, 4094 (2014).
- 801 9. Fu, Q. *et al.* The genetic history of Ice Age Europe. *Nature* **534**, 200–205 (2016).
- 802 10. Posth, C. *et al.* Pleistocene Mitochondrial Genomes Suggest a Single Major Dispersal
803 of Non-Africans and a Late Glacial Population Turnover in Europe. *Curr. Biol.* **26**, 827–
804 833 (2016).
- 805 11 Mathieson, I. *et al.* The genomic history of southeastern Europe. *Nature* **555**, 197–203
806 (2018).
- 807 12. Peresani, M. *et al.* Hunter-gatherers across the great Adriatic-Po region during the Last
808 Glacial Maximum: Environmental and cultural dynamics. *Quaternary International*
809 (2020) doi:[10.1016/j.quaint.2020.10.007](https://doi.org/10.1016/j.quaint.2020.10.007).
- 810 13. Ravazzi, C. *et al.* The latest LGM culmination of the Garda Glacier (Italian Alps) and
811 the onset of glacial termination. Age of glacial collapse and vegetation
812 chronosequence. *Quat. Sci. Rev.* **105**, 26 – 47 (2014).
- 813 14. Monegato, G., Scardia, G., Hajdas, I., Rizzini, F. & Piccin, A. The Alpine LGM in the
814 boreal ice-sheets game. *Sci. Rep.* **7**, 2078 (2017).
- 815 15. Gazzoni, V. *et al.* Late Upper Palaeolithic human diet: first stable isotope evidence
816 from Riparo Tagliente (Verona, Italy). *Bull. Mém. Société Anthropol. Paris* **25**, 103–117
817 (2013).
- 818 16. Reimer, P. J. *et al.* The IntCal20 Northern Hemisphere Radiocarbon Age Calibration
819 Curve (0–55 cal kBP). *Radiocarbon* **62**, 725–757 (2020).
- 820 17. Ramsey, C. B. Methods for Summarizing Radiocarbon Datasets. *Radiocarbon* **59**,
821 1809–1833 (2017).
- 822 18. Fu, Q. *et al.* A Revised Timescale for Human Evolution Based on Ancient
823 Mitochondrial Genomes. *Current Biology* **23**, 553–559 (2013).
- 824 19. Antonio, M. L. *et al.* Ancient Rome: A genetic crossroads of Europe and the
825 Mediterranean. *Science* **366**, 708–714 (2019).

- 826 20. Villalba-Mouco, V. *et al.* Survival of Late Pleistocene Hunter-Gatherer Ancestry in the
827 Iberian Peninsula. *Curr. Biol.* **29**, 1169–1177.e7 (2019).
- 828 21. Montoya, C. & Peresani, M. Nouveaux éléments de diachronie dans l'Épigravettien
829 récent des Préalpes de la Vénétie. in *D'un monde à l'autre : les systèmes lithiques*
830 *pendant le Tardiglaciaire autour de la Méditerranée nord-occidentale : actes de la*
831 *table-ronde internationale, Aix-en-Provence, 6-8 juin 2001* (ed. Montoya, J.-P. B. & C.)
832 vol. 40 123–138 (Société préhistorique française, 2005).
- 833 22. Cancellieri, M., Over the hills and far away. Last Glacial Maximum lithic technology
834 around the Great Adriatic Plain (Archaeopress Publishing, 2015)
- 835 23. Boric, D. & Cristiani, E. Social networks and connectivity among the Palaeolithic and
836 Mesolithic foragers of the Balkans and Italy. in *Southeast Europe Before Neolithisation:*
837 *Proceedings of the International Workshop within the Collaborative Research Centres*
838 *SFB 1070 "RessourcenKulturen", Schloss Hohentübingen, 9th of May 2014* (eds.
839 Krauss, R. & Floss, H.) 73–112 (Universität Tübingen, 2016).
- 840 24. Tomasso, A., L'Épigravettien: variabilité diachronique et géographique. In: Olive, M.
841 (ed.), *Campo delle Piane: un habitat de plein air épigravettien dans la Vallée du*
842 *Gallero (Abruzzes, Italie centrale)* 13-21 (École Française de Rome, 2017).
- 843 25. Bertola, S., Fontana, F. & Visentin, D. Lithic raw material circulation and settlement
844 dynamics in the Upper Palaeolithic of the Venetian Prealps (NE Italy). A key-role for
845 palaeoclimatic and landscape changes across the LGM? in *Palaeolithic Italy.*
846 *Advanced Studies on Early Human Adaptations in the Apennine Peninsula* 219–246
847 (Sidestone Press, 2018).
- 848 26. Montoya, C., Duches, R., Fontana, F., Peresani, M. & Visentin, D. Peuplement
849 tardiglaciaire et holocène ancien des Préalpes de la Vénétie (Italie Nord Orientale):
850 éléments de confrontation in L'Aquitaine à la fin des temps glaciaires. Les sociétés de
851 la transition du Paléolithique final au début du Mésolithique dans l'espace Nord
852 aquitain. in *Actes de la table ronde organisée en hommage à Guy Célérier, Les*
853 *Eyzies-de-Tayac, 24-26 juin 2015, PALEO, numéro spécial.* 193–202 (Musée national
854 de Préhistoire, 2018).
- 855 28. Cristiani, E. Epigravettian osseous technology from the eastern Alpine region of Italy:
856 The case of Riparo Dalmeri (Trentino). in *Palaeolithic Italy. Advanced studies on early*
857 *human adaptation in the Apennine Peninsula* 311–334 (Sidestone Press, 2018).
- 858 29. Wirsig, C., Zasadni, J., Ivy-Ochs, S., Christl, M., Kober, F., Schlichter, C. A deglaciation
859 model of the Oberhasli, Switzerland. *J. Quat. Sci.* **31**, 46–59 (2016).

- 860 30. Monegato, G., Ravazzi, C., The Late Pleistocene multifold glaciation in the Alps:
861 updates and open questions. *Al. Med. Quat.* **31**, 225–229 9 (2018).
- 862 31. Bolland, A., Rey, F., Gobet, E., Tinner, W. & Heiri, O. Summer temperature
863 development 18,000–14,000 cal. BP recorded by a new chironomid record from
864 Burgäschisee, Swiss Plateau. *Quaternary Science Reviews* **243**, 106484 (2020).
- 865 32. Fontana, A., Mozzi, P., Marchetti, M., 2014. Alluvial fans and megafans along the
866 southern side of the Alps. *Sediment. Geol.* **301**, 150–171 (2014).
- 867 33. Terlato, G. *et al.* Chronological and Isotopic data support a revision for the timing of
868 cave bear extinction in Mediterranean Europe. *Hist. Biol.* **31**, 474–484 (2019).
- 869 34. Romandini M., Nannini N., Chasseurs épigravettiens dans le territoire de l'ours des
870 cavernes: le cas du Covolo Fortificato di Trene (Vicenza, Italie). *L'anthropologie*, **116**,
871 39-56 (2012).
- 872 35. Romandini M., Bertola S. & Nannini N., Nuovi dati sul Paleolitico dei Colli Berici:
873 risultati preliminari dello studio archeozoologico e delle materie prime litiche della
874 Grotta del Buso Doppio del Broion (Lumignano, Longare, Vicenza). *Studi di Preistoria
875 e Protostoria*, **2**, 53-59 (2015).
- 876 36. Carrera, L., Pavia, M., Romandini, M. & Peresani, M. Avian fossil assemblages at the
877 onset of the LGM in the eastern Alps: A palaeological contribution from the Rio Secco
878 Cave (Italy). *Comptes Rendus Palevol* **17**, 166–177 (2018).37. Peresani, M. Cultures
879 et traditions du Paléolithique supérieur dans les régions nord-méditerranéennes. in *La
880 Cuenca Mediterránea durante el Paleolítico Superior (38.000-10.000 años)* 408–429
881 (Fundación Cueva de Nerja, Nerja, 2006).
- 882 37. Peresani, M. Cultures et traditions du Paléolithique supérieur dans les régions nord-
883 méditerranéennes. in *La Cuenca Mediterránea durante el Paleolítico Superior (38.000-
884 10.000 años)* 408–429 (Fundación Cueva de Nerja, Nerja, 2006).
- 885 38. Straus, L. G. After the Deep Freeze: Confronting “Magdalenian” Realities in Cantabrian
886 Spain And Beyond. *J Archaeol Method Theory* **20**, 236–255 (2013).
- 887 39. Tallavaara, M., Luoto, M., Korhonen, N., Järvinen, H. & Seppä, H. Human
888 populatiodynamics in Europe over the Last Glacial Maximum. *Proc. Natl. Acad. Sci.*
889 **112**, 8232–8237 (2015).
- 890 40. Timmermann, A. & Friedrich, T. Late Pleistocene climate drivers of early human
891 migration. *Nature* **538**, 92–95 (2016).
- 892 41. Berto, C., Luzi, E., Canini, G. M., Guerreschi, A. & Fontana, F. Climate and landscape
893 in Italy during Late Epigravettian. The Late Glacial small mammal sequence of Riparo

