Journal of Archaeological Science: Reports 71 (2026) 105692

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

The influence of fragmentation on a combined ZooMS and zooarchaeological study at Geißenklösterle Cave in the Swabian Jura, Southwestern Germany

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ARTICLE INFO

Keywords:
ZooMS
Palaeoproteomics
Palaeolithic
Hominin evolution
Archaeology
Zooarchaeology
Bioarchaeology

ABSTRACT

Geißenklösterle Cave, a Palaeolithic site located in the Swabian Jura of southern Germany, has yielded multiple Middle Palaeolithic strata and some of the earliest evidence for the Aurignacian and Gravettian in Europe. Rich assemblages of three-dimensional figurines, personal ornaments, and musical instruments position Geißenklösterle Cave, and the complex of caves in the region, as significant in our understanding of the Palaeolithic in Europe. Extensive osseous assemblages preserved through the Palaeolithic layers of the site have allowed for thorough zooarchaeological research, aimed at reconstructing site use and human behavior. Drawing from this established research, we applied ZooMS (Zooarchaeology by Mass Spectrometry) to 988 morphologically non-identifiable bone fragments from Geißenklösterle Cave to develop strategies for the integration of non-diagnostic material into the previously established datasets. Our results indicate excellent preservation conditions for collagen, with a 98.4% success rate for ZooMS. The inclusion of taphonomic analyses in our study suggests predators played a significantly bigger role in bone fragmentation at the site than previously assumed, with 31% of bones included in this study exhibiting some kind of carnivore damage. Rare instances of anthropogenic modifications on bones were also identified, including the earliest instance of a cut-mark on a woolly rhinoceros (*Coelodonta antiquitatis*) bone in the Swabian Jura. Finally, we demonstrate the potential biases introduced through sampling strategies regarding the size of bone fragments analyzed in our study. Our results provide valuable insights for the discourse on both Palaeolithic archaeology as well as the best-practice integration of ZooMS into the zooarchaeological workflow.

1. Introduction

Understanding how our Palaeolithic ancestors navigated through and interacted with their respective environments necessarily relies on the study of an incomplete archaeological record. Osseous assemblages, which are crucial in unraveling the means by which hominins accumulated, processed, managed, and consumed their food (Outram, 2001; Peters et al., 2022; Sinet-Mathiot et al., 2019; Stiner, 1994) are often subject to fragmentation and loss of diagnostic landmarks, meaning macroscopic taxonomic identification is frequently not possible (Morin et al., 2017). Although the search for patterns within fragmented assemblages and attempts to determine the underlying causes for fragmentation can lead to important insights in its own right, the addition of taxonomic identification to these fragmented bones can aid in a more complete picture of hominin subsistence strategies (Buckley et al., 2014; Sinet-Mathiot et al., 2019).

Geißenklösterle Cave is a Palaeolithic site located in the Swabian Jura of southwestern Germany (Fig. 1). The site is part of a series of caves containing Palaeolithic material within the Ach Valley and the neighboring Lone Valley. Following Wagner's test excavation in 1973,

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https://doi.org/10.1016/j.jasrep.2026.105692
Received 7 July 2025; Received in revised form 2 February 2026; Accepted 4 March 2026
Available online 16 March 2026

Hahn (1988) led a major phase of excavations between 1974 and 1991 that documented the rich Upper Palaeolithic sequence and the upper portion of the Middle Palaeolithic strata. Conard headed excavations from the base of the Aurignacian down to bedrock in 2001 and 2002, thereby extending the sequence to an age of ca. 95 ka (Goldberg et al., 2019; Richard et al., 2019).

The site spans the Middle and Upper Palaeolithic with some of the earliest dates for the Aurignacian and Gravettian technocomplexes (Higham et al., 2012; Richard et al., 2019). Organic preservation at the site is good and a highly sophisticated array of cultural objects have been discovered there (Conard, 2011, 2010; Hahn, 1988). The rate of morphologically identifiable bone at Geißenklösterle Cave is high at around 50%, but bone fragments excavated from the site are still frequently small and lack diagnostic features (Münzel, 2019). Extensive zooarchaeological analysis has been conducted on the morphologically identifiable bones of the macrofauna (Münzel, 2019) as well as the micro- (Böhme, 2019; Rhodes et al., 2018; Ziegler, 2019) and avifauna (Krönneck, 2019). While zooarchaeological analysis has been very successful in contextualising hominin behaviour, osseous fragmentation at Geißenklösterle Cave presents an opportunity for biomolecular analysis. The necessity of overcoming the issues of fragmentation is further compounded by the low density of finds in the Middle Palaeolithic (MP, 94–55 ka BP) in comparison with the Upper Palaeolithic (UP) layers (Aurignacian beginning ca. 42.5 ka BP and the Gravettian potentially beginning as early as ca. 37 ka BP; Goldberg et al., 2019; Higham et al., 2012 Richard et al., 2019). Bone fragmentation, driven by hominins, non-human predators, and environmental pressures like weathering, also appears to have removed rare taxa from the zooarchaeological record, potentially obscuring subsistence strategies that are key to understanding hominin lifeways (Münzel, 2019). The long history of research at Geißenklösterle Cave therefore provides ample footing for the integration of the non-diagnostic fragments into the established zooarchaeological record.

Peptide mass fingerprinting or Zooarchaeology by Mass Spectrometry (ZooMS) is an efficient biomolecular technique that allows for taxonomic identification of morphologically unidentifiable bones (Buckley et al., 2009; Richter et al., 2022). ZooMS takes advantage of small differences in the amino-acid sequences of type I collagen (COL1) between species, making it possible to differentiate between taxa (Buckley et al., 2009). The application of ZooMS to assemblages of non-diagnostic bone fragments from several Palaeolithic sites has led to new insights into diet, subsistence strategies, and the detection of rare hominin remains (Brown et al., 2022, 2021b, 2016; Martisius et al., 2020; Pothier Bouchard et al., 2020; Sinet-Mathiot et al., 2019, 2023; Welker et al., 2016; Xia et al., 2024). These studies have demonstrated that in combination with taphonomic analyses, ZooMS may be able to provide a more complete understanding of the osseous assemblages within sites. However, optimal approaches to sample selection and pathways to integrate these results into the zooarchaeological record present important ongoing challenges.

ZooMS was applied to unidentified fragments from the MP, Aurignacian, and Gravettian horizons at Geißenklösterle Cave. Additionally, each of these fragments underwent a taphonomic analysis, which mirrored the work carried out in previous zooarchaeological research for the site. Comparison to the morphologically identified material focused on diagnostic bones; other osseous materials like teeth, ivory, and antler were excluded. The aims of this study were to (1) understand the comparative species distribution between the highly fragmented and morphologically identifiable components of the osseous assemblage at Geißenklösterle Cave and (2) find novel means of integrating ZooMS-data into the zooarchaeological record. Through this research we also propose best-practices for fragment size inclusion and taphonomic

