Prevalence of cranial trauma in Eurasian Upper Paleolithic humans

Judith Beier | Nils Anthes | Joachim Wahl | Katerina Harvati

1Paleoanthropology, Senckenberg Centre for Human Evolution and Palaeoenvironment, University of Tübingen, Tübingen, Germany
2Animal Evolutionary Ecology Group, Institute of Evolution and Ecology, University of Tübingen, Tübingen, Germany
3DFG Center for Advanced Studies “Words, Bones, Genes, Tools”, University of Tübingen, Tübingen, Germany

Correspondence
Judith Beier, Paleoanthropology, Senckenberg Centre for Human Evolution and Palaeoenvironment, University of Tübingen, Rümelinstraße 23, 72070 Tübingen, Germany. Email: judith.beier@uni-tuebingen.de

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Abstract
Objectives: This study characterizes patterns of cranial trauma prevalence in a large sample of Upper Paleolithic (UP) fossil specimens (40,000–10,000 BP).

Materials and Methods: Our sample comprised 234 individual crania (specimens), representing 1,285 cranial bones (skeletal elements), from 101 Eurasian UP sites. We used generalized linear mixed models (GLMMs) to assess trauma prevalence in relation to age-at-death, sex, anatomical distribution, and between pre- and post-Last Glacial Maximum (LGM) samples, while accounting for skeletal preservation.

Results: Models predicted a mean cranial trauma prevalence of 0.07 (95% CI 0.003–0.19) at the level of skeletal elements, and of 0.26 (95% CI 0.08–0.48) at the level of specimens, each when 76–100% complete. Trauma prevalence increased with skeletal preservation. Across specimen and skeletal element datasets, trauma prevalence tended to be higher for males, and was consistently higher in the old age group. We found no time-specific trauma prevalence patterns for the two sexes or age cohorts when comparing samples from before and after the LGM. Samples showed higher trauma prevalence in the vault than in the face, with vault remains being affected predominantly in males.

Discussion: Cranial trauma prevalence in UP humans falls within the variation described for Mesolithic and Neolithic samples. According to our current dataset, UP males and females were exposed to slightly different injury risks and trauma distributions, potentially due to different activities or behaviors, yet both sexes exhibit more trauma among the old. Environmental stressors associated with climatic changes of the LGM are not reflected in cranial trauma prevalence. To analyze trauma in incomplete skeletal remains we propose GLMMs as an informative alternative to crude frequency calculations.

KEYWORDS
bioarchaeology, crania, generalized linear mixed models, trauma, Upper Paleolithic

INTRODUCTION

Technological, cultural, and behavioral innovations are unique characteristics of the Upper Paleolithic (UP) period (ca. 40,000–10,000 BP). It has been suggested that marked climatic and environmental fluctuations over the course of several millennia exposed anatomically modern humans to climate change induced stresses, which prompted biocultural adaptations of survival strategies regarding subsistence,
technology, and social life, buffering against environmental stressors (Banks et al., 2008; Banks, D’Errico, & Zilhão, 2013; Burke et al., 2017; Holt, 2018; Straus, 2015; Zuckerman, 2018; Zuckerman, Martin, & Debra, 2016; Zuckerman, Turner, & Armelagos, 2011). Frequent marked climate oscillations and a gradual temperature decline (Barron, van Andel, & Pollard, 2003; Clark et al., 2009; Davies & Gollup, 2003; Mix, 2001; van Andel, 2003) changed vegetation and habitats of prey mammals, the main subsistence resource of Paleolithic hunter-gatherers, thus affecting habitat suitability (Burke et al., 2017; Holt, 2018). At around 26,500–19,000 BP, climate deteriorations culminated in the Last Glacial Maximum (LGM), when ice sheets reached their maximum extent and covered most of Northern and Central Europe (Clark et al., 2009). As a consequence, human populations in northern latitudes may have gone extinct or retreated to environmentally more favorable regions in southern glacial refugia (Brewster, Meiklejohn, von Cramon-Taubadel, & Pinhasi, 2014; Burke et al., 2017; Chase, Straus, Debénath, Dibble, & McPherron, 2010; Clark et al., 2009; Djindjian, 2016; Maier & Zimmerman, 2017; Straus, 2015; Tallavaara, Luoto, Korhonen, Järvinen, & Seppä, 2015; Wygal & Heidenreich, 2014). Local population extinctions, the fragmentation and reduction of suitable habitats, and limitations to maintain social networks, likely entailed high levels of demographic and environmental stress (Burke et al., 2017; Djindjian, 2016; Maier, 2017; Maier et al., 2016; Straus, 2015).

These scenarios of stress and adaptation mainly rest on archaeological evidence, such as site distributions, animal bone assemblages, and material culture (Banks et al., 2008; Banks et al., 2013; Djindjian, 2016; Langlais et al., 2012; Maier & Zimmerman, 2017; Naudinot et al., 2017; Straus, 2016). Another line of evidence derives directly from human fossil remains. For example, a variety of dental and skeletal stress markers (e.g., dental hypoplasia, Harris lines, periostitis, arthritis, and trauma) indicate some support for health deterioration from pre-LGM to post-LGM populations (Brennan, 1991; Formicola & Holt, 2007; Holt & Formicola, 2008; Trinkaus, 2013). Human groups before and after the LGM differ markedly in their morphology in terms of body height, robusticity, and craniofacial and dental dimensions (Brennan, 1991; Brewster, Meiklejohn, et al., 2014; Brewster, Pinhasi, & Meiklejohn, 2014; Cox, Ruff, Maier, & Mathieson, 2019; Formicola & Giannecehini, 1999; Formicola & Holt, 2007; Holt, 2018; Holt et al., 2018; Holt & Formicola, 2008; Meiklejohn & Babb, 2011; Niskanen, Ruff, Holt, Sládek, & Berner, 2018; Ruff, 2002). These morphological features can result from changing levels of stress (Frayer, 1981), but may also be associated with a large-scale population turnover during recolonization after the LGM as suggested by genetic evidence (Feldman et al., 2019; Fu et al., 2016; Posth et al., 2016).

