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Evidence from personal ornaments suggest nine distinct cultural groups between 34,000 and 24,000 years ago in Europe

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1 **Editor summary:**

2 The study of personal ornaments worn by Ice Age European hunter gatherers between 34,000 and 24,000 years ago identifies nine regional
3 groups, which align with the known genetic diversity of that period.

4 **Peer review information:**

5 Nature Human Behaviour thanks the anonymous reviewers for their contribution to the peer review of this work.

6 **Inventory of Supporting Information**

7
8
9

1. Extended Data

Figure or Table #	Figure/Table title	Filename	Figure/Table Legend
Extended Data Fig. 1	Geographical distribution of the Gravettian burials yielding personal ornaments.	Baker et al. Extended Data Figure 1 final submission correct size.jpg	<i>Extended Data Figure 1 - a) Geographical distribution of the Gravettian burials yielding personal ornaments. BS1, Krems-Wachtberg; BS2, Lagar Velho; BS3, Paviland; BS4, Arene Candide; BS5, Kostenki 14; BS6, Ostuni; BS7, Fanciulli; BS8, Paglicci; BS9, Dolni Vestonice; BS10, Brno; BS11, Cro-Magnon; BS12, Baouso da Torre; BS13, Barma Grande; BS14, Grotta del Caviglione; BS15, Veneri Parabita; BS16, Predmosti; BS17, Borsuka Cave. b) Geographical distribution of the Gravettian occupation sites yielding personal ornaments in Europe with the Dordogne region enlarged at the bottom right (c). S1, Poiana Ciresului-Piatra Neamt; S2, Kostenki 17; S3, Foradada Cave; S4, Riparo Mochi; S5, Franchthi Cave; S6, Mitoc-Malu Galben; S7, Brinzeni Cave; S8, Duruitoarea Veche Cave; S9, Cosauti; S10, Climauti; S11, Molodova V; S12, Gargas Cave; S13, Brillenhohle; S14, Geisenklosterle; S15, Hohle Fels; S16, Ollersdorf/Heidenberg; S17, Mainz-Linsenberg; S18, Nerja Cave; S31, Isturitz Cave; S32, Abri des Pecheurs; S33, Baume Perigaud; S34, Pushkari; S35, Grotta della Serratura; S36, Vale Boi; S37, El Cuco; S38, Sire; S39, Tibrinu; S40, Gura Cheii-Rasnov Cave; S41, Garma A; S42, Cova Gran de Santa Linya; S43, La</i>

			<p><i>Grotte du Figuier; S44, Cova de les Cendres; S45, Cova del Comte; S47, Grub-Kranawetberg; S48, Grotte du Renne; S49, Krakow Spadzista; S50, Grotte du Pape; S52, Kostenki 21; S53, Kostenki 8; S54, Kostenki 4; S55, Aitzbitarte; S56, Amiens-Renancourt; S57, Mollet; S58, Arbreda Cave; S59, Jaksice; S60, Les Bossats; S61, La Bergerie; S62, Lapa do Picareiro; S63, La Fuente del Salin; S66, Krems-Wachtberg; S67, Willendorf; S70, Buran-Kaya; S71, Weinberghohlen; S72, Krems-Hundsteig; S73, Obere Klause; S74, Betche-aux-Rotches de Spy; S75, Goyet; S77, Dolni Vestonice 1; S80, Le Blot; S81, Pavlov; S82, Oblazowa Cave; S83, Ciooarei Cave; S84, Reclau Viver Cave; S85, Paviland; S86, La Vina; S87, Cueto de la Mina; S88, Cueva Morin; S89; Bolinkoba; S90, Amalda; S91, Alkerdi; S92, Antolinako Koba; S93, Abric Romani; S94, Cueva de Ardales; S95, Gruta do Caldeirao; S96, Cova Beneito; S97, Zajara; S98, Los Morceguillos. c) Geographical distribution of the Gravettian occupation sites yielding personal ornaments from the Dordogne region. S19, Le Facteur; S21, Labattut; S20, Le Flageolet; S22, Laussel; S23, Le Poisson; S24, Les Rochers de l'Acier; S25, Le Roque-Saint-Christophe; S26, Le Ruth-Pages; S27, Grotte de Tourtoirac; S28, Abri Laroux; S29, Grotte de Pairnon-Pair; S30, Le Roc de Gavaudun; S46, Le Fourneau du Diable; S51, La Gravette; S64, Les Vachons; S65, La Ferrassie; S68, Le Petit-Puyrouseau; S69, Abri Pataud; S78, Laugerie-Haute; S79, Masnaigre. Maps created on QGIS using ETOPO1 Global Relief Model data with a modern and Gravettian coastline at -100 m¹⁴².</i></p>
Extended Data Fig. 2	Two-tailed Mantel correlogram established for the bead-type associations recorded at Gravettian occupation sites.	Baker et al. Extended Data Figure 2 final submission correct size.jpg	<i>Extended Data Figure 2 - Two-tailed Mantel correlogram established for the bead-type associations recorded at Gravettian occupation sites (a), and burial sites (b). Unit of geographic distance for a1 and b1: 500 km, a2 and b2: 250 km, a3 and b3: 100 km. Black squares indicate significant P-values, white squares non-significant P-values.</i>
Extended Data Fig. 3	Boxplot of radiocarbon ages associated with Gravettian occupation and burial sites yielding personal ornaments in	Baker et al. Extended Data Figure 3 final submission correct size.jpg	<i>Extended Data Figure 3 - Boxplot of radiocarbon ages associated with Gravettian occupation and burial sites yielding personal ornaments in different regions of Europe. Maximum value = 36,280.5 years, Minimum = 23,525 years. Dark grey = occupation sets, light grey = burial sets. The box extends from the lower to upper quartile, with the whisker variability indicating outside the upper and lower quartiles. "Eastern Europe" = N=8,</i>

	different regions of Europe.		"South Iberia" = N=8, "Northwestern Europe" = N=4, "North Iberia" = N=8, "Central Europe" = N=9, "Eastern (Burials)" = N=9, "North Italy (Burials)" = N=11, "South Italy (Burials)" = N=6. Total = N=63.
Extended Data Table. 1	Results of the two-tailed Mantel tests calculated for the bead-type associations recorded at Gravettian occupations and burial sites.	Extended Data Table 1.jpg	<i>Results of the two-tailed Mantel tests calculated for the bead-type associations recorded at Gravettian occupations and burial sites.</i>
Extended Data Table. 2	Results of the two-tailed Partial Mantel tests calculated for the bead-type associations recorded at Gravettian burial sites.	Extended Data Table 2.jpg	<i>Results of the two-tailed Partial Mantel tests calculated for the bead-type associations recorded at Gravettian burial sites.</i>
Extended Data Table. 3	Results of the two-tailed Mantel tests calculated for the bead-type associations recorded at Gravettian burial sites in Western and Eastern Europe.	Extended Data Table 3.jpg	<i>Results of the two-tailed Mantel tests calculated for the bead-type associations recorded at Gravettian burial sites in Western and Eastern Europe.</i>

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1. Supplementary Information:

12

A. PDF Files

13

Item	Present?	Filename	A brief, numerical description of file contents.
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Supplementary Information	Yes	All SI combined.pdf	Supplementary Results 1 and 2, Supplementary Figures 1-5, Supplementary Tables 1-4.
Reporting Summary	Yes	Baker_RS.pdf	
Peer Review Information	No		

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15 **B. Additional Supplementary Files**

16

Type	Number	Filename	Legend or Descriptive Caption
Supplementary Table	1	Bead Coding SUPP TAB 1_2 nd .xlsx	Bead coding. An excel spreadsheet containing each of the discrete bead types and the code used for each.
Supplementary Table	2	All datasets SUPP TAB 2_2 nd .xlsx	All datasets. An excel spreadsheet containing 7 separate worksheets.
Supplementary Table	3	Occupation Table SUPP TAB 3_2 nd .xlsx	Occupation Table. An excel spreadsheet which contains the attributes and personal ornaments of the occupation sites.
Supplementary Table	4	Burial Table SUPP TAB 4_2 nd _SR.xlsx	Burial Table. An excel spreadsheet which contains the attributes and personal ornaments of the buried individuals.
Supplementary Table	5	All distance matrices SUPP TAB 5_2 nd .xlsx	All distance matrices. An excel spreadsheet containing 14 separate worksheets.
Supplementary Table	6	Modelling datasets SUPP TAB 6.xlsx	All datasets used for the Mantel test modelling. An excel

17

			spreadsheet containing 5 separate worksheets.
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19 **Evidence from personal ornaments suggest nine distinct cultural groups**
20 **between 34,000 and 24,000 years ago in Europe**

21

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34 **Abstract:**

35 Mechanisms governing the relationship between genetic and cultural evolution are the subject of
36 debate, data analysis and modelling efforts. Here we present a new georeferenced dataset of personal
37 ornaments worn by European hunter-gatherers during the so-called Gravettian technocomplex (34-
38 24,000 years ago), analyse it with multivariate and geospatial statistics, model the impact of distance
39 on cultural diversity, and contrast the outcome of our analyses with up-to-date paleogenetic data. We
40 demonstrate that Gravettian ornament variability cannot be explained solely by isolation-by-distance.
41 Analysis of Gravettian ornaments identified nine geographically discrete cultural entities across
42 Europe. While broadly in agreement with paleogenetic data, our results highlight a more complex
43 pattern with cultural entities located in areas not yet sampled by paleogenetics, and distinctive entities
44 in regions inhabited by populations of similar genetic ancestry. Integrating personal ornament and
45 biological data from other Palaeolithic cultures will elucidate the complex narrative of population
46 dynamics of Upper Palaeolithic Europe.

47 **Keywords:** beads, Gravettian, grave goods, seriation, neighbour-joining, neighbour-net, Mantel test,
48 ethnicity, modelling

49

50 Introduction

51

52 Paleolithic archaeologists have long sought means to identify past cultural entities, their geographic
53 extension, social organisation and evolution¹⁻³. For the Upper Paleolithic (*circa* 42-10 ka), lithic and, to
54 a lesser extent, bone and antler technologies have been the privileged proxies for exploring
55 Palaeolithic cultural diversity and settlement dynamics⁴⁻⁶. It is only recently that these elements of
56 material culture have been supplemented by paleogenomics⁷⁻¹⁰. The correspondence between genetic
57 and cultural features is, however, the subject of ongoing debate and it has been argued that
58 amalgamating these two types of evidence together may lead to biased interpretations if not
59 supported by explicit reasoning¹¹⁻¹³.

60 It is generally accepted that artefacts with exclusively symbolic functions, such as personal ornaments
61 and mobiliary art, are more informative than functional objects when characterising cultural and social
62 systems as well as individuals' role within society^{14,15}. Many authors argue that they are essential tools
63 for exploring past cultural dynamics¹⁶⁻²⁰.

64 The earliest instances of personal ornaments consist of marine shells found in Northwestern and
65 Southern Africa and the Levant and are dated between 140 to 70 thousand years (ka)²¹⁻²⁴. Only a single
66 or a few species are used as ornaments at these sites. In Northern Africa, these sites are spread over a
67 large geographic area encompassing inland regions. From *circa* 52 ka marine shells are replaced in
68 Eastern Africa and by *circa* 42 ka in Southern Africa by discoid ostrich eggshell beads²⁵. It has recently
69 been proposed that a split in their size occurred *circa* 33 ka between East and Southern Africa²⁵. It is
70 only after *circa* 45 ka in Eurasia that we observe the spread of ornamental traditions involving the use
71 of hundreds of different bead types made of a range of raw materials (*e.g.*, ivory, bone, antler, teeth,
72 shells, stone, fossil, amber, jet etc.). This is the moment in which personal ornaments acquire a degree
73 of diversity enabling researchers to more precisely investigate their role as cultural markers. The idea
74 behind this approach, supported by ethnographic evidence²⁶⁻²⁸, is that personal ornaments are a
75 communication technology used to convey privileged information on group affiliation and social
76 status^{29,30}.

77 Working within this framework, Newell et al.³¹ reached the conclusion, after analysing a dataset of
78 Mesolithic personal ornaments, that their distribution supported the hypothesis that they reflected

79 geographically structured and hierarchically nested ethnic groups in Western Europe³². Vanhaeren and
80 d’Errico²⁰ interpreted a georeferenced database of Aurignacian personal ornaments as reflecting the
81 ethnolinguistic geography of Europe just after its peopling by modern humans. Applying a similar
82 approach, d’Errico and Vanhaeren³³ analysed personal ornaments and grave goods associated with
83 Gravettian burials and proposed the existence of two main distinct cultural regions during this period.
84 Rigaud et al.¹⁸ reached the conclusion, after analysing an extensive database of Mesolithic and Early
85 Neolithic personal ornaments, that this cultural proxy was able to identify the cultural geography of
86 Europe before and after the spread of the Neolithic. These authors also showed that stronger
87 continuity in personal ornament use was observed in the Baltic compared to the Central Europe and
88 Mediterranean areas, with the former interpreted as a resilience in fashion and systems of belief.

89 An alternative theoretical framework is proposed by some authors to interpret these and similar
90 archaeological datasets^{1,34–38} according to which the observed regional differences are better
91 explained as the result of isolation-by-distance (IBD), a mechanism well known in population
92 genetics^{39,40}, according to which individuals are more likely to exchange genes with more
93 geographically proximate conspecifics. When applied to material culture, this mechanism predicts that
94 similarity in cultural features will be determined by the geographic distances between
95 contemporaneous sites. The corollary of this view is that other factors such as linguistic diversity,
96 topography, environment, phenotypic diversity and economy would play a negligible role in structuring
97 cultural diversity and in creating long-lasting boundaries between groups. It also implies that
98 populating events by groups possessing different cultural features will result in an almost immediate
99 dilution of cultural systems following the IBD scenario. Determining which of these two theoretical
100 frameworks more accurately explains past cultural variability is crucial for understanding the function
101 of technologies for culturalising the human body in past societies and their evolutionary trajectories.