- 894 Tagliente (Stallavena di Grezzana, Verona, Italy). *Quaternary Science Reviews* **184**,
895 132–142 (2018).
- 896 42. Lugli, F. *et al.* Strontium and stable isotope evidence of human mobility strategies
897 across the Last Glacial Maximum in southern Italy. *Nature Ecology & Evolution* **3**, 905–
898 911 (2019).
- 899 43. Cristiani, E., Farbstein, R. & Miracle, P. Ornamental traditions in the Eastern Adriatic:
900 The Upper Palaeolithic and Mesolithic personal adornments from Vela Spila (Croatia).
901 *J. Anthropol. Archaeol.* **36**, 21 – 31 (2014)
- 902 44. Catalano, G. *et al.* Late Upper Palaeolithic hunter-gatherers in the Central
903 Mediterranean: New archaeological and genetic data from the Late Epigravettian burial
904 Oriente C (Favignana, Sicily). *Quat. Int.* **537**, 24 – 32 (2020).
- 905 45. Pini, R., Ravazzi, C. & Reimer, P. J. The vegetation and climate history of the last
906 glacial cycle in a new pollen record from Lake Fimon (southern Alpine foreland, N-
907 Italy). *Quat. Sci. Rev.* **29**, 3115–3137 (2010).
- 908 46. Finsinger, W. *et al.* Temporal patterns in lacustrine stable isotopes as evidence for
909 climate change during the late glacial in the Southern European Alps. *J Paleolimnol* **40**,
910 885–895 (2008).
- 911 47. Cooper, A. *et al.* Abrupt warming events drove Late Pleistocene Holarctic megafaunal
912 turnover. *Science* **349**, 602–606 (2015).
- 913 48. Rasmussen, S. O. *et al.* A stratigraphic framework for abrupt climatic changes during
914 the Last Glacial period based on three synchronized Greenland ice-core records:
915 refining and extending the INTIMATE event stratigraphy. *Quat. Sci. Rev.* **106**, 14 – 28
916 (2014).
- 917 49. Karmin, M. *et al.* A recent bottleneck of Y chromosome diversity coincides with a global
918 change in culture. *Genome Res.* **25**, 459–466 (2015).
50. Bartolomei, G., Broglio, A., Guerreschi, A. & *et al.* Una sepoltura epigravettiana nel
deposito pleistocenico del Riparo Tagliente in Valpantena (Verona). *Riv. Sci.*
Preistoriche **29**, 101–152.
51. Fontana, F., Cilli, C., Cremona, M. G., Giacobini, G. & Gurioli, F. Recent data on the
Late Epigravettian occupation at Riparo Tagliente, Monti Lessini (Grezzana, Verona): a
multidisciplinary perspective. *Preistoria Alp.* **44**, 51–59 (2009).
52. Corrain, C. Un frammento di mandibola umana, rinvenuto a “Riparo Tagliente” in
Valpantena (Verona). *Atti Dell’Istituto Veneto Sci. Lett. Ed Arti* **CXXIV**, 23–26 (1966).
53. Corrain, C. I resti scheletrici umani della sepoltura epigravettiana del Riparo Tagliente
in Valpantena (Verona). *Boll. Mus. Civ. Storia Nat. Verona* **4**, 35–79.

- 919 54. Hughes, A. L. C., Gyllencreutz, R., Lohne, Ø. S., Mangerud, J. & Svendsen, J. I. The
920 last Eurasian ice sheets - a chronological database and time-slice reconstruction,
921 DATED-1. *Boreas* **45**, 1–45 (2016).
- 922 55. Seguinot, J. *et al.* Modelling last glacial cycle ice dynamics in the Alps. *The Cryosphere*
923 **12**, 3265–3285 (2018).
56. Luetscher, M. *et al.* North Atlantic storm track changes during the Last Glacial
Maximum recorded by Alpine speleothems. *Nat. Commun.* **6**, 6344 (2015).
57. Lofverstrom, M. A dynamic link between high-intensity precipitation events in
southwestern North America and Europe at the Last Glacial Maximum. *Earth Planet.
Sci. Lett.* **534**, 116081 (2020).
58. Ivy-Ochs, S. *et al.* Chronology of the last glacial cycle in the European Alps. *J. Quat.
Sci.* **23**, 559–573 (2008).
59. Pellegrini, C. *et al.* Anatomy of a compound delta from the post-glacial transgressive
record in the Adriatic Sea. *Mar. Geol.* **362**, 43–59 (2015).
60. Maselli, V. *et al.* Delta growth and river valleys: the influence of climate and sea level
changes on the South Adriatic shelf (Mediterranean Sea). *Quat. Sci. Rev.* **99**, 146–163
(2014).
61. Münzel, S. C. *et al.* Pleistocene bears in the Swabian Jura (Germany): Genetic
replacement, ecological displacement, extinctions and survival. *Quat. Int.* **245**, 225–237
(2011).
62. Fortes, G. G. *et al.* Ancient DNA reveals differences in behaviour and sociality between
brown bears and extinct cave bears. *Mol. Ecol.* **25**, 4907–4918 (2016).
63. Stuart, A. J. & Lister, A. M. Patterns of Late Quaternary megafaunal extinctions in
Europe and northern Asia. *Cour Forsch-Inst Senckenberg* **259**, 287–297.
64. Barnosky, A. D., Koch, P. L., Feranec, R. S., Wing, S. L. & Shabel, A. B. Assessing the
Causes of Late Pleistocene Extinctions on the Continents. *Science* **306**, 70–75 (2004).
65. Lorenzen, E. D. *et al.* Species-specific responses of Late Quaternary megafauna to
climate and humans. *Nature* **479**, 359–364 (2011).
66. Pacher, M. & Stuart, A. J. Extinction chronology and palaeobiology of the cave bear
(*Ursus spelaeus*). *Boreas* **38**, 189–206 (2009).
67. Stuart, A. J. Late Quaternary megafaunal extinctions on the continents: a short review.
Geol. J. **50**, 338–363 (2015).
68. Gretzinger, J. *et al.* Large-scale mitogenomic analysis of the phylogeography of the
Late Pleistocene cave bear. *Sci. Rep.* **9**, 10700 (2019).

69. Lowe, J. J. *et al.* Synchronisation of palaeoenvironmental events in the North Atlantic region during the Last Termination: a revised protocol recommended by the INTIMATE group. *Quat. Sci. Rev.* **27**, 6–17 (2008).
70. Moran, A. P., Ivy-Ochs, S., Schuh, M., Christl, M. & Kerschner, H. Evidence of central Alpine glacier advances during the Younger Dryas–early Holocene transition period. *Boreas* **45**, 398–410 (2016).
71. Oeggl, K. & Wahlmüller, N. *Vegetation and climate history of a high alpine mesolithic camp site in the Eastern Alps*. (Museo Tridentino di Scienze Naturali, 1994).
72. Fontana, F., Guerreschi, A. & Peresani, M. The visible landscape: Inferring Mesolithic settlement dynamics from multifaceted evidence in the south-eastern Alps. in *Hidden Landscapes of Mediterranean Europe: Cultural and Methodological Biases in Pre- and Protohistoric Landscape Studies. Proceedings of the International Meeting (Siena 2007)* vol. 2320 71–81 (2011).
73. Fontana, F. & Visentin, D. Between the Venetian Alps and the Emilian Apennines (Northern Italy): Highland vs. lowland occupation in the early Mesolithic. *Quat. Int.* **423**, 266–278 (2016).
- 924 74. Stiner, M. C., Kuhn, S. L., Weiner, S. & Bar-Yosef, O. Differential Burning,
925 Recrystallization, and Fragmentation of Archaeological Bone. *J. Archaeol. Sci.* **22**,
926 223–237 (1995).
- 927 75. Longin, R. New Method of Collagen Extraction for Radiocarbon Dating. *Nature* **230**,
928 241–242 (1971).
- 929 76. Brown, T. A., Nelson, D. E., Vogel, J. S. & Southon, J. R. Improved Collagen
930 Extraction by Modified Longin Method. *Radiocarbon* **30**, 171–177 (1988).
- 931 77. Higham, T. F. G., Jacobi, R. M. & Ramsey, C. B. AMS Radiocarbon Dating of Ancient
932 Bone Using Ultrafiltration. *Radiocarbon* **48**, 179–195 (2006).
- 933 78. Brock, F., Bronk Ramsey, C. & Higham, T. Quality Assurance of Ultrafiltered Bone
934 Dating. *Radiocarbon* **49**, 187–192 (2007).
- 935 79. Korlević, P., Talamo, S. & Meyer, M. A combined method for DNA analysis and
936 radiocarbon dating from a single sample. *Sci. Rep.* **8**, 4127 (2018).
- 937 80. van Klinken, G. J. Bone Collagen Quality Indicators for Palaeodietary and Radiocarbon
938 Measurements. *J. Archaeol. Sci.* **26**, 687–695 (1999).
- 939 81. Kromer, B., Lindauer, S., Synal, H.-A. & Wacker, L. MAMS – A new AMS facility at the
940 Curt-Engelhorn-Centre for Archaeometry, Mannheim, Germany. *Nucl. Instrum. Methods*
941 *Phys. Res. Sect. B Beam Interact. Mater. At.* **294**, 11–13 (2013).

