LETTER

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Similar cranial trauma prevalence among Neanderthals and Upper Palaeolithic modern humans

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Neanderthals are commonly depicted as leading dangerous lives and permanently struggling for survival. This view largely relies on the high incidences of trauma that have been reported[1,2] and have variously been attributed to violent social behaviour[3,4], highly mobile hunter-gatherer lifestyles[2] or attacks by carnivores[5]. The described Neanderthal pattern of predominantly cranial injuries is further thought to reflect violent encounters with large prey mammals, resulting from the use of close-range hunting weapons[1]. These interpretations directly shape our understanding of Neanderthal lifestyles, health and hunting abilities, yet mainly rest on descriptive, case-based evidence. Quantitative, population-level studies of traumatic injuries are rare. Here we reassess the hypothesis of higher cranial trauma prevalence among Neanderthals using a population-level approach—accounting for preservation bias and other contextual data—and an exhaustive fossil database. We show that Neanderthals and early Upper Palaeolithic anatomically modern humans exhibit similar overall incidences of cranial trauma, which are higher for males in both taxa, consistent with patterns shown by later populations of modern humans. Beyond these similarities, we observed species-specific, age-related variation in trauma prevalence, suggesting that there were differences in the timing of injuries during life or that there was a differential mortality risk of trauma survivors in the two groups. Finally, our results highlight the importance of preservation bias in studies of trauma prevalence.

Neanderthals are commonly depicted as robust hominins who led stressful, dangerous lives[1,6–9]. Traumatic injuries, considered to be common among remains of adult Neanderthals[1], are a major piece of evidence supporting this hypothesis: not only are Neanderthals proposed to suffer from a high prevalence of trauma[2,3,10,11], but they are also thought to exhibit more traumatic injuries than early modern humans[9,12,13]. Explanations for this include violent social behaviour[3,4], a highly mobile hunter-gatherer lifestyle in glacial environments[2] and attacks by carnivores[5]. Moreover, Neanderthals are thought to show unusually high levels of head and neck injuries, attributed to their hypothesized reliance on close-range hunting leading to confrontations with large prey mammals[1]. These interpretations have important implications for reconstructions of Neanderthal palaeobiology and behaviour, and have shaped the prevailing perception of the species. However, they are largely based on anecdotal evidence, because trauma among Palaeolithic humans is often reported on a descriptive, case-by-case basis. The few systematic, quantitative studies that have been conducted to date have yielded contradictory results[2,4,11,14,15], but question the prevailing view of 'the highly traumatized Neandertal'[15].

Current research into Palaeolithic trauma suffers from several limitations. Most previous work assessed the proportional distribution of lesions throughout the body in injured Neanderthal skeletons, comparing the derived ratios to those of recent humans[1,5,15–17]. Such approaches provide insights into individual life histories, but—because they focus exclusively on the injured—cannot elucidate population-level trauma prevalence. The latter requires an examination of both injured and uninjured individuals. Furthermore, contextual factors such as age at death, sex and skeletal preservation are rarely accounted for in these approaches[15]. These variables can markedly affect trauma prevalence variation[18–21] and lesion visibility in the fossil record, and should thus be integral to population-level analyses. Moreover, Neanderthals are routinely compared to recent humans—clinical[1] or forensic[5] samples, rodeo riders[1] and Holocene hunter-gatherers or nomads[2,4,15,16]—but only rarely to Upper Palaeolithic modern humans[17]. However, the latter are the most appropriate comparative sample, sharing similar environments and comparable mobile hunter-gatherer lifestyles. Finally, small sample sizes have hampered the validity of the statistical inferences of most previous research.

Here we assess the hypothesis of higher prevalence of cranial trauma among Neanderthals relative to Upper Palaeolithic modern humans using a population-level comparison, including contextual data and using the largest fossil dataset that is currently available. We systematically compiled published information on fossil crania from the Middle and Upper Palaeolithic of Eurasia, dating to roughly 80–20 thousand years ago (Fig. 1). Cranial injuries—considered typical for Neanderthals[1]—are a particularly reliable trauma archive, because they heal with only minor bone remodelling and therefore leave visible lesions even after full recovery[22].

For each specimen, we recorded whether trauma was present (0 or 1), the taxon (Neanderthals or Upper Palaeolithic modern humans), sex (male, female or unknown), age at death (juvenile to young adult, old adult or indeterminate), preserved skeletal element(s) (14 major cranial bones), the preservation percentage of each skeletal element ($\leq$25%, 25–50%, 50–75% and 75–100%) and location (five geographical regions within Eurasia; see Supplementary Tables 1, 2). We then used generalized linear mixed models (GLMMs) to assess differences in trauma prevalence with taxon, sex, age and preservation as explanatory variables, while accounting for variation among skeletal elements and locations.

Our systematic literature survey revealed 21 specimens with one or several cranial lesions (9 Neanderthals and 12 Upper Palaeolithic modern humans; Supplementary Table 3) in our sample of 114 specimens of Neanderthals and 90 specimens of Upper Palaeolithic modern humans (Supplementary Tables 1, 2). At the level of skeletal elements, this corresponds to 14 out of 295 cranial elements of Neanderthals, and 25 out of 541 cranial elements of Upper Palaeolithic modern humans, exhibiting at least one traumatic lesion.

We calculated separate models to predict trauma prevalence at the specimen and the skeletal-element level. Our analysis comprised two sets of four GLMM models each that were based on hierarchically nested subsets of the raw data. The first set (models 1–4; Fig. 2) followed an element-based approach, with skeletal elements being the unit of analysis; the second set (models 5–8; Fig. 3) was based on individuals (see Methods). Trauma was modelled as a binary response variable in all models, either per skeletal element or per specimen. The random component of the GLMMs comprised skeletal element and location in models 1–4, and only location in models 5–8.

