

ANALYSES OF CRANIAL TRAUMA
IN NEANDERTHAL AND
MODERN HUMAN FOSSIL REMAINS

JUDITH BEIER



DISSERTATION

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Analyses of cranial trauma in Neanderthal and modern human fossil remains

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Dekan:

Prof. Dr. Thilo Stehle

1. Berichterstatterin:

Prof. Dr. Katerina Harvati

2. Berichterstatterin:

PD Dr. Miriam Noël Haidle

3. Berichterstatterin:

Prof. Dr. Eugénia Cunha

Contents

Acknowledgements	1
Abstract.....	3
Zusammenfassung.....	5
List of publications for cumulative dissertation.....	7
1. Introduction	8
1.1. Theoretical and methodological background of trauma research	8
1.2. Trauma research in Neanderthal and modern human fossil remains	12
2. Objectives.....	17
3. Material and Methods	20
3.1. Qualitative trauma analysis: Case study Apidima (Paper III)	20
3.1.1. The Apidima site and human fossils.....	20
3.1.2. Timing the cranial breakage of the Apidima fossils	20
3.2. Quantitative trauma analyses: Neanderthals and Upper Paleolithic humans (Papers I and II)	22
3.2.1. Data collection.....	22
3.2.2. Assessing trauma prevalence with GLMMs	24
4. Results and Discussion	26
4.1. Qualitative trauma analysis: Case study Apidima (Paper III)	26
4.2. Quantitative trauma analyses: Neanderthals and Upper Paleolithic humans (Papers I and II)	28
4.2.1. Testing a research opinion: the highly traumatized Neanderthal? (Paper I).....	29
4.2.2. Cranial trauma prevalence throughout the Upper Paleolithic (Paper II).....	33
4.2.3. GLMM-predicted trauma prevalence and crude trauma frequencies (Papers I and II).....	38
5. Concluding remarks	40
References	41

Appendix A: Paper I

Appendix B: Paper II

Appendix C: Paper III

Abbreviations

CT	computed tomography
CI	credible interval
GLMM	generalized linear mixed models
ka BP	thousand years before present
LGM	Last Glacial Maximum
MCMC	Markov chain Monte Carlo

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Abstract

Traumatic injuries in fossil skeletal remains of Neanderthals and Paleolithic modern humans bear witness of past accidents, the involvement in risky activities, or violent conflict, and therefore provide crucial insights for reconstructing lifestyles, behaviours, and living environments of these past humans. This cumulative dissertation aimed at furthering our understanding of cranial trauma in fossil remains of Neanderthals and Paleolithic modern humans using qualitative and quantitative approaches and addressed three major objectives. First, the cranial breakage patterns of two late Middle Pleistocene crania from the Apidima caves in Greece were investigated to assess the timing of breakage and evaluate whether the fracture lines represent postmortem taphonomic damage or perimortem fractures, and thus possibly traumatic injuries. Second, the cranial trauma prevalence of Neanderthals was quantified and contrasted with that of early to mid-Upper Paleolithic humans to test the common perception that Neanderthals experienced exceptional high levels of trauma. Third, the cranial trauma prevalence throughout the entire early to late Upper Paleolithic period was characterized, and it was investigated whether the stressors associated with the climatic conditions before and after the Last Glacial Maximum (LGM) are reflected in different levels of trauma. To address the first objective, I employed virtual methods using computed tomography scanning of the fragmented Apidima crania and examined several diagnostic criteria of the endo- and ectocranial aspects of fracture lines to differentiate fresh from dry bone breakage. Most fracture lines of the crania gave inconclusive results regarding the timing of breakage, suggesting that the criteria used for differentiation were insufficient or may not be readily applicable to fossil remains, especially when their depositional and taphonomic history is complex. To address the second and third objectives, I performed an extensive literature review and compiled a large dataset comprising several hundred cranial fossil specimens from western Eurasia, dating to about 80,000 to 10,000 years ago. To quantify and statistically compare trauma prevalence between groups, I used generalized linear mixed models (GLMMs) employing a Markov chain Monte Carlo algorithm. This approach allowed me to assess trauma prevalence in relation to multiple contextual variables, including sex, age-at-death, affected cranial region, and time period, while accounting for the differential preservation of the fossil remains. Results indicated similar prevalence of cranial trauma in Neanderthals and Upper Paleolithic modern humans, contradicting previous suggestions of exceptionally high trauma rates in Neanderthals. In both taxa, trauma prevalence was higher for males than females, but results showed

differences between the taxa in age-specific trauma prevalence, suggesting differences in the age of acquisition of trauma or in the mortality risk of trauma survivors. The characterization of cranial trauma prevalence patterns of early to late Upper Paleolithic humans showed that the high levels of environmental stress likely associated with the severe climatic changes before and after the LGM are not reflected in cranial trauma prevalence. Trauma prevalence throughout the Upper Paleolithic period was similar to trauma rates found in Mesolithic and Neolithic samples. Moreover, males were slightly more often injured than females, and both sexes exhibited more trauma among the old age group. The statistical approach using GLMMs provides a powerful alternative to conventional crude trauma frequencies for investigations of past trauma prevalence, especially when skeletal preservation is poor as in the fossil record. This dissertation highlights the importance of considering both qualitative and quantitative approaches to study trauma, and of including multiple contextual variables when evaluating trauma in fossil human remains.

Zusammenfassung

Verletzungsspuren an fossilen Skelettresten von Neandertalern und modernen Menschen aus dem Paläolithikum zeugen von Unfällen, risikoreichen Aktivitäten oder gewaltsamen Konflikten und liefern somit aufschlussreiche Erkenntnisse für die Rekonstruktion der Lebenswelt und Verhaltensweisen der damaligen Menschen. Ziel dieser kumulativen Dissertation war es, neue Erkenntnisse über Schädelverletzungen bei Fossilien von Neandertalern und modernen Menschen des Paläolithikums zu gewinnen. Dafür wurden mittels qualitativer und quantitativer Untersuchungen drei zentrale Fragestellungen bearbeitet. Zunächst wurden die kranialen Bruchmuster von zwei spätmittelpleistozänen Schädeln aus den Apidima-Höhlen in Griechenland hinsichtlich des Zeitpunkts des Knochenbruchs untersucht. Die Untersuchung sollte klären, ob die Bruchkanten postmortal oder perimortal entstanden sind, also taphonomische Beschädigungen darstellen oder aber perimortale Brüche, bei welchen es sich um Schädeltraumata handeln könnte. Die zweite Untersuchung widmete sich der Prävalenz von Schädelverletzungen bei Neandertalern. Durch den Vergleich der Schädeltraumahäufigkeit von Neandertalern mit jener moderner Menschen des frühen bis mittleren Jungpaläolithikums sollte die vorherrschende Auffassung, dass Neanderthaler außergewöhnlich viele Verletzungen aufwiesen, überprüft werden. Als Drittes wurde die Prävalenz von Schädelverletzungen während des gesamten frühen bis späten Jungpaläolithikums charakterisiert sowie der Frage nachgegangen, ob die Stressoren, die mit den klimatischen Bedingungen vor und nach dem letzten glazialen Maximum (LGM) einhergingen, in unterschiedlichen Traumahäufigkeiten Niederschlag fanden. In der ersten Untersuchung wurden die fragmentierten Apidima-Schädel mittels Computertomographie virtuell analysiert. Ich untersuchte mehrere diagnostische Kriterien der endo- und ectocranialen Aspekte der Bruchlinien, um frischen von sprödem Knochenbruch zu differenzieren. Die meisten Bruchlinien lieferten kein eindeutiges Ergebnis hinsichtlich des Zeitpunktes des Knochenbruchs. Dies legt nahe, dass die verwendeten Kriterien zur Unterscheidung ungenügend waren oder nicht unmittelbar für fossile Knochenreste verwendet werden können, insbesondere wenn Ablagerungsgeschichte und Fundkontext komplex sind. Die zweite und dritte Untersuchung basieren auf einem Datensatz, den ich durch eine umfangreiche Literaturrecherche zusammengetragen habe. Dieser umfasst mehrere hundert fossile Schädelreste aus dem westlichen Eurasien aus dem Zeitraum zwischen 80.000 und 10.000 Jahren vor heute. Ich verwendete generalisierte lineare gemischte Modelle (GLMM) mit einem Markow-Chain-Monte-Carlo-Algorithmus, um die Häufigkeit von

Traumata zu ermitteln und zwischen Gruppen zu vergleichen. Diese Methode ermöglichte es, verschiedene kontextuelle Variablen wie Geschlecht, Sterbealter, betroffene Schädelregion und Datierung in die Analyse einzubeziehen sowie dabei den unterschiedlichen Überlieferungsgrad der Fossilien zu berücksichtigen. Die Ergebnisse zeigen ähnlich hohe Traumahäufigkeiten bei Neandertalern wie bei jungpaläolithischen modernen Menschen und stehen damit im Widerspruch zu bisherigen Annahmen, denen zufolge Neandertaler ungewöhnlich viele Verletzungen aufweisen. Sowohl bei Neandertalern als auch bei Jungpaläolithikern fanden sich mehr Verletzungen bei Männern als bei Frauen, jedoch unterschieden sich die beiden Taxa hinsichtlich ihrer altersabhängigen Verletzungshäufigkeiten. Dies könnte darin begründet liegen, dass sich entweder das Alter unterschied, in denen Verletzungen erworben wurden, oder das Sterberisiko von Individuen mit überlebten Verletzungen. Die Charakterisierung der Verletzungshäufigkeiten früh- bis spät-jungsteinzeitlicher moderner Menschen zeigte, dass sich die vermeintlich hohen Level an Umweltstress, die mit den klimatischen Veränderungen vor und nach dem LGM einhergingen, nicht in der Traumaprävalenz widerspiegeln. Die Traumahäufigkeit während des Jungpaläolithikums ist ähnlich wie bei mesolithischen und neolithischen Skelettserien. Ferner zeigte die Untersuchung, dass Männer etwas häufiger verletzt waren als Frauen und dass bei beiden Geschlechtern mehr Traumata innerhalb der älteren Altersgruppe auftraten. Der statistische Auswertungsansatz mittels GLMMs stellt eine leistungsstarke Alternative zu konventionellen Frequenzberechnungen für die Analyse von prähistorischen Traumahäufigkeiten dar – besonders dann, wenn die Skelettüberlieferung wie im Fossilbericht spärlich ist. Diese Dissertation verdeutlicht, wie wichtig es für die Erforschung von Traumata an fossilen Skelettresten ist, qualitative wie auch quantitative Untersuchungsansätze zu berücksichtigen sowie kontextuelle Variablen in die Auswertung einzubeziehen.

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1. Introduction

The human skeleton is key to understanding how humans lived, adapted, and died in the distant past. Skeletal remains – often the only record left of past humans – can preserve traces of lived experiences such as adaptations to everyday activities, or developmental, nutritional or health challenges a person faced during life, as well as the measures the organism took to cope with them. Thereby, habitual activities, episodes of deficiencies and disease, individual behaviors, cultural practices, and sometimes even the cause of death can become stored in the skeleton, serving as an archive of past life events that can be “read” by the osteologist (Grauer and Armelagos, 1998; Agarwal and Glencross, 2011; Martin et al., 2013; Agarwal, 2016; Martin and Harrod, 2016; Larsen, 2018; Schrader, 2019).

Among these traces, traumatic lesions reveal insights into individual fates and behaviors, given that they result from accidents or violent encounters. In anthropology, trauma refers to a bodily injury caused by an extrinsic agent. Traumatic lesions appear as partially or completely fractured bones, and in the form of altered bone surfaces or depressions. Even though a large number of traumatic lesions remain restricted to the soft tissue in the living (Novak, 2006), and therefore go unnoticed in the skeletal record, anthropological trauma analyses have nevertheless shown to be a powerful tool for reconstructions of past human lives yielding insights into individual or group-specific social, cultural, and environmental life realities (e.g., Wilkinson and van Wagenen, 1993; Martin et al., 2010; Wahl and Trautmann, 2012; Larsen, 2015; Martin and Harrod, 2015; Allen et al., 2016; Martin and Harrod, 2016; Mirazón Lahr et al., 2016; Redfern, 2017a, 2017b).

1.1. Theoretical and methodological background of trauma research

Cranial blunt force trauma

Bone is elastic and hard at the same time, owing to its composition of organic (collagen fibers) and inorganic components (minerals). Bone is therefore both flexible and robust to resist mechanical forces, encountered for example during locomotion or physical activities (Symes et al., 2012). When impacted, cranial bone behaves in a biomechanically determined way because of its global shape and its layered structure with two layers of cortical bone (inner and outer tables) and a layer of trabecular bone (diploë) in between. Yet, the manner of reaction depends on the velocity and

magnitude of the applied force and differs between slow loadings (i.e. force moving at speeds of kilometers per hour, such as blows, falls, or motor vehicle accidents) and rapid loadings (i.e. force moving at speeds of meters per second, such as ballistics and explosives) (Symes et al., 2012). In the context of this thesis, only slow loads causing blunt force trauma are of interest since the latter is irrelevant for Paleolithic times. As a general rule, owing from its viscoelastic properties, bone is about twice as strong against compression than against tension, and will therefore always fracture first under tensile loads (Berryman and Symes, 1998; Symes et al., 2012). When bone is impacted by a slow load, it first bends and deforms. Such deformation is reversible, and the bone will return to its original shape when the load is removed (elastic phase). However, if the load persists and surpasses the elastic capacity of the bone matrix, damages at the microscopic level occur, that result in a non-reversible plastic deformation (plastic phase). Finally, if the load has still not dissipated, failure occurs – that is, cranial trauma (König and Wahl, 2006; Passalacqua and Fenton, 2012; Symes et al., 2012; Loe, 2016).

Cranial traumatic lesions represent a more persistent life-course record than long-bone trauma. The latter heal forming a callus, and usually disappear completely after some months or years – if not severely misaligned – because of remodeling and mechanical loads (Mays, 1998; Nehrlich et al., 2003; Schumpelick et al., 2010; Boyd, 2018). In contrast, cranial bone possesses less regenerative capacity than long bones due to biologically different properties, like the relative dearth in bone marrow, relatively little blood supply, and a lack of mechanical loads, except for mastication (Schmitz and Hollinger, 1986; Nehrlich et al., 2003). As a consequence, adult cranial bones are thought to not naturally fill in defects with new bone tissue (Schmitz and Hollinger, 1986; Campillo, 1991; Carlson, 2007; Szpalski et al., 2010), which is why modern clinical treatment of skull fractures commonly involves materials and procedures like growth stimulation substances, bone grafts, or biomaterial scaffolds to stimulate and support the bony bridging of a defect (Szpalski et al., 2010; Lappalainen, 2016). Nevertheless, also if clinically untreated, a non-lethal cranial defect will heal. Signs of healing occur earliest one to two weeks after injury and involve osteoclastic and osteoblastic responses, namely the removal of necrotic bone tissue and the formation of new bone (Campillo, 1991; Barbian and Sledzik, 2008; Boer et al., 2015). Subsequently, lesion edges and exposed diploë get covered up by the deposition of new bone, but the gap itself is usually bridged by a hard soft-tissue matrix instead of bone (Beck et al., 1991; Boyd, 2018), leaving a visible gap in the archaeological dry bone specimen. Hence, even long healed cranial trauma is

commonly recognizable in human skeletal remains, providing a record of a deceased person's sustained but survived cranial injuries.

Ante-, peri- and postmortem trauma or breakage

Healing is the most striking and defining characteristic of antemortem trauma, that is, an injury sustained during life. An injury that was not survived long enough to start healing, is called perimortem trauma (around the time of death), but definitions of the term perimortem differ between disciplines. According to the clinical definition, perimortem refers to the dying process, i.e. to the time interval between being injured and death (Symes et al., 2012). In anthropology, in contrast, perimortem describes any fresh bone breakage lacking signs of healing, regardless of whether it was sustained before or after death. The latter definition considers the fact that bone can pertain a fresh (wet) state for weeks, months or even years after death, depending on the depositional conditions of the skeletal remains (Maples, 1986; Moraitis and Spiliopoulou, 2006; Galloway et al., 2014; Cunha and Pinheiro, 2016; Sorg, 2019). The transition of wet bone to a dry state involves the progressive loss of organic material during decomposition and is a gradual and non-uniform process (Moraitis and Spiliopoulou, 2006; Passalacqua and Fenton, 2012; Cunha and Pinheiro, 2016; Sorg, 2019). Dry bone is bone that has lost (most of) its organic components. Its breakage occurs postmortem by definition and represents taphonomic damage rather than trauma.

Assessing the timing of injury

How much load bone can absorb before it fractures depends on the ratio of organic to inorganic components and the amount of moisture. These conditions change with advancing age of a person (Schmitt et al., 2010; Wescott, 2013), and, even more so, after death when organic components progressively decompose and thereby also change related biomechanical behaviours. In contrast to fresh wet bone, decomposed dry bone is brittle and fails immediately without undergoing the elastic and plastic phases beforehand (König and Wahl, 2006; Symes et al., 2012; Christensen et al., 2019; Wescott, 2019). This produces distinct fracture morphologies that allow for the distinction between fresh (perimortem) and dry (postmortem) bone breakage in well-preserved skeletal remains.

Several morphological features have been suggested as characteristic for the two types of breakage. A perimortem blunt force impact typically causes a fracture pattern resembling a spider-web with primary fractures at the point of impact, fracture lines radiating from it, and possibly concentric fractures, if the applied force has not yet

dissipated beforehand (Symes et al., 2012; Christensen et al., 2019; Ribeiro et al., 2020). Perimortem fracture lines exhibit distinct morphological features including oblique fracture edges/beveling, smooth undulated margins, cortical delamination, peels, plastic deformation, hinging/bridges, flake defects, bone scales, fissures and crushed margins, that differentiate them from dry bone breakages (Wahl and König, 1987; Berryman and Haun, 1996; Churchill and Formicola, 1997; Berryman and Symes, 1998; Symes et al., 2012; Fleming-Farrell et al., 2013; Jordana et al., 2013a; Kranioti, 2015; Ribeiro et al., 2020). Because dry bones possess no plastic capacity, they shatter in several smaller fragments when impacted, producing fragments with jagged and brittle edges. Dry bone breakage lines are discontinuous and do not show plastic deformation (Maples, 1986; Wahl and König, 1987; Lovell, 1997; Sauer, 1998; Fleming-Farrell et al., 2013; Jordana et al., 2013a, 2013b; Galloway et al., 2014; Loe, 2016; Sala et al., 2016; Wescott, 2019; Ribeiro et al., 2020). The edges of fresh bone breakages have furthermore been suggested to break at obtuse or acute angles, while those of dry bones have been suggested to break at roughly right angles, but deviations from this rule of thumb have also been observed (Wahl and König, 1987; Lovell, 1997; König and Wahl, 2006; Fleming-Farrell et al., 2013; Jordana et al., 2013a, 2013b; Kranioti, 2015; Sala et al., 2016). Knowing the timing of fracture helps identify the processes that have acted on the skeletal remains under study, such as taphonomic (depositional damage) or behavioral (e.g., intravital injury or processing of remains after death).

Trauma prevalence and preservation

The preservation of human bone in terms of condition and completeness is of particular importance for trauma analyses. First, poor preservation such as damaged surfaces may obscure signs of trauma and hamper explicit diagnoses of bony lesions in paleopathological assessments of skeletal remains. Second, estimates of trauma prevalence highly depend on the preservation of skeletal remains because traumatic lesions once present in a skeleton may be missing from the archaeological skeletal record when remains are incomplete (Judd, 2002, 2004; Pankowská et al., 2019). Hence, the less complete skeletal remains are, the higher the uncertainty of trauma prevalence estimates. Several studies therefore suggest using preservation thresholds to address this issue and consider only bones with a defined minimum preservation such as 75% complete in their analyses (Judd, 2002; Fibiger et al., 2013; Cohen et al., 2014; Schulting and Fibiger, 2014; Gheggi, 2016; Torres-Rouff et al., 2018). This ensures comparability of obtained trauma prevalence estimates within and between samples that follow the same preservation threshold, but negatively impacts sample

sizes and may result in the exclusion of large parts of a sample when skeletal preservation is poor. The use of preservation thresholds is therefore not straightforward for fossil skeletal remains, considering their small sample sizes and incomplete preservation.

1.2. Trauma research in Neanderthal and modern human fossil remains

Since the discovery of Neanderthal fossils more than 150 years ago (Schmerling, 1833; Fuhlrott, 1859; Schaaffhausen, 1859; King, 1864; Menez, 2018), paleoanthropological research has been concerned with reconstructing the taxonomic position of these hominins, their biology, behaviour, culture, and lifestyle, and investigating the reasons behind their disappearance and replacement by *H. sapiens*, the only extant *Homo* taxon. The perception of Neanderthals has changed substantially in the last few decades in view of new concepts, methods, sites and specimens, through which our understanding of these past humans has constantly enhanced and refined (Drell, 2000; Schlager and Wittwer-Backofen, 2015; Madison, 2020; Peeters and Zwart, 2020). Among these perceptions, the depiction of Neanderthals as robust hominins living harsh and dangerous lives has long prevailed in academia and the public alike. Traumatic injuries, thought to occur frequently in Neanderthal skeletal remains (Courville, 1967; Kunter, 1986; Berger and Trinkaus, 1995; Underdown, 2006; Nakahashi, 2017), and also more often than in early modern humans (McBrearty and Brooks, 2000; Klein, 2009; Trinkaus et al., 2014), are, alongside other lines of evidence, believed to demonstrate the stresses and struggles in the lives of Neanderthals (Trinkaus, 1978; Berger and Trinkaus, 1995; Pettitt, 2000; Davies and Underdown, 2006; Klein, 2009; Overmann and Coolidge, 2013). Proposed explanations for traumatic injuries in Neanderthals include: (1) a violent social behaviour among and between groups (Courville, 1950, 1967; Jurmain, 2001; Hutton Estabrook and Frayer, 2014); (2) hunting techniques without long distance-weapons resulting in violent encounters with large prey mammals (Berger and Trinkaus, 1995; Gaudzinski-Windheuser et al., 2018); (3) a highly mobile hunter-gatherer-lifestyle in a glacial environment where accidental falls were common (Underdown, 2006); and (4) attacks by carnivores like bears or cave lions (Camarós et al., 2016). These interpretations exemplify the significance of trauma studies in reconstructing the lifestyles of Neanderthals and Paleolithic modern humans alike.

Types of trauma analyses

Trauma analyses can be applied targeting at a wide range of research questions and, accordingly, manifold approaches have been utilized. A general distinction of previous approaches in Paleolithic research can be made between qualitative trauma analyses and quantitative trauma analyses.

Qualitative trauma analyses aim to describe bony lesions, diagnose whether such represent a trauma, and discuss alternative diagnoses or alternative causes, such as taphonomic damages. Hence, qualitative trauma assessments are usually case studies examining single individuals or coherent skeletal series. They are commonly performed in targeted and specialized paleopathological investigations, or as part of the standard protocol in osteological examinations aiming at comprehensively studying and describing newly discovered human skeletal remains. Qualitative trauma studies can inform about individual fates and the injuries that formed part of a person's life. Building upon individual qualitative trauma diagnoses, quantitative trauma analyses estimate and statistically compare the quantity or frequency of traumatic lesions in pre-defined units within or between different samples. Quantitative trauma analyses have been employed in two different ways, either to explore the anatomical distribution of traumata across the body, or to investigate the prevalence of trauma within a sample, group, or population. Anatomical trauma patterns refer to the proportional distribution of lesions throughout the skeleton, and analyses therefore consider exclusively injured individuals. In contrast, prevalence studies focus on the quantity of trauma occurrence in a sample and therefore assess the proportion of injured to uninjured individuals.

Previous qualitative trauma research

Trauma among Neanderthals and Upper Paleolithic human fossil remains has predominantly been addressed in anecdotal reviews of skeletal remains with traces of injury (e.g., Courville, 1950; Roper, 1969; Dastugue and Lumley, 1976; Kunter, 1981; Ullrich, 1982; Pettitt, 2000; Holt and Formicola, 2008; Klein, 2009; Trinkaus, 2013), as well as in numerous individual qualitative case studies (for cranial trauma e.g., Trinkaus and Zimmerman, 1982; Trinkaus, 1983, 1985; Zollikofer et al., 2002; Mann and Monge, 2006; Schultz, 2006; Teschler-Nicola et al., 2006; Trinkaus et al., 2006; Coqueugniot et al., 2014; Giemsch et al., 2015; Sala et al., 2015; Sala et al., 2016; Kranioti et al., 2019; see also references in Supplementary Table 3 of Paper I and Table S2 of Paper II).

Although the circumstances and causes of traumatic injuries are often not readily discernible, evaluations of individual accounts of trauma have yielded revealing

insights into the lives and deaths of single Neanderthals and Upper Paleolithic specimens. For example, the Upper Paleolithic specimen Cioclovina 1 (Kranioti et al., 2019) and the pre-Neanderthal specimen Sima de los Huesos Cr-17 (Sala et al., 2015) likely sustained lethal blows to their skulls, suggesting violent deaths. The Upper Paleolithic specimens Grotte des Enfants 2 (Henry-Gambier, 2001) and San Teodoro 4 (Bachechi et al., 1997) were possibly shot or stabbed, as indicated by lithics found embedded in their postcranial bones. Similar projectile or stabbing injuries were also observed in the skeletal remains of the Upper Paleolithic specimen Sunghir 1 (Trinkaus and Buzhilova, 2012) and the Neanderthal specimen Shanidar 3 (Trinkaus, 1983; Churchill et al., 2009). However, it could not be distinguished whether these injuries resulted from an accidental (e.g., hunting accident) or violent cause. Some instances of trauma observed in fossil human remains likely involved significant consequences, such as temporary or permanent disabilities and impairments (e.g., Trinkaus and Zimmerman, 1982; Trinkaus, 1983; Zollikofer et al., 2002; Coqueugniot et al., 2014), fostering discussion about the provision of care for the injured in Paleolithic times (Hublin, 2009; Tilley, 2015b; Thorpe, 2016; Spikins et al., 2018; Spikins et al., 2019).

More recently, virtual techniques such as computed tomography are complementing examinations of fossil remains and have extended the scope of qualitative trauma investigations by allowing for the non-destructive investigation of otherwise inaccessible specimens and features (e.g., unprepared fossils or internal structures, such as cross-sectional aspects of fractures) (Fleming-Farrell et al., 2013; Schultz and Schmidt-Schultz, 2015; Villa et al., 2019; Coqueugniot et al., 2020). Especially signs of perimortem trauma are likely to go unnoticed in fragmented and partial skeletal remains because characteristic perimortem breakage patterns, such as an impact site with concentric and radiating fractures, are not immediately apparent. Using virtual approaches, both antemortem trauma and perimortem fractures have successfully been identified in fossil crania of Neanderthals and early modern humans (Zollikofer et al., 2002; Coqueugniot et al., 2014; Kranioti et al., 2019), as well as in other hominin fossil crania (Indriati, 2006; Wu et al., 2011; Sala et al., 2015; Sala et al., 2016; Wu et al., 2021). Moreover, these techniques were also used to distinguish between pathological and taphonomic alterations of Paleolithic fossil cranial remains (Ponce De León, 2002; Gómez-Olivencia et al., 2018; Fernández-Jalvo and Andrews, 2019).

Previous quantitative trauma research

Despite the common application of quantitative approaches to the study of trauma patterns in skeletal samples from Holocene times (e.g., Walker, 1989; Pijoan Aguadé and Lory, 1997; Tung, 2007; Jurmain et al., 2009; Andrushko and Torres, 2011; Šlaus et al., 2012; Fibiger et al., 2013), there are only few systematic large-scale assessments of trauma patterns in Neanderthals and Upper Paleolithic humans.

Most of the research focused on anatomical injury patterns and on Neanderthals (Berger and Trinkaus, 1995; Gardner, 2004; Hutton Estabrook, 2007, 2009; Trinkaus, 2012; Camarós et al., 2016). Representing one of the most influential studies in this context, Berger and Trinkaus (1995) investigated the anatomical distribution pattern of traumatic lesions in a sample of 17 Neanderthal specimens and identified a high proportion of skull and neck injuries (~30%) in the sample. This injury pattern resembled that of today's rodeo riders. The authors hypothesized that, owing to their hunting technique lacking long-distance weapons, Neanderthals had to get very close to their hunting prey and, like rodeo riders, suffered from many accidental injuries caused by regular encounters with large ungulates (Berger and Trinkaus, 1995). A similar anatomical trauma pattern with high rates of skull injuries was also observed in two other Neanderthal skeletal series, one from Krapina (n=14-82, depending on the estimate), and one Eurasian-wide Neanderthal sample (n=15) (Hutton Estabrook, 2007), which largely corresponds to the sample already analysed by Berger and Trinkaus (1995). Among the first studies comprehensively considering contextual factors that may affect trauma distributions in Neanderthals, Hutton Estabrook (2009) investigated whether distribution patterns in a sample of injured Neanderthals (n=22) co-vary with several factors (date, geography, preservation, body side, age-at-death, sex, and severity of injury), and identified correlations of trauma distribution with age-at-death, preservation, and age-at-death along with sex. A predominance of skull and neck lesions has long been considered Neanderthal-specific (Berger and Trinkaus, 1995), until it was found to be common in Upper Paleolithic modern humans, too, prompting a revision of the rodeo rider hypothesis (Trinkaus, 2012). Proposed alternative, non-mutually exclusive explanations for this trauma pattern include inter-human violence, commonly targeting the upper body region (Trinkaus, 2012; Hutton Estabrook and Frayer, 2014), and the necessity to maintain locomotion and mobility. Considering the relative dearth of lower limb trauma in the fossil record, it has been suggested that immobile individuals may have been left behind and their remains did not preserve (Berger and Trinkaus, 1995; Trinkaus, 2012; but see Hutton Estabrook and Frayer, 2014). Another explanation for the Paleolithic injury pattern with high levels of cranial trauma has been proposed

by Camarós et al. (2016), who showed that the injury patterns exhibited by nowadays victims of violent encounters with large carnivores are almost identical to those described by Berger and Trinkaus (1995) and Trinkaus (2012) for Neanderthals and Upper Paleolithic humans.

Population-related trauma patterns of Neanderthals and Upper Paleolithic humans have barely been researched, and the few studies conducted so far yielded widely varying findings. Cranial trauma prevalence estimates of 30–40% have been suggested for Neanderthals (Courville, 1967; Kunter, 1986). However, these estimates are not based on systematic quantitative evidence, but on casuistic impressions from compilations of injured specimens. By extrapolating observed trauma rates from incomplete bones to complete skeletons, Nakahashi (2017) estimated a Neanderthal population-related trauma frequency of 79–94% using all skeletal remains, and 28–38% using crania only. By contrast, Brennan (1991) investigated stress indicators and trauma in a regional sample of Neanderthals and Upper Paleolithic humans from southern France and found a trauma frequency as low as 2% across a lumped Middle and Upper Paleolithic sample (n=209). Other research compared postcranial (Underdown, 2006; Hutton Estabrook, 2009) and cranial (Hutton Estabrook and Frayer, 2014) trauma frequencies of Neanderthals to that of recent hunter-gatherer groups, finding contrasting results. While Underdown (2006) found a long bone trauma frequency of 32% in Neanderthal specimens (n=31), which exceeded the injury frequencies of modern hunter-gatherer comparative samples, Hutton Estabrook (2009) and Estabrook and Frayer (2014) identified largely similar trauma rates in Neanderthals when compared to recent hunter-gatherers, proposing that "*the highly traumatized Neandertal' is a cliché*" (Hutton Estabrook, 2009, p. 338).

2. Objectives

This dissertation research aimed at furthering our understanding of cranial trauma in Neanderthal and modern human fossil remains by qualitative and quantitative means. The primary objectives were threefold: (1) to investigate the cranial breakage patterns of two late Middle Pleistocene crania from the Apidima caves in Greece in a qualitative manner (Paper III); (2) to contrast cranial trauma prevalence of Neanderthals with that of Upper Paleolithic modern humans by quantitative means (Paper I); and (3) to characterize population-related quantitative trauma prevalence patterns among Upper Paleolithic modern humans (Paper II).