Trauma patterns can serve as an important measure of the lifestyle, organization, and stresses of past human populations, since traumatic injuries are directly linked to violent encounters (Churchill, Franciscus, McKeen-Peraza, Daniel, & Warren, 2009; Kranioti, Grigorescu, & Harvati, 2019; Larsen, 2015; Martin, Debra, & Anderson, 2014; Martin, Debra, & Harrod, 2015; Mirazón Lahr et al., 2016; Redfern, 2017b; Sala et al., 2015; Wahl & Trautmann, 2012; Walker, 2001), accidents (Kappelman et al., 2016; L’Abbé et al., 2015; Marinho & Cardoso, 2016; Petaros et al., 2013), impairments and care for the injured (Spikins et al., 2019; Spikins, Needham, Tilley, & Hitchens, 2018; Stoddler, 2017; Tilley, 2015, 2017; Trinkaus, 1983), and reflect the various injury risks resulting from occupational, environmental or social conditions (Collier & Primeau, 2019; Delgado-Darias, Alberto-Barroso, & Velasco-Vázquez, 2018; Lambert & Welker, 2017). Nevertheless, population-wide trauma patterns in UP humans have barely been researched. Trinkaus (2012) and Beier, Anthes, Wahl, and Harvari (2018) analyzed trauma in larger samples of UP fossils from Eurasia. They compared their findings to those of Neanderthals and found similar distribution patterns and trauma prevalence in the two groups. However, these studies focused on the between-taxa comparison and not on a comprehensive characterization of the UP period, neglecting large numbers of later UP fossils postdating 20,000 BP.

Here, we present a population-wide characterization of cranial trauma among fossil skeletal remains from the entire UP period of western Eurasia. We performed a comprehensive review of published fossil cranial remains with and without traumatic injuries to characterize patterns of cranial trauma prevalence. The aims of the study were the following:

1. To quantify the overall cranial trauma prevalence for fossil remains from the entire UP period. This estimate allows for diachronic comparisons to Middle Paleolithic, Mesolithic, and Neolithic samples.
2. To examine the contribution of basic demographic variables, namely sex and age-at-death, on cranial trauma prevalence. Previous trauma research suggested a higher prevalence of cranial trauma among older and male individuals (Beier et al., 2018), consistent with the proposed intensification of sexual division of labor in the UP period (Brennan, 1991; Karakostis, Hotz, Tourloukis, & Harvati, 2018; Kuhn & Stiner, 2006; Stiner & Kuhn, 2009; Villotte, Churchill, Doutour, & Henry-Gambier, 2010; Villotte & Knüsel, 2014; Zilhão, 2014).
3. To contrast cranial trauma prevalence of pre- and post-LGM UP humans to investigate possible differences through time. This comparison provides additional data to scrutinize the earlier suggestions of increasing stress and declining health in the late UP (Brennan, 1991; Formicola & Holt, 2007; Holt & Formicola, 2008; Trinkaus, 2013).
4. To examine the distribution of traumatic lesions across the skull to assess whether remain of the cranial vault (neurocranium) or the face (viscerocranium) were more likely to exhibit traumatic lesions. Although trauma distribution within a sample can provide insights into the circumstances of injury, such as violent encounters (Kremer, Racette, Dionne, & Sauvageau, 2008; Kremer & Sauvageau, 2009; Lessa & de Souza, 2006; Martin et al., 2015; Novak, 2006; Redfern, 2017a; Walker, 1989, 1997), little is known about the patterns of trauma in UP remains (Trinkaus, 2012).

Trauma prevalence estimates depend highly on the preservation status of skeletal remains, because once present traumatic lesions may not be preserved in the skeletal record when skeletal.
preservation is poor (Judd, 2002, 2004; Pankovská, Galeta, Uhlik Spěváková, & Nováček, 2019). Consequently, the uncertainty of trauma prevalence estimates increases with decreasing completeness of the remains. Skeletal samples are therefore commonly restricted to a predefined preservation threshold, such as >75% complete (Cohen et al., 2014; Fibiger, Ahlström, Bennike, & Schulting, 2013; Gheggi, 2016; Judd, 2002; Schulting & Fibiger, 2014; Torres-Rouff, Hubbe, & Pestle, 2018) when calculating trauma frequencies. This procedure, however, diminishes sample sizes when skeletal preservation is poor, such as in fossil human remains. We therefore pursued an approach different from crude frequency calculations and used generalized linear mixed models (GLMM) to calculating trauma prevalence. This approach enabled us to include skeletal remains of any preservation status and to determine the effects of different variables (sex, age-at-death, time period, anatomical location) on trauma prevalence, while accounting for the differential preservation of skeletal remains. Contrasting the two analytical approaches of crude frequencies and GLMM, we outline the particular suitability of the latter for predicting trauma prevalence of incomplete human skeletal remains using multiple predictor variables.

2 | MATERIALS AND METHODS

2.1 | Data collection

We collected data about trauma on UP human cranial remains from western Eurasia, dating between circa 40,000 and 10,000 years BP, from the literature. We compiled relevant literature using a snowball approach. We also used library and online search engines (e.g., Google Scholar, Web of Science) but did not restrict the literature search to those, because some key references for specific sites and fossils date back to the 1800s and are therefore not systematically indexed. In total, 234 UP specimens, representing 1,285 skeletal elements, from 101 archaeological sites were analyzed (Figure 1, Table S1, see Supplementary References for literature used to compile data). We considered only specimens preserving cranial remains, excluding those represented exclusively by teeth. We included adult and adolescent specimens yielding an estimated age-at-death of at least ca. 12 years. We excluded younger children to avoid bias in data collection due to higher bone remodeling rates in growing immature bone, which may obscure signs of antemortem trauma (Redfern & Roberts, 2019). In contrast, such signs remain visible in adult cranial bone, even when fully healed (Campillo, 1991; Lewis, 2006; Redfern, 2017b; Walker, 1989). Our literature review revealed cases of cranial trauma that have remained largely unnoticed aside from their mention in the anthropological reports of the respective fossils, especially among late UP individuals. A descriptive catalogue of single (possible) traumatic lesions of specimens postdating 20 ka BP is provided in Table S2 and represents an update and follow-up of the trauma catalogue in Supplementary Table S3 of Beier et al. (2018).