- 942 82. Meyer, M. & Kircher, M. Illumina Sequencing Library Preparation for Highly Multiplexed
943 Target Capture and Sequencing. *Cold Spring Harb. Protoc.* **2010**, pdb.prot5448-
944 pdb.prot5448 (2010).
- 945 83. Orlando, L. *et al.* Recalibrating Equus evolution using the genome sequence of an
946 early Middle Pleistocene horse. *Nature* **499**, 74–78 (2013).
- 947 84. Malaspinas, A.-S. *et al.* Two ancient human genomes reveal Polynesian ancestry
948 among the indigenous Botocudos of Brazil. *Curr. Biol.* **24**, R1035–R1037 (2014).
- 949 85. Magoç, T. & Salzberg, S. L. FLASH: fast length adjustment of short reads to improve
950 genome assemblies. *Bioinformatics* **27**, 2957–2963 (2011).
- 951 86. Martin, M. Cutadapt removes adapter sequences from high-throughput sequencing
952 reads. *EMBnet.journal* **17**, 10 (2011).
- 953 87. Li, H. & Durbin, R. Fast and accurate short read alignment with Burrows-Wheeler
954 transform. *Bioinformatics* **25**, 1754–1760 (2009).
- 955 88. Li, H. *et al.* The Sequence Alignment/Map format and SAMtools. *Bioinformatics* **25**,
956 2078–2079 (2009).
- 957 89. McKenna, A. *et al.* The Genome Analysis Toolkit: A MapReduce framework for
958 analyzing next-generation DNA sequencing data. *Genome Res.* **20**, 1297–1303
959 (2010).
- 960 90. Jónsson, H., Ginolhac, A., Schubert, M., Johnson, P. L. F. & Orlando, L.
961 mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage
962 parameters. *Bioinformatics* **29**, 1682–1684 (2013).
- 963 91. Jones, E. R., Zarina, G., Moiseyev, V., Lightfoot, E., Nigst, P. R., Manica, A., Pinhasi,
964 R., & Bradley, D. G. (2017). The Neolithic Transition in the Baltic Was Not Driven by
965 Admixture with Early European Farmers. *Current Biology: CB*, **27**(4), 576–582
- 966 92. Skoglund, P., Storå, J., Götherström, A. & Jakobsson, M. Accurate sex identification of
967 ancient human remains using DNA shotgun sequencing. *J. Archaeol. Sci.* **40**, 4477–
968 4482 (2013).
- 969 93. Fu, Q. *et al.* Genome sequence of a 45,000-year-old modern human from western
970 Siberia. *Nature* **514**, 445–449 (2014).
- 971 94. Weissensteiner H., Pacher D., Kloss-Brandstätter A., Forer L., Specht G., Bandelt H.-
972 J., Kronenberg F., Salas A., Schönherr S. 2016. HaploGrep 2: mitochondrial
973 haplogroup classification in the era of high-throughput sequencing. *Nucl. Acids. Res.*
974 *2016 Apr 15; doi:10.1093/nar/gkw233*

- 975 95. The 1000 Genomes Project Consortium *et al.* Punctuated bursts in human male
976 demography inferred from 1,244 worldwide Y-chromosome sequences. *Nat. Genet.* **48**,
977 593–599 (2016).
- 978 96. Korneliussen, T. S., Albrechtsen, A. & Nielsen, R. ANGSD: Analysis of Next
979 Generation Sequencing Data. *BMC Bioinformatics* **15**, 356 (2014).
- 980 97. Quinlan, A. R. BEDTools: The Swiss-Army Tool for Genome Feature Analysis:
981 BEDTools: the Swiss-Army Tool for Genome Feature Analysis. *Curr. Protoc.*
982 *Bioinforma.* **47**, 11.12.1-11.12.34 (2014).
- 98 98. S14. Smith, B. H. Patterns of molar wear in hunter-gatherers and agriculturalists. *Am.*
J. Phys. Anthropol. **63**, 39–56 (1984).
99. S15. Young, S. K., Markowitz, N. R., Sullivan, S., Seale, T. W. & Hirschi, R. Familial
gigantiform cementoma: Classification and presentation of a large pedigree. *Oral Surg.*
Oral Med. Oral Pathol. **68**, 740–747 (1989).
100. Henthorn, P. S., Raducha, M., Fedde, K. N., Lafferty, M. A. & Whyte, M. P. Different
missense mutations at the tissue-nonspecific alkaline phosphatase gene locus in
autosomal recessively inherited forms of mild and severe hypophosphatasia. *Proc.*
Natl. Acad. Sci. **89**, 9924–9928 (1992).
101. Divisato, G. *et al.* ZNF687 Mutations in Severe Paget Disease of Bone Associated
with Giant Cell Tumor. *Am. J. Hum. Genet.* **98**, 275–286 (2016).
102. Carpten, J. D. *et al.* HRPT2, encoding parafibromin, is mutated in
hyperparathyroidism–jaw tumor syndrome. *Nat. Genet.* **32**, 676–680 (2002).
103. Behjati, S. *et al.* Distinct H3F3A and H3F3B driver mutations define chondroblastoma
and giant cell tumor of bone. *Nat. Genet.* **45**, 1479–1482 (2013).
104. Fittall, M. W. *et al.* Recurrent rearrangements of FOS and FOSB define
osteoblastoma. *Nat. Commun.* **9**, 2150 (2018).
- 983 105. Patterson, N. *et al.* Ancient Admixture in Human History. *Genetics* **192**, 1065–1093
984 (2012).
- 985 106. Skoglund, P. *et al.* Genetic evidence for two founding populations of the Americas.
986 *Nature* **525**, 104–108 (2015).
- 987 107. Nei M. and Kumar S. (2000). *Molecular Evolution and Phylogenetics*. Oxford
988 University Press, New York.
- 989 108. Kumar S., Stecher G., Li M., Knyaz C., and Tamura K. (2018). MEGA X: Molecular
990 Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and*
991 *Evolution* **35**:1547-1549.

