Beier, J., Anthes, N., Wahl, J. *et al.* Similar cranial trauma prevalence among Neanderthals and Upper Palaeolithic modern humans. Accepted manuscript, published in *Nature* **563,** 686–690 (2018) doi:10.1038/s41586-018-0696-8

https://doi.org/10.1038/s41586-018-0696-8

# Similar cranial trauma prevalence among Neanderthals and Upper Paleolithic humans

Authors: Judith Beier[1], Nils Anthes[2], Joachim Wahl[1,3], Katerina Harvati[*1,4]

[1] Paleoanthropology, Senckenberg Centre for Human Evolution and Palaeoenvironment, University of Tübingen, Rümelinstraße 23, 72070 Tübingen, Germany

[2] Animal Evolutionary Ecology Group, Institute of Evolution and Ecology, University of Tübingen, Auf der Morgenstelle 28E, 72076 Tübingen, Germany

[3] State Office for Cultural Heritage Management Baden-Württemberg, Osteology, Stromeyersdorfstraße 3, 78467 Konstanz, Germany

[4] DFG Center for Advanced Studies 'Words, Bones, Genes, Tools', University of Tübingen, Rümelinstraße 23, 72070 Tübingen, Germany

**Neanderthals are commonly depicted as leading dangerous lives and permanently struggling for survival. This view largely relies on their reported high incidences of trauma[1,2], variously attributed to violent social behavior[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, close encounters with large prey mammals resulting from a lack of long-distance 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 using an exhaustive new fossil database. We show that Neanderthals and Upper Paleolithic modern humans exhibit similar overall incidences of cranial trauma, which are higher for males in both taxa, consistent with patterns shown by later modern human**

**populations. Beyond these similarities we observed species-specific age-related variation in trauma prevalence, suggesting either differences in the timing of injuries during life, or 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 leading stressful, dangerous lives[1,6–9]. Traumatic injuries, considered common among adult Neanderthal remains[1], are a major piece of evidence supporting this hypothesis: not only are Neanderthals proposed to suffer from high trauma prevalence[2,3,10,11], they are also thought to exhibit more traumatic injuries than early modern humans[9,12,13]. Explanations for this include violent social behavior[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 paleobiology and behavior, and have shaped the prevailing perception of the species. However, they are largely based on anecdotal evidence, since trauma among Paleolithic humans is often reported on a descriptive, case-by-case basis. The few systematic, quantitative studies conducted to date have yielded contradictory results[2,4,11,14,15], but question the prevailing view of 'the highly traumatized Neandertal'[15].

Current Paleolithic trauma research 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, since they focus exclusively on the injured, cannot elucidate population-level trauma prevalence. The latter requires an examination of both injured and non-injured individuals. Furthermore, contextual factors such as age-at-death, sex, and skeletal preservation, are rarely accounted for[15]. These variables can significantly 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 / nomads[2,4,15,16] – but only rarely to Upper Paleolithic 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 hampered the validity of statistical inference of most previous research.

Our analysis is the first to assess the hypothesis of higher cranial trauma prevalence among Neanderthals (NEA) relative to Upper Paleolithic modern humans (UPH) through a population-level comparison, including contextual data and using the currently largest fossil dataset available. We systematically compiled published information on fossil crania from the Middle and Upper Paleolithic of Eurasia, dating to roughly 80-20 ka BP (Fig. 1). Cranial injuries, considered typical for NEA[1], are a particularly reliable trauma archive because they heal with only minor bone remodeling and therefore leave visible lesions even after full recovery[22].

For each specimen we recorded whether a trauma was present (0 or 1), the taxon (NEA, UPH), sex (male, female, unknown), age-at-death (juvenile/young adult, old adult, indeterminate), preserved skeletal element(s) (14 major cranial bones), the preservation percentage of each skeletal element (≤ 25 %, 25-50 %, 50-75 %, 75-100 %), and location (five geographical regions within Eurasia; Supplementary Tables 1 and 2). We then used generalized linear mixed models (GLMM) to assess differences in trauma prevalence among 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 NEA, 12 UPH; Supplementary Table 3) in our sample of 114 NEA and 90 UPH specimens

(Supplementary Tables 1 and 2). At the level of skeletal elements, this corresponds to 14 of 295 NEA, and 25 of 541 UPH cranial elements 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 on hierarchically nested subsets of the raw data. The first set (models 1-4) followed an element-based approach, with skeletal elements being the unit of analysis; the second set (models 5-8) was based on individuals (see Methods). Trauma was modeled 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.