Data collection followed the procedure described in Beier et al. (2018). For each fossil, we recorded whether the specimen exhibits an injury or not, and if so, which skeletal elements, that is, cranial bones, are affected. Trauma was recorded as present or absent (binary), thus multiple traumata on the same skeletal element were not accounted for. We followed the diagnoses of the original specimens’ examiners and registered a lesion as a trauma if its diagnosis has been stated so or if trauma was considered a possible differential diagnosis of a lesion. We included both antemortem and perimortem trauma in our data and did not differentiate between them in the statistical analyses. Perimortem breakages, however, were only recorded as trauma when the original examiners of the fossil specimens explicitly stated that a perimortem breakage was caused by a traumatic impact during lifetime, and not by an event after the death of the individual, such as during burial, deposition, or postmortem manipulation of the remains. This applies to remains from Le Placard, Gough’s Cave, Isturitz, Burkhartshöhle, Maszycka, Röthekopf, and Brillenhöhle, where, for example, cut and percussion marks and breakage morphology suggest intentional human modification of the skeletal remains, carnivore activity, or postmortem damage as causative agents for perimortem breakages (see Supplementary Information for details and references). We acknowledge that the methods used by the original fossils’ examiners to diagnose traumatic lesions vary in detail and thoroughness. Nevertheless, the majority of cited references to compile our dataset are scientific publications whose quality was assured by measures of peer-review and editorial services. We thus consider them a reliable source of information and current best knowledge.

Moreover, for each fossil, we recorded the preserved skeletal elements and their completeness. This allowed us to account for bias in trauma prevalence resulting from the differential preservation status of the skeletal remains. Preservation affects the likelihood that an injury will be observed on a bone and thus can bias calculations of trauma prevalence (Beier et al., 2018; Judd, 2002, 2004). We used published pictures, drawings or descriptions to rate the completeness of each of the 14 major cranial bones (skeletal elements). These were the frontal and occipital bones, as well as the left and right elements of the parietal, temporal, maxilla, mandible, zygomatic and nasal bones. Compared with a complete bone, we visually rated how much of each skeletal element is preserved as a percentage using four preservation categories: category 0.25 comprises all elements with a preserved portion of 1–25%, category 0.5 elements with a preserved portion of about 26–50%, category 0.75 elements with about 51–75% preserved, and category 1 with 76–100% preserved. Due to their small size, the nasal and zygomatic bones were rated in just two categories (category 0.5:1–50% and category 1:51–100%). Several UP cranial remains could not be considered in the present study, because the available information was insufficient to quantify their state of preservation in this manner (e.g., no published pictures). Likewise, some specimens could only be partially quantified, for example, when a cranium was depicted only in one view in a publication. Thus, the preservation scores in our sample do not always reflect the actual completeness of a fossil, but its quantifiable portions in the context of the current study.

For each specimen, we recorded the individual demographic parameters sex (male, female, or indeterminate) and age-at-death...
(<30 years, >30 years, or indeterminate) as published by the examiners of the original fossils. We differentiated age dichotomously because wide and overlapping age-at-death ranges of several specimens precluded the use of more narrow age cohorts. Specimens with an age determination of about 25–35 years were assigned to the young age cohort (<30 years).

We assigned each specimen to either the pre-LGM period or the post-LGM period according to proposed direct dates, archaeological contexts, or chronostratigraphic position of the remains within the sites. Where available, we used uncalibrated radiocarbon dates (BP) for assignments. Our division in pre- and post-LGM is grounded on archaeological and paleoclimatological reasoning, separating...
samples by the onset of the Magdalenian culture, which appeared in different regions at different times, with earliest appearances at around 17 ka BP in the glacial refugia of Iberia and southern France (Djindjian, 2016; González Sainz & Utrilla Miranda, 2005; Straus, 2013). This culturally significant transition to a new technocomplex is thought to roughly coincide with a deglaciated landscape and the repopulation of central Europe after its presumed abandonment during the maximum glaciation of the LGM (Clark et al., 2009; Djindjian, 2016). The pre-LGM period as used in this study dates to roughly 40–16 ka BP (Aurignacian to onset Magdalenian), the post-LGM period to roughly 17–10 ka BP (Magdalenian to onset Holocene).

Finally, we assigned each site in our sample to one of four larger geographic regions within Europe (location: South, East, Central, Iberia). Each region is a coherent area, with geographic barriers such as coastlines and mountain ranges as natural boundaries between them (Figure S1).

Overall sample sizes of the different variable levels are provided in Table S3. The raw data used for this research are available in Beier (2020) at http://doi.org/10.5281/zenodo.3979485.

2.2 Assessing trauma prevalence with GLMMs

To assess overall cranial trauma prevalence in UP human remains and to statistically compare trauma prevalence between subsamples divided by basic demographic variables such as age cohorts and sexes, we used GLMMs with a Markov chain Monte Carlo (MCMC) algorithm as implemented in the MCMCglmm package (Hadfield, 2010) in R version 3.6.1 (R Core Team, 2019). Most importantly, this approach enabled us to include skeletal remains with any preservation status in the analyses and to predict trauma prevalence across different levels of preservation. Moreover, GLMMs simultaneously assess the explanatory power of multiple predictor variables on trauma prevalence and account for variation in trauma prevalence arising from random variables such as between-region differences (see Konigsberg & Frankenberg, 2013 for other applications of Bayesian methods in bioarchaeology). As a result, estimated overall trauma frequencies (here termed “prevalence”) take into account unbalanced sampling between the different variable levels, and thus avoid potential sampling biases that can easily confound crude trauma frequency estimates. We modeled trauma presence or absence as a binary response variable with a binomial error distribution and a logit-link function.

2.2.1 Element- and specimen-level

We performed all GLMMs twice, once at the level of skeletal elements and once at the level of specimens. The element-level approach enabled us to account for variation in trauma prevalence between skeletal elements and to derive marginal predictions for trauma prevalence beyond element identity—a crucial aspect because previous research (Delgado-Darias et al., 2018; Fibiger et al., 2013; Scaffidi & Tung, 2020; Walker, 1997; Wilkinson, 1997), as well as our own data have shown that some cranial regions such as the frontal and parietal bones exhibit trauma more frequently than others. In our present sample, the frontal and right parietal bones are the skeletal elements most often affected by trauma (11.6 and 9.1%; Table 1). However, the element-level approach may be subject to pseudoreplication when lesions extend over two or more skeletal elements and are thus counted more than once. The second, more conservative approach at the level of specimens overcomes the issue of pseudoreplication but cannot take variation in trauma prevalence between skeletal elements into account. For the specimen-level models, we scored cranial trauma absence or presence for each specimen instead of each skeletal element, and used specimen preservation as a measure of cranial completeness instead of element preservation. This was determined by adding up the element-preservation categories (0.25, 0.5, 0.75, and 1) of all preserved skeletal elements assigned to one specimen, divided by 14 (maximum number of elements per specimen).