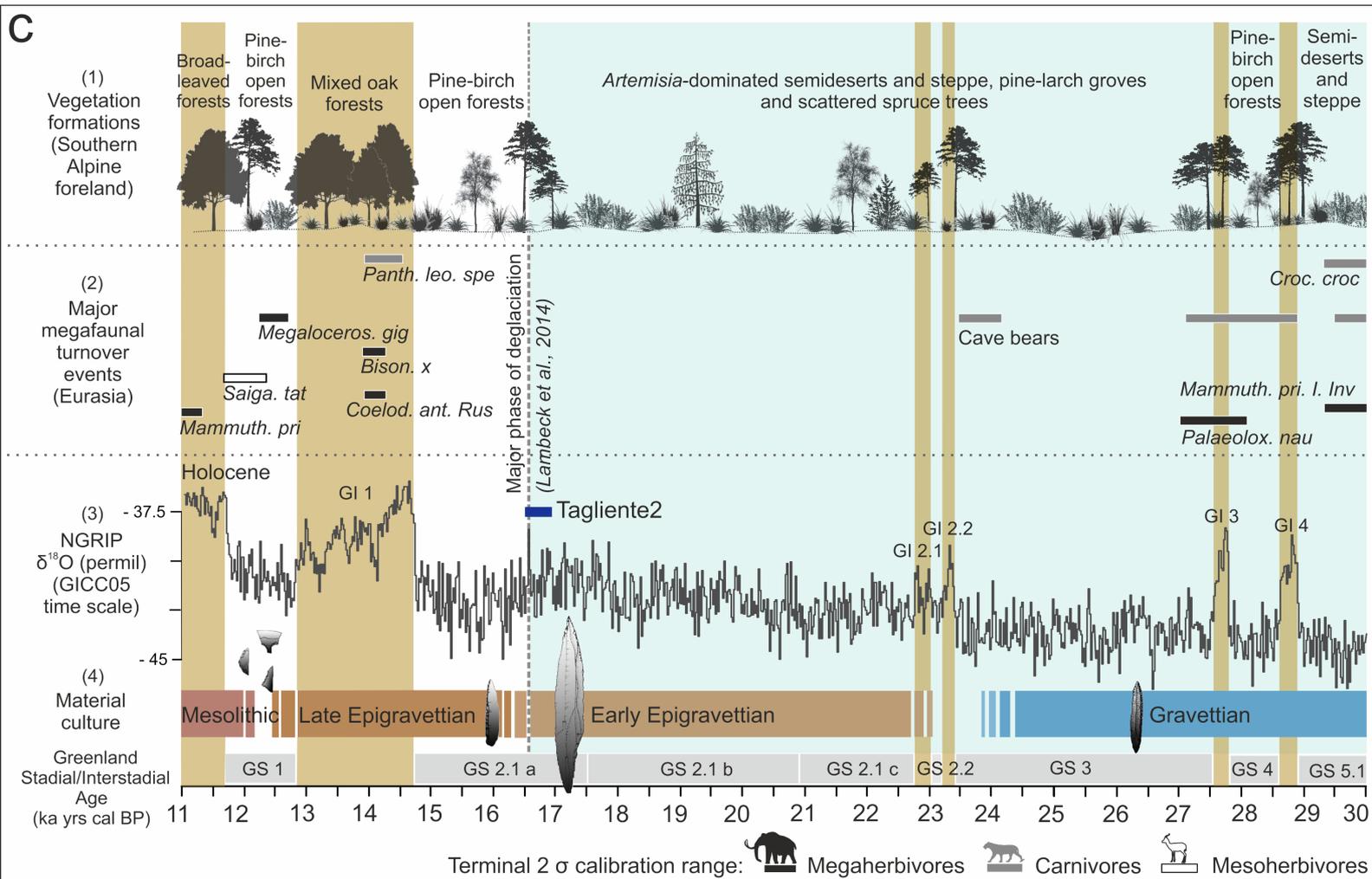
992 109. Stecher G., Tamura K., and Kumar S. (2020). Molecular Evolutionary Genetics
993 Analysis (MEGA) for macOS. *Molecular Biology and Evolution*
994 (<https://doi.org/10.1093/molbev/msz312>).

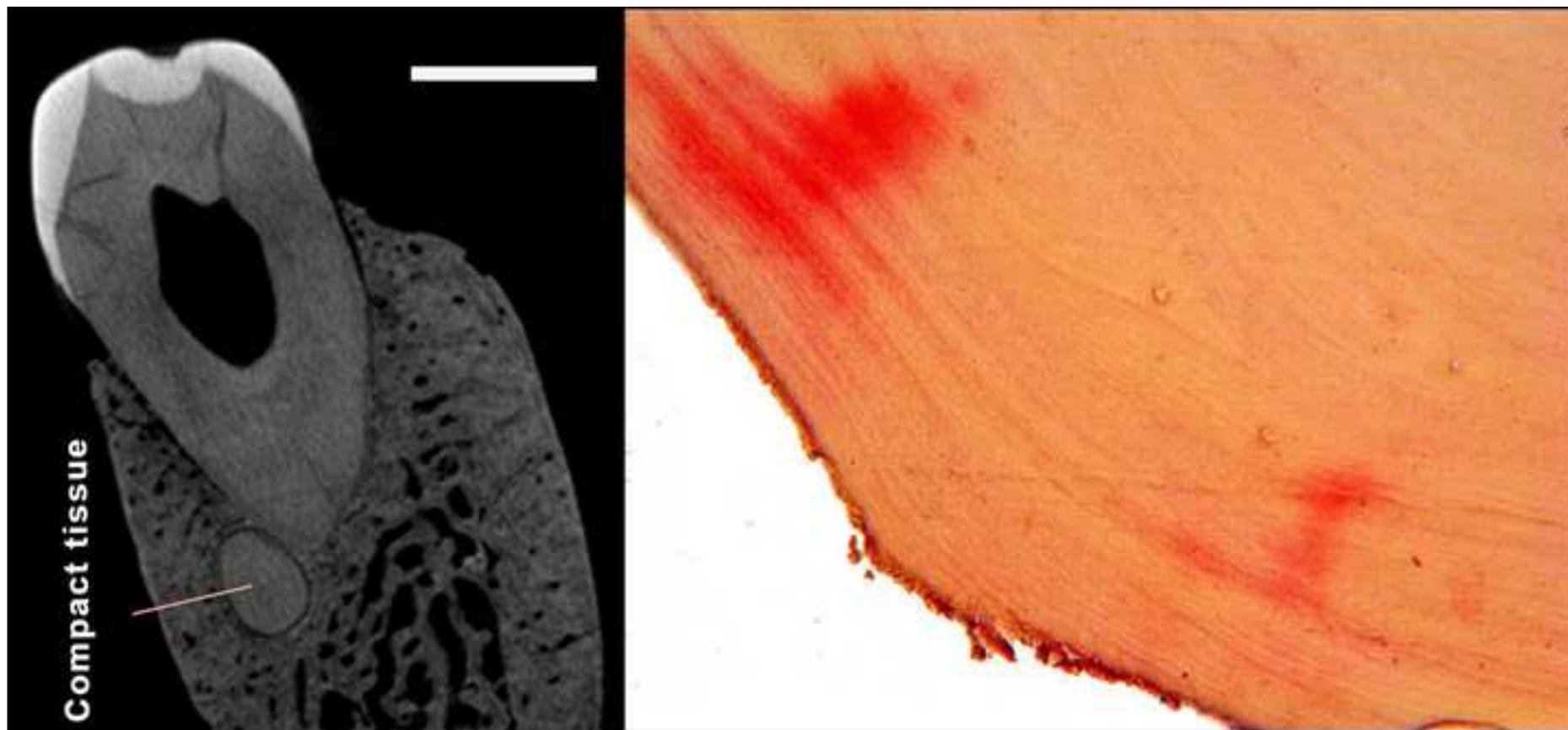
KEY RESOURCES TABLE

REAGENT or	SOURCE	IDENTIFIER
Biological Samples		
Human archaeological remains – left hemimandible from Riparo Tagliente	This paper	Tagliente2
Critical Commercial Assays		
High Pure Viral Nucleic Acid Large Volume Kit	Roche	05114403001
NEBNext DNA Library Prep	New England	E6070
Master Mix Set for 454	Biolabs	
Deposited Data		
Tagliente2 genome	This study	https://evolbio.ut.ee/Bortolini_2020/
Ancient DNA comparison dataset	David Reich's lab, Harvard	https://reich.hms.harvard.edu/datasets
Human reference genome NCBI build 37, GRCh37	Genome Reference Consortium	http://www.ncbi.nlm.nih.gov/projects/genome/assembly/grc/human/
Software and Algorithms		
FLASH	[62]	DOI: 10.1093/bioinformatics/btr507
cutadapt-1.11	[63]	https://doi.org/10.14806/ej.17.1.200
Burrows-Wheeler Aligner (BWA)	[64]	http://bio-bwa.sourceforge.net/
Samtools	[65]	http://samtools.sourceforge.net/
Picard 2.12	Broad Institute 2019	http://broadinstitute.github.io/picard/index.html
GATK	[66]	https://software.broadinstitute.org/gatk/
mapDamage2.0	[67]	https://ginolhac.github.io/mapDamage/
sex identification algorithm	[69]	http://www.sciencedirect.com/science/article/pii/S0305440313002495
HaploGrep2	[71]	doi:10.1093/nar/gkw233 https://github.com/seppinho/haplogrep-cmd