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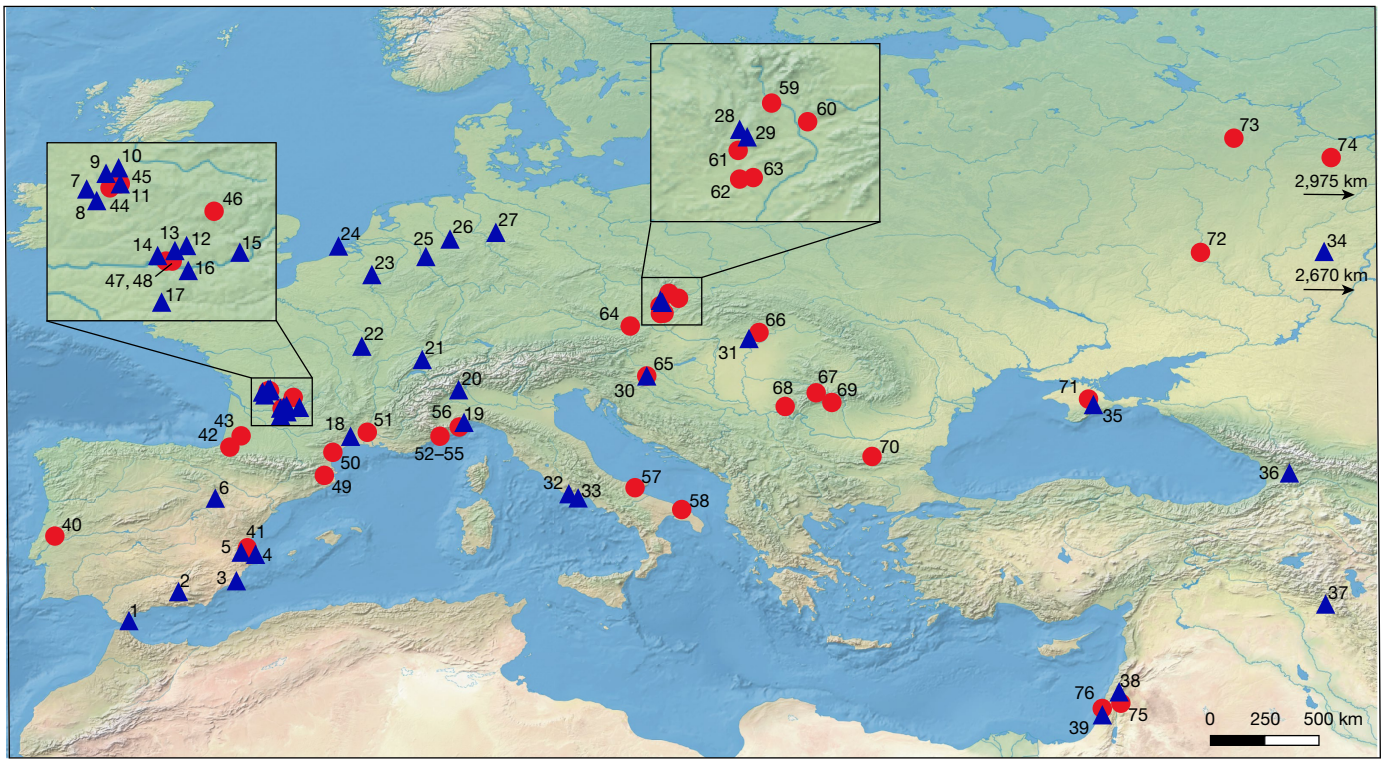

▲ Neanderthal sites

1	Gibraltar (1,10)	14	La Ferrassie (2,14)	27	Sarstedt (2,2)		
2	Horá (1,1)	15	La Chapelle (1,12)	28	Kůlna (2,2)		
3	Palomas (3,9)	16	Combe Grenal (6,6)	29	Ochoz (1,2)		
4	Cova Foradà (1,3)	17	Monsempron (2,2)	30	Vindija (26,33)		
5	Cova Negra (2,2)	18	Hortus (2,3)	31	Subalyuk (1,3)		
6	Gegant (1,2)	19	Fate (2,2)	32	Grotta Breuil (1,1)		
7	Petit-Puymoyen (3,4)	20	Ciota Ciara (1,1)	33	Guattari (3,14)		
8	La Quina-Amont (9,21)	21	Cotencher (1,2)	34	Chagyrskaya (1,1)		
9	Pradelles/Marillac (16,19)	22	Genay (1,5)	35	Zaskalnaya VI (1,1)		
10	St. Césaire (1,8)	23	Spy (2,16)	36	Sakajia (1,1)		
11	Fontéchevade (1,3)	24	Zeeland Ridges (1,1)	37	Shanidar (6,49)		
12	Régourdou (1,2)	25	Neanderthal (1,8)	38	Amud (3,14)		
13	Le Moustier (1,12)	26	Warendorf (1,1)	39	Kebara (2,3)		

