

## 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:

The study of personal ornaments worn by Ice Age European hunter gatherers between 34,000 and 24,000 years ago identifies nine regional
 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.

## Inventory of Supporting Information

## 78 1. Extended Data

9

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	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, Baousso 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

			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, Ciaoarei 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 Laraux; S29, Grotte de Pair- non-Pair; S30, Le Roc de Gavaudun; S46, Le Fourneau du Diable; S51, La Gravette; S64, Les Vachons; S65, La Ferrassie; S68, Le Petit-Puyrousseau; 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 m <sup>142</sup> .
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	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.
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	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" = $N=8$ ,

	different regions of		"South Iberia" = N=8, "Northwestern Europe" = N=4, "North Iberia" = N=8,
	Europe.		"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-	Extended Data Table	Results of the two-tailed Mantel tests calculated for the bead-type
	tailed Mantel tests	1 ing	associations recorded at Gravettian occupations and hurial sites
	calculated for the	-168	
	bead-type associations		
	recorded at Gravettian		
	occupations and burial		
	sites.		
Extended Data Table. 2	Results of the two-	Extended Data Table	Results of the two-tailed Partial Mantel tests calculated for the bead-
	tailed Partial Mantel	2.jpg	type associations recorded at Gravettian burial sites.
	tests calculated for the		
	bead-type associations		
	recorded at Gravettian		
	burial sites.		
Extended Data Table. 3	Results of the two-	Extended Data Table	Results of the two-tailed Mantel tests calculated for the bead-type
	tailed Mantel tests	3.jpg	associations recorded at Gravettian burial sites in Western and Eastern
	calculated for the		Europe.
	bead-type associations		
	recorded at Gravettian		
	burial sites in Western		
	and Eastern Europe.		

## **1. Supplementary Information:**

A. PDF Files

Item Present? Filename A brief, numerical description of file contents.	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		

## 15 B. Additional Supplementary Files

	Number	Filename	Legend or Descriptive Caption
Туре			
			Bead coding. An excel
			spreadsheet containing each of
			the discrete bead types and the
Supplementary Table	1	Bead Coding SUPP TAB 1_2 <sup>nd</sup> .xlsx	code used for each.
			All datasets. An excel spreadsheet
Supplementary Table	2	All datasets SUPP TAB 2_2nd.xlsx	containing 7 separate worksheets.
			Occupation Table. An excel
			spreadsheet which contains the
			attributes and personal
		Occupation Table SUPP TAB	ornaments of the occupation
Supplementary Table	3	3_2nd.xlsx	sites.
			Burial Table. An excel spreadsheet
			which contains the attributes and
		Burial Table SUPP TAB	personal ornaments of the buried
Supplementary Table	4	4_2nd_SR.xlsx	individuals.
			All distance matrices. An excel
		All distance matrices SUPP TAB	spreadsheet containing 14
Supplementary Table	5	5_2nd.xlsx	separate worksheets.
		Modelling datasets SUPP TAB	All datasets used for the Mantel
Supplementary Table	6	6.xlsx	test modelling. An excel

	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 debate, data analysis and modelling efforts. Here we present a new georeferenced dataset of personal 36 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

Paleolithic archaeologists have long sought means to identify past cultural entities, their geographic 52 extension, social organisation and evolution<sup>1-3</sup>. For the Upper Paleolithic (*circa* 42-10 ka), lithic and, to 53 54 a lesser extent, bone and antler technologies have been the privileged proxies for exploring Palaeolithic cultural diversity and settlement dynamics<sup>4–6</sup> It is only recently that these elements of 55 material culture have been supplemented by paleogenomics<sup>7–10</sup>. The correspondence between genetic 56 57 and cultural features is, however, the subject of ongoing debate and it has been argued that amalgamating these two types of evidence together may lead to biased interpretations if not 58 supported by explicit reasoning<sup>11–13</sup>. 59

It is generally accepted that artefacts with exclusively symbolic functions, such as personal ornaments
 and mobiliary art, are more informative than functional objects when characterising cultural and social
 systems as well as individuals' role within society<sup>14,15</sup>. Many authors argue that they are essential tools
 for exploring past cultural dynamics<sup>16–20</sup>.

64 The earliest instances of personal ornaments consist of marine shells found in Northwestern and Southern Africa and the Levant and are dated between 140 to 70 thousand years  $(ka)^{21-24}$ . Only a single 65 or a few species are used as ornaments at these sites. In Northern Africa, these sites are spread over a 66 large geographic area encompassing inland regions. From circa 52 ka marine shells are replaced in 67 Eastern Africa and by *circa* 42 ka in Southern Africa by discoid ostrich eggshell beads<sup>25</sup>. It has recently 68 been proposed that a split in their size occurred *circa* 33 ka between East and Southern Africa<sup>25</sup>. It is 69 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 behind this approach, supported by ethnographic evidence<sup>26–28</sup>, is that personal ornaments are a 74 communication technology used to convey privileged information on group affiliation and social 75 status<sup>29,30</sup>. 76

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

geographically structured and hierarchically nested ethnic groups in Western Europe<sup>32</sup>. Vanhaeren and 79 d'Errico<sup>20</sup> interpreted a georeferenced database of Aurignacian personal ornaments as reflecting the 80 81 ethnolinguistic geography of Europe just after its peopling by modern humans. Applying a similar approach, d'Errico and Vanhaeren<sup>33</sup> analysed personal ornaments and grave goods associated with 82 Gravettian burials and proposed the existence of two main distinct cultural regions during this period. 83 Rigaud et al.<sup>18</sup> reached the conclusion, after analysing an extensive database of Mesolithic and Early 84 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 Mediterranean areas, with the former interpreted as a resilience in fashion and systems of belief. 88

89 An alternative theoretical framework is proposed by some authors to interpret these and similar 90 archaeological datasets<sup>1,34–38</sup> 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<sup>39,40</sup>, 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, topography, environment, phenotypic diversity and economy would play a negligible role in structuring 96 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 data<sup>9</sup>.

112

#### 113 **The Gravettian**

The Gravettian technocomplex (circa 34 – 24 ka cal. BP<sup>41–43</sup>) succeeds the Aurignacian in Europe<sup>20,35,44–</sup> 114 <sup>48</sup> and endured until just before the Last Glacial Maximum. Recent palaeogenomic work has shown 115 116 that individuals associated with Gravettian assemblages from Western Europe had a different genetic 117 ancestry from contemporaneous Gravettian groups from Central and Southern Europe<sup>9</sup>. It has also highlighted that Gravettian individuals from Western Europe genetically resemble those from the 118 preceding Aurignacian culture. The Gravettian (sensu lato) is characterised by geographically diverse 119 120 lithic technologies having in common the widespread production of straight backed points<sup>42,49–54</sup>, the ubiquitous production of anthropomorphic figurines<sup>55,56</sup> and it is when we first witness the systematic 121 production of primary burials with rich grave goods and personal ornaments<sup>33,57</sup>. The internal 122 123 heterogeneity observed within the Gravettian lithic record has been accounted for with multiple hypotheses by various authors (e.g., regionally distinct populations<sup>9,58</sup>, various site functions<sup>59,60</sup> and 124 different ecological adaptions<sup>54,61</sup>), whilst many publications have attempted to describe and explain 125 the European-wide phenomenon of the Gravettian anthropomorphic figurines<sup>56,62,63</sup>. However, the 126 127 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 archaeological layers to be attributed to different *facies*<sup>52,54,64,65</sup>. Thirdly, it presents personal 134 135 ornaments of discrete types which are found in numerous, well-dated sites, which enables the investigation of both regional and temporal evolutionary trends in ornamental practices. Finally, the 136 137 Gravettian provides abundant ornaments in both burial and occupation contexts<sup>3</sup>. While burials provide a single 'snapshot' event of ornamental behavioural practices, occupation sites represent a 138 139 diachronic palimpsest of these behaviours. In modern-day traditional societies, the position, order and association of personal ornaments often play an important role in their social meaning<sup>14,66,67</sup>. 140 Therefore, having personal ornaments preserved in their 'real-life' state gives an additional dimension 141 142 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

size of burials compared to occupation sites, the existence of personal ornaments in the latter providesan 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<sup>20,35,44–48</sup> and the well-established Gravettian geographic lithic variability<sup>42,49–54</sup>, 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 corpus of data available in the literature, only a small number of studies<sup>68–71</sup> directly tackle the subject 150 151 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 meaningful discussion on the broad evolutionary mechanisms which were at play during the 154 155 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 Mediterranean shores, and 50 shell taxa which can be found at both the Mediterranean and Atlantic 166 167 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, unknown Felis sp., Wolf), eleven from mammal herbivore species (i.e., European Elk, Horse, Rabbit, 170 Red Deer, Steppe Bison, unknown Bovid sp., unknown herbivore sp.), one belonged to a fish species 171 172 (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 <i>circa</i> 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	(S66. Austria).
200	
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>i.e.</i> 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

clockwise, Cluster 1 (B2-B1) is composed of Eastern Europe burials characterized by ornaments made
of carnivore teeth (*i.e.*, Fox canine and Wolf canine) and symmetric ivory pendants. The association of *C. elaphus* canines with Mediterranean shells (*i.e.*, *T. neritea/pellucida* and *Cypraea* sp.) and
asymmetric ivory pendants is characteristic of burials found in North Italy and one burial from South
Italy (B8, Ostuni 1), all grouped in Cluster 2 (B8-B21). Cluster 3 (B9-B30) is composed of South Italy
burials characterized by ornaments made of *C. elaphus* canines and *Cypraea* sp.

- 260
- 261

#### Figure 7

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The Delta score for the occupation sites neighbour-net is 0.2 with a q-residual of 0.00469. The Delta score for burials is 0.2387 with a q-residual of 0.0166. These values indicate that the amount of reticulation is greater in the burial sites than in the occupation sites Neighbor-net. This implies that 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 occupation268 sites.

269

#### 270 Effect of geographic and chronological distances

The degree of correlation between the cultural, spatial and temporal distances are different for the 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.

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

Our five simulations of the effects of spatial and cultural barriers on bead diversity produce notably different Mantel Test Z values (Supplementary Result, 'Modelling the effect of spatial and cultural boundaries'), with two simulations closely matching the results obtained for our occupation and burial datasets (respectively Model 2 and 3). Model 2, which assumes a slight geographical overlap of sites with partially shared cultural attributes, yields a low but significant Mantel Test Z value (Mantel Z Value (109) = 0.1296, p = < 0.001). Model 3, which assumes a clear separation of geographical and cultural traits, results in a relatively strong and significant Mantel Test Z value (Mantel Z Value (109) = 0.3517, p = < 0.001). Model 1 (Mantel Z Value (109) = -0.01053, p = 0.7885), Model 4 (Mantel Z Value (109) = -0.009945, p = 0.8093) and Model 5 (Mantel Z Value (109) = -0.01871, p = 0.9318) each result in a nonsignificant, 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 comprising nine clusters, of which six are occupation and three are burial. The occupation clusters 313 314 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 geographic distance of 100 km. The Mantel test performed on the Eastern and Western Europe subsets 339 340 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 reflects the very small chronological overlap between burials from East and West Europe. Burials 345 346 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.

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

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

The neighbour-net analyses demonstrate a clear East and West separation in the sites and identified clusters, with the burial clusters being more geographically discrete than those of the occupations. The higher Delta score and q-residuals obtained from the burial neighbour-net analyses indicate that beadtypes found in burial contexts were more likely to be circulated and exchanged within a small regionthan those found at occupation sites.

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

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

377 A third possibility is that the observed difference is caused by social stratification<sup>33,79–81</sup>: 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)<sup>82</sup> and Cussac cave (France)<sup>83</sup>) is consistent with this hypothesis. The presence of non-adult ornamented burials in our dataset (n=6)<sup>84-87</sup> also supports this hypothesis, as these 381 382 individuals did not have a chance to personally merit an elaborate burial. However, the large proportion of elaborately buried individuals with signs of disfiguring diseases (n=14) instead supports 383 the well-documented principle of 'bad death'<sup>88-92</sup> influencing who was selected to be elaborately 384 385 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.

The analysis of Gravettian grave goods conducted by d'Errico and Vanhaeren<sup>33</sup> identified marginally different groups to those in this study. This minor difference resulted from their inclusion of burials formally attributed to the Gravettian (i.*e.*, Sunghir, Russia<sup>93,94</sup>), our inclusion of newly discovered burials (*i.e.*, Borsuka Cave, Poland<sup>87</sup>) and our exclusion of grave goods which were not personal ornaments (*e.g.*, awls and mammoth scapulae). The very similar results underpin the robustness of the geographic clusters in personal ornament associations in Gravettian burial practices.

394 The recent paleogenomic study conducted by Posth et al.<sup>9</sup> 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 of different regions of Europe, already predicted by other authors<sup>78,95–97</sup> contradict the hypothesis that 397 398 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.<sup>9</sup> 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

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

#### 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 ornaments and simulations modelling the impact of distance on cultural traits, that the sense of 432 433 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 converted into calibrated ages using OxCal 4.498, which applies the IntCal20 Northern Hemisphere 451 radiocarbon age calibration curve<sup>99</sup>. The above resulted in the creation of two distinct datasets, one 452 453 for occupation sites and the other for burial sites.

454 We created mutually exclusive bead-types (Supplementary Table 1) taking into account cross-cultural studies on the classification of beads<sup>100–103</sup> and on criteria used to classify archaeological artefacts<sup>103–</sup> 455 456 <sup>105</sup>. 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 published<sup>102,106,107</sup>. As such, care was taken to verify that species in older literature were updated to 460 461 modern nomenclature. To prevent attribution to multiple taxa when referring to the same shell

species, we used WoRMS, the World Register of Marine Species (https://www.marinespecies.org), tocharacterise the species.

For animal teeth, the genus, species and anatomical attribution were taken into account. For fully or partially shaped ornaments made of other raw material (bone, ivory, stone etc.), the type of raw material and morphology of the ornaments were considered to create mutually exclusive types. Few perforated bones, described as ornaments, bear features typical of bone fragments regurgitated by carnivores<sup>108</sup>. These were not included in the dataset.

469

#### 470 Statistical analyses

Seriation analysis sorts individuals based on their shared attributes<sup>109</sup>. Application of this method with 471 472 PAST software<sup>110</sup> to personal ornament presence/absence data from burial and occupation sites enabled the identification of sets, defined as associations of at least three geographically proximate 473 474 sites sharing a minimum of one bead type<sup>20</sup>. 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 Modularity<sup>111</sup> test and a Permutational Multivariate Analysis of Variance (perMANOVA)<sup>112,113</sup>. 478 479 (Supplementary Results, 'Modularity test and permutational MANOVA').

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

485 We quantified personal ornament dissimilarity between sites by creating a distance matrix using a Jaccard distance index<sup>114–116</sup> (Supplementary Table 5). This index is particularly well adapted to 486 archaeological enquiry as it does not give weight to absence data, possibly due in archaeology to field 487 investigation biases<sup>38,117</sup>. When constructing the distance matrices, we did not include sites which 488 shared no personal ornaments types with other sites<sup>118</sup>. Personal ornament distance matrices of burial 489 490 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 because it uses binary data<sup>119</sup>. In order to investigate the branching and clustering between sites, we 492

entered the distance matrices into a Neighbour-joining tree analysis<sup>120</sup>. This was performed using 1000
bootstrap replications with Knossos (Crete, Greece), a Neolithic site, as an outgroup to root the tree<sup>121</sup>.

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<sup>2,122–124</sup>. However, an effective 497 application of these techniques to this domain is somewhat hampered by the fact that cultural evolution involves horizontal transmission of cultural traits<sup>125,126</sup>. The Neighbour-Net technique<sup>120,127</sup> 498 499 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 account<sup>128</sup>. The shape and amount of reticulation shown within the resultant network reflect the 501 502 degree of horizontal transfer between sites. We performed the Neighbour-net joining method in SplitsTree6 software using default settings<sup>129</sup> on both occupation and burial cultural distance matrices. 503 504 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 is<sup>125,130</sup> 506

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 associations<sup>18,38</sup>. In evolutionary biology, IBD model predicts the presence of a positive correlation 509 between geographical and genetic distances within a meta-population<sup>38,40,131</sup>. In order to evaluate the 510 role of geography we use a Mantel test<sup>132</sup> which quantifies the degree of correlation between the 511 512 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 pairwise comparisons at the same geographic location. In order to assess the degree of spatial 520 521 autocorrelation (i.e., higher than average similarity between sites for a given geographic distance) we additionally conducted a Mantel correlogram<sup>133,134</sup> for both of the datasets. A positive significant value 522 523 for each geographic distance class indicates that sites at a given geographic distance from one another are more similar than expected by the Mantel test (*i.e.*, they spatially autocorrelate)<sup>135</sup>. Since patterns 524 525 observable at one scale can be lost at another, it is recommended that any Mantel correlogram analysis be carried out at multiple scales<sup>136</sup>. We therefore generated a Mantel correlogram for each dataset 526

using three geographic distance scales. Simply put, whereas a Mantel test investigates the overall
relationship between two distance matrices, a Mantel correlogram probes deeper into the internal
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<sup>2</sup>) 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) library<sup>137</sup>. 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 conducted on each of the simulated datasets so as to assess the relationship between these characters. 537 538 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.

To investigate the impact of time on variations in personal ornament associations, we employed two different strategies, one for the occupation and one for the burial dataset due to the different nature 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 test<sup>138</sup> that enabled the partial 550 correlation between two matrices while holding for the effect of the third<sup>139</sup>. The midpoints of these 551 ranges were then calibrated using the IntCal20 Calibration Curve<sup>99</sup> 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

- 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

Figure 1 – Material used for Gravettian personal ornaments. a) Types of teeth used as ornaments identified at
 occupation and burial sites attributed to the Gravettian. 1, Bear canine; 2, Bear incisor; 3, Bovid incisor
 (archaeological, adapted from Baker et al. 2022<sup>140</sup>); 4, European elk canine (Collection PACEA); 5, Felis canine; 6,
 Fox canine; 7, Fox incisor; 8, Hare tooth (incisor) (Collection PACEA), 9, Herbivore incisor; 10, Horse incisor; 11,
 Human tooth (canine); 12, Hyena canine; 13, Lynx canine; 14, Red Deer vestigial canine; 15, Red Deer incisor; 16,
 Sparus auratus tooth (archaeological, adapted from Zilhão et al. 2021<sup>141</sup>); 17, Steppe bison canine (Collection
 PACEA); 18, Steppe bison incisor (Collection PACEA); 19, Wolf canine; 20, Wolf incisor. Scale bar = 2 cm. (modified

after Vanhaeren and d'Errico 2006<sup>20</sup>), b) Shaped ornaments and modified bones identified at occupation and
burial sites attributed to the Gravettian. 1, Amber Pendant; 2, Anthropomorphic bone bead; 3, Asymmetric ivory
pendant; 4, Bear phalange; 5, Bilobated ivory bead; 6, Ellipsoidal ivory pendant; 7, Elongated ivory pendant; 8,
Fishtail ivory pendant; 9, Fish Vertebrae; 10, Herbivore diaphysis fragment; 11, Ivory bracelet; 12, Ivory breast
bead; 13, Ivory cylindrical bead; 14, Ivory diadem; 15, Ivory pin; 16, Notched herbivore diaphysis; 17, Owl-shaped
ivory beads; 18, Rectangular ivory pendant; 19, Red deer femur head; 20, Stone pendant; 21, Stone Ring; 22,
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

Figure 5 – a) Seriation analysis of the bead database of Gravettian burial sites. Squares are indicative of
 occurrences of ornament type at burial sites, ages are from calibrated radiocarbon dates. b) Seriation analysis of
 the bead-type database of Gravettian burials performed under time constraint. Squares indicate occurrence of
 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 = 0.2, Q-residual = 0.00469). b) Neighbour-Net analysis performed on the bead database for Gravettian burial 619 = 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

Figure 8 - Map of Europe showing the location of human remains attributed to the Gravettian analysed by Posth
et al.<sup>9</sup>. S1 = Dolní Vestonice (13, 14, 15, 16), S2 = Krems-Wachtberg (individual 3), S3 = Ostuni 1, S4 = Paglicci 12,
S5 = Pavlov 1, S6 = Goyet (2878-15, 2878-18, Q-1, Q100-8, Q376-19, Q53-1, Q56-16), S7 = Fournol 85, S8 = La
Rochette, S9 = Mollet III (GER-33), S10 = Reclau Viver (GER-8). Map created on QGIS<sup>142</sup> using ETOPO1 Global Relief
Model<sup>143</sup> data with a modern and Gravettian coastline at -100 m<sup>144</sup>.

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a Brno 2	<i>Trivia</i> sp. <i>Columbella</i> sp. <i>Pecten</i> sp. <i>L. lurida</i> Bovid Incisor <i>C. elaphus</i> Canine Asymmetric Ivory Pendant Bilobated Ivory Pendant Bilobated Ivory Bead <i>L. littorea</i> <i>L. littorea <i>L. littore</i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i></i>	<b>b</b> • 32 - 29.5 ka • 29.5 - 28.5 ka • 28.5 - 24 ka	<i>Trivia</i> s <i>Columbella</i> s <i>Pecten</i> s <i>L. lurid</i> Bovid Incise <i>Cypraea</i> s <i>T. neritea/pellucid</i> <i>C. elaphus</i> Canir Asymmetric Ivory Pendau Fish Vertebra Bone Pendau Bilobated Ivory Bea Symmetric Ivory Pendau <i>C. lupus</i> Canir <i>Theodoxus</i> s <i>Vulpes</i> sp. Canir
Predmosti			
Borsuka Cave		Kostenki 15	
Krems-Wachtberg 2		Dolni Vestonice 16	
Kostenki 15		Krems-Wachtberg 1B	
Dolni Vestonice 3		Dolni Vestonice 3	
Doini Vestonice 15		Dolni Vestonice 15	
Krems-Wachtherg 1B		Krems-Wachtberg 1A	
Dolni Vestonice 13		Dolni Vestonice 13	
Dolni Vestonice 14		Dolni Vestonice 14	
Krems-Wachtberg 1A		Barma Crando 2	
Cro-Magnon		Barma Grande 3	
Lagar Velho I		Barma Grande 2	
Paviland		Barma Grande 4	
Arene Candide		Barma Grande 6	
Barma Grande 3 Barma Grando 2		Barma Grande 5	
Barma Grande 4		Grotta del Caviglione	
Barma Grande 6		Ostuni 1	
Barma Grande 5		Paglicci II	
Grotta del Caviglione		Arene Candide	
Fanciulli 5		Fanciulli 5	
Fanciulli 6		Fanciulli 6	
Baousso da Torre 2		Bacusso da Torro 2	
Baousso da Torre 1			
Veneri Parabita 2		Baousso da Torre I	
		Veneri Parabita 2	
Paglicci II		Veneri Parabita 1	
Paglicci III		Ostuni 2	
Ostuni 1		Paglicci III	













# Dataset Z value (R<sup>2</sup>) P-value Occupation 0.1941563 < 0.001</td> Burial 0.3257094 0.0093

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

## Dataset Z value (R<sup>2</sup>) P-value Western burial 0.4559727 0.0266 Eastern burial 0.855131 0.16667