Objective 1: Qualitative assessment of the cranial breakage patterns of two late Middle Pleistocene crania from Apidima, Greece (Paper III)

In the first study of this cumulative dissertation, I qualitatively investigated the cranial breakage patterns of two highly fragmented and partially damaged late Middle Pleistocene crania from the Apidima cave site in the southern Peloponnese, Greece (Apidima 1 and 2). In a previous forensic examination of Apidima 2, cranial fractures on its frontal bone were interpreted to be the result of two traumatic blows (Coutselinis et al., 1991, 1995). Later, however, this interpretation was revised, and the fractures were instead suggested to result from sediment pressure during deposition and to represent taphonomic damage (Geanacos, 2001; Pitsios, 2007; Pitsios et al., 2007). The second partial cranium, Apidima 1, has so far not been investigated from a forensic or taphonomic point of view. In this study, I assessed the timing of breakage of the two Apidima crania to evaluate whether the fractures represent postmortem taphonomic damage or perimortem fractures, and thus possibly traumatic injuries. This study is the first to systematically analyze the cranial breakage patterns of Apidima 1 and re-evaluate the cranial breakage patterns of Apidima 2. To do so, I employed virtual methods using computed tomography (CT) scanning of the two crania which allowed for non-destructive examination of the endo- and ectocranial aspects of fracture lines despite adhesive breccia. I aimed at differentiating between perimortem (fresh) and postmortem (dry) bone breakages of the two Apidima fossil crania by examining five morphological breakage features (breakage outline, path of least resistance, breakage angle, texture, and plastic response).

Objective 2: Quantifying cranial trauma prevalence in Neanderthals and Upper Paleolithic modern humans (Paper I)

In the second study of this cumulative dissertation, I quantified the population-related cranial trauma prevalence of Neanderthals and Upper Paleolithic modern humans from western Eurasia to test the hypothesis of more trauma in Neanderthals relative to Upper Paleolithic humans. The study aimed at testing a long-lasting research opinion in paleoanthropology – the view of a commonly high trauma prevalence in Neanderthals – which has prevailed for years in the scientific and public opinion (Trinkaus, 1978; Berger and Trinkaus, 1995; Pettitt, 2000; Klein, 2009), although recent research cast doubts on the validity of this assertion (Hutton Estabrook, 2009). To do so, I performed a comprehensive literature review of published fossil remains with and without traces of traumatic injuries and contrasted cranial trauma prevalence patterns between the two taxa using generalized linear mixed models (GLMMs). This approach allowed me to account for contextual factors, such as age-at-death, sex, and skeletal preservation, which have rarely been accounted for in previous Paleolithic trauma studies. These contextual factors have been shown to significantly affect trauma prevalence variation and visibility of traumatic lesions in skeletal remains (Larsen, 1997; Jurmain, 1999; Judd, 2002; Hutton Estabrook, 2009; Martin and Harrod, 2015; Redfern, 2017b), and are therefore critical for quantitative estimates of trauma rates.

Objective 3: Characterizing population-related trauma prevalence patterns in Upper Paleolithic modern humans (Paper II)

In the third study of this cumulative dissertation, I quantified the population-related cranial trauma prevalence among fossil skeletal remains from the Upper Paleolithic of western Eurasia to arrive at a large-scale characterization of trauma prevalence patterns, revealing insights into the lifestyles and stresses during the Upper Paleolithic. The objectives of the study were fourfold: (1) to quantify, to my knowledge for the first time, the overall cranial trauma prevalence for skeletal remains from the entire period of the Upper Paleolithic and compare the estimates to samples from Middle Paleolithic, Mesolithic, and Neolithic times; (2) to evaluate how cranial trauma prevalence in Upper Paleolithic humans varies with basic demographic variables, such as age-at-death and sex, because previous research identified higher rates of cranial trauma among male individuals (Paper II), which is consistent with the suggested sexual division of labor in Upper Paleolithic humans (Brennan, 1991;

Balme and Bowdler, 2006; Kuhn and Stiner, 2006; Stiner and Kuhn, 2009; Villotte et al., 2010; Villotte and Knüsel, 2014; Zilhão, 2014; Karakostis et al., 2018; Beaune, 2019); (3) to investigate possible differences in cranial trauma prevalence before and after the Last Glacial Maximum (LGM) to further scrutinize previous suggestions of higher levels of stress as well as a health deterioration in the late Upper Paleolithic (Brennan, 1991; Formicola and Holt, 2007; Holt and Formicola, 2008; Trinkaus, 2013); and (4) to assess whether the cranial vault (neurocranium) or the face (viscerocranium) were more likely injured, because the anatomical distribution of trauma may yield insights into the circumstances of injury, such as violence (Walker, 1989, 1997; Lessa and Souza, 2006; Novak, 2006; Kremer et al., 2008; Kremer and Sauvageau, 2009; Martin and Harrod, 2015; Redfern, 2017a). To do so, I collected a dataset of fossil cranial remains with and without trauma through a comprehensive literature review and assessed patterns of cranial trauma prevalence with GLMMs.

3. Material and Methods

3.1. Qualitative trauma analysis: Case study Apidima (Paper III)

3.1.1. The Apidima site and human fossils

The fossil bearing site Apidima is located in proximity to the village Areopolis at the coast of Mani Peninsula in the southern Peloponnese in Greece (Harvati, in press; Harvati et al., 2009; Harvati, 2016). The five caves of the site (A,B,C,D and E), which today are only accessible by boat, are filled with progressively eroding Middle and Late Pleistocene terrestrial sediments (Pitsios, 1999; Harvati et al., 2011; Bräuer et al., 2019). In the late 1970s, a team of researchers from the Museum of Anthropology of the School of Medicine, National and Kapodistrian University of Athens, discovered two partial human crania (Apidima 1 and 2), enclosed in breccia, in the cave walls of cave A. The two specimens, deposited circa 15 cm apart from each other, were excavated *en bloc* and later prepared in the laboratory to mechanically remove the enclosing breccia (Pitsios, 1999). The crania are highly fragmented but nevertheless adhere together owing to the remaining breccia on their insides.

Apidima 1 (also labeled LAO1/S1) comprises a major part of the left parietal, the superior right parietal bone, a portion of the occipital bone and the posterior left temporal squama. A large piece of rock is still attached to it (Harvati et al., 2019). The more complete second cranium, Apidima 2 (also labeled LAO1/S2), exhibits a nearly complete facial skeleton lacking the mandible, and an almost complete cranial vault lacking the cranial base and the occipital bone (Harvati et al., 2019).

Apidima 2 is thought to represent a Neanderthal specimen, dating to more than 170 thousand years before present (ka BP) (Harvati et al., 2011; Bartsiokas et al., 2017; Bräuer et al., 2019; Harvati et al., 2019). Apidima 1 has recently been dated to older than 210 ka BP and is taxonomically classified as early *Homo sapiens* (Harvati et al., 2019; although Lumley, 2019 and Lumley et al., 2020 arrive at a different assignment, but see Harvati, in press; Harvati et al., 2020). Thus, Apidima 1 currently represents the oldest known anatomically modern human outside of Africa.

3.1.2. Timing the cranial breakage of the Apidima fossils

To evaluate the timing of breakage of the Apidima cranial fossils, a virtual anthropological approach was employed. Using computed tomography (CT) scanning of the crania, the breakage lines were assessed by evaluating five morphological breakage features: (1) breakage outline (straight, stepped, curved), (2) path of least

resistance (yes or no), (3) breakage angle (measured on two to seven points along each breakage line or defect in CT cross sections), (4) texture (smooth or jagged; assessed at each point where an angle was measured), and (5) plastic response (yes or no) (see Table 1). These five features were assessed for 15 breakage lines in Apidima 1, and for 37 breakage lines in Apidima 2. Additionally, the edges of four defects in Apidima 2 (damages or holes partly filled with breccia or plaster on the ectocranial surface) were examined by assessing the latter three features (breakage angle, texture, plastic response), since the other two do not apply. Based on the joint assessments of the single features, each breakage line was classified as fresh or dry bone breakage, or as inconclusive regarding the timing of breakage.

Table 1. Criteria used to distinguish peri- or postmortem timing of cranial breakages in the Apidima crania (table modified from Paper III, see Appendix C).

Feature (references)	Description	Fresh bone	Dry bone	Inconclusive	Criteria evaluated in this study
Outline	General course of breakage line along ectocranial surface	Curved	Stepped	Straight	Classification of each breakage line as curved, stepped, or straight
Path of least resistance (Symes et al., 2012; Fleming-Farrell et al., 2013; Galloway and Wedel, 2014a; Loe, 2016)	Propagation of breakages towards structurally weaker areas of the skull	Present	Absent	-	Evaluation of whether a breakage line runs towards a structurally weaker area of the skull (yes, no)
Angle (Fleming-Farrell et al., 2013; Jordana et al., 2013b; Kranioti, 2015; Sala et al., 2016)	Angulation between endocranial cortical surface and breakage edge	Oblique (acute: <70°, or obtuse: >110°)	Right (70°-110°)	-	Measurement of the angle between the ecto- and endocranial surface at several (2-7) points along each breakage line and defect in cross-sectional 2D view
Texture (Fleming-Farrell et al., 2013; Jordana et al., 2013a; Sala et al., 2016)	Texture of breakage edge (exposed surface of outer table, diploë, inner table)	Smooth	Jagged	-	Assessment of the texture of breakage edges as smooth or jagged at each point, where an angle was measured
Plastic response (Symes et al., 2012; Fleming-Farrell et al., 2013; Kranioti, 2015)	Permanent plastic deformation (applied force exceeded elastic capacity of bone)	Present	-	Absent	Investigation whether any signs of plastic response are associated with breakage lines (yes, no)

3.2. Quantitative trauma analyses: Neanderthals and Upper Paleolithic humans (Papers I and II)

3.2.1. Data collection

Data for the population-related analyses of cranial trauma in Neanderthals and Upper Paleolithic humans were collected from the literature. The publications used to compile the data comprised for the largest part scientific publications such as peer-reviewed papers, book chapters and monographs, as well as few 'grey' literature resources, including conference contributions, archaeological excavation reports, master's theses, museum databases, and personal communications with examiners of original fossils. All references used to compile the datasets analyzed in Papers I and II are provided in the associated supplementary materials allowing for transparency and reproducibility.

The literature of several hundred Middle- and Upper Paleolithic sites were researched to check whether fossil human remains were preserved and met the following three criteria to be included in the studies: (1) the preserved cranial remains (except isolated teeth) belong to classic Neanderthals or Upper Paleolithic modern humans, and can securely be assigned to a time period from around 80 to 10 ka BP by direct dating or archaeological context (that is, stratigraphic position or associated finds), (2) available pictures, drawings or verbal anatomical descriptions of preserved cranial specimens allow for quantification of their completeness, and (3) estimated age-at-death of the cranial specimens is at least about 12 years. Remains of younger children were not considered, because the higher bone remodeling and healing rates in growing bone may erase once present signs of antemortem trauma (Boyd, 2018; Redfern and Roberts, 2019), thereby introducing bias in data collection. In adult cranial remains, on the contrary, such signs persist, even when fully healed (Walker, 1989; Campillo, 1991; Lewis, 2006; Redfern, 2017b).

To account for bias in trauma prevalence by the differential preservation of the cranial remains, it was registered which of the 14 skeletal elements (frontal, occipital, as well as left and right elements of parietal, temporal, maxillary, mandibular, zygomatic and nasal bones) were preserved in each specimen and how complete they were. The completeness of each skeletal element was visually rated in four preservation categories (ca. 1–25%, 26–50%, 51–75% and 76–100%), except for zygomatic and nasal bones, which were rated in two categories due to their small size (ca. 1–50% and 51–100%).

For each skeletal element it was registered whether it exhibits a trauma or not. Trauma was recorded in a binary fashion (present/absent) per skeletal element, thus, multiple injuries on the same element were not considered. Trauma diagnoses were adopted from the original specimens' examiners, and a lesion was counted as a trauma if the original examiners stated so or if they considered trauma a possible differential diagnosis. Both antemortem and perimortem trauma was considered and not differentiated in the analyses. However, perimortem breakages suggested to result from an event after death, such as burial, deposition, or postmortem manipulation by original authors, were excluded.

Of each preserved cranial specimen, the following contextual parameters were recorded: taxon (Neanderthal or Upper Paleolithic modern human), and for the latter, the time period within the Upper Paleolithic (pre-LGM or post-LGM, with the onset of the Magdalenian period as the cut-off criterion); sex (male, female or indeterminate); age-at-death (young: 12–30 years; old: >30 years; or indeterminate: >12 years but no more detailed estimate available). The age of 30 years offered a good cut-off point to separate samples because there were the least overlapping age ranges, and samples could be divided without having too many specimens that fell in both cohorts. The few specimens with age determinations at around 30 years (e.g., 25–35 years or ~30 years) were attributed to the young cohort. Finally, each site providing cranial remains was assigned to one of five geographic regions within Eurasia in Paper I (Iberia, South, Central, East, Near East) and to one of four in Paper II (Iberia, South, Central, East). All assignments of trauma, taxon, sex, age-at-death, and date followed published reports of the respective specimens. These assignments were performed by several different researchers and may thus be affected by observer bias or the use of different approaches. They are nevertheless considered reliable and assumed to represent current best knowledge, given that they were gathered from scientific publications, whose quality is assured by peer-review and editorial work.

Paper I contrasts Neanderthals (ca. 80–30 ka BP) with early and mid-Upper Paleolithic humans (ca. 35–20 ka BP) and samples comprised 114 Neanderthal specimens, corresponding to 295 skeletal elements, and 90 Upper Paleolithic specimens, corresponding to 541 skeletal elements. Paper II comprised Upper Paleolithic humans from the entire Upper Paleolithic (ca. 40–10 ka BP) and the sample amounts to a total of 234 specimens, or 1,285 skeletal elements, respectively. Data analysed in Paper II are publicly available at the Zenodo Data Repository (Beier, 2020).

3.2.2. Assessing trauma prevalence with GLMMs

The relative scarcity of trauma cases as opposed to the numerous cranial specimens without trauma, plus the variety of contextual variables that should be accounted for in the analyses, eventuated in the need for an advanced multivariate statistical approach. Cranial trauma prevalence was therefore assessed and compared between different subsamples using GLMMs with a Markov chain Monte Carlo (MCMC) algorithm implemented in the MCMCglmm package (Hadfield, 2010) in the statistics software R (R Core Team, 2019). With this approach, skeletal remains of any preservation status could be included in the analyses and trauma prevalence could be predicted across different levels of preservation.

Models were fitted with trauma as the binary dependent variable with a binomial error distribution and a logit-link function. All model variants were calculated twice, (1) at the level of cranial elements, and (2) at the level of cranial specimens. In the element-level approach, it could be accounted for potential variation in trauma prevalence between the 14 different skeletal elements by adding them as a random component to the models. This is crucial because trauma has been observed not to be equally frequent across different skull regions (Walker, 1997; Wilkinson, 1997; Fibiger et al., 2013; Delgado-Darias et al., 2018; Scaffidi and Tung, 2020). The element-level approach, however, may be affected by pseudoreplication because traumatic lesions extending over more than one skeletal element are counted several times. The specimen-level approach, where cranial trauma absence or presence was scored for each specimen instead of each skeletal element, overcomes the issue of pseudoreplication, but it cannot be accounted for variation in trauma prevalence between different skeletal elements. Preservation at the specimen-level was scored by adding up the element-preservation categories of each preserved skeletal element belonging to one specimen and divide the sum by 14 (maximum number of elements per specimen).

Analyses in Papers I and II comprised several model variants using different data subsets and different variable combinations of the fixed two-level predictors taxon (Neanderthals or Upper Paleolithic humans), period (pre-LGM or post-LGM), age (young or old), sex (male or female), as well as the four-level covariate element preservation (0.25, 0.5, 0.75, and 1) in the element-level models, or the continuous covariate specimen preservation in the specimen-level models. Models also included different interaction terms to assess relationships between specific variables. Intercepts for skeletal elements were added as random component to the element-level models to account for trauma prevalence variation between different skeletal elements. Geographic location was added as a second random component to element-

level models, and as the only random component to specimen-levels models, to account for the possibility that trauma prevalence may vary by geographic region. From the generated posterior distributions, parameter estimates were derived as posterior means with lower and upper 95% credible intervals (CI), and p-values for posterior means (pMCMC) were calculated. Based on the model estimates, mean predictions of trauma prevalence with 95% CIs were computed for each fixed factor combination. Predictions of trauma prevalence are estimates of the probability that a skeletal element or specimen exhibits trauma. They are marginalized over random effects, meaning that predictions are merged over variation in trauma prevalence across geographic regions and, in the element-level models, skeletal elements. The different model variants and data subsets, as well as technical details how the specific models of each study were fitted and validated, are provided in the methods sections of Papers I and II (Appendices A and B). Statistical inference and interpretation of results were based on predicted model coefficients (effect sizes), p-values of posterior means, and the model-predicted trauma prevalence patterns.

4. Results and Discussion

4.1. Qualitative trauma analysis: Case study Apidima (Paper III)

This study assessed the breakage patterns of the two Apidima cave fossil crania through the evaluation of five morphological fracture features to differentiate between perimortem (fresh) and postmortem (dry) bone fractures. In both crania, most of the examined fractures and defects remained inconclusive regarding their timing of breakage (66.7% in Apidima 1 and 73.0% in Apidima 2). In Apidima 1, 26.7% of the fractures show a morphology that is compliant or rather compliant with fresh bone fractures, whereas 6.7% of the fractures are rather compliant with dry bone fracture morphology. In Apidima 2, 13.5% of the fractures exhibit a morphology compliant or rather compliant with fresh bone fracture, and also 13.5% are rather compliant with dry bone breakage.

Fractures in the frontal bone of Apidima 2, that were previously suggested to result from blunt force trauma (Coutselinis et al., 1991, 1995), but were later attributed to taphonomic damages that had happened during deposition (Geanacos, 2001; Pitsios, 2007; Pitsios et al., 2007), gave inconclusive results regarding the timing of breakage. Therefore, despite the re-assessment carried out in this study, neither of the two previous interpretations can be supported.

Besides many inconclusive expressions of features, several fracture lines (53.3% in Apidima 1, as well as 43.2% of fractures and 25.0% of defects in Apidima 2) were found to show fresh and dry bone breakage morphologies at the same time – although the morphology within one fracture or defect is expected to exhibit predominantly either fresh or dry bone breakage characteristics. Results regarding the timing of breakage were also inconsistent between the two features breakage angle and texture although the morphology of these two features should be correlated, since perimortem breakage edges are considered to be oblique and smooth, and postmortem edges to be right-angled and jagged. Nevertheless, only 53.3% of the assessed breakage edges in Apidima 1, and 62.6% of the assessed edges in Apidima 2 corresponded to this expected association between breakage angle and texture.

The findings of a large portion of inconclusive expressions of features, the observed mix of fresh and dry bone breakage characteristics between the five features within a single fracture line, and the lack of association between breakage angle and texture, could relate to different explanations.

Possibly, the number and type of features used to differentiate fresh from dry bone breakage were too few or not specific enough to adequately capture morphological differences. Features such as cortical delamination, hinging and flaking, suggested to be good indicators of fresh bone breakage (Fleming-Farrell et al., 2013; Jordana et al., 2013a; Kranioti, 2015; Sala et al., 2016), could not be assessed, because the insufficient resolution of the available medical CT scans precluded their evaluation. This represents a major limitation to the study. Cortical delamination larger than 10.5 mm has been suggested to be indicative of fresh bone breakage in isolated human remains, whereas in skeletal series, a combination of the features breakage angle, roughness, cortical delamination and fracture outline were found to be good indicators (Jordana et al., 2013a). The consideration of additional features would likely improve determinations of the timing of breakage, even though the Apidima crania are isolated. This limitation could be addressed by using high-resolution micro-CT scans of the crania for the investigation of breakage timing (Fleming-Farrell et al., 2013; Sala et al., 2016), when such are available in the future. Likewise, considering that several breakage lines were not observable and thus not evaluable in the available CT scans, the use of micro-CT scans could likely also improve the rate of successful observations of the features assessed here.

Alternative explanations for the heterogenous findings of fresh and dry bone fracture morphologies could be associated with the fossilized state of preservation and the depositional history of the Apidima remains. Assessments of the timing of breakage are hampered in bones deposited in wet conditions, first, because the changed decomposition rates in water-logged environments may prolong the perimortem interval (Haglund and Sorg, 2002; Galloway et al., 2014; Augias et al., 2017; Stuart and Ueland, 2017), and second, because the breakage behavior of rehydrated dry bone can resemble that of fresh bone (Broz et al., 1993; Moraitis and Spiliopoulou, 2006; Augias et al., 2017; King, 2017). In addition, diagnostic characteristics of breakage edges are more likely obscured in water environments, owing to abrasive sediment movements (Haglund and Sorg, 2002; Moraitis and Spiliopoulou, 2006). Wet conditions were possibly present at several times during the depositional history of the Apidima crania. The crania were found in close proximity, although U-series dating indicates that they are temporally separated by about 40 thousand years (Harvati et al., 2019). A potential scenario proposed to explain this find situation involves the downwards displacement of the specimens, each deposited at distinct times, which was caused by out-washing of underlying sediments (Harvati et al., 2019). Moreover, recurring sea level changes during Pleistocene and post-Pleistocene times contributed both to the formation of the Apidima caves, nowadays located only

few meters above sea level, and to the erosion of the cave sediments (Pitsios, 1999; Harvati et al., 2011; Bräuer et al., 2019). Hence, the Apidima fossils were presumably affected by sea water on different occasions during their depositional history, as well as by a possible mudflow event. Geoarchaeological investigations could help clarify if and to what extent wet conditions were present in the sediments surrounding the Apidima crania, and help evaluate how these conditions may have affected the taphonomy and breakage behavior of the remains.

Furthermore, bone breakage could also have occurred after the two Apidima crania had fossilized. It is assumed that mineralized bone behaves differently than both fresh and dry bone when being impacted (Morlan, 1984; Gifford-Gonzalez, 2018). Fossil bone rather breaks like a stiff and uniform material, because the original bone tissue with its viscoelastic and brittle properties (Symes et al., 2012) had been replaced by minerals with biomechanically different properties (Morlan, 1984; L'Abbé et al., 2015; Gifford-Gonzalez, 2018). Assessing the timing of fracture using fresh and dry bone characteristics might be pointless for bone that fractured after mineralization. However, breakage behavior and breakage characteristics of mineralized fossil cranial bone has, to my knowledge, not been thoroughly studied and described so far. Such investigations would be crucial for future assessments of the timing of trauma in fossil remains, but would require study designs with experimental or modeling approaches that do not involve damaging or destroying precious fossils.

4.2. Quantitative trauma analyses: Neanderthals and Upper Paleolithic humans (Papers I and II)

The second and third objectives of this thesis addressed the prevalence of cranial trauma in Neanderthals and Upper Paleolithic humans through a comprehensive quantitative population-level analysis including contextual data and using a large fossil dataset. The analyses employed in Papers I and II ground on data collected by means of a thorough review of Middle and Upper Paleolithic human fossil remains from western Eurasia, spanning a time from 80 to 10 ka BP and a geographic range from Great Britain to the Near East and from Portugal to Siberia. Only a fraction of the several hundred fossil specimens reviewed was eligible to be included in analyses and thus considered in the population-related assessment of cranial trauma prevalence. Samples of the two studies of Papers I and II sum up to a total of 348 quantified cranial specimens (114 Neanderthal, 234 Upper Paleolithic human) from

140 sites (39 Neanderthal, 101 Upper Paleolithic human), representing 1,580 skeletal elements (295 Neanderthal, 1,285 Upper Paleolithic human).

Among these, 32 specimens sustained cranial trauma (9 Neanderthal, 23 Upper Paleolithic human), exhibiting a total of 63 single traumatic lesions (15 Neanderthal, 48 Upper Paleolithic human; lesions extending over two or more elements counted once). This corresponds to 14 cranial elements of Neanderthals and 42 cranial elements of Upper Paleolithic humans exhibiting one or several traumatic cranial lesions.

This systematic literature review revealed cases of cranial trauma, especially in late Upper Paleolithic fossil remains, which have remained largely unnoticed aside their mention in the anthropological reports of the respective fossils. Accordingly, these cases are also missing in recent inventories of injured Paleolithic specimens, such as Sala et al. (2015) and Wu et al. (2011). An important outcome of this doctoral research is a comprehensive trauma catalogue, where all single lesions of the studied specimens are listed and shortly described by paraphrasing the diagnoses of the original fossils' examiners and providing original references. The catalogue, split in two sections, can be found in the supplementary materials of Paper I (Neanderthals and Upper Paleolithic humans until about 20 ka BP) and Paper II (Upper Paleolithic humans post-dating 20 ka BP). Through the integration of available, but so far often overlooked Paleolithic trauma cases, the catalogue provides a significant contribution to Paleolithic trauma research and can serve as a reference resource to future studies.

4.2.1. Testing a research opinion: the highly traumatized Neanderthal?

(Paper I)

To scrutinize the long-lasting and prevailing view of Neanderthals as leading dangerous and exhaustive lives (Trinkaus, 1978; Berger and Trinkaus, 1995; Pettitt, 2000; Klein, 2009; Overmann and Coolidge, 2013), this study aimed at testing whether Neanderthals exhibit more cranial trauma than Upper Paleolithic modern humans, and whether trauma prevalence in the two taxa is (differentially) affected by contextual variables, including age-at-death, sex, and preservation.

Across all model variants and subsets of the data, trauma prevalence was found to be similar between Neanderthals and Upper Paleolithic humans. Therefore, the hypothesis of more cranial trauma in Neanderthals as compared to early and mid-Upper Paleolithic modern humans is rejected. The mean model-predicted trauma prevalence for Neanderthals was 3–17% for skeletal elements and 4–33% for specimens, and for Upper Paleolithic humans 2–12% for skeletal elements and 2–34% for specimens (minimum and maximum mean predictions of models 1–8 in

Paper I, predicted for skeletal elements when 50–75% complete, and for mean specimen-preservation scores, respectively). The estimates for Neanderthals are at the very limit of previous suggestions of about 30–40% prevalence of cranial trauma in Neanderthals (Courville, 1967; Kunter, 1981; Nakahashi, 2017). Furthermore, the prevalence estimates for both Neanderthals and Upper Paleolithic humans are similar to the prevalence of cranial trauma in Holocene humans, such as Mesolithic hunter-gatherers (Bennike, 1985; Terberger, 2006), Neolithic agriculturalists (Bennike, 1985; Fibiger et al., 2013), and modern hunter-gatherers (Davies and Underdown, 2006; Hutton Estabrook, 2009).

The analyses revealed that trauma prevalence is strongly related to sex. In Neanderthals and Upper Paleolithic humans, males have higher trauma prevalence than females. Such trauma pattern has been observed in Neanderthals in previous studies (Trinkaus, 1983; Hutton Estabrook, 2009) and is also commonly found in modern human skeletal remains from later periods (e.g., Jurmain and Bellifemine, 1997; Larsen, 1997; Walker, 2001; Jiménez-Brobeil et al., 2009; Fibiger et al., 2013; Cohen et al., 2014; Schwitalla et al., 2014; Milner et al., 2015; Allen et al., 2016; Redfern, 2017b; Scaffidi and Tung, 2020; Standen et al., 2020). It might suggest that male individuals exposed themselves more often to risky situations and activities, such as physical conflict, or hazardous leisure activities, that involve a high chance for accidental injuries (Sutherland, 2002; O'Jile et al., 2004; Kwan et al., 2011; Martin and Harrod, 2015; Judd, 2017; Redfern, 2017b). Differences in trauma prevalence between the sexes may also be related to culturally determined sex-specific behaviours and activities within a group, exposing males to higher or females to lower risks for injuries, such as division of labour, warfare or initiation rites (Larsen, 1997; Martin and Harrod, 2015; Redfern, 2017b).

Beyond these similarities, analyses revealed age-dependent differences between the two taxa in the element-based models. Neanderthals exhibited more trauma in young compared to old skeletal elements, whereas Upper Paleolithic humans showed a roughly similar trauma prevalence between young and old skeletal elements. In other words, Neanderthals younger than about 30 years were more likely injured than modern humans of the same age, but the two taxa were similarly often injured when older than about 30 years. This finding contrasts – at least as far as cranial trauma is concerned – with previous suggestions that injured Neanderthals were predominantly of older age (Trinkaus, 1983; Hutton Estabrook, 2009). Given that in both taxa most injuries were healed, it furthermore contradicts the suggestion that trauma accumulates with age, as a result of the longer period of exposure to potentially hazardous situations (Glencross and Sawchuk, 2003) in combination with

the condition that signs of cranial trauma remain visible due to the limited capacity of cranial bone to fully bridge and remodel cranial lesion during healing (Walker, 1989; Campillo, 1991; Lewis, 2006; Redfern, 2017b). However, a linear relationship between the number of traumatic lesions and increasing age does not necessarily apply to death assemblages, such as a skeletal series (Boldsen et al., 2015; Milner and Boldsen, 2017). Clinical and anthropological research has shown that individuals with a record of trauma have a higher relative risk of dying than individuals who never sustained injury, even if the injury had fully healed (Boldsen et al., 2015; Eriksson et al., 2016; Mitchell et al., 2017). Compared to individuals who were never injured, trauma survivors are more likely to die sooner, i.e., they have an increased mortality, and thus occur in the death assemblage at relatively younger ages (Boldsen et al., 2015). In this study, both taxa deviate from the linear accumulation of trauma with increasing age when considering skeletal elements, and neither Neanderthals nor Upper Paleolithic humans show a markedly higher trauma prevalence in old compared to young elements. This can be interpreted as indicating an increased mortality risk of trauma survivors relative to non-injured individuals in both taxa, which is, however, further elevated among Neanderthals. The interpretation of age-related trauma prevalence in skeletal remains is not straightforward because once healed, it usually cannot be assessed from the skeletal remains alone at what age a trauma was acquired, but only that an individual of a certain age, who sustained a traumatic injury sometime earlier in life, died. Therefore, the distinct age-related trauma patterns between Neanderthals and Upper Paleolithic humans found here could be explained by two alternative scenarios, that are, however, not mutually exclusive: (1) Neanderthals had a higher likelihood of injury when young compared to Upper Paleolithic humans; and/or (2) the trauma prevalence was similar for both Neanderthals and Upper Paleolithic humans when young, but young Neanderthal trauma survivors had a more elevated risk of dying than young Upper Paleolithic human trauma survivors. Under the second scenario, injured young Upper Palaeolithic modern humans were more likely to survive into the old age cohort – which is where the trauma is recorded in the death assemblage, although it was originally sustained when young. Several possible reasons can account for different age-specific injury proneness or mortality risks. For example, different activities or different individual temperaments, either more or less cautious, lead to different exposures to hazardous situations. Furthermore, the severity of injuries and resulting long-term consequences, such as impairments, or differences in the provision of care for the injured can likewise affect injury-related mortality risks at the individual or group-level (Tilley, 2015a, 2015b; Thorpe, 2016; Stodder,

2017; Tilley, 2017; Spikins et al., 2018; Tornberg and Jacobsson, 2018; Spikins et al., 2019).

The results and interpretations of this study are limited by several aspects. First, analyses were restricted to cranial fossil remains and interpretations are therefore limited to this body region. The additional consideration of postcranial remains is important since postcranial trauma patterns might be distinct from the findings presented here and should therefore be integrated in future research to arrive at more exhausting interpretations about injury patterns of Neanderthals and Upper Paleolithic humans. The present study provides a conceptual template for that.

The inclusion of postcranial remains would also significantly increase the number of available samples as well as cases of trauma, further improving analytical GLMM performance. The few cases of trauma in the samples relative to the many remains without trauma, represent a second concern of this study, affecting model convergence and analytical power. A trade-off exists between model convergence and the number of variables and variable levels that can be included in analysis. As the number of variables or variable levels increases, there are proportionally fewer trauma cases in each variable level that can be used as reference to assess the explanatory power of single variables in the model computations. In fact, poor model convergence turned out to be a major challenge during study design, which could finally be addressed by employing the MCMC-GLMM approach. Nevertheless, credible intervals of coefficient estimates and predictions, indicating the uncertainty associated with the estimates, were still rather large. Possibly, analytical performance could be improved by using refined computational algorithms.

A third limitation is that data was collected from the literature. The use of secondary published data carries a risk that should be acknowledged as data might be affected by observational bias due to different methods and varying expertise of original examiners. Ideally, every cranial specimen would have been examined by the same well-experienced person to diagnose traumatic lesions and to determine age-at-death and sex. However, many fossils have restricted access or no longer exist (for example, destroyed in World War II). This makes previously collected and published data the only information available and precludes systematic (re-)assessment by a single person. Here, data collection was sought to be as comprehensive and complete as possible by combining published evidence from past research with more recent results, reflecting best-practice of research in the field. Importantly, misclassifications of traumatic lesions, age-at-death, or sex are assumed to be equally likely in Neanderthals and Upper Paleolithic humans, and therefore are not expected to introduce systematic bias into the group comparisons.