● Upper Palaeolithic modern human sites

40	Caldeirão (1,1)	53	Barma Grande (3,28)	66	Tapolca (1,1)		
41	Parpallo (1,11)	54	Caviglione (1,13)	67	Cioclovina (1,8)		
42	Isturitz (1,2)	55	Grotte des Enfants (2,28)	68	Oase (2,14)		
43	Brassempouy (1,2)	56	Arene Candide (1,13)	69	Muierii (2,12)		
44	Vilhonneur (1,4)	57	Grotta Paglicci (9,20)	70	Bacho Kiro (1,1)		
45	Fontéchevade (1,1)	58	Ostuni (1,14)	71	Buran Kaya III (3,4)		
46	Cussac (1,9)	59	Mladeč (9,42)	72	Kostenki (3,24)		
47	Cro Magnon (3,29)	60	Predmost (11,85)	73	Sunghir (3,26)		
48	Abri Pataud (1,14)	61	Brno (2,11)	74	Pokrovka (1,1)		
49	Mollet (1,5)	62	Pavlov (3,13)	75	Ohalo II (1,14)		
50	Crouzade (2,3)	63	Dolní Věstonice (6,67)	76	el-Wad (3,3)		
51	La Balauzière (2,8)	64	Willendorf (1,2)				
52	Baousso da Torre (1,4)	65	Vindija (3,4)				

Fig. 1 | Neanderthal and Upper Palaeolithic modern human sites. Neanderthal sites, blue triangles; Upper Palaeolithic modern human sites, red dots. Numbers in brackets indicate number of specimens/number of skeletal elements, respectively. Sites Chagyrskaya (34) and Pokrovka (74) were projected 2,670 and 2,975 km west for better visualization. The map was generated using the QGIS Geographic Information System (https://www.qgis.org) and Natural Earth (http://naturalearthdata.com/).

Model 1 comprised the full dataset of all skeletal elements ($n = 836$) to exclusively assess overall taxon differences in trauma prevalence, while ignoring the incompletely scored contextual variables. Model 2 ($n = 604$) excluded skeletal elements of unknown sex and indeterminate age, thus assessing the additional influence of age, sex, element preservation, and the interaction between age and taxon. Given trauma

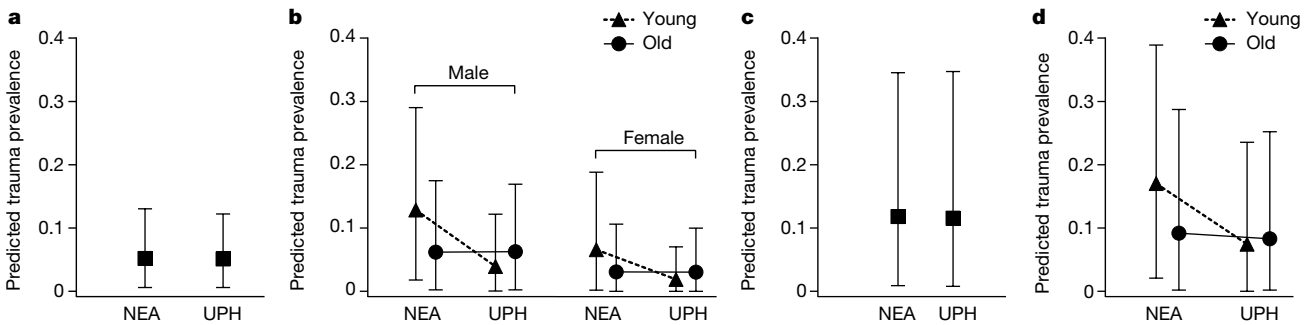

Fig. 2 | Predicted cranial trauma prevalence in skeletal elements from Neanderthals and Upper Palaeolithic modern humans. a, Model 1 includes taxon as the predictor variable (full dataset, $n = 836$). **b**, Model 2 includes the variables taxon, sex, age, element preservation and the interaction between age and taxon, but excludes sex unknown and age indeterminate skeletal elements ($n = 604$). **c**, Model 3 includes taxon as the variable, but excludes female and sex unknown skeletal elements ($n = 462$). **d**, Model 4 includes the variables taxon, age, element preservation, and the interaction between age and taxon, but excludes female, sex unknown and age indeterminate skeletal elements ($n = 407$). Predictions are given for skeletal elements when 50–75% complete; predictions for other preservation categories scale linearly. Predictions are based on posterior estimates of the four GLMMs using a Markov chain Monte Carlo (MCMC) algorithm. Sample sizes represent single skeletal elements, treated as biologically independent samples in models 1–4 (see Methods). Markers denote the predicted means, bars show lower and upper 95% credible intervals. NEA, Neanderthals; UPH, Upper Palaeolithic modern humans.