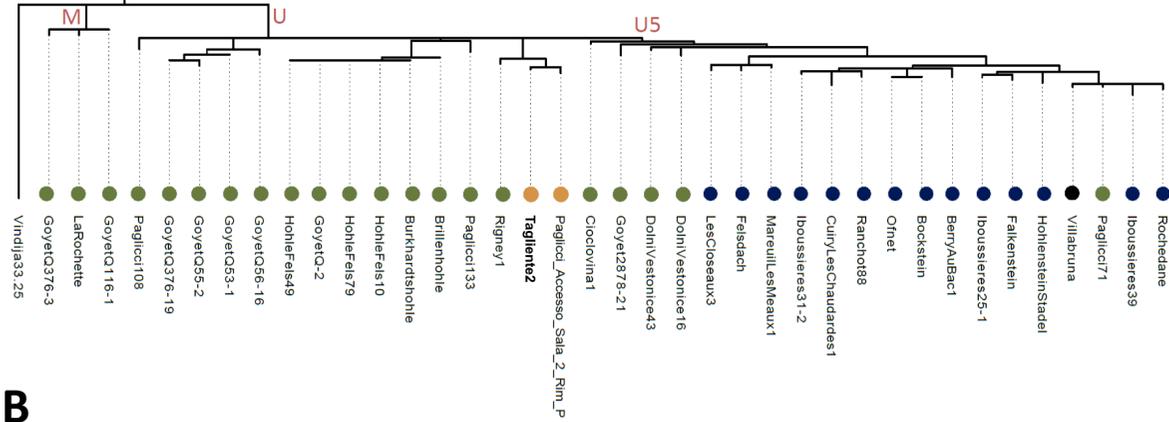
ANGSD	[73]	http://www.popgen.dk/angsd/index.php/ANGSD
BEDTools 2.19	[74]	http://bedtools.readthedocs.io/en/latest/
f3, f4, qpGraph, ADMIXTOOLS	[75]	https://github.com/DReichLab/AdmixTools
popstats	[76]	https://github.com/pontussk/popstats/blob/master/README.md
MEGA X	[78, 79]	https://academic.oup.com/mbe/article/37/4/1237/5697095 https://www.megasoftware.net/
Geomagic Design X (Fig. 1b)	3D System	https://www.3dsystems.com/software/geomagic-design-x
NIS D 3.0	Nikon	https://www.nikon.com/products/microscope-solutions/support/download/software/imgsfw/nis-d_v5020364.htm
Other		
Data for palaeogeographic map (Fig. 1a): DEM (base topography)	Copernicus Land Monitoring Service 2019 (CLMS)	http://land.copernicus.eu/pan-european
Data for palaeogeographic map (Fig. 1a): Bathymetric data (base topography)	General Bathymetric Chart of the Oceans (GEBCO 2019 grid)	doi:10.5285/836f016a-33be-6ddc-e053-6c86abc0788e
Data for palaeogeographic map (Fig. 1a): Sea level drop at – 110 m	[1]	https://doi.org/10.1073/pnas.141176211
Data for palaeogeographic map (Fig. 1a): mountain glaciers at LGM and freshwater systems	[6]	http://dx.doi.org/10.1016/j.quaint.2019.09.024

Data for palaeogeographic map (Fig.1a): Scandinavian and British Islands ice sheets at 17ka ago	[49]	https://doi.org/10.1111/bor.12142
Data for palaeogeographic map (Fig.1a): Alpine Glaciers extent at 17ka ago	[50]	https://doi.org/10.5446/35164