Finally, the quantitative findings of this study should in the future be complemented by qualitative assessments of the traumatic lesions. Qualitative investigations provide more in-depth details about individual injuries and could help to further interpret and contextualize the observed trauma rates and patterns. In a similar manner, antemortem and perimortem trauma, that were not differentiated in this study, could be considered separately to further elucidate questions of injury severeness, survival and mortality.

4.2.2. Cranial trauma prevalence throughout the Upper Paleolithic (Paper II)

To characterize trauma in Upper Paleolithic fossil remains, a comprehensive and systematic assessment of population-related cranial trauma prevalence patterns of western Eurasian humans from the entire Upper Paleolithic period, dating to around 40 to 10 ka BP, was performed. The objectives addressed were fourfold: (1) to estimate the overall cranial trauma prevalence for fossil remains from the Upper Paleolithic, (2) to evaluate if and how trauma prevalence varies with variables such as sex and age-at-death, (3) to investigate whether cranial trauma prevalence differs in human groups before and after the LGM, and (4) to examine whether the cranial vault (neurocranium) or the face (viscerocranium) were more likely injured.

The Upper Paleolithic sample exhibits an overall mean trauma prevalence of 3-7% at the level of skeletal elements, and of 8-26% at the level of specimens (mean predictions of models 1.1 and 1.2 in Paper II, predicted for remains at their lowest and highest preservation categories/scores, respectively). These estimates are largely similar to the estimates for Neanderthals ranging between 3 and 17% for skeletal elements, and between 4 and 33% for specimens (lowest and highest mean predictions of models 1-8 in Paper I, predicted for skeletal elements when 50-75% complete, and for specimens at mean specimen-preservation scores).

To enable comparisons with previous trauma studies of Mesolithic and Neolithic cranial samples, crude trauma frequencies were calculated in addition to the GLMM-predicted prevalence (see 4.2.3. for a discussion of the two approaches). The Upper Paleolithic crude frequencies (3.3–3.5% for elements, 9.8–21.4% for specimens, calculated for the full sample irrespective of preservation and for remains >75% complete, respectively) largely correspond to the range of crude trauma frequencies found in samples from Mesolithic and Neolithic times. For example, Mesolithic cranial specimens revealed crude trauma frequencies of 4.7% (Roksandic, 2006), 5–19% (Terberger, 2006), 9.5% (Papathanasiou, 2012), and 43.8% (Bennike, 1985), however, this latter estimate was adjusted downwards after the assessment of additional samples (Schulting, 2006). Samples of Neolithic cranial specimens yielded crude

trauma frequencies of 3.4% (Roksandic, 2006), 3.5% (Papathanasiou, 2012), 8.9% (Schulting and Wysocki, 2005), 9.4% (Bennike, 1985), 11.5% (Jiménez-Brobeil et al., 2009), and 9–17% (and 1–6% for skeletal elements instead of specimens; (Fibiger et al., 2013).

Trauma prevalence was higher in male compared to female Upper Paleolithic remains, although the difference is rather small. A distinct male to female cranial trauma prevalence can result from sex-specific activities or behaviors that involve different exposures to risky situations. Such would be consistent with a sexual division of labor, proposed to have intensified during Upper Paleolithic times (Brennan, 1991; Balme and Bowdler, 2006; Kuhn and Stiner, 2006; Stiner and Kuhn, 2009; Villotte et al., 2010; Villotte and Knüsel, 2014; Zilhão, 2014; Karakostis et al., 2018; Beaune, 2019). However, anthropological reconstructions of past sex-specific behaviors and tasks rest on morphological or genetic sex determinations of the human remains which cannot ultimately be equated with the genders lived by those individuals. Interpretations about the cultural and social organization of past human groups and their gender roles as drawn from skeletal remains alone, are therefore limited and require specifically designed studies considering contextual information (Sofaer, 2006; Martin et al., 2010; Agarwal and Glencross, 2011; Wood and Eagly, 2012; Agarwal and Wesp, 2017; Matic and Jensen, 2017; Zuckerman and Crandall, 2019). The prevalence of cranial trauma varied between age cohorts in the Upper Paleolithic sample. Cranial elements and specimens in the old age cohort were more often injured than elements and specimens in the young age cohort. This pattern, found in both males and females, is rather consistent with the proposed, yet debated, accumulation of trauma with increasing age (Glencross and Sawchuk, 2003; Boldsen et al., 2015; Milner and Boldsen, 2017; and see 4.2.1. (p. 30-31) for a discussion of age-related trauma patterns and selective mortality). This pattern is distinct from the age-related trauma pattern found for skeletal elements of Upper Paleolithic humans pre-dating the LGM in Paper I. However, the age pattern found in Paper I refers to the interaction term taxon-by-age and should be considered relative to the comparative sample of Neanderthals. In Paper II, by contrast, age-related variation in trauma prevalence was assessed across the full sample (entire Upper Paleolithic period; age as fixed predictor) and per time period (pre-LGM/post-LGM; age-by-period interaction). Moreover, it should be noted that the predictions of trauma prevalence in the two studies refer to different preservation categories (50-75% complete in Paper I, 76-100% complete in Paper II). Thus, the different age patterns found in Papers I and II need not represent contradicting results; such could only be revealed by using all three comparative samples in a single analysis. In general, age-related trauma

patterns obtained from skeletal remains are challenging to interpret as it is unknown for healed injuries at which time during life they were acquired. They would be best addressed using several and more narrow age cohorts than the two broad categories used here (young and old), because the upper limit of each age cohort serves as a *terminus ante quem* for the traumatic injuries observed in the respective cohort. However, the age-at-death determinations available for the fossil skeletal remains studied here often comprise very wide age ranges, ruling out the possibility to form narrower age categories. Ranges are inherent to any age-at-death determination as they reflect uncertainties due to individual variation in the expression of age-related morphological features, methodological limits of adult age determinations, and incomplete preservation. Issues of wide-ranging age-at-death determinations in reconstructions of age-related trauma patterns and associated mortality in Upper Paleolithic human remains may be addressed by using refined age-at-death determination methods and more specific study designs, including for example demographic modeling (Boldsen et al., 2015).

Samples from before and after the LGM showed no time-specific cranial trauma prevalence, but similar trauma rates and patterns in the two sexes and age cohorts across both time periods. During the Late Pleistocene, modern humans faced several millennia of major climatic and environmental changes, involving marked oscillations in climatic conditions (Mix, 2001; Barron et al., 2003; Davies and Gollop, 2003; van Andel, 2003; Clark et al., 2009) and deteriorations in habitat suitability (Burke et al., 2017; Holt, 2018). These changes finally culminated in the LGM, a period when average global temperature dropped significantly, and ice sheets covered most of Europe (Clark et al., 2009; Tierney et al., 2020). In consequence, human populations are assumed to either have gone extinct or retreated to southern refugia, leaving large parts of central Europe uninhabited (Brewster et al., 2014a; Wygal and Heidenreich, 2014; Straus, 2015; Tallavaara et al., 2015; Djindjian, 2016; Maier et al., 2016; Burke et al., 2017; Maier and Zimmermann, 2017). Following the LGM, a population discontinuity and turnover are suggested by paleogenetic and craniometric data (Brewster et al., 2014a; Brewster et al., 2014b; Fu et al., 2016), and morphological differences in body height and robusticity between humans before and after the LGM have also been observed (Brennan, 1991; Formicola and Giannecchini, 1999; Ruff, 2002; Formicola and Holt, 2007; Holt and Formicola, 2008; Meiklejohn and Babb, 2011; Holt et al., 2018; Holt, 2018; Niskanen et al., 2018; Cox et al., 2019). The climatic conditions during the Upper Paleolithic likely exposed human populations to high levels of demographic and environmental stress (Straus, 2015; Djindjian, 2016; Maier et al., 2016; Burke et al., 2017; Maier, 2017). Nevertheless, skeletal remains

were found to exhibit only minor indications of declined health or worsening living conditions, as was inferred from skeletal stress markers such as dental hypoplasia and Harris lines, and from the decrease in body height among late Paleolithic humans, which was suggested to result from reduced gene flow and nutritional deficiencies (Brennan, 1991; Formicola and Giannecchini, 1999; Formicola and Holt, 2007; Holt and Formicola, 2008). Similarly, in this study, no time period-specific cranial trauma patterns were found for pre- and post-LGM samples that would reflect the stressors likely accompanying the climatic instabilities and associated large-scale changes in subsistence and population composition.

Comparing the prevalence of cranial lesions between the viscerocranium and the neurocranium, the neurocranium was found to be slightly more often injured than the viscerocranium. In both cranial regions, trauma prevalence was higher among old remains, but the two regions differed in their trauma prevalence between the sexes. In males, trauma occurred more frequently in the neurocranium, while females exhibited trauma more often in viscerocranial remains. Although the anatomical distribution of trauma across the skull can help to identify violent or accidental causes of injury (Walker, 1989, 1997; Lessa and Souza, 2006; Novak, 2006; Brink, 2009; Martin and Harrod, 2015; Redfern, 2017a), the various modes of injury and manifold intents of violence can lead to very different, sample-specific trauma patterns. Their interpretation often requires broad contextualization and conclusions usually remain restricted to the studied sample. Nevertheless, a commonly used concept called “hat brim line rule” suggests that blunt force trauma located above the hat brim line (area around the largest circumference of the cranial vault) is more likely caused by violent blows, while trauma in the hat brim line area more likely results from accidental falls (Kremer et al., 2008; Kremer and Sauvageau, 2009; Galloway and Wedel, 2014b). Following this rule, Upper Paleolithic males would have sustained violent blows more often than females. There are many exceptions, however, where the rule does not apply, which limits its straightforward and sole use for reconstructing causes of injury (Geserick et al., 2014; Kranioti, 2015). Not only trauma to the vault, but also trauma to the face can be indicative of violence, as is the case in domestic violence, for example (Novak, 2006; Guyomarc'h et al., 2010). In this study, model convergence precluded the consideration of more than two cranial regions and interpretations regarding the anatomical trauma pattern therefore remain sketchy. In addition, to arrive at detailed reconstructions of the different etiologies of Upper Paleolithic cranial injuries, quantitative findings as provided here should in the future be complemented by thorough qualitative trauma assessments.

This study is affected by several limitations which largely correspond to those of Paper I, given the similar study designs. Results refer exclusively to cranial remains since postcranial remains were not considered. Interpretations are thus limited in scope, and analyses should be extended to the postcranium in the future for a whole-body perspective of trauma prevalence patterns in Upper Paleolithic humans. Furthermore, although results ground on a large dataset of fossil skeletal remains, data was collected from the literature and assessments of trauma, sex, and age-at-death were performed by several different researchers and by using different methods. Inter-observer bias can therefore not be ruled out. This also applies to the diagnosis of traumatic lesions presented in the literature, which vary in detail and thoroughness, as the intentions of the cited publications range from specialized and highly detailed trauma examinations to general descriptions of fossil remains, where trauma is only briefly mentioned as part of a basic anthropological investigation. In this study, all lesions were recorded as trauma if original authors explicitly stated that a lesion or breakage edge represents a trauma, or if trauma was suggested as one of several possible causes of a lesion. Results could therefore be biased towards overestimating rates of trauma, when lesions for which trauma is mentioned among several explanations in a differential diagnosis are actually not trauma. Uncertainty in the diagnosis of bony lesions, however, cannot be ruled out completely, even if primary data from original specimens would be available, because manifold pathological or physiological processes evoke uniform bodily reactions, resulting in similar, unspecific bony manifestations (Klaus and Lynnerup, 2019). To address such potential bias, analyses were repeated on a reduced trauma data set, removing all skeletal elements/specimens from the trauma sample where original examiners of the fossils stated alternative explanations for a lesion besides trauma in a differential diagnosis. It should be noted, however, that the provision of a differential diagnosis does not necessarily indicate an undiagnostic trauma finding, but could, on the contrary, indicate a thorough and differentiated examination. The exclusion of cases, where trauma was among the possible differential diagnoses, could thus bias results just like their inclusion. The two approaches, using the full and the reduced trauma datasets, yielded very similar results in both overall effect patterns and credible interval ranges (see Supplementary Information of Paper II: p.14, Table S4, and Figure S2). Minor deviations in mean coefficient estimates and larger credible intervals in the analysis using the reduced trauma dataset can be explained by the fewer cases of trauma in the sample. As discussed in the limitations of Paper I (see 4.2.1., p. 32), fewer cases of trauma negatively affect model convergence and result in increased uncertainty of estimated model parameters. The trade-off between model

convergence and the number of variables or variable levels that can be accounted for in a model given a limited number of trauma cases likewise precluded the assessment of more than two cranial areas (neuro- and viscerocranium) in the examination of the distribution of traumatic lesions across the skull. These analytical issues could perhaps be addressed by employing GLMMs with a different computational algorithm.

4.2.3. GLMM-predicted trauma prevalence and crude trauma frequencies (Papers I and II)

To quantify the trauma prevalence of Neanderthals and Upper Paleolithic humans, a different method than the commonly used crude frequency calculations was used in Papers II and III of this thesis, namely, GLMMs. They allow for considering the effects of multiple predictor variables and variable interactions on trauma prevalence simultaneously. By including preservation as a variable in the analyses, it could be accounted for the differential preservation states and sample sizes of the cranial samples. The GLMM approach therefore represents a valuable alternative to crude trauma frequencies for assessments of past trauma rates, especially when dealing with poorly preserved incomplete human skeletal material.

Crude trauma frequencies are closely linked to skeletal preservation, because the less complete the skeletal remains are, the more likely a once present traumatic lesion is missing from the record. A common practice to account for this uncertainty and avoid potential bias in trauma frequencies is to consider only skeletal remains with a minimum preservation state, such as 75% complete, and exclude all less complete remains from analyses (Judd, 2002; Fibiger et al., 2013; Cohen et al., 2014; Schulting and Fibiger, 2014; Gheggi, 2016; Torres-Rouff et al., 2018). This procedure, however, severely diminishes sample sizes in poorly preserved samples such as the fossil record. In Paper II, for example, about 30% of sampled skeletal elements and more than 90% of sampled specimens would have to be excluded, if a preservation threshold of >75% was applied. While in the samples of Paper II the application of such preservation threshold would barely change crude frequencies at the level of skeletal elements (3.5% for elements that are >75% complete, and 3.3% for all elements irrespective of preservation), the crude trauma frequency for specimens that are >75% complete (21.4%) would be more than twice as high than the crude frequency of specimens irrespective of preservation (9.8%). The GLMM-predicted mean cranial trauma prevalence for remains that are 76-100% complete (Paper II; 7% for skeletal elements, and 26% for specimens) is slightly higher than the crude frequencies of remains that are >75% complete (3.5% for elements, 21.4% for

specimens). Yet, crude frequencies of the studied sample lie well within the GLMM-predicted 95% credible intervals.

The comparison of the GLMM-based trauma prevalence estimates of Papers I and II with previous trauma prevalence research is limited because this approach has, to my knowledge, so far not been applied in bioarchaeological trauma studies (but see Konigsberg and Frankenberg, 2013 for other applications of Bayesian methods in bioarchaeology, and Alonso-Llamazares et al., 2020 for a recent application of GLMMs to studying the prevalence of degenerative joint disease). It should be acknowledged that the comparability of crude trauma frequencies with GLMM-predicted prevalence is possible in very general terms, but not straightforward. In a similar vein, however, comparability of crude trauma frequencies between different studies is not straightforward either, because various approaches can be employed for their calculation (e.g., different preservation thresholds applied, or bone count vs. segment count; Judd, 2002). Future research should therefore explicitly evaluate the utility of GLMMs and crude frequencies for estimating trauma prevalence in poorly preserved samples, for example by using an artificial dataset with a known trauma prevalence and simulations of different amounts of missing data. Such study design could help to assess how closely the two approaches correspond to the known trauma prevalence of the sample and which approach provides more accurate estimates with increasing amounts of missing data.

5. Concluding remarks

In this dissertation, I researched cranial trauma in fossil remains of Neanderthals and modern humans using qualitative and quantitative analyses. Both approaches provide distinct insights into past humans' lives. While qualitative trauma analyses are concerned with the diagnosis of possible traumatic lesions to reconstruct individual fates, quantitative trauma analyses are concerned with larger-scale estimations and comparisons of trauma rates within and between samples to unravel similarities or differences in behaviors and lifestyles of past populations. With the latter quantitative approach, trauma patterns as well as possible changes in patterns through time and space can be recognized and related to social, cultural or environmental processes, if interpreted alongside contextual data. However, each quantitative investigation depends ultimately on the thoroughness of single qualitative trauma diagnoses that constitute their data base. Paper III exemplifies some of the methodological challenges that can be associated with qualitative trauma assessments of fossil remains, especially when the taphonomic and depositional history is complex. In future research, these might be overcome by using refined virtual methods and including further contextual information. Taking a quantitative approach, Papers I and II demonstrate the potential of employing advanced statistical techniques and highlight the importance of considering contextual anthropological and archaeological variables in analyses of fossil trauma. In doing so, this dissertation revealed hitherto unknown patterns of cranial trauma in Neanderthals and Upper Paleolithic modern humans. Future studies should expand the scope of analysis to postcranial remains to arrive at more comprehensive interpretations, and the analytical approach used here provides a methodological template for that. When seeking to decipher Paleolithic lives from skeletal lesions, it requires the combined evidence of qualitative and quantitative analyses, each contributing distinct yet equally important bits and pieces to our understanding of Paleolithic trauma.

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Appendix A
Paper I

**Similar cranial trauma prevalence among Neanderthals and Upper
Palaeolithic modern humans**

Judith Beier, Nils Anthes, Joachim Wahl, Katerina Harvati

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Similar cranial trauma prevalence among Neanderthals and Upper Palaeolithic modern humans

Judith Beier¹, Nils Anthes², Joachim Wahl^{1,3} & Katerina Harvati^{1,4*}

¹ Paleoanthropology, Senckenberg Centre for Human Evolution and Palaeoenvironment, University of Tübingen, Tübingen, Germany. ² Animal Evolutionary Ecology Group, Institute of Evolution and Ecology, University of Tübingen, Tübingen, Germany. ³ State Office for Cultural Heritage Management Baden-Württemberg, Osteology, Konstanz, Germany. ⁴ DFG Center for Advanced Studies ‘Words, Bones, Genes, Tools’, University of Tübingen, Tübingen, Germany. *Corresponding author: katerina.harvati@ifu.uni-tuebingen.de

Neanderthals are commonly depicted as leading dangerous lives and permanently struggling for survival. This view largely relies on the high incidences of trauma that have been reported^{1,2} and have variously been attributed to violent social behaviour^{3,4}, highly mobile hunter-gatherer lifestyles² or attacks by carnivores⁵. The described Neanderthal pattern of predominantly cranial injuries is further thought to reflect violent encounters with large prey mammals, resulting from the use of close-range hunting weapons¹. These interpretations directly shape our understanding of Neanderthal lifestyles, health and hunting abilities, yet mainly rest on descriptive, case-based evidence. Quantitative, population-level studies of traumatic injuries are rare. Here we reassess the hypothesis of higher cranial trauma prevalence among Neanderthals using a population-level approach—accounting for preservation bias and other contextual data—and an exhaustive fossil database. We show that Neanderthals and early Upper Palaeolithic anatomically modern humans exhibit similar overall incidences of cranial trauma, which are higher for males in both taxa, consistent with patterns shown by later populations of modern humans. Beyond these similarities, we observed species-specific, age-related variation in trauma prevalence, suggesting that there were differences in the timing of injuries during life or that there was a differential mortality risk of trauma survivors in the two groups. Finally, our results highlight the importance of preservation bias in studies of trauma prevalence.

Neanderthals are commonly depicted as robust hominins who led stressful, dangerous lives^{1,6–9}. Traumatic injuries, considered to be common among remains of adult Neanderthals¹, are a major piece of evidence supporting this hypothesis: not only are Neanderthals proposed to suffer from a high prevalence of trauma^{2,3,10,11}, but they are also thought to exhibit more traumatic injuries than early modern humans^{9,12,13}. Explanations for this include violent social behaviour^{3,4}, a highly mobile hunter-gatherer lifestyle in glacial environments² and attacks by carnivores⁵. 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 mammals¹. These interpretations have important implications for reconstructions of Neanderthal palaeobiology and behaviour, and have shaped the prevailing perception of the species. However, they are largely based on anecdotal evidence, because trauma among Palaeolithic humans is often reported on a descriptive, case-by-case basis. The few systematic, quantitative studies that have been conducted to date have yielded contradictory results^{2,4,11,14,15}, but question the prevailing view of ‘the highly traumatized Neanderthal’¹⁵.

Current research into Palaeolithic trauma suffers from several limitations. Most previous work assessed the proportional distribution of lesions throughout the body in injured Neanderthal skeletons, comparing the derived ratios to those of recent humans^{1,5,15–17}. Such approaches provide insights into individual life histories, but—because they focus exclusively on the injured—cannot elucidate population-level trauma prevalence. The latter requires an examination of both injured and uninjured individuals. Furthermore, contextual factors such as age at death, sex and skeletal preservation are rarely accounted for in these approaches¹⁵. These variables can markedly affect trauma prevalence variation^{18–21} and lesion visibility in the fossil record, and should thus be integral to population-level analyses. Moreover, Neanderthals are routinely compared to recent humans—clinical¹ or forensic⁵ samples, rodeo riders¹ and Holocene hunter-gatherers or nomads^{2,4,15,16}—but only rarely to Upper Palaeolithic modern humans¹⁷. However, the latter are the most appropriate comparative sample, sharing similar environments and comparable mobile hunter-gatherer lifestyles. Finally, small sample sizes have hampered the validity of the statistical inferences of most previous research.

Here we assess the hypothesis of higher prevalence of cranial trauma among Neanderthals relative to Upper Palaeolithic modern humans using a population-level comparison, including contextual data and using the largest fossil dataset that is currently available. We systematically compiled published information on fossil crania from the Middle and Upper Palaeolithic of Eurasia, dating to roughly 80–20 thousand years ago (Fig. 1). Cranial injuries—considered typical for Neanderthals¹—are a particularly reliable trauma archive, because they heal with only minor bone remodelling and therefore leave visible lesions even after full recovery²².

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

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

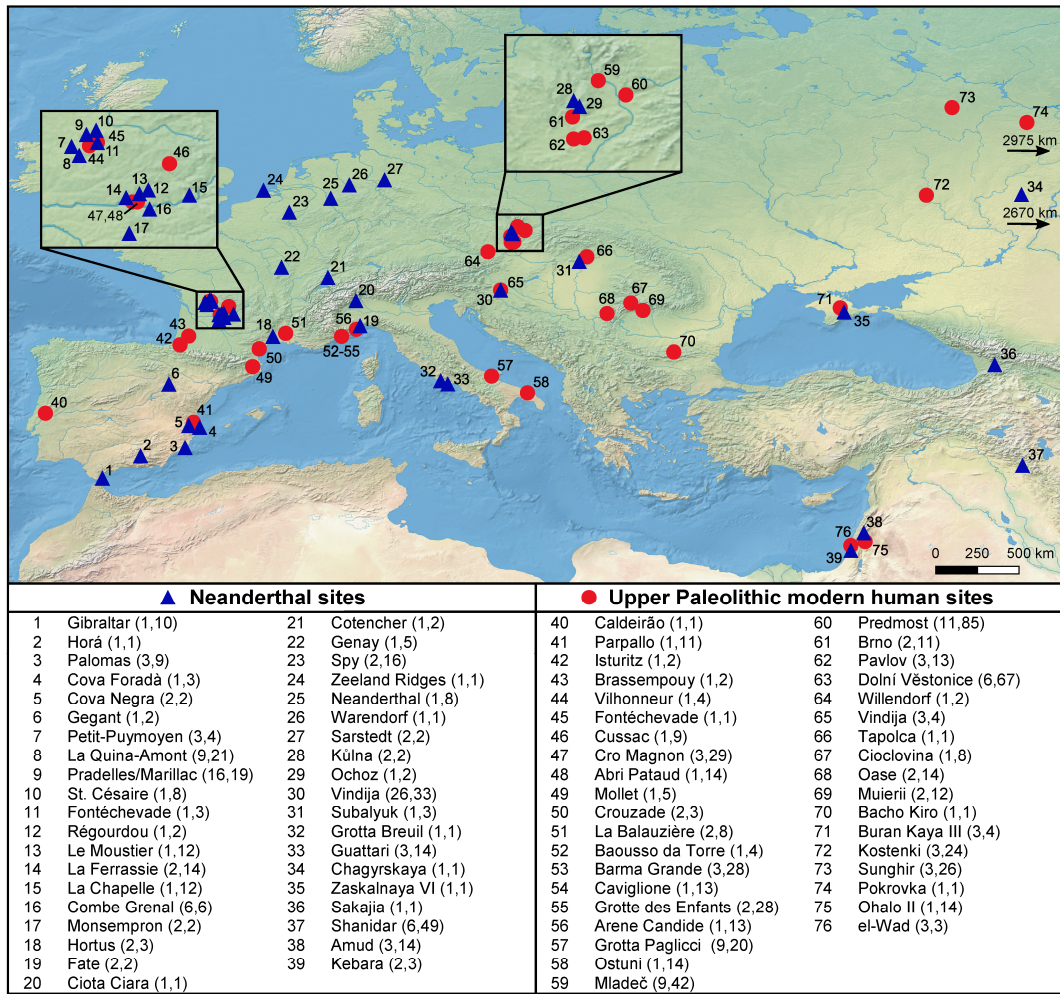


Fig. 1 | Neanderthal and Upper Palaeolithic modern human sites. Neanderthal sites, blue triangles; Upper Palaeolithic modern human sites, red dots. Numbers in brackets indicate number of specimens/number of skeletal elements, respectively. Sites Chagyrskaya (34) and Pokrovka (74) were projected 2,670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

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

Model 1 comprised the full dataset of all skeletal elements ($n = 836$) to exclusively assess overall taxon differences in trauma prevalence, while ignoring the incompletely scored contextual variables. Model 2 ($n = 604$) excluded skeletal elements of unknown sex and indeterminate age, thus assessing the additional influence of age, sex, element preservation, and the interaction between age and taxon. Given trauma predominance in males, we repeated these models on male-only subsets in models 3 ($n = 462$) and 4 ($n = 407$).

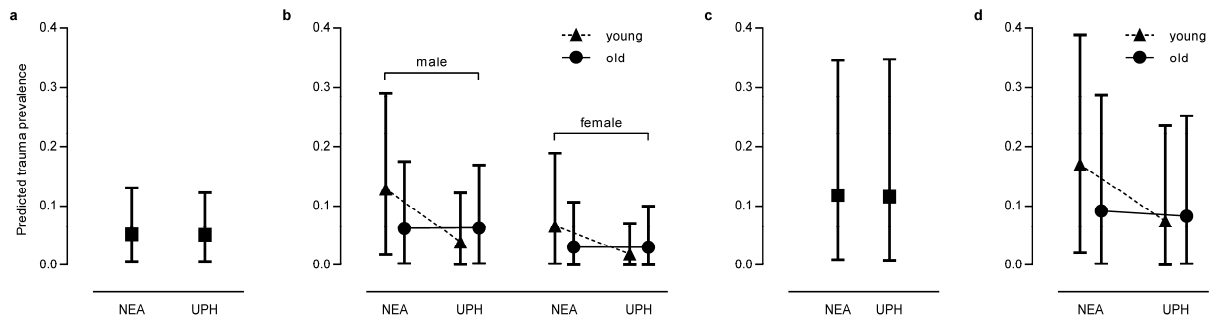


Fig. 2 | Predicted cranial trauma prevalence in skeletal elements from Neanderthals and Upper Palaeolithic modern humans. a, Model 1 includes taxon as the predictor variable (full dataset, $n = 836$). b, Model 2 includes the variables taxon, sex, age, element preservation and the interaction between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

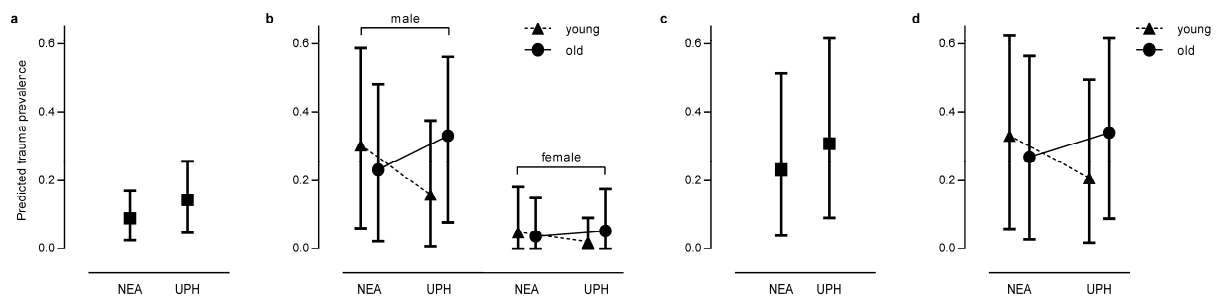


Fig. 3 | Predicted cranial trauma prevalence in individual cranial specimens from Neanderthal and Upper Palaeolithic modern humans. a, Model 5 includes taxon as the predictor variable (full dataset, $n = 204$). b, Model 6 includes the variables taxon, sex, age, specimen preservation and the interaction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

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

None of the models showed a quantitative difference in cranial trauma prevalence between Neanderthals and Upper Palaeolithic modern humans (taxon effect in models 1–8 in Table 1 and Figs. 2a–d, 3a–d). Instead, we found a significantly higher prevalence of trauma in males compared to females (sex effect in models 2 and 6; Table 1 and Figs. 2b, 3b). Furthermore, trauma prevalence significantly increased with preservation status, indicating a greater probability to detect trauma on more complete skeletal elements or individuals (preservation

effect in models 2, 4, 6 and 8; Table 1 and Extended Data Fig. 1a). Finally, in the element-based models, trauma prevalence varied between age classes with distinct patterns for the two taxa (age-by-taxon interaction in models 2 and 4; Table 1, Fig. 2b, d and Extended Data Fig. 1b): Neanderthals had a significantly higher prevalence of trauma when young, whereas Upper Palaeolithic modern humans showed a similar prevalence of trauma across age cohorts. Although a similar pattern appeared to be present in the specimen-level models (Fig. 3b, d), the interaction failed to reach statistical significance.

Table 1 | Summary statistics of the GLMMs

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

Trauma prevalence was modelled using a MCMC algorithm in two model sets with four data subsets each: models 1–4 comprise skeletal elements, models 5–8 comprise cranial specimens. Parameter estimates are given as their posterior mean with 95% credible intervals (CI) and statistical significance (*PMCMC*; ****P* < 0.01, ***P* < 0.05, **P* < 0.10). See Methods for details.

^a Full dataset.

^b Exclusion of sex unknown and age indeterminate elements or specimens.

^c Exclusion of female and sex unknown elements or specimens.

^d Exclusion of female, sex unknown and age indeterminate elements or specimens.

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

On the basis of our results, we reject the hypothesis that Neanderthals exhibit more cranial trauma than Upper Palaeolithic modern humans in western Eurasia—rather, we show that the two taxa exhibited a similar overall prevalence of cranial injuries. Previously suggested values of 30–40% cranial trauma prevalence for Neanderthals^{3,10} represent the very limit of the predictions of our models for Neanderthals (mean prevalence of 3–17% for skeletal elements and 4–33% for individual specimens); these values are comparable to those found for Upper Palaeolithic modern humans (2–12% for skeletal elements and 2–34% for individual specimens) and that have been reported for Mesolithic hunter-gatherers²³, Neolithic agriculturalists^{24,25} and recent hunter-gatherers²⁶. Nevertheless, trauma prevalence derived from skeletal remains must not be equated to the actual numbers of injuries that were experienced during an individual’s lifetime and comparisons of crude trauma frequencies should be considered with caution, because the methods used for their estimation are not always comparable among studies.

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

Both taxa showed mostly healed traumata and we did not find a markedly higher prevalence of trauma among ‘old’ skeletal elements in either group. This finding contradicts the expectation that healed traumatic injuries accumulate with increasing age as a result of longer exposure to dangerous situations²⁸, given that cranial defects remain visible over long-term periods owing to the limited regenerative bridging capacity of cranial bone healing²². However, death assemblages are likely to deviate from such an expected accumulation pattern^{29,30}, because injured individuals—even if they survived their injuries—had an increased risk of dying relative to individuals who were never injured^{31,32}. Thus, our observed age pattern across taxa is consistent with the well-documented increased mortality risk of trauma survivors.