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 age-by-taxon interaction. Given trauma 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 sex unknown and age indeterminate specimens to assess how age, sex, specimen-preservation, and the age-by-taxon interaction 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 NEA and UPH (taxon effect in models 1-8 in Tab. 1, Fig. 2a-d, 3a-d). Instead, we found significantly higher trauma prevalence in males compared to females (sex effect in models 2 and 6, Tab. 1, Fig. 2b, 3b). Furthermore, trauma prevalence significantly increased with preservation status, indicating a greater probability to detect a trauma on more complete skeletal elements / individuals (preservation effect in models 2, 4, 6 and 8, Tab. 1, 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, Tab 1, Fig. 2b,d, Extended Data Fig. 1b): NEA had significantly higher trauma prevalence when young, while UPH maintained similar trauma prevalence across age cohorts. While a similar pattern appeared to be present in the specimen-level models (Fig. 3b,c), the interaction failed to reach statistical significance.

The mean model-predicted trauma prevalence for skeletal elements in preservation category 50-75 % ranged between 0.03 and 0.17 (0.0002-0.39 95 % CI) for NEA, and between 0.02 and 0.12 (0.00006-0.35 95 % CI) for UPH (Fig. 2a-d). For specimens at their mean preservation score these values ranged between 0.04 and 0.33 (0.000002-0.62 95 % CI) for NEA, and between 0.02 and 0.34 (0.000001-0.62 95 % CI) for UPH (Fig. 3a-d).

Our results reject the hypothesis that Neanderthals exhibit more cranial trauma than Upper Paleolithic modern humans in Western Eurasia, and rather indicate that the two taxa exhibited a similar overall prevalence of cranial injuries. Previously suggested values of 30-40 % cranial trauma prevalence for NEA[3,10] represent the very limit of our models' predictions for NEA (mean prevalence of 3-17 % for skeletal elements, and 4-33 % for individual specimens), values comparable to those found for UPH (2-12 % for skeletal elements, 2-34 % for specimens), and reported for later modern humans, including Mesolithic hunter-gatherers[23], Neolithic agriculturalists[24,25], and recent hunter-gatherers[26]. Nevertheless, trauma prevalence derived from skeletal remains must not be equated with actual numbers of injuries experienced during an individual's lifetime, and comparisons of crude trauma frequencies should be considered with caution since 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 behaviors (division of labor, initiation rites, or violent conflict)[18,20,21]. Trauma prevalence was further affected by the preservation state of skeletal remains, with more complete crania / cranial elements more likely to preserve traumatic lesions. We therefore caution against quantitative trauma analyses that do not address preservation bias.

Both taxa presented mostly healed traumata, and we did not find markedly higher trauma prevalence among 'old' skeletal elements in either. 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 in the long term due 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 their injuries were survived, exhibit 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 age-by-taxon interaction in trauma prevalence was found by our element-based analysis. For NEA, this result suggests that cranial trauma was sustained early in life (before 30 years) 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, UPH were either less likely than NEA to sustain trauma when 'young'; and/or they sustained trauma in a similar frequency when 'young', but 'young' UPH trauma survivors had lower mortality risk relative to 'young' NEA trauma survivors. In other words, 'young' UPH injured individuals had 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 trauma prevalence.

Our study addressed the controversial topic of trauma prevalence in the Paleolithic by reassessing cranial trauma data using a novel state-of-the-art methodological approach. It is the largest population-level investigation of Neanderthal cranial trauma to date and the first to account for differential skeletal preservation and contextual explanatory variables using Upper Paleolithic modern humans as a comparative sample. The available evidence indicates similar overall trauma prevalence in Neanderthals and Upper Paleolithic 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 trauma-survivor mortality risk.