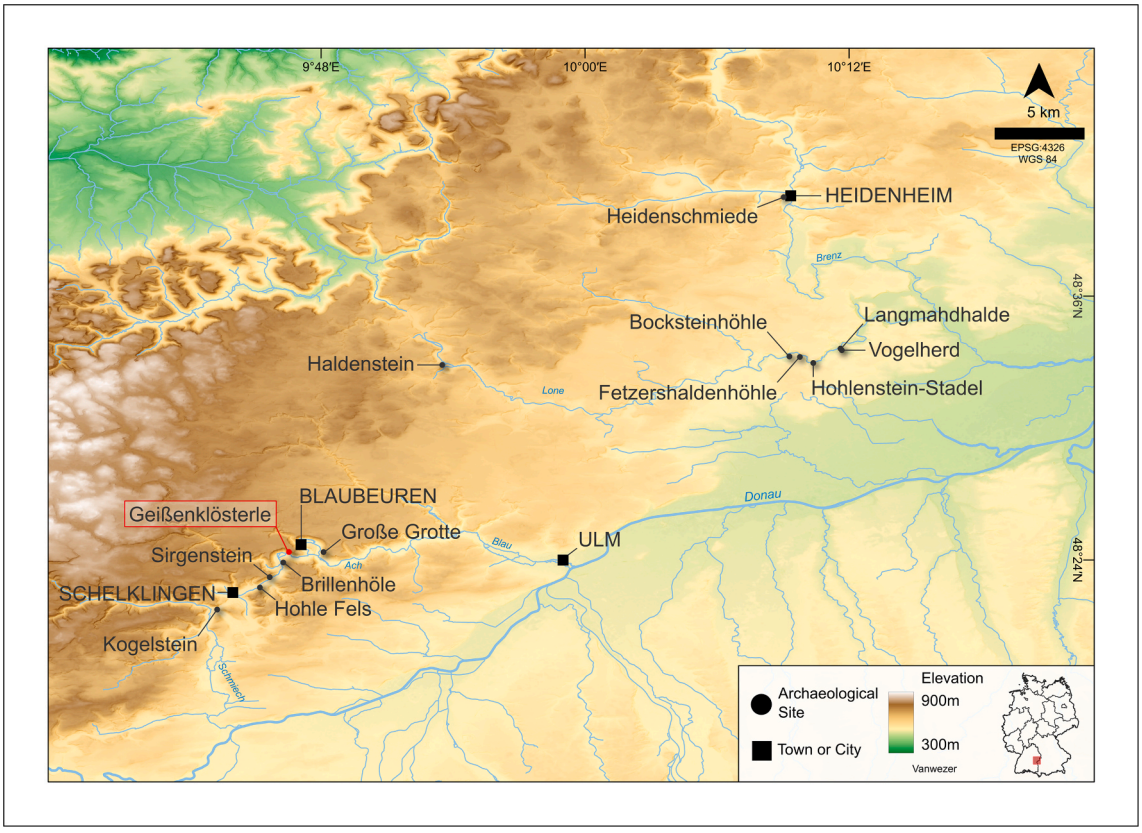

Fig. 1. Location of Geißenklösterle Cave in the Swabian Jura. Geißenklösterle Cave is situated in the Ach Valley of the Swabian Jura alongside notable sites Brillenhöhle, Hohle Fels, and Sirgenstein. The Lone Valley is shown to the north-east where Vogelherd, Hohlenstein-Stadel, and Langmahdhalde are located. Map by Nils Vanwezer.

recording for fragmented assemblages analyzed using ZooMS.

2. Material

988 mainly long and flat bone fragments with intact cortical surfaces were sampled from the three main cultural horizons at Geißenklösterle: the MP (n = 336), Aurignacian (n = 343), and Gravettian (n = 309). Cancellous bone was largely avoided as it tends to exhibit a decrease in biomolecular preservation due to lower bone density (Buckley et al., 2014). While in most comparable studies bone fragments under 2 cm are preferably avoided (see for instance Brown et al., 2021b; Pothier Bouchard et al., 2020; Sinet-Mathiot et al., 2019), in this study we explicitly included those fragments in the hopes of capturing small mammals, like hares, foxes, and mustelids which are known to the site. Further, we aimed to determine if a 2 cm threshold may bias the results towards medium and large mammals. Fragments of less than 1 cm were not included as ZooMS reference libraries for micromammals and birds are not established to a degree that would allow for confident identifications. We selected bones from two assemblages excavated from the site, those bones which were large enough for piece plotting during excavation (n = 279) and those typically smaller than 3 cm which formed part of the hand-picked or screened finds (n = 709). These two assemblages were combined and we established three distinct fragment size classes (SC) for inclusion in our study: bones with a maximum length of 1–2 cm (SC1; n = 376); 2–3 cm (SC2; n = 309), and greater than 3 cm (SC3; n = 303. A summary of samples included in the study can be found in Table 1.

3. Methods

Each bone fragment was weighed and analyzed taphonomically, mirroring previous zooarchaeological analysis conducted at the site (Münzel, 2019, supplementary information), including an analysis of anthropogenic and carnivore damage. ZooMS analysis was carried out following an established acid-insoluble protocol (Brown et al., 2020; Buckley et al., 2009). Analysis of the results was carried out using our in-house protocol for mammal identifications (following the baseline, smoothing, and signal-to-noise thresholds recorded in Brown, 2021 via mMass (version 6.0.2 – Niedermeyer and Strohalm, 2012; Strohalm et al., 2008)). The comparative reference library was compiled from previously published literature (Buckley et al., 2017, 2016, 2011, 2009; Buckley and Kansa, 2011; Janzen et al., 2021; Jensen et al., 2020; Prendergast et al., 2017; Welker et al., 2016) using established nomenclature (Brown et al., 2021a) and based on known species at the site and within the region (Münzel, 2019). A list showing all the ZooMS-taxa present at Geißenklösterle Cave, and the most specific category these taxa can be assigned to, can be found in Table 2. Given the homogeneity of COL1 and ZooMS identifications most taxa fall into broad genus or family categories like Canidae or Cervidae. Some species-specific exceptions are possible, however, including *Vulpes vulpes* and *Capreolous capreolous* which can be distinguished beyond their family groups Table 2).

To better understand the inherent biases in sample selection for ZooMS analysis, we investigated the correlation between maximum fragment size length and identified taxa. Once samples were taxonomically identified, the ZooMS-taxa were grouped into size-classes. The ZooMS-taxa of Canidae, Cervidae and Crocuta/Panthera were excluded here, since they are comprised of species of considerable size differences (see Table 2). Statistical analysis was carried out using R (4.1.1) and the package dyplr (1.1.4; Wickham et al., 2025; Supplementary Data 2). The analysis was conducted by performing a linear model with the size classes as factorial predictors. The assumptions necessary for applying a linear model – normality, variance homogeneity and absence of influential outliers within the raw data – were visually confirmed via residual analysis. Using fragment length resulted in deviance from normality, which was eliminated by log-transforming the data. Pairwise differences between size classes were assessed with Tukey-HSD post hoc tests that correct for multiple testing.

Finally, in order to provide a more informative means through which our ZooMS data could be incorporated into the zooarchaeological record for Geißenklösterle Cave, we explored bone weight (Uerpmann, 1973) as a means to circumvent issues with NISP-based analyses. Bone weight represents a less derivative measurement than NISP because it is not affected by rates of fragmentation. Our hypothesis was that one could add the ZooMS-derived bone weight to the values established from morphological analyses and enhance the general understanding of how strong the different taxa are represented at a site according to their biomass (Münzel, 2019).

Table 1
Sample sizes for the different cultural horizons included in the ZooMS assemblage. Indexed numerals denote size classes SC1 (1), SC2 (2), and SC3 (3).

Size classes	SC1	SC2	SC3	Total (n)
Gravettian	139	112	58	**309**
Aurignacian	119	115	109	**343**
Middle Paleolithic	118	82	136	**336**
Total	**376**	**309**	**303**	**988**

4. Results

4.1. ZooMS

Of the 988 analyzed bone fragments, we were able to identify 972 successfully to ZooMS-taxon, which translates to a success rate of 98.4% (Table 3). Six specimens could only be identified to a broader taxonomic group (0.6%), while 10 specimens failed to produce sufficient collagen for identification (1.0%). A further six specimens were identified as Aves (Buckley et al., 2009). 13 ZooMS-taxa were identified for this study (Table 3; supplementary information). Failed and imprecisely identified samples, i.e., those samples which could not be identified to their most specific ZooMS category as described in Table 2, as well as the six specimens identified as 'Aves', were omitted from the more detailed presentation of the results to facilitate comparability with the morphologically identifiable fauna at Geißenklösterle. To aid in this comparison, the morphological data for bones previously reported (Münzel, 2019) were also converted according to their most specific ZooMS-taxon. A summary of the results per cultural horizon can be found in the supplementary information and Table 4.