2.2.2 Model variants

We ran different models using different data subsets and different variable combinations of the fixed two-level predictors age (young or old), sex (male or female), period (pre-LGM or post-LGM), as well as the z-transformed four-level covariate element preservation (0.25, 0.5, 0.75, and 1) for element-level models, or the z-transformed continuous covariate specimen preservation for specimen-level models. We added the age-by-sex interaction to account for potentially different age-effects in the two sexes, as well as the age-by-period and the sex-by-period interactions to account for potential variation in the period effect with age class or sex. Table 2 (see Section 3) provides an overview of the different model variants.

In Models 4.1 and 4.2, we examined whether there is variation in trauma prevalence between different cranial regions in UP humans. The trade-off between analytical power and model complexity, given that model convergence is negatively affected by the increasing number of variable levels per predictor, required merging the 14 skeletal elements into just two predictor levels. We therefore assigned skeletal elements to either the neurocranium (frontal, left and right parietal bones, occipital, left, and right temporal bones) or the viscerocranium (left and right mandible, maxilla, nasal, and zygomatic bones) and used anatomy (viscerocranium or neurocranium) as a fixed two-level predictor. To account for potential variation in the anatomy effect with age class or sex, we added the anatomy-by-age and the anatomy-by-sex interactions to these models.

We added intercepts per skeletal element as a random component to all element-level models to predict trauma prevalence while accounting for its variation between skeletal elements. Moreover, given that trauma prevalence may vary regionally, we added location as a second random intercept to the element-level models. To the specimen-level models, we added location as the only random intercept.
2.2.3 Model fitting, validation, and statistical inference

Trauma was modeled as a binary response variable, both for skeletal elements and for specimens. We used an inverse Gamma prior for random effects and fixed the residual variance at 1 (Gelman & Hill, 2006; Hadfield, 2019). We chose model parameters as to maximize model fit, as indicated by: (a) an autocorrelation value between posterior parameter estimates \( \leq 0.1 \) (Hadfield, 2019); (b) parameter estimates reaching convergence between four independent model chains, visible with the potential scale reduction factor <1.01 (Gelman & Rubin, 1992); and (c) observed trauma prevalence falling within the 95% highest posterior density intervals of their respective posterior distribution. After 5,100,000 MCMC iterations, a burn-in of 100,000, and a thinning interval of 1,000, these criteria were generally met in Models 1.1–3.2, generating posterior distributions with >3,600 samples each. Only the variance distribution for the random component skeletal element consistently produced autocorrelation values >0.1 in Models 1.1, 2.1 and 3.1, owing to the inherently small sample sizes in some of its levels, which resulted in smaller effective samples sizes between 1,580 and 2,400 samples. In Model 4.1, we used 7,500,000 MCMC iterations, a burn-in of 200,000, and a thinning interval of 1,500 to meet the above-mentioned criteria, and in Model 4.2, we used 10,000,000 MCMC iterations, a burn-in of 200,000, and a thinning interval of 2,000. This generated posterior distributions with >3,700 samples each, except for the anatomy-by-age and anatomy-by-sex interactions in Model 4.2, whose autocorrelation values >0.1 resulted in slightly fewer effective samples of approximately 3,000.

From the posterior distributions, we derived the posterior mean as a coefficient point estimate and the lower and upper 95% credible intervals (CI). Additionally, we calculated \( p \)-values for the posterior mean (\( p_{\text{MCMC}} \)). However, we emphasize that, in line with recent developments in the interpretation of statistical results and the debate about thresholds for statistical significance (Amrhein, Greenland, & McShane, 2019; Amrhein, Korner-Nievergelt, & Roth, 2017; Smith, 2020; Wasserstein, Schirm, & Lazar, 2019), we interpret \( p_{\text{MCMC}} \) values as graded evidence, and refrain from using them for null hypothesis significance testing. Rather, we focus our statistical inference on effect sizes (predicted model coefficients) and observed patterns of predicted trauma prevalence.

2.2.4 Model predictions

From the posterior model estimates, we computed predictions of trauma prevalence displayed as their means ± 95% CIs, indicating the probability for a skeletal element or specimen to exhibit a trauma. These predictions are marginalized over the distribution of random effects, that is, the trauma prevalence modeled for each fixed factor combination represents a global prediction that is merged over all investigated geographic regions and skeletal elements.

For skeletal elements, we predicted trauma prevalence at preservation category 1 (i.e., 76–100% complete) in Models 2.1, 3.1, and 3.2.
4.2. For specimens, we predicted trauma prevalence for preservation score 1.0 (i.e., 76–100% complete) in Models 2.2 and 3.2. To produce predictions using worst-to-best-preserved skeletal remains, we predicted trauma prevalence in Models 1.1 and 4.1 separately for each of the four preservation categories of skeletal elements (0.25, 0.5, 0.75, and 1). Accordingly, in Model 1.2 we predicted cranial trauma prevalence once for the least complete crania in our sample (score 0.018), as well as for approximately half-complete crania (score 0.5) and most complete crania (score 1.0). In all cases, predictions linearly scale across the other preservation categories/scores, generating lowest trauma prevalence among the least complete elements/specimens and increasing values with each better preservation category/score. Therefore, qualitative effect patterns do not change when predicting for different preservation categories/scores.

To account for uncertainty in trauma diagnoses, we repeated all model variants with a reduced trauma dataset comprising only "securely diagnosed" trauma. For this, we excluded lesions where the authors of the original publications considered trauma one of several possible causes of a lesion. When no alternative causes were given, and a lesion was exclusively referred to as (certain, likely, or possible) trauma, we kept this lesion in the trauma dataset. Results of the reduced trauma dataset are similar to the results of the full trauma dataset and both overall effect patterns and CI ranges are largely consistent (see Supplementary Information, p. 14, Table S4, Figure S2).