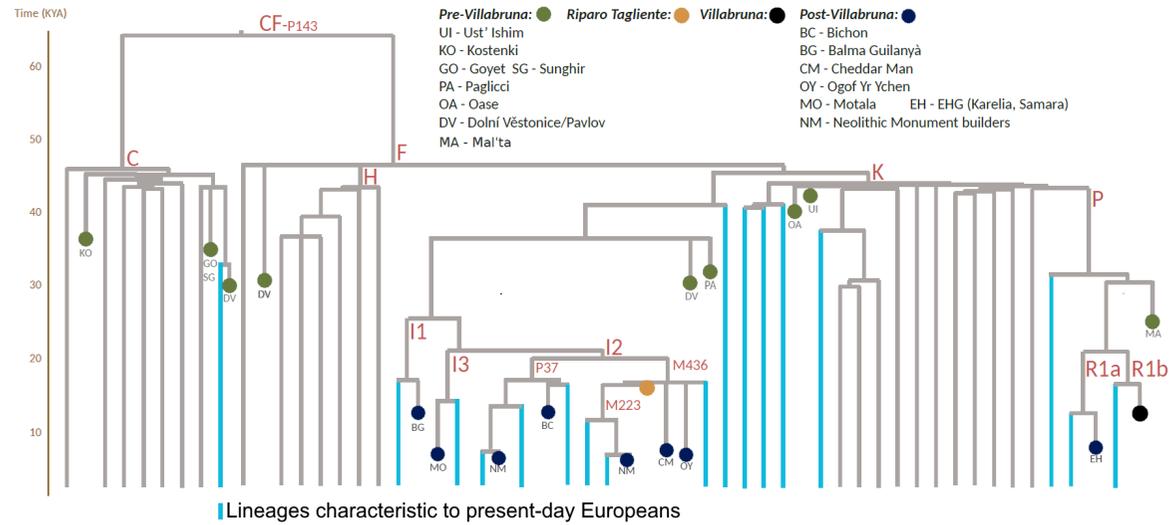




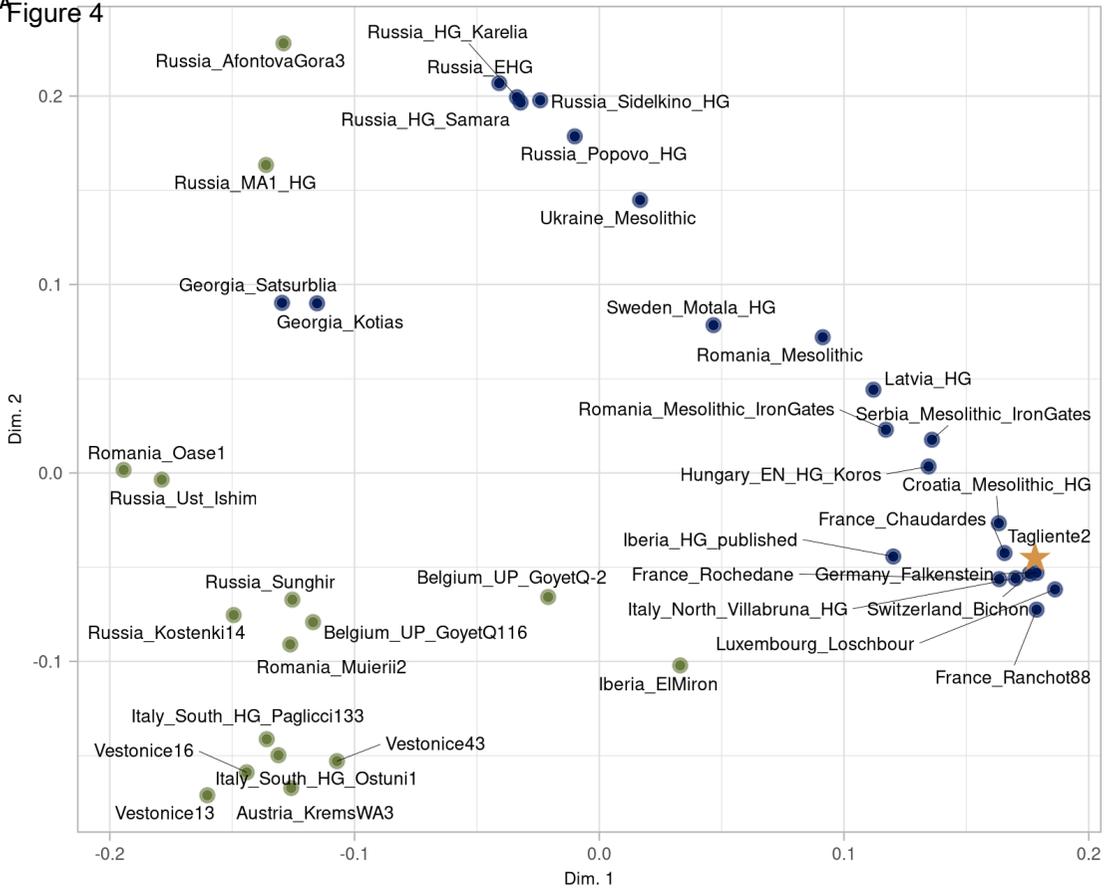
Agure 3



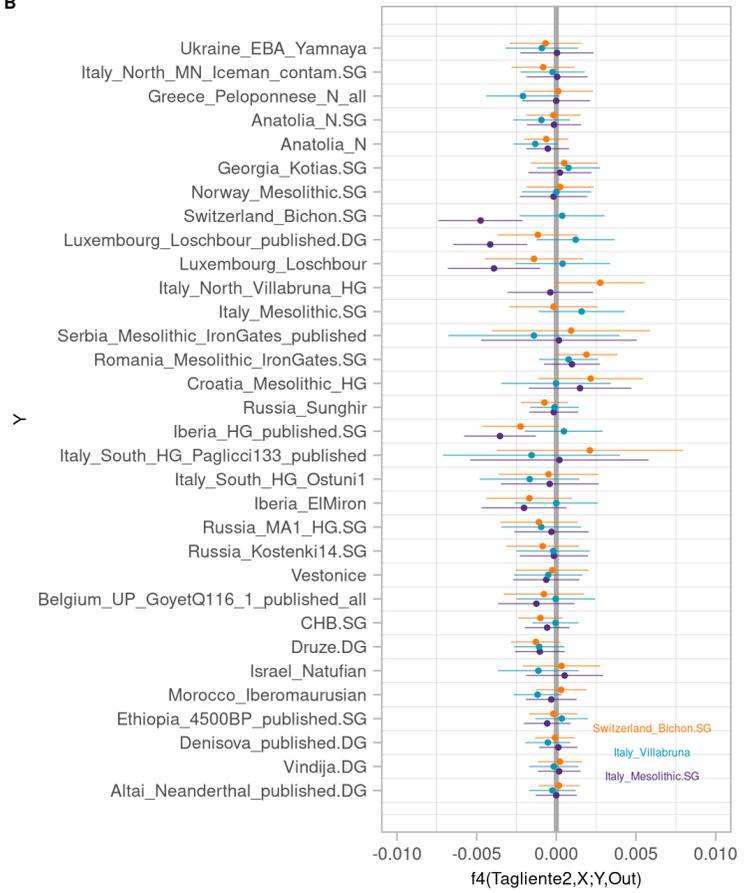
B



A Figure 4



B



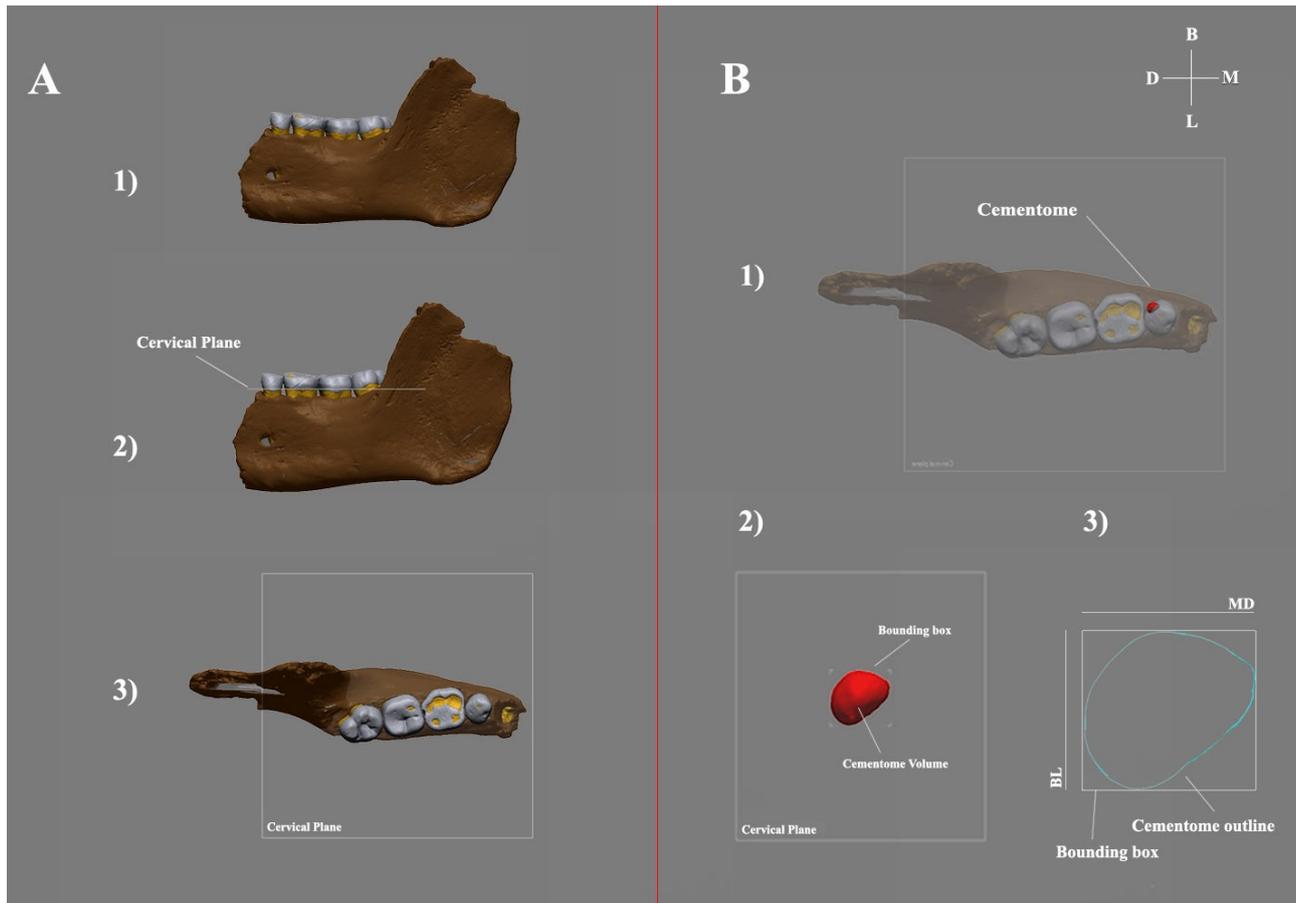


Figure S1. Digital reconstruction of the hemimandible Tagliente2. Related to Figure 1 and Figure 2: Digital reconstruction of the hemimandible. A1) A spline curve was digitized at the cervical line of each crown dentine. A2) A best-fit plane (cervical plane) was obtained. A3) The hemimandible was oriented with the best-fit plane computed at the cervical lines (i.e., the cervical plane that best fits a spline curve digitized at the cervical line), parallel to the xy-plane of the Cartesian coordinate system and rotated along the z-axis to have its lingual aspect parallel to the x-axis. B1) Virtual model oriented in occlusal view. Transparency level set at 72% to highlight the lesion (in red). B2) Cementome in occlusal view. It was excluded from the context to calculate the Volume and diameters. B3) the outline corresponds to the silhouette of the oriented cementome as seen in occlusal view and projected onto the cervical plane. The contour of the section identified by 335 the cervical plane represents the cementome outline. The size of the bounding box enclosing the silhouette was used to collect mesiodistal (MD) and buccolingual (BL) diameters. M= Mesial; B=Buccal; D=Distal; L=Lingual. The hemimandible Tagliente2 was found in 1963 during the first excavation campaigns in the site within disturbed sediments located immediately outside the Riparo Tagliente shelter^{S1}. According to excavators such sediments could come from the inner area of the shelter and have been removed during historical excavations in the uppermost deposits which had led to destruction of part of the prehistoric stratigraphic sequence and dumping of sediments outside the shelter entrance. The analysis of seasonality shows an occupation spanning from the beginning of the spring season to the end of autumn^{S2, S3, S4, S5}. This record consists of dwelling structures, several fireplaces, and some thick soils rich in lithic assemblages, faunal and ochre remains, along with some osseous tools and some beads obtained from marine shells and red deer canines^{S6, S7, S8, S9}. An emphasis on processing of the rich lithic, mineral and biological resources offered by the Lessini area is recorded. The variety and abundance of finds indicate an excellent knowledge of the territory surrounding the site, which was intensively exploited at least from the valley-bottom to the top of the plateau^{S2, S10}. Such occupations occurred on a seasonal basis, especially during the period of the year between early spring and late autumn. Despite this rich record the absence of evidence referring to the time span between 17 and 16 kyrs cal. BP all over the north Italian peninsula does not allow to support any hypothesis on the annual range of mobility of these groups. Nonetheless, the presence of few artefacts and cores manufactured on cherts from the Northern Adriatic Apennines (Umbria-Marche basin) among the wide quantity of items and discarded elements obtained on the local high quality siliceous rocks suggests the persistence of contacts with this area until at least this age^{S11}. Long distance

mobility and/or contacts are also supported by marine shells beads from this layers amounting to some hundreds^{S2}.