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

Our study addresses the controversial topic of trauma prevalence in the Palaeolithic by reassessing cranial trauma data using a state-of-the-art methodological approach. It is, to our

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

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Author contributions

J.B., J.W. and K.H. conceived the study. J.B. collected data. J.B., J.W., K.H. and N.A. developed the methods. J.B. and N.A. analysed the data. J.B., J.W., K.H. and N.A. wrote the manuscript.

Methods

Data collection. We collected data through a comprehensive literature review and aimed at gathering a full-evidence dataset comprising all currently known fossil crania with and without traumatic lesions. We focused on Eurasian Middle and Upper Palaeolithic sites that had yielded skull remains from classic Neanderthals (around 80–30 thousand years ago) and early to mid-Upper Palaeolithic modern humans (around 35–20 thousand years ago) (Fig. 1; Supplementary Tables 1, 2 provide information on the studied specimens). We excluded specimens that consisted of only dental remains and restricted our sample to adolescent and adult specimens with a minimum estimated age-at-death of 12 years³³. For each specimen we recorded the taxon (Neanderthal or Upper Palaeolithic modern human), sex (male, female or unknown), age (young, 12–30 years; old, >30 years; or indeterminate, if there was no further estimate published), the skeletal element with its preservation status (see ‘Quantification’), and whether the skeletal element was affected by trauma (binary). Because trauma prevalence may vary across geographical regions owing to differing social or environmental conditions, we furthermore recorded the location of each specimen (five geographical regions: Iberia, south, central, east, Near East). We adopted the assignments of taxon, sex, age and the diagnoses of traumatic lesions as published by the examiners of the specimens. These literature-based assignments may be influenced by observer bias or by the use of different methods. Nevertheless, we decided in favour of a full-evidence approach based on all available published data in order to keep data collection as consistent and complete as possible. Moreover, many

fossil specimens are not available for original examination, precluding a single-method- based systematic assessment. We conducted an extensive literature review seeking to combine past research with the most recent results, so as to base our data on a complete synthesis of all available evidence, representing best-practice of research in the field. Notably, we expect misclassifications of traumatic lesions, age or sex to be equally likely in Neanderthals and Upper Palaeolithic modern humans, and this therefore should not introduce systematic biases into our group comparisons. Supplementary Table 3, a catalogue of specimens with described traumata, provides detailed descriptions of each lesion as published by the respective authors. A case was recorded as (possible) trauma once an author expressed confidence that a lesion represents a trauma, or considered a traumatic origin to be an alternative explanation for an observed lesion. No statistical methods were used to predetermine sample size. The investigators were not blinded to allocation during analyses.

Quantification. Skeletal preservation has a direct effect on the census of trauma prevalence, because an injury is more likely to be detected on a more complete bone³⁴. In chronologically older fragments, the preservation of skeletal remains commonly deteriorates and fragmentation of both single bones and associated skeletons increases. Moreover, the assignment of fragmented and commingled remains to specific individuals is often impossible or insecure. To account for differential skeletal preservation among sites and specimens, and to remove bias between geologically older Neanderthals and younger Upper Palaeolithic modern humans, we quantified the preservation status for each of the 14 major skull bones, that is, skeletal elements, separately. These are the frontal and occipital bones, as well as the left and right elements of the parietal, temporal, maxilla, mandible, zygomatic and nasal bones. Except for the zygomatic and nasal bones, we rated the completeness of skeletal elements in four preservation categories: up to 25%, 25–50%, 50–75% and 75–100%. Owing to their small size, the left and right zygomatic and the nasal bones were rated in just two categories: up to 50% and 50–100%. We performed the quantification procedure by visually judging the preserved portion of a given skeletal element in comparison to its complete equivalent using published pictures, sketches, virtual representations and verbal anatomical descriptions. Skeletal elements for which the preservation could not be quantified were excluded from the sample. In total, we collected data on 836 skeletal elements from 204 specimens. The quantification revealed a differential preservation among skeletal remains of Neanderthals and Upper Palaeolithic modern humans, with Neanderthals being biased towards incompletely preserved skeletal remains (see Extended Data Fig. 2a–e).

Statistical methods. We predicted trauma prevalence using GLMMs. To obtain robust GLMM estimates despite a large proportion of trauma absences (zeros) in our dataset, we used a Markov chain Monte Carlo (MCMC) algorithm as implemented in the MCMCglmm package³⁵ for R version 3.4.3³⁶. Trauma presence or absence was modelled as a binary response variable with a binomial error distribution using a logit-link function.

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

Element-level models (models 1–4). We entered the two-level predictors taxon (Neanderthals or Upper Palaeolithic modern humans), age (young or old, with 30 years as the cut-off) and sex (male or female), as well as the z-transformed four-level covariate element preservation (0.25, 0.5, 0.75 and 1) as fixed predictor variables. Visual data inspection indicated

a potential for variation in the taxon effect with age class but not with sex, so we added the age-by-taxon interaction to the models.

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

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

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

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

As suggested for binary response variables³⁸, we fixed the residual before 1 and chose an inverse Gamma prior for random effects³⁹. Model parameters were chosen to maximize model fit, visible with (i) an autocorrelation value³⁸ between posterior parameter estimates ≤ 0.05 ; (ii) parameter estimates reaching convergence between four independent model chains⁴⁰ as reflected in the potential scale reduction factor < 1.01 ; and (iii) observed trauma prevalence falling within the 95% highest posterior density intervals of their respective posterior distribution. These criteria were met after 5,100,000 MCMC iterations, a burn-in of 100,000, and a thinning interval of 1,000, resulting in approximately 5,000 samples in all posterior distributions. From these posterior distributions, we derived the highest posterior density intervals (or credible intervals) for each parameter estimate and denoted them statistically significant ($***P < 0.01$, $**P < 0.05$) or statistical trend ($*P < 0.10$) when not including zero. These intervals formed the basis for statistical inference and hypothesis testing. Plots in Fig. 2 show model predictions for element-preservation category 50–75%, plots in Fig. 3 show the predicted trauma prevalence

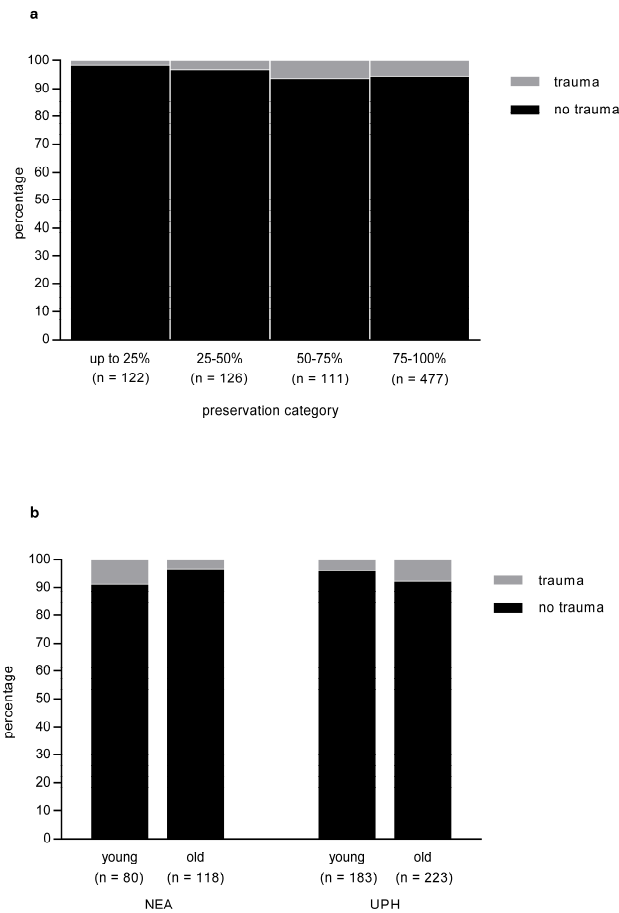
for specimens at their mean preservation score. In both cases, predictions linearly scale with the other preservation categories, generating overall slightly larger or smaller values but no change in the effect pattern for taxon, sex, age and the age-by-taxon interaction.

Data availability

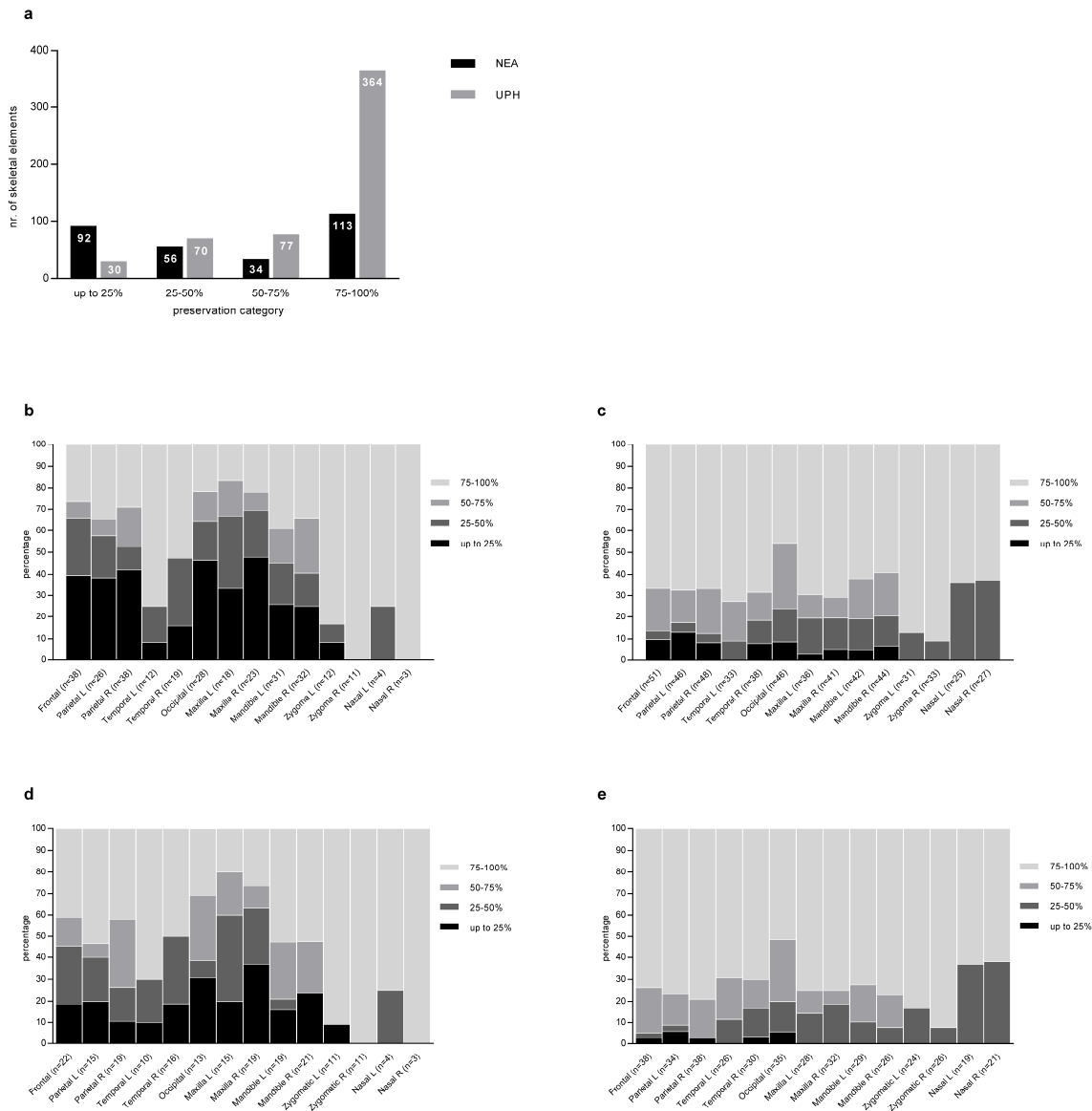
Specimen-level data that support the findings of this study are provided in Supplementary Tables 1, 2. Quantification data for skeletal elements are available from the corresponding author upon reasonable request. Source Data for Figs. 2, 3 and Extended Data Figs. 1, 2 are provided in the online version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

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



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

Source data of Extended Data Figures 1 and 2 are available at <https://doi.org/10.1038/s41586-018-0696-8>.

Supplementary Materials

Similar cranial trauma prevalence among Neanderthals and Upper Paleolithic humans

Judith Beier, Nils Anthes, Joachim Wahl, Katerina Harvati

Content

Supplementary Table 1.....	2
Supplementary Table 2.....	6
Supplementary Table 3.....	9
Supplementary References.....	16

Supplementary Table 1: Neanderthal (NEA) specimens used in this study. Data collected from cited references. Column "n" displays the number of skeletal elements, column "sp-pres" displays specimen-preservation (rounded to the second decimal place).

Country	Specimen	Taxon	Region	Age	Sex	n	sp-pres	Trauma	Ref.
Belgium	Spy 1	NEA	Central	old	male	8	0.48	no	43-46
	Spy 2	NEA	Central	young	male	8	0.46	no	43,45,46
Crimea Croatia	Zaskalnaya 5/Zsk VI-78	NEA	East	young	indet.	1	0.02	no	47,48
	Vindija 202	NEA	East	indet.	male	1	0.02	no	49-51
	Vindija 204/302	NEA	East	indet.	male	2	0.04	no	49-51
	Vindija 205	NEA	East	indet.	female	1	0.02	no	49-51
	Vindija 206	NEA	East	young	male	2	0.07	no	49-52
	Vindija 207	NEA	East	indet.	female	1	0.04	no	49,50,53-55
	Vindija 224	NEA	East	indet.	male	1	0.02	no	49-51
	Vindija 226/265	NEA	East	old	female	2	0.09	no	49-51
	Vindija 227/254	NEA	East	young	female	1	0.04	no	49-51
	Vindija 231	NEA	East	old	female	2	0.07	no	49-51
	Vindija 250	NEA	East	indet.	male	1	0.05	no	49-51
	Vindija 257	NEA	East	indet.	female	1	0.02	no	49-51
	Vindija 260	NEA	East	indet.	female	1	0.02	no	49-51
	Vindija 261/275	NEA	East	indet.	male	1	0.04	no	49-51
	Vindija 262	NEA	East	indet.	female	1	0.02	no	49-51
	Vindija 280	NEA	East	old	female	1	0.02	no	49-51
Vindija 281	NEA	East	indet.	female	1	0.02	no	49-51	
Vindija 282	NEA	East	indet.	female	1	0.02	no	49-51	
Vindija 284-230-255-256/11.19-11.22-11.37-11.35	NEA	East	young	female	3	0.11	no	54	
Czech Republic	Vindija 296	NEA	East	indet.	female	1	0.02	no	49-51
	Vindija 298	NEA	East	indet.	female	1	0.02	no	49-51
	Vindija 299	NEA	East	indet.	female	1	0.02	no	49-51
	Vindija 301	NEA	East	indet.	male	1	0.04	no	49-51
	Vindija 303	NEA	East	indet.	female	1	0.02	no	49-51
	Vindija 304	NEA	East	old	male	1	0.02	no	49-51
	Vindija 305	NEA	East	indet.	male	1	0.02	no	49-51
	Vindija 306	NEA	East	indet.	female	2	0.04	no	49-51
	Kůlna 1	NEA	East	young	male	1	0.04	no	43,56-60
	Kůlna 2	NEA	East	young	male	1	0.05	no	43,56-61
	Ochoz 1	NEA	East	indet.	indet.	2	0.07	no	43,60,62,63

Country	Specimen	Taxon	Region	Age	Sex	n	sp-pres	Trauma	Ref.
France	Chapelle-aux-Saints 1	NEA	Central	old	male	12	0.86		43,64-68
	Combe Grenal A	NEA	Central	indet.	indet.	1	0.02	no	69
	Combe Grenal B	NEA	Central	indet.	indet.	1	0.02	no	69
	Combe Grenal C	NEA	Central	indet.	indet.	1	0.02	no	69
	Combe	NEA	Central	young	indet.	1	0.04	no	69
	Grenal III								
	Combe	NEA	Central	young	indet.	1	0.02	no	69
	Grenal IV								
	Combe	NEA	Central	indet.	indet.	1	0.04	no	69
	Grenal 149								
	Ferrassie 1	NEA	Central	old	male	12	0.8	no	70-75
	Ferrassie 2	NEA	Central	young	female	2	0.07	no	70,71,73,74
	Fontéchevade 6	NEA	Central	old	male	3	0.16	no	76-78
	Genay 1	NEA	Central	old	male	5	0.11	no	79-84
	Hortus IV	NEA	Central	young	female	2	0.13	no	43,85,86
	Hortus V	NEA	Central	young	indet.	1	0.02	no	85,86
	Marillac 1	NEA	Central	indet.	indet.	1	0.02	no	85,87
	Marillac 2	NEA	Central	indet.	indet.	3	0.2	no	85,88
	Marillac 3	NEA	Central	indet.	indet.	2	0.05	no	87,89
	Marillac 12	NEA	Central	indet.	indet.	1	0.02	no	87
	Monsempron M8-95.2	NEA	Central	indet.	indet.	1	0.02	no	90
	Monsempron Grot1-	NEA	Central	indet.	indet.	1	0.07	no	90
	Hom Rem 1								
	Le Moustier 1	NEA	Central	young	male	12	0.75	yes	91-98
	Petit-Puymoyen 2	NEA	Central	young	indet.	1	0.02	no	99-101
	Petit-Puymoyen 3	NEA	Central	young	indet.	2	0.05	no	99,100
	Petit-Puymoyen 7	NEA	Central	young	indet.	1	0.02	no	99,100
	Les Pradelles 31	NEA	Central	old	indet.	1	0.02	yes	87
	Les Pradelles 32 bis etc	NEA	Central	indet.	indet.	1	0.04	no	87,88
	Les Pradelles 34	NEA	Central	indet.	indet.	1	0.02	no	87
	Les Pradelles 42	NEA	Central	indet.	indet.	1	0.02	no	87
	Les Pradelles 44/44bis	NEA	Central	indet.	indet.	1	0.02	no	87
	Les Pradelles 50	NEA	Central	indet.	indet.	1	0.02	no	87
Les Pradelles 58	NEA	Central	indet.	indet.	1	0.02	no	87	
Les Pradelles 60	NEA	Central	indet.	indet.	1	0.02	no	87	
Les Pradelles 64	NEA	Central	indet.	indet.	1	0.02	no	87	
Les Pradelles 73	NEA	Central	indet.	indet.	1	0.02	no	87	
Les Pradelles 74/74bis	NEA	Central	indet.	indet.	1	0.02	no	87	

Country	Specimen	Taxon	Region	Age	Sex	n	sp-pres	Trauma	Ref.
France	Les Pradelles 78/78bis/78ter/ 78quater	NEA	Central	indet.	indet.	1	0.02	no	87
	La Quina H5	NEA	Central	indet.	indet.	10	0.59	no	43,102-104
	La Quina H9	NEA	Central	indet.	indet.	1	0.07	no	105,106
	La Quina H10	NEA	Central	indet.	indet.	1	0.07	no	43,85,103
	La Quina- Amont 23a	NEA	Central	indet.	indet.	1	0.02	no	107,108
	La Quina- Amont 23b	NEA	Central	indet.	indet.	2	0.04	no	107,108
	La Quina- Amont 23c	NEA	Central	indet.	indet.	1	0.02	no	107,108
	La Quina H 27	NEA	Central	indet.	indet.	1	0.07	no	43,85,103,109
	La Quina 28	NEA	Central	old	indet.	1	0.02	no	107,110
	La Quina 34	NEA	Central	indet.	indet.	3	0.07	no	107,110
	Régourdou 1	NEA	Central	young	male	2	0.13	no	111-114
	St. Césaire 1	NEA	Central	young	male	8	0.36	yes	115,116
Georgia	Sakajia 1	NEA	Near East	young	indet.	1	0.02	no	117-119
Germany	Feldhofer 1	NEA	Central	old	male	8	0.36	yes	120-123
	Sarstedt II	NEA	Central	indet.	indet.	1	0.04	no	52,124,125
	Sarstedt III	NEA	Central	indet.	indet.	1	0.04	no	52,124,125
	Warendorf- Neuwarendorf	NEA	Central	young	indet.	1	0.04	yes	52,126,127
Gibraltar	Gibraltar 1	NEA	Iberia	old	female	10	0.66	no	43,128-130
Hungary	Subalyuk 1	NEA	East	young	female	3	0.09	no	63,131
Iraq	Shamidar 1	NEA	Near East	old	male	12	0.73	yes	132-135
	Shamidar 2	NEA	Near East	young	male	12	0.52	no	133,135
	Shamidar 4	NEA	Near East	old	male	12	0.48	no	133,135
	Shamidar 5	NEA	Near East	old	male	10	0.61	yes	133-136
	Shamidar 6	NEA	Near East	young	female	2	0.04	no	133,135
	Shamidar 8	NEA	Near East	young	female	1	0.02	no	133,135
Israel	Amud 1	NEA	Near East	young	male	12	0.71	no	137-141
	Amud 2	NEA	Near East	indet.	male	1	0.02	no	137,139,140
	Amud 14	NEA	Near East	indet.	indet.	1	0.04	no	142
	Kebara 2	NEA	Near East	old	male	2	0.14	no	134,143-149
	Kebara 6	NEA	Near East	old	indet.	1	0.02	no	144,149
Italy	Breuil 1	NEA	South	indet.	indet.	1	0.04	no	150-152
	Ciota Ciara 1	NEA	South	indet.	indet.	1	0.04	no	151

Country	Specimen	Taxon	Region	Age	Sex	n	sp-pres	Trauma	Ref.
Italy	Fate 3	NEA	South	old	indet.	1	0.04	no	106,153
	Fate 4	NEA	South	indet.	indet.	1	0.02	no	106,153
	Guattari 1	NEA	South	old	male	11	0.77	no	43,106,151,154-156
	Guattari 2	NEA	South	old	male	2	0.11	no	43,101,106,151,154,156
	Guattari 3	NEA	South	young	male	1	0.07	no	43,101,106,151,154,156
Netherlands	Zeeland Ridges	NEA	Central	indet.	male	1	0.02	no	157
	Chagyrskaya 5	NEA	East	indet.	indet.	1	0.04	no	158
Russia	Cova Foradà I	NEA	Iberia	old	female	3	0.07	no	159-161
	Cova Negra Parietal I	NEA	Iberia	young	male	1	0.07	yes	162-165
	Cova Negra Parietal II	NEA	Iberia	young	indet.	1	0.05	no	164
Spain	Gegant 1	NEA	Iberia	young	indet.	2	0.07	no	166-168
	Horá 1	NEA	Iberia	young	indet.	1	0.02	yes	169
	Palomas 1	NEA	Iberia	old	indet.	2	0.09	no	170-172
	Palomas 59	NEA	Iberia	young	indet.	1	0.04	no	170,171
	Palomas 96	NEA	Iberia	young	female	6	0.21	no	173
	Contencher	NEA	Central	old	female	2	0.05	no	174-177
Switzerland									

Supplementary Table 2: Early Upper Paleolithic modern human (UPH) specimens used in this study. Data collected from cited references. Column "n" displays the number of skeletal elements, column "sp-pres" displays specimen-preservation (rounded to the second decimal place).

Country	Specimen	Taxon	Region	Age	Sex	n	sp-pres	Trauma	Ref.
Austria	Willendorf 2	UPH	East	indet.	female	2	0.04	no	178,179
Bulgaria	Bacho Kiro 3575	UPH	East	old	indet.	1	0.02	no	180-182
Crimea	Buran Kaya III (1)	UPH	East	indet.	indet.	1	0.02	no	183
	Buran Kaya III (2)	UPH	East	indet.	indet.	1	0.02	no	183
	Buran Kaya III (3)	UPH	East	indet.	indet.	2	0.04	no	183
Croatia	Vindija 210/267	UPH	East	indet.	female	2	0.13	no	49,50,54
	Vindija 235	UPH	East	indet.	male	1	0.02	no	49,50,54
	Vindija n.n.	UPH	East	indet.	indet.	1	0.02	no	49,50,54
Czech Republic	Brno I	UPH	East	young	male	2	0.14	no	43,184,185
	Brno II	UPH	East	old	male	9	0.46	no	43,185-190
Dolní Věstonice	Dolní Věstonice 3	UPH	East	old	female	14	0.93	yes	191-199
	Dolní Věstonice 11/12	UPH	East	old	male	5	0.25	yes	191-193,196,198,198,200
	Dolní Věstonice 13	UPH	East	young	male	12	0.86	yes	191-196,200,201
Dolní Věstonice	Dolní Věstonice 14	UPH	East	young	male	12	0.75	no	191-196,201
	Dolní Věstonice 15	UPH	East	young	male	12	0.84	yes	191-196,201-203
	Dolní Věstonice 16	UPH	East	old	male	12	0.82	yes	191-196,198,199,204
Mladeč	Mladeč 1	UPH	East	young	female	12	0.84	no	205-208
	Mladeč 2, 7	UPH	East	young	female	9	0.48	no	205-208
	Mladeč 5	UPH	East	old	male	6	0.39	yes	205-211
	Mladeč 6	UPH	East	old	male	6	0.27	yes	205-208,210,211
	Mladeč 8	UPH	East	old	male	2	0.07	no	205-208,210
	Mladeč 39	UPH	East	young	male	1	0.02	no	205,206,208,210
	Mladeč 40	UPH	East	young	male	2	0.04	no	205,206,208,210
	Mladeč 48, 49, 52	UPH	East	young	indet.	2	0.07	no	205,206,208,210
	Mladeč 54	UPH	East	indet.	male	2	0.09	no	205,206,208,210
	Pavlov 1	UPH	East	old	male	11	0.64	yes	191-193,195,196
Pavlov	Pavlov 3	UPH	East	young	indet.	1	0.02	no	191,192,195
	Pavlov 4	UPH	East	young	indet.	1	0.02	no	191,192,195
	Predmost 1	UPH	East	young	male	12	0.79	no	212-214
Predmost	Predmost 3	UPH	East	young	male	14	0.98	no	85,212-214
	Predmost 4	UPH	East	old	male	14	0.98	no	85,212-214
Predmost	Predmost 9	UPH	East	young	female	13	0.91	no	85,212-214
	Predmost 10	UPH	East	young	indet.	14	0.96	no	85,212-214
Predmost	Predmost 10	UPH	East	young	indet.	14	0.95	no	85,212-214

Country	Specimen	Taxon	Region	Age	Sex	n	sp-pres	Trauma	Ref.
Czech Republic	Predmost 14	UPH	East	old	male	7	0.39	no	85,212-214
	Predmost 18	UPH	East	young	male	6	0.18	no	85,212-214
	Predmost 19	UPH	East	indet.	female	1	0.04	no	85,212-214
	Predmost 21	UPH	East	indet.	female	1	0.05	no	85,212,214,215
	Predmost 26	UPH	East	indet.	female	1	0.05	no	85,212,214
	Predmost 30	UPH	East	young	indet.	2	0.11	no	214
	Abri Pataud 1	UPH	Central	young	female	14	1.00	no	43,216,217
	La Balauzière 1	UPH	Central	old	female	3	0.13	no	218,219
	La Balauzière 2	UPH	Central	young	indet.	5	0.14	no	218,219
	Brassempouy 316	UPH	Central	old	indet.	2	0.04	no	220-222
France	Cro Magnon 1	UPH	Central	old	male	14	0.95	no	223-226
	Cro Magnon 2	UPH	Central	old	female	11	0.61	no	223-226
	Cro Magnon 3	UPH	Central	old	male	4	0.27	no	223-225
	Crouzade 5	UPH	Central	indet.	indet.	2	0.09	no	227-229
	Crouzade 6	UPH	Central	young	indet.	1	0.02	no	227-229
	Cussac LZA	UPH	Central	indet.	male	9	0.64	no	230,231
	Fontéchevade 5 (Homo I)	UPH	Central	indet.	female	1	0.02	no	76,77,85,232
	Isturitz 70	UPH	Central	indet.	indet.	2	0.09	no	229,233
	Vilhonneur 1	UPH	Central	young	male	4	0.29	no	77,234,235
	Tapolca 1	UPH	East	young	female	1	0.05	no	85,236-238
	el-Wad EM 3915	UPH	Near East	indet.	indet.	1	0.07	no	239-241
	el-Wad EM 3916	UPH	Near East	young	female	1	0.07	no	239-241
	el-Wad EM 3936	UPH	Near East	indet.	indet.	1	0.04	no	240,241
Italy	Ohalo II H2	UPH	Near East	old	male	14	0.98	no	148,242-246
	Arene Candide	UPH	South	young	male	13	0.89	no	199,247,248
	"Principe"								
	Baouso da Torre 1	UPH	South	indet.	male	4	0.14	no	151,249,250
	Barma Grande 1	UPH	South	old	male	8	0.36	no	234,251,252
	Barma Grande 2	UPH	South	old	male	7	0.46	no	252-254
	Barma Grande 5	UPH	South	indet.	male	13	0.86	no	43,251-253,255
	Caviglione 1	UPH	South	old	female	13	0.09	no	256
	Grotta Paglicci 14 B	UPH	South	old	male	1	0.02	no	151,257,258
	Grotta Paglicci 15 C	UPH	South	indet.	male	1	0.64	no	151,257,258
	Grotta Paglicci 16 D	UPH	South	indet.	indet.	1	0.02	no	151,257
	Grotta Paglicci 20 I	UPH	South	young	female	1	0.09	no	151,257-259
	Grotta Paglicci 24 N	UPH	South	indet.	female	1	0.29	no	151,257-259

Country	Specimen	Taxon	Region	Age	Sex	n	sp-pres	Trauma	Ref.
Italy	Grotta Paglicci 25	UPH	South	young	female	12	0.05	no	151,260,261
	Grotta Paglicci 34	UPH	South	indet.	male	1	0.07	no	151,257,262
	Grotta Paglicci 36	UPH	South	young	male	1	0.07	no	151,257,262
	Grotta Paglicci 37	UPH	South	young	male	1	0.04	no	151,257,262
	Grotte des Enfants 4	UPH	South	indet.	male	14	0.98	no	43,151,263
Portugal	Grotte des Enfants 5	UPH	South	old	female	14	0.89	no	43,151,263,264
	Ostuni 1	UPH	South	young	female	14	0.14	no	151,265
	Caldeirão 1	UPH	Iberia	indet.	female	1	0.36	no	266,267
	Cioclovina 1	UPH	East	old	indet.	8	0.46	yes	268-271
	Muierii 1	UPH	East	old	male	11	0.86	no	237,272-274
Romania	Muierii 2	UPH	East	old	female	1	0.09	no	273-275
	Oase 1	UPH	East	young	male	2	0.14	no	275-278
	Oase 2	UPH	East	young	male	12	0.71	no	275-277,279
	Kostenki 2 Zamiatnin	UPH	East	young	indet.	12	0.71	no	280,281
	Kostenki 8 Telmanskaia	UPH	East	old	male	9	0.54	no	281-283
Russia	Kostenki 14	UPH	East	old	male	1	0.04	yes	284-289
	Markina Gora	UPH	East	young	male	14	1.00	yes	
	Pokrovka 2	UPH	East	young	indet.	1	0.05	no	288
	Sunghir 1	UPH	East	young	male	14	1.00	no	290-295
	Sunghir 5	UPH	East	old	male	10	0.48	no	293-295
Spain	Sunghir 6	UPH	East	old	indet.	2	0.11	yes	293-295
	Mollet III 379	UPH	Iberia	young	indet.	5	0.3	no	296
	Parpallo 1	UPH	Iberia	old	female	11	0.73	no	258,297-299

Supplementary Table 3: Cranial traumatic lesions of Neanderthals (NEA) and early Upper Paleolithic modern humans (UPH). Descriptions are summarized from cited references and reproduce the original authors' descriptions and diagnoses.