3 | RESULTS

In our sample of 234 quantified UP cranial specimens, 23 specimens exhibit at least one traumatic lesion (9.8%), corresponding to 42 of 1,285 skeletal elements with one or multiple traumatic lesions (3.3%). Table 1 shows crude trauma frequencies of the overall UP cranial sample by skeletal element and preservation category, calculated by dividing the number of skeletal elements with trauma per preservation category by the total number of elements in that preservation category. Overall crude trauma frequency for skeletal remains with >75% completeness in our sample (i.e., preservation category 1 for skeletal elements, and preservation score 1.0 for specimens) is 3.5% (30/850) for skeletal elements and 21.4% (3/14) for specimens.

Results of the different GLMMs are summarized in Table 2. Posterior coefficient means with their 95% CIs are graphically displayed in Figure S1. Notably, in each model variant, element-level and specimen-level models provided largely consistent estimates of posterior coefficient means and CIs. Hence, effect sizes for element- and specimen-level models are jointly considered in the following. Smaller sample sizes in the specimen-level models resulted in slightly larger CIs for the estimated posterior means when compared to element-level model CIs.

In general, we found trauma prevalence to vary with the preservation status of the skeletal remains of UP modern humans, that is, increasing with skeletal completeness in the two overall analyses (preservation effects in Models 1.1 and 1.2; Table 2) as well as across all other models taking further covariates into account (preservation effects in Models 2.1–4.2; Table 2).

3.1 | How prevalent is cranial trauma in UP skeletal remains?

Our models predicted a mean cranial trauma prevalence of 0.03 for UP human skeletal elements that are 1–25% complete (CI: 0.0002–0.11). When 76–100% complete, models predicted a mean prevalence of 0.07 (CI: 0.003–0.19; Figure 2a; Table S5a). For cranial specimens (Figure 2b; Table S5b), mean predicted trauma prevalence was 0.08 (CI: 0.008–0.20) at the smallest observed preservation (score 0.018), and 0.26 (CI: 0.08–0.48) for 76–100% complete crania (score 1.0).

3.2 | Does cranial trauma prevalence in UP remains vary by age class or sex?

When restricting our sample to sex- and age-determined skeletal elements and specimens of the UP (Models 2.1 and 2.2, Figure 3a,b), we found cranial trauma prevalence to be slightly higher in males (sex effect in Models 2.1 and 2.2; Table 2). Cranial trauma prevalence clearly varied between age classes (age effect in Models 2.1 and 2.2; Table 2), with old elements or specimens being more often injured than young elements or specimens (Figure 3a,b). Males and females did not differ in their age-specific trauma prevalence (age-by-sex-interaction in Models 2.1 and 2.2; Table 2).

When accounting for age- and sex-dependent variation in trauma prevalence (exclusion of sex-unknown and age-indeterminate cranial remains), overall mean trauma prevalence estimates ranged between 0.03 and 0.10 (CI: 0.00005–0.25) for skeletal elements, and between 0.12 and 0.38 (CI: 0.0009–0.62) for specimens, each when 76–100% complete (Figure 3a,b; Table S6a,b).

3.3 | Does cranial trauma prevalence in UP remains vary by time period?

The comparisons between samples from pre- and post-LGM UP humans (Models 3.1 and 3.2, Figure 4a,b) provided no indication that cranial trauma prevalence varied between time sections (period effect in Models 3.1 and 3.2; Table 2). Across samples, cranial trauma prevalence varied between age cohorts (age effect in Models 3.1 and 3.2; Table 2) with a clearly and consistently higher prevalence among the old. With respect to sex, male remains tended to exhibit slightly higher trauma prevalence than female remains (sex effect in Models 3.1 and 3.2; Table 2). These age- and sex-specific patterns where consistent between pre- and post-LGM periods (age-by-period- and sex-by-period-interactions in Models 3.1 and 3.2; Table 2).

The mean model predicted trauma prevalence for pre-LGM cranial remains across ages and sexes (exclusion of sex-unknown and age-indeterminate cranial remains) varied between 0.04 and 0.10 (CI: 0.0006–0.26) for skeletal elements, and between 0.13 and 0.40 (CI: 0.003–0.68) for specimens, each when 76–100% complete. The mean model predicted trauma prevalence for post-LGM cranial remains across ages and sexes varied between 0.03 and 0.11 (CI:
### TABLE 2  Summary statistics of GLMMs. Model coefficients are given as their posterior mean with 95% CIs and the associated pMCMC. Values are rounded to their third decimal position. Reference levels for the factorial predictors age, sex, period, and anatomy are old, female, post-LGM, and neurocranium. See Figure S2 for graphical display of effect sizes and further explanations.