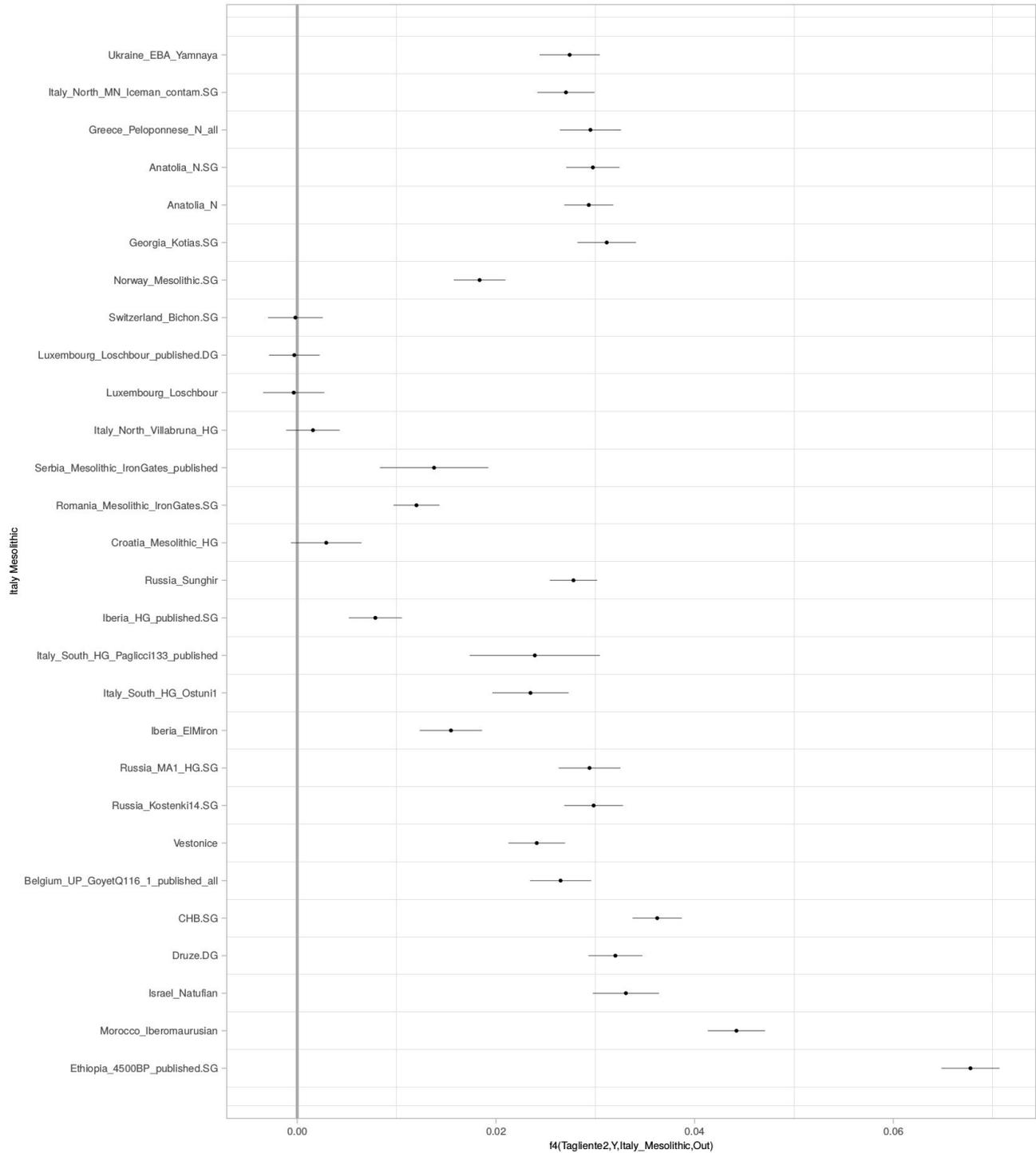


Figure S2. Results of F4 tests. Related to Figure 4: F4 tests in form (Tagliente, X, Mesolithic_Italian_Continenza,Mbuti), where X is one of the populations reported along the Y axis and consistent with Figure 3 B, showing that the available SNPs are sufficient to yield significance in a f4 test.

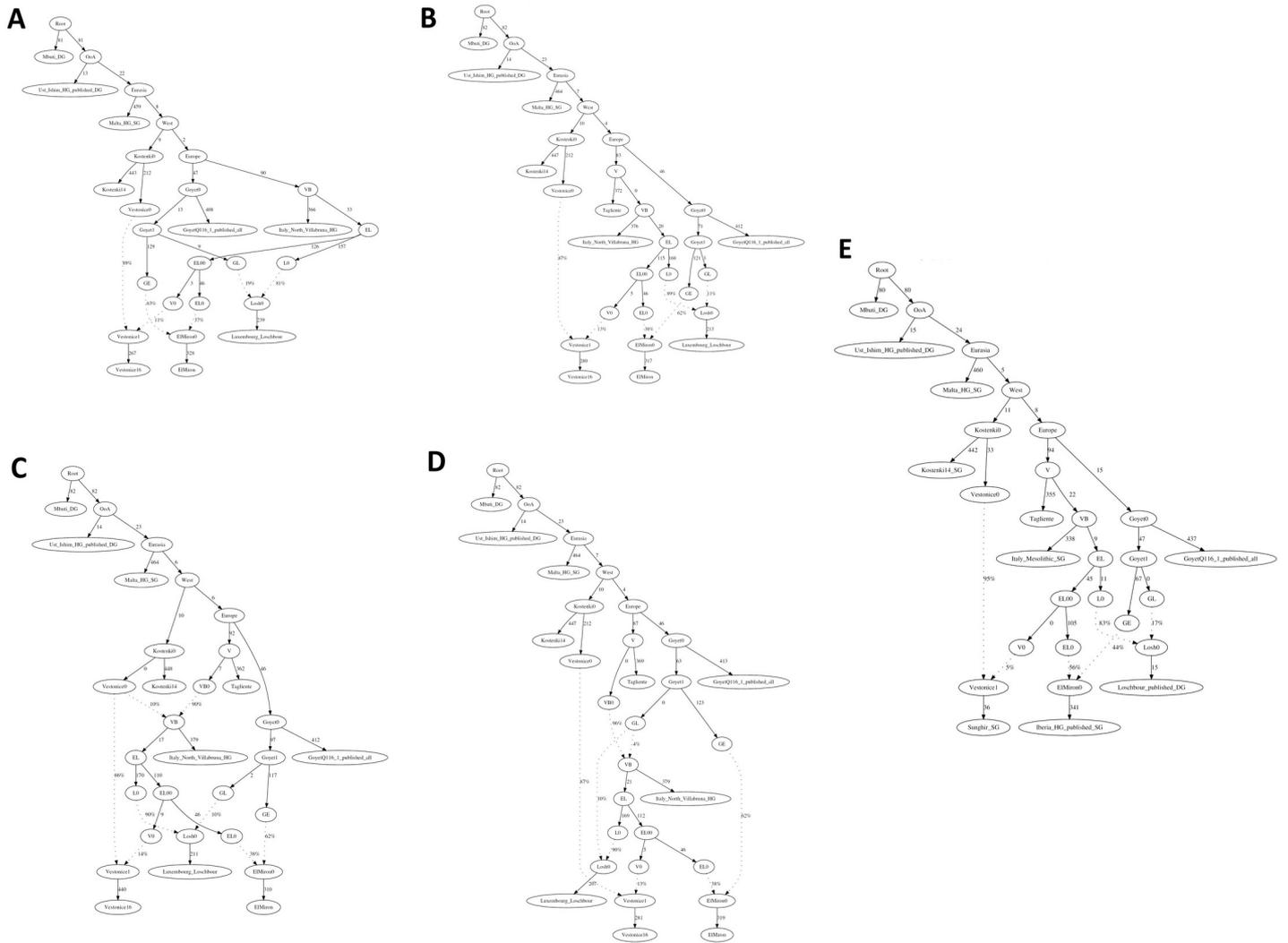


Figure S3. Tagliente2 within the Fu et al. 2016^{S12} qpGraph model. Related to Figure 4. We started from the qpGraph originally proposed in Fu et al. 2016 (Panel A: Final Score 37628.736; dof: 8; no f2 outliers; worst f4: Mbu,Ust,Goy,Ita $Z=-3.330$) and informed by the f4 stats shown in Figure 3 placed Tagliente 2 as a basal branch of the Villabruna cluster (Panel B: Final Score 38182.359; dof: 15; no f2 outliers; worst f4: Mbu,Ust,Goy,Ita $Z=-3.330$). We also explored alternative scenarios featuring Villabruna as an admixture of pre-existing Vestonice (Panel C: Final Score 39471.021; dof: 14; no f2 outliers; worst f4: Mbu,Ust,Goy,Ita $Z=-3.330$) or Goyet (Panel D: Final Score 37245.412; dof: 14; no f2 outliers; worst f4: Ust,Ita,Goy,Ita $Z=3.503$) clusters. Notably, since the number of events and degrees of freedom (dof) are different across different graphs, final scores are not directly comparable. Panel E: to minimize the bias introduced by using capture and shotgun data within the same analysis, we report also the tree proposed as in panel B using, with the exception of Goyet, only shotgun data. Final Score: 34431.549; Degrees of freedom: 15; One f2 outlier: Mal, Sun , $Z=2.346$; Worst f4: Mbu,Ust,Sun,Goy, $Z=3.541$