Specimen	Taxon	Skeletal element	Traumatic lesions	Timing	Examination method	Ref
Les Pradelles 31	NEA	maxilla right	(1) <i>hypervascularization on right maxillary torus, inconclusive etiology:</i> Mussini (2011) describes a developed hypervascularization on the right maxillary torus above first molar, with a size of 18x4 mm. Localized areas of hypervascularization and intensified bone remodeling can stem from various conditions like infectious, traumatic, neurovascular, or tumourous, she reports.	antemortem	macroscopic	87
Le Moustier 1	NEA	frontal	(1) <i>lesion on left orbit/superciliary arch:</i> Ullrich (2005) describes a defect (18x24 mm) centered above the left orbital margin. The external table chipped off (17x5 mm), exposing diploë and the frontal sinus. The defect shows an irregular medial margin and a regular, slightly curved lateral margin. Ullrich identifies several bone fragments at the margins of the lesion which are depressed yet still attached, and describes a fracture line originating from the upper margin of the lesion. He interprets the lesion to be the result of a strong impact when the bone was still fresh. (2) <i>defect on left parietal, possibly perimortal, inconclusive etiology:</i> On the left parietal bone, Ullrich (2005) describes an area of missing bone reaching from the coronal to the lambdoid suture. The defect has a more regular superior and an irregular inferior margin and exhibits no fissures or fracture lines. Previously, this defect has been interpreted as an intentional blow to the head by Gieseler (1952). Yet, the defect's margins exhibit edges at right angles to the bone surface as well as splintered-off regions exposing diploë and the inner table. According to Ullrich the former would suggest a postmortem defect, while the latter could indicate a perimortal fracture, therefore precluding the defect from a definite diagnosis. (3) <i>comminuted fracture to right parietal:</i> The right parietal bone was reconstructed from several fragments. Ullrich (2005) describes eight radiating fracture lines originating from a central fractured area (35x24 mm) close to the parietal tuber (25 mm from the sagittal, and 50 mm from the lambdoid sutures), as well as some concentric fractures. Most of the fracture lines are also visible endocranially. On the inside of the skull the internal table is splintered-off (40x40 mm) at the location of the central fractured area. Ullrich concludes that such characteristic are clearly indicative of a comminuted perimortal fracture. (4) <i>healed mandibular fracture, deformed mandibular condyle:</i> The origin - whether pathologic or taphonomic - of the deformed left mandibular condyle of Moustier 1 and its elevated left mandibular ramus has been debated since its discovery. Ponce de Léon & Zollikofer (1999, 2005) argue for a condylar neck fracture resulting from a fall or	perimortal	macroscopic	95
		parietal left		peri- or postmortem	macroscopic	95,300
		parietal right		perimortal	macroscopic	95
		mandible left		antemortem	macroscopic	95,301

				115
St. Césaire 1	NEA	frontal	<p>blunt trauma. They observe bone resorption and apposition of the left condylar neck, as well as remodeling extending to the ramus mandibulae and external acoustic meatus. They rule out a taphonomic origin of the deformation because the deformed condyle fits well into the glenoid fossa. As differential diagnosis they propose condylar ankylosing spondylitis.</p> <p>(1) <i>healed trauma on frontal bone, extending to right parietal:</i></p> <p>Zollikofer et al. (2002) interpret the rounded medial margins (68 mm long) of aligned fronto-parietal fragments as antemortem trauma. The rounded edges are covered with cortical bone and do not exhibit diploté, excluding postmortem damage as an explanation. Regarding its location at an oblique angle right of the mediansagittal plane, and its rather smooth edges, the authors argue against the possibility that the margin could represent a cranial suture, ossicle or remnants of a fontanelle. Instead, they interpret that the lesion was inflicted by a sharp implement, and that the site of impact was close to the coronal suture, as indicated by a fractured and dislocated inner bone table. Advanced bone remodeling evidences a survival of the injury.</p>	CT Scan
Feldhofer 1	NEA	frontal	<p>(2) <i>healed lesion on right parietal:</i></p> <p>Continuation of lesion (1) described above.</p> <p>(1) <i>healed trauma above right orbit:</i></p> <p>Schultz (2006) describes a healed rounded lesion (15x6 mm) above the right orbit, characterized by an upper and a lower facet within the depression of the lesion, of which the latter exhibits irregular ridges. He interprets these features to be the result of a sharp and pointed impact causing bone loss, most likely by a stone tool or a fall on a sharp rock. The lesion is well healed.</p>	CT Scan
Warendorf-Neuwarendorf	NEA	parietal right	<p>(1) <i>lesion with inflammatory signs on right parietal:</i></p> <p>The surface of the external table of the parietal fragment is irregularly thickened and porotic. Czarnetzki & Trellisó Carreño (1999) suggest that this vascularization could be post-traumatic, and could have resulted from an osteomyelitis, caused by an injury to the scalp and its subsequent inflammation.</p>	antemortem macro- & microscopic (magnifying glass, binocular low magnifying microscope) macroscopic, x-ray 126,302
Shanidar 1	NEA	frontal	<p>(1) <i>healed superficial lesions on right side of frontal:</i></p> <p>Trinkaus (1983) mentions healed ectocranial lesions (not specified how many) on the right frontal bone, close to the frontal tuber. These probably resulted from injuries that damaged the periosteum but not the bone itself.</p> <p>(1.1) <i>healed trauma to left orbit, extending to left zygomatic:</i></p> <p>On the left side of the face, Trinkaus (1983) diagnoses a healed trauma which affected the orbit and zygomatic bone and resulted in an irreversible facial deformity. He reports a flattened lateral orbital margin with signs of bone healing, and a reduced breadth of the left orbit compared to the right. Trinkaus assumes that this lesion caused blindness to the left eye.</p>	antemortem macroscopic antemortem macroscopic 132,133

	zygoma left		(2) <i>deformed zygomatic bone, caused by same traumatic event as (1.1):</i> Continuation of lesion (1.1) described above. Like the orbit, the left zygomatic bone is altered in shape and exhibits an enlarged craniocaudal height, as well as signs of healing across the entire bone.	antemortem	macroscopic	132,133
Shanidar 5	frontal	NEA	(1) <i>healed superficial lesion on frontal:</i> The frontal squama exhibits a depressed, rough groove (5mm wide) running anteriorly, but roughly parallel to the coronal suture, from the midline to left stephanion. The diploë and inner table are not affected. Trinkaus and Zimmermann (1982) suggest that the groove was caused by an injury to the scalp which damaged the periosteum. The lesion is fully healed.	antemortem	macroscopic	132,133
Cova Negra Parietal I	parietal right	NEA	(1) <i>lesion on right parietal:</i> In its anterosuperior portion, the Cova Negra parietal shows a rough surface (25 mm wide) between the temporal line and the sagittal suture. Additionally, bone thickness appears to be reduced. Fusté (1953) attributes these features to represent bone remodeling following a trauma which did not affect the inner table.	antemortem	macroscopic	163,165
Horá I	frontal	NEA	(1) <i>notch of possible traumatic origin, inconclusive etiology:</i> Haber Uriarte (2002) mentions a little notch on the Horá fragment which might be related to a trauma during lifetime (no further information provided).	if trauma: antemortem?	macroscopic	169
Dolní Věstonice 3	frontal	UPH	(1) <i>healed minor lesion on frontal:</i> There is a shallow, healed lesion to the frontal bone (16.5x13 mm), which is restricted to the outer bone table. Trinkaus et al. (2006) conclude a minor trauma to the periosteum and outer table. Remodeled bone indicates healing.	antemortem	macroscopic	198
	temporal left		(1.1) <i>deformation left orbit:</i> Same traumatic event as lesion (3). See description below.	antemortem	macroscopic	198
	mandible left		(2) <i>deformation left temporal:</i> Same traumatic event as lesion (3). See description below. (3) <i>fractured left mandibular condyle:</i> The viscerocranium of DV3 shows facial asymmetry. Trinkaus et al. (2006) favor the explanation that a trauma fracturing the left mandibular condyle (and possibly the zygomatic bone) caused these changes. Remodeling processes, both during healing and as a secondary response to altered biomechanical loads, resulted in the observed altered morphology of the mandibular ramus, zygomatic and frontal bones (orbit), and caused the arthritic condition in the glenoid fossa of the left temporal. Nevertheless, the injury was survived and healed.	antemortem	macroscopic	198
	zygoma left		(4) <i>deformation left zygomatic:</i> Same traumatic event as lesion (3). See description above.	antemortem	macroscopic	198

Dolní Věstonice 11/12	UPH	frontal	<p>(1) <i>healed depressed trauma on frontal squamous:</i> There is a healed, depressed lesion (27x19 mm) above the right orbit which left traces on both fragments DV11 and 12 (not aligned). The DV12 fragment exhibits a pronounced depression with an irregular surface, resulting from bone remodeling. The traumatic impact was severe enough to not only damage the external table and diploë, but also leave a permanent yet minor deformation of the internal table. Nevertheless, the injury is well healed. As described by Trinkaus et al. (2006), the same traumatic lesion is observable on the DV11 calotte. Right of the midline, the frontal fragment of the calotte exhibits a bevelled and rounded inferior edge (17 mm wide) with vascular porosities, which Trinkaus interprets to be the superior edge of the lesion.</p>	antemortem	macroscopic	198,303
(1.1) <i>abnormal thinning of squamous frontal:</i>	<p>Along the edge of DV12's lateral left side, Trinkaus et al. (2006) distinguish a rounded bevelled edge (5 mm long), exhibiting no diploë, from neighbouring postmortem damage and recognize a thinning of the frontal squama. The authors argue for a traumatic origin of the lesion. As a less likely differential diagnosis, they propose senile thinning of the frontal squama.</p>	not specified, but presumably antemortem	macroscopic	198,303		
(2) <i>lesion on right parietal, inconclusive etiology:</i>	parietal right	<p>The DV11 calotte exhibits a shallow depression (11x15 mm) in the right parietal, located in the anteromedial angle between the coronal and sagittal sutures. While Vlček (1991) interprets this lesion to be a healed minor trauma, Trinkaus et al. (2006) express uncertainty about its etiology.</p>	if trauma: antemortem	macroscopic	198,303	
Dolní Věstonice 13	UPH	frontal	<p>(1) <i>minor healed frontal trauma:</i> The frontal bone shows a shallow depression (20 x 8 mm) located 40 mm above the right orbit, close to the midline. The diploë is not affected. There is root-etching in the area of interest, too, but Trinkaus et al. (2006) identify signs of bone remodeling and therefore argue for a traumatic origin of this healed minor lesion.</p>	antemortem	macroscopic	198
(2) <i>healed lesion on right parietal:</i>	parietal right	<p>There is a minor lesion (12 x 11 mm) in the anteromedial angle of the right parietal bone. Trinkaus et al. (2006) cannot specify whether the trauma affected the diploë or was restricted to the periosteum and the outer bone table. Anyway, the lesion is healed.</p>	antemortem	macroscopic	198	
(3) <i>bone deposit on occipital:</i>	occipital	<p>Trinkaus et al. (2006) mention a raised formation of new bone (20 x 6.5 mm) at the superior nuchal line of the occipital bone, located close to the left mastoid process. The authors assume an association of this muscle attachment irregularity with a minor trauma.</p>	not specified	macroscopic	198	
Dolní Věstonice 15	UPH	frontal	<p>(1) <i>small healed lesion on frontal:</i> The frontal bone exhibits an irregularly shaped shallow lesion (12x9 mm) left of the median-sagittal line below bregma. The minor injury was fully healed as indicated by remodeling.</p>	antemortem	macroscopic	198

			antemortem	macroscopic	198
parietal right	(2) <i>healed depression on right parietal:</i> A small lesion (7 mm in diameter) with circular edges is observable on the right parietal bone. Even though it is very shallow, Trinkaus et al. (2006) assume that the outer bone table was fractured and the lesion was not only superficial. Yet, the edges are well healed.				
	(2.1) <i>vertical notch on right parietal, inconclusive etiology:</i> Also in the right parietal, Trinkaus et al. (2006) identify a groove (13 mm long) located alongside the squamosmastoid suture. The authors mention morphological similarities with a healed trauma, but, since it could also be remnants of the suture, its etiology remains unclear.		if trauma: antemortem	macroscopic	
Dolní Věstonice 16	(1) <i>healed frontal lesion:</i> Trinkaus et al. (2006) describe a lesion (ca. 18x13 mm) located approx. in the midline of the frontal bone, close to the coronal suture. It remains unclear whether the well-healed lesion was a superficial trauma to the periosteum, or damaged the outer bone table, too. Either way, it did not affect the diploë. (1.1) <i>small lesion on frontal:</i> Just 23 mm away from lesion (1), there is a second superficial minor lesion (ca. 9x7 mm) on the frontal bone of DV16. Trinkaus et al. (2006) speak of either “a small compression fracture or scrape” (Trinkaus et al. 2006, 446) which is healed. (1.3) <i>groove on frontal, inconclusive etiology:</i> Above the right orbit, there is a linear groove (ca. 15 mm long), which could either represent a unilateral frontal groove or a healed injury, as stated by Trinkaus et al. (2006).		antemortem	macroscopic	198,303
	(2) <i>groove on occipital:</i> Another groove (25 mm long) is located on the left side of the occipital bone at the nuchal line, and is bulging at its inferior end. Trinkaus et al. (2006) speak of it being a possible healed injury.		antemortem	macroscopic	198,303
maxilla left	(3) <i>maxilla malposition:</i> The viscerocranium of DV16 appears asymmetric due to an anterosuperior displacement of the left maxilla, involving morphological alterations to the orbit, zygomatic bone and mandibular occlusion. Trinkaus et al. (2006) argue for a congenital or developmental etiology of the features, but discuss an antemortem traumatic origin as an alternative, yet less likely, explanation.		if trauma: antemortem	macroscopic	198,303
Mladeč 5	(1) <i>healed traumatic lesion on frontal:</i> There is a depressed lesion (12 x 8 mm) with an irregular ground surface above the left orbit, which damaged the outer bone table and diploë. Bone remodeling indicates full healing of this suggested antemortem blunt force trauma.		antemortem	macroscopic, CT Scan	207,210

parietal right		<p>(2) depression on right parietal, etiology and timing inconclusive: In its anterior part the right parietal bone exhibits a large depression (40 x 25/30 mm). Szombathy (1925) described this to be an injury which was associated with a sagittally oriented fracture line (35 mm long) on the internal table. Macroscopically, Teschler-Nicola et al. (2006) could not verify this endocranial fracture line due to recent restoration work. Yet, CT images revealed an involvement of both the outer and inner tables, but no signs of healing or remodeling which would verify the depression as antemortem trauma. Frayer et al. (2006) discuss whether the depression was caused postmortem, or if it might represent an anatomical feature (parasagittal depression). Its etiology and possible timing remains unclear.</p>	inconclusive macroscopic, CT Scan	207,209,210
<p>Mladeč 6 This specimen is only preserved by a cast, hampering pathological diagnoses.</p>	UPH frontal	<p>(2.1) healed lesion on right parietal: There is another lesion (9x6 mm) on the right parietal bone, located posterior to the parietal tuber. The ground of the depression, which is limited to the external table, is slightly porous. Teschler-Nicola et al. (2006) and Frayer et al. (2006) suggest an antemortem, fully healed traumatic lesion.</p>	antemortem macroscopic	207,210
	parietal right	<p>(1.1) minor depression, inconclusive etiology: Frayer et al. (2006) mention a second minor depression on the frontal bone, which may also represent a healed trauma. However, since the specimen is a cast, its etiology is not definite.</p>	if trauma: macroscopic antemortem	207
	parietal right	<p>(2, 2.1) two porous areas on right parietal, inconclusive etiology: Two areas of severe porotic hyperostosis can be found on the right parietal bone. Such porosities are often related to malnutrition, but can also result from soft tissue inflammations following a trauma, as suggested by Teschler-Nicola et al. (2006).</p>	if trauma: macroscopic antemortem	207
<p>Pavlov 1</p>	UPH parietal left	<p>(1) healed lesion on left parietal: Trinkausk et al. (2006) describe a curved depressed line (60 mm long, max. 5 mm wide) running from the the left temporal line towards bregma. He interprets the shallow groove as a healed minor injury to the scalp.</p>	antemortem macroscopic	198
	parietal right	<p>(2) small depression on right parietal: There is a small depression (9 mm in diameter) in the inferior part of the right parietal, close to the lambdoid suture, exhibiting small bony outgrowths. Trinkausk et al. (2006) describe this lesion, but without providing an interpretation.</p>	not specified macroscopic	198
		<p>(2.1) depression on right parietal, inconclusive etiology: Trinkausk et al. (2006) describe a second lesion, identifiable as a depressed area (10-15 mm in diameter), located between the coronal and sagittal sutures and the right parietal tuber.</p>	if trauma: macroscopic antemortem	

However, the authors express uncertainty about its etiology (healed minor trauma, depression evoked by swellings along the coronal and sagittal sutures, or normal anatomical variation).

Cioclovina 1	UPH	frontal	(1) <i>healed lesion above nasion:</i> First mentioned by Rainer & Simionescu (1942), there is a traumatic depression (12 mm in diameter) on the frontal bone, right of the midline (ca. 50 mm above nasion). The minor lesion, restricted to the outer bone table, is well healed.	antemortem	macroscopic	269,304
			(1.1) <i>healed lesion above right orbit:</i> On the right side of the frontal bone, above the right orbit, there is a second minor healed traumatic lesion (9 mm in diameter), which is also limited to the outer bone table.	antemortem	macroscopic	
Kostenki 8 Telmanskaia	UPH	frontal	(1) <i>healed lesion on frontal bone, probably trepanation:</i> The frontal bone exhibits a marked cone-shaped depression (8 mm) on its right squamous portion, which did not extend to the inner bone table. Mednikova et al. (2012) suggest an intravital trepanation as the most likely explanation for the lesion. They discuss a tumour or blunt force trauma as alternative explanations but assume them less conclusive regarding morphological features. The rounded margins of the lesion reveal it was fully healed.	antemortem	macroscopic, x-ray	282
Kostenki 14 Markina Gora	UPH	frontal	(1) <i>healed trauma on right side of frontal bone:</i> On the right side of the frontal bone Kostenki 14 exhibits a healed lesion (10-12 mm).	antemortem	macroscopic, CT scan	287,289
		parietal right	(1) <i>healed trauma on right parietal:</i> The right parietal bone shows a healed lesion. The authors also identified an intracranial calcified hemorrhaging in the right parietal, possibly caused by a traumatic blow.	antemortem	macroscopic, CT scan	287,289
Sunghir 5	UPH	frontal	(1) <i>healed minor lesion on frontal:</i> Trinkaus et al. (2014) report a minor healed trauma, indicated by a small depressed area just above the right orbital margin. The latter appears slightly vaulted downwards.	antemortem	macroscopic	295

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Appendix B
Paper II

**Prevalence of cranial trauma in Eurasian Upper Paleolithic
humans**

Judith Beier, Nils Anthes, Joachim Wahl, Katerina Harvati

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RESEARCH ARTICLE



WILEY

Prevalence of cranial trauma in Eurasian Upper Paleolithic humans

Judith Beier¹ | Nils Anthes² | Joachim Wahl¹ | Katerina Harvati^{1,3}

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

1 | 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,

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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 & Gollop, 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 & Zimmermann, 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 & Zimmermann, 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 & Giannecchini, 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, McKean-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; Stodder, 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 Harvati (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, Dutour, & 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 remains 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; Pankowská, Galeta, Uhlík Spěváčková, & 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, Burkhardtshöhle, Maszycka, Röhkopf, 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



FIGURE 1 Geographical distribution of sites with Upper Paleolithic human cranial remains. Sites Afontova Gora II (100) and Pokrovka (101) were projected 2,982 and 3,035 km west for better visualization. The map was generated using the open source software QGIS Geographic Information System (<https://www.qgis.org>) and the free map repository Natural Earth (<http://naturalearthdata.com/>). † Numbers refer to site names, not to fossil specimens

(<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.

TABLE 1 Crude trauma frequencies by skeletal element and preservation category

Skeletal element	Element preservation category												Total		
	1–25%			26–50%			51–75%			76–100%					
	<i>n</i>	With trauma	%	<i>n</i>	With trauma	%	<i>n</i>	With trauma	%	<i>n</i>	With trauma	%	<i>n</i>	With trauma	%
Frontal	9	0	0	16	1	6.3	29	5	17.2	75	9	12.0	129	15	11.6
Mandible left	5	0	0	10	0	0	16	0	0	76	2	2.6	107	2	1.9
Mandible right	8	0	0	13	0	0	24	0	0	67	0	0	112	0	0.0
Maxilla left	6	0	0	12	0	0	11	0	0	60	1	1.7	89	1	1.1
Maxilla right	6	0	0	11	0	0	17	0	0	61	0	0	95	0	0.0
Nasal left ^a	–	–	–	12	0	0	–	–	–	43	0	0	55	0	0.0
Nasal right ^a	–	–	–	17	0	0	–	–	–	41	0	0	58	0	0.0
Occipital	13	0	0	15	0	0	23	1	4.3	51	2	3.9	102	3	2.9
Parietal left	15	0	0	14	1	7.1	15	0	0	67	4	6.0	111	5	4.5
Parietal right	12	0	0	13	0	0	22	2	9.1	74	9	12.2	121	11	9.1
Temporal left	8	0	0	8	0	0	14	1	7.1	50	1	2.0	80	2	2.5
Temporal right	8	0	0	9	0	0	11	0	0	53	2	3.8	81	2	2.5
Zygoma left ^a	–	–	–	8	1	12.5	–	–	–	62	0	0	70	1	1.4
Zygoma right ^a	–	–	–	5	0	0	–	–	–	70	0	0	75	0	0.0
Total	90	0	0	163	3	1.8	182	9	5.0	850	30	3.5	1,285	42	3.3

^aNasal and zygomatic bones were rated in just two preservation categories (1–50% and 51–100%).

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 ≤ 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 sample 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 (pMCMC). 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 pMCMC 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 \pm 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

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 results 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 UP 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 were 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	Model coefficients			
				Posterior mean	Lower 95% CI	Upper 95% CI	pMCMC
Trauma prevalence overall in UP?	Model 1.1	1,285 ^a	Element preservation	0.574	0.129	1.105	0.010
	Model 1.2	234 ^a	Specimen preservation	0.754	0.250	1.220	0.003
Trauma prevalence variation in UP by age and sex?	Model 2.1	959 ^b	Element preservation	0.536	0.037	1.074	0.032
			Age	-1.898	-3.981	-0.034	0.041
			Sex	0.537	-0.620	1.713	0.360
	Model 2.2	118 ^b	Age × sex	0.806	-1.625	2.918	0.470
			Specimen preservation	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 ^b	Element preservation	0.559	0.040	1.097	0.022
			Period	1.025	-1.108	3.139	0.355
			Age	-1.247	-3.308	0.640	0.211
			Sex	1.504	-0.500	3.805	0.138
			Period × age	-0.103	-2.458	2.052	0.894
	Model 3.2	118 ^b	Period × sex	-1.003	-3.526	1.636	0.452
			Specimen preservation	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 viscerocranium and neurocranium?	Model 4.1	1,285 ^a	Element preservation	0.608	0.148	1.103	0.005
			Anatomy	-2.772	-4.317	-1.407	0.001
Trauma prevalence of the viscerocranium and neurocranium by age and sex?	Model 4.2	959 ^b	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.

^aFull dataset.

^bExclusion of sex unknown and age indeterminate skeletal elements or specimens, that is, no more precise age determination than >12 years.

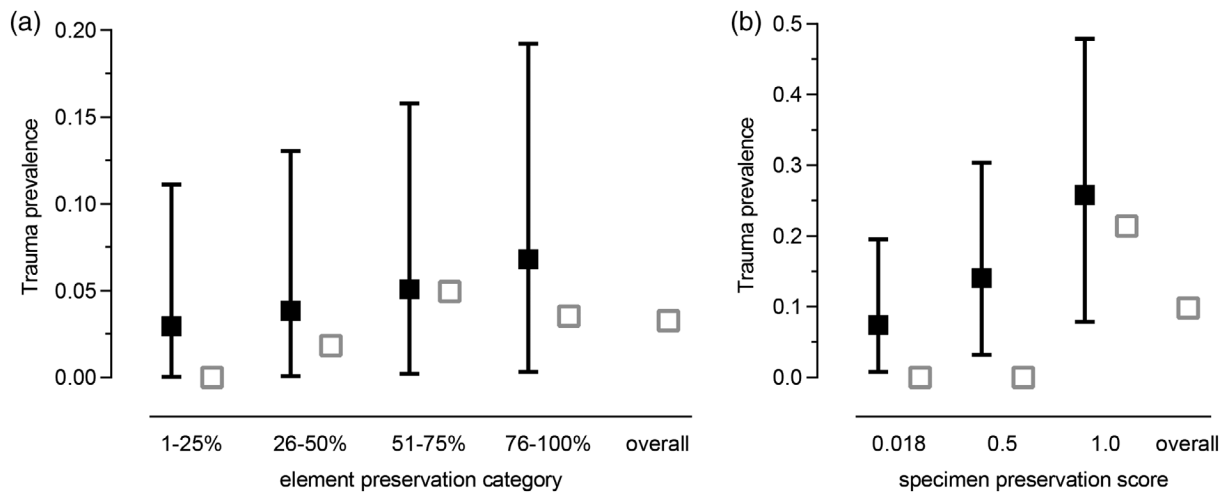


FIGURE 2 Cranial trauma prevalence of Upper Paleolithic modern human cranial remains. Solid markers denote predicted means based on posterior estimates of Markov chain Monte Carlo generalized linear mixed models (MCMC GLMMs), bars show lower and upper 95% credible intervals. Open markers denote crude 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

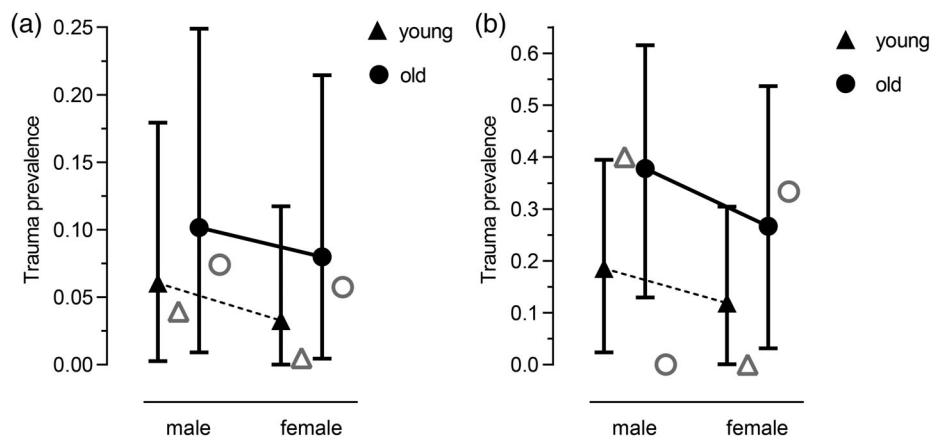


FIGURE 3 Cranial trauma prevalence of Upper Paleolithic modern human cranial remains by age and sex. Solid markers denote predicted means based on posterior estimates of Markov chain Monte Carlo generalized linear mixed models (MCMC GLMMs), bars show lower and upper 95% credible intervals. Open markers 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

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).

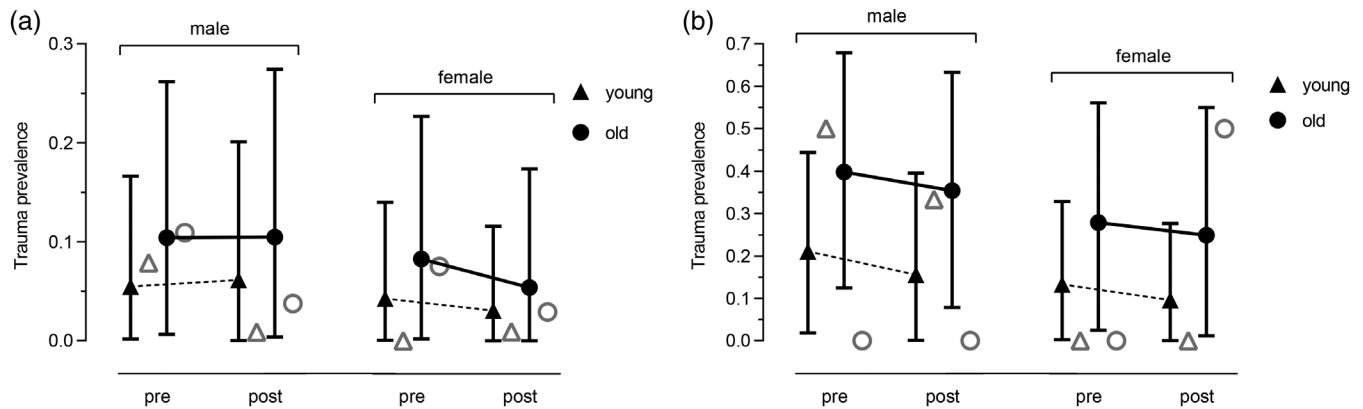


FIGURE 4 Cranial trauma prevalence of Upper Paleolithic modern human cranial remains by time period, age, and sex. Solid markers denote predicted means based on posterior estimates of Markov chain Monte Carlo generalized linear mixed models (MCMC GLMMs), bars show lower and upper 95% credible intervals. Open markers denote crude trauma frequencies. (a) Predicted trauma prevalence (Model 3.1) and crude trauma frequencies of skeletal elements when 76–100% complete. (b) Predicted trauma prevalence (Model 3.2) 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 S7a,b for predicted values. Note the different scales of the y-axes

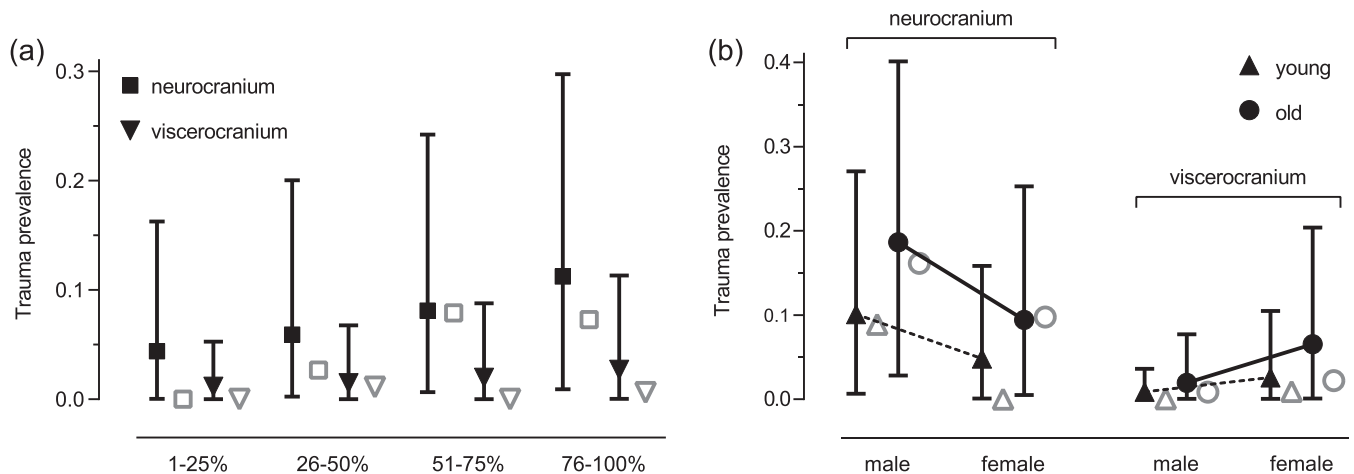


FIGURE 5 Cranial trauma prevalence of viscerocranial and neurocranial remains of Upper Paleolithic humans. Solid markers denote predicted means based on posterior estimates of Markov chain Monte Carlo generalized linear mixed models (MCMC GLMMs), bars show lower and upper 95% credible intervals. Open markers denote crude trauma frequencies. (a) Predicted trauma prevalence (Model 4.1) and crude trauma frequencies for preservation categories 1–25%, 26–50%, 51–75%, and 76–100%. (b) Predicted trauma prevalence (Model 4.2) and crude trauma frequencies by age and sex of skeletal elements when 76–100% complete. See Table S8a,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; Pankowska 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 than 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. Crude 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-Brobeil, Du Souich, & Al Oumaoui, 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; CI: 0.178–2.921; pMCMC: 0.017 for skeletal elements, and posterior mean: 3.533; CI: 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-Brobeil et al., 2009; Larsen, 1997; Milner, Boldsen, Weise, Lauritsen, & Freund, 2015; Redfern, 2017b; Scaffidi & Tung, 2020; Schwitalla, Jones, Pilloud, Coddling, & 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 rapid adaptations 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 neurocranial 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, Krockner, & Wirth, 2014 for a critical review). Injuries predominantly affecting the face can equally indicate violence, as is the case in domestic violence (Guyomarc'h, 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.

This study contributes to our sparse understanding of trauma prevalence in the UP. The study provides a methodological template for future trauma research on the human fossil record, and the provided raw data can be used for comparative studies with skeletal remains from preceding and subsequent time periods. Only the accumulative evidence from a multitude of trauma assessments of Paleolithic humans with different research foci will lead to a better understanding and more detailed reconstructions of the injury risks and consequences that prehistoric humans faced during their lives.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Judith Beier: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; software; visualization; writing-original draft; writing-review and editing. **Nils Anthes:** Methodology; software; writing-review and editing. **Joachim Wahl:** Conceptualization; funding acquisition; methodology; supervision; writing-review and editing. **Katerina Harvati:** Conceptualization; funding acquisition; methodology; supervision; writing-review and editing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are publicly available in the Zenodo Data Repository at <http://doi.org/10.5281/zenodo.3979485>.