## References


1. Berger, T. D. & Trinkaus, E. Patterns of Trauma among the Neandertals. J. Archaeol. Sci. 22, 841–852 (1995).

2. Underdown, S. A comparative approach to understanding Neanderthal trauma. Period. Biolog. 108, 485–493 (2006).

3. Courville, C. B. in Diseases in antiquity, edited by D. R. Brothwell & A. T. Sandison (C.C. Thomas1967), pp. 606–622.

4. Hutton Estabrook, V. & Frayer, D. W. in The Routledge Handbook of the Bioarchaeology of Human Conflict, edited by C. J. Knüsel & M. J. Smith (Routledge, London/New York, 2014), pp. 67–89.

5. Camarós, E., Cueto, M., Lorenzo, C., Villaverde, V. & Rivals, F. Large carnivore attacks on hominins during the Pleistocene. A forensic approach with a Neanderthal example. Archaeol. Anthropol. Sci. 8, 635–646 (2016).

6. Trinkaus, E. Hard times among the Neanderthals. Nat. Hist. 87, 58–63 (1978).

7. Trinkaus, E. Neanderthal Mortality Patterns. J. Archaeol. Sci. 22, 121–142 (1995).

8. Pettitt, P. B. Neanderthal lifecycles. developmental and social phases in the lives of the last archaics. World Archaeology 31, 351–366 (2000).

9. Klein, R. G. The Human Career. Human biological and cultural origins. 3rd ed. (University of Chicago Press, Chicago/London, 2009).

10. Kunter, M. Gewalt- und Arbeitsverletzungen in alter Zeit. Knochenfunde als Geschichtsquelle (1986).

11. Nakahashi, W. The effect of trauma on Neanderthal culture: A mathematical analysis. HOMO (2017).

12. McBrearty, S. & Brooks, A. S. The revolution that wasn't: a new interpretation of the origin of modern human behavior. J. Hum. Evol. 39, 453–563 (2000).

13. Trinkaus, E., Buzhilova, A. P., Mednikova, M. B. & Dobrovolskaya, M. V. in The People of Sunghir, edited by E. Trinkaus, A. P. Buzhilova, M. B. Mednikova & M. V. Dobrovolskaya (Oxford University Press, Oxford, New York, 2014), pp. 269–294.

14. Brennan, M. U. Health and disease in the Middle and Upper Paleolithic of southwestern France: a bioarcheological study (New York, 1991).

15. Hutton Estabrook, V. Sampling Biases and New Ways of Addressing the Significance of Trauma in Neandertals (2009).

16. Hutton Estabrook, V. Is Trauma at Krapina like all Other Neandertal Trauma? A Statistical Comparison of Trauma Patterns in Neandertal Skeletal Remains. Period. Biolog. 109, 393–400 (2007).

17. Trinkaus, E. Neandertals, early modern humans, and rodeo riders. J. Archaeol. Sci. 39, 3691–3693 (2012).

18. Larsen, C. S. Bioarcheology. Interpreting behavior from the human skeleton (Cambridge University Press, Cambridge [etc.], 1997).

19. Jurmain, R. Stories from the skeleton. Behavioural reconstruction in human osteology (Gordon & Breach, Amsterdam, 1999).

20. Martin, D. L. & Harrod, R. P. Bioarchaeological contributions to the study of violence. Am. J. Phys. Anthropol. 156 Suppl 59, 116–145 (2015).

21. Redfern, R. C. Injury and trauma in bioarchaeology. Interpreting violence in past lives (Cambridge University Press, Cambridge, United Kingdom, 2016).

22. Campillo, D. Healing of the Skull Bone after Injury. J. Paleopathol. 3, 137–149 (1991).

23. Terberger, T. in Frühe Spuren der Gewalt, edited by J. Pieck & T. Terberger (Landesamt für Kultur und Denkmalpflege, Schwerin, 2006), pp. 129–154.

24. Fibiger, L., Ahlström, T., Bennike, P. & Schulting, R. J. Patterns of Violence-Related Skull Trauma in Neolithic Southern Scandinavia. Am. J. Phys. Anthropol. 150, 190–202 (2013).

25. Jiménez-Brobeil, S. A., Du Souich, P. & Al Oumaoui, I. Possible relationship of cranial traumatic injuries with violence in the south-east Iberian Peninsula from the Neolithic to the Bronze Age. Am. J. Phys. Anthropol. 140, 465–475 (2009).