| Research question                                      | Model       | N   | Predictor variable | Posterior mean | Lower 95% CI | Upper 95% CI | pMCMC |
|--------------------------------------------------------|-------------|-----|--------------------|----------------|--------------|--------------|-------|
| Trauma prevalence overall in UP?                        | Model 1.1   | 1,285<sup>a</sup> | Element preservation | 0.574          | 0.129        | 1.105        | 0.010 |
|                                                        | Model 1.2   | 234<sup>a</sup>  | Specimen preservation | 0.754          | 0.250        | 1.220        | 0.003 |
| Trauma prevalence variation in UP by age and sex?       | Model 2.1   | 959<sup>b</sup>  | Element preservation | 0.536          | 0.037        | 1.074        | 0.032 |
|                                                        | Model 2.2   | 118<sup>b</sup> | Specimen preservation | -1.898        | -3.981       | -0.034       | 0.041 |
|                                                        |             |     | Age                | 0.537          | -0.620       | 1.713        | 0.360 |
|                                                        |             |     | Sex                | 0.806          | -1.625       | 2.918        | 0.470 |
|                                                        |             |     | Age × sex          | 0.372          | -0.251       | 1.011        | 0.258 |
|                                                        |             |     | Age                | -1.446         | -3.676       | 0.971        | 0.209 |
|                                                        |             |     | Sex                | 0.786          | -0.931       | 2.698        | 0.392 |
|                                                        |             |     | Age × sex          | 0.023          | -2.747       | 2.851        | 0.989 |
| Trauma prevalence by age and sex in pre- and post-LGM times? | Model 3.1   | 959<sup>b</sup>  | Element preservation | 0.559          | 0.040        | 1.097        | 0.022 |
|                                                        | Model 3.2   | 118<sup>b</sup> | Specimen preservation | 1.025          | -1.108       | 3.139        | 0.355 |
|                                                        |             |     | Period             | -1.247         | -3.308       | 0.640        | 0.211 |
|                                                        |             |     | Age                | 1.504          | -0.500       | 3.805        | 0.138 |
|                                                        |             |     | Sex                | -0.103         | -2.458       | 2.052        | 0.894 |
|                                                        |             |     | Period × age       | -1.003         | -3.526       | 1.636        | 0.452 |
|                                                        |             |     | Period × sex       | 0.387          | -0.260       | 1.019        | 0.228 |
|                                                        |             |     | Period             | 0.290          | -2.330       | 3.101        | 0.840 |
|                                                        |             |     | Age                | -1.664         | -3.846       | 0.640        | 0.134 |
|                                                        |             |     | Sex                | 0.840          | -1.394       | 3.170        | 0.477 |
|                                                        |             |     | Period × age       | 0.335          | -2.440       | 3.211        | 0.829 |
|                                                        |             |     | Period × sex       | -0.053         | -3.104       | 2.990        | 0.985 |
| Trauma prevalence of the viscero- and neurocranium?     | Model 4.1   | 1,285<sup>a</sup> | Element preservation | 0.608          | 0.148        | 1.103        | 0.005 |
|                                                        |             |     | Anatomy             | -2.772         | -4.317       | -1.407       | 0.001 |
| Trauma prevalence of the viscero- and neurocranium by age and sex? | Model 4.2   | 959<sup>b</sup>  | Element preservation | 0.616          | 0.102        | 1.131        | 0.011 |
|                                                        |             |     | Anatomy             | -0.772         | -3.163       | 1.442        | 0.503 |
|                                                        |             |     | Age                | -1.235         | -2.212       | -0.288       | 0.011 |
|                                                        |             |     | Sex                | 1.392          | 0.309        | 2.622        | 0.011 |
|                                                        |             |     | Anatomy × age       | -0.715         | -4.108       | 2.197        | 0.695 |
|                                                        |             |     | Anatomy × sex       | -3.807         | -7.032       | -0.788       | 0.009 |

Note: Trauma prevalence was modeled using a MCMC algorithm: Models 1.1, 2.1, 3.1, 4.1, and 4.2 comprise skeletal elements, Models 1.2, 2.2, and 3.2 comprise cranial specimens. See Section 2 for details.

Abbreviations: CI: credible interval; GLMM, generalized linear mixed model; LGM, Last Glacial Maximum; MCMC, Markov chain Monte Carlo algorithm; UP, Upper Paleolithic.

<sup>a</sup>Full dataset.

<sup>b</sup>Exclusion of sex unknown and age indeterminate skeletal elements or specimens, that is, no more precise age determination than >12 years.
0.00002–0.27) for skeletal elements, and between 0.10 and 0.35 (CI: 0.0003–0.63) for specimens, each when 76–100% complete (Figure 4a,b; Table S7a,b).

### 3.4 Does cranial trauma prevalence differ between the neuro- and the viscerocranium of UP remains?

Comparing the prevalence of cranial lesions between the facial skeleton and the braincase, we found the neurocranium to be (at least tentatively) more often injured in UP human remains than the viscerocranium (anatomy effect in Models 4.1 and 4.2; Table 2). After restricting our sample to age and sex determined remains, we further found that old remains were more likely to show traumatic injuries than young skeletal elements (age effect in Model 4.1, Table 2), consistently in both cranial regions (anatomy-by-age-interaction in Model 4.2, Table 2). However, the two anatomical regions differed in their trauma prevalence between the sexes (anatomy-by-sex-interaction in Model 4.2, Table 2), insofar as male remains had a higher trauma prevalence than female remains in the neurocranium, but a reverse pattern for the viscerocranium (Figure 5b).

**FIGURE 2** Cranial trauma prevalence of Upper Paleolithic modern human cranial remains. Solid markers denote predicted means based on posterior estimates of Markov chain Monte Carlo generalized linear mixed models (MCMC GLMMs), bars show lower and upper 95% credible intervals. Open markers denote crude trauma frequencies. (a) Predicted trauma prevalence (Model 1.1) and crude trauma frequencies of skeletal elements for preservation categories 1–25%, 26–50%, 51–75%, and 76–100%, and overall crude frequency across all preservation categories. (b) Predicted trauma prevalence (Model 1.2) and crude trauma frequencies for the least complete cranial specimens in the sample (score 0.018), for half (score 0.5) and most complete crania (score 1.0), and overall crude trauma frequency across all preservation scores. See Table S5a, b for predicted values. Note the different scales of the y-axes.

**FIGURE 3** Cranial trauma prevalence of Upper Paleolithic modern human cranial remains by age and sex. Solid markers denote predicted means based on posterior estimates of Markov chain Monte Carlo generalized linear mixed models (MCMC GLMMs), bars show lower and upper 95% credible intervals. Open markers denote crude trauma frequencies. (a) Predicted trauma prevalence (Model 2.1) and crude trauma frequencies of skeletal elements when 76–100% complete. (b) Predicted trauma prevalence (Model 2.2) and crude trauma frequencies of specimens when 76–100% complete. Predictions for lower preservation categories/scores scale down linearly. Sex unknown and age indeterminate skeletal elements/specimens are excluded. See Table S6a,b for predicted values. Note the different scales of the y-axes.
4 | DISCUSSION

In this study, we quantified the prevalence of cranial trauma in UP modern humans using different predictor variables (sex, age-at-death, pre- and post-LGM time periods, and anatomical location on the cranium). For this, we employed a GLMM approach as an alternative method to commonly used crude trauma frequency estimates. It allowed us to account for differential sample sizes and skeletal preservation in the fossil record and to assess the effects of multiple predictor variables and variable interactions on trauma prevalence simultaneously. We performed all analyses twice, once at the level of skeletal elements and once at the level of specimens. We found a mean cranial trauma prevalence in UP humans of 0.07 (95% CI 0.003–0.19) at the level of skeletal elements, and of 0.26 (95% CI 0.08–0.48) at the level of specimens, each for skeletal remains that are 76–100% complete. Across specimen and skeletal element datasets, trauma prevalence tended to be higher for males, and was consistently higher in the old age group. When comparing samples from before and after the LGM, we found no substantial difference in trauma prevalence patterns for the two sexes or age-cohorts. Samples showed higher trauma prevalence in neuro- than in viscerocranial remains, with neurocrania being affected predominantly in males. Consistently, we found that trauma prevalence increased with skeletal preservation.