4.2. Overall species composition

The species composition of the ZooMS- and morphological components largely agree with one another, with the exception of *C. capreolus* (roe deer) and Mustelidae (including *Mustela erminea, M. putorius*, and *Gulo gulo*), which have been identified previously at the site but were absent from the ZooMS identified assemblage (compare Tables 3 and 4). For all studied contexts, the ZooMS identified bones are dominated by Ursidae, which mirrors the composition of the diagnostic bones. The most notable difference between the ZooMS identified fragments and the morphologically identifiable bones are visible in the bones originating from the MP. Our ZooMS analysis identified several *Bos/Bison* (n = 12, including *Bos primigenius* and *Bison priscus*), Elephantidae (n = 12, in this case *Mammuthus primigenius*), and Rhinocerotidae (n = 23, *Coelodonta antiquitatis*) bones, none of which had previously been identified within the diagnostic bones for the MP of Geißenklösterle, although they had previously been identified within the teeth assemblage which had been morphologically identified at the site. The identification of *Bos/Bison* remains has been exceedingly rare for all contexts at the site, with only a single third phalanx having been previously identified within the lower Aurignacian horizon (Münzel, 2019). The 12 fragments identified in this study as *Bos/Bison* thus represent the first detection of those taxa

Table 2
List of all relevant ZooMS-taxa and their constituents for Geißenklösterle Cave (derived from data published by Münzel, 2019).

ZooMS taxon	Family	Genus	Species	Common Name
Bos/Bison	Bovidae	*Bos*	*B. primigenius*	Aurochs
	Bovidae	*Bison*	*B. priscus*	Steppe bison
Canidae	Canidae	*Canis*	*C. lupus*	Wolf
	Canidae	*Vulpes*	*V. lagopus*	Arctic fox
Capra	Bovidae	*Capra*	*C. ibex*	Ibex
C. Capreolus	Cervidae	*Capreolus*	*C. capreolus*	Roe deer
Cervidae	Cervidae	*Cervus*	*C. elaphus*	Red deer
	Cervidae	*Megaloceros*	*M. giganteus*	Irish elk
Crocuta/Panthera	Felidae	*Panthera*	*P. leo spelaea*	Cave lion
	Hyaenidae	*Crocuta*	*C. crocuta spelaea*	Cave hyena
Elephantidae	Elephantidae	*Mammuthus*	*M. primigenius*	Woolly mammoth
Equidae	Equidae	*Equus*	*E. ferus*	Wild horse
Felidae	Felidae	*Lynx*	*L. lynx*	European Lynx
Homo	Hominidae	*Homo*	*H. sapiens*	AMH
	Hominidae	*Homo*	*H. neanderthalensis*	Neanderthal
Leporidae	Leporidae	*Lepus*	*L. europaeus*	European hare
	Leporidae	*Lepus*	*L. timidus*	Mountain hare
Mustelidae	Mustelidae	*Mustela*	*M. erminea*	Stoat
	Mustelidae	*Mustela*	*M. putorius*	European polecat
	Mustelidae	*Gulo*	*G. gulo*	Wolverine
Rangifer	Cervidae	*Rangifer*	*R. tarandus*	Reindeer
Rhinocerotidae	Rhinocerotidae	*Coelodonta*	*C. antiquitatis*	Woolly rhinoceros
Rupicapra	Bovidae	*Rupicapra*	*R. rupicapra*	Chamois
Ursidae	Ursidae	*Ursus*	*U. spelaeus/ingressus*	Cave bear
	Ursidae	*Ursus*	*U. arctos*	Brown bear
V. vulpes	Canidae	*Vulpes*	*V. vulpes*	Red fox

Table 3
The results for the 988 analyzed samples. Failed here includes both samples without an ID and those with an imprecise ID.

ZooMS-Taxon	Middle Palaeolithic		Aurignacian		Gravettian		Total	
	NISP (%)	**Weight (%)**	**NISP (%)**	**Weight (%)**	**NISP (%)**	**Weight (%)**	**NISP**	**Weight**
Aves	3 (0.9%)	0.69 g (0.1%)	1 (0.5%)	0.10 g (0.0%)	2 (0.7%)	0.45 g (0.2%)	**6 (0.6%)**	**1.24 g (0.1%)**
Bos/Bison	12 (3.6%)	15.97 g (2.8%)	4 (1.2%)	4.46 g (0.8%)	–	–	**16 (1.6%)**	**20.43 g (1.4%)**
Canidae	4 (1.2%)	2.39 g (0.4%)	–	–	4 (1.3%)	4.13 g (1.5%)	**8 (0.8%)**	**6.52 g (0.4%)**
Capra	48 (14.3%)	48.41 g (8.48%)	17 (5.0%)	17.13 g (2.9%)	17 (5.5%)	12.61 g (4.5%)	**82 (8.3%)**	**78.15 g (5.4%)**
Cervidae	7 (2.1%)	33.62 g (5.9%)	3 (0.9%)	8.40 g (1.4%)	6 (1.9%)	2.51 g (0.9%)	**16 (1.6%)**	**44.53 g (3.1%)**
Crocuta/Panthera	5 (1.5%)	20.96 g (3.7%)	–	–	–	–	**5 (0.5%)**	**20.96 g (1.4%)**
Elephantidae	12 (3.6%)	38.49 g (6.7%)	26 (7.6%)	70.80 g (11.9%)	21 (6.8%)	44.76 g (16.1%)	**59 (6.0%)**	**154.05 g (10.6%)**
Equidae	23 (6.9%)	55.98 g (9.8%)	37 (10.8%)	84.55 g (14.2%)	20 (6.5%)	17.44 g (6.3%)	**80 (8.1%)**	**157.97 g (10.9%)**
Leporidae	4 (1.2%)	0.98 g (0.2%)	6 (1.8%)	1.37 g (0.2%)	22 (7.1%)	5.86 g (2.1%)	**32 (3.2%)**	**8.21 g (0.6%)**
R. tarandus	36 (10.7%)	33.87 g (5.9%)	29 (8.5%)	51.92 g (8.7%)	21 (6.8%)	19.02 g (6.8%)	**86 (8.7%)**	**104.81 g (7.2%)**
Rhinocerotidae	23 (6.9%)	52.21 g (9.1%)	12 (3.5%)	41.84 g (7.0%)	–	–	**35 (3.5%)**	**94.05 g (6.5%)**
R. rupicapra	1 (0.3%)	0.28 g (0.1%)	–	–	–	–	**1 (0.1%)**	**0.28 g (0.0%)**
Ursidae	152 (45.2%)	251.72 g (44.1%)	201 (58.6%)	309.09 g (51.8%)	189 (61.2%)	154.45 g (55.6%)	**542 (54.9%)**	**715.26 g (49.3%)**
V. vulpes	1 (0.3%)	0.10 g (0.0%)	2 (0.6%)	0.92 g (0.2%)	1 (0.3%)	0.27 g (0.1%)	**4 (0.4%)**	**1.29 g (0.1%)**
Failed	5 (1.5%)	15.46 g (2.7%)	5 (1.5%)	10.86 g (1.8%)	6 (1.9%)	16.53 g (6.0%)	**16 (1.6%)**	**42.85 (3.0%)**
Total	**336**	**571.13 g**	**343**	**601.44 g**	**309**	**278.03 g**	**988**	**1450.60 g**

within the MP at the site.