ORCID

Judith Beier  <https://orcid.org/0000-0002-5375-6958>

Nils Anthes  <https://orcid.org/0000-0003-4189-7849>

Joachim Wahl  <https://orcid.org/0000-0002-5733-8905>

Katerina Harvati  <https://orcid.org/0000-0001-5998-4794>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Supplementary Information

Content

Table S1. Upper Paleolithic modern human cranial specimens used in this study.....	2
Table S2. Cranial remains with traumatic lesions	7
Perimortem cranial breakages of human cranial remains post-dating 20 ka BP	11
Figure S1. Assigned locations of Upper Paleolithic sites	12
Table S3. Overall sample sizes of each variable level.....	13
Analyses with reduced trauma dataset.....	14
Table S4. Summary statistics of generalized linear mixed models of the reduced trauma dataset	16
Figure S2. Plot of effect sizes of models 1.1–4.2 (full and reduced trauma datasets).....	17
Table S5a. Predicted trauma prevalence values of model 1.1	18
Table S5b. Predicted trauma prevalence values of model 1.2.....	18
Table S6a. Predicted trauma prevalence values of model 2.1.....	19
Table S6b. Predicted trauma prevalence values of model 2.2.....	19
Table S7a. Predicted trauma prevalence values of model 3.1	20
Table S7b. Predicted trauma prevalence values of model 3.2.....	20
Table S8a. Predicted trauma prevalence values of model 4.1	21
Table S8b. Predicted trauma prevalence values of model 4.2.....	21
Supplementary References	22

Table S1. Upper Paleolithic modern human cranial specimens used in this study. Data provided in Beier (2020)¹ were collected from cited references.

Country	Specimen	Ref.
Austria	Willendorf 2	2,3
Britain	Kent's Cavern 4	4–10
	Gough's Cave GC2	11–15
	Gough's Cave GC6	11–13
	Gough's Cave GC7	11–13,16
	Gough's Cave GC86:55-GC87:139-230A-230B-253	12,13
	Gough's Cave GC87:190-162	12,13
	Gough's Cave GC87:25-29-49-87	12,13
	Kendrick's Lower Cave 074	17–22
Bulgaria	Bacho Kiro 3575	23–25
	Buran Kaya III #56	26,27
	Buran Kaya III BK3-55	26,27
	Buran Kaya III Frontoparietal	26,27
Croatia	Sandalja 14013-14016-14024	28–30
	Sandalja 14015	28–30
	Sandalja 14019	28–30
	Sandalja 14021	28–30
	Sandalja 14022	28–30
	Sandalja 14026	28–30
Czech Republic	Brno I	31–34
	Brno II	32,33,35–39
	Dolní Věstonice 3	40–49
	Dolní Věstonice 11/12	40–42,45,47,47,50
	Dolní Věstonice 13	40–45,50,51
	Dolní Věstonice 14	40–45,51
	Dolní Věstonice 15	40–45,51–53
	Dolní Věstonice 16	40–45,47,48,54
	Kůlna 6	55–58
	Mladeč 1	59–62
	Mladeč 2, 7	59–62
	Mladeč 5	59–65
	Mladeč 6	59–62,64,65
	Mladeč 8	59–62,64
	Mladeč 39	59,60,62,64
	Mladeč 40	59,60,62,64
	Mladeč 48, 49, 52	59,60,62,64
	Mladeč 54	59,60,62,64
	Pavlov 1	40–42,44,45,48,66
	Pavlov 3	40,41,44
	Pavlov 4	40,41,44
	Předmostí 1	67–70
	Předmostí 3	67–71
	Předmostí 4	67–71
	Předmostí 5	67,69–71
	Předmostí 9	67–71
	Předmostí 10	67–71
	Předmostí 14	67–71
	Předmostí 18	67–71
	Předmostí 19	67–71
	Předmostí 21	67,69–72
	Předmostí 26	67,69–71

	Předmostí 30	69,70
	Zlatý kůň ZK1+2	24,32,66,73-78
France	Abri Pataud 1	33,79-82
	La Balauzière 1	83,84
	La Balauzière 2	83,84
	Brassempouy 316	85-87
	Bruniquel-Lafaye 24	71,88-92
	Cap Blanc 1	71,93-97
	Chancelade 1	33,97-104
	Cro Magnon 1	105-108
	Cro Magnon 2	105-108
	Cro Magnon 3	105-107
	Crouzade V	109-112
	Crouzade VI	109-112
	Cussac L2A	113-115
	Farincourt 1	71,116-119
	Farincourt 2	71,116,117
	Farincourt 3	71,93,116,117
	Fontéchevade 5 (Homo I)	71,120-122
	Iboussières A	123-125
	Isturitz 1	33,111,126,127
	Isturitz 14	111,126
	Isturitz 23	111,126,128
	Isturitz 25	111,126,127
	Isturitz 37+98	33,111,126
	Isturitz 41	111,126,128
	Isturitz 50+79	111,126,127
	Isturitz 52	33,111,126,129
	Isturitz 53	111,126,128
	Isturitz 59	111,126,127
	Isturitz 69	33,111,126,127
	Isturitz 70	111,126
	Isturitz 71	33,111,126,129
	Isturitz 72	111,126,129
	Jaurias 1+2	71,130,131
	Lachaud 1	71,132,133
	Lachaud 2	71,132,133
	Lachaud 3	71,132,133
	Lachaud 5	71,132,133
	Laugerie-Basse 4	71,90,134-138
	Limeuil-village 3	111,139
	Lussac-Marche LC1	121,140
	Lussac-Tannerie LC5	71,121,140
	Madeleine 1	71,90,111,136,141
	Madeleine 3	71,90,111,139
	Mas-d'Azil 3	142
	Montgaudier 4	71,111,143
	Peyrat LP5	71,144,145
	Placard 15	111,146-150
	Placard 17	71,111,146-150
	Placard 19	111,146-151
	Placard 20	111,146-150
	Placard 21	111,146-150
	Placard 23	111,146-150
	Placard C-61387	111,146-151

	Placard I-56022	111,146–150
	Rigney-1 Mandibule	111,117,152,153
	Roc-de-Cave 1	90,93,154,155
	Rochereil 1	71,156–158
	Romains 2	111,159
	St-Germain-Rivière STG1	90,111,130,160–162
	St-Germain-Rivière STG2	111,130,162
	St-Germain-Rivière STG3	111,130,162
	St-Germain-Rivière STG4	111,130,162
	Sorde 1	91,163
	Sorde 3	91,163,164
	Veyrier II	165–168
	Vilhonneur 1	34,121,169
Germany	Bonn-Oberkassel 1	170–175
	Bonn-Oberkassel 2	170–175
	Brillenhöhle Calotte	176–180
	Brillenhöhle Temp-le	176–180
	Brillenhöhle Temp-ri-1	176–180
	Brillenhöhle Temp-ri-2	176–180
	Brillenhöhle Occ	176–180
	Brillenhöhle Zyg	176–180
	Burkhardtshöhle 111+113	177,181
	Dietfurt M6c-307+M6c-306.5+M6c305-310	182,183
	Dietfurt M6c-308.5	182,183
	Hohle-Fels HF79IIb876	177,184
	Neuessing 2	179,185–188
	Neuwied-Irlich 1	187,189
	Rhünda	187,190–193
	Röthekopf	194–196
Greece	Theopetra THE1	197,198
Hungary	Tapolca 1	71,199–201
Israel	el-Wad EM 3915	202–204
	el-Wad EM 3916	202–204
	el-Wad EM 3936	203,204
	Ohalo II H2	205–210
Italy	Arene Candide "Principe"	48,211–215
	Arene Candide AC2	213,214,216–218
	Arene Candide AC3	213,214,216,217,219
	Arene Candide AC4	213,214,216,217,220
	Arene Candide AC5	213,214,216,217,221
	Arene Candide AC12	213,214,216,217,221
	Arene Candide AC16	213,214,216,217,222
	Arene Candide AC17	213,214,216,217
	Arene Candide AC18	213,214,216,223
	Baouso da Torre 1	213,224–226
	Baouso da Torre 3	213,224–226
	Barma Grande 1	34,213,227,228
	Barma Grande 2	213,228–230
	Barma Grande 3	213,228,229
	Barma Grande 4	213,228,229,231
	Barma Grande 5	33,227–229,232
	Caviglione 1	48,155,233–236
	Fossellone 1	213,237
	Grotta Paglicci 12	213,238–242
	Grotta Paglicci 14 B	129,213,238

	Grotta Paglicci 15 C	129,213,238
	Grotta Paglicci 16 D	213,238
	Grotta Paglicci 20 I	129,213,238,243
	Grotta Paglicci 24 N	129,213,238,243
	Grotta Paglicci 25	213,241,242,244,245
	Grotta Paglicci 34	213,238,246
	Grotta Paglicci 36	213,238,246
	Grotta Paglicci 37	213,238,246
	Grotte des Enfants 4	33,213,247
	Grotte des Enfants 5	33,155,213,247
	Maritza 2	71,213,248–250
	Oriente C	251–255
	Ortucchio 1	213,256
	Ortucchio 2	213,257
	Ostuni 1	184,213
	Punta 1	129,213,256,257
	Romanelli 4+5	213,258
	Romanelli 7	213,258
	Romanelli 8	213,258
	Romanelli 9	213,258
	Romanelli 11	213,258
	Romito 1	213,247,248,259
	Romito 2	213,247,248,259–261
	Romito 3	213,247,248,259
	Romito 4	213,247,248,259,260
	Romito 5	213,247,248,259,260
	Romito 6	213,247,248,259
	Romito 7	247,248,262,263
	San Teodoro 1	213,264–271
	San Teodoro 2	213,264,266,267,270–272
	San Teodoro 3	213,264,266,267,271,273
	San Teodoro 5	213,264,266,267,273
	San Teodoro 6	213,267,273,274
	San Teodoro 7	213,267,273,275
	Vado all'Arancio A	276,277
	Villabruna 1	213,278
Netherlands	Eurogeul	279
Poland	Maszycka 1-1	280,281
	Maszycka 1-5	280,281
	Maszycka 541	280,282
Portugal	Caldeirão 1	283,284
Romania	Cioclovina 1	285–291
	Climente-II M1	292–296
	Muierii 1	200,297–300
	Muierii 2	298,299
	Oase 1	301–305
	Oase 2	301–303,305,306
Russia	Afontova Gora II_Mandible	184,307,308
	Kostenki 2 Zamiatnin	309,310
	Kostenki 8 Telmanskaia	310–312
	Kostenki 14 Markina Gora	309,313–318
	Pokrovka 2	317
	Sunghir 1	313,319–325
	Sunghir 2	313,319,321–325
	Sunghir 5	322–325

Slovakia	Moča 1	326–328
Spain	Balma Guilanya BG-92-S2-E-1206/1209	329–332
	Barranc Blanc 2	71,331,333–337
	Beneito 1	129,331,338,339
	Castillo level 8 Frontal1	71,331,333,340–344
	Castillo level 8 Frontal2	71,331,333,340–344
	Chora 1	331,333,345
	Chora 2	331,333,345
	Lloseta craneo	331,343,346
	Mirón 1	331,347–349
	Mollet III 379	350
	Nerja 1/B	331,333,351,352
	Nerja 2/A	331,333,351,352
	Parpallo 1	129,333,334,353,354
	Parpallo 3	333,355
	Pasiega 1	331,333,342,356
	Rascaño Ra.IXB.152.427	331,357
Switzerland	Bichon 1	166,358–362

Table S2. Cranial remains with traumatic lesions.

This catalogue is a follow-up to the descriptive trauma catalogue in Beier et al. 2018, Supplementary Table 3³⁶³. We here present cranial lesions exhibited by Upper Paleolithic specimens post-dating 20,000 years ago, and, in the case of Cioclovina 1, we added recently published additional lesions not included in the previous catalogue. Descriptions are summarized from cited references and reproduce the original authors' presentations and diagnoses.

Specimen	Skeletal element	Traumatic lesions	Timing	Examination method	Ref
Beneito 1	frontal	<i>(1) healed trauma on frontal:</i> Iturbe et al. 1993 describe a small trauma on the right orbit. The injury was probably caused by a blow and is healed.	antemortem	macroscopic	338
Bonn Oberkassel 1	parietal left	<i>(1) healed lesion on left parietal:</i> There is a small depression (ca. 14x12 mm) located in the antero-inferior part of the left parietal bone, representing a well-healed blunt force trauma. The injury could have been caused by an accident, a blow with a stone or an angular object, or a projectile, such as a slingshot.	antemortem	macroscopic	171,175
Chancelade 1	parietal right	<i>(1) healed trauma on right parietal bone:</i> The skull shows a large trauma of oval shape (ca. 63x50 mm (Testut 1889) resp. 63x32 mm (Sollas 1927)) comprising the inferior part of the right parietal bone and the superior part of the temporal squama. The fractured fragments were bent inwards, thus, the outer surface appears as a depressed area with marked edges and discernible fracture lines. Although clearly recognizable externally, the trauma is barely visible endocranially. Testut 1889 suggests a strong and direct blow as the only possible explanation for this lesion, which nevertheless has healed completely. Courville 1950 refers to a trauma on the left parietal, which we assume to be a typo, because we found no other mention of an injury to the left parietal in the literature.	antemortem	macroscopic	98-101
	temporal right	<i>(2) healed trauma on the superior part of the right temporal squamous:</i> Continuation of lesion (1) described above.	antemortem	macroscopic	98-101
Cioclovina 1 (for frontal bone trauma see Beier et al. 2018)	parietal right	<i>(2, numeration continued from Beier et al. 2018) depressed trauma on right parietal bone:</i> The right parietal bone exhibits a depressed trauma, ca. 2 cm above the inferior temporal line, with radiating fracture lines crossing the left temporal, right and left parietal bones. The lesion shows no signs of healing and typical perimortem characteristics, such as plastic deformation, bony flakes and sharp lesion edges. Kranioti et al. 2019 suggest that the semicircular shape (35 mm radius) of a displaced bone fragment results from a blow with a rounded object, such as a club.	perimortem (but see comments below)	macroscopic, CT scan	289-291

<p>(2.1) <i>perimortem trauma on right parietal bone:</i> Associated with the depressed trauma, the Cioclovina cranium exhibits a linear fracture line extending over the occipital, right parietal, right temporal and right sphenoid bones (sphenoid bones not considered in this study). Kranioti et al. 2019 reason it was sustained prior to the depressed trauma; it shows perimortem characteristics, too. Both a fall and a blow with a club-like object could have caused this lesion.</p>	<p>perimortem (but see comments below)</p>	<p>macroscopic, CT scan</p>
<p>Soficaru and Trinkaus 2020 disagree with the interpretation by Kranioti et al. 2019 and suggest that the breakages on the parietal, temporal and occipital bones are postmortem damages. Because the breakages were not visible on the original photographs by Rainer and Simionescu 1942, they argue that they were probably caused during the World War II bombing of the University of Bucharest and the restoration of the skull (but see Kranioti et al.'s reply, submitted).</p>		
<p>In this study Cioclovina 1's lesions 2, 2.1, 3, 4, 5, 6 were included as perimortem trauma in the analyses presented in the main text, but excluded in the analyses of the reduced trauma data set (where we excluded trauma cases for which alternative interpretations are provided, see below: Supplementary Information p. 14-17). The healed antemortem frontal lesions 1 and 1.1 were included in both analyses.</p>		
<p>parietal left</p>	<p>(3) <i>perimortem fracture line:</i> Continuation of lesion (2) described above.</p>	<p>perimortem (but see comments above) macroscopic, CT scan</p>
<p>occipital</p>	<p>(4) <i>perimortem fracture line:</i> Continuation of lesion (2.1) described above.</p>	<p>perimortem (but see comments above) macroscopic, CT scan</p>
<p>temporal right</p>	<p>(5) <i>perimortem fracture line:</i> Continuation of lesion (2.1) described above.</p>	<p>perimortem (but see comments above) macroscopic, CT scan</p>
<p>temporal left</p>	<p>(6) <i>perimortem fracture line:</i> Continuation of lesion (2) described above.</p>	<p>perimortem (but see comments above) macroscopic, CT scan</p>

Eurogeul	parietal left	<i>(1) vault pitting on left parietal, inconclusive etiology:</i> Amkreutz et al. 2018 describe shallow pits along the sagittal suture on the ectocranial surface of the left parietal bone. The underlying spongiosa is not altered. The lesion could result from an episode of porotic hyperostosis during adolescence owing to anemia, or, alternatively, from scurvy, rickets or an inflammation of the scalp owing to trauma or infection. The lesion is not associated with any diagnostic features which would help to determine the etiology of the pitting (see discussion in Supplementary Material of Amkreutz et al. 2018). The pitting is well healed.	antemortem	macroscopic, CT scan	279
Farincourt 1	mandible left	<i>(1) bone deposition on left mandible:</i> The left mandible ramus exhibits a localized bone deposition on its external surface. A histopathological study revealed that the bone deposit formed shortly before death by connective tissue metaplasia, probably owing to inflammation. It is suggested that the deposition could be the result of a hematoma, possibly after a trauma.	antemortem/ perimortem	macroscopic, microradiography	116,119
Lachaud 1	parietal right	<i>(1) lesion on right parietal:</i> There is a shallow depression in the middle superior part of the right parietal bone. The lesion is oval in shape (ca. 15x10 mm) and was probably caused by a blow.	not specified	macroscopic	132
Maszycka 1/1	parietal right	<i>(1) perimortem trauma on parietal bone:</i> The right parietal tuber region exhibits a rounded breakage with smooth edges, oblique angles and an inwardly displaced bone flake; the inner table shows delamination and beveling. Considering its location, Orschiedt et al. 2017 suggest a violent, or, alternatively, accidental cause for this perimortem lesion, while they rule out the fabrication of a skull cup.	perimortem	macro- and microscopic	189
Moča 1	parietal left	The left parietal bone exhibits three different oval lesions on its posterior portion, which are restricted to the external table of the skull. They are probably the result of superficial injuries to the skull, potentially sustained in initiation ceremonies as suggested by Šečáková et al. 2011.			327
		<i>(1) lesion on left parietal:</i> Size ca. 9x11 mm	not specified	macroscopic, X-ray	
		<i>(1.1) lesion on left parietal:</i> Size ca. 18x14 mm	not specified	macroscopic, X-ray	
		<i>(1.2) lesion on left parietal:</i> Size ca. 8x4 mm	not specified	macroscopic, X-ray	

Röthekopf 1	frontal	<p><i>(1) trauma on frontal bone:</i> There is a relatively large lesion in the middle of the frontal squama, which exhibits characteristics of a perimortem trauma. It was potentially caused by a lethal blow to the forehead.</p> <p>Previously, Gerhardt 1977 suggested that the specimen had been reworked as a skull cap and, additionally to the frontal lesion, he described a lesion on the right parietal bone, which he assumed to be either traumatic or to have been caused during the processing of the remains. However, in a reanalysis in 2011, one of the authors (JW) could not verify these assumptions and diagnosed the perimortem trauma to the frontal as the only verifiable lesion.</p>	perimortem	macroscopic	194,195,364
San Teodoro 1	frontal	<p><i>(1) small lesion on frontal:</i> Graziosi 1947 mentions a small cavity on the right side of the frontal bone, which is either of pathological origin or represents a healed trauma.</p>	antemortem	macroscopic	264
San Teodoro 2	frontal	<p><i>(1) small lesion on frontal:</i> This specimen exhibits a small cavity of pathological or traumatic origin on the right side of the frontal bone. Compared to San Teodoro 1, the lesion is a bit deeper and is located more superior.</p> <p><i>(1.1) small lesion on frontal:</i> There is another lesion of the same nature, but shallower, circa in the middle of the frontal bone.</p> <p><i>(1.2) small lesion on frontal:</i> A third small depression is located close to the previous one.</p>	not specified	macroscopic	264

Perimortem cranial breakages of human cranial remains post-dating 20 ka BP

We recorded perimortem breakages on Upper Paleolithic cranial remains only as trauma when the authors who examined the original fossils explicitly stated that the breakage was caused by an antemortem traumatic impact and not by an event following the death of the individual, such as burial, deposition or intentional postmortem manipulation of the remains.

Hence, we recorded the following remains in our sample as having no trauma, although all of them have been suggested to exhibit perimortem damages, such as cut marks, percussion marks or perimortem breakages:

- Placard 15, 17, 19, 20, 21, 23, C-61387, I-56022 ^{146,147,149–151}
- Gough's Cave GC 2, GC 6, GC 7, GC86:55-GC87:139-230A-230B-253, GC87:190-162, GC87:25-29-49-87 ¹³
- Isturitz 1, 25, 50+79, 59 ^{126,127,150}
- Burkhardtshöhle 88/111 + 88/113 ^{177,181}
- Maszycka 1/5 ²⁸¹
- Brillenhöhle Calotte ^{176,177,179,180}

For Röthekopf 1 we only recorded the frontal lesion as trauma and neglected other breakages and a lesion on the right parietal, previously proposed as traumatic¹⁹⁴, as no trauma because more recent examinations of the latter breakages suggest them to be postmortem damages rather than perimortem trauma³⁶⁴.

Figure S1. Assigned locations of Upper Paleolithic sites. See Figure 1 for site names and further details.

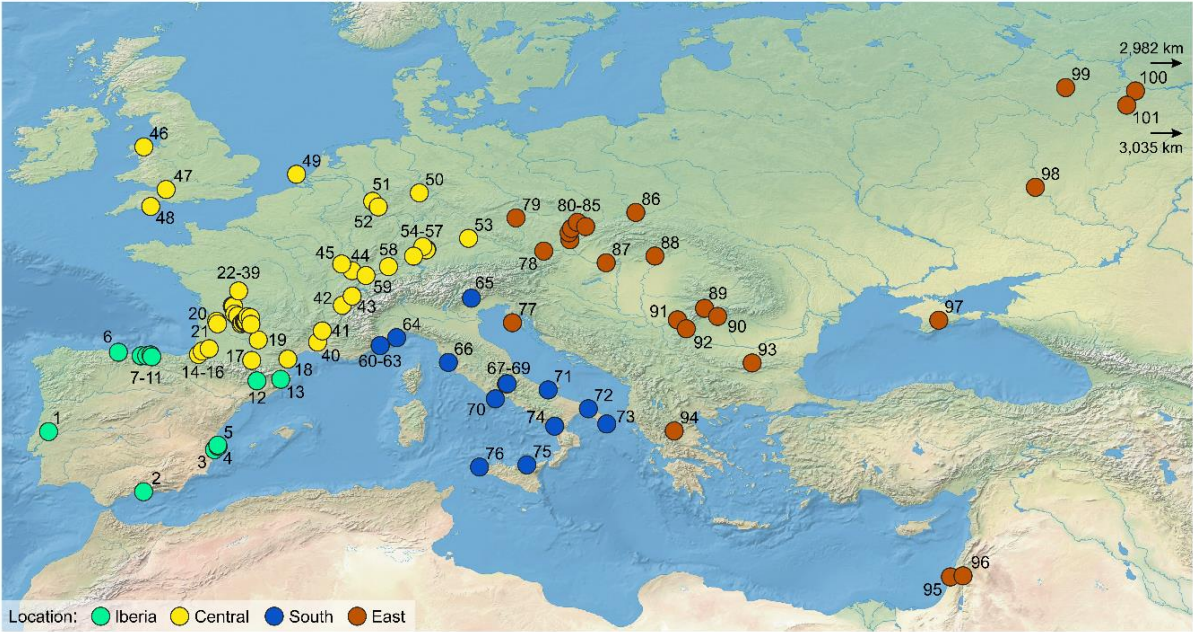


Table S3. Overall sample sizes of each variable level

Variable	Variable level	n total (n with trauma)	
		Skeletal elements	Specimens ¹
preservation	1-25%	90 (0)	NA
	26-50%	163 (3)	NA
	51-75%	182 (9)	NA
	76-100%	850 (30)	NA
period	pre-LGM	644 (32)	111 (14)
	post-LGM	641 (10)	123 (9)
age	young (<30 y)	574 (10)	82 (6)
	old (>30 y)	470 (30)	61 (15)
	indeterminate	241 (2)	91 (2)
sex	female	400 (8)	57 (5)
	male	707 (31)	98 (15)
	indeterminate	178 (3)	79 (3)
anatomy	viscerocranium	661 (4)	NA
	neurocranium	624 (38)	NA
skeletal element	frontal	129 (15)	NA
	mandible left	107 (2)	NA
	mandible right	112 (0)	NA
	maxilla left	89 (1)	NA
	maxilla right	95 (0)	NA
	nasal left	55 (0)	NA
	nasal right	58 (0)	NA
	occipital	102 (3)	NA
	parietal left	111 (5)	NA
	parietal right	121 (11)	NA
	temporal left	80 (2)	NA
	temporal right	81 (2)	NA
	zygoma left	70 (1)	NA
	zygoma right	75 (0)	NA
location	south	423 (2)	56 (2)
	east	394 (32)	69 (14)
	central	404 (7)	92 (6)
	Iberia	64 (1)	17 (1)

¹ NA: variable levels not applicable to specimens. Specimens are skeletal elements belonging to the same individual (e.g. adhering together) and can be composed of up to 14 skeletal elements (see Materials and Methods for further details).

Analyses with reduced trauma dataset

Compared to the full trauma dataset as employed in the main text of the article, in the reduced trauma dataset we excluded lesions when original authors provided an alternative cause for a lesion besides trauma. This was the case for 23 lesions in our Upper Paleolithic cranial dataset. However, some of these lesions were located on skeletal elements that exhibited one or several other lesions identified as trauma. Because trauma was recorded binary (present/absent) per skeletal element, finally 13 skeletal elements were excluded in the reduced trauma dataset, i.e. they were recorded as “not injured”. The same applied to specimens, where four specimens, formerly recorded as “injured” were recorded as “not injured” in the reduced trauma dataset. See skeletal catalogues in Table S2 and Beier et al. 2018, Supplementary Table 3 for single lesion descriptions and lesion number given below.

Excluded lesions (authors provided alternative explanations):

Lesions located on skeletal elements that exhibit another trauma (elements remain as “injured” in the reduced trauma dataset)

- Dolní Věstonice 11/12 lesion 1.1 (frontal)
- Dolní Věstonice 15 lesion 2.1 (parietal right)
- Dolní Věstonice 16 lesion 1.3 (frontal)
- Mladeč 5 lesion 2 (parietal right)
- Mladeč 6 lesion 1.1 (frontal)

Lesions located on skeletal elements that do not exhibit another trauma (elements recorded as “not injured” in the reduced trauma dataset)

- Dolní Věstonice 11/12 lesion 2 (parietal right)
- Dolní Věstonice 16 lesion 3 (maxilla left)
- Mladeč 6 lesions 2, 2.1 (parietal right)
- Pavlov 1 lesions 2, 2.1 (parietal right)
- Cioclovina 1 lesions 2, 2.1 (parietal right), lesion 3 (parietal left), lesion 4 (temporal right), lesion 5 (temporal left), lesion 6 (occipital)
- Kostenki 8 lesion 1 (frontal)
- Eurogeul lesion 1 (parietal left)
- San Teodoro 1 lesion 1 (frontal)
- San Teodoro 2 lesions 1, 1.1., 1.2. (frontal)

Specimens recorded as “not injured” in the reduced trauma dataset:

- Kostenki 8
- Eurogeul
- San Teodoro 1
- San Teodoro 2

We employed the same model variants and setup as for the full trauma dataset (described in Materials and Methods; reduced trauma dataset models are labelled “-b”). We used 5,100,000 MCMC iterations, a burn-in of 100,000, and a thinning interval of 1,000 in the reduced specimen-level models 1.2-b, 2.2-b and 3.2-b, generating posterior distributions with >1900 samples each. In the skeletal-element-level

models, autocorrelation was high due to the fewer trauma cases in the reduced trauma dataset and the resulting small sample sizes in variable levels. We therefore increased iterations to 10,000,000 MCMC iterations, a burn-in of 200,000, and a thinning interval of 2,000 in the reduced skeletal element-level models 1.1-b, 2.1-b and 3.1-b and 4.1-b, and used 15,000,000 MCMC iterations, a burn-in of 300,000, and a thinning interval of 3,000 in model 4.2-b. This did not overcome high autocorrelation in every case, and effective sample sizes for some of the skeletal element-level models were as small as >160 in the random component.

Results of analyses with the reduced trauma dataset are provided in Table S4 and graphically contrasted with results of the full trauma dataset in Figure S2. Overall, effect patterns are similar and produced credible intervals largely consistent with the full trauma dataset.

Table S4. Summary statistics of generalized linear mixed models of the reduced trauma dataset. Model coefficients are given as their posterior mean with 95 % credible intervals 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. UP: Upper Paleolithic, CI: credible interval.

Model	N	Predictor variable	Model coefficients			
			posterior mean	lower 95 % CI	upper 95 % CI	pMCMC
model 1.1-b	1285 †	element preservation	0.725	0.140	1.380	0.007
model 1.2-b	234 †	specimen preservation	0.840	0.305	1.404	0.004
model 2.1-b	959 ‡	element preservation	0.575	-0.004	1.223	0.045
		age	-2.086	-4.076	-0.204	0.021
		sex	-0.552	-1.778	0.671	0.365
		age x sex	1.932	-0.369	4.221	0.089
model 2.2-b	118 ‡	specimen preservation	0.376	-0.343	1.062	0.300
		age	-1.493	-3.876	0.946	0.222
		sex	0.248	-1.610	2.339	0.835
		age x sex	0.150	-2.977	3.211	0.935
model 3.1-b	959 ‡	element preservation	0.572	-0.042	1.199	0.045
		period	0.562	-1.685	2.815	0.640
		age	-1.943	-5.093	0.574	0.142
		sex	0.610	-1.745	3.095	0.624
		period x age	1.375	-1.599	4.527	0.373
		period x sex	-0.678	-3.529	2.164	0.642
model 3.2-b	118 ‡	specimen preservation	0.375	-0.353	1.056	0.300
		period	-0.126	-3.059	2.772	0.918
		age	-2.476	-5.663	0.512	0.083
		sex	-0.181	-3.037	2.735	0.895
		period x age	1.369	-1.996	5.138	0.448
		period x sex	0.685	-2.744	4.251	0.700
model 4.1-b	1285 †	element preservation	0.752	0.142	1.383	0.003
		anatomy	-2.754	-4.666	-0.907	0.002
model 4.2-b	959 ‡	element preservation	0.680	0.017	1.322	0.020
		anatomy	-0.656	-3.161	1.799	0.618
		age	-0.649	-1.685	0.410	0.216
		sex	0.795	-0.389	1.933	0.176
		anatomy x age	-1.091	-4.701	2.141	0.529
		anatomy x sex	-154.951	-307.746	-19.051	<0.0002

Trauma prevalence was modelled using a Markov chain Monte Carlo algorithm: models 1.1-b, 2.1-b, 3.1-b, 4.1-b and 4.2-b comprise skeletal elements, models 1.2-b, 2.2-b and 3.2-b comprise cranial specimens. See Methods for detail. † full dataset; ‡ exclusion of sex unknown and age indeterminate skeletal elements or specimens, i.e. no more precise age determination than >12 years.

Figure S2. Plot of effect sizes of models 1.1–4.2 (full and reduced trauma datasets).

Effect sizes of full trauma dataset displayed in black, reduced trauma dataset effect sizes in orange. Given are the coefficient estimates (posterior means) with 95% credible intervals. Open symbols for element-level and solid symbols for specimen-level models. Model coefficients are given on the logit scale (scale of the link function). Plot shows the effect of one predictor while keeping the effects of all other predictors constant. Reference levels for the factorial predictors age, sex, period and anatomy are old, female, post-LGM and neurocranium. Hence, for example, a positive model coefficient value for sex (with female as reference level) indicates that male remains have a higher cranial trauma prevalence than female remains.