102 In this study we created and analysed a georeferenced database of personal ornaments from burial
103 and occupation contexts dated to the Gravettian, a major Palaeolithic archaeological culture spanning
104 across Europe between 34 – 24 ka cal. BP. Our aim is to establish whether personal ornaments could
105 be used to identify the geography and evolution of past cultural entities and, if so, accomplish this task
106 for the ten-thousand-year time span covered by the Gravettian. Unlike the Aurignacian (41.5 – 30 ka
107 cal. BP), the culture preceding the Gravettian, personal ornaments are found in the latter at occupation
108 and numerous burial sites, which enable comparative analysis of the two records and evaluation of
109 contrasting interpretations. Our archaeological and modelling results support the view that personal
110 ornaments are reliable proxies for reconstructing past cultural diversity and reflect to a large extent
111 past population dynamics highlighted by palaeogenomic data⁹.

112

113 **The Gravettian**

114 The Gravettian technocomplex (*circa* 34 – 24 ka cal. BP^{41–43}) succeeds the Aurignacian in Europe^{20,35,44–}
115 ⁴⁸ and endured until just before the Last Glacial Maximum. Recent palaeogenomic work has shown
116 that individuals associated with Gravettian assemblages from Western Europe had a different genetic
117 ancestry from contemporaneous Gravettian groups from Central and Southern Europe⁹. It has also
118 highlighted that Gravettian individuals from Western Europe genetically resemble those from the
119 preceding Aurignacian culture. The Gravettian (*sensu lato*) is characterised by geographically diverse
120 lithic technologies having in common the widespread production of straight backed points^{42,49–54}, the
121 ubiquitous production of anthropomorphic figurines^{55,56} and it is when we first witness the systematic
122 production of primary burials with rich grave goods and personal ornaments^{33,57}. The internal
123 heterogeneity observed within the Gravettian lithic record has been accounted for with multiple
124 hypotheses by various authors (*e.g.*, regionally distinct populations^{9,58}, various site functions^{59,60} and
125 different ecological adaptations^{54,61}), whilst many publications have attempted to describe and explain
126 the European-wide phenomenon of the Gravettian anthropomorphic figurines^{56,62,63}. However, the
127 third characteristic of the Gravettian, *i.e.*, burials and personal ornaments, remains relatively
128 understudied on a European scale.

129

130 **Gravettian ornaments**

131 Gravettian beads have several key attributes which lend themselves well to statistical analysis. Firstly,
132 the Gravettian is Pan-European in nature and thus it provides a wide geographical canvas upon which
133 one can apply statistical analyses. Secondly, it presents typological variation which allows different
134 archaeological layers to be attributed to different *facies*^{52,54,64,65}. Thirdly, it presents personal
135 ornaments of discrete types which are found in numerous, well-dated sites, which enables the
136 investigation of both regional and temporal evolutionary trends in ornamental practices. Finally, the
137 Gravettian provides abundant ornaments in both burial and occupation contexts³. While burials
138 provide a single ‘snapshot’ event of ornamental behavioural practices, occupation sites represent a
139 diachronic palimpsest of these behaviours. In modern-day traditional societies, the position, order and
140 association of personal ornaments often play an important role in their social meaning^{14,66,67}.
141 Therefore, having personal ornaments preserved in their ‘real-life’ state gives an additional dimension
142 of inquiry and, especially in the case of multiple burials, offers a unique opportunity to study the
143 internal social organisation of these groups of people. However, given the relatively smaller sample

144 size of burials compared to occupation sites, the existence of personal ornaments in the latter provides
145 an additional large dataset which can complement the conclusions drawn from the former.

146 Considering the progress made to unravel the social and cultural evolution of the preceding
147 Aurignacian culture^{20,35,44–48} and the well-established Gravettian geographic lithic variability^{42,49–54}, the
148 opportunity to perform in-depth analyses on Gravettian personal ornaments presents itself as a next
149 step to further elucidate the cultural narrative of Upper Palaeolithic Europe. Despite the extensive
150 corpus of data available in the literature, only a small number of studies^{68–71} directly tackle the subject
151 of Gravettian ornamental practices in an effort to characterize regional and temporal trends. These
152 studies, unfortunately, do not examine personal ornaments at large geographic or continental scales,
153 tending instead to focus on single sites or smaller regional scales. This has hitherto prevented
154 meaningful discussion on the broad evolutionary mechanisms which were at play during the
155 Gravettian.

156

157 Main Text

158 Results

159 Dataset description

160 Our dataset includes 134 discrete types of ornaments (Fig. 1a & 1b, Supplementary Information,
161 Supplementary Table 1 & 2) found at 112 Gravettian sites, (97 occupation and 17 burial sites, with two
162 sites harbouring both a burial and occupation layers) (Supplementary Table 3 & 4). The burial sites
163 housed 32 individual human skeletons (Extended Data Fig. 1). Of these discrete ornament types, 79
164 were made of shells, 26 of teeth and 29 shaped from other raw materials. Ornaments fashioned from
165 shells comprise eight taxa only available on Atlantic shores, eleven taxa only available from
166 Mediterranean shores, and 50 shell taxa which can be found at both the Mediterranean and Atlantic
167 coasts. Two taxa were available from freshwater sources and eight taxa are found at fossil outcrops
168 throughout Europe. Our database records ornaments made from various teeth (Fig. 1a): canines,
169 incisors and molars. Ten types come from mammal carnivoran species (*i.e.*, Bear, Fox, Hyena, Lynx,
170 unknown *Felis* sp., Wolf), eleven from mammal herbivore species (*i.e.*, European Elk, Horse, Rabbit,
171 Red Deer, Steppe Bison, unknown *Bovid* sp., unknown herbivore sp.), one belonged to a fish species
172 (*i.e.*, Gilt-head Bream) and four belonged to humans. They feature two techniques of suspension,
173 perforation and grooving. Of the shaped ornaments (Fig. 1b), sixteen types were fashioned out of ivory
174 (*e.g.*, bilobated, cylindrical, and, in the rare case of Dolní Věstonice (Czech Republic), breast-shaped
175 beads etc.), eight types from bone (*e.g.*, tubular beads made of mammal long bone diaphyses and

176 perforated *Ursus spelaeus* phalange etc.), two of stone and single types from amber, jet, and fish
177 vertebrae.

178

179 *Figure 1*

180

181 **Multivariate analysis of the occupation dataset**

182 The seriation identifies 6 sets (Fig. 2). Set 1 groups sixteen sites from Eastern Europe, Set 2 twelve sites
183 from Central Europe, Set 3 thirty sites from Northwestern Europe, Set 4 fourteen sites from Southern
184 Iberia, Set 5 twelve sites from Northern Iberia, Set 6 three sites from the Mediterranean region. Ten
185 sites are not included in any set. The seriation criterion score was 0.18562. The Modularity test and
186 the perMANOVA performed on the groups identified by the seriation indicate that they are
187 significantly different, and their diversity explains 14% of the variance in the data ($R^2(5) =$
188 0.14070246985803 , $p = 0.001$) (Supplementary Results, 'Modularity test and permutational
189 MANOVA').

190

191 *Figure 2*

192

193 Within each geographic set identified by the seriation *circa* 20% to 32% of the bead types are present
194 in two or three chronological phases (Early, Middle and Late) of the Gravettian (Fig. 3). This continuity
195 is observed to a lesser extent within the Northwestern set, however, with only 4.3% of the bead-types
196 used in different chronological phases.

197

198 *Figure 3*

199

200 The first PCoA axis of the occupation dataset, accounting for 8.62% of variation, shows two overlapping
201 clusters, one associating sites from Western Europe and the other associating sites from Central and
202 Eastern Europe (Fig. 4a). The slight overlap is mainly caused by Abri Pataud (S69, France), without
203 which the two clusters would plot almost separately.

204 The neighbour-joining tree analysis identifies two groups of sites following the same geographic
205 pattern identified by the PCoA (Fig. 4b). One group (Fig. 4b1) clusters sites from Western Europe and

206 the other (Fig. 4b2) clusters sites mainly from Central and Eastern Europe with the inclusion of some
207 Northwestern Europe sites. The only exception in the Western group is the site of Krems-Wachtberg
208 (S66, Austria).

209

210

Figure 4

211

212 **Multivariate analysis of the burial dataset**

213 The seriation identifies three sets (Fig. 5a). Overall, the seriation highlights two major groups, one
214 includes burials located in Eastern Europe (set 1), and another group that includes burials located in
215 Western Europe (mostly South and North Italy). North Italy burials make up set 2 while burials from
216 South Italy make up set 3. The criterion score is 0.577181. The Modularity test and the perMANOVA
217 performed on the groups identified by the seriation indicate that they are significantly different and
218 their diversity explains 53% of the variation in the data ($R^2(2) = 0.533373821394103$), $p = 0.001$
219 (Supplementary Results, 'Modularity test and permutational MANOVA').

220

221

Figure 5

222

223 The seriation made under chronological constraint (Fig. 5b), *i.e.* phase by phase, shows that the two
224 major groups of burials (*i.e.*, Eastern and Western Europe burials) only overlap for a period of one
225 thousand years. Burials older than 29.5 ka are only found in the Eastern group whereas burials younger
226 than 28.5 ka are only found in the Western group. This seriation highlights a continuity in bead-type
227 associations found in Eastern Europe burials during the Early and Middle Gravettian (50%) and a
228 continuity in bead-type associations found in Western Europe burials (North (57.14%) and South (50%)
229 Italy) during the Middle and Late Gravettian.

230 The first PCoA axis of the burial dataset, accounting for 35.93% of variation, shows a marked separation
231 between the Western and Eastern Europe burials and a less compelling one between burials from the
232 North and South of Italy (Fig. 6a).

233 The neighbour-joining analysis identifies a clear separation between burials from Eastern Europe,
234 South Italy and North Italy (Fig. 6b), with the only exception being the Southern Italian burial of Ostuni
235 1 (B8, Italy), which plot with the burials from the North of the Italian peninsula. The Southern Italian

236 subgroup also includes the Lagar Velho burial (B4, Portugal) due to the presence of *C. elaphus* canines.
237 Paviland (B5, Wales, United Kingdom) and Cro-Magnon (B20, France) cluster together as a distinct sub-
238 group.

239

240 *Figure 6*

241

242 **Neighbour-net analysis of occupation and burial sites**

243 *The occupation neighbour-net tree identified four clusters of sites (*

244 *Figure 7*

245 [Fig. 7a](#)). Moving clockwise, Cluster 1 (S7-S58) includes a mix of Western and Eastern Europe sites
246 characterized by ornaments made of *Glycymeris* sp. and *Pecten* sp. shells. Cluster 2 (S11-84) is mostly
247 composed of Central and Eastern Europe sites characterized by the use of ornaments made of
248 symmetric ivory pendants and *Vulpes* sp. canines. Cluster 3 (S72-S24) groups Mediterranean and
249 Northwestern Europe sites in which *Turritella* sp. and *Dentalium* sp. shells are frequently found. North
250 and South Iberian sites are included in cluster 4 (S90-S44), which is characterized by perforated *N.*
251 *lapillus* and *L. obtusata* shells.

252 The neighbour-net tree built with the burial dataset identifies the three geographically distinct clusters
253 of sites ([Fig. 7b](#)) previously identified by the seriation and the Neighbour-joining analyses. Moving
254 clockwise, Cluster 1 (B2-B1) is composed of Eastern Europe burials characterized by ornaments made
255 of carnivore teeth (*i.e.*, Fox canine and Wolf canine) and symmetric ivory pendants. The association of
256 *C. elaphus* canines with Mediterranean shells (*i.e.*, *T. neritea/pellucida* and *Cypraea* sp.) and
257 asymmetric ivory pendants is characteristic of burials found in North Italy and one burial from South
258 Italy (B8, Ostuni 1), all grouped in Cluster 2 (B8-B21). Cluster 3 (B9-B30) is composed of South Italy
259 burials characterized by ornaments made of *C. elaphus* canines and *Cypraea* sp.

260

261 *Figure 7*

262

263 The Delta score for the occupation sites neighbour-net is 0.2 with a q-residual of 0.00469. The Delta
264 score for burials is 0.2387 with a q-residual of 0.0166. These values indicate that the amount of
265 reticulation is greater in the burial sites than in the occupation sites Neighbor-net. This implies that
266 the data are moderately tree-like for both occupation and burial datasets, and the personal ornament

267 diversity identified in burials is even less tree-like than bead-type associations diversity at occupation
268 sites.

269

270 **Effect of geographic and chronological distances**

271 The degree of correlation between the cultural, spatial and temporal distances are different for the
272 occupation and burial datasets ([Extended Data Table 1](#)).

273 Occupation site personal ornament diversity shows a statistically significant correlation with
274 geographic distances, with approximately 19.4% (Mantel Z Value (95) = 0.1941563, $p < 0.001$) of the
275 variability explained by the latter. The perMANOVA conducted on the occupation sites attributed to
276 one Gravettian phase (Early, Middle, Late), shows that 5.5% of the bead-type diversity is explained by
277 chronology ($R^2(2) = 0.0550199468252677$, $p = 0.005$) ([Supplementary Results, 'Modularity test and
278 permutational MANOVA'](#)).

279 Burial data show significant correlation with distance in space and time, with approximately 32.6%
280 (Mantel Z Value (15) = 0.3257094, $p = 0.0093$) of the variability explained by geography ([Extended Data
281 Table 1](#)) and 32.9% (Mantel Z Value (15) = 0.3288, $p = 0.0052$) explained by chronology ([Extended Data
282 Table 2](#)). Because there is only a small degree of chronological overlap between the burials from
283 Western (North and South Italy) and Eastern Europe, we performed a separate Mantel test for each
284 geographic burial subset. These tests ([Extended Data Table 3](#)) reveal a relatively strong and significant
285 correlation between cultural and geographic distances for the former (Mantel Z Value (6) = 0.4559727,
286 $p = 0.0266$) and no significant correlation for the latter (Mantel Z Value (1) = 0.855131, 0.16667),
287 although this may be due to the small sample size.