26. Schwitalla, A. W., Jones, T. L., Pilloud, M. A., Codding, B. F. & Wiberg, R. S. Violence among foragers: The bioarchaeological record from central California. Journal of Anthropological Archaeology 33, 66–83 (2014).

27. Cohen, H. et al. Trauma to the Skull. A Historical Perspective from the Southern Levant (4300BCE–1917CE). Int. J. Osteoarchaeol. 24, 722–736 (2014).

28. Glencross, B. & Sawchuk, L. The person-years construct. Ageing and the prevalence of health related phenomena from skeletal samples. Int. J. Osteoarchaeol. 13, 369–374 (2003).

29. Boldsen, J. L., Milner, G. R. & Weise, S. Cranial vault trauma and selective mortality in medieval to early modern Denmark. Proc. Natl. Acad. Sci. USA 112, 1721–1726 (2015).

30. Milner, G. R. & Boldsen, J. L. Life not death: Epidemiology from skeletons. International Journal of Paleopathology 17, 26–39 (2017).

31. Eriksson, M., Brattström, O., Larsson, E. & Oldner, A. Causes of excessive late death after trauma compared with a matched control cohort. Br J Surg 103, 1282–1289 (2016).

32. Mitchell, R. J., Cameron, C. M. & McClure, R. Higher mortality risk among injured individuals in a population-based matched cohort study. BMC public health 17, 150 (2017).

Acknowledgements: We thank Jiří Svoboda, Sandra Sázelová (Paleolithic and Paleoanthropology Research Center, Dolní Věstonice), Martin Oliva and Zdeněk Tvrdý (Moravian Museum, Anthropos Institute, Brno) for permission to study the Dolní Věstonice, Pavlov and Brno collections, and Laura Limmer for her contribution. This research is funded by the German Research Foundation (DFG-HA-5258/12-1, DFG-WA-2808/2-1) and supported by the University of Tübingen and Senckenberg Gesellschaft für Naturforschung. K. Harvati is supported by ERC-CoG-724703 and DFG-FOR-2237.

Author Contributions:

J.B., J.W., K.H. conceived the study. J.B.: data collection. J.B., J.W., K.H., N.A.: methods development. J.B., N.A.: data analysis. J.B., J.W., K.H., N.A.: wrote the manuscript.

Author Information:



The authors declare no competing interests.

Correspondence and requests for materials should be addressed to katerina.harvati@ifu.uni-tuebingen.de.

**Table 1. Summary statistics of generalized linear mixed models.**

| 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 x 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 x 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 x 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 x taxon | 1.584 | -1.762 | 4.621 | 0.320 |

Trauma prevalence was modelled using a Markov chain Monte Carlo algorithm in two model sets with four data subsets each: models 1-4 comprise skeletal elements, models 5-8 comprise cranial specimens. Parameter estimates 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 detail. [a] full dataset; [b] exclusion of sex unknown and age indeterminate elements/specimens; [c] exclusion of female and sex unknown elements/specimens; [d] exclusion of female, sex unknown, and age indeterminate elements/specimens.

**Fig. 1. Neanderthal and Upper Paleolithic modern human sites.**

NEA sites: blue triangles, UPH sites: red dots. Numbers in brackets indicate number of specimens / number of skeletal elements respectively. Sites Chagyrskaya (34) and Pokrovka (74) were projected 2670 and 2975 km west respectively for better visualization.

**Fig. 2. Predicted cranial trauma prevalence for skeletal elements of Neanderthals (NEA) and Upper Paleolithic modern humans (UPH).**

Predictions based on posterior estimates of four GLMMs using a Markov chain Monte Carlo algorithm. Sample sizes represent single skeletal elements, treated as biologically independent samples in models 1-4 (see Methods). Markers denote predicted means, bars lower and upper 95 % credible intervals for (a) model 1 (full dataset, n = 836) comprising the predictor variable taxon; (b) model 2 (excluding sex unknown and age indeterminate skeletal elements, n = 604) comprising variables taxon, sex, age, element-preservation, and the age-by-taxon interaction; (c) model 3 (excluding female and sex unknown skeletal elements, n = 462) comprising the variable taxon; and (d) model 4 (excluding female, sex unknown, and age indeterminate skeletal elements, n = 407) comprising variables taxon, age, element-preservation, and the age-by-taxon interaction. Predictions given for skeletal elements when 50-75 % complete; predictions for other preservation categories scale linearly.