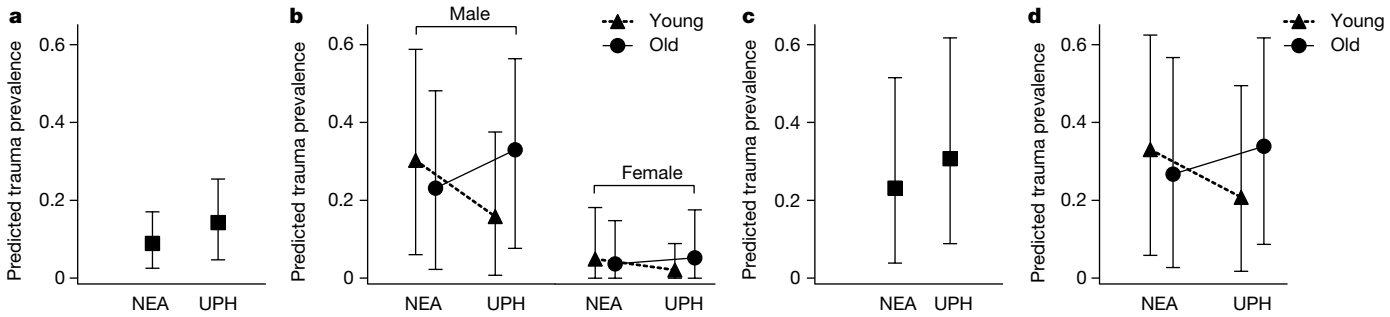

Fig. 3 | Predicted cranial trauma prevalence in individual cranial specimens from Neanderthal and Upper Palaeolithic modern humans. **a**, Model 5 includes taxon as the predictor variable (full dataset, $n = 204$). **b**, Model 6 includes the variables taxon, sex, age, specimen preservation and the interaction between age and taxon, but excludes sex unknown and age indeterminate specimens ($n = 89$). **c**, Model 7 includes taxon as the variable, but excludes female and sex unknown specimens ($n = 76$). **d**, Model 8 includes the variables taxon, age, specimen preservation and the interaction between age and taxon, but excludes female, sex unknown and age indeterminate specimens ($n = 59$). Predictions are given for mean specimen-preservation scores; predictions for other preservation scores scale linearly. Predictions are based on posterior estimates of the four GLMMs using a Markov chain Monte Carlo algorithm. Samples sizes in models 5–8 represent cranial specimens, comprising one or several skeletal elements of the same cranium (see Methods). Markers denote the predicted means, bars indicate lower and upper 95% credible intervals.

predominance in males, we repeated these models on male-only subsets in models 3 ($n = 462$) and 4 ($n = 407$).

Model 5 comprised all specimens ($n = 204$) and, corresponding to model 1, assessed overall taxon differences in trauma prevalence. Model 6 ($n = 89$) excluded specimens of unknown sex and indeterminate age to assess how age, sex, specimen preservation and the interaction between age and taxon affected trauma prevalence. We repeated these models for male-only subsets in models 7 ($n = 76$) and 8 ($n = 59$).

None of the models showed a quantitative difference in cranial trauma prevalence between Neanderthals and Upper Palaeolithic modern humans (taxon effect in models 1–8 in Table 1 and Figs. 2a–d, 3a–d). Instead, we found a significantly higher prevalence of trauma in males compared to females (sex effect in models 2 and 6; Table 1 and Figs. 2b, 3b). Furthermore, trauma prevalence significantly increased with preservation status, indicating a greater probability to detect trauma on more complete skeletal elements or individuals (preservation effect in models 2, 4, 6 and 8; Table 1 and Extended Data Fig. 1a). Finally, in the element-based models, trauma prevalence varied between age classes with distinct patterns for the two taxa (age-by-taxon interaction in models 2 and 4; Table 1, Fig. 2b, d and Extended Data Fig. 1b): Neanderthals had a significantly higher prevalence of trauma when young, whereas Upper Palaeolithic modern humans showed a similar

Table 1 | Summary statistics of the GLMMs

Model	*n*	Predictor variable	Parameter estimates			
			Posterior mean	Lower 95% CI	Upper 95% CI	P_{MCMC}
Model 1	836[a]	Taxon	0.020	−0.889	0.933	0.965
Model 2	604[b]	Taxon	−0.060	−2.017	1.687	0.949
		Sex	1.515	0.178	2.921	0.017**
		Age	−0.973	−2.154	0.210	0.100
		Element preservation	0.866	0.232	1.514	0.006***
		Age × taxon	2.595	0.573	4.645	0.008***
Model 3	462[c]	Taxon	0.052	−1.167	1.329	0.940
Model 4	407[d]	Taxon	0.220	−1.934	2.439	0.863
		Age	−0.340	−1.553	1.050	0.605
		Element preservation	0.671	0.048	1.376	0.037**
		Age × taxon	2.149	0.048	4.355	0.046**
Model 5	204[a]	Taxon	−0.651	−1.719	0.472	0.231
Model 6	89[b]	Taxon	−0.715	−2.864	1.650	0.522
		Sex	3.533	0.865	6.397	0.002***
		Age	−1.490	−3.454	0.561	0.137
		Specimen preservation	0.882	0.054	1.730	0.032**
		Age × taxon	2.019	−1.190	5.030	0.196
Model 7	76[c]	Taxon	−0.743	−2.443	0.749	0.354
Model 8	59[d]	Taxon	−0.513	−2.902	1.858	0.660
		Age	−1.153	−3.333	0.736	0.255
		Specimen preservation	0.739	−0.106	1.623	0.082*
		Age × taxon	1.584	−1.762	4.621	0.320

Trauma prevalence was modelled using a MCMC algorithm in two model sets with four data subsets each: models 1–4 comprise skeletal elements, models 5–8 comprise cranial specimens. Parameter estimates are given as their posterior mean with 95% credible intervals (CI) and statistical significance (P_{MCMC}; ***$P < 0.01$, **$P < 0.05$, *$P < 0.10$). See Methods for details.
[a]Full dataset.
[b]Exclusion of sex unknown and age indeterminate elements or specimens.
[c]Exclusion of female and sex unknown elements or specimens.
[d]Exclusion of female, sex unknown and age indeterminate elements or specimens.

prevalence of trauma across age cohorts. Although a similar pattern appeared to be present in the specimen-level models (Fig. 3b, d), the interaction failed to reach statistical significance.

The mean model-predicted prevalence of trauma for skeletal elements in preservation category 50–75% was between 0.03 and 0.17 (95% credible interval, 0.0002–0.39) for Neanderthals, and between 0.02 and 0.12 (95% credible interval, 0.00006–0.35) for Upper Palaeolithic modern humans (Fig. 2a–d). For specimens, predictions were calculated for the mean specimen preservation score (a proxy for skull completeness and average preservation category of its constituent elements; see Methods). These model-predicted trauma prevalence values ranged between 0.04 and 0.33 (95% credible interval, 0.000002–0.62) for Neanderthals and between 0.02 and 0.34 (95% credible interval, 0.000001–0.62) for Upper Palaeolithic modern humans (Fig. 3a–d).