288 The occupation Mantel correlograms display significant positive autocorrelation up to geographic
289 distances of approximately 1000 km and significant negative autocorrelation at geographic distances
290 over 1500 km ([Extended Data Fig. 2a](#)). The burial dataset Mantel correlograms displays positive
291 autocorrelation at geographic distances up to 100 km and no significant autocorrelation at other
292 geographic distances ([Extended Data Fig. 2b](#)).

293 Our five simulations of the effects of spatial and cultural barriers on bead diversity produce notably
294 different Mantel Test Z values ([Supplementary Result, 'Modelling the effect of spatial and cultural
295 boundaries'](#)), with two simulations closely matching the results obtained for our occupation and burial
296 datasets (respectively Model 2 and 3). Model 2, which assumes a slight geographical overlap of sites
297 with partially shared cultural attributes, yields a low but significant Mantel Test Z value (Mantel Z Value
298 (109) = 0.1296, $p = < 0.001$). Model 3, which assumes a clear separation of geographical and cultural

299 traits, results in a relatively strong and significant Mantel Test Z value (Mantel Z Value (109) = 0.3517,
300 $p = < 0.001$). Model 1 (Mantel Z Value (109) = -0.01053, $p = 0.7885$), Model 4 (Mantel Z Value (109) = -
301 0.009945, $p = 0.8093$) and Model 5 (Mantel Z Value (109) = -0.01871, $p = 0.9318$) each result in a non-
302 significant, low and negative Mantel Test Z value.

303

304 Discussion

305 The first aim of our study was to establish whether prehistoric material culture variability was solely
306 determined by geographic distance between archaeological sites or better explained by a combination
307 of factors. Due to their ubiquitous and discrete nature, personal ornaments are ideal proxies to test
308 these competing hypotheses. If the first hypothesis were to be proven wrong, the second aim was to
309 explore the potential of personal ornaments to reconstruct the cultural geography of Gravettian
310 populations and contrast it with available population data. Our results identify consistent differences
311 in Gravettian personal ornament associations across Europe. Seriation, PCoA and neighbour-joining
312 analyses reveal distinct geographic clusters. Ornaments broadly identify an East to West cline
313 comprising nine clusters, of which six are occupation and three are burial. The occupation clusters
314 encompass the regions of Eastern and Central Europe, the Eastern and Western (South Iberia)
315 Mediterranean, Northwestern Europe and the North of the Iberian Peninsula. The burial clusters of
316 the Northern and Southern Italian peninsula are contained within the Western Mediterranean
317 occupation cluster, whereas the Eastern European burial cluster is found over areas contained within
318 both the Central and Eastern European occupation entities.

319 Our results support the view that geographic distance is not the only factor determining prehistoric
320 material culture variability during the Gravettian. Our simulations indicate that the bead-type
321 associations identified in the Gravettian occupation dataset conform to a scenario in which
322 neighbouring cultural entities displaying culturally driven boundaries, and characterized by specific
323 bead-types, shared some of them with neighbouring groups due to synchronic or diachronic
324 fluctuations of cultural boundaries. They also indicate that the bead-type associations identified in the
325 Gravettian burial dataset is consistent with a scenario in which geographically distinct groups use
326 different bead-types. The highest Mantel Z value produced by this simulation theoretically indicates
327 isolation by geographic distance being a main driver of the archaeological bead diversity. However,
328 this hypothesis is contradicted, in our archaeological instance, by the temporal divide between the
329 identified burial clusters and their chronological and spatial exclusivity, thus suggesting that IBD does
330 not account for the observed archaeological diversity.

331 The significant, albeit weak, positive correlation identified by the Mantel test between geographic
332 distance and bead-type diversity for the occupation dataset also supports the view that geographic
333 distance does not explain all of the bead-type association diversity. The occupation dataset displays
334 significant positive autocorrelation at short geographic distances (100 - 1000 km) and significant
335 negative autocorrelation at geographic distances greater than 1500 km. This negative autocorrelation
336 at longer geographic distances suggests a significant role of factors other than geographic distance in
337 determining bead-type associations. The correlation is markedly stronger in the burial dataset.
338 However, the burial Mantel correlograms reveal that the correlation substantially drops after a
339 geographic distance of 100 km. The Mantel test performed on the Eastern and Western Europe subsets
340 shows that geographic distance did not significantly affect the bead-type diversity identified in the
341 Eastern Europe burial subset, the small size of the sample (n=3) unfortunately prevents any meaningful
342 discussion of this result.

343 Our results show that temporal distance affects the bead-type diversity identified in the burial dataset
344 to a higher extent than the bead-type diversity identified in the occupation dataset. This pattern
345 reflects the very small chronological overlap between burials from East and West Europe. Burials
346 appear to have been a cultural trait possessed by Early and Middle Gravettian people in Eastern
347 Europe, but these people apparently stopped burying their dead during the Late Gravettian.
348 Conversely, in Western Europe (South and North Italy) there were no burials during the Early
349 Gravettian but numerous examples during the Middle and Late Gravettian. Within each region over
350 half of the bead-types were continuously used during multiple phases, suggesting that the symbolic
351 meanings encoded within personal ornaments remained relatively unchanged over time.

352 The use of a small number of bead-types is maintained through time within the occupation sites. This
353 pattern indicates that the messages encoded by personal ornaments changed through time but some
354 symbols used to culturalise the human body were transmitted over long time periods.

355 In summary, our results are consistent with the view that when choosing their personal ornaments,
356 Gravettian hunter-gatherers followed, at least to some extent, conventions dictated by their sense of
357 belonging to a cultural group, and that slightly permeable cultural boundaries existed between groups
358 as supported by our modelling results ([Supplementary Result, 'Modelling the effect of spatial and
359 cultural boundaries'](#)). This, of course, does not deny the likely role of factors such as ecology and raw
360 material availability but rather it entails that these factors were largely incorporated in cultural choices.

361 The neighbour-net analyses demonstrate a clear East and West separation in the sites and identified
362 clusters, with the burial clusters being more geographically discrete than those of the occupations. The
363 higher Delta score and q-residuals obtained from the burial neighbour-net analyses indicate that bead-

364 types found in burial contexts were more likely to be circulated and exchanged within a small region
365 than those found at occupation sites.

366 What factors other than geographic distance could explain the differences observed between these
367 two contexts? One obvious possibility is that the burials and occupations represent two culturally
368 distinct time periods of the Gravettian. However, we can dismiss this possibility owing to the large
369 overlap in the radiocarbon ages of both contexts in each region ([Extended Data Fig. 3](#)).

370 A second possibility is that occupation sites represent diachronic palimpsests, whilst burials represent
371 snapshots in time. Therefore, whereas occupation sites accrued personal ornaments lost over
372 extended periods by different Gravettian sub-groups, burials reflect the cultural affiliation of
373 individuals at the time of death. The greater clarity of the burial clusters identified by our PCoA analysis
374 is consistent with this reasoning, with additional factors such as seasonal mobility^{72,73}, exogamy^{74,75}
375 and climate induced fluctuations of cultural boundaries^{76–78} further contributing to the overlapping
376 convex hulls of the occupation clusters.

377 A third possibility is that the observed difference is caused by social stratification^{33,79–81}: mortuary
378 practices for “common” individuals tend to be different from, and simpler than, those of individuals
379 with a special social status. The existence of Gravettian burials without personal ornaments (*e.g.*, Brno
380 3 (Czech Republic)⁸² and Cussac cave (France)⁸³) is consistent with this hypothesis. The presence of
381 non-adult ornamented burials in our dataset ($n=6$)^{84–87} also supports this hypothesis, as these
382 individuals did not have a chance to personally merit an elaborate burial. However, the large
383 proportion of elaborately buried individuals with signs of disfiguring diseases ($n=14$) instead supports
384 the well-documented principle of ‘bad death’^{88–92} influencing who was selected to be elaborately
385 buried. Regardless of the exact reasons determining who was buried in the Gravettian, it appears that
386 not everyone was elaborately buried, which may have contributed to the observed differences
387 between burial and occupation sites’ bead associations.

388 The analysis of Gravettian grave goods conducted by d’Errico and Vanhaeren³³ identified marginally
389 different groups to those in this study. This minor difference resulted from their inclusion of burials
390 formally attributed to the Gravettian (*i.e.*, Sunghir, Russia^{93,94}), our inclusion of newly discovered
391 burials (*i.e.*, Borsuka Cave, Poland⁸⁷) and our exclusion of grave goods which were not personal
392 ornaments (*e.g.*, awls and mammoth scapulae). The very similar results underpin the robustness of the
393 geographic clusters in personal ornament associations in Gravettian burial practices.

394 The recent paleogenomic study conducted by Posth et al.⁹ has highlighted the importance of
395 population dynamics, largely influenced by climate change, on the genetic history of the Upper

396 Palaeolithic European human population. The periodic abandonment and subsequent recolonization
397 of different regions of Europe, already predicted by other authors^{78,95–97} contradict the hypothesis that
398 the genetic variability of Upper Palaeolithic populations reflect a gradual process of homogenisation
399 determined by IBD following a first colonisation by a modern human population. The population
400 dynamics revealed by Posth and colleagues do not necessarily entail, however, a one-to-one
401 correspondence between genetic and cultural traits. Cultural drift and cultural contact implicit in some
402 identified population events, which possibly led to cultural assimilation, acculturation or hybridization,
403 may have created a discordance between genetic and cultural heritage.

404 Posth *et al.*⁹ argue for a correspondence between genetic ancestry and mortuary practices in the
405 Gravettian by comparing genetic data and available data on the treatment of dead (*e.g.*, cannibalism,
406 interment location, presence of ochre etc.). However, their paleogenomic analyses only concerned a
407 small number of individuals of this period and left the vast majority of the European territory
408 genetically unexplored. Their analysis of cultural traits associated with burials did not investigate
409 personal ornaments as a source of information. While in broad agreement with theirs, our results
410 appear to reconstruct the geography of Gravettian cultural entities at a finer scale (Fig. 8). Personal
411 ornaments associated with burials identify two cultural entities in the Italian Peninsula where their
412 genomic and cultural data envision a single entity. Ornaments found at occupation sites, on the other
413 hand, identify two cultural entities in the Iberian Peninsula, an area for which only a single individual
414 with genomic data is available and identify a region covering present day France and Belgium as a
415 single cultural entity, in which human remains genetically attributed to different ancestries are located.
416 Our dataset also distinguishes an easternmost European cultural entity, in a vast region for which
417 genomic data are not yet available, from a Central European entity associated with a Věstonice
418 ancestry.

419

420

Figure 8

421

422 Future analyses in the field of paleogenomics will have to establish the extent to which the finer
423 cultural geography established from the ornamental objects is matched by the genetic data. Should
424 this correspondence show significant inconsistencies, it will be crucial to document when and where
425 these occurred and what factors have determined divergences. Contrasting the two types of data,
426 rather than simply equating human history to its genetic dimension, is essential to obtain an integrated
427 view of the history of human society and culture.

428

429 Conclusion

430 Human history is complex and multifaceted, extending well beyond the simple interaction of genes
431 and ecology. We have demonstrated here, through the multivariate analysis of Gravettian personal
432 ornaments and simulations modelling the impact of distance on cultural traits, that the sense of
433 belonging felt by all humans today is deeply rooted in our shared history and played an important role
434 in determining how Gravettian people adorned themselves. On a larger scale, our study identified nine
435 distinct geographic sub-groups in the Gravettian who wore different personal ornaments in both life
436 and death. The results obtained for occupation and burial sites demonstrate that it is paramount that
437 site function is taken into account in future research. Comparison of our results with those of genomic
438 studies has shown that symbolic material culture can reveal patterns not detectable by
439 palaeogenomics. Integrating personal ornament and biological data from other Paleolithic cultures will
440 therefore help to elucidate the complex narrative of the earliest humans in Europe.

441

442 Materials and Methods

443 Our datasets include the site name, country, geographical coordinates of the site, associated
444 radiocarbon ages, and personal ornaments found within each layer ([Supplementary Table 3](#),
445 [Supplementary Table 4](#)). For occupation sites, we also recorded archaeological information pertaining
446 to the Gravettian phase to which a site or a layer are attributed. At sites featuring both occupation
447 layers and burials, the attribution of personal ornaments to the latter was based on contextual
448 information provided in the literature. In the case of multiple burials, ornaments from each individual
449 were recorded separately. The information regarding the personal ornament types which were present
450 at a given site was obtained through a systematic literature search. The radiocarbon ages were
451 converted into calibrated ages using OxCal 4.4⁹⁸, which applies the IntCal20 Northern Hemisphere
452 radiocarbon age calibration curve⁹⁹. The above resulted in the creation of two distinct datasets, one
453 for occupation sites and the other for burial sites.

454 We created mutually exclusive bead-types ([Supplementary Table 1](#)) taking into account cross-cultural
455 studies on the classification of beads^{100–103} and on criteria used to classify archaeological artefacts^{103–}
456 ¹⁰⁵. Ornaments types were categorised by raw material and then by mode of suspension (*i.e.*, groove,
457 perforation). For shell ornaments, the genus and species were considered. If multiple species of a
458 genus were indistinguishable to the naked eye, only the genus was recorded. Shell species taxonomy
459 has undergone significant development since the earliest papers detailing Palaeolithic ornaments were
460 published^{102,106,107}. As such, care was taken to verify that species in older literature were updated to
461 modern nomenclature. To prevent attribution to multiple taxa when referring to the same shell

462 species, we used WoRMS, the World Register of Marine Species (<https://www.marinespecies.org>), to
463 characterise the species.

464 For animal teeth, the genus, species and anatomical attribution were taken into account. For fully or
465 partially shaped ornaments made of other raw material (bone, ivory, stone etc.), the type of raw
466 material and morphology of the ornaments were considered to create mutually exclusive types. Few
467 perforated bones, described as ornaments, bear features typical of bone fragments regurgitated by
468 carnivores¹⁰⁸. These were not included in the dataset.