**Fig. 3. Predicted cranial trauma prevalence for Neanderthal (NEA) and Upper Paleolithic modern human (UPH) individual cranial specimens.**

Predictions based on posterior estimates of 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 predicted means, bars lower and upper 95 % credible intervals for (a) model 5 (full dataset, n = 204) comprising the predictor variable taxon; (b) model 6 (excluding sex unknown and age indeterminate specimens, n = 89) comprising variables taxon, sex, age, specimen-preservation, and the age-by-taxon interaction; (c) model 7 (excluding female and sex unknown specimens, n = 76) comprising the variable taxon; and (d) model 8 (excluding female, sex unknown, and age indeterminate specimens, n = 59) comprising variables taxon, age, specimen-preservation, and the age-by-taxon interaction. Predictions given for mean specimen- preservation scores; predictions for other preservation scores scale linearly.

## 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 Paleolithic sites yielding skull remains from classic Neanderthals (NEA, ca. 80-30 ka BP) and early to mid-Upper Paleolithic modern humans (UPH, ca. 35-20 ka BP) (Fig. 1[33,34]; Supplementary Tables 1 and 2 provide information on studied specimens). We excluded specimens comprising only dental remains and restricted our sample to adolescent and adult specimens with a minimum estimated age-at-death of 12 years[35]. For each specimen we recorded the taxon (NEA or UPH), 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 below), and if the skeletal element was affected by trauma (binary). Because trauma prevalence may vary across geographical regions due 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 specimens' examiners. These literature-based assignments may be influenced by observer bias or by the use of different methods. Nevertheless, we decided in favor 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 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. Importantly, we expect misclassifications of traumatic lesions, age, or sex to be equally likely in NEA and UPH, and therefore not to 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.

Quantification

Skeletal preservation has a direct impact on the census of trauma prevalence, because it is more likely to detect an injury on a more complete bone[36]. 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 NEA and younger UPH, we quantified the preservation status for each of the 14 major skull bones, i.e. skeletal elements, separately. These are the frontal and occipital bones, as well as each left and right 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 %. Due 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 whose 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 NEA and UPH skeletal remains, with NEA being biased towards incompletely preserved skeletal remains (see Extended Data Fig. 2a-e).

Statistical methods

We predicted trauma prevalence using generalized linear mixed models (GLMM). 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[37] for R version 3.4.3[38]. Trauma presence or absence was modeled 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 GLMM models on subsets of the raw data. The first set (models 1-4) followed a skeletal element-level approach, while 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 (NEA vs. UPH), age (young vs. old, with 30 years as the cut-off), and sex (male vs. female), as well as the z-transformed four-level covariate element-preservation (0.25, 0.5, 0.75, 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 all models.

Because traumata are not equally frequent in the different cranial regions[24,27,39], we entered intercepts for skeletal element into the random component of 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 sub-sets and different explanatory variable combinations, while maintaining the same two random components in each case. Model 1 comprised taxon as the only fixed predictor. The exclusion of the other, incompletely scored, contextual predictor variables enabled us to analyze the full dataset of n = 836 skeletal elements. Model 2 comprised all fixed predictors, i.e. 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 results), 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) comprised 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 allow to 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[40], we fixed the residual prior to 1 and chose an inverse Gamma prior for random effects[41]. Model parameters were chosen so as to maximize model fit, visible with (i) an autocorrelation value[40] between posterior parameter estimates ≤ 0.05, (ii) parameter estimates reaching conversion between four independent model chains[42] as reflected in the so-called potential scale reduction (PSRI) factor < 1.01, and (iii) observed trauma prevalence falling within the 95 % highest posterior density (HPD) 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 1000, resulting in approx. 5000 samples in all posterior distributions. From these posterior distributions, we derived HPD intervals (= credible intervals) for each parameter estimate and denoted them statistically significant (at 99 % = ** or 95 % = *) or statistical trend (at 90 % = (*)) 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 age-by-taxon interaction.