On the basis of our results, we reject the hypothesis that Neanderthals exhibit more cranial trauma than Upper Palaeolithic modern humans in western Eurasia—rather, we show that the two taxa exhibited a similar overall prevalence of cranial injuries. Previously suggested values of 30–40% cranial trauma prevalence for Neanderthals[3,10] represent the very limit of the predictions of our models for Neanderthals (mean prevalence of 3–17% for skeletal elements and 4–33% for individual specimens); these values are comparable to those found for Upper Palaeolithic modern humans (2–12% for skeletal elements and 2–34% for individual specimens) and that have been reported for Mesolithic hunter-gatherers[23], Neolithic agriculturalists[24,25] and recent hunter-gatherers[26]. Nevertheless, trauma prevalence derived from skeletal remains must not be equated to the actual numbers of injuries that were experienced during an individual's lifetime and comparisons of crude trauma frequencies should be considered with caution, because the methods used for their estimation are not always comparable among studies.

The significant relationship between trauma prevalence and sex in both taxa is consistent with observations of greater trauma prevalence among males in later periods[18,21,24–27], generally explained by sex-specific differences in activities and behaviours (division of labour, initiation rites or violent conflict)[18,20,21]. Trauma prevalence was further affected by the preservation state of skeletal remains; more complete crania or cranial elements were more likely to have preserved traumatic lesions. We therefore caution against quantitative trauma analyses that do not address preservation bias.

Both taxa showed mostly healed traumata and we did not find a markedly higher prevalence of trauma among 'old' skeletal elements in either group. This finding contradicts the expectation that healed traumatic injuries accumulate with increasing age as a result of longer exposure to dangerous situations[28], given that cranial defects remain visible over long-term periods owing to the limited regenerative bridging capacity of cranial bone healing[22]. However, death assemblages are likely to deviate from such an expected accumulation pattern[29,30], because injured individuals—even if they survived their injuries—had an increased risk of dying relative to individuals who were never injured[31,32]. Thus, our observed age pattern across taxa is consistent with the well-documented increased mortality risk of trauma survivors.

An interaction between age and taxon in trauma prevalence was found by our element-based analysis. For Neanderthals, this result suggests that cranial trauma was sustained early in life (before 30 years of age) and that trauma survivors were more likely to die while still 'young'—therefore accumulating in the 'young' age cohort in the fossil record. Once a trauma is healed, it is not possible to determine when it was acquired. Therefore, Upper Palaeolithic modern humans were either less likely to sustain trauma than Neanderthals when 'young'; and/or they sustained trauma in a similar frequency when 'young', but 'young' Upper Palaeolithic modern human trauma survivors had a lower mortality risk relative to 'young' Neanderthal trauma survivors. In other words, 'young' Upper Palaeolithic modern human injured individuals had a greater probability to survive into the 'old' age cohort. Possible explanations for these patterns include cultural or individual differences in injury proneness and healing, and different long-term consequences of healed trauma, resulting from (for example) differences in injury severity or differential treatment of the injured—which did not, however, affect the overall prevalence of trauma.

Our study addresses the controversial topic of trauma prevalence in the Palaeolithic by reassessing cranial trauma data using a state-of-the-art methodological approach. It is, to our knowledge, the largest population-level investigation of Neanderthal cranial trauma to date and accounts for differential skeletal preservation and contextual explanatory variables using Upper Palaeolithic modern humans as a comparative sample. The available evidence indicates similar overall trauma prevalence in Neanderthals and Upper Palaeolithic modern humans in western Eurasia, rejecting earlier hypotheses of highly traumatized Neanderthals. Beyond this overall similarity, our observed age-dependent differences between the taxa also suggest possible differences in the likely age of trauma acquisition or in the mortality risk of trauma survivors.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at https://doi.org/10.1038/s41586-018-0696-8.

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Competing interests The authors declare no competing interests.

Additional information
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METHODS

Data collection. We collected data through a comprehensive literature review and aimed at gathering a full-evidence dataset comprising all currently known fossil crania with and without traumatic lesions. We focused on Eurasian Middle and Upper Palaeolithic sites that had yielded skull remains from classic Neanderthals (around 80–30 thousand years ago) and early to mid-Upper Palaeolithic modern humans (around 35–20 thousand years ago) (Fig. 1; Supplementary Tables 1, 2 provide information on the studied specimens). We excluded specimens that consisted of only dental remains and restricted our sample to adolescent and adult specimens with a minimum estimated age-at-death of 12 years[33]. For each specimen we recorded the taxon (Neanderthal or Upper Palaeolithic modern human), sex (male, female or unknown), age (young, 12–30 years; old, >30 years; or indeterminate, if there was no further estimate published), the skeletal element with its preservation status (see 'Quantification'), and whether the skeletal element was affected by trauma (binary). Because trauma prevalence may vary across geographical regions owing to differing social or environmental conditions, we furthermore recorded the location of each specimen (five geographical regions: Iberia, south, central, east, Near East). We adopted the assignments of taxon, sex, age and the diagnoses of traumatic lesions as published by the examiners of the specimens. These literature-based assignments may be influenced by observer bias or by the use of different methods. Nevertheless, we decided in favour of a full-evidence approach based on all available published data in order to keep data collection as consistent and complete as possible. Moreover, many fossil specimens are not available for original examination, precluding a single-method-based systematic assessment. We conducted an extensive literature review seeking to combine past research with the most recent results, so as to base our data on a complete synthesis of all available evidence, representing best-practice of research in the field. Notably, we expect misclassifications of traumatic lesions, age or sex to be equally likely in Neanderthals and Upper Palaeolithic modern humans, and this therefore should not introduce systematic biases into our group comparisons. Supplementary Table 3, a catalogue of specimens with described traumata, provides detailed descriptions of each lesion as published by the respective authors. A case was recorded as (possible) trauma once an author expressed confidence that a lesion represents a trauma, or considered a traumatic origin to be an alternative explanation for an observed lesion. No statistical methods were used to predetermine sample size. The investigators were not blinded to allocation during analyses.