469

470 **Statistical analyses**

471 Seriation analysis sorts individuals based on their shared attributes¹⁰⁹. Application of this method with
472 PAST software¹¹⁰ to personal ornament presence/absence data from burial and occupation sites
473 enabled the identification of sets, defined as associations of at least three geographically proximate
474 sites sharing a minimum of one bead type²⁰. For both datasets we calculated the criterion score, the
475 index that describes the level of concentration of individuals along the diagonal of the seriation. A
476 score of 1 denotes a maximum and a score of 0 a minimum concentration. In order to assess the
477 significance of the groups identified by the seriations, we performed two complimentary analyses, a
478 Modularity¹¹¹ test and a Permutational Multivariate Analysis of Variance (perMANOVA)^{112,113}.
479 ([Supplementary Results, 'Modularity test and permutational MANOVA'](#)).

480 We also performed a seriation on the ornament types from burial sites attributed to the identified
481 sets, in which we highlighted their belonging to different Gravettian phases, Early (34-30 ka cal. BP),
482 Middle (31-29 ka cal. BP) and Late Gravettian (29-24 ka cal. BP), using available radiocarbon ages. A
483 similar seriation was performed on occupation sites attributable to one of the phases of the Gravettian
484 based on radiocarbon ages and chronocultural attribution.

485 We quantified personal ornament dissimilarity between sites by creating a distance matrix using a
486 Jaccard distance index¹¹⁴⁻¹¹⁶ ([Supplementary Table 5](#)). This index is particularly well adapted to
487 archaeological enquiry as it does not give weight to absence data, possibly due in archaeology to field
488 investigation biases^{38,117}. When constructing the distance matrices, we did not include sites which
489 shared no personal ornaments types with other sites¹¹⁸. Personal ornament distance matrices of burial
490 and occupation sites were processed with a Principal Coordinates Analysis (PCoA), which was
491 performed in PAST software. A PCoA was preferentially chosen amongst other ordination techniques
492 because it uses binary data¹¹⁹. In order to investigate the branching and clustering between sites, we

493 entered the distance matrices into a Neighbour-joining tree analysis¹²⁰. This was performed using 1000
494 bootstrap replications with Knossos (Crete, Greece), a Neolithic site, as an outgroup to root the tree¹²¹.
495 These techniques, originally conceived to identify phylogenies with biological data, are also applicable
496 to the diversity of material culture items found at archaeological sites^{2,122–124}. However, an effective
497 application of these techniques to this domain is somewhat hampered by the fact that cultural
498 evolution involves horizontal transmission of cultural traits^{125,126}. The Neighbour-Net technique^{120,127}
499 largely overcomes this problem by exploring horizontal transfers of traits which are not visible in other
500 network-based methods and thus directly takes the horizontal transmission of cultural traits into
501 account¹²⁸. The shape and amount of reticulation shown within the resultant network reflect the
502 degree of horizontal transfer between sites. We performed the Neighbour-net joining method in
503 SplitsTree6 software using default settings¹²⁹ on both occupation and burial cultural distance matrices.
504 SplitsTree6 also provides the Delta score and Q-residuals for each network. These statistics both
505 calculate and describe the amount of reticulation within a network and how ‘tree-like’ the network
506 is^{125,130}.

507 Incorporating geographic distances between sites into these analyses is essential to fully appreciate
508 whether geography determines and, if so, to what extent, differences in ornament type
509 associations^{18,38}. In evolutionary biology, IBD model predicts the presence of a positive correlation
510 between geographical and genetic distances within a meta-population^{38,40,131}. In order to evaluate the
511 role of geography we use a Mantel test¹³² which quantifies the degree of correlation between the
512 Euclidean geographic distance between sites and Jaccard distance matrices based on the cultural data.
513 We carried out this test for both the burial and occupation sites. The burial dataset was also divided
514 into two subsets: one dataset which contained burials located in Eastern Europe and one dataset which
515 contained burials located in Western Europe (North and South Italy). A Mantel test was performed on
516 each subset. Unlike the other analyses (*i.e.*, PCoA, Neighbour-joining, Neighbour-Net), we included all
517 sites when constructing these distance matrices because the interpretation of the Mantel test does
518 not rely on the sets identified by the seriation analyses. In the case of multiple burials, the personal
519 ornaments found on each skeleton were condensed into a single site in order to avoid too many
520 pairwise comparisons at the same geographic location. In order to assess the degree of spatial
521 autocorrelation (*i.e.*, higher than average similarity between sites for a given geographic distance) we
522 additionally conducted a Mantel correlogram^{133,134} for both of the datasets. A positive significant value
523 for each geographic distance class indicates that sites at a given geographic distance from one another
524 are more similar than expected by the Mantel test (*i.e.*, they spatially autocorrelate)¹³⁵. Since patterns
525 observable at one scale can be lost at another, it is recommended that any Mantel correlogram analysis
526 be carried out at multiple scales¹³⁶. We therefore generated a Mantel correlogram for each dataset

527 using three geographic distance scales. Simply put, whereas a Mantel test investigates the overall
528 relationship between two distance matrices, a Mantel correlogram probes deeper into the internal
529 structure of this relationship.

530 We modeled the effects of spatial segregation and cultural barriers with different degree of
531 permeability on the Mantel test Z value (R^2) score. We created and analysed five simulated datasets
532 including three synthetic Gravettian cultural groups and different bead-type associations across
533 mainland Europe ([Supplementary Result, 'Modelling the effect of spatial and cultural boundaries'](#)).
534 Simulating random coordinate values was facilitated by the spatstat (v.3.0) library¹³⁷. Jaccard
535 dissimilarity values were calculated for each simulation from the matrices of cultural attributes. The
536 great circle distance was used to calculate the geographic distance between sites. Mantel tests were
537 conducted on each of the simulated datasets so as to assess the relationship between these characters.
538 All simulations (Random spatial and cultural attributes, Slight spatial overlap and partially shared
539 cultural attributes, Marked spatial and cultural boundaries, Different cultural attributes, Random
540 spatial distribution, Random cultural attributes, Marked spatial boundaries) were performed using the
541 base R (v.4.3.0) programming language.

542 To investigate the impact of time on variations in personal ornament associations, we employed two
543 different strategies, one for the occupation and one for the burial dataset due to the different nature
544 of the information on the sites chronology.

545 For the occupation dataset we performed a perMANOVA on the sites attributable to one of the
546 Gravettian phases (Early, Middle, Late) ([Supplementary Results, 'Modularity test and permutational
547 MANOVA'](#)).

548 Our radiocarbon ages dataset for Gravettian burials was used to create a chronological distance matrix
549 calculated with the Euclidian distances. We computed a Partial Mantel test¹³⁸ that enabled the partial
550 correlation between two matrices while holding for the effect of the third¹³⁹. The midpoints of these
551 ranges were then calibrated using the IntCal20 Calibration Curve⁹⁹ with a 1-sigma error of 150 years to
552 ensure that all dates were comparable. For the few burial sites with no associated direct or indirect
553 radiocarbon age (N=3), we used the generally accepted age range provided in the literature.

554 For every statistical test used, the data met all of the various assumptions.

555

556 **Data availability**

557 The data used for the statistical tests can be found in the Supplementary tables.

558 **Code availability**

559 Code used is available upon request from the corresponding author and is detailed in the
560 Supplementary Information.

561

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573

574 **Author Contributions**

575 JB, SR and FD wrote the paper. JB, SR, DP, LAC and FD conceived and designed the experiments. JB, DP,
576 LAC performed the experiments. JB, SR, DP, LAC and FD analysed the data.

577

578 **Competing interests**

579 The authors declare no competing interests.

580

581 **Figure Legends**

582

583 **Figure 1** – Material used for Gravettian personal ornaments. a) Types of teeth used as ornaments identified at
584 occupation and burial sites attributed to the Gravettian. 1, Bear canine; 2, Bear incisor; 3, Bovid incisor
585 (archaeological, adapted from Baker et al. 2022¹⁴⁰); 4, European elk canine (Collection PACEA); 5, Felis canine; 6,
586 Fox canine; 7, Fox incisor; 8, Hare tooth (incisor) (Collection PACEA), 9, Herbivore incisor; 10, Horse incisor; 11,
587 Human tooth (canine); 12, Hyena canine; 13, Lynx canine; 14, Red Deer vestigial canine; 15, Red Deer incisor; 16,
588 Sparus auratus tooth (archaeological, adapted from Zilhão et al. 2021¹⁴¹); 17, Steppe bison canine (Collection
589 PACEA); 18, Steppe bison incisor (Collection PACEA); 19, Wolf canine; 20, Wolf incisor. Scale bar = 2 cm. (modified

590 after Vanhaeren and d'Errico 2006²⁰), b) Shaped ornaments and modified bones identified at occupation and
591 burial sites attributed to the Gravettian. 1, Amber Pendant; 2, Anthropomorphic bone bead; 3, Asymmetric ivory
592 pendant; 4, Bear phalange; 5, Bilobated ivory bead; 6, Ellipsoidal ivory pendant; 7, Elongated ivory pendant; 8,
593 Fishtail ivory pendant; 9, Fish Vertebrae; 10, Herbivore diaphysis fragment; 11, Ivory bracelet; 12, Ivory breast
594 bead; 13, Ivory cylindrical bead; 14, Ivory diadem; 15, Ivory pin; 16, Notched herbivore diaphysis; 17, Owl-shaped
595 ivory beads; 18, Rectangular ivory pendant; 19, Red deer femur head; 20, Stone pendant; 21, Stone Ring; 22,
596 Symmetric ivory pendant; 23, Tubular bone bead. Scale bar = 1 cm.

597

598 **Figure 2** - Seriation analysis of the bead database for Gravettian occupation sites. Squares indicate the occurrence
599 of ornament types at sites.

600

601 **Figure 3** - Seriation analysis of the bead database of Gravettian occupation sites attributable to Gravettian phases
602 (Early, Middle and Late). Squares indicate the occurrence of ornament types at sites. Shaded background colours
603 represent geographical sets identified in Figure 2.

604

605 **Figure 4** - Principal Coordinate Analysis (a) and Neighbour-Joining analysis (b) of the bead-type associations
606 recorded at Gravettian occupation sites.

607

608 **Figure 5** – a) Seriation analysis of the bead database of Gravettian burial sites. Squares are indicative of
609 occurrences of ornament type at burial sites, ages are from calibrated radiocarbon dates. b) Seriation analysis of
610 the bead-type database of Gravettian burials performed under time constraint. Squares indicate occurrence of
611 ornament types at sites. Shaded background colours represent geographical sets identified in Figure 5a.

612

613 **Figure 6** - Principal Coordinate Analysis (a) and Neighbour-Joining analysis (b) of the bead-type associations
614 recorded at Gravettian burial sites.

615

616 **Figure 7** - a) Neighbour-Net analysis performed on the bead database for Gravettian occupation sites (Delta score
617 = 0.2, Q-residual = 0.00469). b) Neighbour-Net analysis performed on the bead database for Gravettian burial
618 sites (Delta score = 0.2387, Q-residual = 0.0166). Thick black lines separate distinct clusters.

619

620 **Figure 8** - Map of Europe showing the location of human remains attributed to the Gravettian analysed by Posth
621 et al.⁹. S1 = Dolní Vestonice (13, 14, 15, 16), S2 = Krems-Wachtberg (individual 3), S3 = Ostuni 1, S4 = Paglicci 12,
622 S5 = Pavlov 1, S6 = Goyet (2878-15, 2878-18, Q-1, Q100-8, Q376-19, Q53-1, Q56-16), S7 = Fournol 85, S8 = La
623 Rochette, S9 = Mollet III (GER-33), S10 = Reclau Viver (GER-8). Map created on QGIS¹⁴² using ETOPO1 Global Relief
624 Model¹⁴³ data with a modern and Gravettian coastline at -100 m¹⁴⁴.