RIP001.all.hs37d5.sorted.remDup

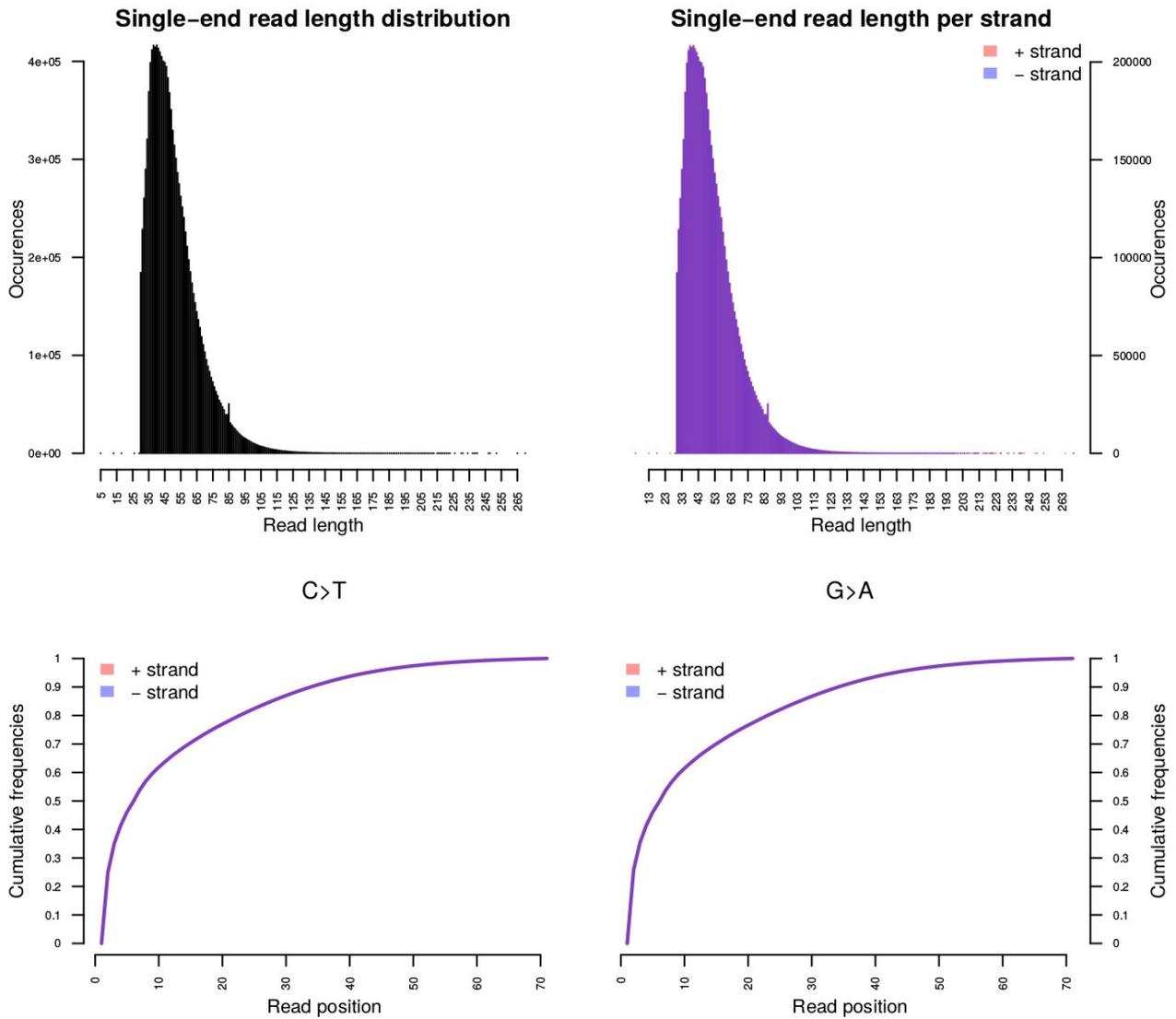


Figure S4. Sequencing read length and substitution rate for Tagliente2 whole genome sequence. Related to Figure 3 and Figure 4

Supplemental References

- S1. Corrain, C. Un frammento di mandibola umana, rinvenuto a “Riparo Tagliente” in Valpantena (Verona). *Atti Dell'Istituto Veneto Sci. Lett. Ed Arti* **CXXIV**, 23–26 (1966).
- S2. Fontana, F., Cilli, C., Cremona, M. G., Giacobini, G. & Gurioli, F. Recent data on the Late Epigravettian occupation at Riparo Tagliente, Monti Lessini (Grezzana, Verona): a multidisciplinary perspective. *Preistoria Alp.* **44**, 51–59 (2009).
- S3. Fontana, F. *et al.* Re-colonising the Southern alpine fringe: diachronic data on the use of sheltered space in the late Epigravettian site of Riparo Tagliente. in *Palaeolithic Italy. Advanced studies on early human adaptation in the Apennine Peninsula* 287–310 (Sidestone Press, 2018).
- S4. Gazzoni, V. *et al.* Late Upper Palaeolithic human diet: first stable isotope evidence from Riparo Tagliente (Verona, Italy). *Bull. Mém. Société Anthropol. Paris* **25**, 103–117 (2013).
- S5. Rocci Ris, A. I macromammiferi di Riparo Tagliente. Archeozoologia e tafonomia dei livelli epigravettiani. (Universita degli Studi di Torino, Dipartimento di Anatomia, Farmacologia e Medicina Legale, 2006).
- S6. Bietti, A. *et al.* Inorganic Raw Materials Economy and Provenance of Chipped Industry in Some Stone Age Sites of Northern and Central Italy. *Coll Antropol* **14** (2004).
- S7. Cavallo, G. *et al.* Sourcing and processing of ochre during the late upper Palaeolithic at Tagliente rock-shelter (NE Italy) based on conventional X-ray powder diffraction analysis. *Archaeol. Anthropol. Sci.* **9**, 763–775 (2017).
- S8. Cavallo, G. *et al.* Textural, microstructural, and compositional characteristics of Fe-based geomaterials and Upper Paleolithic ocher in the Lessini Mountains, Northeast Italy: Implications for provenance studies. *Geoarchaeology* **32**, 437–455 (2017).
- S9. Peretto, C., Biagi, P., Boschian, G. & Broglio, A. Living-Floors and Structures From the Lower Paleolithic to the Bronze Age in Italy. *Coll. Antropol.* **28**, 63–88 (2004).
- S10. Bertola, S., Broglio, A. & Cassoli, PF. L'Epigravettiano recente nell'area prealpina e alpina orientale. in *L'Italia tra 15.000 e 10.000 anni fa. Cosmopolitismo e regionalità nel Tardoglaciale* 39–94 (Museo Fiorentino di Preistoria “Paolo Graziosi”, 2007).
- S11. Bertola, S., Fontana, F. & Visentin, D. Lithic raw material circulation and settlement dynamics in the Upper Palaeolithic of the Venetian Prealps (NE Italy). A key-role for palaeoclimatic and landscape changes across the LGM? in *Palaeolithic Italy. Advanced Studies on Early Human Adaptations in the Apennine Peninsula* 219–246 (Sidestone Press, 2018).
- S12. Fu, Q. *et al.* The genetic history of Ice Age Europe. *Nature* **534**, 200–205 (2016).