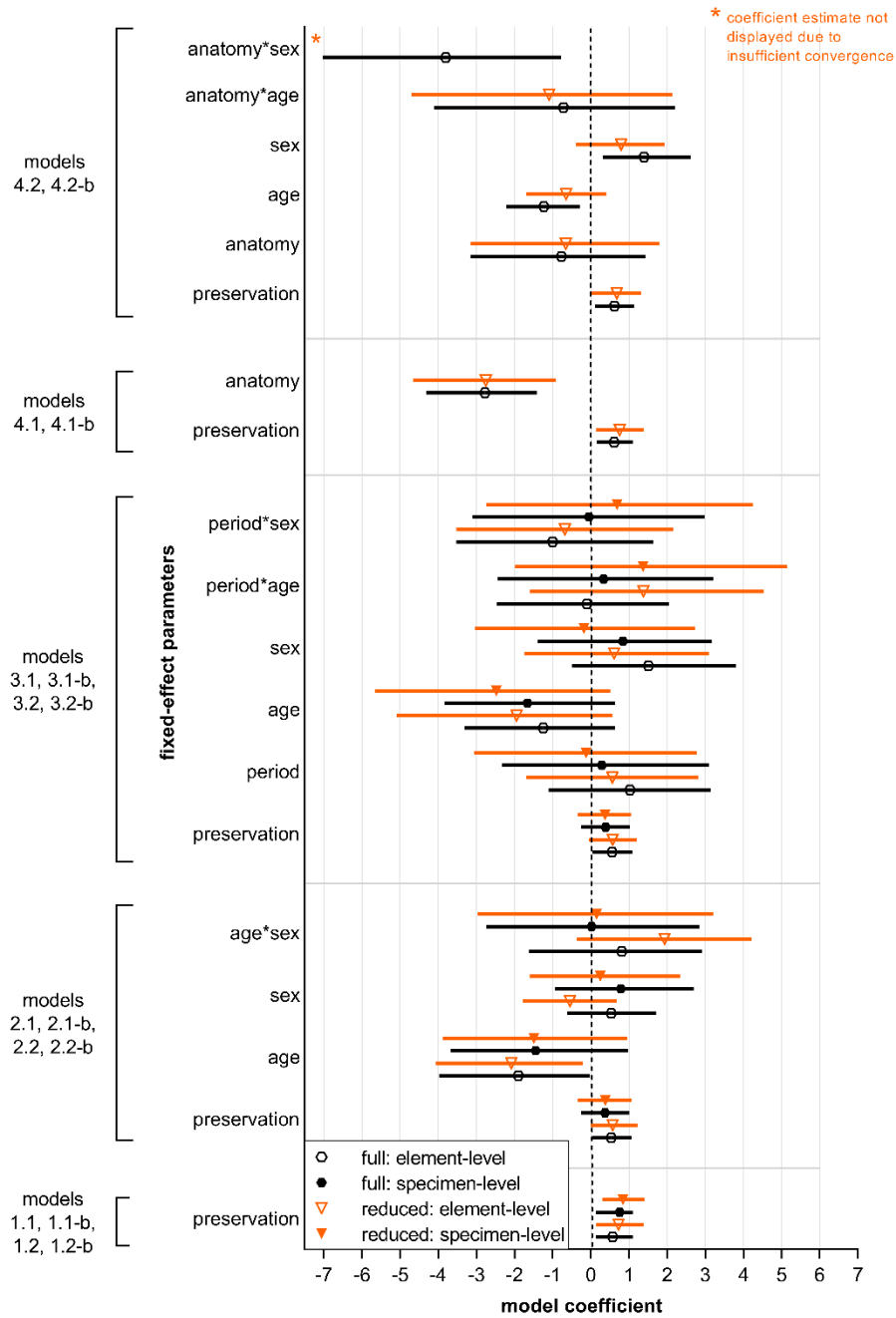


Table S5a. Predicted trauma prevalence values of model 1.1.

element-preservation category	mean	lower 95% CI	upper 95% CI
1-25%	0.030	0.0002	0.111
26-50%	0.038	0.001	0.130
51-75%	0.051	0.002	0.158
76-100%	0.068	0.003	0.192

Table S5b. Predicted trauma prevalence values of model 1.2.

specimen-preservation score	mean	lower 95% CI	upper 95% CI
0.018	0.075	0.008	0.196
0.5	0.141	0.032	0.304
1	0.258	0.078	0.479

Table S6a. Predicted trauma prevalence values of model 2.1.

sex	age	mean	lower 95% CI	upper 95% CI
male	young	0.060	0.003	0.179
	old	0.102	0.009	0.249
female	young	0.033	0.0001	0.117
	old	0.080	0.005	0.215

Table S6b. Predicted trauma prevalence values of model 2.2.

sex	age	mean	lower 95% CI	upper 95% CI
male	young	0.185	0.024	0.395
	old	0.378	0.130	0.616
female	young	0.119	0.001	0.305
	old	0.266	0.031	0.537

Table S7a. Predicted trauma prevalence values of model 3.1.

period	sex	age	mean	lower 95% CI	upper 95% CI
pre-LGM	male	young	0.055	0.002	0.166
		old	0.104	0.007	0.262
	female	young	0.043	0.001	0.140
		old	0.083	0.002	0.227
post-LGM	male	young	0.062	0.0003	0.201
		old	0.105	0.004	0.274
	female	young	0.031	0.00002	0.116
		old	0.054	0.0002	0.174

Table S7b. Predicted trauma prevalence values of model 3.2.

period	sex	age	mean	lower 95% CI	upper 95% CI
pre-LGM	male	young	0.211	0.019	0.444
		old	0.398	0.124	0.679
	female	young	0.133	0.003	0.328
		old	0.279	0.025	0.561
post-LGM	male	young	0.156	0.001	0.395
		old	0.354	0.079	0.633
	female	young	0.096	0.0003	0.277
		old	0.249	0.012	0.550

Table S8a. Predicted trauma prevalence values of model 4.1.

element-preservation category	anatomy	mean	lower 95% CI	upper 95% CI
1-25%	neurocranium	0.044	0.0003	0.163
	viscerocranium	0.012	0.000003	0.053
26-50%	neurocranium	0.059	0.003	0.200
	viscerocranium	0.015	0.00002	0.068
51-75%	neurocranium	0.081	0.007	0.242
	viscerocranium	0.020	0.0003	0.088
76-100%	neurocranium	0.112	0.009	0.297
	viscerocranium	0.027	0.0004	0.113

Table S8b. Predicted trauma prevalence values of model 4.2.

anatomy	sex	age	mean	lower 95% CI	upper 95% CI
neurocranium	male	young	0.101	0.007	0.271
		old	0.187	0.028	0.401
	female	young	0.048	0.001	0.158
		old	0.094	0.005	0.253
viscerocranium	male	young	0.009	0.00000004	0.036
		old	0.019	0.0000003	0.077
	female	young	0.026	0.000003	0.105
		old	0.065	0.0004	0.204

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Appendix C

Paper III

Analysis of cranial breakage patterns of two late Middle Pleistocene crania from Apidima Cave, Greece: peri- or postmortem?

Judith Beier, Mirsini Kouloukoussa, Vassilis G. Gorgoulis, Joachim Wahl,
Katerina Harvati

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Analysis of cranial breakage patterns of two late Middle Pleistocene crania from Apidima Cave, Greece: peri- or postmortem?

Judith Beier¹, Mirsini Kouloukoussa^{2,3}, Vassilis G. Gorgoulis^{3,4,5}, Joachim Wahl¹,
Katerina Harvati^{1,2,6}

¹ Paleoanthropology, Senckenberg Centre for Human Evolution and Palaeoenvironment, University of Tübingen, Tübingen, Germany. ² Museum of Anthropology, Medical School, National and Kapodistrian University of Athens, Athens, Greece. ³ Department of Histology and Embryology, Medical School, National and Kapodistrian University of Athens, Athens, Greece. ⁴ Biomedical Research Foundation of the Academy of Athens, Athens, Greece. ⁵ Division of Cancer Sciences, Faculty of Biology, Medicine and Health, Manchester Academic Health Science Centre, Manchester Cancer Research Centre, NIHR Manchester Biomedical Research Centre, University of Manchester, Manchester, UK. ⁶ DFG Center for Advanced Studies 'Words, Bones, Genes, Tools', University of Tübingen, Tübingen, Germany.

This study investigates the cranial breakage patterns of two late Middle Pleistocene partial fossil crania from the Apidima cave site in Mani peninsula, Peloponnese, southern Greece. To assess the timing of breakage and evaluate whether the fracture lines represent postmortem taphonomic damage or perimortem fractures, we employed virtual anthropological methods using computed tomography (CT) scanning of the two crania. We differentiated between perimortem (fresh) and postmortem (dry) bone breakages by examining five morphological features of the endo- and ectocranial aspects of fracture lines: breakage outline, path of least resistance, breakage angle, texture, and plastic response. Most fractures of the two crania gave inconclusive results regarding the timing of breakage, while some likely represent fresh bone breakage and few were found to be consistent with dry bone breakage. About half of all examined fracture lines exhibit a mix of fresh and dry bone breakage morphologies, suggesting that the features used for differentiation were insufficient or may not be readily applicable to fossil remains. We discuss the methodological challenges involved in determining the timing of trauma in isolated fossil remains, especially when the depositional context is complex.

1. Introduction

The cave site of Apidima, Mani peninsula, Peloponnese, southern Greece, has yielded two partial fossil human crania (Apidima 1 and 2) from Middle to Late Pleistocene deposits, which were discovered in the late 1970s during research activities by the Museum of Anthropology of the School of Medicine, National and Kapodistrian University of Athens. Apidima 2 dates to more than 170 thousand years ago (Bartsiokas et al., 2017; Harvati et al., 2019), and is taxonomically classified as Neanderthal (Harvati et al., 2011; Bräuer et al., 2019; Harvati et al., 2019). Apidima 1, the less complete of the two crania, had until recently received only little scientific attention. Harvati et al. (2019) used virtual reconstruction, comparative 3D geometric morphometric shape analysis and direct laser ablation U-series dating to evaluate this specimen. Results indicated that it is > 210 ka old, and it displays a combination of primitive and derived modern human features. Harvati et al. (2019) proposed that it represents an early *Homo sapiens*, making Apidima 1 the oldest known such

specimen outside of Africa (Harvati et al., 2019 – although a different conclusion was reached by Lumley, 2019; Lumley et al., 2020; but see Harvati, in press; Harvati et al., 2020). Crucially, questions remain about the context, taphonomy and depositional history of both Apidima specimens. Here we investigate their cranial fractures from a taphonomic and paleopathological perspective, so as to contribute to the understanding of the depositional history of the remains and provide insights into their potential behaviors and life events.

The two crania, extracted from a block of breccia wedged near the cave ceiling between the cave walls, are highly fragmented and partially damaged. Whilst showing some taphonomic deformation (Harvati et al., 2019), the fragments cohere together in near correct anatomical position due to the breccia infill of the endocranium, which was not removed during the preparation of the fossils (Pitsios, 1999). Previous work by Coutselinis et al. (1991; 1995) employed a macroscopic forensic examination of Apidima 2 and interpreted cranial fractures on its frontal bone as the result of two traumatic blows with an object such as a pointed stone (Coutselinis et al., 1991, 1995). Later, however, this interpretation was revised, and the Apidima 2 fractures were instead attributed to taphonomic damage from sediment pressure after deposition (Geanacos, 2001; Pitsios, 2007; Pitsios et al., 2007). Apidima 1 has not been investigated from a taphonomic perspective until now.

In this study we re-evaluate the question of whether the cranial fractures of Apidima 2 result from postmortem taphonomic damage or from perimortem breakage that could potentially represent traumatic injuries. Moreover, we perform the first assessment of the cranial fracture patterns of Apidima 1. Our work is based on virtual methods using computed tomography (CT) scanning of the two crania. Recently, virtual assessments of fossil remains have been widely used for the diagnosis of traumatic lesions and the determination of the timing of breakage (e.g. Zollikofer et al., 2002; Indriati, 2006; Wu et al., 2011; Coqueugniot et al., 2014; Sala et al., 2015; Kappelman et al., 2016; Sala et al., 2016; Gómez-Olivencia et al., 2018; Kranioti et al., 2019; Coqueugniot et al., 2020), and to differentiate between pathological and taphonomic alterations of fossil cranial remains (Ponce De León, 2002; Shang et al., 2008; Sanz et al., 2018; Fernández-Jalvo and Andrews, 2019; Wu et al., 2021). Virtual methods are particularly suitable for analysis of fossil remains, because they allow for non-destructive examination even of inaccessible areas, such as internal structures or anatomical regions covered in adhesive sediments. We aim at differentiating between perimortem (fresh) and postmortem (dry) bone breakages of the Apidima fossil crania by examining five morphological breakage features (breakage outline, path of least resistance, breakage angle, texture, and plastic response).

2. Material and Methods

2.1. The Apidima human fossils

The site Apidima is located at the coast of Mani Peninsula in Southern Peloponnese, Greece, close to the village Areopolis (Harvati, in press; Harvati et al., 2009; Harvati, 2016; Fig. 1). It comprises five caves on a steep cliff, which today can only be accessed by boat. All caves were filled with Middle and Late Pleistocene terrestrial sediments, which later progressively eroded by recurrent flooding events caused by changing sea levels throughout the Middle-Late Pleistocene and Holocene

(Pitsios, 1999; Harvati et al., 2011; Bräuer et al., 2019). The two crania were found about 15 cm apart from each other in the cave wall breccia of Cave A near the ceiling.

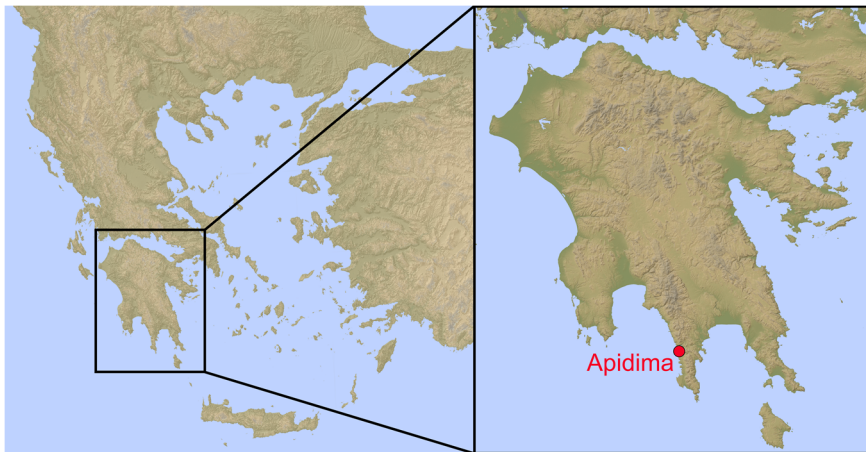


Fig. 1. Location of the Apidima cave site in Mani Peninsula, Southern Greece. (Figure created using maps kindly provided for download by the American School of Classical Studies at Athens (<https://www.ascsa.edu.gr>)).

Apidima 1 (LAO1/S1) is the less complete of the two Middle Pleistocene crania and preserves a major portion of the left parietal bone, the superior portion of the right parietal along the sagittal suture, the squamous part of the occipital bone and the posterior portion of the left temporal squama (Harvati et al., 2019; Fig. 2d-f). A large rock is still attached to its left side. Apidima 2 (LAO1/S2) preserves an almost complete viscerocranium without the mandible, and most of the cranial vault, lacking the occipital and the cranial base (Harvati et al., 2019; Fig. 2a-c).

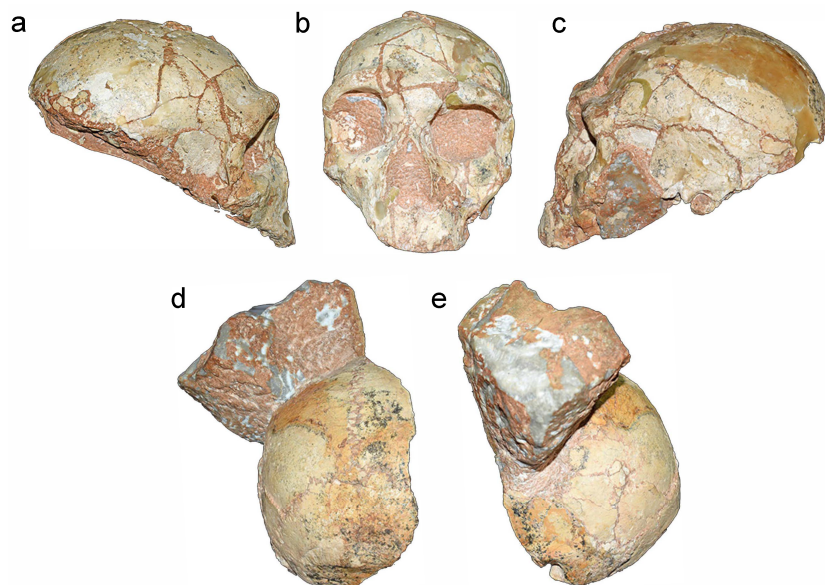


Fig. 2. The fossil crania of Apidima 2 (a-c) and Apidima 1 (d, e). a: Right lateral view. b: Frontal view. c: Left lateral view. d: Posterior view. e: Left lateral view. (Figure modified from Harvati et al., 2019; Photos by K. Harvati; Copyright: K. Harvati and Museum of Anthropology, Athens).

2.2. Bone, biomechanics and timing of breakages

Bone tissue is elastic and flexible due to its organic components (collagen fibers), and rigid and hard due to its inorganic components (minerals). The combination makes bone both robust and flexible to withstand mechanical forces, encountered for example during locomotion or physical activities. Given its material composition and morphology, cranial bone reacts in a biomechanically determined manner when exposed to extrinsic forces (loadings), yet differently to slow loadings (i.e. a force moving at speeds of kilometers per hour) or rapid loadings (i.e. a force moving at speeds of meters per second) (Symes et al., 2012). The latter, primarily associated with ballistics and explosives, does not apply to Paleolithic times. Therefore, the following refers exclusively to slow impacts.

When force is applied, bone initially gets deformed. As long as the force is not exceeding a threshold point, the deformation is reversible, and the bone will return to its original shape after removal of the force (elastic phase). When surpassing the threshold point, microscopic structural damages occur in the bone matrix, causing a non-reversible plastic deformation (plastic phase). Persistent loading will finally lead to material failure and disruption (fracture) (König and Wahl, 2006; Passalacqua and Fenton, 2012; Symes et al., 2012; Loe, 2016). The elastic capacity of a bone, i.e., how much load it can absorb before structural damage occurs, is determined by the amount of organic material and moisture in a bone. The ratio of organic to inorganic components in bone changes with increasing age (Schmitt et al., 2010; Wescott, 2013), and after death, when bone progressively loses its organic components during decomposition. In a decomposed (dry) state bone is brittle, and, unlike fresh (wet) bone, it fractures without undergoing the elastic and plastic phases (König and Wahl, 2006; Symes et al., 2012; Christensen et al., 2019; Wescott, 2019), thereby producing a breakage morphology discernible from fresh bone fractures.

The terms ante-, peri- and postmortem are commonly used to define whether an injury or breakage on human skeletal remains occurred before, around, or after death. The most striking characteristic of antemortem trauma, an injury sustained during life, is healing. Signs of healing, which occur one to two weeks after injury at the earliest, involve osteoclastic and osteoblastic responses, namely the removal of necrotic bone tissue and the formation of new bone (Campillo, 1991; Barbian and Sledzik, 2008; Boer et al., 2015). In anthropology, the term perimortem relates to any fresh bone breakage without signs of healing, regardless of whether it was sustained before or after death – as opposed to the clinical definition, where perimortem relates to the dying process, i.e. the period between an injury and the death of a person (Symes et al., 2012). Dry bone breakages, on the other hand, occur postmortem by definition.

The transition of a bone from fresh to dry state is a gradual and non-uniform process (Moraitis and Spiliopoulou, 2006; Passalacqua and Fenton, 2012; Cunha and Pinheiro, 2016; Sorg, 2019). Consequently, the perimortem interval is no uniformly defined time span, but can extend to weeks, months or even years after death, depending on the depositional conditions of the skeletal remains (Maples, 1986; Moraitis and Spiliopoulou, 2006; Wahl and Zink, 2013; Galloway et al., 2014; Cunha and Pinheiro, 2016; Sorg, 2019). Additionally, the breakage behavior of dry bones may be altered by rehydration so as to resemble wet bone breakage morphology (Broz et al., 1993; Moraitis and Spiliopoulou, 2006; Augias et al., 2017; King, 2017), obscuring the assessment of breakage timing. Contextual information, such as the find situation of the remains or the association of multiple breakages, can ultimately

help to reconstruct under which circumstances a perimortem breakage occurred and whether it may be indicative of a lethal injury or post-mortem processing of remains.

Although challenging, the breakage morphology of fresh and wet bone breakages is discernible in well-preserved skeletal remains. A typical perimortem (fresh bone) blunt force trauma on the cranium involves a spider-web-like fracture pattern comprising primary fractures at the impact point of the blunt force, fractures radiating from the impact point, and, if the applied force is not yet dissipated by then, also concentric fractures (Symes et al., 2012; Christensen et al., 2019; Ribeiro et al., 2020). In addition to the overall pattern, which may not be possible to assess in incomplete or highly fragmented remains, several macroscopic morphological characteristics of the fractured edges have been suggested as indicators of perimortem trauma. These include oblique fracture edges/beveling, smooth undulated margins, cortical delamination, peels, plastic deformation, hinging/bridges, flake defects, bone scales, fissures and crushed margins (Berryman and Haun, 1996; Churchill and Formicola, 1997; Berryman and Symes, 1998; Symes et al., 2012; Fleming-Farrell et al., 2013; Jordana et al., 2013a; Kranjoti, 2015; Ribeiro et al., 2020). Dry bones, on the contrary, shatter without undergoing a plastic phase, which results in smaller fragments with jagged and brittle edges. Postmortem dry bone breakages exhibit irregular breakage patterns following discontinuous paths and show no plastic deformation (Maples, 1986; Lovell, 1997; Sauer, 1998; Fleming-Farrell et al., 2013; Jordana et al., 2013a, 2013b; Galloway et al., 2014; Loe, 2016; Sala et al., 2016; Wescott, 2019; Ribeiro et al., 2020). As a rule of thumb, it is also suggested that fresh bone breakages rather exhibit edges with obtuse or acute angles, whereas dry bone breakages show edges at roughly right angles – but deviations from this rule have been noticed (Lovell, 1997; Fleming-Farrell et al., 2013; Jordana et al., 2013a, 2013b; Kranjoti, 2015; Sala et al., 2016). For example, in spider-web-like fresh bone fractures, it has been observed that radial fractures located beyond the innermost concentric fracture lines enclosing the point of impact can exhibit fracture edges at roughly right angles (Wahl & König 1987, König & Wahl 2006). These exceptions limit the sole use of the breakage edge angle to distinguish peri- from postmortem breakage.

2.3. Data collection

The ectocranial surfaces of Apidima 1 and 2 were visually inspected and photographically documented. The endocrania of both specimens are filled with breccia, as are all gaps between the skull fragments. Moreover, many parts of the ectocranial surface of Apidima 2 are covered with plaster, which was applied to damaged areas. These conditions precluded a macroscopic assessment of the endocranial surface appearance and the edge morphology of inner and outer bone tables along the breakage lines. As shown by Sala et al., 2016 and Fleming-Farrell et al., 2013, criteria to distinguish between peri- and postmortem breakages can be successfully assessed in virtual representations of (fossil) skeletal remains. We therefore examined the breakage patterns in a non-destructive virtual setting using computed tomography (CT) scans of the two crania. The scans were prepared at the First Department of Radiology of the National and Kapodistrian University of Athens using a multidetector computed tomography scanner (Philips) with the following scanning parameters: tube voltage 120 kV, tube current–time product 599 mAs, 16 × 0.75 collimation, 0.8 mm slice thickness, slice increment 0.4 mm, field of view 249 mm, matrix 768 × 768, pitch 0.44, rotation time 0.75 s, convolution kernel detailed

(D) and ultra-high focal spot resolution. The CT scans of both individuals show isotropic pixel sizes of 0.31 and 0.32 mm, respectively.

We examined the following five morphological features of each breakage line to assess the timing of breakage in the Apidima specimens: a) outline, b) path of least resistance, c) angle, d) texture, and e) plastic response (Tab. 1). In contrast to the studies by Sala et al. (2016) and Fleming-Farrell et al. (2013), the features of cortical delamination (Jordana et al., 2013a; Kranioti, 2015; Sala et al., 2016) and hinging (Fleming-Farrell et al., 2013) could not be observed in sufficient detail owing to insufficient resolution of the medical CT scans. They were therefore not considered in the present study.

We focused on the cranial vault bones (of the two Apidima specimens. We excluded the facial bones of Apidima 2 from breakage analyses because cranial vault bones consisting of two tables of cortical bone with a layer of trabecular bone (diploë) in between, such as frontal, parietal and occipital bones, are more diagnostic than the thin one-layered bones of the face for the analysis of breakage patterns (Sala et al., 2016). Neither of the two Apidima specimens preserve a cranial base.

Table 1. Criteria to distinguish the peri- or postmortem timing of cranial breakages.

Feature	Description	Fresh bone	Dry bone	Inconclusive	Reference
Outline	General course of breakage line along ectocranial surface	Curved	Stepped	Straight	
Path of least resistance	Propagation of breakages towards structurally weaker areas of the skull	Present	Absent	-	(Symes et al., 2012; Fleming-Farrell et al., 2013; Galloway and Wedel, 2014; Loe, 2016)
Angle	Angulation between endocranial cortical surface and breakage edge	Oblique (acute: <70°, or obtuse: >110°)	Right (70°-110°)	-	(Fleming-Farrell et al., 2013; Jordana et al., 2013b; Kranioti, 2015; Sala et al., 2016)
Texture	Texture of breakage edge (exposed surface of outer table, diploë, inner table)	Smooth	Jagged	-	(Fleming-Farrell et al., 2013; Jordana et al., 2013a; Sala et al., 2016)
Plastic response	Permanent plastic deformation (applied force exceeded elastic capacity of bone)	Present	-	Absent	(Symes et al., 2012; Fleming-Farrell et al., 2013; Kranioti, 2015)

Outline: Because the Apidima crania are highly fragmented, it was not a priori evident whether some breakage lines are associated, i.e. belong to one point of impact. We therefore classified each breakage line separately as curved, straight or stepped, depending on its course over the ectocranial skull surface. In general, curved fracture lines are more likely indicative of perimortem trauma, as they can represent concentric fracture lines following blunt force trauma. A straight course of a breakage

line can either represent a radiating fracture line and would thus be related to perimortem trauma, or, alternatively, result from postmortem dry bone breakage. The latter more likely produces numerous, smaller, and angled fragments, whose breakage lines are usually short and do not cover long distances as is more likely the case in fresh bone breakage.

Path of least resistance: We recorded whether a breakage line runs towards a structurally weaker area of the skull, such as foramina, cranial sutures, or vessel imprints. Fresh bone breakages propagate along the path of least resistance, circumvent cranial buttresses, and often end in pre-existing breakages or cranial sutures, where the kinetic energy dissipates (Berryman and Symes, 1998; Symes et al., 2012; Fleming-Farrell et al., 2013; Galloway and Wedel, 2014; Kranioti, 2015; Loe, 2016; Kranioti et al., 2019, 2020). On the contrary, dry bone breakages may cross through cranial buttresses and robust cranial regions irrespective of bone density.

Angle: To examine the edge cross-morphology of the cranial breakage lines, we used the Slice module in Avizo Lite Version 9.2.0. Depending on their lengths, we manually chose 2 to 7 points at roughly similar distances along each breakage line and placed the two outermost points slightly away from the points of intersection with other breakage lines. At each of these points, we measured the angle between the ectocranial and the endocranial surface in cross-section. To do so, we set a slicing plane and, using the “rotate” function, manually aligned it so that it intersected both the breakage line and the ectocranial surface at approximately right angles. This is crucial, because a slice cut obliquely to either of these two reference lines (breakage edge and ectocranial surface) appears larger, thus biasing measured angles. We measured the angles with the in-built “measurement” tool on the sliced images, i.e. the 2D cross-sections, employing the ectocranial surface as base line. If possible, angles were measured on the same side of each breakage line, mostly on the left and/or posterior sides. We followed Sala et al. (2016) in considering angles between 70° and 110° as right angles, and angles <70° and >110° as oblique angles.

Texture (tactile roughness): At each of the defined points, where an angle was measured, we also assessed the texture of the breakage edge in the 2D cross-sections and recorded whether its morphology was smooth or jagged. Texture describes the surface structure of the surface, which is exposed by the breakage, i.e. a section through the outer and inner tables and diploë. It has been suggested that the breakage surface tends to be macroscopically smooth in fresh bone, but rough and jagged in dry bone breakages (Johnson, 1985; Wahl and König, 1987; Wheatley, 2008; Fleming-Farrell et al., 2013; Jordana et al., 2013a; Kranioti, 2015; Sala et al., 2016; Christensen et al., 2019).

Plastic response: We recorded whether any sign of plastic deformation is associated with a breakage line. Irreversible plastic deformation indicates bending before bone failure and is commonly associated with slow impacts on fresh bone. In contrast, dry bone breaks without undergoing the plastic phase and therefore does not exhibit permanent deformation (Symes et al., 2012; Fleming-Farrell et al., 2013; Galloway et al., 2014; Kranioti, 2015; Christensen et al., 2019). When present, plastic deformation is a fairly reliable indicator of fresh bone breakage, but its absence, conversely, does not indicate dry bone breakage (Fleming-Farrell et al., 2013). Especially in fossil remains, taphonomic processes should be considered an alternative cause for observed distortions and deformations.

We selected 15 breakage lines in Apidima 1, and 37 breakage lines in Apidima 2 to be examined. We furthermore examined the edges of four defects in Apidima 2, i.e.

holes or damages on the ectocranial surface, partly filled with breccia or plaster. Figures 3 and 4 provide an overview of all examined single breakage lines of the two crania. For each breakage line we assessed the five morphological features breakage outline (straight, stepped, curved), path of least resistance (yes, no), breakage angle (measured on 2 to 7 points along each breakage line or defect in CT cross section), texture (smooth, jagged), and plastic response (yes, no). For defects we only assessed the latter three morphological features since the former two do not apply.

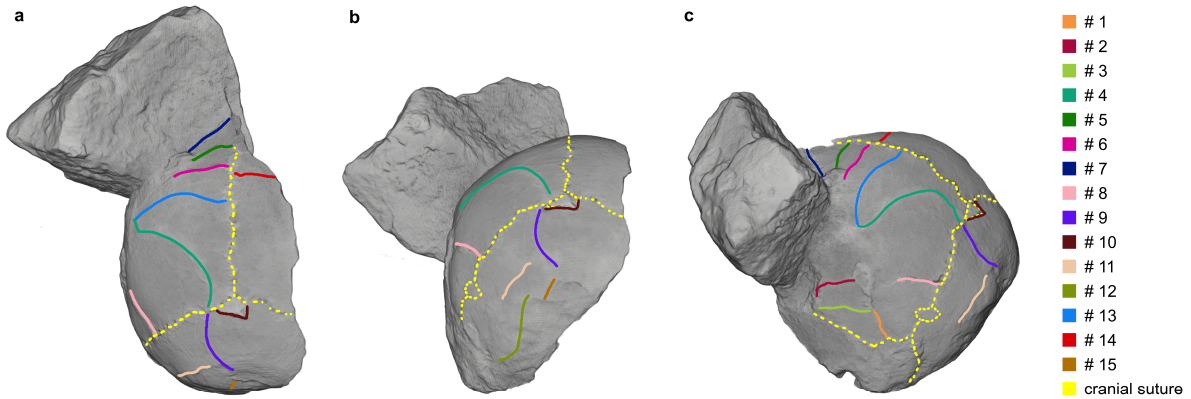


Fig. 3. Overview of the 15 breakages lines examined in Apidima 1. a: Superior view. b: Posterior view. c: Left superolateral view.