References

33. "Natural Earth". Free vector and raster map data (naturalearthdata.com) (2018).

34. QGIS Development Team. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org (2018).

35. J. Buikstra & D. H. Ubelaker (eds.). Standards for data collection from human skeletal remains. Proceedings of a seminar at the Field Museum of Natural History (Arkansas Archeological Survey, Fayetteville, Ark., 1994).

36. Judd, M. A. Comparison of Long Bone Trauma Recording Methods. J. Archaeol. Sci. 29, 1255–1265 (2002).

37. Hadfield, J. D. MCMC Methods for Multi-Response Generalized Linear Mixed Models. The MCMCglmmR Package. J. Stat. Softw. 33 (2010).

38. R Core Team. R: A language and environment for statistical computing. Available at http://www.R-project.org/ (2017).

39. Walker, P. L. Cranial injuries as evidence of violence in prehistoric southern California. Am. J. Phys. Anthropol. 80, 313–323 (1989).

40. Hadfield, J. MCMCglmm Course Notes. Available at https://cran.r-project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf (2017).

41. Gelman, A. & Hill, J. Data Analysis Using Regression and Multilevel/Hierarchical Models (Cambridge University Press, Cambridge, 2006).

42. Gelman, A. & Rubin, D. B. Inference from Iterative Simulation Using Multiple Sequences. Stat. Sci. 7, 457–472 (1992).

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

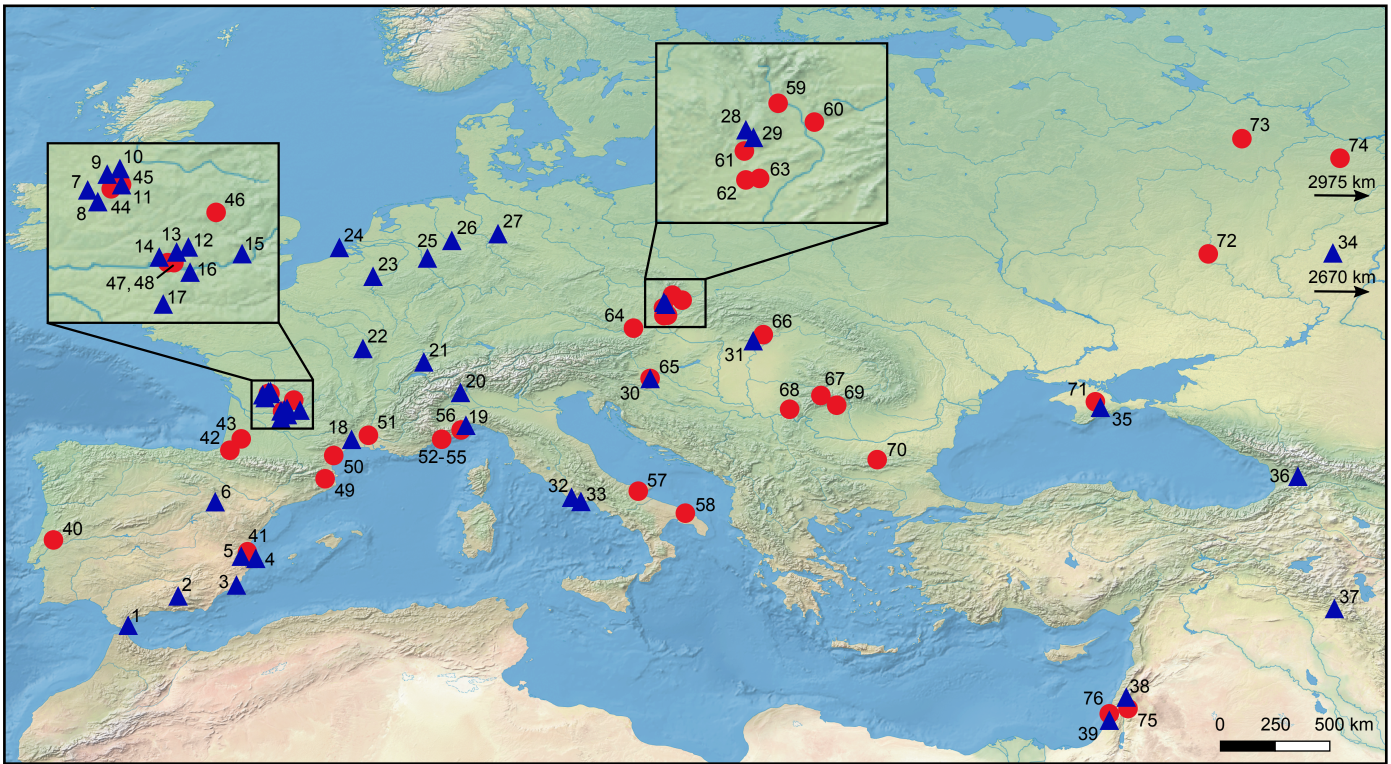
Code availability: The R code used to analyze the data in this study is available upon request.