4.3. Fragment size and weight

Comparing NISP and bone weight across all studied layers, we observe a similar pattern in both our ZooMS data and the previously published zooarchaeological data for the diagnostic bone assemblage. Bone fragments identified as belonging to a taxon with a larger body size represent a high percentage of the overall assemblage using bone weight, but frequently have a lower relative NISP count. For large mammals, Rhinocerotidae are represented by 35 bone fragments (3.5% of the assemblage by NISP), weighing a total of 94.05 g (6.5% of the assemblage by weight) and Elephantidae are represented by 59 bone fragments (6.0%), weighing a total of 154.05 g (10.6%).

As summarized in Table 5, the average fragment weight tracks body size relatively well. Thus, fragments of woolly rhino and woolly mammoth bone in the mean are heavier than those of medium to large mammals, like *Bos/Bison*, Equidae and *Rangifer tarandus*. An exception is presented by Cervidae (*C. elaphus*, *M. giganteus*), whose fragments were among the heaviest. Very few predators were identified within the ZooMS assemblage but interestingly, Crocuta/Panthera, which were only detected for the MP, have the largest average bone weight for any group identified using ZooMS of 4.19 g, though the sample size is low. In comparison, Canidae bones identified are among the lightest on average. Ursidae were the most abundant by NISP (n = 542; 54.9% of the assemblage) and bone weight (715.3 g; 49.3% of the assemblage) for all cultural horizons, with an average bone weight of 1.3 g. Average bone weight for Ursidae decreased through the sequence from MP to Gravettian among the ZooMS assemblage, but there is not a similar trend in the morphologically identified assemblage. Leporidae, the smallest mammals present within the ZooMS assemblage, have high NISP counts (32 fragments – 3.2% of the assemblage) and the lowest average fragment weight overall (0.26 g), making up only 0.6% of the assemblage by bone weight. Red fox bone fragments were similarly very small, with an average weight of 0.30 g.

The results of the linear model of fragment length size classes can be seen in Fig. 2. It shows that maximum fragment length differs significantly between the chosen body-size classes (ANOVA, $F_{2,934}$, P =

Table 4
NISP and Bone Weight of the morphologically identified bones (excluding teeth) shown per cultural horizon (following Münzel, 2019). Note: morphologically-identified taxa were converted to ZooMS-taxa for comparability.

ZooMS-Taxon	Middle Palaeolithic		Aurignacian		Gravettian		Total	
	NISP (%)	**Weight (%)**	**NISP (%)**	**Weight (%)**	**NISP (%)**	**Weight (%)**	**NISP**	**Weight**
Bos/Bison	–	–	1 (0.05%)	12.5 g (0.06%)	–	–	**1 (0.03%)**	**12.5 g (0.04%)**
Canidae	14 (5.47%)	84.9 g (3.62%)	107 (5.52%)	445.8 g (2.23%)	31 (3.52%)	55.6 g (0.8%)	**152 (4.94%)**	**586.3 g (0.2%)**
Capra	9 (3.52%)	171.2 g (7.29%)	78 (4.02%)	446.2 g (2.23%)	27 (3.07%)	200.3 g (2.9%)	**114 (3.71%)**	**817.7 g (2.8%)**
C. capreolus	2 (0.78%)	5.9 (0.25%)	3 (0.15%)	18.5 g (0.09%)	–	–	**5 (0.16%)**	**24.4 (0.08%)**
Cervidae	3 (1.17%)	61.30 g (2.61%)	9 (0.46%)	110.8 g (0.55%)	–	–	**12 (0.39%)**	**172.1 g (0.59%)**
Crocuta/ Panthera	2 (0.78%)	12.4 g (0.53%)	3 (0.15%)	12.2 g (0.06%)	1 (0.11%)	0.9 g (0.01%)	**6 (0.2%)**	**25.6 g (0.09%)**
Elephantidae	–	–	117 (6.03%)	2922.3 g (14.63%)	40 (4.55%)	1453.5 g (21.02%)	**157 (5.1%)**	**4375.8 g (14.96%)**
Equidae	11 (4.30%)	178.1 g (7.59%)	356 (18.35%)	5094.3 g (25.5%)	80 (9.09%)	999.9 g (14.46%)	**456 (14.82%)**	**6272.3 g (21.45%)**
Felidae	–	–	1 (0.05%)	1,2g (0.01%)	–	–	**1 (0.03%)**	**1.2 g (<0.01%)**
Leporidae	5 (1.95%)	8.2 g (0.35%)	183 (9.43%)	216.4 g (1.08%)	169 (19.2%)	232.3 g (3.36%)	**357 (11.61%)**	**456,6g (1.56%)**
Mustelidae	1 (0.39%)	0.2 (0.01%)	4 (0.21%)	1.1 (0.01%)	2 (0.23%)	0.4 g (0.01%)	**7 (0.23&)**	**1.7 (0.01%)**
R. tarandus	17 (6.64%)	113.8 g (4.85%)	227 (11.7%)	1476.8 g (7.39%)	98 (11.14%)	566.5 g (8.19%)	**342 (11.12%)**	**2157.1 g (7.38%)**
Rhinocerotidae	–	–	9 (0.46%)	261.6 g (1.31%)	2 (0.23%)	17.5 (0.25%)	**11 (0.36%)**	**279.1 g (0.95%)**
R. rupicapra	1 (0.39%)	7.5 g (0.32%)	18 (0.93%)	68.7 g (0.34%)	4 (0.45%)	31.7 g (0.46%)	**23 (0.75%)**	**107.9 g (0.37%)**
Ursidae	191 (74.61%)	1704.3 g (72.59%)	812 (41.86%)	8879.1 g (44.44%)	421 (48.84%)	3339.6 g (48.31%)	**1424 (46.29%)**	**13923.0 g (47.61%)**
V. vulpes	–	–	12 (0.62%)	14.0 g (0.07%)	5 (0.57%)	15.0 g (0.22%)	**17 (0.55%)**	**29.0 g (0.1%)**
Total	**256**	**2347.8 g**	**1940**	**19981.5 g**	**880**	**6913.2 g**	**3076**	**29242.5 g**

Table 5
Average ZooMS-fragment weight (g) per taxon per horizon. Standard deviation for each weight group is shown in brackets, along with the number of fragments for each group.

	Middle Palaeolithic	Aurignacian	Gravettian	Overall
Zooms-taxon	Avg. fragment weight (g)	Avg. fragment weight	Avg. fragment weight	Avg. fragment weight
Bos /Bison	1.33 (± 1.13; n = 12)	1.12 (± 1.07; n = 4)	–	1.28 (± 1.08; n = 16)
Canidae	0.60 (± 0.20; n = 4)	–	1.03 (± 0.76; n = 4)	0.82 (± 0.57; n = 8)
Capra	1.01 (± 0.84; n = 48)	1.01 (± 0.72; n = 17)	0.74 (± 0.44; n = 17)	0.95 (± 0.77; n = 82)
Cervidae	4.80 (± 2.33; n = 7)	2.80 (± 0.87; n = 3)	0.42 (± 0.25; n = 6)	2.78 (± 2.54; n = 16)
Crocuta/ Panthera	4.19 (± 3.66; n = 5)	–	–	4.19 (± 3.66; n = 5)
Elephantidae	3.21 (± 3.15; n = 12)	2.72 (± 2.45; n = 26)	2.13 (± 4.03; n = 21)	2.61 (± 3.20; n = 59)
Equidae	2.43 (± 3.36; n = 23)	2.28 (± 3.23; n = 37)	0.87 (± 0.70; n = 20)	1.97 (± 2.90; n = 80)
Leporidae	0.25 (± 0.08; n = 4)	0.23 (± 0.06; n = 6)	0.27 (± 0.21; n = 22)	0.26 (± 0.17; n = 32)
R. tarandus	0.95 (± 1.33; n = 36)	1.79 (± 3.46; n = 29)	0.91 (± 0.90; n = 21)	1.22 (± 2.23; n = 86)
Rhinocerotidae	2.27 (± 2.69; n = 23)	3.49 (± 3.92; n = 12)	–	2.69 (± 3.16; n = 35)
R. rupicapra	0.28 (n = 1)	–	–	0.28 (n = 1)
Ursidae	1.66 (±2.07; n = 152)	1.54 (± 2.58; n = 201)	0.82 (± 1.20; n = 189)	1.32 (± 2.08; n = 542)
V. Vulpes	0.10 (n = 1)	0.46 (± 0.11; n = 2)	0.27 (n = 1)	0.32 (± 0.19; n = 4)

<0.001), which explains about 3.4% of the total variation in log fragment length (R^2). The post-hoc tests revealed that fragments of the small mammal size class are significantly smaller than those of the others and

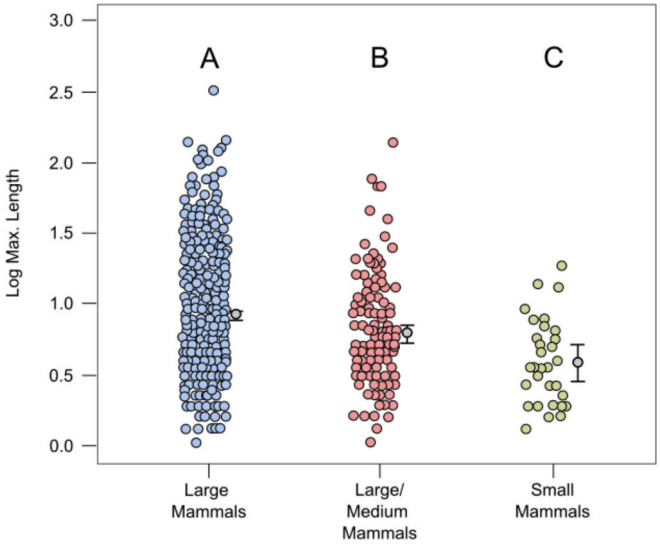

Fig. 2. Results of the linear analysis of the fragment size per body size class, demonstrating that maximum fragment length differs significantly between the chosen body-size classes (ANOVA, F2,934, P = <0.001), which explains about 3.4% of the total variation in log fragment length (R2). Blue, red, green circles depict raw data, grey circles and flags model the predicted group means and their 95% CI. Non-matching capital letters indicate significant post-hoc differences (Tukey HSD). P-values for the differences are: Large/Medium – Large Mammals: 0.001; Small Mammals – Large/Medium Mammals: 0.012; Small Mammals – Large Mammals: <0.001. Y-axis shows log-transformed values of fragment lengths. Body-size class therefore can be seen as a reliable predictor for fragment size.

large mammal fragments are significantly larger.

This pattern highlights an important consideration when selecting bone fragments for biomolecular studies. Despite heavy fragmentation at the site, which would suggest that large fauna would be found in all fragment size classes, large fauna dominate the larger and heavier bone fragments and are infrequently found in the smaller fragment sizes. In comparison, small mammals like fox and hare are most frequently found among the smallest fragments (SC1, n = 24), they decrease in SC2 (n = 9), and are almost completely absent within SC3 (n = 3; Fig. 3). We

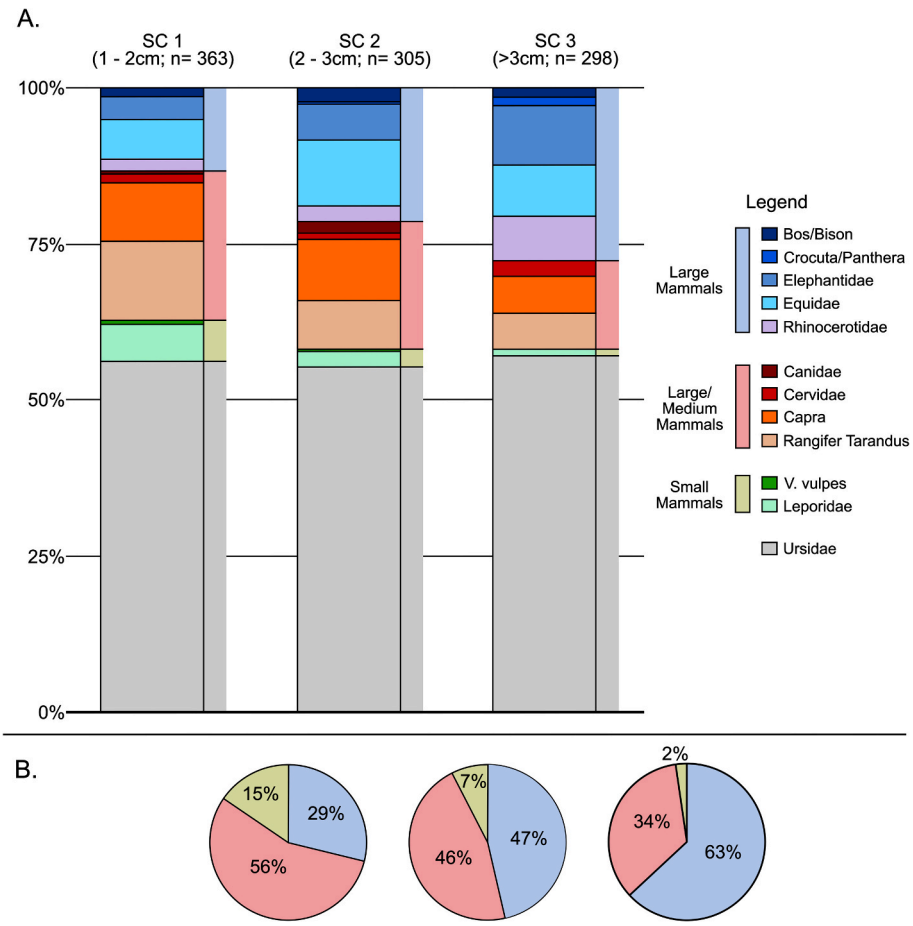

Fig. 3. A) Bar graphs report the ZooMS taxons identified per fragment size class: SC1 (bones between 1–2 cm; n = 363), SC2 (bones between 2–4 cm; n = 305), and SC3 (bones larger than 3 cm; n = 298). Bars in blue, red, and green indicate small, large/medium, and large mammals. Ursidae are shown in grey; B) Ursidae are removed from the pie charts and all other ZooMS taxa are divided by body size class, demonstrating the decline of smaller fauna as fragment size increases. In comparison, larger fauna (with the exclusion of Ursidae) decrease in number as the fragment size decreases.

therefore suggest that recording bone weight and length is worthwhile since it can be used as a means for contextualizing the NISP.

4.4. Taphonomy

Gnawing marks, including bite marks, drag marks, puncture marks and traces of digestion, were more frequent on the non-diagnostic bone fragments than on those bones which could be morphologically identified (Fig. 4). Around one third of all ZooMS-analyzed fragments from MP (34.9%) and Aurignacian (33.1%) contexts show carnivore damage, while within the morphological component only 16.7% (MP) and 7.5% (Aurignacian) do. Within the Gravettian assemblage the difference is less stark but nevertheless notable, with 24.3% and 11.3% of bones demonstrating some carnivore damage for the ZooMS and morphological assemblage, respectively.

Anthropogenic marks were far less numerous than carnivore damage within the ZooMS-component. Among the morphologically identifiable bones, one secure and four possible cut marks had been identified. In comparison, in this study only two clear and three possible cut marks were detected for the entire ZooMS assemblage (Figs. 5-6). Additionally, one fragment (ZGK 515) preserves a potential group of pits and microstriations that could indicate attempts at opening the bone for marrow, although this identification is less secure than the other examples presented here (Vettese et al., 2020). This amounts to four secure anthropogenic marks and seven potential ones, distributed without apparent pattern across the ZooMS-taxa and cultural horizons (Table 6). Focusing on the certain instances of anthropogenic marks, fragments with cut marks were taxonomically identified as Rhinocerotidae (MP, ZGK 355), Ursidae (Aurignacian, ZGK 563), and Equidae (Gravettian, ZGK 254), while ZGK 515, which showed possible evidence for a group of pits and striations, was identified as *Capra* (MP, Figs. 5-6).

5. Discussion

Previous zooarchaeological analyses of the Geißenklösterle Cave faunal material (Münzel, 2019) indicated that hominins lived within the mammoth steppe and exploited the species found there, including woolly mammoth (*Mammuthus primigenius*), wild horse (*Equus ferus*), reindeer (*Rangifer tarandus*), and woolly rhinoceros (*Coelodonta antiquitatis*) (Münzel, 2002, 2019), a pattern largely borne out in the current study. Previous research on Geißenklösterle Cave established cave bear (*Ursus spelaeus/U. ingressus*), a species that naturally frequented and used the cave as a den during hibernation, as the most dominant taxon within the Palaeolithic layers (Münzel, 2019). In the morphological analysis, the MP layers (n = 769 identified to species) show a significantly smaller assemblage and mass than the Aurignacian (n = 5848) and Gravettian (n = 2234) horizons (Münzel, 2019). The MP shows the highest percentage of large and middle-sized carnivores (3.9%, compared to 1.8% and 0.8%), and small ruminants (3.3%, compared to 2.3% and 2.1%). The main prey species, mammoth, wild horse and reindeer, show an opposite pattern (10.8% compared to 40.1% in the Aurignacian and 20.6% in the Gravettian layers). Münzel (2019) associated these patterns with differences in subsistence behavior between AMH and Neanderthals, as well as a lower occupation intensity during

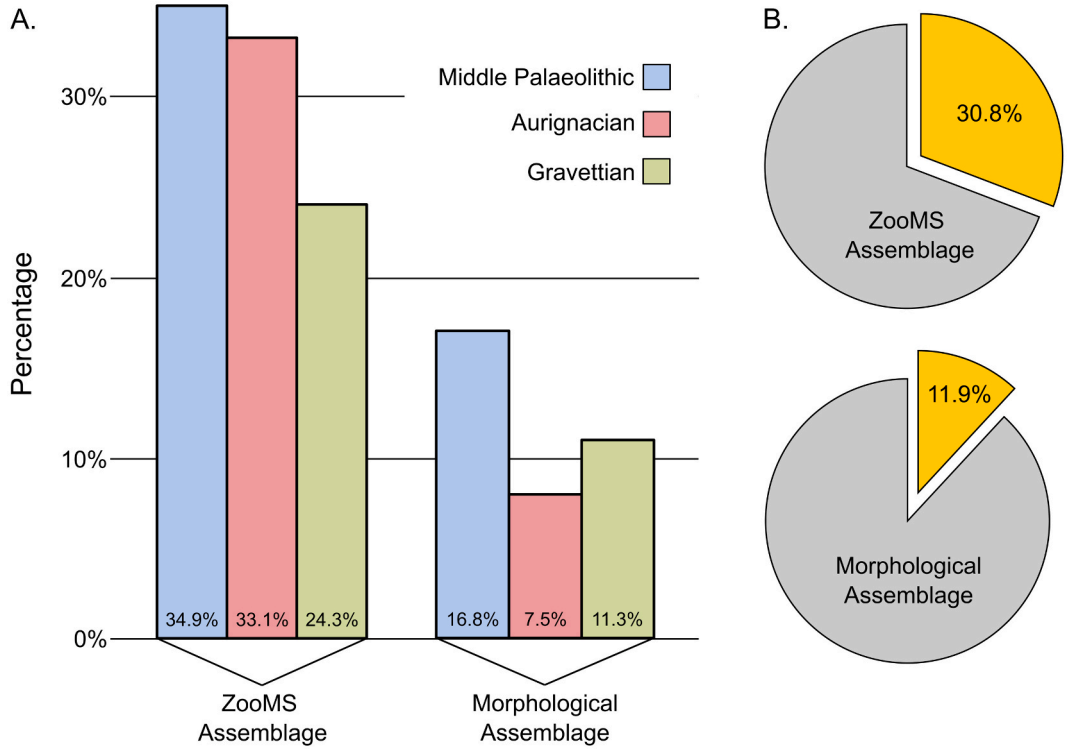

Fig. 4. Comparison of the frequency of occurrence of gnawing marks within the cultural horizons between the morphologically identifiable and the ZooMS-components. A break-down by species of carnivore damage can be found in the supplementary information and in the supplementary database. A. Reports the percentage of bones with gnawing marks per cultural horizon. B. Pie charts report the total percentage per assemblage of bones with gnawing marks.

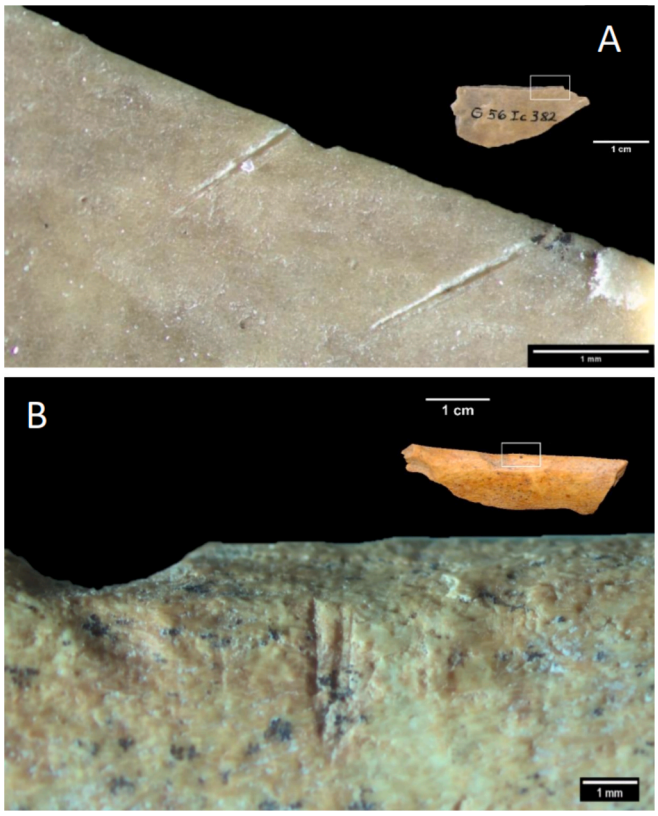

Fig. 5. A. cut marks on zgk 254 (equidae); sharp incisions with clear v-profile; b. cut marks on zgk0355 (rhinocerotidae); clearly v-shaped, parallel striae.

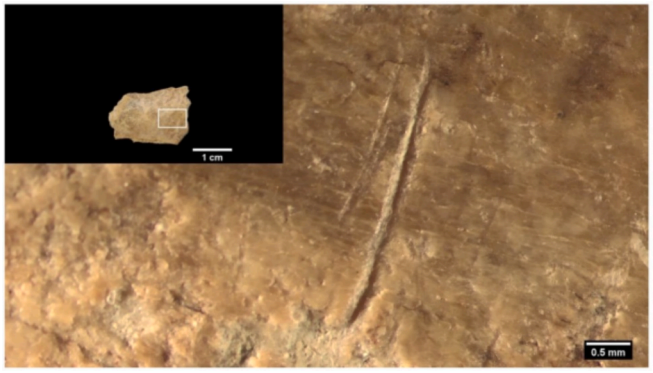

Fig. 6. Cut marks on ZGK 563 (Ursidae); one deep v-shaped straight incision, one parallel shallow one.