Quantification. Skeletal preservation has a direct effect on the census of trauma prevalence, because an injury is more likely to be detected on a more complete bone[34]. In chronologically older fragments, the preservation of skeletal remains commonly deteriorates and fragmentation of both single bones and associated skeletons increases. Moreover, the assignment of fragmented and commingled remains to specific individuals is often impossible or insecure. To account for differential skeletal preservation among sites and specimens, and to remove bias between geologically older Neanderthals and younger Upper Palaeolithic modern humans, we quantified the preservation status for each of the 14 major skull bones, that is, skeletal elements, separately. These are the frontal and occipital bones, as well as the left and right elements of the parietal, temporal, maxilla, mandible, zygomatic and nasal bones. Except for the zygomatic and nasal bones, we rated the completeness of skeletal elements in four preservation categories: up to 25%, 25–50%, 50–75% and 75–100%. Owing to their small size, the left and right zygomatic and the nasal bones were rated in just two categories: up to 50% and 50–100%. We performed the quantification procedure by visually judging the preserved portion of a given skeletal element in comparison to its complete equivalent using published pictures, sketches, virtual representations and verbal anatomical descriptions. Skeletal elements for which the preservation could not be quantified were excluded from the sample. In total, we collected data on 836 skeletal elements from 204 specimens. The quantification revealed a differential preservation among skeletal remains of Neanderthals and Upper Palaeolithic modern humans, with Neanderthals being biased towards incompletely preserved skeletal remains (see Extended Data Fig. 2a–e).

Statistical methods. We predicted trauma prevalence using GLMMs. To obtain robust GLMM estimates despite a large proportion of trauma absences (zeros) in our dataset, we used a Markov chain Monte Carlo (MCMC) algorithm as implemented in the MCMCglmm package[35] for R version 3.4.3[36]. Trauma presence or absence was modelled as a binary response variable with a binomial error distribution using a logit-link function.

Our statistical analysis of trauma prevalence comprised two sets of four GLMMs on subsets of the raw data. The first set (models 1–4) followed a skeletal element-level approach, whereas the second set (models 5–8) represented an individual specimen-level approach.

Element-level models (models 1–4). We entered the two-level predictors taxon (Neanderthals or Upper Palaeolithic modern humans), age (young or old, with 30 years as the cut-off) and sex (male or female), as well as the z-transformed four-level covariate element preservation (0.25, 0.5, 0.75 and 1) as fixed predictor variables. Visual data inspection indicated a potential for variation in the taxon effect with age class but not with sex, so we added the age-by-taxon interaction to the models.

Because traumata are not equally frequent in the different cranial regions[24,27,37], we added intercepts for skeletal element as a random component for all element-level models, enabling us to derive marginal predictions for trauma prevalence beyond element identity while statistically accounting for variation in trauma prevalence between skeletal elements. Moreover, given that trauma prevalence may vary regionally, we added location as a second random intercept to the models.

We ran four separate models to assess trauma prevalence using four data subsets and different explanatory variable combinations, while maintaining the same two random components in each case. Model 1 included taxon as the only fixed predictor. The exclusion of the other, incompletely scored, contextual predictor variables enabled us to analyse the full dataset of $n = 836$ skeletal elements. Model 2 included all fixed predictors, that is, taxon, age, sex, element preservation and the age-by-taxon interaction. We excluded all sex unknown and age indeterminate skeletal elements from model 2, resulting in a reduced sample of $n = 604$. Given a prevalence of trauma in male individuals (see Fig. 2), we reproduced these two model variants using a male-restricted data subset. In model 3 ($n = 462$), we exclusively tested for taxon differences, excluding female and sex unknown skeletal elements. Model 4 ($n = 407$) included the predictors taxon, age, element preservation and the age-by-taxon interaction. We excluded female, sex unknown and age indeterminate skeletal elements from this model.

Specimen-level models (models 5–8). As a complementary conservative approach, we repeated the above analyses on the specimen level. This overcomes potential pseudo-replication of trauma incidence when lesions extend over multiple skeletal elements of the same cranium, or a single cranium exhibits several lesions, but does not take variation in trauma incidences between skeletal elements into account.

Specimen-level models 5–8 were identical to the element-based models 1–4, respectively, as described above. Cranial trauma presence or absence, however, was here scored at the level of specimens, resulting in sample sizes of $n = 204$ in model 5, $n = 89$ in model 6, $n = 76$ in model 7 and $n = 59$ in model 8. The preservation score in these models (specimen preservation) is a combined proxy of skull completeness and its average preservation category, calculated as the sum of all available element-based preservation scores divided by 14 skeletal elements. Location was added as the only random intercept in models 5–8.

As suggested for binary response variables[38], we fixed the residual before 1 and chose an inverse Gamma prior for random effects[39]. Model parameters were chosen to maximize model fit, visible with (i) an autocorrelation value[38] between posterior parameter estimates ≤ 0.05; (ii) parameter estimates reaching conversion between four independent model chains[40] as reflected in the potential scale reduction factor < 1.01; and (iii) observed trauma prevalence falling within the 95% highest posterior density intervals of their respective posterior distribution. These criteria were met after 5,100,000 MCMC iterations, a burn-in of 100,000, and a thinning interval of 1,000, resulting in approximately 5,000 samples in all posterior distributions. From these posterior distributions, we derived the highest posterior density intervals (or credible intervals) for each parameter estimate and denoted them statistically significant ($^{***}P < 0.01$, $^{**}P < 0.05$) or statistical trend ($^{*}P < 0.10$) when not including zero. These intervals formed the basis for statistical inference and hypothesis testing. Plots in Fig. 2 show model predictions for element-preservation category 50–75%, plots in Fig. 3 show the predicted trauma prevalence for specimens at their mean preservation score. In both cases, predictions linearly scale with the other preservation categories, generating overall slightly larger or smaller values but no change in the effect pattern for taxon, sex, age and the age-by-taxon interaction.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Code availability. The R code used to analyse the data in this study is available upon request from the corresponding author.