**Extended Data Fig. 1: Ratio of skeletal elements with and without trauma.**

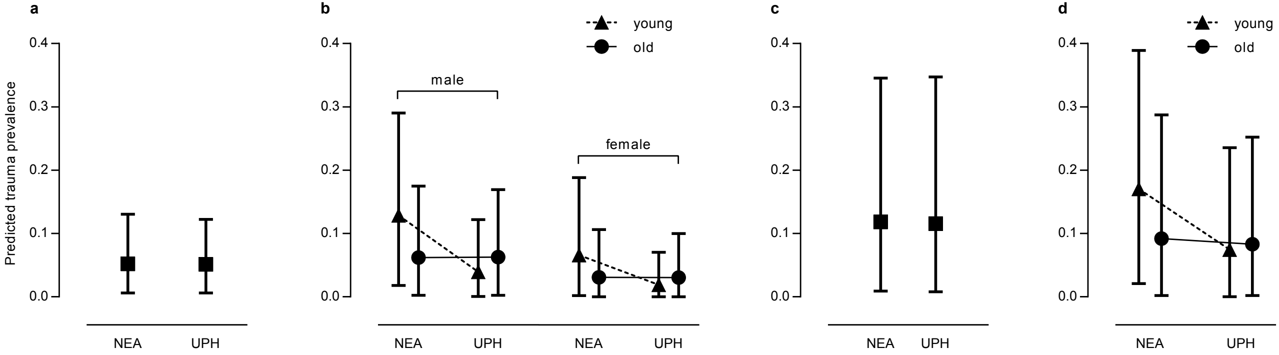
Bars indicate ratios of skeletal elements with and without trauma, (a) per preservation category for the full dataset of n = 836 skeletal elements, and (b) per age cohort (young/old) and taxon (NEA/UPH) excluding sex unknown and age indeterminate skeletal elements (n = 604). Sample sizes given below bars represent numbers of skeletal elements of each subsample.

**Extended Data Fig. 2: Preservation of NEA and UPH skeletal elements.**

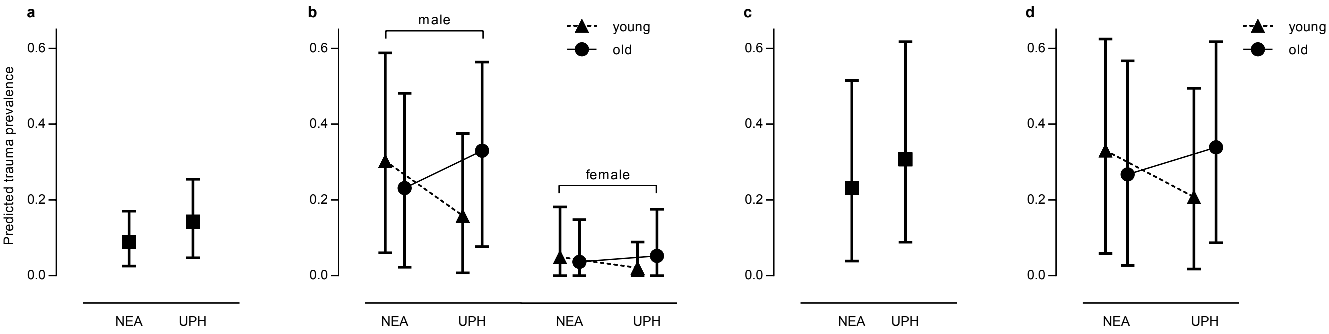
(a) Bars and white labels illustrate the number of skeletal elements in each preservation category for NEA and UPH for the full dataset of n = 836 skeletal elements. Graphs b-e display the percentages of the four preservation categories for each skeletal element for (b) NEA (full dataset, n = 295 skeletal elements), (c) UPH (full dataset, n = 541 skeletal elements), (d) NEA (reduced dataset excluding age indeterminate and sex unknown elements, n = 198), and (e) UPH (reduced dataset excluding age indeterminate and sex unknown elements, n = 406).