Table 6
Overview of all the anthropogenic modifications evidenced among the ZooMS-analyzed fragments. "C" indicates cut marks are defined and "I" indicates impact/percussion/cone marks. Additional details on the taphonomic analysis for each bone can be found in the supplementary information.

Cultural Horizon	Sample Number	Modification	ZooMS-ID
Gravettian	ZGK 254	C	Equidae
	ZGK 266	C?	*Capra*
	ZGK 863	C?	Leporidae
	ZGK 906	C?	Ursidae
Upper Aurignacian	ZGK 208	C?	Equidae
	ZGK 563	C	Ursidae
Lower Aurignacian	ZGK 176	C?	Elephantidae
	ZGK 580	C?	Leporidae
Middle Palaeolithic	ZGK 355	C	Rhinocerotidae
	ZGK 470	C?	*Bos/Bison*
	ZGK 515	Retoucher?; I?	Capra

the MP, allowing for a higher influence of non-human predators on the respective material. Within the UP horizons, a much stronger anthropogenic input becomes apparent through organic tool industry with formal tool types such as projectiles and smoothers; mammoth ribs and ivory were crafted into osseous points, horse long bones frequently into retouchers, and reindeer antlers, metatarsals and tibias into awls, split bone points, *bâtons percés*, or chisels (Barth et al., 2009; Conard and Bolus, 2003; Münzel, 2005, 2002, 2001; Toniato et al., 2018). This led Münzel (2019) to conclude that during the UP, Geißenklösterle Cave was primarily frequented for the production of organic tools (Barth et al., 2009; Münzel, 2019).

While the ZooMS-data generally agrees with the species abundances from previous research, we did observe some relative and absolute differences across the cultural horizons. One taxon that had been virtually absent in the morphological component at the site is *Bos/Bison*. Within the archaeological horizons relevant to this study, bison was previously only represented at Geißenklösterle Cave by a single third phalanx from the lower Aurignacian (Münzel 2019). The ZooMS results now contribute an additional twelve specimens to the MP and four to the Aurignacian record. Previous zooarchaeological studies in the Swabian Jura show evidence for bison at various sites within the region and demonstrate: (1) bison is more abundant among the Lone Valley sites (Fig. 1), (2) evidence for that taxon declines over time, and (3) neither aurochs nor steppe bison were ever the main prey species of hominin populations in the Swabian Jura (Barth et al., 2009; Bertacchi et al., 2021; Boger et al., 2014; Kitagawa et al., 2012; Riek, 1973). While we did not observe any clear taphonomic patterns regarding gnawing marks (on 25% of the fragments) or anthropogenic modifications (ZGK 470 is one possible instance) that would explain the ZooMS-signal, half of the *Bos/Bison* specimens did show green breaks, indicating that a significant amount of fragmentation took place pre- or *peri*-depositionally. Put into a larger context, this result fits well into an emerging interregional pattern as multiple ZooMS-studies have by now been published for sites in Central Europe that show a higher abundance of *Bos/Bison* within the non-diagnostic material (Brown et al., 2021b; Pothier Bouchard et al., 2020; Sinet-Mathiot et al., 2019).

A second pattern that has emerged from this study that sets the ZooMS data apart from the morphologically-derived data is in regards to bear remains. While bear dominates the MP morphological assemblage, it is 25% lower by NISP among the assemblage identified with ZooMS. The opposite is true in the Aurignacian and Gravettian, where percentages of bear remains are 15–20% higher in the ZooMS assemblage compared to the morphological assemblage. A possible explanation for this is that the majority of bear remains in the MP were from animals that died naturally and then underwent only a minor amount of scavenging from bone ravaging carnivores (or hominins; Münzel, 2019), resulting in relatively lower fragmentation rates and fewer fragments of bear bones in the size class considered for ZooMS, in comparison to the many large pieces identified in the morphological analysis (Münzel, 2019). Conversely, in the Upper Palaeolithic, hominins appear to have exploited bears more frequently and were more likely to access nutritious within-bone marrow, likely resulting in more heavily fragmented assemblages and greater identification by ZooMS (Toniato et al., 2024). Support for this comes from a recent study by Toniato and colleagues (2024), who established the regular hunting and butchery of bears for meat and fur by hominins in the Swabian Jura. While there is occasional evidence for such behavior in the MP, it becomes more common in the Aurignacian and Gravettian periods (Toniato et al., 2024).

5.1. Hominin activity

Butchering traces are rare in general for both the MP and the UP at Geißenklösterle Cave and such anthropogenic modifications on megafauna bones are otherwise lacking from the extensive faunal collections of other sites in the Swabian Jura which have well-preserved bones like Vogelherd, Hohle Fels, and Brillenhöhle (Barth et al., 2009; Niven, 2006). The number of anthropogenic modifications on the studied material in the ZooMS assemblage from the site is extremely low, accounting for 1.1% of all fragments studied including 'potential' anthropogenic modifications. Despite their rarity, the anthropogenic marks that were identified highlight the informational value of combining ZooMS with taphonomic analyses. The three small parallel cut marks found on the Rhinocerotidae bone fragment (ZGK 355; Fig. 5b) represent the earliest evidence for anthropogenic activity on woolly rhinoceros at Geißenklösterle Cave. As megafauna, Rhinocerotidae bones might be particularly resistant to marks from cutting the bones directly, given the density of their bones and the surrounding tissues (Haynes and Krasinski, 2021; Starkovich et al., 2020). Circumstantial evidence for the general use of Rhinocerotidae bones has been observed through the manufacture of several bone points from the site which fall into the mammoth/rhino size class (Wolf et al., 2016). These bone points date to the Aurignacian and as yet no biomolecular analysis has been carried out to confirm whether they are from woolly rhinoceros or mammoth. At present, ZGK 355 is the earliest Rhinocerotidae bone with anthropogenic marks discovered in the Swabian Jura. Evidence for Neanderthal's hunting of the woodland rhinoceros (*Stephanorhinus kirchbergensis*) is present elsewhere in Germany, for example, at the Palaeolithic site of Taubach, Thuringia (Bratlund, 1999). However it remains unclear if the cut-mark on ZGK 355 represents hunting or scavenging.