Data availability

Specimen-level data that support the findings of this study are provided in Supplementary Tables 1, 2. Quantification data for skeletal elements are available from the corresponding author upon reasonable request. Source Data for Figs. 2, 3 and Extended Data Figs. 1, 2 are provided in the online version of the paper.

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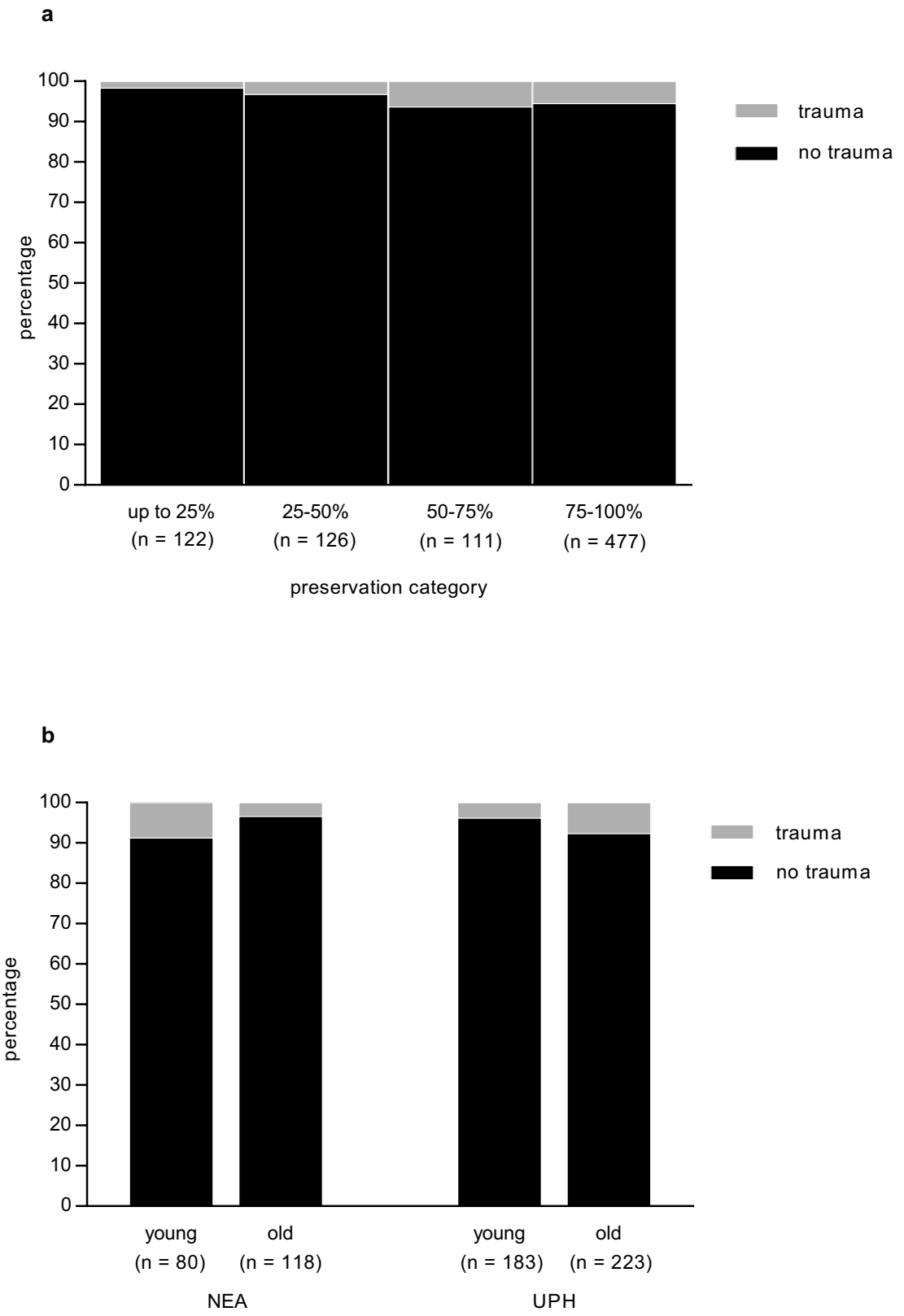
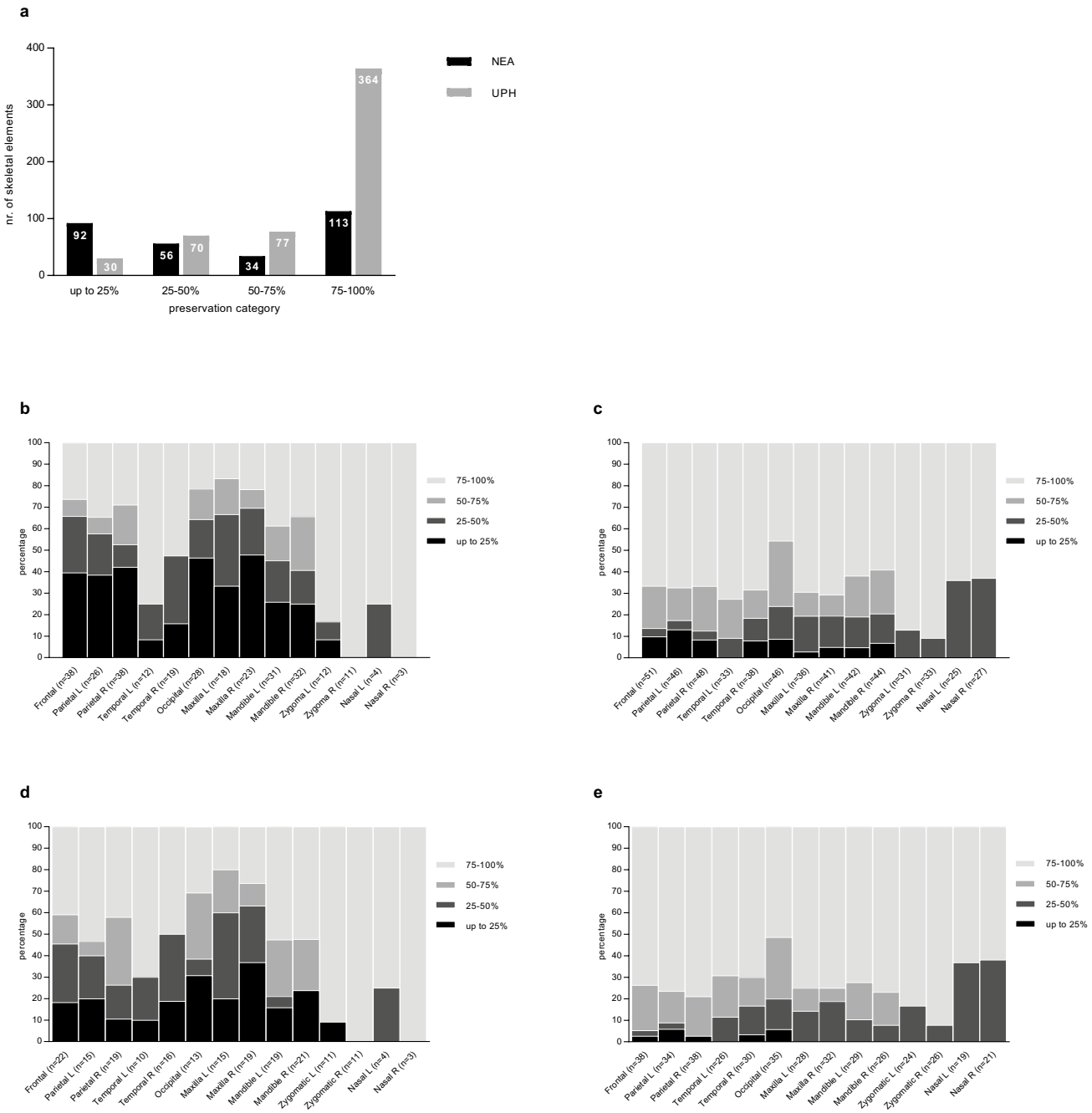