| Neanderthal sites | | | | Upper Paleolithic modern human sites | | | |
|---|---|---|---|---|---|---|---|
| 1 | Gibraltar (1,10) | 21 | Cotencher (1,2) | 40 | Caldeirão (1,1) | 60 | Predmost (11,85) |
| 2 | Horá (1,1) | 22 | Genay (1,5) | 41 | Parpallo (1,11) | 61 | Brno (2,11) |
| 3 | Palomas (3,9) | 23 | Spy (2,16) | 42 | Isturitz (1,2) | 62 | Pavlov (3,13) |
| 4 | Cova Foradà (1,3) | 24 | Zeeland Ridges (1,1) | 43 | Brassempouy (1,2) | 63 | Dolní Věstonice (6,67) |
| 5 | Cova Negra (2,2) | 25 | Neanderthal (1,8) | 44 | Vilhonneur (1,4) | 64 | Willendorf (1,2) |
| 6 | Gegant (1,2) | 26 | Warendorf (1,1) | 45 | Fontéchevade (1,1) | 65 | Vindija (3,4) |
| 7 | Petit-Puymoyen (3,4) | 27 | Sarstedt (2,2) | 46 | Cussac (1,9) | 66 | Tapolca (1,1) |
| 8 | La Quina-Amont (9,21) | 28 | Kůlna (2,2) | 47 | Cro Magnon (3,29) | 67 | Cioclovina (1,8) |
| 9 | Pradelles/Marillac (16,19) | 29 | Ochoz (1,2) | 48 | Abri Pataud (1,14) | 68 | Oase (2,14) |
| 10 | St. Césaire (1,8) | 30 | Vindija (26,33) | 49 | Mollet (1,5) | 69 | Muierii (2,12) |
| 11 | Fontéchevade (1,3) | 31 | Subalyuk (1,3) | 50 | Crouzade (2,3) | 70 | Bacho Kiro (1,1) |
| 12 | Régourdou (1,2) | 32 | Grotta Breuil (1,1) | 51 | La Balauzière (2,8) | 71 | Buran Kaya III (3,4) |
| 13 | Le Moustier (1,12) | 33 | Guattari (3,14) | 52 | Baousso da Torre (1,4) | 72 | Kostenki (3,24) |
| 14 | La Ferrassie (2,14) | 34 | Chagyrskaya (1,1) | 53 | Barma Grande (3,28) | 73 | Sunghir (3,26) |
| 15 | La Chapelle (1,12) | 35 | Zaskalnaya VI (1,1) | 54 | Caviglione (1,13) | 74 | Pokrovka (1,1) |
| 16 | Combe Grenal (6,6) | 36 | Sakajia (1,1) | 55 | Grotte des Enfants (2,28) | 75 | Ohalo II (1,14) |
| 17 | Monsempron (2,2) | 37 | Shanidar (6,49) | 56 | Arene Candide (1,13) | 76 | el-Wad (3,3) |
| 18 | Hortus (2,3) | 38 | Amud (3,14) | 57 | Grotta Paglicci (9,20) | | |
| 19 | Fate (2,2) | 39 | Kebara (2,3) | 58 | Ostuni (1,14) | | |
| 20 | Ciota Ciara (1,1) | | | 59 | Mladeč (9,42) | | |



a
b
c
d
young
old
Predicted trauma prevalence
0.0
0.1
0.2
0.3
0.4
male
female
NEA
UPH


a
b
c
d
Predicted trauma prevalence
0.0
0.2
0.4
0.6
male
female
young
old
NEA
UPH