5.2. Carnivore activity

Carnivore damage is almost three times more frequent on the ZooMS assemblage (31%) in comparison with the bones that were morphologically identified (12%) (Fig. 4). 16.7% of bones exhibit such damage in the MP, 7.5% in the Aurignacian, and 11.3% in the Gravettian. In comparison, the extent of carnivore damage remains constant within the ZooMS identified assemblage from MP (34.9%) to the Aurignacian (33.1%) and then drops to 24.3% in the Gravettian. The consistency of observed carnivore damage and the higher frequency on indeterminate bone fragments highlights the impact of carnivores re-processing bone accumulated at Geißenklösterle Cave. In this study, we mainly sampled long bone shaft and flat bone fragments, which largely excludes epiphyseal specimens. Since bone gnawing by non-human predators affects the epiphyses first (Pickering et al., 2013), the high frequency with which those marks appear on the analyzed fragments therefore indicates intensive fragmenting most characteristic for carnivores like wolves, foxes, and especially hyenas (Starkovich and Conard, 2015). The fact that the frequency of gnawing marks is so much higher on the ZooMS-analyzed than the diagnostic bones supports this assessment. Hyenas are well-known for crushing and consuming bone, which is why assemblages affected by them tend to show a high quantity of gnawing marks (Egeland et al., 2008; Münzel and Conard, 2004). Hyenas are represented within the faunal assemblage of Geißenklösterle Cave in small numbers (0.1% of the total morphological assemblage, while Crocuta/Panthera make up 1.9% of the ZooMS-analyzed fragments from the MP) but are known to have utilised the nearby site of Kogelstein as a den (Münzel and Conard, 2004, 2019). All this suggests that predators, likely hyenas, played a bigger role in the accumulation history of the Geißenklösterle Cave faunal assemblage than previously assumed. Moreover, the extent of gnawing shown by the high quantity of marks on the small fragments analyzed here indicates at least periods of absence of hominins at the site, during which the predators would have had the time and freedom to exploit the bones. This would support Münzel's hypothesis that hominins did not occupy the cave year-round but rather migrated through the Swabian Jura in a seasonal cycle (Münzel, 2019). The relatively lower frequency of carnivore damage within the Gravettian material might further be explained by longer yearly occupation periods of the cave by hominins (Münzel, 2019) and the more intense exploitation of carnivores by hominins (Kitagawa et al., 2012) during that time. Future ZooMS analysis with a specific focus on bones

exhibiting carnivore damage from Geißenklösterle Cave and other sites in the Swabian Jura could further test this hypothesis.

5.3. Sample selection for ZooMS studies of indeterminate bones

The inclusion of bone weight and fragment size has the potential to contextualise ZooMS results of fragmented bones. Our analysis of bone weight demonstrated the biasing effect of utilizing NISP alone. Furthermore, the correlation between fragment-size and body-size has important implications for best-practice sampling strategies for ZooMS analysis. In this study, we demonstrate that including only those fragments with a larger than 2 cm maximum length can dampen or even erase the taxonomic signal of small animals. The fragments identified as Leporidae and red fox are statistically significantly smaller on average, with 21 of the 32 hare specimens and three of the four red fox specimens falling within SC1. To further illustrate this point, the average fragment length of the specimens identified as red fox/hare is 1.85 cm, while the average fragment length of mammoth/rhino is 3.32 cm. Bone fragments from larger-sized taxa were also frequently overrepresented within bone weight relative to NISP-counts. For instance, both Elephantidae (7%) and Leporidae (7.3%) make up a similar proportion for all Gravettian bones identified using ZooMS at Geißenklösterle Cave by NISP. By bone weight, Elephantidae make up a much larger percentage of the assemblage than Leporidae, 17.1% vs 2.2% respectively. So while 22 Leporidae bones were identified, they contribute significantly less biomass than the Elephantidae bones (n = 21). This is repeated across all fauna with large mammals (Elephantidae and Rhinocerotidae) accounting for 17.4% of the overall assemblage by bone weight and 9.7% of NISP, in comparison with small mammals (Leporidae and *V. vulpes*), that show the reverse pattern (0.7% bone weight and 3.7% NISP).

Consequently, the exclusion of bones smaller than 2 cm for this study would have biased the faunal representation we can see in our ZooMS data. We would therefore recommend for future ZooMS-studies with a focus on understanding the zooarchaeological record to include fragments of all size classes or to at least explicitly state the rationale for excluding specific fragment sizes. In this study, we excluded fragments smaller than 1 cm, under the assumption that they would predominantly be Avian and micromammalian fauna for which there are very few ZooMS reference databases. Likely, by excluding these smaller fragments, we have introduced a bias into our own reconstruction of the fragmented assemblage at Geißenklösterle Cave. Recent studies of micromammals in South Africa and voles and lemmings in the United Kingdom represent much needed contributions to the ZooMS reference literature (Buckley et al., 2018; Nel et al., 2023). The eventual development of reference databases of European micromammals and birds will be invaluable.

6. Conclusions

Archaeological and zooarchaeological research has been carried out for the cave sites of the Ach and Lone valleys since the beginnings of the Palaeolithic research in the 1860s and 1870s, resulting in a detailed understanding of the populations inhabiting the region during the Middle and Upper Palaeolithic. While fragmentation of bones persists, the biomolecular preservation is outstanding, demonstrated by our own analysis in which only 16 bones failed to produce sufficient protein for taxonomic identification. At Geißenklösterle Cave we are able to draw on an established zooarchaeological record to contextualise the ZooMS analysis of indeterminate fragmented bones and perhaps provide a framework for further analysis of sites in the region.

In this study, we show that a combination of ZooMS and a detailed taphonomic analysis of the studied fragments, including ones smaller than 2 cm length, leads to valuable insights, contextualizing and adding to the understanding of human-animal interactions that arose out of previous zooarchaeological work (Baumann et al., 2020; Kitagawa et al., 2012; Münzel, 2019). High levels of carnivore damage, frequent even on the fragments of smaller size, demonstrate that the impact of carnivores on the accumulation of the faunal assemblage has been stronger than previously assumed and might be responsible for the removal of rare taxa like Bos/Bison from the record. Moreover, we were able to find the earliest case of anthropogenic modifications on a woolly rhinoceros bone in the Swabian Jura, and provide supporting evidence for existing hypotheses regarding bear exploitation.

Our experimental inclusion of fragments of a size smaller than 2 cm has made clear that the range of fragment sizes included in a study has an influence on the absolute and relative NISP-results and can thus lead to biased results. The parameter of fragment length should thus receive more attention during research design to try and make the results as representative as possible.

Finally, adding bone weight as a data point proved valuable in contextualizing NISP (Münzel 2019; Uerpmann, 1973). We consequently recommend recording it in future studies, also as a potential avenue for integrating data generated by ZooMS and zooarchaeology, as a way to circumvent issues caused by fragmentation rates.

Overall, we were able to show the potential of ZooMS to provide a more complete view of how the osseous assemblages from the Swabian Jura were accumulated. More studies which specifically consider the fragmentation of non-diagnostic bones in the future, paired with further exploration and experimentation of best practice ZooMS-applications will allow this research to continue to make meaningful insights into the past.

CRediT authorship contribution statement

Luca E. Lee-Michaelis: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Susanne C. Münzel:** Writing – review & editing, formal data analysis. **Keiko Kitagawa:** Writing – review & editing, formal data analysis. **Megan A. Saunders:** Writing – review & editing. **Fei Yang:** Writing – review & editing. **Britt M. Starkovich:** Writing – review & editing, Resources, Methodology, formal data analysis. **Nicholas J. Conard:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Samantha Brown:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Angel Blanco-Lapaz, Alexander Janas, and Gregor Bader for their assistance in accessing the material and the database, and providing necessary equipment. We are grateful to the Institute of Organic Chemistry at the Universität Tübingen for use of their facilities, in particular we would like to thank Norbert Grzegorzek. We thank Nils Vanwezer for creating the map of the Swabian Jura for this publication. We thank Erin Scott for assistance in preparing supplementary data for publication.

This project was funded thanks to the Universität Tübingen's Excellence Initiative. The excavations at Geißenklösterle Cave were funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under the project SFB 275, "Climate Coupled Processes in the Meso- and Cenozoic". The zooarchaeological research at the site was additionally supported by DFG grant, "Die Höhle Geißenklösterle: Ökonomie und Ökologie" and by the Hochschulsonderprogramms II zur Förderung von Frauen program, "Archäozoologische

Auswertung der Faunenreste aus den Gravettien-Horizonten der Geißenklösterle im Achtal bei Blaubeuren". We are grateful to the Ministry of Science of Baden-Württemberg and the Alb-Donau-Kreis for their finanacial support throughout the excavations and research at the site.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2026.105692.

Data availability

The research data has been deposited in a publicly accessible online depository.

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