We consider the GLMM approach a valuable alternative to conventional crude trauma frequencies for the study of past trauma
prevalence, especially when skeletal preservation is poor. Crude trauma frequency estimates are in general highly dependent on the completeness of the skeletal remains under study, because the less complete the remains are, the higher is the chance for a traumatic lesion to go unnoticed, resulting in a proportionally growing number of false negative findings in the sample (Judd, 2002, 2004; Pankowšká et al., 2019). In trauma research, skeletal samples are therefore sometimes restricted to a predefined preservation threshold, such as >75% complete, to account for the preservation status of skeletal remains and avoid biased trauma frequencies (Cohen et al., 2014; Fibiger et al., 2013; Gheggi, 2016; Judd, 2002; Schulting & Fibiger, 2014; Torres-Rouff et al., 2018). This approach ensures data quality and comparability, but at the same time severely reduces sample sizes if remains are poorly preserved, hence impairing generalizations and statistical validity of trauma frequency estimates. This issue especially applies to the human fossil record, which is characterized by highly fragmented and incomplete remains. In our study, restriction of the sample to the commonly employed >75% preservation threshold would result in the loss of about 30% of sampled skeletal elements and more than 90% of sampled specimens. For skeletal elements, the crude trauma frequency for skeletal remains with >75% completeness is 3.5% (30/850), and therefore very similar to the crude frequency of 3.3% (42/1285) for the full sample (i.e., all skeletal elements irrespective of preservation). In contrast, the crude trauma frequency for specimens with >75% completeness is 21.4% (3/14), and thus more than twice as high as the crude frequency of 9.8% (23/234) for all specimens irrespective of preservation. To dispense the necessity to exclude large parts of the sample, we examined trauma prevalence using a GLMM approach, which can account for small sample sizes and differential skeletal preservation. The GLMM-predicted mean trauma prevalence values for remains that are 76–100% complete (7% for skeletal elements, and 26% for specimens) are slightly higher than the crude trauma frequencies of remains which are >75% complete (3.5% for skeletal elements, and 21.4% for specimens), though the crude frequencies fall well within the GLMM-predicted confidence intervals (Figure 2a,b). Future research should evaluate, by using artificial data and simulations, for example, how closely model-based GLMM predictions and crude frequencies conform to the "real" trauma prevalence of a sample, and whether the two approaches perform equally well.

Comparability of trauma prevalence estimates between different studies is generally not straightforward. So far, only a few studies employed a GLMM approach to investigate past trauma prevalence. For example, Beier et al. (2018) assessed the cranial trauma prevalence of classic Neanderthals using GLMMs and found a mean prevalence ranging between 4 and 33% for specimens, and between 3 and 17% for skeletal elements. Thus, cranial trauma prevalence seems largely similar in humans of the Middle and Upper Paleolithic, although Beier et al. (2018) predicted trauma prevalence at a slightly lower preservation status of remains (50–75% complete) than in the present study (76–100% complete). In contrast, many studies report crude trauma frequencies. The crude frequencies for UP humans in this study (as calculated for all remains irrespective of preservation, and for remains >75% preserved) fall well within the range of variation in cranial trauma frequencies found in different early Holocene human skeletal samples. Cranial trauma frequencies obtained from Mesolithic cranial specimens yielded values of 4.7% (Roksandic, 2006), 5–19% (Terberger, 2006), 9.5% (Papathanasiou, 2012), and even 43.8% (Bennike, 1985; but this estimate was revised downward after additional samples were studied (Schulting, 2006)). Collections of Neolithic specimens revealed crude trauma frequencies of crania of 3.4% (Roksandic, 2006), 3.5% (Papathanasiou, 2012), 8.9% (Schulting & Wysocki, 2005), 9.4% (Bennike, 1985), 11.5% (Jiménez-Brobiel, Du Souich, & Al Oumaouil, 2009), and 9–17% (and 1–6% for skeletal elements instead of specimens; Fibiger et al., 2013). However, between-study comparison of trauma frequencies and prevalence should be treated with caution due to the various approaches used for their calculation, such as different preservation thresholds, model-settings, or bone count vs. segment count (Judd, 2002).

We found slightly higher cranial trauma prevalence in male compared to female skeletal remains in our overall comparison of UP samples (Models 2.1 and 2.2). A similar result was obtained when we performed the comparison for pre- and post-LGM samples individually (Models 3.1 and 3.2). These results are in agreement with previous findings of higher cranial trauma prevalence in male compared to female skeletal remains in a sample of Neanderthals and UP skeletal remains from ca. 80,000 to 20,000 years ago (Beier et al., 2018). The sex effect in the previous study (posterior mean: 1.515; Cl: 0.178–2.921; pMCMC: 0.017 for skeletal elements, and posterior mean: 3.533; Cl: 0.865–6.397; pMCMC: 0.002 for specimens) was more pronounced than in the present study (Table 2). Furthermore, a higher male than female cranial trauma prevalence is consistent with the common bioarchaeological finding that male skeletal remains are more likely to show injuries than female remains (Cohen et al., 2014; Fibiger et al., 2013; Jiménez-Brobiel et al., 2009; Larsen, 1997; Milner, Boldsen, Weise, Lauritsen, & Freund, 2015; Redfern, 2017b; Scaffidi & Tung, 2020; Schiwatta, Jones, Pilloud, Coddin, & Wiberg, 2014; Standen et al., 2020; Walker, 2001), which might suggest that males exposed themselves more frequently to risky situations, such as physical confrontations, warfare, or risky leisure activities (Judd, 2017; Kwan, Cureton, Dozier, & Victorino, 2011; Martin et al., 2015; O’Jile, Ryan, Parks-Levy, Betz, & Gouvier, 2004; Redfern, 2017b; Sutherland, 2002). The observed, yet small, difference in cranial trauma prevalence between the sexes in our study might indicate different exposures to hazardous situations, for example, because of different behaviors or the involvement in different activities. This would be consistent with the proposed intensification of sexual division of labor in the UP (Brennan, 1991; Karakostis et al., 2018; Kuhn & Stiner, 2006; Stiner & Kuhn, 2009; Villotte et al., 2010; Villotte & Knüsel, 2014; Zilhão, 2014). However, such bioarchaeological interpretations about past sex-specific activities and behaviors are grounded on morphological or genetic sex determinations of the skeletal remains, but these do not necessarily equate with the lived genders of the individuals and are not per se informative about a past culture’s social organization, especially when the number and cultural practice of gender roles is unknown (Agarwal & Glencross, 2011; Agarwal & Wesp, 2017; Martin, Debra, Harrod, & Fields, 2010;
Matić & Jensen, 2017; Sofaer, 2006; Wood & Eagly, 2012; Zuckerman & Crandall, 2019).