625

627

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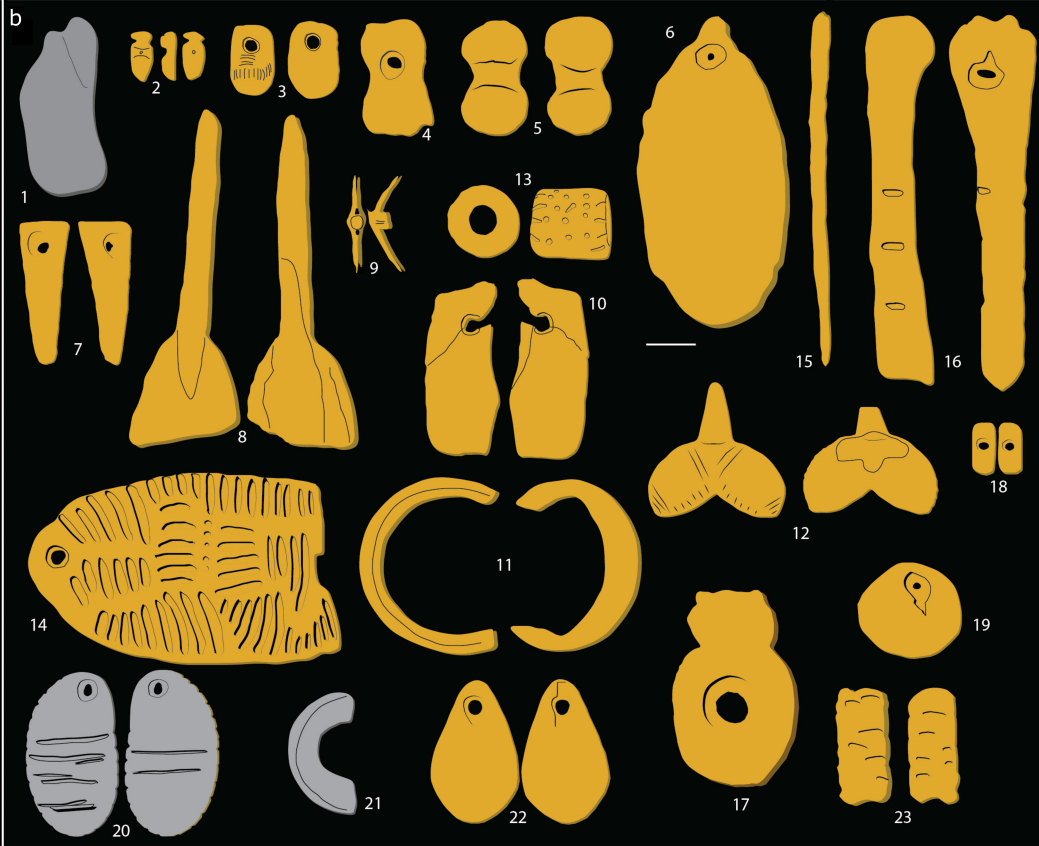
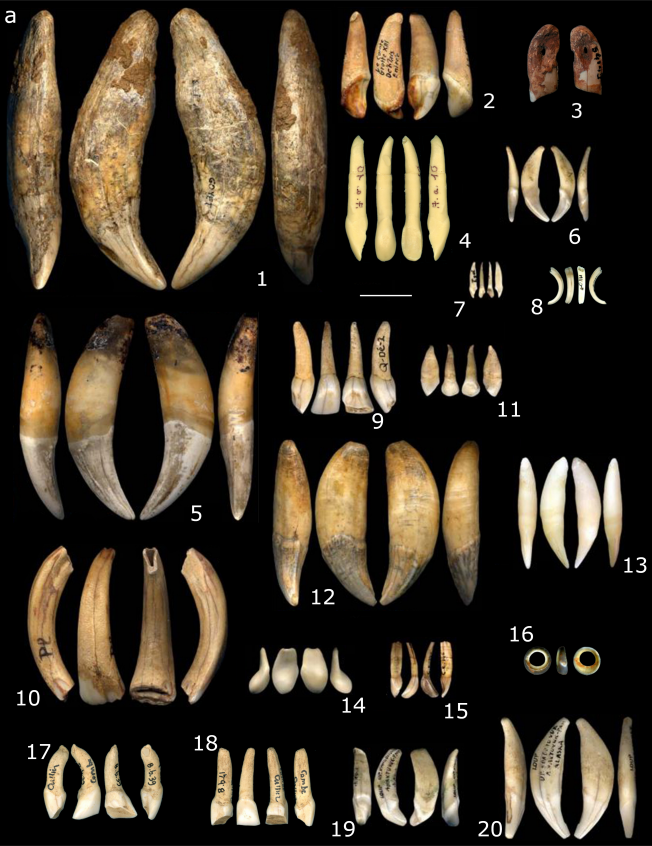
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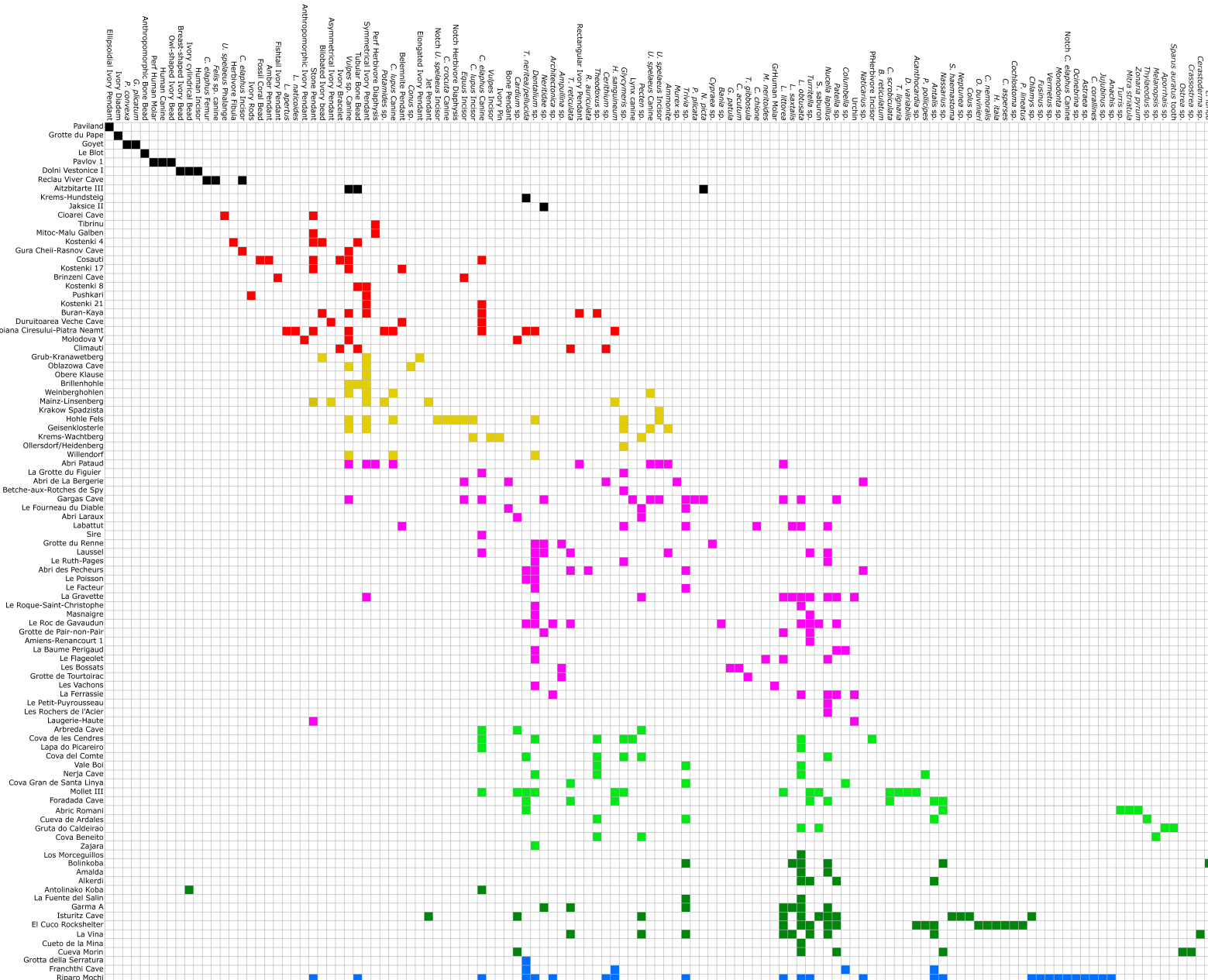
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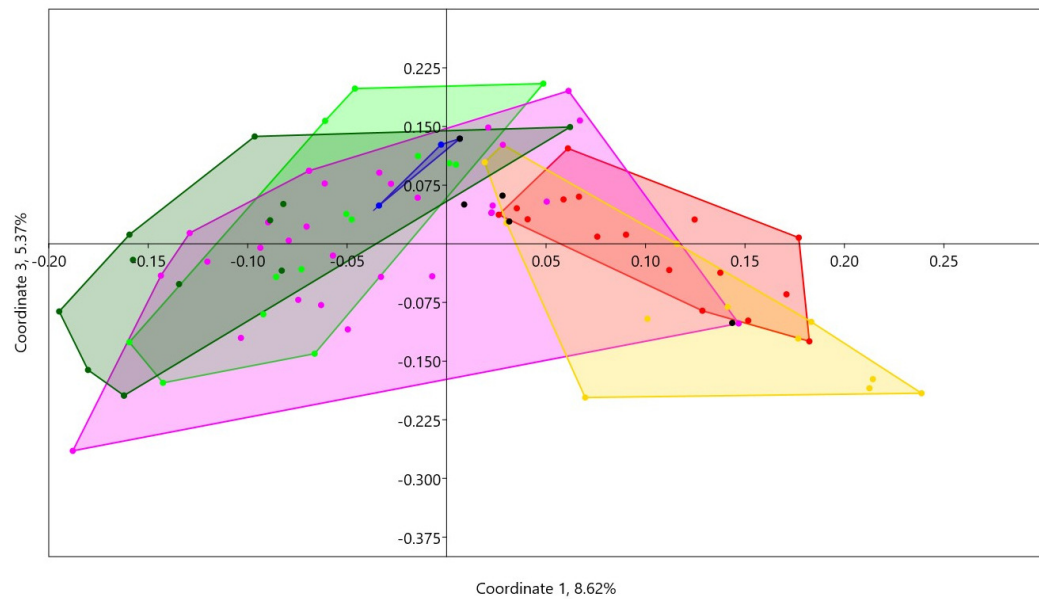
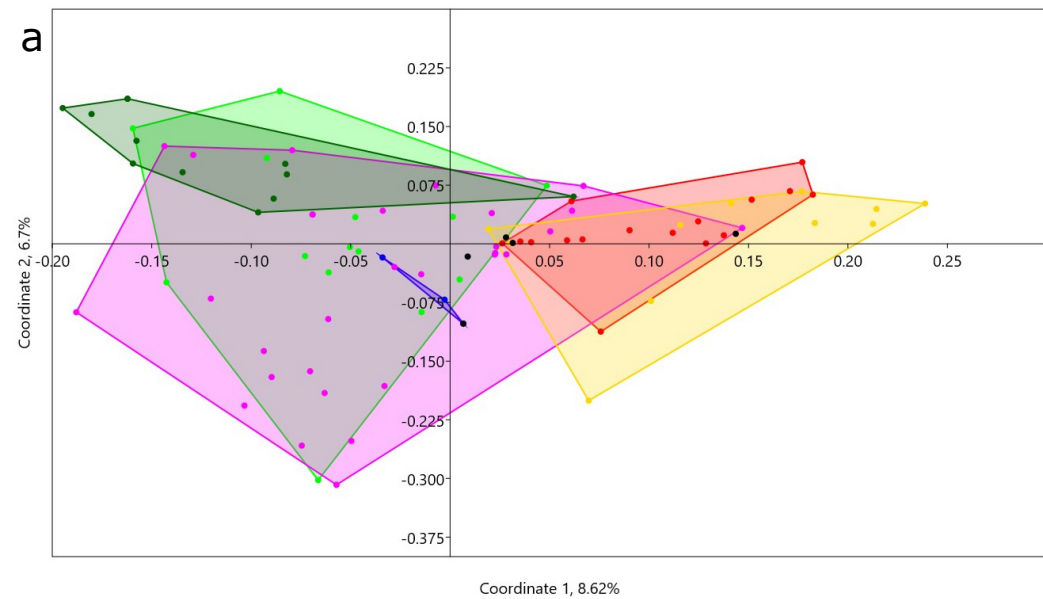
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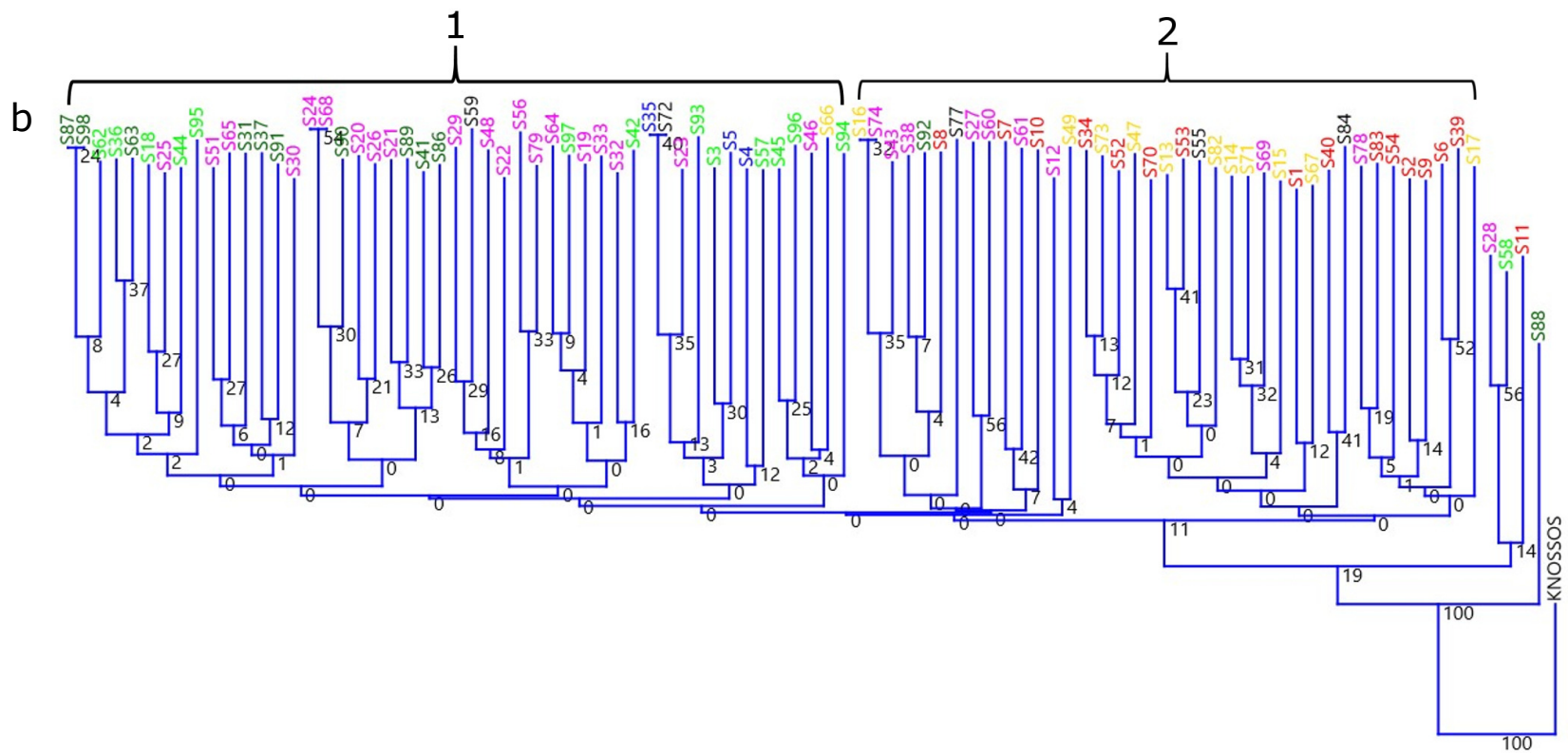