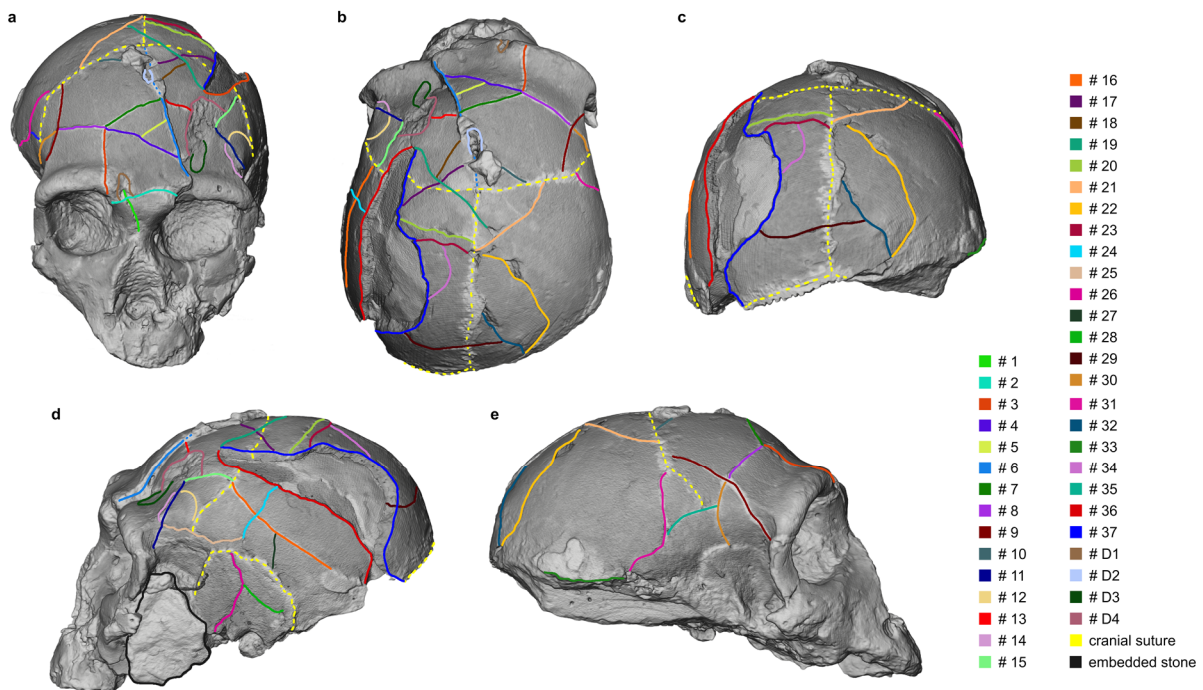


Fig. 4. Overview of the 37 breakages lines and four defects examined in Apidima 2. a: Frontal view. b: Superior view. c: Posterior view. d: Left lateral view. e: Right lateral view.

We first assessed each feature per breakage line and defect, and attributed it as fresh, dry, or inconclusive. Considering these assignments jointly, we classified each breakage line and defect to be more concordant with fresh or dry bone breakage morphology, or to be inconclusive regarding the timing of breakage.

We rated the feature angle as inconclusive when the breakage angle could only be measured at one of the several points along a breakage line in cross-sectional view. The same applies to the feature texture, which we also rated inconclusive when the

sample size of points that could be assessed along one breakage line in cross-sectional view was $n=1$. At the level of breakage lines or defects, we rated them as inconclusive when a) too few features, i.e. only two or fewer of the five features were possible to evaluate for a breakage line or defect, b) when they exhibited morphological features of both kinds (fresh and dry) in roughly similar numbers, and c) when most of the features of one breakage line or defect showed an inconclusive morphology.

3. Results

Apidima 1:

In Apidima 1, we examined 15 breakage lines (#1-15), of which ten are located on the left parietal bone and five on the occipital bone. For each breakage line we assessed five morphological features useful for distinguishing between fresh and dry bone breakage (breakage outline, path of least resistance, breakage angle, texture, and plastic response). The results are shown in Table 2.

In 13 breakage lines (86.7%), all five morphological features could be examined, while in two breakage lines (13.3%) only three morphological features could be examined. These latter two breakage lines (#7 and #13) were not visible in CT cross-sectional view, which precluded assessments of their breakage angle and texture. In total, we were able to measure breakage angles and assess textures at 37 of the 66 sampled points along the 15 breakage lines (results shown in Figure 5). In the remainder cases, breakage edges were not visible clearly enough in cross-sectional view to allow for an assessment.

Our examination revealed inconsistent results regarding the timing of breakage within single breakage lines (i.e. between the five examined features; Tab. 2), but also within single features (i.e. between the different examined points along one breakage line for the features angle and texture; Fig. 5). We found no distinct association between breakage angle and texture, which deviates from the expectation that breakage edges with oblique angles are smooth and edges with roughly right angles are jagged. Only 16 of the 37 assessed breakages edges (43,2%) conform to the expected association (Fig. 5).

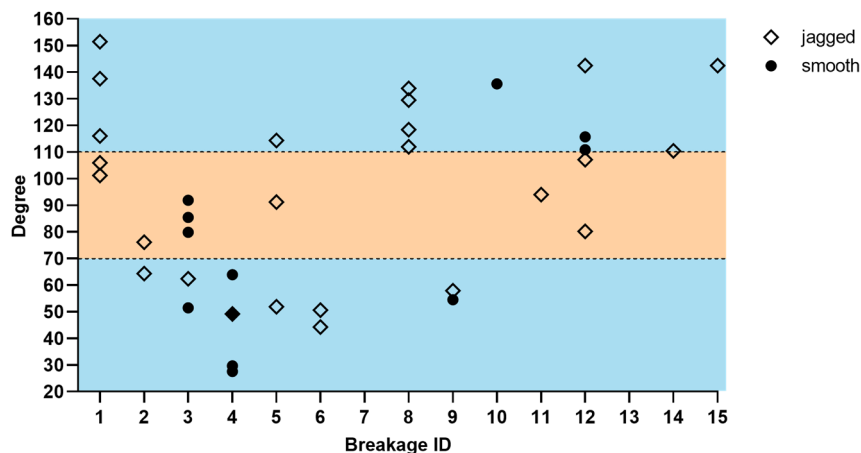


Fig. 5. Results for the features angle and texture for Apidima 1. For each breakage line and defect (x-axis) the breakage angles at the different points along one breakage line are shown (y-axis), as well as the respective texture at each of these sampling points (solid circle: smooth, open diamond: jagged).

Table 2. Results of the examination of the five morphological features per breakage line in Apidima 1. OL: Outline, LR: Least Resistance, A: Angle, T: Texture, PR: Plastic Response. Orange: consistent with dry bone breakage, blue: consistent with fresh bone breakage, grey: inconclusive.

Bone	#	OL	LR	A						T			PR	
				n (total)	n (assess-able)	n (fresh)	%	n (dry)	%	n (smooth)	%	n (jagged)		%
parietal left	1	stepped	yes	5	5	3	60,0	2	40,0	0	0,0	5	100	no
parietal left	2	straight/stepped	no	5	2	1	50,0	1	50,0	0	0,0	2	100	no
parietal left	3	curved	yes	5	5	2	40,0	3	60,0	4	80,0	1	20,0	no
parietal left	4	curved	yes	5	5	5	100	0	0,0	4	80,0	1	20,0	no
parietal left	5	curved	yes	5	3	1	33,3	2	66,7	0	0,0	3	100	no
parietal left	6	straight/stepped	yes	5	2	2	100	0	0,0	0	0,0	2	100	no
parietal left	7	straight	yes	5	0	-	-	-	-	-	-	-	-	no
parietal left	8	straight	yes	4	4	4	100	0	0,0	0	0,0	4	100	yes
occipital	9	curved	yes	3	2	2	100	0	0,0	1	50,0	1	50,0	no
occipital	10	stepped	yes	5	1	1	100	0	0,0	1	100	0	0,0	yes
occipital	11	curved	no	3	1	0	0,0	1	100	0	0,0	1	100	no
occipital	12	curved	no	5	5	3	60,0	2	40,0	2	40,0	3	60,0	no
parietal left	13	curved	yes	5	0	-	-	-	-	-	-	-	-	no
parietal left	14	straight/stepped	yes	3	1	1	100	0	0,0	0	0,0	1	100	no
occipital	15	straight	no	3	1	1	100	0	0,0	0	0,0	1	100	no

Table 3 provides the summary assessments of the timing of breakage for each of the 15 breakage lines that ground on the assessments of the single morphological features (see Tab. 2). The morphology of one breakage line (#4) is consistent with a fresh bone breakage, and those of three breakage lines (#3, #8 and #9) are indicative of possible fresh bone breakages. One breakage line (#2) exhibits morphological features indicative of a possible dry bone breakage. Most breakage lines (#1, #5, #6, #7, and #10-15) remain inconclusive regarding their timing of breakage (Fig. 6).

Three of the fresh or rather fresh-looking breakage lines (#3, #4, #8) are located on the left parietal. The other rather fresh breakage line (#9) is located on the left occipital bone, adjacent to the course of breakage line #4 on the left parietal (Fig. 3, 6).

Table 3. Summary assessment of the morphological features of Apidima 1 regarding the timing of breakage. Abbreviations: f: fresh, d: dry, f?: possibly fresh, d?: possibly dry, i: inconclusive, n.a.: not assessable.

#	Outline	Path of least Resistance	Angle	Texture	Plastic Response	Result	Comment
1	d	f	i	d	i	i	
2	d	d	i	d	i	d?	
3	f	f	i	f	i	f?	
4	f	f	f	f	i	f	
5	f	f	i	d	i	i	
6	d	f	f	d	i	i	
7	i	f	n.a.	n.a.	i	i	breakage not traceable in CT cross-sectional view
8	i	f	f	d	f	f?	
9	f	f	f	i	i	f?	
10	d	f	i	i	f	i	probably ossicle, no breakage
11	f	d	i	i	i	i	
12	f	d	i	i	i	i	
13	f	f	n.a.	n.a.	i	i	breakage not traceable in CT cross-sectional view
14	d	f	i	i	i	i	
15	i	d	i	i	i	i	

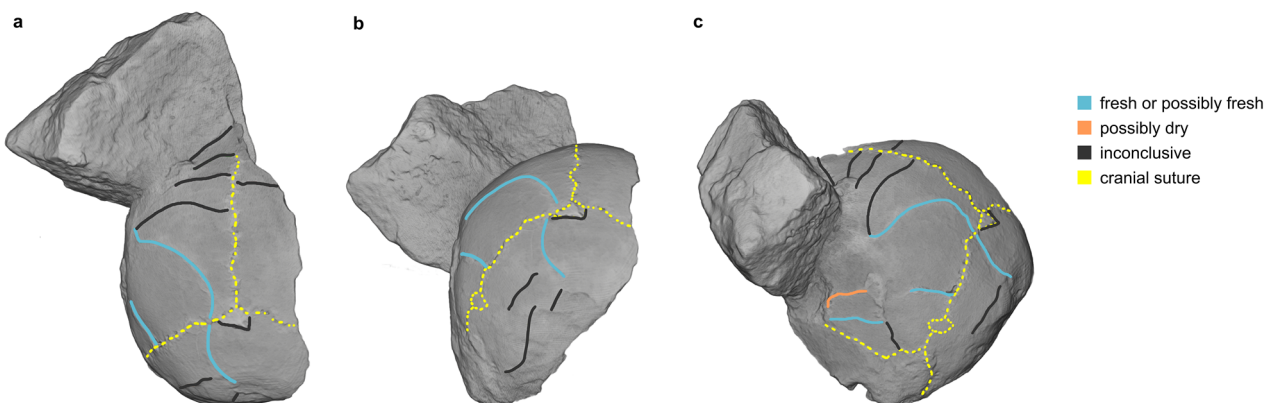


Fig. 6. Timing of breakage of the 15 breakages lines examined in Apidima 1. a: Superior view. b: Posterior view. c: Left superolateral view.

Apidima 2:

In Apidima 2 we examined 37 breakage lines (#1 to #37) as well as the edges of four defects. The defects are located on the frontal bone, as are most breakage lines (n=17; 46.0%). Eight breakage lines are located on the left parietal bone (21.6%), five on the right parietal bone (13.5%), and two on the left temporal bone (5.4%). Five breakage lines extend over two or three different cranial bones (13.5%).

Table 4 shows the results of the assessment of the five morphological features (breakage outline, path of least resistance, breakage angle, texture, and plastic response) for each breakage line and defect.

In 28 of the 37 breakage lines (75.7%), all five morphological features could be examined. For the remainder nine breakages (24.3%), it was possible to assess only three features because we could not identify the breakage lines in the CT cross-sections. The features outline and least resistance do not apply to defects. We could assess the three features angle, texture, and plastic response for defect #D2, but not for defects #D1, #D3 and #D4. In total, breakage angles and textures were possible to evaluate for 123 of the 165 examined breakage edges at defined points along breakage lines and defects in cross-sectional view (74.6%).

As in Apidima 1, the breakage lines of Apidima 2 also revealed a mix of fresh and dry bone breakage characteristics within single breakage lines (Tab. 4), and within the features breakage angle and texture (Fig. 7). Of the 123 assessable breakages edges, 77 (62.6%) correspond to the expected association of oblique angles and smooth edges as well as right angles and jagged edges (Fig. 6), which is a slightly larger portion than in Apidima 1 (43,2%).

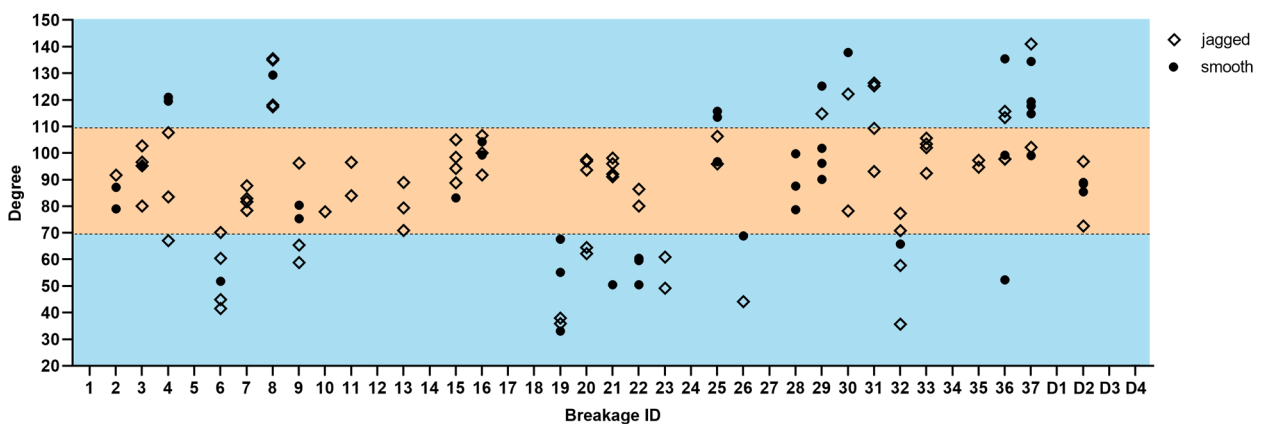


Fig. 7. Results for the features angle and texture for Apidima 2. For each breakage line and defect (x-axis) the breakage angles at the different points along one breakage line are shown (y-axis), as well as the respective texture at each of these sampling points (solid circle: smooth, open diamond: jagged).

Table 4. Results of the examination of the five morphological features per breakage line in Apidima 2. OL: Outline, LR: Least Resistance, A: Angle, T: Texture, PR: Plastic Response. Orange: consistent with dry bone breakage, blue: consistent with fresh bone breakage, grey: inconclusive. * in continuation (i.e. outside the course examined in this study).

Bone	#	OL	LR	A					T					PR		
				n (total)	n (assess-able)	n (fresh)	%	n (dry)	%	n (smooth)	%	n (jagged)	%			
frontal	1	straight	yes	5	0	-	-	-	-	-	-	-	-	-	-	no
frontal	2	straight	no	5	3	0	0,0	3	100	2	66,7	1	33,3	33,3	33,3	no
frontal	3	straight	no	5	5	0	0,0	5	100	1	20,0	4	80,0	80,0	80,0	no
frontal	4	straight	no	5	5	3	60,0	2	40,0	2	40,0	3	60,0	60,0	60,0	no
frontal	5	straight	no	-	-	-	-	-	-	-	-	-	-	-	-	no
frontal	6	straight	yes*	5	5	4	80,0	1	20,0	1	20,0	4	80,0	80,0	80,0	yes
frontal	7	straight	no	5	5	0	0,0	5	100	0	0,0	5	100	100	100	no
frontal	8	straight	no	5	5	5	100	0	0,0	1	20,0	4	80,0	80,0	80,0	no
frontal	9	curved	yes	5	5	2	40,0	3	60,0	2	40,0	3	60,0	60,0	60,0	no
frontal	10	straight	yes	2	1	0	0,0	1	100	0	0,0	1	100	100	100	no
frontal	11	straight	no	5	2	0	0,0	2	100	0	0,0	2	100	100	100	no
frontal	12	curved	yes	-	-	-	-	-	-	-	-	-	-	-	-	no
frontal	13	straight	no	3	3	0	0,0	3	100	0	0,0	3	100	100	100	no
frontal	14	stepped	no	-	-	-	-	-	-	-	-	-	-	-	-	no
frontal	15	straight	yes	5	5	0	0,0	5	100	1	20,0	4	80,0	80,0	80,0	no
parietal left	16	curved	yes	5	5	0	0,0	5	100	2	40,0	3	60,0	60,0	60,0	no
frontal, parietal left	17	straight	yes	5	0	-	-	-	-	-	-	-	-	-	-	no
frontal	18	stepped	no	-	-	-	-	-	-	-	-	-	-	-	-	no
frontal, parietal left + right	19	curved	yes	5	5	5	100	0	0,0	3	60,0	2	40,0	40,0	40,0	no
parietal left	20	straight	yes	5	5	2	40,0	3	60,0	0	0,0	5	100	100	100	no
parietal right	21	curved	yes	5	5	1	20,0	4	80,0	1	20,0	4	80,0	80,0	80,0	yes

Table 5 provides the summary assessments of the timing of breakage for each of the 37 breakage lines and four defects that build upon the single features' assessments (see Tab. 4). The morphology of one breakage line (#37) is consistent with a fresh bone breakage. Four breakage lines (#6, #19, #23, #29) are indicative of possible fresh bone breakages. The morphology of five breakage lines (#3, #7, #11, #13, #33) is indicative of possible dry bone breakages. Most breakage lines (n=27) are inconclusive in their morphology regarding the timing of breakage (#1, #2, #4, #5, #8-10, #12, #14-18, #20-22, #24-28, #30-32, #34-36; Fig. 8).

The breakage lines with a fresh or rather fresh-looking morphology are extending over the frontal, left and right parietal and left temporal bones. Four of the rather dry-looking bone breakages are located on the frontal bone, and one on the right parietal bone (Fig. 4, 8).

The morphology of one defect (#D2) was inconclusive regarding its timing of breakage. Two defects (#D3, #D4) were found to be only superficial ectocranial damages covered with plaster and no actual breakages, which is why we could not assess any of the morphological features and thus classified them as inconclusive. The same accounts for defect #D1, which could not be assessed either, because it is located on the pneumatic bone of the frontal sinus and therefore does not exhibit an inner and outer table and diploë.

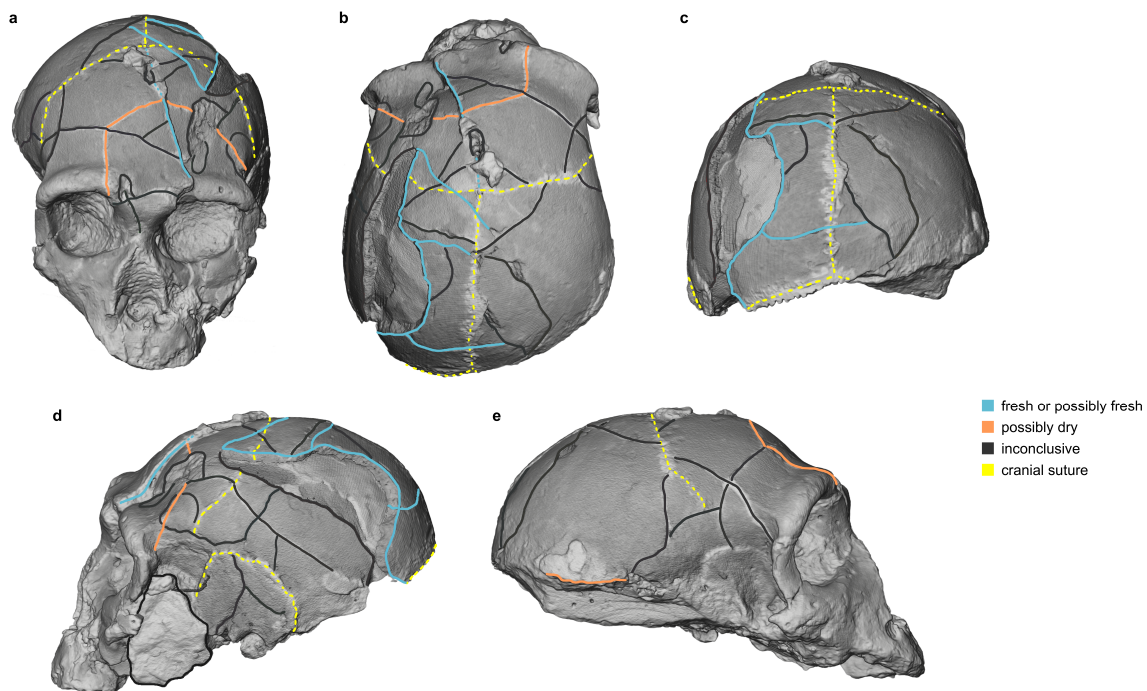


Fig. 8. Timing of breakage of the 37 breakages lines and four defects examined in Apidima 2. a. Frontal view. b: Superior view. c: Posterior view. d: Left lateral view. e. Right lateral view.

Table 5. Summary assessment of the morphological features of Apidima 2 regarding the timing of breakage. f: fresh, d: dry, f?: possibly fresh, d?: possibly dry, i: inconclusive, n.a.: not assessable, n/a: not applicable.

#	Outline	Path of least Resistance	Angle	Texture	Plastic Response	Result	Comment
1	i	f	n.a.	n.a.	i	i	breakage not traceable in CT cross-sectional view
2	i	d	d	i	i	i	
3	i	d	d	d	i	d?	
4	i	d	i	i	i	i	
5	i	d	n.a.	n.a.	n.a.	i	breakage not traceable in CT cross-sectional view
6	i	f	f	d	f	f?	
7	i	d	d	d	i	d?	
8	i	d	f	d	i	i	
9	f	f	i	i	i	i	
10	i	f	i	i	i	i	
11	i	d	d	d	i	d?	
12	f	f	n.a.	n.a.	i	i	breakage not traceable in CT cross-sectional view
13	i	d	d	d	i	d?	
14	d	d	n.a.	n.a.	i	i	breakage not traceable in CT cross-sectional view
15	i	f	d	d	i	i	
16	f	f	d	i	i	i	
17	i	f	n.a.	n.a.	i	i	breakage not traceable in CT cross-sectional view
18	d	d	n.a.	n.a.	i	i	breakage not traceable in CT cross-sectional view
19	f	f	f	i	i	f?	
20	i	f	i	d	i	i	
21	f	f	d	d	f	i	
22	f	f	i	i	i	i	
23	f	f	f	d	i	f?	
24	i	f	n.a.	n.a.	i	i	breakage not traceable in CT cross-sectional view
25	d	f	i	i	i	i	
26	d	f	f	i	i	i	
27	d	f	n.a.	n.a.	i	i	breakage not traceable in CT cross-sectional view
28	d	f	d	f	i	i	
29	f	f	i	f	i	f?	
30	f	f	i	i	i	i	
31	f	f	i	d	i	i	
32	i	f	i	d	i	i	
33	f	d	d	d	i	d?	
34	f	d	n.a.	n.a.	i	i	breakage not traceable in CT cross-sectional view
35	f	f	d	d	i	i	
36	f	f	i	i	i	i	
37	f	f	f	f	i	f	
D1	n/a	n/a	n.a.	n.a.	n.a.	i	not measurable, pneumatic bone, no inner & outer tables
D2	n/a	n/a	d	i	f	i	
D3	n/a	n/a	n.a.	n.a.	n.a.	i	superficial damage filled with plaster
D4	n/a	n/a	n.a.	n.a.	n.a.	i	superficial damage filled with plaster

4. Discussion

In this study, we analyzed fracture patterns of the fossil crania Apidima 1 and 2 aiming at differentiating between perimortem (fresh) and postmortem (dry) bone breakages using virtual CT scan data. We did so by examining five morphological fracture features (breakage outline, path of least resistance, breakage angle, texture, and plastic response). In Apidima 1, the combined evidence of the five morphological features suggests that 66.7% (10/15) of the examined cranial fractures are inconclusive with regard to the timing of fracture, 26.7% (4/15) are compliant or rather compliant with a fracture morphology found in fresh bone fractures and 6.7% (1/15) are rather compliant with a dry bone fracture morphology. In Apidima 2, we found a portion of 73.0% (27/37) fractures plus four defects exhibiting inconclusive fracture morphologies, 13.5 % (5/37) fractures with a morphology compliant or rather compliant with fresh bone fracture, and 13.5 % (5/37) fractures which are rather compliant with the morphology of dry bone fractures.

Previous research interpreted cranial fractures on the frontal bone of Apidima 2 to be the result of traumatic blows with an object such as a stone with a blunt point (Coutselinis et al., 1991, 1995). The fractures that were suggested to result from blunt force trauma (traumatisme B and D in Coutselinis et al., 1991, and fractures 2 and 4 in Coutselinis et al., 1995, respectively) correspond to defects #D1 and #D2 in our study. Later, this interpretation was revised, and the two fractures (and all other fracture lines of Apidima 2) were instead attributed to taphonomic damages from sediment pressure during deposition (Geanacos, 2001; Pitsios, 2007; Pitsios et al., 2007). Our reassessment remains inconclusive regarding the timing of breakage for both #D1 and #D2. Because of its location on the frontal sinus, we could not assess any of the morphological features of #D1. In contrast, #D2 was possible to evaluate, but showed both fresh, dry, and inconclusive bone fracture characteristics. Hence, our reassessment of those two cranial damages cannot clarify either the timing of breakage or the interpretation of the fractures as postmortem damage that happened during deposition (Geanacos, 2001; Pitsios, 2007; Pitsios et al., 2007).

We followed a rather conservative approach by investigating each cranial fracture line individually and separating fracture lines at crossings with other fracture lines or cranial sutures. It is possible that in some cases we thereby separated lines that should be considered jointly because they actually represent the same fracture. In Apidima 1, this might apply to the following adjacent fractures: a) #4 and #8; and b) #6 and #14. We would expect corresponding morphological characteristics in the adjacent fractures lines if they indeed represented a single fracture. The two adjacent fractures #4 and #8 exhibit a fresh and a possible fresh fracture morphology. Fractures #6 and #14 are both inconclusive. Considering the adjacent fracture lines jointly, the combined fracture line #4/8, therefore, is consistent with fresh bone breakage, and the combined fracture line #6/14 is inconclusive.

In Apidima 2, the following fractures may belong together: a) #11 and #13; b) #15 and #16; c) #19 and #22; d) #4, #8 and #30; and e) #6, #10 and defect #D2. fractures 11 and 13 both exhibit a morphology of possible dry bone fractures, and the same result is obtained when assessed jointly (#11/13). The combined fracture #15/16 remains inconclusive regarding its timing of breakage, equaling the results of the two single fractures #15 and #16. The same accounts for the morphology of the combined fracture #4/8/30 that yields an inconclusive breakage morphology, as do its separate

fracture lines. Fracture #6 exhibits a possibly fresh breakage morphology when examined individually, while fractures #10 and #D2 remain inconclusive. The joint assessment of the combined fractures #6/10/D2 gives an inconclusive result.

The matching breakage morphologies between the adjacent fracture lines indicates that the subdivision of fracture lines into smaller sections, as employed in this study, does not bias the overall assessment of fracture morphology regarding the timing of fracture.

The five different features characterizing each fracture line provided heterogeneous results regarding the timing of breakage, as did the three features characterizing defect D2. This mix of fresh and dry bone breakage morphologies within one fracture line or defect resulted in a large quantity of inconclusive findings, and contrasts with the expectation that fractures should exhibit either a predominantly fresh or a predominantly dry bone breakage morphology (possibly combined with some features showing an inconclusive morphology) across all investigated features. This deviation could be due to the kind of morphological features used in this study. It is possible that our selected features were too few or too unspecific to adequately capture and differentiate fresh and dry bone breakage morphologies. For example, features such as flaking, hinging or cortical delamination have been suggested to be particularly suitable for identifying fresh bone breakage (Fleming-Farrell et al., 2013; Jordana et al., 2013a). However, the resolution of the available medical CT scans did not allow their evaluation in the present study. For isolated bones, Jordana et al. (2013a) suggested cortical delamination >10.5 mm as the only stand-alone criterion to indicate fresh bone breakage. By contrast, other features (breakage angle, cortical delamination, roughness and breakage outline) were found to work effectively in combination with each other in skeletal series (Jordana et al., 2013a). Though the Apidima crania are isolated, the inclusion of additional features not considered here would likely improve the differentiation between fresh and dry bone fractures. They should therefore be addressed in the future, for example by using high-resolution micro-CT scans (Fleming-Farrell et al., 2013; Sala et al., 2016), to complement our findings.

Other explanations for the mix of fresh and dry bone characteristics within fracture lines (i.e., between features), but also between the features angle and texture (i.e., between the different measurements/assessments) could relate to the depositional context of the Apidima crania, and their fossilized condition. Bones deposited in aquatic environments are problematic for the assessment of fresh vs. dry bone breakage because water-logged microenvironments change decomposition rates and may artificially prolong the perimortem interval (Haglund and Sorg, 2002; Galloway et al., 2014; Augias et al., 2017; Stuart and Ueland, 2017). In addition, rehydrated dry bone can retrieve breakage behavior mimicking fresh breakages (Broz et al., 1993; Moraitis and Spiliopoulou, 2006; King, 2017). Ultimately, the high levels of abrasion due to sediment movement in water environments are more likely to round off diagnostic breakage edges (Haglund and Sorg, 2002; Moraitis and Spiliopoulou, 2006), which further complicates their identification. The Apidima crania were possibly affected by wet conditions during some periods of their depositional history. The two crania were found next to each other in a brecciated block between the cave walls, yet U-series dating produced dates that are about 40 ka BP apart (210 ka BP for Apidima 1 and 170 ka BP for Apidima 2). Harvati et al., 2019 suggested that the mixing of crania could have happened by down-movement

of materials from the top of the talus cone, where the crania had originally been deposited independently from each other at two distinct times. In such a scenario, after infiltrating water had washed out sediments from the limestone cliffs and thereby opened spaces, the crania were dislocated downwards and deposited next to each other in one of these opened spaces, for example by a mudflow event. At around 150 ka BP the sediments consolidated and solidified them in their final position (Harvati et al., 2019). Moreover, sea level changes contributed to the formation of the Apidima caves during Pleistocene-times (see Harvati et al. (2011) for a detailed discussion of site formation), and post-Pleistocene sea level highstands are successively eroding the brecciated Pleistocene terrestrial sediments in Cave A (Pitsios, 1999; Harvati et al., 2011; Bräuer et al., 2019). It is currently impossible to evaluate to what extent water-logged conditions could affect the sediments that enclosed the Apidima fossils and which effect this could have had on the cranial bones and their depositional history. Future geoarchaeological assessment at the site might help clarify this point.

Another issue regarding the timing of breakage relates to the possibility that breakage occurred after fossilization. The breakage behavior of fossil bone is likely very distinct from the breakage behavior of both fresh and dry bone because the original bone tissue has been replaced by minerals with inherently different mechanical properties (Morlan, 1984; Gifford-Gonzalez, 2018). Fossils are therefore expected to behave like a uniform stiff material such as rock when impacted, and resulting damages are assumed to be localized and restricted to the point of impact (Brain, 1972; L'Abbé et al., 2015). The breakage dynamics and the breakage morphology of fossilized cranial bone has, to our knowledge, not been studied so far – which is not surprising, considering that precious fossils would have to be damaged or destroyed to do so. Future taphonomic and experimental studies may assist in the clarification of these issues.

Previous research has shown that the combination of taphonomic and forensic criteria can be an effective tool to reconstruct past hominin behaviors (Sala et al., 2015; Sala et al., 2016; Sanz et al., 2018). Here, we reassessed and for the first time systematically investigated the cranial breakage patterns of the Apidima fossil crania using virtual CT scan data. Our study demonstrates the hurdles of applying forensic techniques to fossils, especially when the depositional context of the remains is complex. While most fractures therefore remained inconclusive regarding the timing of breakage, our investigation revealed few fracture lines with morphological features rather consistent with fresh bone breakage that should be further investigated in the future, for example using high-resolution CT scans and microscopy. This might help to evaluate geological, biological or anthropogenic causes of the (possible) perimortem fractures, such as natural deposition, dislocation, scavenging, as well as traumatic injury, (secondary) burial, or postmortem processing of the remains, thought to be part of the behavioral repertoire of Pleistocene humans (e.g. Buisson and Gambier, 1991; Le Mort and Gambier, 1992; Defleur et al., 1999; Orschiedt, 1999; Rosas et al., 2006; Bello et al., 2011; Saladié et al., 2012; Bello et al., 2015; Sala et al., 2015; Sala et al., 2016; Sala and Conard, 2016; Orschiedt et al., 2017; Kranioti et al., 2019).

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