We found a marked difference in cranial trauma prevalence between old and young age cohorts in our sample of UP human remains. More trauma on skulls of old compared to young individuals is consistent with a hypothesized accumulation of trauma with increasing age. Such accumulation has been suggested to result from a longer exposure time to potentially hazardous situations (Glencross & Sawchuk, 2003), considering that non-lethal cranial injuries usually remain visible for extended periods of time due to the limited capacity of cranial bone to bridge and fully remodel lesions during healing (Campillo, 1991; Walker, 1989). It is debated, however, whether the accumulation of traumata with age is expected to be observed in a skeletal sample. Clinical and anthropological research has shown that traumatic injuries, even if survived, are linked to an increased risk of dying compared to individuals who never sustained trauma (Boldsen, Milner, & Weise, 2015; Eriksson, Brattström, Larsson, & Oldner, 2016; Mitchell, Cameron, & McClure, 2017). Death assemblages therefore are expected to deviate from a strictly linear accumulation of trauma with age (Boldsen et al., 2015; Milner & Boldsen, 2017) because trauma survivors are more likely to die earlier than individuals who were never injured, that is, entering the skeletal population at relatively younger ages. Specifically designed studies using more narrow age cohorts than the present analysis may be helpful in future research to further characterize age-specific trauma patterns and selective mortality of UP humans under a life-course perspective.

Our comparisons of cranial trauma prevalence in human skeletal remains before and after the LGM revealed no time-specific prevalence of the sexes or age cohorts. The LGM, the most severe climatic event since the appearance of modern humans in Europe, was preceded by several millennia of major climatic and environmental changes, and resulted in drastic lowering of sea levels, in ice sheet cover extending over large parts of Europe, and in a depopulation of central Europe and an assumed retreat of human populations to southern refugia (Brewster, Meiklejohn, et al., 2014; Burke et al., 2017; Chase et al., 2010; Clark et al., 2009; Djindjian, 2016; Maier et al., 2016; Maier & Zimmermann, 2017; Straus, 2015; Tallavaara et al., 2015; Wygal & Heidenreich, 2014). Paleogenetic and morphological data moreover suggest a population disruption and large-scale turnover after the LGM (Brewster, Meiklejohn, et al., 2014; Brewster, Pinhasi, & Meiklejohn, 2014; Fu et al., 2016). Although this marked environmental instability is likely associated with elevated stress levels and the need for rapidadaptations of the human populations regarding subsistence and technology, skeletal remains have revealed only minor indicators of declined health or worsening living conditions, such as a decrease in body height in the late Paleolithic, likely due to reduced gene flow and nutritional deficiencies (Brennan, 1991; Formicola & Giannecchini, 1999; Formicola & Holt, 2007; Holt & Formicola, 2008). In a similar vein, our results indicate largely unchanged stress levels before and after the LGM as far as these are reflected by cranial trauma prevalence. The proposed large-scale changes in human subsistence, mobility and population composition of the LGM seemingly did not manifest in different levels of cranial trauma.

Trauma prevalence was in general found to be higher in neuro- than in viscerocranial remains. In both anatomical regions, trauma occurred more frequently among the old. Moreover, males exhibited trauma more often than females in neurocranial remains, while females tended to be more often affected by viscerocranial trauma than males. The distribution of injuries across different regions of the skull can be indicative of the origin of injury, such as violent or accidental (Brink, 2009). However, interpretations of trauma distribution patterns are highly sample-specific because different modes of injury and intents of violence can produce various patterns. The concept of the “hat brim line rule” states that blunt force trauma above the hat brim line (an area roughly around the largest circumference of the cranial vault, see Kremer & Sauvageau, 2009 for details) is more often related to violent blows, whereas a fall rather results in trauma in the hat brim line area (Galloway & Wedel, 2014; Kremer et al., 2008; Kremer & Sauvageau, 2009). According to this rule, UP males would have been involved in violent encounters more often than women. However, the “hat brim line rule” has been contested as being too simplistic and not readily applicable (see for example, Kranioti, 2015 and Geserick, Krocker, & Wirth, 2014 for a critical review). Injuries predominantly affecting the face can equally indicate violence, as is the case in domestic violence (Guyomar’ch, Campagna-Vaillancourt, Kremer, & Sauvageau, 2010; Novak, 2006). The resolution of analysis regarding the distribution patterns of cranial trauma in this study, employing only two cranial areas, is too coarse to arrive at conclusive interpretations about possible causes of injury. However, model convergence precluded the assessment of more cranial areas (see Section 2.2.2). Moreover, to distinguish between different etiologies of UP injuries, a detailed qualitative assessment should complement quantitative findings as provided here in the future.

We note that this study is limited by several factors. First, our study exclusively comprises cranial remains and our conclusions are therefore limited to this body region. Further research should focus on an assessment of trauma prevalence in postcranial remains to arrive at overall trauma prevalence estimates. Furthermore, although our analyses comprise the probably largest samples currently available for the study of UP trauma, our data were collected from the literature, and are based on the assessments of many different researchers. We therefore cannot exclude observational biases in the underlying assessments of trauma, age, and sex. The identification and reporting of traumatic lesions in the literature we used to compile our data is highly dependent on the intention of these studies (e.g., site report versus detailed paleopathological examination) as well as on the thoroughness of investigation. The latter is particularly relevant regarding the challenging endeavor of interpreting perimortem breakages, which usually remain inconclusive with regard to their origin. Whether perimortem breakages represent an actual injury or were caused during deposition or postmortem manipulation can, if at all, only be disentangled when skeletal preservation allows for a detailed examination, and when contextual evidence is available and fully considered.
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