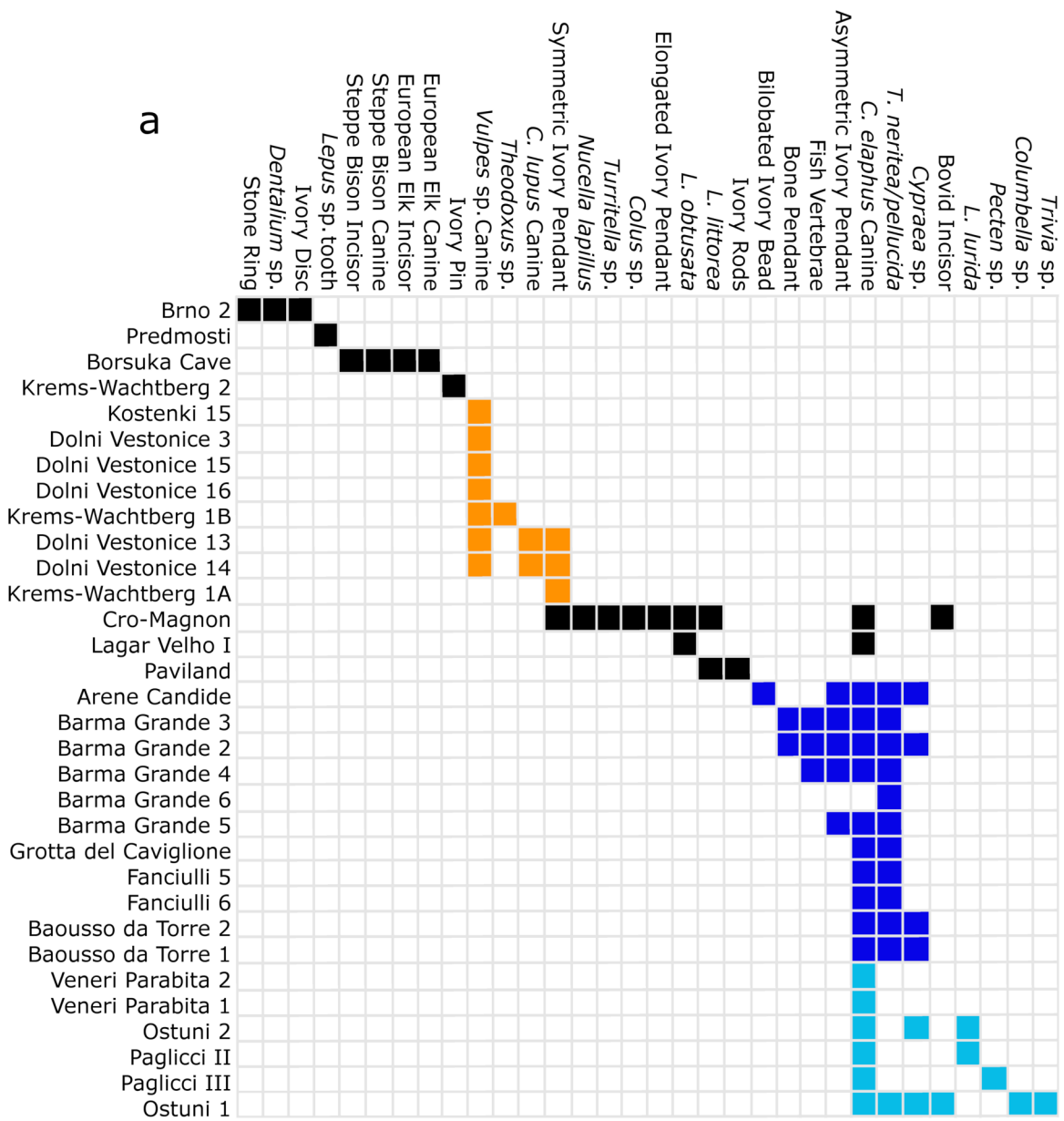
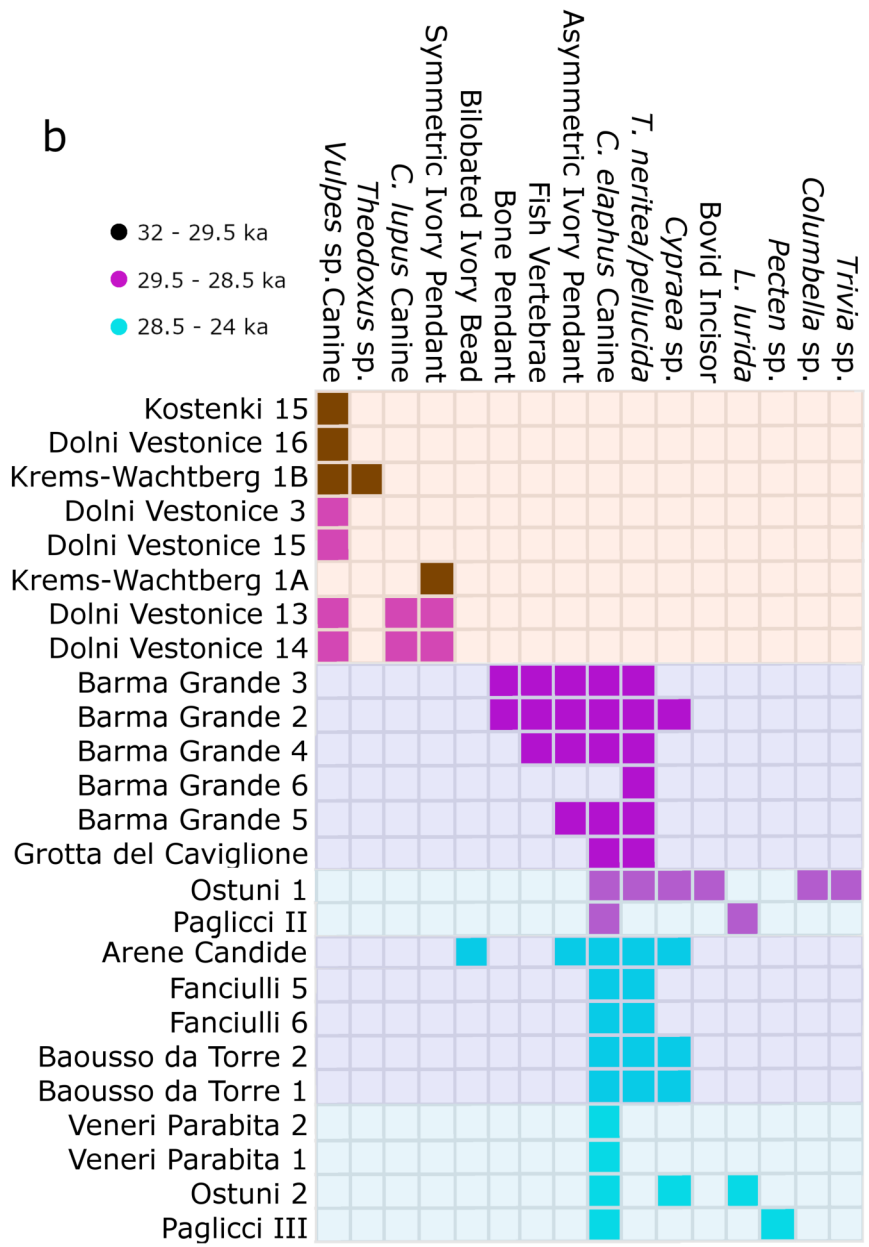


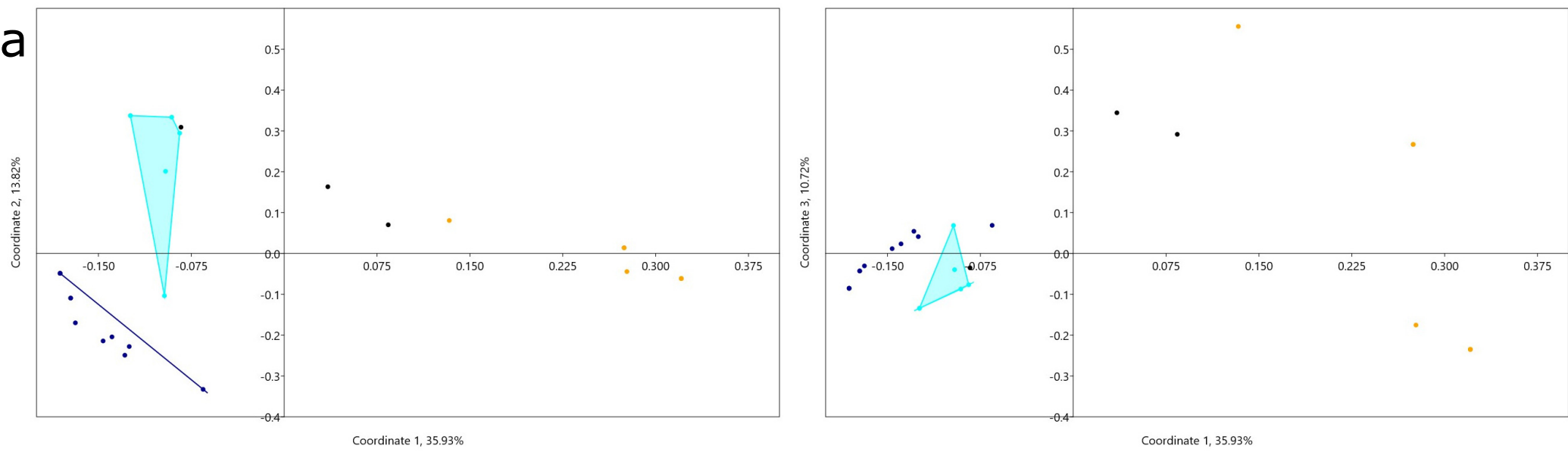




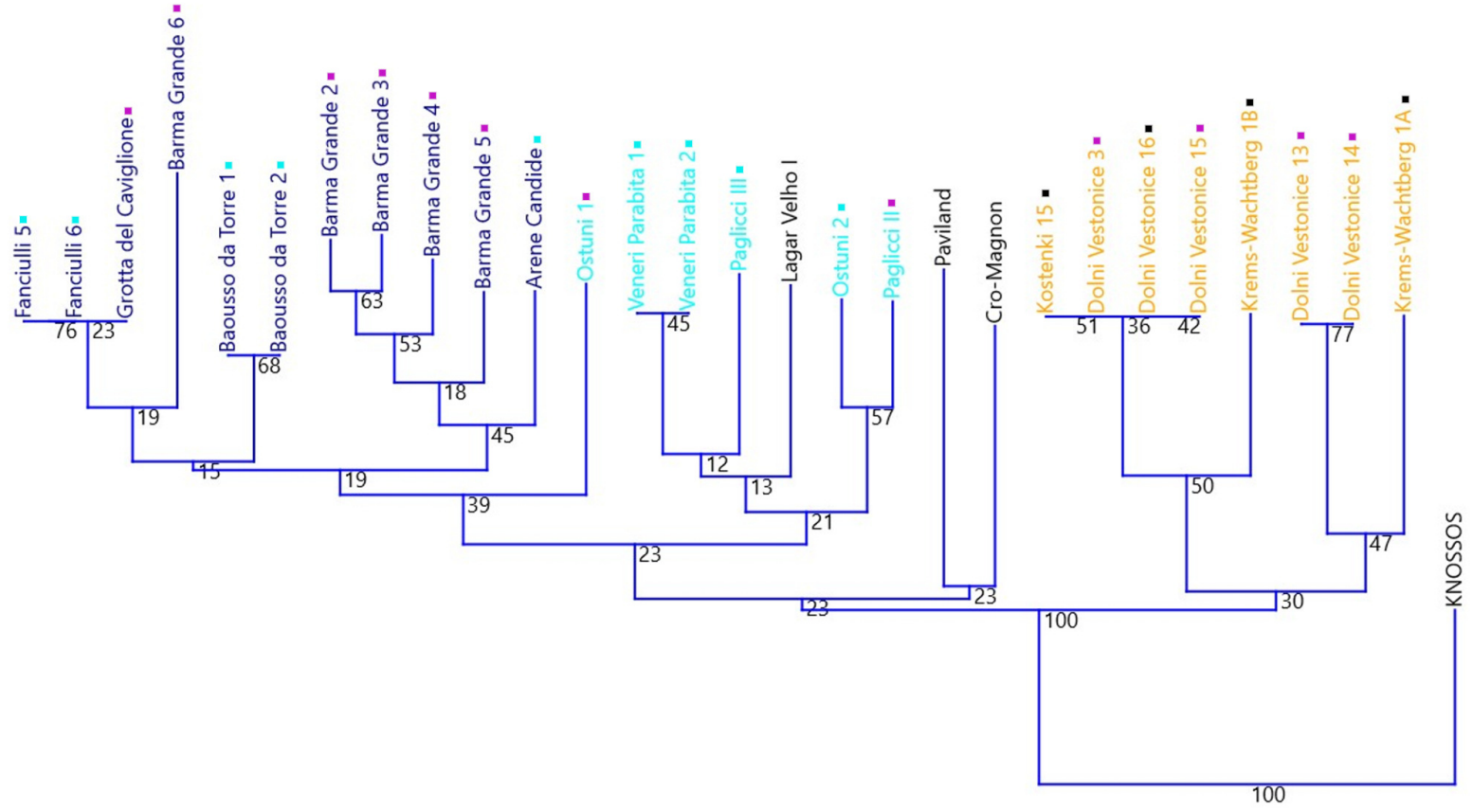
- Eastern Europe (N=16)
- Central Europe (N=12)
- Northwestern Europe (N=30)
- North Iberia (N=12)
- South Iberia (N=14)
- Mediterranean (N=3)
- Not in set (N=5)

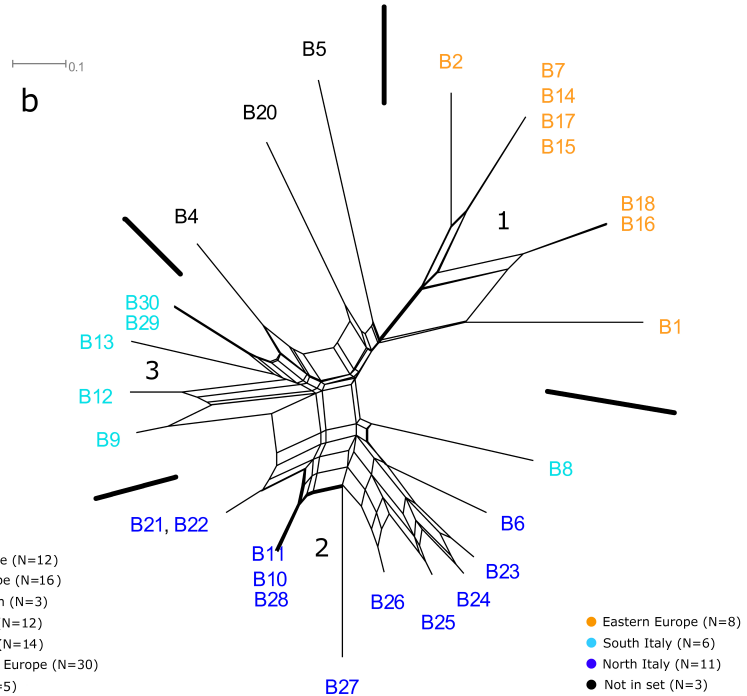
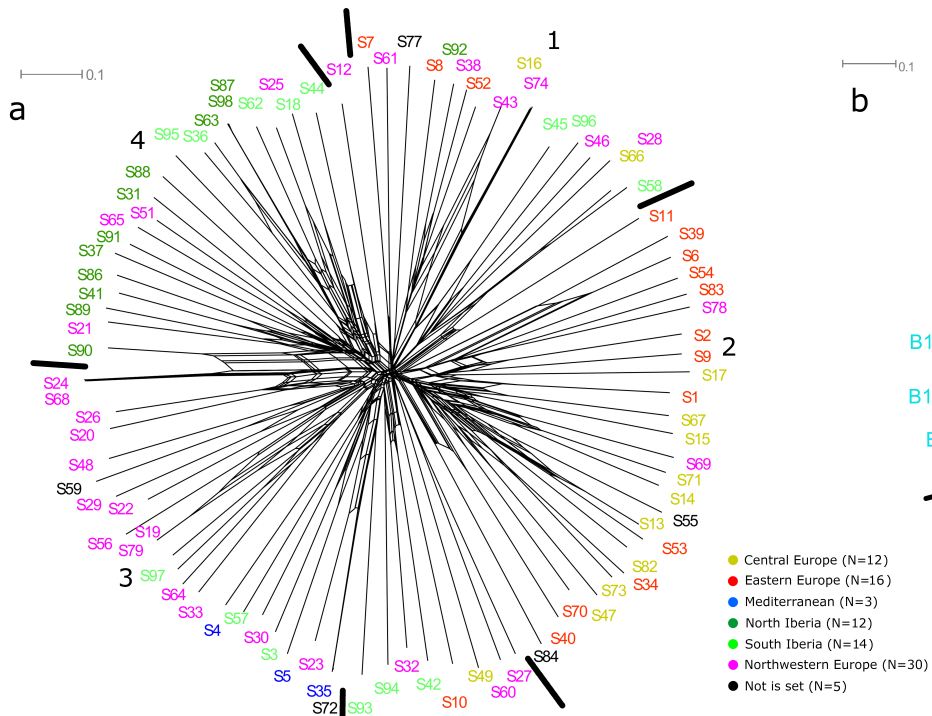


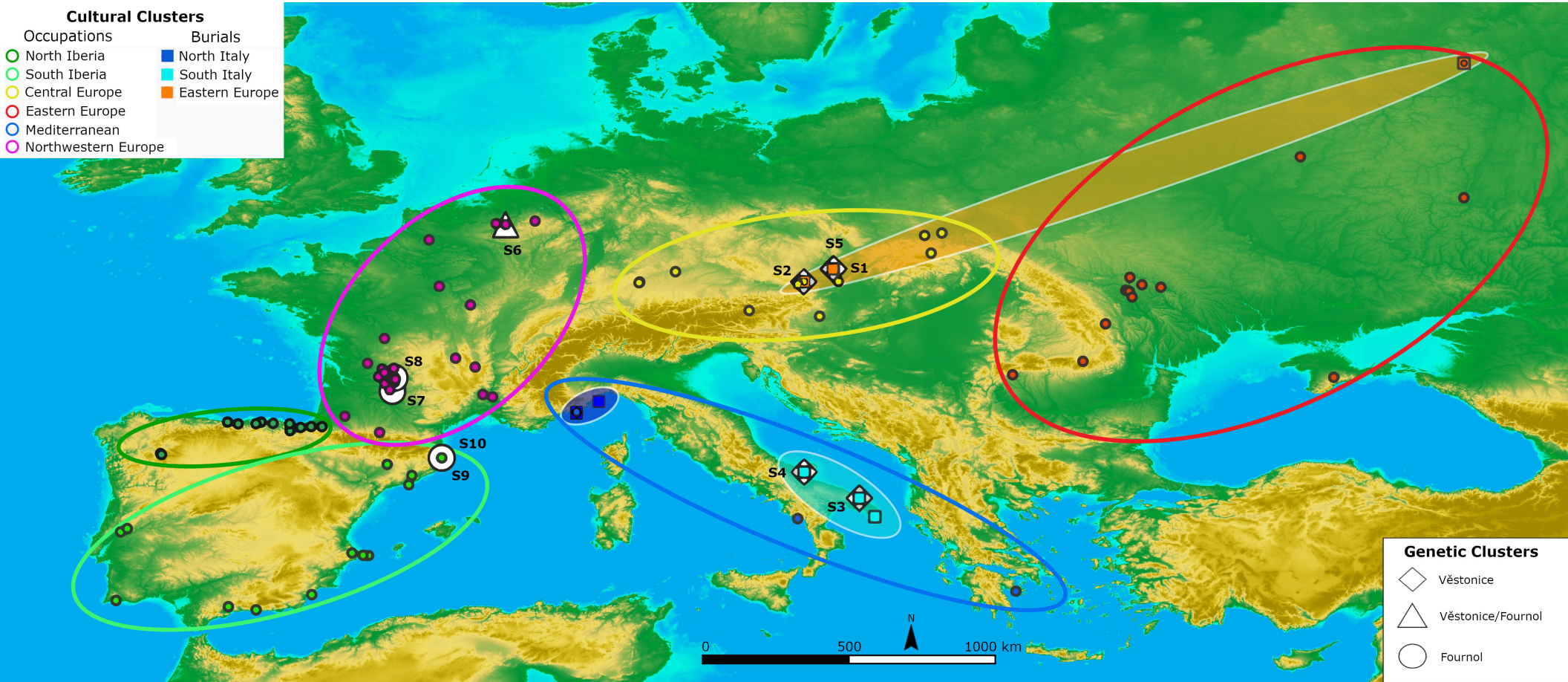


a

- North Italy (N=11)
 - South Italy (N=6)
 - East Europe (N=8)
 - Not in set (N=3)
-
- 32 - 29.5 ka
 - 29.5 - 28.5 ka
 - 28.5 - 24 ka

b





Cultural Clusters

Occupations

- North Iberia
- South Iberia
- Central Europe
- Eastern Europe
- Mediterranean
- Northwestern Europe

Burials

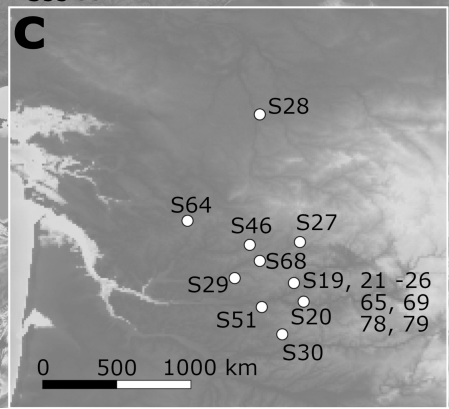
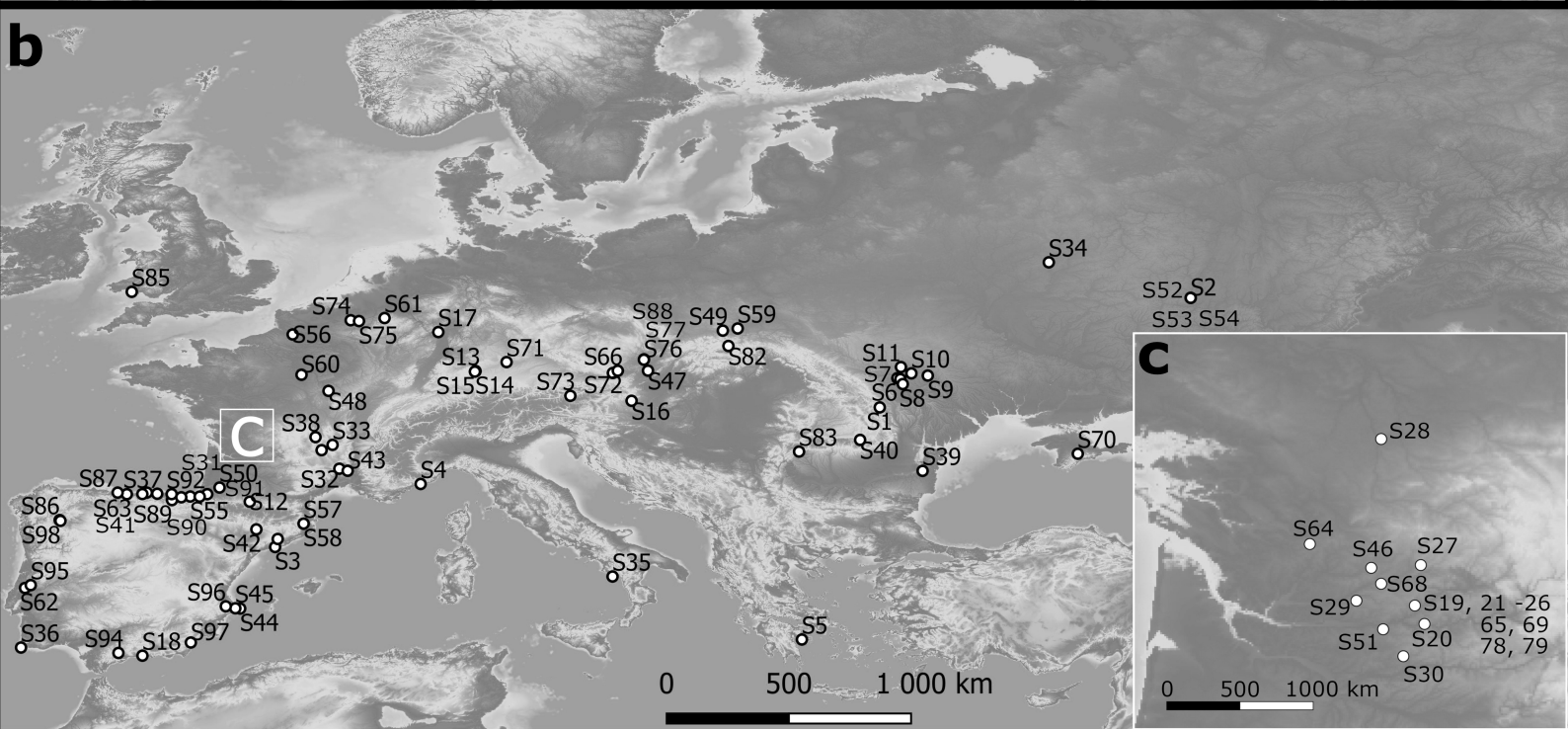
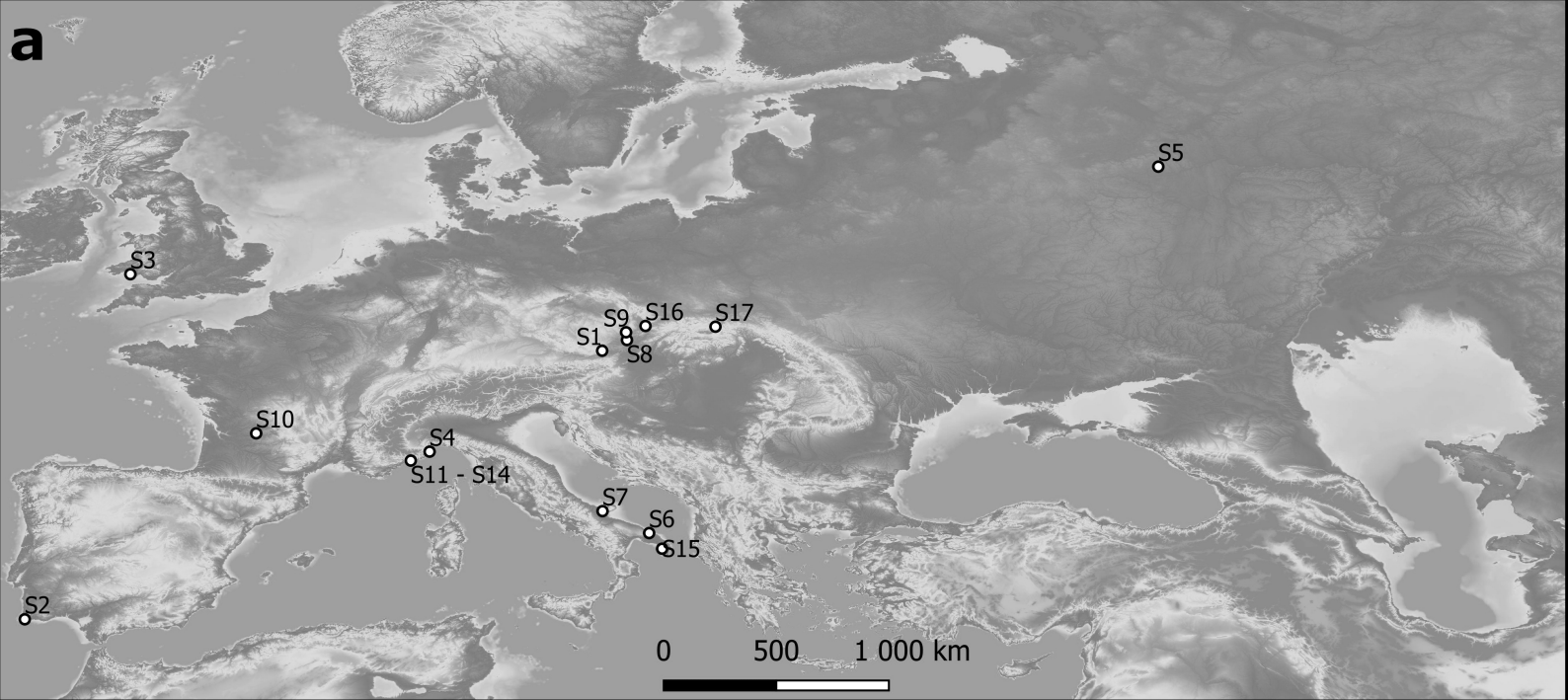
- North Italy
- South Italy
- Eastern Europe

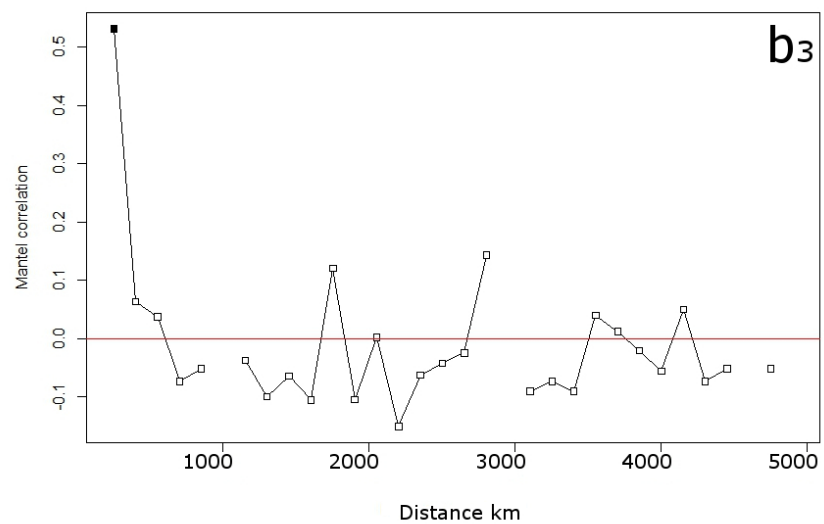
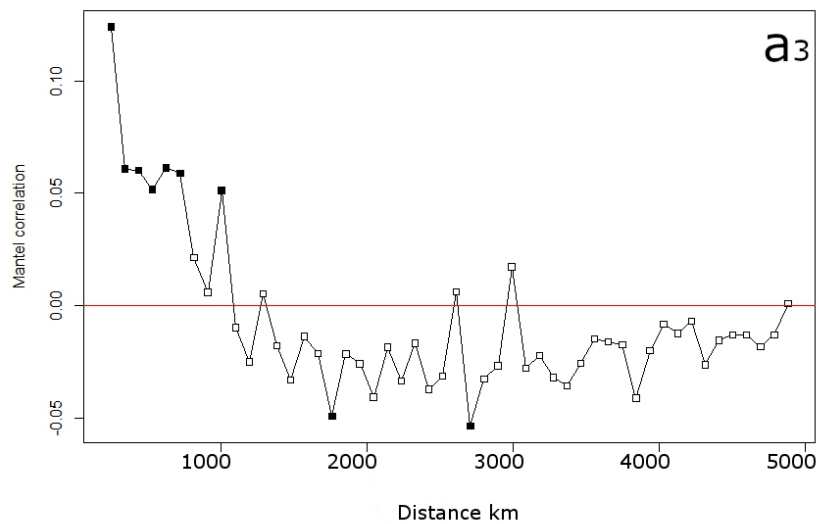
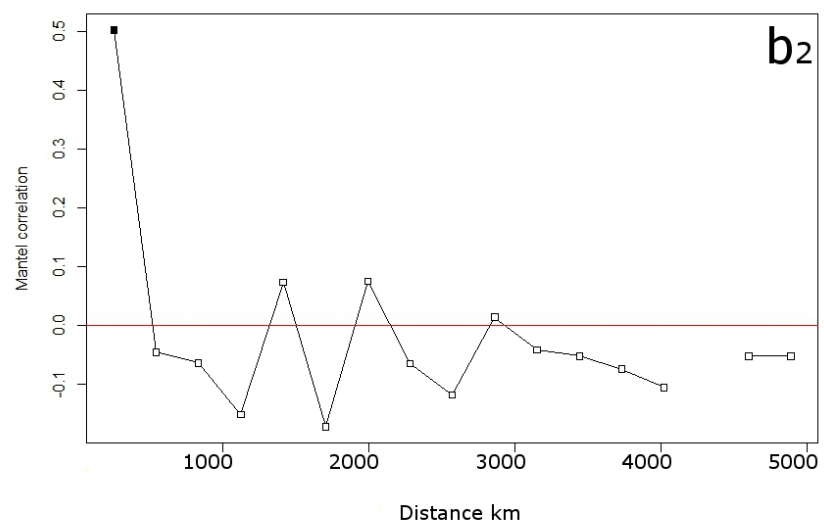
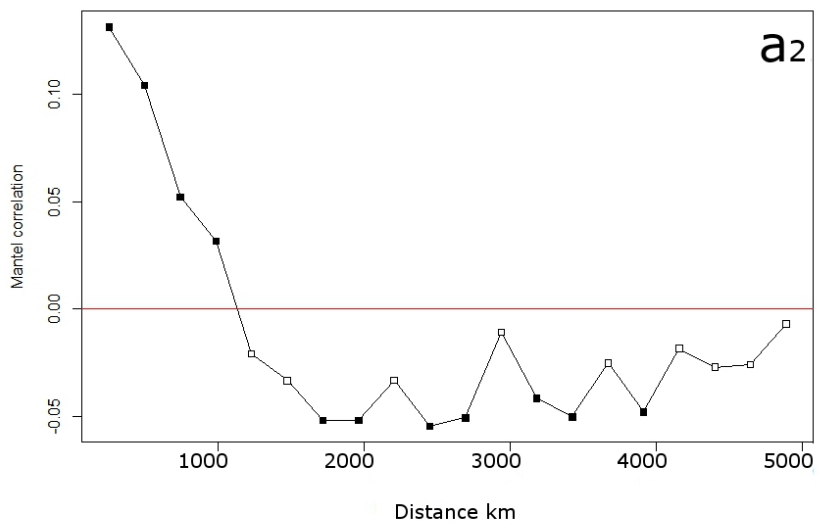
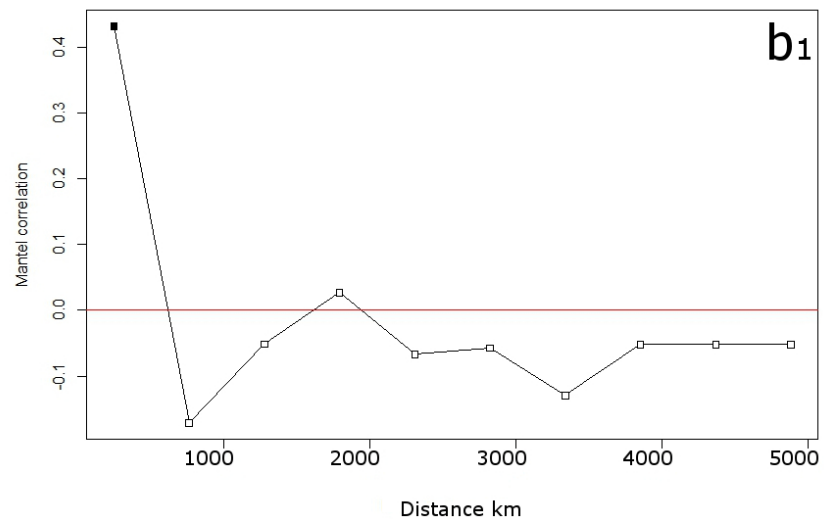
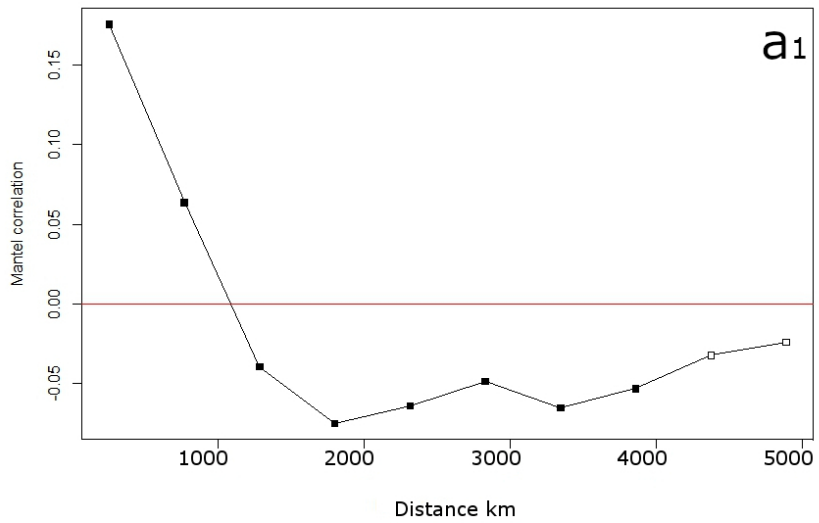
Genetic Clusters

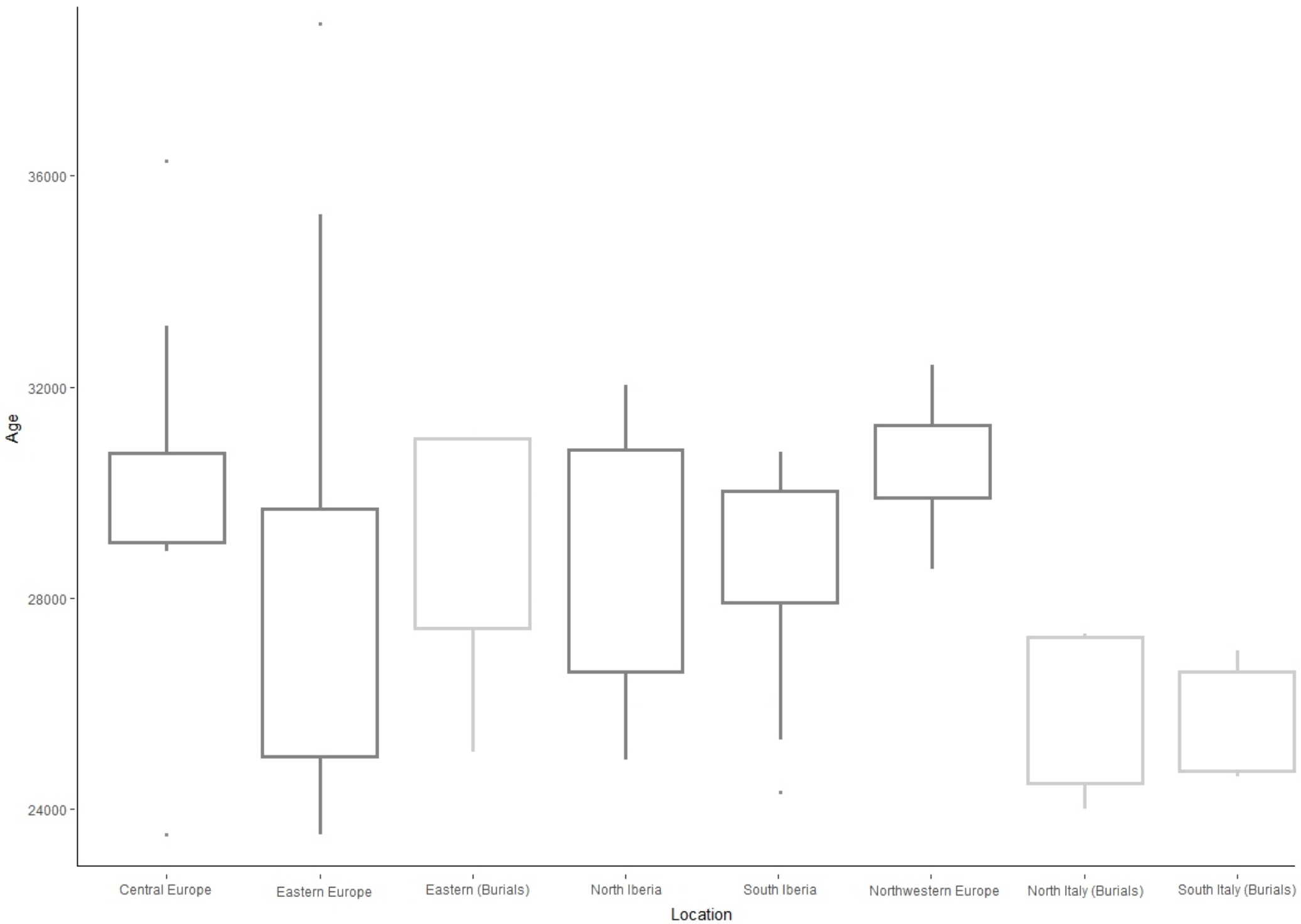
- ◊ Věstonice
- △ Věstonice/Fournol
- Fournol

0 500 1000 km

N







Dataset	Z value (R^2)	P-value
Occupation	0.1941563	< 0.001
Burial	0.3257094	0.0093

Dataset	Z value (R^2)	P-value
Burial vs Geography (Holding time)	0.2572	0.0398
Burial vs Time (Holding geography)	0.3288	0.0052

Dataset	Z value (R^2)	P-value
Western burial	0.4559727	0.0266
Eastern burial	0.855131	0.16667