Extended Data Fig. 1 | Ratio of skeletal elements with and without trauma. a, Ratios of skeletal elements with and without trauma per preservation category for the full dataset of $n = 836$ skeletal elements. **b**, Ratios of skeletal elements with and without trauma per age cohort (young or old) and taxon (Neanderthals or Upper Palaeolithic modern humans), excluding sex unknown and age indeterminate skeletal elements ($n = 604$). Sample sizes given below bars represent numbers of skeletal elements of each subsample.



Extended Data Fig. 2 | Preservation of skeletal elements of Neanderthals and Upper Palaeolithic modern humans. a, Number of skeletal elements in each preservation category for Neanderthals and Upper Palaeolithic modern humans for the full dataset of $n = 836$ skeletal elements. **b**–**e**, Percentages of the four preservation categories for each skeletal element for Neanderthals (**b**; full dataset, $n = 295$ skeletal elements), Upper Palaeolithic modern humans (**c**; full dataset, $n = 541$ skeletal elements), Neanderthals (**d**; reduced dataset, excluding age indeterminate and sex unknown elements, $n = 198$) and Upper Palaeolithic modern humans (**e**; reduced dataset, excluding age indeterminate and sex unknown elements, $n = 406$). L and R indicate left and right, respectively.

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☐	☒	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	No software was used for data collection.
Data analysis	We used the MCMCglmm package for R version 3.4.3 for data analysis.

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Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	We did not determine or restrict sample size a priori but collected as many fossil specimens as possible from available published resources when the following criteria were met: (1) age-at-death > 12 years , (2) from a time period between ca. 80-20 ka BP, and (3) quantifiable, i.e. published with anatomical descriptions, or depictions like photos, scans, etc.
Data exclusions	We analyzed the full data set without any exclusions in models 1 and 5. Subsequently, in models 2 to 4 and 6 to 8, we used different data subsets enabling us to add more predictors into the models by excluding incompletely scored variables. We therefore excluded sex unknown, age indeterminate or female skeletal elements in different combinations in these model variants.
Replication	We did not perform experiments. Our data was collected from the literature and trauma diagnoses were adopted from the original specimens' examiners, i.e. all data analyzed in this study is publicly available. Results can be recalculated using our data and methods and are therefore replicable.
Randomization	Randomization is not relevant to our study because no experiments were performed. All biological categories used in our study (taxon, sex, age) are predetermined by assessments of the original specimens' examiners. We adopted those assessments to allocate fossil specimens into our sample groups. We assigned each skeletal element to one of four preservation categories based on its completeness. In this respect we considered a 25 % grading a good balance between detailed data recording and analytical applicability. We allocated sites providing fossil specimens to geographical locations based on conglomerates of sites and geographical barriers in Eurasia.
Blinding	Our analytical framework did not require blinding because we did not perform experiments but data was collected from the literature.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging