Of Mice and (Neanderthal) Men: The small mammal record of the Middle to Upper Paleolithic transition in the Swabian Jura, Germany

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I Abbreviations

NISP – Number of Identified Specimens
MNI – Minimum Number of Individuals
NTAXA – Number of Taxonomic Designations at the genera and/or species level.
AMH – Anatomically Modern Humans
OIS – Oxygen Isotope Stage
GS – Greenland Stadial
GIS – Greenland Interstadial
D-O – Dansgaard-Oeschger event (numbered)
H – Heinrich event (numbered)
ACC – anterioconid complex
AL – anterior lobe
PL – posterior lobe
BRA – buccal re-entrant angle
LRA – lingual re-entrant angle
BSA – buccal salient angle/edge
LSA – lingual salient angle/edge
T – triangle (numbered)
Qu. – quadrant
SDQ – Schmelz-Dicken-Quotient
LE – leading edge
TE – trailing edge
LUF – length of upper condylar facet
LLF – length of lower condylar facet
HC – height of the condyle
TRW – trogonid width
TAW – talonid width
W – width
L - length

II Acknowledgements

By any measure of the word, the undertaking of a thesis project is a *community* effort. I consider myself exceptionally lucky to have had a true community of colleagues, friends, and family from which I drew guidance, strength, and motivation over the past four and a half years.

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III Summary

The Middle to Upper Paleolithic transition and the loss of Neanderthal populations across Central and Western Europe has been a dominant area of archaeological research throughout the 20th century. In particular, the role interspecies competition, genetic interbreeding, and the climatic instability of Oxygen Isotope Stage 3 (OIS 3) played in the extinction of Neanderthal groups has been heavily debated. The Swabian Jura in southwestern Germany, houses a number of important caves and rock shelters preserving detailed faunal, geoarchaeological, and cultural records spanning this biological and technological transition. In particular, chronological and stratigraphic records indicating that Neanderthals and anatomically modern humans occupied the valley with little to no overlap or interaction, as well as the exceptional record of early Aurignacian technological innovation and complex symbolic expression, make this an important region for our understanding of human cultural and biological evolution during this time.

This thesis contributes a high-resolution and taphonomically robust terrestrial paleoenvironmental record derived from small mammal material recovered from Hohle Fels and Geißenklösterle caves, located in the Ach Valley, to the long history of archaeological research in the Swabian Jura. The effect of high amplitude stadial-interstadial oscillations, recognizable in the Greenland ice core records, on local vegetation patterns is explored. Particularly, the continued applicability of climatically driven explanatory models for the Neanderthal abandonment of the region is assessed in light of this new paleoecological record, and alternative hypotheses emphasizing the interaction of multiple factors in shaping Neanderthal settlement dynamics are discussed.

Small mammals, such as rodents, insectivores, and bats, are valuable paleoenvironmental proxies due to their narrow climatic and vegetative habitats. In addition, their short life spans and fast reproductive rates drive population level response to environmental change over short time periods. This change can be quantified diachronically within stratified deposits to produce a high-resolution record of small mammal turnover and related vegetative change in response to climatic variables in the past. Furthermore, the application of a robust taphonomic analysis allows for the recognition of inherent biases in the taxonomic composition of small mammal assemblages due to predator behaviour and post-depositional destruction.

This new paleoenvironmental record reveals that the Ach Valley Middle Paleolithic landscape was characterized by substantial woodlands, as well as meadows and grasslands alongside gradually increasing cold and dry tundra areas. A number of stadial-interstadial oscillations are identified based on shifts in the proportion of woodland and tundra adapted small mammal species, and these are broadly correlated with high-resolution records from the Greenland ice cores. Importantly, there is no indication of dramatic climatic instability directly preceding or during the nearly-culturally sterile deposits interstratified between the Middle Paleolithic and Aurignacian periods at both sites. The Ach Valley was substantially colder and dryer during the initial Upper Paleolithic compared with earlier periods, as cold tundra landscapes continued to expand and temperate forests retract. The role that this challenging environment played in the development of the exceptional cultural and symbolic material culture of the local Aurignacian groups, which includes the earliest examples of figurative art and musical instruments, is also discussed. My taphonomic analysis indicates the small mammal material was accumulated primarily by opportunistic predators such as the great grey owl, snowy owl, European eagle owl, and kestrel, and therefore accurately reflects the taxonomic composition of the small mammal community and the diversity of landscapes present around the sites in the past.

Overall, this new paleoenvironmental record fits well with past studies of the paleoecology of the Ach Valley, and this, combined with recent calibrated radiocarbon ages suggests that the most striking regional climatic pattern - a gradual cooling and drying beginning in the Middle Paleolithic and extending into the early Upper Paleolithic - can be confidently correlated with the cooling trend spanning Dansgaard-Oeschger cycles 12 – 9 seen elsewhere in Western and Central Europe. The lack of a clear signal for dramatic climatic change around the time of Neanderthal abandonment of the valley suggests that deteriorating environmental conditions, and the resultant decrease in resource availability, was not the decisive factor in this demographic shift. Instead, a multi-factor explanation is outlined, taking into account documented low genetic variability within Neanderthal groups, small group sizes, and highly mobile lifeways, as well as a growing signal of Neanderthal niche fragmentation resulting from climatic instability recognized throughout Central and Eastern Europe.

III Zusammenfassung

Der Übergang vom Mittel- zum Jungpaläolithikum und das Verschwinden der Neandertaler in Zentral- und Westeuropa ist eines der zentralen Forschungsthemen der Urgeschichtlichen Archäologie des 20. Jahrhunderts. Dabei wird ganz besonders debattiert, welche Rolle artübergreifende Rivalitäten, genetische Vermischung und die klimatische Instabilität der Sauerstoff-Isotopenstufe 3 (OIS3) für das Aussterben der Neandertaler spielten. Die Schwäbische Alb in Südwestdeutschland beherbergt eine Vielzahl wichtiger Höhlen und Abris in denen Faunenreste, geoarchäologische Daten und kulturelle Überreste besonders gut überliefert sind und anhand derer sich dieser biologische und technologische Wandel greifen lässt. Chronologische und stratigraphische Daten deuten darauf hin, dass Neandertaler und anatomisch moderne Menschen diese Region mit wenig oder keinen Überschneidungen nutzten. Zudem macht die außergewöhnliche Fülle an technologischen Innovationen und komplexer Symbolik des Frühaurignacien dieses Tal zu einer Schlüsselregion für Studien zur kulturellen und biologischen Evolution des Menschen.

Diese Dissertation leistet einen weiteren Beitrag zur Forschungsgeschichte der Schwäbischen Alb und generiert einen hochauflösenden und taphonomisch robusten Datensatz zur Rekonstruktion der Paläoumwelt aufgrund von Kleinsäugerresten aus den Höhlen des Hohle Fels und des Geißenklösterles im Achtal. Untersucht wird der Effekt von stark schwankenden stadial-interstadialen Oszillationen − die in den grönländischen Eiskernaufzeichnungen erkennbar sind − auf lokale Vegetation. Dabei wird insbesondere die häufige Anwendung klimabedingter Erklärungsmodelle für das Verschwinden der Neandertaler in der Region anhand der in dieser Dissertation neu generierten paläoökologischen Daten bewertet und alternative Hypothesen diskutiert, die das Zusammenspiel multipler Faktoren bei der Erklärung von Siedlungsdynamiken der Neandertaler berücksichtigen.

Kleinsäuger wie Nagetiere, Insektivore und Fledermäuse, sind aufgrund ihrer klimatisch und vegetativ enggefassten Lebensräume wertvolle paläoökologische Proxys. Darüber hinaus tragen kurze Lebensdauer sowie schnelle Reproduktionsraten dazu bei, dass Kleinsäugerpopulationen in relativ kurzer Zeit auf Umweltveränderungen reagieren. Solche Veränderung können in stratifizierten Ablagerungen quantifiziert werden um eine hochauflösende diachrone Sequenz zu erhalten, an der sich chronologische Umschwünge in Kleinsäugerpopulationen und Vegetation ablesen lassen, die als Reaktion auf Klimaschwankungen in der Vergangenheit zu erklären sind. Darüber hinaus ermöglicht die

Anwendung einer robusten taphonomischen Analyse inhärente Verzerrungen in der taxonomischen Zusammensetzung von Kleinsäugerpopulationen zu erkennen, welche auf Karnivorenaktivitäten oder Ablagerungsstörungen zurückzuführen sind.

Der in dieser Dissertation vorgelegte paläoökologische Datensatz lässt erkennen, dass die mittelpaläolithische Landschaft des Achtals von ausgedehnten Wäldern, Wiesen und Grasland geprägt war, sowie von allmählich zunehmenden kalten und trockenen Tundren. Aufgrund von Verschiebungen des Anteils von Kleinsäugerarten die an Wald und Tundra angepasst sind, kann eine Reihe von stadial-interstadialen Oszillationen festgestellt werden, die weitgehend mit hochauflösenden Aufzeichnungen der grönländischen Eiskerne korrelieren. Es ist zu betonen, dass es in beiden Höhlen keinerlei Anzeichen für eine dramatische Klimainstabilität unmittelbar vor oder während der nahezu kulturell sterilen Ablagerungen gibt, die zeitlich zwischen das Mittelpaläolithikum und das Aurignacien fallen. Das Achtal war während des anfänglichen Jungpaläolithikums im Vergleich zu früheren Perioden wesentlich kälter und trockener, da sich die kalte Tundra ausbreitete und die gemäßigten Wälder zurückwichen. Die Rolle, die dieses herausfordernde Umfeld für die Entwicklung von Kultur und Symbolik in den lokalen Gruppen des Aurignacien spielte − einschließlich der frühesten Belege für figurative Kunst und Musikinstrumente − wird ebenfalls erörtert. Die taphonomische Analyse zeigt, dass die Kleinsäugerreste in den Höhlen hauptsächlich von Allesfressern wie der großen Graueule, der Schneeeule, dem europäischen Uhu und dem Turmfalken angesammelt wurden. Das Untersuchungsmaterial spiegelt somit die taxonomische Zusammensetzung und die Vielfalt von Kleinsäugerarten in den umliegenden urzeitlichen Landschaften der Höhlen wieder.

Zusammenfassend lässt sich sagen, dass sich der in dieser Dissertation vorgestellte paläoökologische Datensatz mit früheren Studien zur Paläoökologie des Achtals deckt. Zusammen mit neu generierten und kalibrierten Radiokohlenstoffdatierungen lässt diese Arbeit den Schluss zu, dass das regionale Klimamuster − eine allmähliche Abkühlung und Trocknung im Mittelpaläolithikum bis hin zum frühen Jungpaläolithikum − mit der generellen Abkühlung in West- und Zentraleuropa während der Dansgaard-Oeschger-Schwankungen 12-9 korreliert. Das Fehlen eines eindeutigen Signals für einen dramatischen Klimawandel für die Zeit in der der Neandertalers das Achtal aufgab lässt darauf schließen, dass die verschlechternden Umweltbedingungen und die daraus resultierende Abnahme der Ressourcenverfügbarkeit keine entscheidenden Faktoren für den demografischen Wandel waren. Stattdessen wird ein multifaktorieller Erklärungsansatz vorgestellt, der geringe genetische Variabilität innerhalb von Neandertalerpopulationen, kleine Gruppengrößen, hochmobile Lebensweisen, sowie die

Fragmentierung der Lebensräume infolge klimatischer Instabilitäten in Mittel- und Osteuropa berücksichtigt.

III Résumé

Tout au long du 20ème siècle, la transition du Paléolithique moyen au supérieur, et la perte de populations de Néandertaliens en Europe centrale et occidentale, ont été un domaine dominant dans la recherche archéologique. Le rôle de la concurrence interspécifique, des croisements génétiques et l'instabilité climatique du stade isotope de l'oxygène 3 (SIO/OIS 3) dans l'extinction des groupes de néanderthaliens sont particulièrement controversés. Le Jura Souabe (dans le sud-ouest de l'Allemagne) abrite des nombreuses grottes et abris sous roches célèbres qui traversent cette transition biologique et technologique et qui conservent des archives détaillées de la faune, la géoarchéologie et la culture. En particulier, les données chronologiques et stratigraphiques qu'indiquant que les Néandertaliens et les humains de l'anatomie moderne occupaient la vallée avec peu ou pas de chevauchement ou d'interaction, ainsi que les occurrences de l'innovation technologique et expression symbolique exceptionnelles du début de l'Aurignacien, en fait une région importante pour notre compréhension de l'évolution culturelle et biologique pendant cette période.

Cette thèse contribue à la longue histoire des recherches archéologiques dans le Jura Souabe, un ensemble de données paléoenvironnementales terrestres, taphonomique robustes et à haute résolution, dérivées de matériel provenant de petits mammifères récupéré dans les grottes de Hohle Fels et Geißenklösterle, situées dans la vallée de l'Ach. L'effet d'oscillations stadialo-interstadiales de forte amplitude, reconnaissables dans les archives de carottes de glace du Groenland, sur les structures de végétation locales est aussi exploré. À la lumière de ces nouvelles données paléoécologiques, l'applicabilité continue de modèles explicatifs basés sur le climat pour les Néandertaliens abandonnant la région est évaluée, et des hypothèses alternatives qui se concentrant à l'interaction de nombreux facteurs dans la formation de la dynamique du peuplement néandertalien sont discutées.

Les petits mammifères, tels que les rongeurs, les insectivores et les chauves-souris, sont de bons indicateurs paléoenvironnementaux en raison de leurs habitats climatiques et végétatifs limités. De plus, leur courte durée de vie et leurs taux de reproduction rapides, poussent les populations à réagir aux changements environnementaux sur de périodes courtes. Ce changement est quantifié diachroniquement dans les dépôts stratifiés afin de produire un témoignage au haute résolution pour le renouvellement des petits mammifères, et le changement végétatif lié, en réponse aux variables climatiques à l'époque. Par ailleurs, l'application d'une analyse taphonomique robuste permet la reconnaissance des biais inhérents

à la composition taxonomique des assemblages de petits mammifères en raison du comportement des prédateurs et la destruction après -dépôt.

Ces nouvelles données paléoenvironnementales montrent que le paysage du Paléolithique moyen de la vallée de l'Ach était caractérisé par des forêts substantielles, ainsi que par des prairies et des herbages, et aussi par des zones de toundra froide et sèche qui se développaient progressivement. Un certain nombre d'oscillations stadio-interstadiales ont été identifiées en fonction de l'évolution de la proportion d'espèces de petits mammifères qui sont adaptées aux zones boisées et à la toundra. Celles-ci sont largement corrélées aux données à haute résolution des carottes de glace du Groenland. Il est important de noter qu’il n'y a aucune indication d'instabilité climatique dramatique directement avant ou pendant les dépôts quasi-culturellement stériles qui sont intercalées entre le Paléolithique moyen et Aurignacien sur les deux sites. La vallée de l'Ach était nettement plus froide et sèche pendant le début de la Paléolithique supérieur par rapport aux périodes précédentes, alors que les paysages de toundra froide continuaient de s'étendre et que les forêts tempérées se rétractaient. Le rôle de cet environnement difficile dans le développement de la culture matérielle et symbolique exceptionnelle des groupes locaux d’Aurignacien, qui comprend les premiers exemples d'art figuratif et instruments de musique, est également discuté. L'analyse taphonomique indique que le matériel de petit mammifère a été accumulée principalement par des prédateurs opportunistes comme le grand hibou gris, chouette harfang des neiges, hibou européen, et crécerelle et, par consequent, reflète fidèlement la composition taxonomique de la communauté des petites mammifères et la diversité des paysages présents autour de les sites dans le passé.

Globalement, ces nouvelles données paléoenvironnementales correspondent bien aux études antérieures sur la paléoécologie de la vallée de l’Ach et ceci, en combinaison aux datations radiocarbone calibrées récentes, suggère que le schéma climatique régional le plus saisissant -- refroidissement et séchage progressifs commençant au Paléolithique moyen et s'étendant jusqu'au Paléolithique supérieur initial -- peuvent être corrélés avec confiance à la tendance au refroidissement observée au cours des cycles de Dansgaard-Oeschger 12 - 9 observés ailleurs en Europe occidentale et centrale. L'absence de signe clair d'un changement climatique spectaculaire au moment de l'abandon de la vallée par les Neanderthaliens suggère que la détérioration des conditions environnementales, et la diminution résultante de la disponibilité des ressources, ne sont pas le facteur décisif de ce changement démographique. Au lieu de cela, une explication multifactorielle est proposée, tenant compte de la faible variabilité génétique documentée au sein des groupes Néandertaliens, de la petite taille des groupes et des modes de vie très mobiles, ainsi qu'un signal croissant de fragmentation de la niche Néandertalienne, résultant d'une instabilité climatique reconnue dans toute l'Europe centrale et orientale.

IV List of Publications

1) **Rhodes, S.E.,** Ziegler, R., Starkovich, B.M., Conard, N.J., 2018. Small mammal taxonomy, taphonomy, and the paleoenvironmental record during the Middle and Upper Paleolithic at Geißenklösterle Cave (Ach Valley, southwestern Germany). Quaternary Science Reviews. 185, 199–221.

2) **Rhodes, S.E**., Starkovich, B.M., Conard, N.J., 2019. Did climate determine Late Pleistocene settlement dynamics in the Ach Valley, SW Germany? PLOS ONE. 14, e0215172

V Personal Contribution

Description of the extend and significance of the personal contribution according to § 6,2 PromO of the University of Tübingen. Numbers follow the order in III List of Publications

1) I was first and corresponding author, as well as the main person responsible for conceiving the study design, conducting the reported research, and lead author of writing the manuscript. The co-authors helped with difficult taxonomic identifications (Reinhard Ziegler), in writing the manuscript and providing editorial input (Reinhard Ziegler, Britt M. Starkovich, Nicholas J. Conard), were principal investigator and director of excavation at the site (Nicholas J. Conard) and oversaw the study as supervisor(s) (Britt M. Starkovich, Nicholas J. Conard).

2) I was first and corresponding author, as well as the main person responsible for conceiving the study design, conducting the reported research, and lead author of writing the manuscript. The co-authors helped in writing the manuscript and gave editorial input (Britt M. Starkovich, Nicholas J. Conard),), were principal investigator and director of excavation at the site (Nicholas J. Conard), sourcing funding for the SEM photographs (Nicholas J. Conard) and oversaw the study as supervisor(s) (Britt M. Starkovich, Nicholas J. Conard).

1.0 Introduction

This section will provide a brief and selective review of the history of Middle and Upper Paleolithic research including the following: the discovery and identification of the Neanderthal type specimen; the characteristics of Neanderthal and anatomically modern human material culture, social behaviour and the interaction between the two groups; the leading theories surrounding the biological and technological shifts which characterize the Middle to Upper Paleolithic transition; and the preeminent hypotheses put forth to explain the extinction of Neanderthal groups throughout Europe.

1.1 Neanderthals in the European Context

> *"Were this the skeleton of the oldest man, then the oldest man was a freak, and in antediluvian times, as today, there must have been malformed human beings such as are welcomed by the adherents of the teaching of the descent of mankind from the apes..."*
>
> *Mayer, 1864*

The first scientifically studied Neanderthal specimens were discovered during quarrying of the Klein Feldhofer Grotte in the Neander Valley, near Düsseldorf in 1856. Initially mistaken for cave bear bones, the calvaria and associated post-cranial remains which make up the Neanderthal type specimens were first described by Hermann Schaaffhausen, Professor of Anatomy at Bonn University and Johann Karl Fuhlrott, a local naturalist familiar with the circumstances of the discovery (Schaaffhausen, 1858). A number of prominent scientists examined and/or commented on the remains, including Charles Lyell, George Busk, Thomas Henry Huxley, and Charles Carter Blake (Madison, 2016) before William King, a geologist at Queen's College Galway in Ireland proposed the specimens be designated *Homo neanderthalensis*, a new species within the human genus (King, 1864). This designation was a pivotal step in the history of Neanderthal research in that it facilitated recognition of other *H. neanderthalensis* specimens, including the previously discovered remains from Engis, Belgium (Schmerling, 1833) and Forbes Quarry in Gibraltar (Menez, 2018). The nature of the relationship between modern humans and Neanderthals, sometimes referred to as *Homo sapiens neanderthalensis* (Hublin, 1983; Gunbin et al., 2015; Bennett, 2017), is still widely debated (Harvati et al., 2004; Harvati and Harrison, 2006). Likewise, many aspects of Neanderthal history and material culture have inspired significant debate, including the question of when and how Neanderthals evolved.

Neanderthals are temporally restricted to the Middle Paleolithic, which spans from 300,000 to 30,000 years before present (BP) and are commonly thought to have evolved from European *Homo heidelbergensis* populations (Hublin 1998; Dean et al., 1998; Leben et al., 2001), potentially anagenetically (Churchill, 2014). The *Accretion* model (Hublin, 1988, 2009) and the *Out of Europe* hypothesis (Serangeli and Bolus, 2008) place the evolution of the Neanderthal phenotype within Europe, whereas the *Local emergence* hypothesis suggests early populations at Tabun in Israel also underwent anagenic evolution while maintaining geneflow with European groups (Trinkaus, 1988 as paraphrased in Churchill, 2014; see Grün and Stringer, 2000 re: early dates for the Tabun C1 specimen). An alternative to this suggests climatic forcing drove European Neanderthals into the Levant during OIS 4 or 3 (Bar-Yosef, 1989), supporting a uniquely European ancestry for all Neanderthal groups

Neanderthal associated lithic technocomplexes include Clark's Mode III (Clark, 1969), in particular Levallois core reduction technology, the Micoquian (also known as the Keilmessergruppen), the Mousterian (De Mortillet, 1883), and the Châtelperronian (Breuil, 1909, 1910, 1911). The presence of hominin remains with Neanderthal characteristics within Châtelperronian deposits at la Roche a Pierrot, Saint-Césaire (Leveque and Vandermeersch, 1980; Morin, 2012) and at Grotte de Renne at Arch-sur-Cure (Bailey and Hublin, 2006) suggests exclusively Neanderthal authorship of this industry (also see Bar-Yosef and Bordes, 2010). Although contested by some (Higham et al., 2010; Gravina et al., 2018) many researchers accept these contextual correlations and attribute production of this transitional industry to Neanderthals, either as an independent cultural development (d'Errico et al., 1998) or as evidence of inter-species acculturation (Mellars, 1990; Hublin et al., 1996, 2012). Additionally, the association of personal ornaments and bone tools at Grotte de Renne (Hublin et al., 1996), as well as the Upper Paleolithic character of most Châtelperronian lithic assemblages (Harrold, 1981, 1983; Connet, 2002 but see Pelegrin, 1995; d'Errico et al., 1998) led to heated debate surrounding the cognitive and innovative capabilities of Neanderthals (Coolidge and Wynn, 2004) and the potential for inter-taxa interaction during the Middle to Upper Paleolithic transition (d'Errico et al., 1998; Mellars, 2005).

The first evidence for the production of composite tools during the Middle Paleolithic was recovered from the Micoquian levels at Königsaue, Germany, and consists of two pieces of birch-bark resin, one with the imprint of a hafted lithic point, directly dated to 43,800 ±

2,100 BP and 48,400 ± 3,700 BP (Hedges et al., 1998). Other examples of hafted tools followed this discovery (Solecki, 1992; Boëda et al., 1999; Rots, 2009, 2013; Villa and Soriano, 2010; Hardy et al., 2013) and the production of resin and the use of cordage, wood, and feathers are now commonly accepted parts of the Neanderthal toolkit (d'Errico, 2003) from as early as MIS 4 (Hardy et al., 2013; see also d'Errico, 2003 for contested earlier dates). Inherent in the argument for Neanderthal hafting abilities is the assumption that they utilized wood as a material for various types of spears, which is attested from the significantly earlier MIS 9 contexts at Schöningen (Thieme, 1999; Schoch et al., 2015), Clacton-on-the-Sea (Allington-Jones, 2015) and Lehringen (Movius Jr, 1950). Woodworking in other contexts is suggested by the wooden pseudomorphs found at Abric Romaní (Carbonell and Castro-Curel, 1992; Castro-Curel and Carbonell, 1995) and possible digging sticks recently recovered from Pogetti Vecchi (Aranguren et al., 2018).

The use of other organic raw materials during the Middle Paleolithic, particularly bone and antler, is more contentious. d'Errico (2003) suggests that bone points, although within the realm of Neanderthal tool-making capability, were incompatible with close-range hunting due to their 'soft nature' (see also Villa and D'errico, 2001). However, the bone tools from Salzgitter-Lebenstedt, which include at least one bone point (Gaudzinski, 1999) challenge this interpretation, and their presence at what may be a mass kill reindeer site (Gaudzinski and Roebroeks, 2000) has been taken by some to indicate the selective use of more reliable (i.e. durable) technology for large-scale resource harvesting (Churchill, 2014). Overall, Middle Paleolithic technology was variable, across both time and space, reflecting what may be adaptive responses to the broad ecogeographic range of Neanderthals (Churchill, 2014).

1.2 The Middle to Upper Paleolithic transition

> *"The (Middle to Upper Paleolithic) transition is like a greased*
> *pig—it is very elusive, slippery, hard to grasp in its entirety,*
> *and prone to generate misunderstanding."*
> *Clark, 2009*

Perhaps more has been written on the Middle to Upper Paleolithic transition than any other period of human prehistory. This is partially due to the nature of the evidence for this 'transition', which encompasses somewhat synchronous biological and cultural shifts, detectable in the archaeological, human paleontological, and genetic records (Clark, 2009). The exceptional level of academic focus on this period, which occurred sometime between

~50,000 and 30,000 BP primarily within Eurasia, is also due to its perceived ability to answer many key questions within modern human origins research, as well as existential questions such as 'what does it mean to be human?'. The dichotomies inherent in our early picture of the transition – archaic vs. modern, other vs. human – are also appealing in their simplicity. Hovers (2009) suggests that the assumedly 'self-explanatory' nature of the early physical evidence for the shift from a Neanderthal to Upper Paleolithic biological 'stage' lead to the development of various models of cultural evolution devoid of an overarching theoretical framework. This view was eventually challenged by the Levantine archaeological record (Vandermeersch, 1982; Rak, 1986; Bar-Yosef, 1998; Shea, 2008) and since then, the definition of this biocultural shift as a definable and sequential 'transition' has been challenged as well (Clark, 2009; Hovers, 2009).

Study of the Middle to Upper Paleolithic transition could be said to have begun in earnest at the end of the 19th Century when Edouard Lartet recognized differences between the Middle Paleolithic and Upper Paleolithic artifacts at Le Moustier (Lartet and Christy 1865 – 1875) and with de Mortillet's (1867, 1897) systematic classification of the UP flake based industries (Trinkaus and Shipman, 1993; Harrold, 2009). The uniquely striking nature of the technological shift from Middle Paleolithic to Aurignacian technologies, specifically, was first recognized by Breuil (1913) along with the coeval biological replacement of Neanderthals with 'Cro-Magnon' anatomically modern humans (AMH) in Western Europe. Breuil believed the Cro-Magnon hominins to be allochthonous, with a North African origin based on Garrod's (1938) discoveries at Skuhl Cave. Variations on this *Replacement model*, also known as the *Out-of-Africa model* or the *Population Replacement model* (Mellars and Stringer, 1989; Harrold, 2009), have since been widely applied in Paleolithic archaeology (White et al., 1982; Mellars and Stringer, 1989; Mellars, 1990, 1995, 2005; Bolus and Conard, 2001; Gilligan, 2007; Klein, 2008; Rigaud, Jean-Philippe, 2010; Bradtmöller et al., 2012).

The *Multiregional hypothesis* often presented as a contrasting model for modern human origins (Stringer and Andrews, 1988; Stringer, 2002), was first proposed by Wolpoff (1984) who credits Franz Weidenreich's *Polycentric hypothesis* as a guiding influence in its development (Wolpoff et al., 1988). Emphasizing continuous gene flow between hominin groups, this model suggests that the human fossil record represents a single continuous evolutionary lineage, and that the morphological differences proposed to indicate species distinctions are more correctly interpreted as clinal variation (Wolpoff et al., 2000, 2001; Stringer, 2002). A large number of variations on the Multiregional hypothesis and the replacement model have been proposed (see Clark, 2009; Stringer, 2010, 2014 for detailed summaries), however, a full description of each, and the heated debate they provoked, is beyond the scope of this thesis (but see Thorne and Wolpoff, 1992; Wolpoff et al., 2000; Stringer Chris, 2002; Clark, 2009; Hovers, 2009; Stringer, 2010, 2014; Otte, 2014).

The development of ancient DNA (aDNA) analysis in the 1980s and 1990s undermined the validity of the main tenants of the *Multiregional hypothesis,* particularly as the unique nature of the Neanderthal genome and the presence of African genetic lineages in modern European human populations became more evident (Cann et al., 1987; Nei, 1995; Relethford, 1998). These studies also revealed that interbreeding between multiple hominin groups had occurred, if rarely, which contradicts early formations of the *Out-of-Africa model* (Stringer, 2014; Caldararo, 2016). As such, the most widely accepted model within the modern human origins debate has been described as the *'mostly out of Africa" model* (Stringer, 2014).

Much of the confusion surrounding the timing and locations at which the Middle to Upper Paleolithic transition occurred has been traced to ill-defined concepts such as 'behavioural modernity' (Clark, 2009) and the Eurocentric nature of the defining attributes of such concepts (McBrearty and Brooks, 2000). It is now well documented that many of these attributes (i.e. the production of pigments and composite tools, long-distance raw material transport, and the exploitation of marine resources) arose in Africa during the Middle Stone Age (Henshilwood et al., 2003, 2004; Wadley, 2005, 2010; Backwell et al., 2008). Furthermore, it has been argued that these innovations did not arise gradually, but rather occurred at punctuated intervals in a spatially inconsistent manner (Klein, 2008), with some disappearing from the later Middle Stone Age record only to reappear at later periods (Hovers, 2006). Recent high-impact research also exemplifies the growing body of evidence for behaviorally modern characteristics within the Neanderthal material culture repertoire (d'Errico, 2003), including the possible symbolic use of marine shells and ochre (Heyes et al., 2016; Hoffmann et al., 2018) and bird feathers and talons (Finlayson et al., 2012; Radovčić et al., 2015; Majkić et al., 2017). Furthermore, it is now well recognized that the long duration of Middle Paleolithic occupation of Central and Western Europe, which spanned 250,000 years and multiple glacial and interglacial periods, likely required dynamic behavioural flexibility and both cultural and social adaptation to deal with shifting climates (Trinkaus and Shipman, 1993; Hovers, 2009; Richter, 2016). That much of the material evidence of this behavioural flexibility remains hidden, or is controversial in nature, is likely the result of various external processes such as research focus and taphonomic bias (Villa and Roebroeks, 2014).

1.3 Theories of Neanderthal extinction

> *Theory is the lifeblood of science, and the value of a theory lies*
> *not so much in whether it is ultimately proven to be true or*
> *false, but in its fruitfulness.*
>
> *Montagu, 1963*

The earliest arguments put forth to explain the extinction of Neanderthal groups across Western and Central Europe were clearly tied to the issue of modern human origins. If Neanderthals represent a phase in the continuum of human evolution culminating in *Homo sapiens*, as suggested by Hrdlička (1927), Weidenreich (1943), and Coon (1962) and supported by Müller-Beck (reply in Brace et al., 1964) and others, then their extinction was the result of anagenic evolution. Many researchers influenced by the Modern Synthesis (and the later Extended Evolutionary Synthesis) and early advances in population genetics supported variants of this explanation, although not without heatedly debating their peers on the active mechanisms of the model (see Dobzhansky et al., 1963).

Alternatively, some believed that the earliest Upper Paleolithic modern humans were contemporaries of Neanderthals, and therefore could not be directly descended from Neanderthal groups. However, early arguments of this type were often based off of infamously misidentified material including the skeletal remains from Swanscombe, Fontéchevade, the Caves of Grimaldi, and Piltdown (Brace et al., 1964). During the 1960s and 1970s, the lack of skeletal material of early AMHs from contexts dated to earlier than 35,000 BP or from outside of Europe meant that neither model was strongly supported, and the imprecise dating techniques available at the time added further confusion to the picture of human evolution available at this time (Brace and comments therein, 1964).

By the late 1980s, there remained a gap in the human skeletal record during the important period between 100,000 and 50,000 BP, however early AMH remains had been found in both Africa and the Levant (Stringer and Andrews, 1988 and ref. therein), lending much needed support to the *Out-of-Africa* hypothesis. Genetic studies identified sub-Saharan African populations as containing the greatest levels of genetic diversity, and genealogical trees of mitochondrial DNA (mtDNA) change pointed to an early (~290,000 – 140,000 years BP) branching event separating a number of highly genetically diverse African groups from other African and Eurasian populations (Cann et al., 1987; Stringer and Andrews, 1988). The dating of modern human remains from Mugharet-es-Skuhl and Djebel Qafzeh in Israel to between 80,000 and 120,000 BP (McDermott et al., 1993; Mercier et al., 1993) along with similar results from Omo-Kibish 1 in Ethiopia, and Border Cave, and Klasies River Mouth in South Africa (Aiello, 1993) effectively closed the chronological gap in our record of early human evolution, and confirmed the presence of modern humans outside of Europe by at least 50,000 years before the European Middle to Upper Paleolithic transition. Recent findings from Morocco may push the date for modern human presence in Africa back even further (Hublin et al., 2017).

As it began to appear more likely that Neanderthals had experienced some sort of rapid extinction event, explanatory scenarios hinging on the superiority of colonizing anatomically modern human groups became plentiful. Perhaps the earliest was put forth by Boule (1912), who contended that violent competition with colonizing AMH lead to the demise of archaic (i.e. Neanderthal) groups. Indeed, many claims have been made that skeletal remains of both Neanderthals and modern humans preserve evidence of damage incurred through conflict (Roper, 1969). The most compelling include Churchill et al.'s (2009) description and experimental replication of damage preserved on a rib from the Shanidar 3 Neanderthal, and the cranial damage preserved on a juvenile Neanderthal from the Châtelperronian deposits at St. Césaire (Zollikofer et al., 2002), however neither have been convincingly linked to intra-species conflict. Shea (2003) suggests that coalitionary killing (Wrangham, 1999) likely played a role in the competitive interactions between Neanderthals and modern humans, yet points out that the risk such conflict carried to small, isolated groups (e.g. the loss of individual lives) was likely prohibitively high.

Competition, particularly the evolutionary concept of competitive exclusion (Banks et al., 2008), is a common thread throughout most extinction theories. A recent review by Villa and Roebroeks (2014) identifies 11 main hypotheses which have structured our current thinking on the extinction of Neanderthals, nine of which incorporate (to some degree) the idea that AMHs out-competed Neanderthals in acquiring various resources. Additionally, they include two theories which posit that climate, particularly dramatic climatic change, was the driving force in Neanderthal extinction. These hypotheses are re-iterated in Table 1, and an updated discussion of the archaeological support and refuting evidence for each is briefly covered here.

Table 1 Hypotheses for the demise of the Neanderthals (adapted from Villa and Roebroeks, 2014).

1)	AMH had “complex symbolic communication systems” and “fully syntactic language”, while Neanderthals did not
2)	Neanderthals had limited capacity for innovations
3)	Neanderthals were less efficient hunters
4)	Neanderthal weaponry was inferior to AMH projectile technology
5)	Neanderthals had a narrow diet, unsuccessful in competition with AMH with their more diverse diets
6)	The use of traps and snares to capture animals was the exclusive domain of AMHs
7)	AMH had larger social networks
8)	The initial AMH populations entering Neanderthal territory were significantly larger than regional Neanderthal populations
9)	Hafting by AMH required complex procedures indicative of modern cognition, while Neanderthals hafting was a simple procedure using naturally available glues
10)	Cold climate around 40 ka was a factor in Neanderthal decline
11)	Eruption of Mount Toba volcano at 75 ka played an indirect role in Neanderthal extinction

Hypothesis 1. Symbolic Expression:

The major proponents of this hypothesis, emphasizing the competitive advantages of complex and symbolic communication, are Mellars (1989, 2005; Mellars and Stringer, 1989) and Conard (Conard, 2006, 2008, 2010, 2011), both of whom emphasize the growing body of evidence for complex symbolic expression in Middle Stone Age Africa (d’Errico et al., 2001, 2005) and Upper Paleolithic Europe (Bolus and Conard, 2001; Conard et al., 2009; Roebroeks et al., 2012; Wolf, 2013, 2015; Wolf et al., 2013; Velliky et al., 2018) as a defining trait of modern human behaviour. They contend that these behaviours likely reflect larger social networks and increased sense of group membership and cohesion, both of which provided advantages during times of resource stress and/or climatic change. Conard’s *Polycentric model* (Conard, 2008, 2010) posits that these behaviours, which include the production and use of portable figurative artworks, decorative beads, pendants and ornaments, figurative and zoomorphic paintings and carvings, and musical instruments, arose in multiple locations at different periods of human history in response to ecological and climatic pressures which characterize marginal regions of the early AMH geographic range.

Hypothesis 2. Neanderthal innovation

Mellars (1995, 1998) and Klein (2003) are credited with formulating the hypothesis that Neanderthal technology exhibits less innovative advancement, as reflected in the slow rate of change within Middle Paleolithic lithic industries, due to the limited cognitive capacities of Neanderthals and/or their small population sizes (Villa and Roebroeks, 2014). In this model, the advent of fully syntactic language within AMH groups is causally linked to their innovative potential, and is claimed by some to have resulted from a genetic mutation within the modern human lineage which took place around 50,000 BP (Klein, 1992, 2003, 2008). Opposing arguments compare the speed of technological change within the Middle Paleolithic of Central and Western Europe with that from the contemporary Middle Stone Age of southern Africa (Hovers, 2009; Porraz et al., 2013, 2013; Otte, 2014, 2017), and cite recent dates which suggest their industries endured for much longer than previously thought (Tribolo et al., 2009, 2013; Porraz et al., 2013). Population dynamic models are often cited as directly linking the innovative potential of a group to the overall population size (Powell et al., 2009), therefore suggesting that low density Neanderthal populations (see Hypothesis 7-8) had lower innovative potential, however, recent studies have begun to question this relationship (Vaesen et al., 2016).

Hypotheses 3 – 6. Neanderthal hunting capabilities

Binford (1981, 1985) was one of the earliest researchers to suggest that Neanderthals were hindered by a reliance on scavenging for meat protein compared to AMHs. A proliferation of evidence for large game hunting by Neanderthal groups has all but disproven this theory (Villa and Roebroeks, 2014 S1 and ref. therein), however, claims that Neanderthals lacked various technologies (i.e. projectiles, snares, and traps) and were restricted to ambush hunting using thrusting-spears, have since been proposed in its place (Berger and Trinkaus, 1995). Evidence for extensive trauma on Neanderthal skeletal remains is often invoked to support these theories, although a multiple studies now suggest that both Neanderthals and AMHs experienced similar levels of physiological trauma (Trinkaus, 2012; Beier et al., 2018). The evidence for bow-and-arrow and spear-throwing technologies in the Middle Paleolithic and/or Middle Stone Age is far more contentious and readers are directed to the detailed overview provided by Villa and Roebroeks (2014, S1) for more information.

Marean (2005) and O'Connell (2006) have suggested that Neanderthals had a narrow diet restricted to large herbivores, which inhibited their ability to compete with the more flexible AMHs who exploited a greater range of subsistence resources. Incorporating the idea that Neanderthals lacked the technology necessary to exploit small game and aquatic resources, this hypothesis is supported by a number of isotopic studies indicating higher nitrogen isotope ratios ($\delta^{15}N$) in AMHs, suggestive of a diet including a high amount of aquatic resources, and slightly lower nitrogen ratios in Neanderthals, indicative of the primarily terrestrial meat based diet of a 'top-level' carnivore (Richards and Trinkaus, 2009). As evidence refuting this theory, Villa and Roebroeks list 16 Mousterian contexts from Israel, Germany, France, Italy, Spain, and Gibraltar (2014; S1) which preserve the remains of small ungulates, rabbit, tortoise, and duck with cut-marks or anthropogenic fracture patterns. A temporal trend towards increased exploitation of small game in the Upper Paleolithic has been confirmed from other Eurasian sites (Stiner et al., 1999; Stiner, 2001; Hockett and Haws, 2005; Starkovich, 2012, 2014, 2017), including many in the Swabian Jura (Starkovich et al., in press; Conard et al., 2013) however, this pattern is more often linked to Upper Paleolithic demographic growth rather than a technological disadvantage among Neanderthals. Recent zooarchaeological, stable isotope and dental calculus analyses also suggest that Neanderthals were much more flexible in terms of exploiting small game and plant resources than previously suggested (Bocherens et al., 2016; Zaatari et al., 2016; Power et al., 2018; Morin et al., 2019) and may have even occupied the same ecological niche, and shared a similar diet, as early Upper Paleolithic AMHs in northern Central Europe (Wißing et al., 2016, 2019).

Lastly, Shipman has proposed that Upper Paleolithic groups may have had a distinct advantage over Neanderthal groups when hunting large game by utilizing pre-domesticated dogs (Shipman, 2015). While undisputed evidence of domesticated dogs doesn’t appear in the archaeological record until the early Holocene, claims for Upper Paleolithic examples come from Předmosti in the Czech Republic (Germonpré et al., 2012) and Goyet in Belgium (Germonpré et al., 2009) and lend tantalizing support to this theory.

Hypothesis 7 – 8. AMHs had larger social networks and larger population sizes.

The archaeological evidence in support of larger group sizes and increasing social networks over long distances in the Upper Paleolithic is relatively strong. Villa and Roebroeks (2014 and ref. therein) cite 23 cases documenting the transport of materials, primarily shells, over distances upwards of 300 km during the Aurignacian, Gravettian, and Magdalenian. However, there are some indications that raw material transport during the Middle Paleolithic may have spanned greater distances in Central and Eastern Europe than is reflected in the Western European record (Floss, H, 1990; Féblot-Augustins, 1999). Villa and Roebroeks point out that MSA groups in Eastern Africa likely had weakly defined intergroup contact based on the quantity and quality of raw materials transported (based on Ambrose, 2012 and contra to McBrearty and Brooks, 2000), however, similarities between contemporary groups in far distant geographic regions does not explain why these behaviours occurred.

Zubrow's (1989) computer model predicting Neanderthal extinction as the result of small demographic advantages in AMH birth rates, life span, or mortality rates is often cited in support of this hypothesis. However, more recent attempts at agent-based modelling provide conflicting results (Sørensen, 2011; Cucart-Mora et al., 2018; Roberts and Bricher, 2018). Mellars and French (2011) used artifact density data from the Aquitaine region of France to determine that population density increased by a factor of ~9 between Neanderthal and AMH groups, although this study has come under intense scrutiny (Dogandžić and McPherron, 2013). Despite inherent issues with calculating group size from the archaeological record, there is convincing evidence from the Swabian Jura that Neanderthal group population densities were uniformly low, and substantially lower than later Aurignacian groups when compared using the same set of variables (Conard et al., 2012). This conclusion is supported by the low number of anthropogenic features and inputs present in the Middle Paleolithic micromorphological record (Miller, 2015), as well. This patterning could also be obtained through a greater focus on group mobility within Neanderthal populations, which may be suggested in the human isotopic record (Richards et al., 2008). Hublin and Roebroeks (2009) also suggest that their position as top carnivores with high metabolic and energetic costs restricted Neanderthals to low population sizes and chronologically discontinuous occupation of regions on the periphery of their ecological range, resulting in repeated local extinctions alongside higher group mobility compared with AMH groups.

Lastly, the low genetic diversity reflected in the mtDNA of Neanderthal groups compared to modern humans suggests they likely suffered from genetic bottlenecks due to sudden declines in population size (Green et al., 2008; Hublin and Roebroeks, 2009). Dalen et al. (2012) propose a large-scale extinction event among Western European Neanderthals following their divergence from Eastern populations sometime between 55,000 and 77,000 BP, predating the arrival of AMHs. Furthermore, their results support Hublin and Roebroeks, (2009) model of repeated range expansion and localized extinction events concurrent with decreasing hospitality of Northern landscapes as a long-term cause for continued reduced genetic diversity within Neanderthal groups. These, and other studies of early hominin population genetics (Fu et al., 2016; Hajdinjak et al., 2018) support a picture of small, and periodically isolated Neanderthal groups occupying Western and Central Europe during OIS 3, particularly in comparison with later Upper Paleolithic populations.

Hypothesis 9. Hafting and cognition

At the heart of this argument is the idea that Neanderthals lacked the cognitive ability to produce compound adhesives; particularly the ability to multitask, think abstractly, and complete multiple steps in a recursive fashion, all of which require advanced working-memory

(Wadley, 2010). Additionally, compound adhesive production generally requires the manipulation of variables involved in the creation and control of fire. While taphonomic issues may be limiting our picture of Neanderthal pyrotechnological capabilities in general, as well as limiting the preservation of prehistoric adhesives, there is little evidence of this technology in the archaeological record before the Upper Paleolithic. Villa and Roebroeks (2014) cite evidence from Königsaue (Koller et al., 2001) and the Capitello Quarry (Mazza et al., 2006) suggesting an MIS 6 or 7 age for the development of compound adhesives by Neanderthals, although later evidence is also found at Inden-Altdorf (Pawlik and Thissen, 2011) and Umm el Tlel (Shimelmitz et al., 2014).

The extent to which Neanderthals were able to produce and control fire has also been questioned (Sandgathe et al., 2011; Dibble et al., 2018). This would factor into their ability to produce birch bark pitch, which requires distillation in an oxygen free atmosphere at precise temperatures (Villa and Roebroeks, 2014:e96424). Furthermore, an inability to produce fire at will would put Neanderthals at a clear disadvantage during periods of climatic stress (see Hypothesis 10 – 11 below). While there is plenty of evidence for Neanderthals using fire (Roebroeks and Villa, 2011) the strongest evidence we have of fire production includes modifications on pyrite and bifaces suggesting the use of the 'strike-a-light' method for fire production (Sorensen et al., 2014). Still, this issue remains contentious and there exists convincing evidence that the ability to produce fire may have been lacking in some Western European Neanderthal groups (Dibble et al., 2018).

Hypothesis 10 – 11: Cold climate due to the Heinrich 4 event, the Campanian Ignimbrite (CI) eruption or the Mount Toba (Sumatra) eruption

The volatile OIS 3 climate has long been invoked as a contributing factor in the extinction of Neanderthal populations across Europe. However, climatic instability and the resulting ecological destabilization and shifts in resource availability are rarely presented as primary or singular causes of Neanderthal extinction. This may be the reason that Villa and Roebroeks (2014) restricted their formal review to claims that the Campanian Ignimbrite (CI) and Mount Toba eruptions resulted in volcanic winter conditions which significantly affected the survival of Neanderthals and AMHs. While the presence of tephra deposits interstratified between final Middle Paleolithic and early Upper Paleolithic layers at sites in Montenegro, Greece, and Bulgaria (Fedele et al., 2002, 2003, 2008) could suggest these events played a role in at least some localized Neanderthal extinctions, the presence of similarly derived deposits within clearly Upper Paleolithic contexts in these same regions raises serious doubts as to the ecological effect this volcanic event invoked (Giaccio et al., 2006). Pollen records from Lake Malawi, which also contains ash deposits from the Mount Toba eruption, have all but disproven the hypothesized effect this volcanic eruption had on the ecological structure of East Africa and its early human populations. As such, there is little evidence that volcanic activity had any bearing in the cultural or biological transition from the Middle Paleolithic to the Upper Paleolithic in Eurasia. However, recognizing that the Middle to Upper Paleolithic transition occurred during a period of climatic instability has led many researchers to incorporate climate as secondary factors in their explanatory models.

Overall, the history of thought on the relationship between human evolution and climate is marked by a mid-Century academic backlash against the racist and eugenic rhetoric of early environmentally deterministic models (Livingstone, 2012 and ref therein). This lead to increased focus on cultural adaptation and the role of human agency in navigating external (particularly environmental) forces, beginning with the work of Boaz (1982). The increasing incorporation of environmental explanations in Neanderthal extinction scenarios from the 1990's onward was mostly driven by the results of two large-scale research projects: the Greenland Ice-core Project (GRIP) (Dansgaard et al., 1993), and the Stage 3 Project (Van Andel and Davies, 2003).

In addition to providing a long-duration and detailed isotopic record of climatic variability, the GRIP revealed that brief, high-frequency temperature oscillations of large amplitude characterized the period from 120,000 – 10,000 BP (Dansgaard et al., 1993). Named after the geochemist pioneers of ice core studies Willy Dansgaard and Hans Oeschger (Dansgaard et al., 1993), the Dansgaard-Oeschger events (D-O events) are recorded as oscillations in the oxygen isotopic ratios in Greenland ice core records corresponding to a succession of twenty-five interstadial (warm) to stadial (cold) episodes. Each D-O event corresponds to three phases of temperature change (measured at the altitude of the Greenland ice sheet) including (1) a gradual decrease of ~5 – 10°C that lasts ~600 – 2,000 years, (2) a rapid decline of ~5 - 10 °C lasting another 300 – 700 years and marking the peak stadial conditions (3) an abrupt increase of between ~3 °C and ~5 °C per century to interstadial conditions (Labeyrie et al., 2007). During the coldest stadial phases of five D-O events, large scale iceberg melting and the collapse of northern hemisphere ice shelves are registered in the ice core records due to the presence of ice rafted debris (IRD). Termed Heinrich (H) events, after Harmut Heinrich who first observed IRD as sand layers in sediment cores from the Northeast Atlantic (Broecker et al., 1990; Bond and Lotti, 1995), this influx of fresh water is believed to have altered the thermohaline circulation patterns of the oceans, causing global climatic fluctuations. The exact causes of these D-O events and associated H events are debated, and too numerous to explore here, although recent studies suggest they are related to changes in the size of the ice sheets (Zhang et al., 2014) and/or gradual shifts in atmospheric CO_2 changes (Zhang et al., 2017). Despite variation in the duration of the phases of D-O events, there is some evidence that the onset of these oscillations occurred periodically every ~1470 years during the past 50,000 years (Schulz, 2002).

This suggested to many that climate may have had a greater impact on human groups and their evolution during this time than previously assumed (Van Andel and Tzedakis, 1996; van Andel, 2003). The GRIP record is reliably dated by a combination of methods (Dansgaard et al., 1993) and can often be directly correlated with similarly well-dated regional records (Tzedakis et al., 2007). However, the extent to which the D-O oscillations affected terrestrial biomes is still in question, with various lines of evidence suggesting the amplitude of temperature changes decreased with distance from the Atlantic seaboard (Stringer et al., 2003; Dalen et al., 2012; Staubwasser et al., 2018).

The Stage 3 Project, which began in 1996 at the Godwin Conference on Oxygen Isotope Stage 3 (OIS-3) at the University of Cambridge, brought the role of climate into the forefront of academic discourse on the Middle to Upper Paleolithic transition. Furthermore, the climatic models and archaeological databases produced by this multidisciplinary project provided the opportunity to test hypotheses with, what was at the time, up-to-date data from across Europe. The project resulted in a number of high impact articles detailing how shifting landscape patterns may have shaped the resources available to Neanderthal and AMH groups during the OIS 3 period (Van Andel and Tzedakis, 1996; Davies, 2001; Van Andel, 2002; Van Andel and Davies, 2003) as well as a resurgence of single-cause (i.e. environmentally driven) theories of Neanderthal extinction (Stewart and Lister, 2001; John R. Stewart et al., 2003; Finlayson, 2004; Finlayson et al., 2004; Stewart, 2004, 2005).

Another theoretical development which can be traced back to these two multidisciplinary studies is the general revision of our picture of the Neanderthal ecological habitat. Claims that the Neanderthal phenotype was distinctly adapted to cold climates, in terms of both skeletal morphology and their metabolic and energetic requirements (Trinkaus, 1981; Smith et al., 1982; Trinkaus and Shipman, 1993; Holliday, 1997; Condemi, 1998; Steegmann Jr et al., 2002) had begun to be questioned (Aiello and Wheeler, 2003; Rae et al., 2011). Since then, a number of studies of Neanderthal biogeography (Richter, 2016; Benito et al., 2017; Nicholson, 2017) and paleoecology (Stewart et al., 2019) suggest that Neanderthals were better adapted to the warm-temperate semi-forested environments of the Mediterranean than the peri-glacial conditions of Northern Europe.

As such, there is currently a dichotomy between researchers that attribute the extinction of Neanderthal groups to (1) competition with modern humans as a result of climatic pressure and (2) climatic and environmental change alone (Stewart, 2005). The first group includes many of the researchers mentioned above, particularly Mellars (1995, 2002), O'Connell (2006), Hublin and Roebroeks (2009), Conard (2011), Sandgathe et al. (2011), Dalen et al. (2012), Shipman (2015), Dibble et al. (2018), as well as d'Errico et al. (1998), d'Errico and Sánchez Goñi (2003), Shea (2003), Hockett and Haws (2005), Svoboda (2005), Gilligan (2007), Banks et al. (2008), Collard et al. (2016), Staubwasser et al. (2018), and Morin et al. (2019) among others. In the majority of these models, climatic deterioration is seen as adding additional stress to already struggling Neanderthal groups, or providing opportunities for newly arrived AMHs to out compete the indigenous Neanderthals.

A commonly cited reason for excluding climatic change as the singular cause of Neanderthal extinction lies in the fact that Neanderthals successfully navigated other stadial and interstadial periods throughout their 250,000 BP occupation of Europe (d'Errico and Sánchez Goñi, 2003; Richter, 2016). However, as Finlayson (2004) points out, it may be naive to expect temporally disparate groups, even of the same species, to have similar responses to similar climatic events outside of the laboratory setting. Based primarily on his work at Gorhams Cave (Finlayson, 2004, 2008), he suggests that habitat loss and landscape fragmentation were the driving forces of Neanderthal population decline and their eventual extinction in Iberia, however he posits a more stochastic explanation for Neanderthal extinction elsewhere, which likely involved a variety of causal forces.

In a similar vein, Stringer et al., (2003) propose that the combination of dramatic temperature changes and the rate or amplitude of these changes near the end of OIS 3, which exceeded that of earlier periods, destabilized the local ecology and decreased the carrying capacity of the landscapes inhabited by already dwindling Neanderthal populations. The fact that AMH groups would have been subject to the same degree of 'climatic stress' is a clear issue, which he explains by appealing to potential 'dynamic adaptive strategies' and 'cultural buffering' among AMH groups (Stringer et al., 2003; 238).

Serangeli and Bolus (2008) present a model of repeated range expansion by Neanderthal groups from 'core-areas' within southern and southwestern Europe during interstadial periods. They emphasize that the moderate climates of the core-areas represent the real adaptive ecology of Neanderthals (perhaps equivalent to their realized niche) as evidenced by their continuous occupation of these regions, a fact emphasized by Hublin and Roebroeks (2009), as well. Both models argue that groups on the northern boundaries of the Neanderthal geographic range likely went extinct with the onset of cold periods associated with stadials and D-O events, although Hublin and Roebroeks emphasize the effect these localized extinctions would have had on the genetic variability of the Neanderthal population as a contributing factor in their demise. Serangeli and Bolus suggest that AMH groups colonizing areas left depopulated by Neanderthal groups gradually encroached on the Neanderthal 'core-areas' until Neanderthal groups were reduced to a few refuge areas, primarily in southern Spain and Croatia (Serangeli and Bolus, 2008; pg. 90). A pattern of staggered repopulation by AMHs of regions depopulated by Neanderthal groups during particularly cold and arid stadial periods has recently been identified in the Carpathians, through the analysis of regional archaeological, genetic, and speleothem records (Staubwasser et al., 2018). While the success of AMH populations in this scenario still hinges on being better adapted to cold, steppe environments, this study suggests that cyclical climatic deterioration may have driven shifts in the demographic pattern seen in many Central and Eastern European regions.

Lastly, working with the Stage 3 Mammalian Database, Stewart (2004, 2005) and Stewart et al. (2003, 2019) propose that the Neanderthal extinction can be seen as just one facet of a series of large mammalian extinctions and biogeographic shifts that took place as climate deteriorated towards the Last Glacial Maximum. Grouping Neanderthals alongside other 'interglacial survivors' such as *Stephanorhinus kirchbergensis, Stephanorhinus hemitoechus,* and *Elaphas antiquus*, they suggest that increasing cold temperatures and a related decrease in the carrying capacity of the landscape (also evidenced by decreasing mammoth populations) lead the interglacial survivors to retreat southward and, with regards to Neanderthals specifically, westward until their eventual extinction (Stewart et al., 2003). They suggest that the climate exhibited a greater degree of continentality in both Western and Central Europe during OIS 3, with particularly strong seasonality in the west, as evidenced by a non-analogous mammalian community structure. Taken to its most extreme, Stewart (2005) suggests that the non-analogue nature of the European landscape during this time, which he characterizes as a mosaic of temperate, boreal, an steppic regions, indicates that any recreation of the Neanderthal ecological niche based on the principle of uniformitarianism would be inherently flawed. While proponents of this model are clear in their assertion that there is no need to invoke competition or interaction with AMHs to explain the extinction of Neanderthals, they are somewhat vague when describing the forces driving the extinction of Neanderthals from their southern refugia regions, and fail to address the fact that AMH groups would have been subject to the same climatic forces towards the end of the Late Pleistocene.

As this brief overview has shown, experts are still far from agreement on which factor(s) played a role in the extinction of Neanderthal populations throughout Europe during the final stages of OIS 3. While most believe that competition with AMH was the driving force, the dramatically variable climate during this time cannot be entirely discounted. Villa and Roebroeks (2014) ultimately reject any single-cause hypotheses, and propose that the process was multifaceted and complex, including factors such as low population density and range retraction in Neanderthal groups, as well as interbreeding and cultural contact with AMHs, perhaps resulting in male hybrid sterility. Certainly, Neanderthal extinction was a *process* which took place over multiple millennia across a vast geographic area and accepting any singular cause for such a process would be naïve. What is more likely is that regional signals contradict each other due to the fact that different forces were in play in different regions. With new advances in the precision of radiocarbon dating producing a more reliable and high-resolution chronology of the Middle to Upper Paleolithic transition (Higham et al., 2012, 2014), new records of the demographic, cultural, and climatic conditions of specific regions are needed before a 'big picture' understanding of the driving forces at play can be achieved (Discamps and Royer, 2017). This is particularly true with regards to the effect that the unstable OIS 3 climate, as documented in the GRIP and NGRIP records, had on ecosystems within Central and Eastern Europe. The work detailed in this thesis represents a small but important step along that path towards a better understanding of the effect that climate had on Neanderthal and AMH population dynamics and behavioural adaptations across the European landscape.

1.4 The Middle and Upper Paleolithic archaeology of the Swabian Jura

1.4.1 The Swabian Jura

The Swabian Jura (German: *Schwäbische Alb*) is located in the modern state of Baden-Württemberg in southwestern Germany, and is defined by the Upper Danube Valley to the east and south and the Neckar Valley to the west (Bolus, 2015a). This karstic plateau formed of Jurassic limestone ranges from 500 to 1500 m.a.s.l. (Barbieri et al., 2018) and contains three archaeologically important river valleys formed by tributaries of the Danube river – the Ach, the Lone, and the Lauchert Valley. Within the Ach Valley, six cave sites have been identified as containing Middle and/or Upper Paleolithic deposits. These sites are shown in Fig. 1 and include Kogelstein, Hohle Fels, Sirgenstein, Geißenklösterle, Brillenhöhle, and Große Grotte.

In the Lone Valley, Haldenstein, Vogelherd, and Heidenschmiede caves and the Bockstein and Hohlenstein site complexes make up the Middle and Upper Paleolithic sites recognized as of yet. The Lauchert Valley contains the sites of Göpfelsteinhöhle, Annakapellenhöhle, Nikolaushöhle, and Schaftstall. Current research projects in this valley include renewed excavation at Schaftstall and re-analysis of the faunal material recovered from early 20th Century excavations at all four sites (G. Toniato, pers. comm.). Overall, the cave sites of the Swabian Jura are some of the most intensively studied sites in central Europe (Conard, 2015) making a complete history of archaeological endeavor in the region beyond the scope of the present study (for general review, see Bolus, 2015; Conard, 2015). As the focus of this thesis is on Hohle Fels and Geißenklösterle caves, a short review of the history of work at these sites follows.

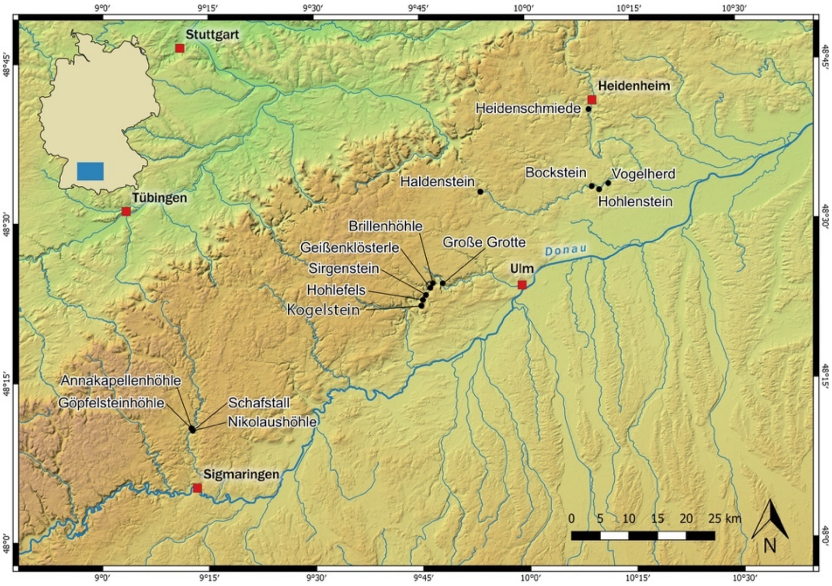

Fig. 1 Map of the Swabian Jura with all Paleolithic sites from the Ach, Lone, and Lauchert Valleys indicated (Map provided by C. Sommer).

1.4.2 Hohle Fels Cave

The Ach Valley likely formed during the early Pleistocene along the path of the Paleo-Danube, which followed the Jura Plateau between Ulm and Schelklingen before migrating southward to its current location at the beginning of the Last Glacial Period (Miller, 2015; Barbieri et al., 2018). Hohle Fels cave is located northeast of the town of Schelklingen and just 7 m above the modern Ach River (Bolus, 2015a; Miller, 2015) which flows into the Blau River, a tributary of the Danube (Miller, 2015). This impressively large cave site has a total volume of 6000 m^3 and includes a 30 m long tunnel passage with a small niche cut into both sides of the tunnel walls, ultimately leading to a 500 m^2 inner cave hall (Bolus, 2015b). Current excavation is focused on the niche area along the tunnel passage, however the earliest archaeological exploration of the site, undertaken by O. Fraas and T. Hartmann in 1870 and 1871, focused on the large cave hall (Schmidt, 1912). R.R. Schmidt continued work at Hohle

Fels in 1906 and published his results as part of the monograph *Die Diluviale Vorzeit Deutschlands* (Schmidt, 1912). Between 1958 and 1960 G. Riek explored the tunnel and cave hall, proving that undisturbed paleolithic deposits remained outside of the cave hall, but unfortunately his results were not published. In 1977, J. Hahn began excavation of the tunnel niche and, with an interruption between 1979 and 1988, excavation in this area has been ongoing annually under the direction of Hahn until 1996 and afterwards under the direction of N. Conard.

The formation of the archaeological strata in both the cave hall and the tunnel leading to the cave mouth are primarily attributed to wind-blown loess, limestone rubble from the roof and walls of the cave, and the downslope movement of sediments accumulated via a chimney and cracks in the hall roof which form a large cone of deposits near the back of the cave (Miller, 2015). Hohle Fels contains materials typologically and chronometrically attributed to the Middle Paleolithic, Aurignacian, Gravettian, Magdalenian, and Holocene. Within the Middle Paleolithic, four archaeological horizons have been delineated (AH IX – VI) which correspond to geological horizons 12 through 9. A hiatus in anthropogenic input is recognizable in the lower half of geological horizon 8 (Miller, 2015), while the upper half of this horizon marks the beginning of Aurignacian occupation of the site which can be divided into seven archaeological horizons (Vb, Vab, Vaa, Va, IV, IIIb, and IIIa) and seven corresponding geological horizons (7b/8, 7ab; 7aa, 7a, 7, 6b, and 6a). Horizon Vab and 7ab are not continuous across the whole site and therefore not present in all stratigraphic and sedimentological profiles. Above these deposits two transitional Aurignacian-Gravettian horizons have been documented, as well as another cultural hiatus followed by a sequence of 3 Gravettian horizons, one Magdalenian horizon, a period of mixed Magdalenian and Holocene materials, and finally purely Holocene deposits.

For the purposes of this thesis, I have looked at small mammal material from the Middle Paleolithic period and the initial Aurignacian (AH IV – Vb; GH 7 – 8) at Hohle Fels, which was excavated by both the Hahn and Conard teams. Continuous sedimentation rates have been suggested for the final MP (GH 8) and the earliest Aurignacian (GH 9) horizons at Hohle Fels (Miller, 2015) and calibrated radiocarbon dates place this technological transition between 39,900 to 44,200 cal BP (95% peak) with the highest probability of the end of the MP occurring between 44,000 and 42,000 cal BP (Bataille and Conard, 2018). The Middle Paleolithic lithic assemblage is made up primarily of Jurassic chert as well as radiolarite and quartzites which can all be sourced locally within 20 km of the Swabian cave sites (Conard et al., 2012). The tools are non-standardized (Bolus, 2015a) and are generally described as Swabian Mousterian based on the presence of clear Levallois cores and debitage (Conard et al., 2012; Bataille and Conard, 2018). The MP find density at Hohle Fels is low – a characteristic which is common throughout the Swabian MP sites (Conard, 2006, 2011; Conard et al., 2012) – although it exceeds that found at Geißenklösterle (see below). The Aurignacian material is characterized by a variety of typical tools including carinated and nosed endscrapers, burins, and various organic tools (Bolus, 2015b) of which split-based points are included from the very earliest deposits (AH Vb).

1.4.3 Geißenklösterle Cave

Geißenklösterle Cave was discovered by R. Blumentritt in 1958. The site is located 60 m above the Ach Valley floor and the entrance to the cave has partially collapsed. Riek opened a small test-pit within the cave shortly after its discovery and E. Wagner directed the first systematic excavation at the site in 1973 (Bolus, 2015b). Hahn continued excavation annually until 1991 and Conard renewed excavation at the site between 2000 and 2002, extending the depth of the excavation through the Middle Paleolithic and reaching bedrock in some areas. Hahn published a monograph on his early finds and their implications in 1988 (Hahn, 1988) while another edited collection focused on the faunal and floral records from the site was recently published (Conard et al., 2019).

Geißenklösterle contains deposits attributed to the Middle Paleolithic, Aurignacian, Magdalenian, and Mesolithic and Holocene periods. A hiatus of cultural inputs is also recognizable at Geißenklösterle (GH 17). Similar 'hiatus' periods have been recognized at Sirgenstein, also located in the Ach Valley, and Vogelherd cave in the Lone Valley. The Middle Paleolithic deposits include 6 geological horizons (GH 23 – 18) and 5 archaeological horizons (VIII, VII, Vi, V, and IV). The Aurignacian deposits include geological horizons 11, 12, 13, 14, and 15/16 and archaeological horizons IIn, IIa, IIb, IId, III, IIIa, and IIIb. These archaeological layers were originally defined by Hahn (1988), however, after extensive work refitting the Aurignacian lithic material revealed clear admixing of the deposits (see Teyssandier et al., 2006 for more details) he argued that the material should be considered as two cultural units – Unit II comprising AH IIn, IIa, and IIb and attributed to the Aurignacian and Unit III including AH IId, III, IIIa, and IIIb (Hahn, 1988; Teyssandier et al., 2006) which Hahn attributed to the Proto- or Pre-Aurignacian.

Thermoluminescence (TL) dating of burnt flints and electron spin resonance (ESR) dating of teeth yielded a date of ~40,000 BP from Unit III and ~38,000 BP from Unit II (Richter et al., 2000). The dozens of radiocarbon dates derived from bone and charcoal at Geißenklösterle do support an early date for these Aurignacian deposits (Conard and Bolus, 2003a, 2008), however they also show wide variation and, in some cases, inconsistency with the stratigraphic sequence of the site (Conard and Bolus, 2008; Higham et al., 2012) despite the use of several different radiocarbon laboratories. Conard and Bolus (2003) suggest that these discrepancies may be due to fluctuations in the radiocarbon production rate or a combination of variable radiocarbon production and other biasing factors increasing the difficulty in producing accurate dates older than 30,000 BP (Conard and Bolus, 2008). Alternative interpretations stress the possibility of post-depositional mixing resultant from cryoturbation and rock falls (Zilhão and d'Errico, 1999, 2003) to explain the anomalous dates. However, various lines of evidence derived from stratigraphic taphonomic, technological, and micromorphological analysis indicate that the degree of mixing was not substantial and unlikely to account for the discrepancies seen in the radiocarbon record (Hahn, 1988; Conard et al., 2003; Teyssandier and Liolios, 2003; Miller, 2015).

Using the ultrafiltration pre-treatment method which claims to eliminate more modern contaminants than traditional methods and therefore produce more accurate (i.e. older) radiocarbon dates, Higham et al. (2012) produced a series of AMS dates for Geißenklösterle based on previously sampled and new materials. The resulting dates are significantly older than most previously published ^{14}C dates and fit well with the stratigraphic sequence of the site (Higham et al., 2012: Figure 4). These results suggests that the Early Aurignacian (Level III) dates to ~43,000 – 41,000 cal BP, overlapping slightly with the Aurignacian (Level II) which dates to ~42,000 – 39,000 cal BP (Higham et al., 2012: Figure 7). This places the Early Aurignacian at Geißenklösterle within the earliest phase of Upper Paleolithic occupation in Europe. Furthermore, these dates suggest that the Swabian Upper Paleolithic pre-dates the H4 cold event, as well as many Proto-Aurignacian and early Aurignacian occupations elsewhere (Higham et al., 2012). The authors report a single ultra-filtrated ^{14}C date of 48,600 ± 3200 BP (OxA-21741) for the Middle Paleolithic at Geißenklösterle, which suggests that the material below AH VII/GH 21 dates to around the radiocarbon limit of ~50,000 BP (Higham et al., 2012: pg. 9). Previous attempts to date the Middle Paleolithic at Geißenklösterle produced a ^{14}C record that did not clearly increase in age with depth (Conard and Bolus, 2003a, 2008) with some dates being younger than Upper Paleolithic dates (Bolus, 2011). This is true for the dating record at Hohle Fels, as well (Bolus, 2011), and therefore both of these cultural sequences can only be said to date to before 50,000 BP.

1.4.4 The Upper Paleolithic Cultural Fluorescence

The early Aurignacian dates from Geißenklösterle also have important implications on our understanding of the development of the wide variety of cultural innovations for which the Aurignacian technocomplex is known. A key feature of the Swabian Aurignacian techno-complex is the fact that it appears with what has been termed the 'full package of early Upper Paleolithic innovations' (Bolus, 2015b: pg. 43). Furthermore, these innovations occur within the very earliest deposits of the period. Split-based bone points have been found in the basal Aurignacian layers (AH Vb) at Hohle Fels, and are otherwise found at Bockstein, Vogelherd, and Geißenklösterle (Conard, 2015). Other organic tools such as ivory projectile points have been found in the lowermost Upper Paleolithic horizons at Geißenklösterle and Hohle Fels (Bolus, 2015b), as well. The variety of new retouched stone tool forms in the early Swabian Aurignacian further suggests the early arrival of a fully formed Aurignacian material culture (Conard and Bolus, 2003b).

The symbolic and musical artifacts for which the Swabian Aurignacian and Gravettian are most well-known are also among the earliest such finds in the world, with many, including the ivory Venus figurine from Hohle Fels, dating to as early as 40,000 BP (Conard, 2009; Bolus, 2015b). Articles of personal adornment, particularly perforated teeth and ivory beads and pendants, are also documented from throughout the Aurignacian period in both the Ach and Lone valleys (Wolf, 2013) with double perforated beads, a characteristically Swabian bead form, being found throughout the entire sequence of Aurignacian deposits at Hohle Fels and within the earliest Upper Paleolithic deposits at Geißenklösterle (Wolf, 2013; Wolf et al., 2013; Bolus, 2015b). The presence of bone and ivory flutes at Geißenklösterle, Hohle Fels, and Vogelherd, the earliest relatively dated to at least 40,000 BP, suggests that musical performance was also a part of the Upper Paleolithic cultural repertoire of the earliest Aurignacian groups in the region (Conard et al., 2009).

The early presence of this complete suite of innovative Aurignacian technologies and forms of symbolic expression in Swabian suggests that AMHs must have moved into southern Germany rapidly following their initial migration into Europe– a key aspect of the Danube Corridor model (Conard, 2002; Conard and Bolus, 2003). Broadly coeval dates from sites along the Danube river, including those from Peștera cu Oase (Zilhão et al., 2007) and elsewhere in the Carpathian Basin (Chu, 2018), support the possible use of the Danube as a migratory pathway, as does the presence of other Aurignacian sites in the Swabian region dated to between 38,000 and 40,000 cal BP (Jöris et al., 2010; Kind et al., 2014 in Hussain and Floss, 2016). The strikingly early dates for the Willendorf II Aurignacian suggested by Nigst et al. (2014) also support this model, although they are not universally accepted (Teyssandier and Zilhão, 2018). More conservative dates for the Willendorf II Aurignacian, as well as those from Kilberg-Kirche (Uthmeier, 1996) and other Upper Paleolithic sites along the middle and lower Danube (i.e. Bacho Kiro) support a continued occupation of the Danube region following initial migration (Bolus and Conard, 2001; Conard and Bolus, 2003a; Chu, 2018). The presence of Franconian tabular chert in the Swabian Gravettian assemblages also suggests a continued use of the Danube region as an east-west conduit of human migration long after initial occupation of central Europe (Burkert and Floss, 1999; Floss and Kieselbach, 2004; Hussain and Floss, 2016).

However, the occurrence of such a complex and regionally homogenous symbolic tradition as that seen in the Swabian Aurignacian has not yet been documented elsewhere in the Mid- and Lower Danube region. Conard and Bolus (2003) acknowledge this may indicate the Aurignacian and Gravettian arose in or nearby the Swabian Jura, but are quick to note that earlier dates from other regions would easily refute this hypothesis. This argument is similar to that of Hussain and Floss (2016), who invoke Davies' (2001) two-phase dispersal model when suggesting early Aurignacian assemblages along the Danube are unlikely to match the 'cultural heritage' develped within Swabian (Hussain and Floss, 2016: pg. 1177). To explain the development of this homogenous symbolic tradition within Swabia, Conard and Bolus (2003) proposed the *Kulturpumpe model,* a series of non-mutually exclusive hypotheses. These hypotheses are:

1) The cultural fluorescence leading to the dramatic increase in symbolic expression and technological advancement is the direct result of the competition between archaic *(Neanderthal)* and modern humans following the initial coloinzation of the upper reaches of the Danube by modern humans around 40,000 BP.
2) These cultural innovations result from innovative problem solving in connection with climatic stress in the harsh environment of the northern foothills of the Alps. Greenland ice cores and other data document a series of major climatic shifts during OIS 3. These dramatic climatic shifts happened within decades and certainly strained the social-economic patterns of the hominins living in Swabia.
3) Cultural innovations of the Aurignacian and Gravettian occurred in connection with social-cultural and demographic changes independent of competition with Neanderthals or the influence of climatic stress. In other periods, important cultural

> innovations are by no means invariably linked to inter-taxa competition or direct responses to environmental change.

The possibility of competition between Neanderthals and modern humans in the Swabian Jura is unlikely, as suggested by the presence of cultural hiatus periods interstratified between the MP and UP at Hohle Fels, Geißenklösterle, Sirgenstein and Vogelherd. The presence of hiatus periods, combined with the high numbers of arctic micromammals found within the Sirgenstein hiatus by Schmidt (1912), lead to the formation of the *Population Vacuume model*, which suggests AMHs occupied the Swabian Jura only after Neanderthal populations had abandoned the region as a consequence of a dramatic cold event (Conard and Bolus, 2006; Conard, 2011). Original connotations of the model suggested the H4 event may be related to this depopulation, however the dates from Geißenklösterle make this unlikely (Higham et al., 2012). With multiple models positing that climate played a role in the settlement dynamics of the Swabian Jura, a number of studies have explored the paleoenvironmental history of the region and the results of these studies are summarized in the following section.

1.5 The Middle and Upper Paleolithic Ach Valley paleoecological record

Our current understanding of the paleoecology of the Ach Valley is derived primarily from sedimentology (including micromophological analysis), the limited botanical record, and faunal analysis (including stable isotope analysis). A brief review of the existing evidence from each of these material records by cultural period is included below.

1.5.1 The Middle Paleolithic paleoenvironmental record

Miller's (2015) micromorphological work at Geißenklösterle and Hohle Fels documents a number of cold/warm osscilations in the Middle Paleolithic and Upper Paleolithic deposits at the sites. The presence of iron depleted clay in the basal deposits of the Middle Paleolithic at both sites suggests the caves were active karstic environments during this time (Miller, 2015). It is important to note that this sedimentary correlation does not necessarily indicate a chronological correlation, as evidence of a continued karstic environment extends throughout the earliest Middle Paleolithic horizons at both sites (GH 23 – 21 at Geißenklösterle and 12-11 at Hohle Fels) (Miller, 2015; pg. 155). Furthermore, exacation at Hohle Fels has yet to reach bedrock. Campen's (1990) sedimentary analysis suggests a moderately cool event beginning during the depostion of GH 19 at Geißenklösterle and continuing until the early Aurignacian (GH 16). They also define the Middle Paleolithic as a predominantly wet environment, based on evidence of alternating periods of heavy and light soliflucation (Campen, 1990; Miller, 2015). This differs from Miller's (2015) characterization of this period as a succession of cold-period deposition with evidence of freeze-thaw events, overwritten by phosphatization and bioturbation during warmer periods (Miller, 2015; pg. 140). Campen (1990) characterizes the hiatus period at Geißenklösterle (GH 17) as colder and damper than preceeding periods, while the micromorphological analysis suggests it began as a cool event that quickly ameliorated, as exemplified by extensive phosphatization and localized clay coatings at both Geißenklösterle and Hohle Fels caves (Miller, 2015; pg. 157). An erosional event is documented at the very top of GH 17 at Geißenklösterle (Conard et al., 2003; Dippon, 2003; Miller, 2015; Goldberg, P. et al., 2019) and is overlaid by deposits with charcoal and burnt bone fragments, suggesting a clear end to the hiatus and the potential loss of some early Aurignacian anthropogenic inputs (Miller, 2015).

There are few other paleoenvironmental records of the Ach Valley during the Middle Paleolithic due primarily to preservation and sample size issues. However, Ziegler's (2019) work with the small mammal record from Geißenklösterle suggests mesic climatic conditions prevaled during the Middle Paleolithic, with particularly warm summers suggested by the low proportion of 'cold' species (i.e. *Dicrostonyx*) in the assemblage. He also notes an increase in forest adapted species, particularly the Holarctic tundra vole (*Microtus oeconomus*) during the final MP horizons (Ziegler, 2019). The herpetofaunal record from Geißenklösterle suggests relatively cold conditions during the Middle Paleolithic, however this is due to limited species representation as a result of poor material preservation (Böhme, 2019). Cave bear (*Ursus spelaeus*) dominate the large faunal record from both Hohle Fels and Geißenklösterle during this time, with much lower proportions of horse (*Equus* sp.), wooly rhino (*Coelodonta antiquitatis*), mammoth (*Mammuthus primigenius*), ruminants (ibex/chamois), cervids (red deer/reindeer), carnivores (*Canis lupus* etc.) and small game (Conard et al., 2013). However, a decrease in the presence of bears and carnivores can be seen through time, as well as an increase in the proportion of reindeer to other cervids between the Middle Paleolithic and Aurignacian in both the Ach and Lone Valleys (Starkovich et al., in press). This suggests an increasingly cold climate and expanding tundra landscapes. Stable istope analysis of horse tooth carbonates from Sirgenstein suggest decreasing temperatures through time (into the Gravettian period) of between 2°C and 4°C (Bertacchi, 2017)[1].

The faunal remains from Große Grotte (Weinstock, 1999) suggest that the majority of the assemblage was deposited during a stadial period within the first half of the Würm (Weichselian) Glacial based on the presence of *Mammuthus, Coelodonta, Equus, Rangifer, Microtus gregalis, Dicrostonyx gulielmi,* and *Lemmus lemmus*. However, since refitted cave bear remains suggest that the material was likely mixed post-depositionally, the material was considered as a single-period accummulation and a more detailed picture of the landscape cannot be derived from the faunal record. The small mammal material from Kogelstein (Ziegler, 2000), which was also treated as a single assemblage, suggests the occurrence of at least one forest dominated interstadial period in the Ach Valley Middle Paleolithic record, based on the relative abundance of the water vole, *Arvicola terrestris*. However, the lack of taphonomic consideration in this study leaves open the possibility that the small mammal material was accummulated by a seletive predator, such as the European eagle owl which is known to have a preference for the large-bodied water vole (Cantrell, n.d.; Andrews, 1990). As such, the signal for open forests and waterways from Kogelstein should be considered cautiously until substantiating evidence is found. Ziegler (2000) attributes this material to an interstadial period between Greenland Insterstadial (GIS) 13 and 16 based on the biostratigraphic small mammal record.

1.5.2 The Aurignacian Paleoenvironmental record

The early Aurignacian at both Hohle Fels and Geißenklösterle is marked by evidence of primarily cold and dry environments. At Hohle Fels, Miller (2015) describes the contact between GH 8 and GH 7 as indicating a substantial change in temperature and a decrease in the presence of water within the deposits indicated by decreased phosphatization. At Geißenklösterle, this shift is seen in the presence of ice lensing features cross cutting the erosional contact of GH 17 and GH 15 (Miller, 2015; pg. 141). The pattern of oscillating cold/dry and warm/moist depositional periods continues throughout the Aurignacian (Miller, 2015) and is documented in all sedimentological studies at the site. Laville and Hahn (1981) also suggest that the earliest Aurignacian at Geißenklösterle is marked by a shift from mild and

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[1] These results should be considered tentative until new radiocarbon dates on the sampled materials confirm their chronological position as some indications that material may have been mixed during or post-excavation have come to light (A. Bertacchi, pers.comm.).

humid conditions to colder temperatures between GH 16 and GH 15. Their climatic record also documents a number of cold to warm oscillations based on increasing and decreasing evidence of cryoclastism and patterns in the sedimentation of allochthonous materials (summarized in Miller, 2015; pg. 20). These include a warm and dry period in GH 13 and 14 followed by lowering temperatures in GH 12, then evidence of increased moisture during a warm period in GH 11 and 10, and finally an osscilation between cool and wamer temperatures in a broadly humid context between GH 9/8 and GH 7 (summarized by Miller, 2015; pg. 20). Campen's (1990) and Miller's (2015; pg. 155) climatic records for this period at Geißenklösterle are broadly similar.

The stratigraphic sequence of upper Aurignacian horizons at Hohle Fels is marked by a number of laterally discontinuous layers and indications of a significant change in temperature as well as water saturation and biological activity (Miller, 2015; pg. 109). The deposits within GH 7, the only laterally continuous horizon, exhibit a platy structure and decreased phosphatization compared to earlier deposits, suggesting relatively colder conditions during its formation (Miller, 2015; pg. 108). The overlying laterally discontinous deposits (GH 6a, 6a bef.1, 6b, 5 and 3bd) are described by Miller as 'strikingly different than GH 7 or any other layers from Hohle Fels' (2015; pg. 108) due to their discontinuous nature and unique matrix components, which are primarily clay but also include a large anthropogenic feature (GH 6a bef.1), evidence of rock falls (GH 5), and guano (GH3bd). Evidence of increased water energy and biogenic agents within these horizons also indicates a change in the active site-formation processes and a potentially significant increase in temperature (Miller, 2015; pg. 108-109). High proportions of *éboulis* within GH 5 have been interpreted as indicitive of a colder climate (Campen, 1990; Laville et al. 1980 cited in Miller, 2015), however Miller points out that a lack of fine sediment (i.e. loess) deposition during this time would give the same indication, while actually resulting from warmer and wetter conditions (2015; pg. 109). Overall, the climatic signal from the Aurignacian sedimentary record at Hohle Fels is less clear, and includes fewer instances of pronounced variability, than that of Geißenklösterle. It should be noted, however, that Goldberg, Miller and Conard (Goldberg et al., 2019) found that frost related microfeatures were more pronounced in the Hohle Fels micromorphological samples in all layers than in those from Geißenklösterle, suggesting this site may have had more moisture content throughout the Aurignacian than elsewhere in the Ach Valley (Miller, 2015; pg. 26).

Botanical remains, including pollen and wood characoal, were recovered from the Aurignacian, Gravettian and Magdalenian deposits at Hohle Fels, although preservation quality was a major factor in limiting the sample size of both material types (Riehl et al., 2015). Six species were recognized in the wood charcoal record, with pine (*Pinus sylvestris/mugo)* being dominant in the early Aurignacian (GH 8 and 7) and willow (*Salix arctica/reticulata*) becoming increasingly present in the upper Aurignacian (GH 6). This suggests the presence of a taiga or forest-steppe biome around Hohle Fels in the early UP with extending snow-covered tundra in later periods (Riehl et al., 2015). Pollen was not recoverable from the early Aurignacian, but limited samples from the upper Aurignaican and Aurignacian/Gravettian transition include cold steppe and woody species with willow continuing to increase in prominence throughout the Gravettian (Riehl et al., 2015). Palynological studies of the UP from Geißenklösterle (Hahn et al., 1977) reveal a similar climatic signal, with tree pollen (*Pinus* and *Betula*) accounting for only 25% of the pollen sample and the remaining vegetation suggesting a generally open environment throughout the Aurignacian and Gravettian periods.

The small mammal record from Geißenklösterle for this period somewhat contradicts the botanical record, as the dominance of cold-adapted taxa (*Dicrostonyx* and to a lesser degree *Lemmus*) suggests that snow-covered tundra was more prominent on the landscape (Hahn et al., 1977; Münzel et al., 1994; Ziegler, 2019). In early studies, boreal adapted species were found in very small amounts (NISP = <5) on average throughout the Upper Paleolithic deposits (Hahn et al., 1977; Münzel et al., 1994). Despite a greater sample size, Ziegler (2019) reports similarly low proportions of forest inhabiting bats and rodents throughout the Aurignacian period. Additionally, his study documents a clear decrease in boreal species from the early to the upper Aurignacian suggesting a decrease in forest patches (e.g. *Microtus oeconomus* decreases from 16.2% of the assemblage in GH 8 to 6.0% in GH 6) (Ziegler, 2019). This community structure remains stable until the Gravettian/Aurignacian transition (GH 5a) when *Myodes glareolus*, the forest-adapted bank vole, becomes more numerous in the small mammal record (Ziegler, 2019).

In the large faunal record, the Aurignacian is characterized by a decrease in the presence of bears and carnivores at the Ach Valley sites and an increase in the amount of small game (Starkovich et al., in press). The latter is particularly marked in the avian record at Sirgenstein (Bertacchi, 2017). However, these trends are likely reflective of human engagement at the sites and the density and/or intensity of site occupation, which artifact density counts suggests was substantially higher during the Aurignacian period (Conard, 2011; Conard et al., 2013). Conversely, an increase in the percentage of reindeer to other cervids between the MP and Aurignacian in both the Lone and Ach valleys is likely driven by both the hunting behaviours of the Upper Paleolithic groups in the region and changing (i.e. cooling) environmental conditions (Starkovich et al., in press). Similarly, shifts in the proportion of Irish elk

(*Megaloceros giganteus)* and saiga antelope (*Saiga tatarica*) between the Middle Paleolithic and Upper Paleolithic at Geißenklösterle has been suggested to reflect changing vegetation from open grasslands to cold and dry steppe biomes (Münzel et al., 1994). Anomalous signals from the herpetological (Böhme, 2019) records from Geißenklösterle suggest a mesic and humid climate during deposition of GH 12, 9/10, and 6/7 which may mark interstadial periods, however this evidence contradicts the sedimentological and faunal records.

Lastly, the small mammal record from Brillenhöhle contains very few specimens for all layers except the most recent Aurignacian (VII) which is dominated by cold tundra adapted species such as *Dicrostonyx torquatus, Lemmus lemmus* and, to a lesser extent, *Arvicola antiquus* (Storch, 1973a). The presence of the ground squirrel, *Spermophilus superciliosus* (*Citellus* cf. *superciliosus*), suggests that open grasslands were present, as well, and that the general make up of the landscape was an open cold steppe (Storch, 1973a).

2.0 Objectives and expected output of research

The primary goal of this thesis is the creation of a high resolution small mammal-based paleoenvironmental record spanning the Middle Paleolithic and earliest Upper Paleolithic of the Ach Valley, which can be integrated with other existing and future paleoecological data to explore the context of the Neanderthal depopulation of the Swabian Jura. This includes the application of a detailed taphonomic analysis to ensure the quality of this paleoenvironmental record in representing past climate and landscape patterns. Despite a long history of small mammal research throughout Germany (Schmidt, 1912; Storch, 1973a, 1973b, 1974; von Koenigswald, 1974; Hahn, and von Koenigswald, 1977; van Kolfschoten, 1990, 1994, 2014; Ziegler, 2000, 2019; Maul, 2002; Maul et al., 2013; Koenigswald and Heinrich, 2007) detailed study of the accumulation of microvertebrate remains within German Paleolithic contexts and the inherent biases introduced by such processes has been absent prior to the publication of the manuscripts included in this thesis (Appendix 1.1, Rhodes et al., 2018; Appendix 1.2, Rhodes et al., 2019). The final goal of this study involves re-assessing the applicability of environmentally driven explanations for the depopulation of the Ach Valley by Neanderthal groups and placing the newly produced paleoecological data within our current understanding of Neanderthal behaviour, population dynamics, and mobility at the end of OIS 3 (~60,000 – 35,000 cal BP) with the objective of eliciting new hypotheses which may explain the loss of Neanderthal populations in the Swabian Jura shortly before the arrival of AMHs. To achieve these goals this research project was structured around five broad questions:

1) How did the small mammal material accumulate in the caves?
2) What was the climate and landscape like in the Ach Valley during the Middle Paleolithic period (~60,000 – 45,000 cal BP)?
3) What was the climate and landscape like during the periods of occupation hiatus directly following the Middle Paleolithic?
4) Is there any evidence of a 'cold snap' or drastic increase in cold and arid environments leading up to or at the time of Neanderthal abandonment of the valley?
5) What was the climate and landscape like when Aurignacian groups first arrived in the Ach Valley (~42,500 cal BP)?

These questions are explored in detail for the material studied from Geißenklösterle Cave in Rhodes et al., 2018 (Appendix 1.1) and for the material studied from Hohle Fels Cave in Rhodes et al., 2019 (Appendix 1.2). Preliminary results, as well as various aspects of the taxonomic and taphonomic analyses included in this project have been presented at a number of professional congress' and conferences over the past 4 years, including meetings of the Hugo Obermaier Society for Quaternary Research and Archaeology of the Stone Age, the European Society for the study of Human Evolution (ESHE), the International Union of Prehistoric Science and Protohistory (UISPP), the International Council of Archaeozoology (ICAZ), and as part of the Universität Tübingen Institut für Naturwissenschaftliche (INA) Kolloqium series, the Tübingen Paleobiology Seminar of the Biogeologie Arbeitsgruppe, the University of Toronto Archaeology Center Colloquium series and the University of Toronto Earth Sciences Rockfest series.

The current milieu of prehistoric archaeological research could arguably be described as focused on the spectacular and/or unique (Wadley, 2014). This emphasis has, in some cases, lead to grand claims that singular answers can be found for complex archaeological questions. A major component of this thesis focuses on producing detailed comparative data which contributes to our understanding of Neanderthal lifeways and extinction, without claiming to answer the big questions of this field in their entirety. It is the firm belief of the author that answers to important questions, such as why and how Neanderthals went extinct, how these groups and modern humans interacted, and how climate change affected these ancestral groups (and will affect modern populations going forward) can only be answered by careful study of local, regional, and landscape scale records derived from reproducible, high-resolution, multi-scalar data derived from diverse archaeological material records. This thesis represents a step along that path and will hopefully survive as a significant, if singular, contribution furthering of our understanding of our vibrant and complex shared past.

3.0 Methods

3.1 Sample

The material analyzed from both Hohle Fels and Geißenklösterle caves was chosen to obtain a relatively uninterrupted stratigraphic sequence spanning the early Aurignacian through to the lowest Middle Paleolithic deposits. At Geißenklösterle this includes material from quadrants (Qu.) 56, 66, and 58 (Appendix 1.1; Rhodes et al., 2018, Fig. 2). Along with Qu. 57, 65, and 67, which were sampled for microfauna in previous studies (Ziegler, 2019), these excavation units comprise the only quadrants at the site with an uninterrupted sequence of Middle Paleolithic and Upper Paleolithic deposits. At Hohle Fels, material from Qu. 30 was preferentially chosen as this unit produced numerous cultural and symbolic finds (including the Hohle Fels Venus figurine) as well as a number of reliable radiocarbon dates. However, as excavation has not yet reached the lowest Middle Paleolithic in this excavation area, material from Qu. 25 was used to complete the stratigraphic sequence (Appendix 1.2; Rhodes et al., 2019 Fig. 2).

The Aurignacian sample from Geißenklösterle includes material from Hahn's excavations from 1973 to 1993 (~GH 11 – 14) and Conard and Malina's excavation from 2001 and 2002 (~GH 14 – 22). The sample from Hohle Fels was recovered as part of the current excavation project (led by N. Conard). The choice of this material also ensures the recovery methods and curation procedures were the same for most of the samples. This is important as variable recovery techniques can produce distinct differences in both the skeletal element representation and taxonomic composition of small mammal assemblages. The substantially larger size of the assemblage from Qu. 25 at Hohle Fels (1.5 times the number of finds recovered from Qu. 30) is most likely because it is located closer to the cave walls near to what was probably a heavily used roosting location for predatory birds. However, as the results of this thesis show, an increase in sample size does not lead to an equal increase in taxonomic richness or significant differences in the taphonomic signal (see Chapter 5: Results and Appendix 1.2; Rhodes et al, 2019, Table 14). Therefore, while selective sampling from areas close to known roosting locations will increase the number of small mammal remains recovered, comparison of these materials with those recovered elsewhere at the site is still warranted.

3.2 Taxonomic identifications

3.2.1 Morphological identification

Taxonomic designations were completed on isolated dental elements including mandibles, maxillae, and both isolated and *in situ* molars. With the exception of those specimens belonging to Soricidae, incisors were not identified taxonomically unless recovered articulated with identifiable dentition. Post-cranial elements were used for taxonomic identification of the families Talpidae, Mustelidae and Chiroptera. The zooarchaeological comparative collection at the Institute für Naturwissenschaftliche Archäologie at the Universität Tübingen was used for preliminary identification and published images and metric measurements for species level determinations. All specimens were examined under 10x – 100x magnification using a Euromax desktop microscope and measurements were taken using a Keyence mounted microscope.

Specimens identified to the subfamily Arvicolinae, including genera *Arvicola*, *Lemmus*, *Dicrostonyx*, *Microtus*, *Chionomys*, and *Myodes* are characterized by high crowned rooted or unrooted molars with a series of triangular cusps and re-entrant angles (also known as synclines). The terminology of van der Meulen (1973; Fig 2) is used herein including the term buccal re-entrant angle (BRA), lingual re-entrant angle (LRA), anterior lobe (AL), posterior lobe (PL), and the anteroconid complex (ACC) which makes up the AL and the first two triangles (T). The edges of each triangle are referred to as salient angles (BSA or LSA) although common taphonomic nomenclature refers to these as salient edges (see Andrews, 1990); both are used interchangeably herein. Additionally, capitalization will be used to indicate maxillary dentition, lower-case lettering to indicate mandibular dentition, and numbers will be used to indicate the location of teeth within the dental arcade (i.e. M1 = upper first molar and i2 = second lower incisor). With the exception of *Myodes*, which is the only Late Pleistocene Arvicolinae genus that exhibits rooted molars, all Arvicolinae species were differentiated based on the number of triangles present, the presence or absence of congruence (opening of the dentine area joining triangles along the central axis of the tooth), the shape of the ACC, and the presence or absence of enamel on the LSA and BSA.

The genera *Lemmus* and *Dicrostonyx* were identified based on a lack of enamel on the BSA and LSA of the triangles, AL, and PL of all molars (van Kolfschoten, 2014). The length of the m1 specimens attributed to *Lemmus* exclude the possibility that they belong to the smaller forest lemming, *Myopus schisticolor* (Weinstock, J., 1999; Appendix 1.1, Rhodes et al., 2018; Table 3). *Dicrostonyx* is primarily distinguishable from *Lemmus* due to a lack of cementum in the LRA and BRA of all molars (van Kolfschoten, 2014). Additionally, these two genera differ in the number of triangles present in the m1, m3 and M3 (Niethammer and Krapp, 1978) and the morphology of the ACC of the m1 (Agadjanian and von Koenigswald, 1977), although variation in ACC morphology was minimal in both analyzed samples. Due to these characteristics, all molars from *Lemmus* and *Dicrostonyx* individuals are theoretically identifiable to genus. This contrasts with the rest of the Arvicolinae assemblage (except for the rooted *Myodes)* for which only some molars, most often the m1, show species-specific morphological features.

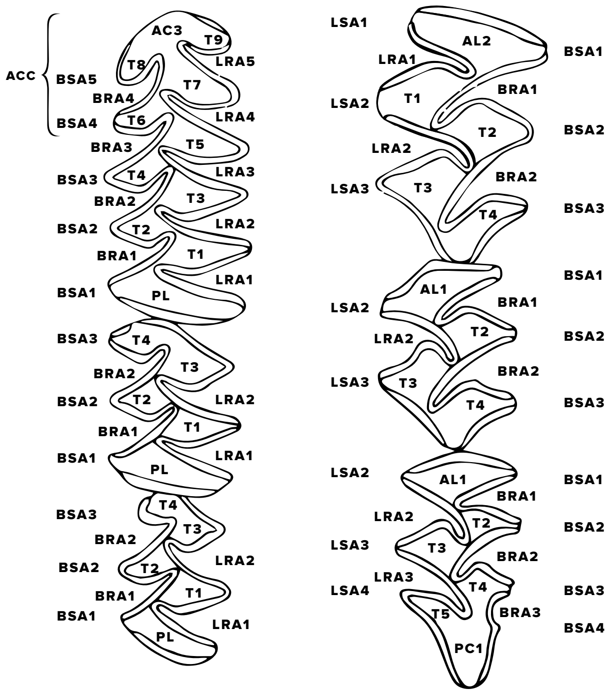


Fig. 2 Terminology of the occlusal morphology of Arvicola dentition (adapted from van der Meulen,1973)

Five fossil species of *Dicrostonyx* have been identified in the Western and Central European Pleistocene record including *D. antiquitatis* Chaline 1972, *D. gulielmi* Sanford 1870, *D. simplicior* Fejfar 1966, *D. intermedius* Heller 1984 and *D. henseli* Hinton 1910. During the Late Pleistocene only *D. gulielmi* and *D. henseli* are documented, although it has been suggested that the *D. henseli* material would be better designated as a sub-species *D. gulielmi henseli* (Agadjanian, 1977; van Kolfschoten, 2014). Agadjanian and von Koenigswald (1977) identified differences in the upper molars of *D. gulielmi* useful in distinguishing *D. g. henseli* from *D. g. rotundus*. These include differences in the shape of the AL and PL of the M1, M2, and M3 which can be categorized into five morphotypes. The dominance of a morphotype within an assemblage suggests the dominance of one of the two subspecies. Identifying the subspecies present can also provide biostratigraphic data, as a transition from *D. g. rotundus* to *D. g. henseli* is documented in the Gravettian of southern Germany (Ziegler, 2019). Each *D. gulielmi* upper molar from Hohle Fels and Geißenklösterle was assigned to one of these morphotypes and the sub-species attribution of both assemblages is discussed in Chapter 5: Results.

The *Arvicola* dentition identified at Hohle Fels and Geißenklösterle present a characteristic *A. terrestris* morphology including congruence of the T4 and T5 in the m1 alongside three closed (i.e. non-congruent) triangles. Additionally, all m1 specimens are rootless with little variation in the form of the ACC. While some specimens exhibit length dimensions which fall within *A. antiquus*, which has been found at a number of German sites of Weichselian age (Storch, 1974), the significant variation in m1 length found in other Weichselian and recent populations of *A. terrestris* raises doubts as to whether size variation can be used to define *A. antiquus* as a separate species (van Kolfschoten, 2014). At Geißenklösterle, the range of *Arvicola* m1 length falls well within that documented for *A. terrestris* from other key sites (Appendix 1.1; Rhodes et al, 2018, Fig. 3). However, the substantially larger Hohle Fels material has been designated *A. terrestris/antiquus* in recognition of its morphological and metric similarity to the material of Brillenhöhle (Storch, 1973a), Kogelstein (Ziegler, 2000), and Weinberghöhle (von Koenigswald, 1974) (Appendix 1.2, Rhodes et al., 2019).

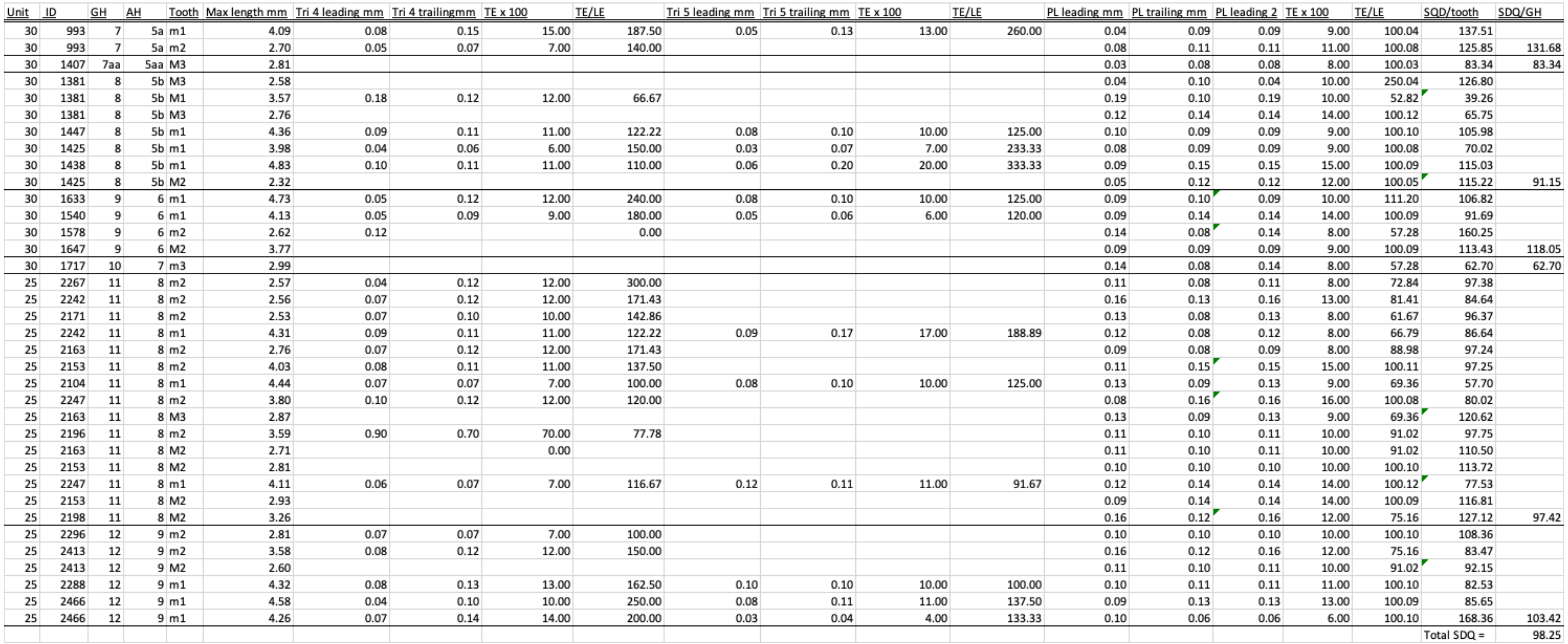
The *Schmelz-Dicken-Quotient* (SDQ) was first proposed by Heinrich (1982) as a method to quantify the disparate width of enamel development on the anterior and posterior borders, referred to as the leading edge (LE) and trailing edge (TE), of the triangles and PL of *Arvicola* molars. The occurrence of thicker enamel on the leading edge compared to the trailing edge width was first noted by Heller (1969) and chronologically correlated by Koenigswald (1973). SDQ is calculated using the following formula:

$$SDQ = TE\, x \frac{100}{LE}$$

The result is then averaged over the whole assemblage (or by stratigraphic boundaries) with lower numbers indicating more recent populations. The loss of enamel development along the trailing edge of *Arvicola* teeth is thought to be advantageous when combined with the renewal of masticatory occlusal surfaces resulting from rapid tooth growth made possible by the loss of molar root development (Koenigswald and Kolfschoten, 1996). Chaline and Sevilla (1990) have shown that the reduction of root development in arvicolids, which likely developed independently among a number of lineages, is due to ‘a heterochronical shift of different phases in ontogeny’ (Chaline and Sevilla, 1990; Koenigswald and Kolfschoten, 1996). The adaptive advantage of rootless dentition lies in the more intensive wear of the occlusal surface that this morphology permits, which in turn allows incorporation of more abrasive foods in an individual’s diet (Koenigswald and Kolfschoten, 1996). The TE and LE measurements recorded from each *Arvicola* specimen and SDQ averages by GH from Hohle Fels Cave are included in Table 2; the material from Geißenklösterle proved too fragmented to produce comparable SDQ measures.

The specimens attributed to *Myodes* (formerly *Clethrionomys*) exhibit thick enamel development, congruence of T4 and T5 in the m1, and the development of two roots in adult specimens. This morphology excludes the Middle Pleistocene species *C. rufocanoides* (Storch, 1973a) and the more recent *M. rufocanus* and *M. rutilis* (Niethammer and Krapp, 1978). In addition to maintaining the ancestral rooted morphology, only small changes in the overall morphology of *Myodes* molars have been documented in the European fossil record suggesting that most Pliocene and Pleistocene fossil species could be attributed to *M. glareolus* (van Kolfschoten, 2014). Whether this status in tooth morphology reflects a lack of adaptability to changing resources or a lack of environmental pressures to expand their potential food sources is not clear. The m1 *Myodes* material from Hohle Fels and Geißenklösterle also exhibits a cap-shaped AL due to a posteriorly slanted labial T6 further confirming the material belongs to *M. glareolus* (Ziegler, 2019; Appendix 1.1, Rhodes et al., 2018).

Table 2 Arvicola enamel thickness quotient (SDQ) measurements from Hohle Fels Cave.



Unit	ID	GH	AH	Tooth	Max length mm	Tri 4 leading mm	Tri 4 trailingmm	TE x 100	TE/LE	Tri 5 leading mm	Tri 5 trailing mm	TE x 100	TE/LE	PL leading mm	PL trailing mm	PL leading 2	TE x 100	TE/LE	SQD/tooth	SDQ/GH
30	993	7	5a	m1	4.09	0.08	0.15	15.00	187.50	0.05	0.13	13.00	260.00	0.04	0.09	0.09	9.00	100.04	137.51	
30	993	7	5a	m2	2.70	0.05	0.07	7.00	140.00					0.08	0.11	0.11	11.00	100.08	125.85	131.68
30	1407	7aa	5aa	M3	2.81									0.03	0.08	0.08	8.00	100.03	83.34	83.34
30	1381	8	5b	M3	2.58									0.04	0.10	0.04	10.00	250.04	126.80	
30	1381	8	5b	M1	3.57	0.18	0.12	12.00	66.67					0.19	0.10	0.19	10.00	52.82	39.26	
30	1381	8	5b	M3	2.76									0.12	0.14	0.14	14.00	100.12	65.75	
30	1447	8	5b	m1	4.36	0.09	0.11	11.00	122.22	0.08	0.10	10.00	125.00	0.10	0.09	0.09	9.00	100.10	105.98	
30	1425	8	5b	m1	3.98	0.04	0.06	6.00	150.00	0.03	0.07	7.00	233.33	0.08	0.09	0.09	9.00	100.08	70.02	
30	1438	8	5b	m1	4.83	0.10	0.11	11.00	110.00	0.06	0.20	20.00	333.33	0.09	0.15	0.15	15.00	100.09	115.03	
30	1425	8	5b	M2	2.32									0.05	0.12	0.12	12.00	100.05	115.22	91.15
30	1633	9	6	m1	4.73	0.05	0.12	12.00	240.00	0.08	0.10	10.00	125.00	0.09	0.10	0.09	10.00	111.20	106.82	
30	1540	9	6	m1	4.13	0.05	0.09	9.00	180.00	0.05	0.06	6.00	120.00	0.09	0.14	0.14	14.00	100.09	91.69	
30	1578	9	6	m2	2.62	0.12			0.00					0.14	0.08	0.14	8.00	57.28	160.25	
30	1647	9	6	M2	3.77									0.09	0.09	0.09	9.00	100.09	113.43	118.05
30	1717	10	7	m3	2.99									0.14	0.08	0.14	8.00	57.28	62.70	62.70
25	2267	11	8	m2	2.57	0.04	0.12	12.00	300.00					0.11	0.08	0.11	8.00	72.84	97.38	
25	2242	11	8	m2	2.56	0.07	0.12	12.00	171.43					0.16	0.13	0.16	13.00	81.41	84.64	
25	2171	11	8	m2	2.53	0.07	0.10	10.00	142.86					0.13	0.08	0.13	8.00	61.67	96.37	
25	2242	11	8	m1	4.31	0.09	0.11	11.00	122.22	0.09	0.17	17.00	188.89	0.12	0.08	0.12	8.00	66.79	86.64	
25	2163	11	8	m2	2.76	0.07	0.12	12.00	171.43					0.09	0.08	0.09	8.00	88.98	97.24	
25	2153	11	8	m2	4.03	0.08	0.11	11.00	137.50					0.11	0.15	0.15	15.00	100.11	97.25	
25	2104	11	8	m1	4.44	0.07	0.07	7.00	100.00	0.08	0.10	10.00	125.00	0.13	0.09	0.13	9.00	69.36	57.70	
25	2247	11	8	m2	3.80	0.10	0.12	12.00	120.00					0.08	0.16	0.16	16.00	100.08	80.02	
25	2163	11	8	M3	2.87									0.13	0.09	0.13	9.00	69.36	120.62	
25	2196	11	8	m2	3.59	0.90	0.70	70.00	77.78					0.11	0.10	0.11	10.00	91.02	97.75	
25	2163	11	8	M2	2.71			0.00						0.11	0.10	0.11	10.00	91.02	110.50	
25	2153	11	8	M2	2.81									0.10	0.10	0.10	10.00	100.10	113.72	
25	2247	11	8	m1	4.11	0.06	0.07	7.00	116.67	0.12	0.11	11.00	91.67	0.12	0.14	0.14	14.00	100.12	77.53	
25	2153	11	8	M2	2.93									0.09	0.14	0.14	14.00	100.09	116.81	
25	2198	11	8	M2	3.26									0.16	0.12	0.16	12.00	75.16	127.12	97.42
25	2296	12	9	m2	2.81	0.07	0.07	7.00	100.00					0.10	0.10	0.10	10.00	100.10	108.36	
25	2413	12	9	m2	3.58	0.08	0.12	12.00	150.00					0.16	0.12	0.16	12.00	75.16	83.47	
25	2413	12	9	M2	2.60									0.11	0.10	0.11	10.00	91.02	92.15	
25	2288	12	9	m1	4.32	0.08	0.13	13.00	162.50	0.10	0.10	10.00	100.00	0.10	0.11	0.11	11.00	100.10	82.53	
25	2466	12	9	m1	4.58	0.04	0.10	10.00	250.00	0.08	0.11	11.00	137.50	0.09	0.13	0.13	13.00	100.09	85.65	
25	2466	12	9	m1	4.26	0.07	0.14	14.00	200.00	0.03	0.04	4.00	133.33	0.10	0.06	0.06	6.00	100.10	168.36	103.42
																			Total SDQ =	98.25

Species of *Microtus* were differentiated based on the presence or absence of congruence between triangles and the shape of the ACC of the m1. The Pleistocene species present in southern Germany all share a generalized m1 occlusal morphology including seven triangles (T1 – T7), five of which are closed (T1 – T5), a pronounced PL with or without enamel on the BSA and LSA, and an ACC comprised of the congruent T6 and T7 and a variably shaped AL (which is also congruent with T6 and T7). Additionally, cementum is present in the BRAs and LRAs. Nadachowski (1982) defined morphotypes to express the variation in the m1 occlusal morphology of *Microtus* species based on material from 18 caves and rock shelters from the late Quaternary of Poland. Although these morphotypes are useful standards for describing variation in species morphology, and may correlate to the evolutionary chronology and biogeography of *Microtus* in the region, they were not employed in this study due to the general morphological homogeneity of the Geißenklösterle and Hohle Fels material, which closely matches the descriptions of other Middle to Late Paleolithic *Microtus* material [i.e. that from Weinberghöhle (von Koenigswald, 1974), Brillenhöhle (Storch, 1973a), and Geißenklösterle (Ziegler, 2019)]. With the exception of seven M3 specimens from Geißenklösterle identifiable to *Microtus arvalis* or *Microtus agrestis* based on the presence or absence of an accessory cusp on the PL (Niethammer and Krapp, 1978), the remaining molariform dentition of the *Microtus* species is so similar in their occlusal morphology that differentiating them is significantly time consuming and produces imprecise results, and therefore was not attempted for this study. Therefore, most m2, m3, M1, M2, and M3 specimens with the generalized *Microtus* morphology were identified to genus *(Microtus*) only.

Microtus gregalis is identified by a poorly pronounced T6 including a lack of cementum development in the BRA 4. This species occlusal pattern is very close to that of *Microtus arvalis* and *Microtus agrestis*, which are indistinguishable from one another except for slight differences in the pronunciation of the PL of the M3 (Niethammer and Krapp, 1978). Since *M. arvalis* and *M. agrestis* occupy the same habitat niche (Mitchell-Jones et al., 1999) they are discussed herein as the combined group *M. arvalis/agrestis*. Their occlusal pattern includes five closed triangles (T1 – T5), congruent T6 and T7, a rounded AL (which is also congruent with T6 and T7), and a pronounced PL. In some cases the similarity in occlusal morphology between *M. gregalis* and *M. arvalis/agrestis* has led to erroneous species attribution of significant portions of fossil assemblages and van Kolfschoten (1985, 2014) proposes the use of metric measures to confirm and correct visual identification of these species. The application of these measurements to the Hohle Fels and Geißenklösterle material is discussed further below. To maintain continuity between past microvertebrate research in the Swabian Alp and the current study, the majority of *M. gregalis* specimens were identified based on the lack of cementum build up in BRA 4 (Ziegler, pers. comm.).

Chionomys nivals differs from the aforementioned species in that the BRA 4 is poorly pronounced and T6 is oriented posteriorly, giving a 'capped' look to the ACC, similar to that of *Myodes*. The BSA and LSA of all triangles are often rounded, in comparison with *M. gregalis* or *M. arvalis/agrestis,* as well. *Microtus oeconomus* also exhibits a lack of BRA 4 pronouncement resulting in a lack of T6 differentiation from the AL and a general rounding to the buccal side of the posterior portion of the ACC. This species also exhibits congruence between T5 and the ACC while all other triangles are closed. Lastly, *M. subterraneus* (previously *Pitymys subterraneus*) was identified by a congruence between T4 and T5, a well pronounced and congruent T6 and T7, and a lack of congruence between the ACC and the posterior portion of the m1.

3.2.2 Metric Identification

Measurements were taken on all *Lemmus, Dicrostonyx, Arvicola, Microtus, Chionomys,* and *Myodes* lower first molar specimens following van Kolfschoten (1985). These include the maximum length of the tooth (L) and width as taken from the salient angle of T4 to T5 (W) (Fig. 3). Additionally, the width of dentine at the junction of T3 and T4 (a), the width of dentine at the junction of the AC and the rest of the tooth (b), the width of dentine at the junction of T4 and T5 (c), the width of the AL (d), the width of the tringles included in the ACC taken from the BSA to LSA (e) and the angle of measure b to f on the buccal side (f) were measured on all *M. gregalis, M. oeconomus, M. nivalis,* and a random sample of *M. arvalis/agrestis* specimens. At Geißenklösterle the number of measured *M. arvalis/agrestis* specimens totaled 187, at Hohle Fels only 50 specimens of *M. arvalis/agrestis* were measured. These measures have proven useful in differentiating Arvicolinae species, although overlap does occur (van Kolfschoten, 2014). By comparison, *M. gregalis* has a low b-value and low f-value, and *M. arvalis* and *M. agrestis* have a lower b-value and high f-value, *C. nivalis* has a lower b-value, high f-value and a high d-value (separating it from *M. arvalis/agrestis*) and *M. oeconomus* has been shown to have a high b-value based on recent and fossil material from Poland and Russia (van Kolfschoten, 2014). Plotting these measurements in a scatterplot allows for the quick recognition of species groupings and allows the identification of any metric outliers. Examples are included in Fig. 4 and Fig. 5.

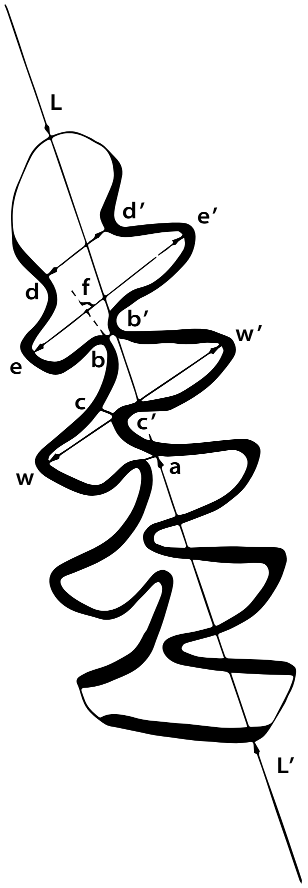


Fig. 3 Occlusal surface of the left m1 of Microtus illustrating the parameters measured (adapted from van Kolfschoten, 2014). See text for description.

The second largest family represented in the Hohle Fels and Geißenklösterle material is Soricidae. The genera *Sorex, Neomys,* and *Crocidura* are present, with the *Crocidura* specimens from Hohle Fels being the first instance this genus has been identified from Paleolithic deposits of the Ach Valley (Appendix 1.2: Rhodes et al., 2019). *Crocidura* was initially differentiated from *Sorex* and *Neomys* due to the lack of red pigmentation on the tips of the cusps and along edges of the lophs of the molariform dentition. However, as this characteristic of Soricinae can be removed in the process of occlusal wear (L. Maul, pers. comm.), identification of *Crocidura* specimens was restricted to visibly unworn dentition. Measurements were taken on all Soricidae dentition and mandible specimens following Reumer (1984). Identification of isolated upper dentition was not attempted as adequate comparative measures could not be sourced in the published literature (L. Maul, pers. comm.).

Specimens of *Sorex* and *Neomys* were differentiated by the presence of a uni-cusped (*Neomys*) or tri-cusped (*Sorex*) incisor and/or the shape of the mandibular condyle. Among *Sorex* species the two facets of the mandibular condyle are connected along the intercondylar axis (Repenning, 1967), whereas in *Neomys* these two facets are clearly separated by a narrow intercondylar space when viewed posteriorly (Reumer, 1984). The length of the upper condylar facet (LUF) and lower condylar facet (LLF) and the height of the condyle (HC) were also compared to confirm these visual identifications (*Neomys* has a greater condyle height ranging from 1.85 – 2.17 mm in the Hohle Fels sample, while *Sorex* ranges from 1.02 – 1.83 mm). In rare cases when the mandibular condyle was not preserved and/or the anterior portion of the mandible was fractured, specimens were identified based on the presence of a mental foramen below the m1 (*Sorex*), the length the tooth row (Lm1-m3), the length of the mandibular body (L), the trigonid width (TRW) and talonid width (TAW) of the m1 and m2 and/or the width (W) and length (L) of the m3 (Ziegler, 2019; Heinrich, 1983; Reumer, 1984; van Kolfschoten, 1985, 1994, 2014). These measurements are illustrated in Fig. 6.

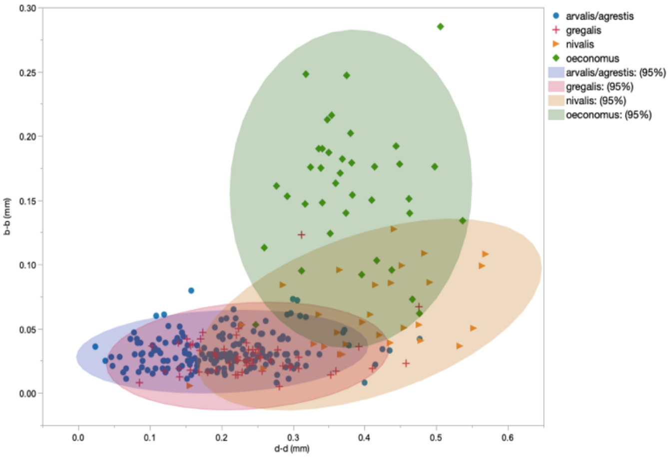


Fig. 5 Scatterplot of the d-value and b-value (in mm) of the m1 of M. arvalis/agrestis, M. gregalis, M. nivalis, and M. oeconomus from all horizons at Geißenklösterle. Ellipses indicate 95% density

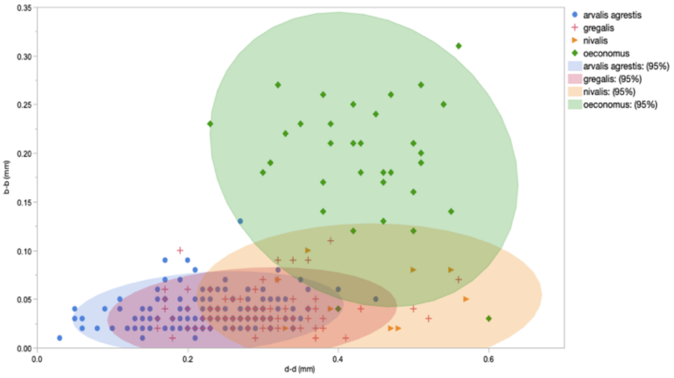


Figure 5 Scatterplot of the d-value and b-value (in mm) of the m1 of M. arvalis/agrestis, M. gregalis, M. nivalis, and M. oeconomus from all horizons at Hohle Fels. Ellipses indicate 95% density

The HC and LLF measurements from Geißenklösterle are compared with those reported from Sesselfelsgrotte (van Kolfschoten, 2014) in Appendix 1.1 (Rhodes et al., 2018, Fig. 4). *Sorex minutus, Sorex araneus,* and *Neomys fodiens* are clearly present at Geißenklösterle, although many of the specimens exceed the LLF length reported by van Kolfschoten (2014). In these cases, other morphological criteria supported the species determination reported by Rhodes et al. (2018). At Hohle Fels, a mandibular toothrow with *in situ* m2 and m3 was identified as *Neomys* cf. *anomalus* based on the m2 length (Heinrich, 1983). As well, 54 specimens were attributed to *Sorex* cf. *araneus* based on the presence of a tricuspid incisor and/or a clear mandibular intercondylar space, as well as HC and LLF lengths intermediate between that reported for *Sorex* and *Neomys* (Heinrich, 1983) despite and an overall size exceeding that of *S. minutus*, *S. araneus* and falling within the range of *Neomys fodiens* (Heinrich, 1983; van Kolfschoten, 2014). The possibility that these specimens are a robust form of *S. araneus* as described from Brillenhöhle (Storch, 1973a) is discussed in further detail in Appendix 1.2 (Rhodes et al., 2019).

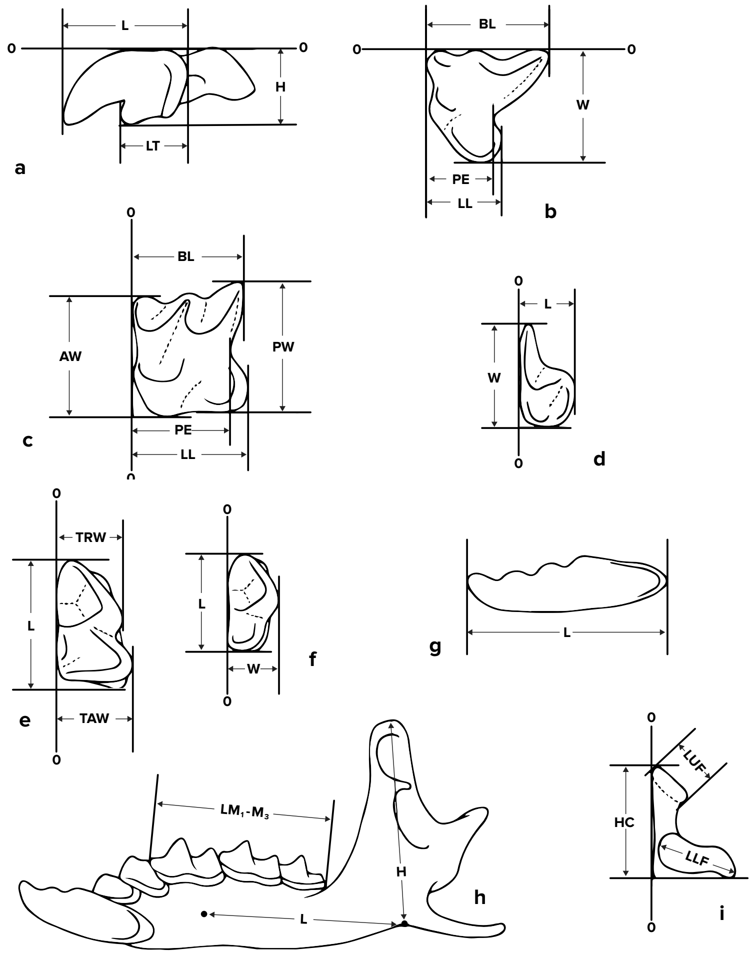


Fig. 6 Measurements taken on Soricidae dentition and mandibles. a) upper incisor, b) P4, c) M1 and M2, d) M3, e) m1 and m2, f) m3, g) lower incisor, h) left mandible, i) mandibular condyle (posterior view). See text for abbreviations. (adapted from Reumer, 1984).

The specimens attributed to *Crocidura leucodon* and *C. leucodon/russula* were initially identified by the lack of red pigment on the cusp tips of the teeth. This genus includes the most species of all mammals (Jenkins et al., 2009) and this, combined with a lack of regional comparative material, makes precise and confident identification to the species level difficult. *C. leucodon/russula* designations are based on comparison of the toothrow length, m1 length, TRW, and the degree of pronouncement of the m1 protocone with that reported by Repenning (1967) and Heinrich (1983). *Drepanosorex* was excluded as none of the Soricid teeth from Hohle Fels exhibit the pale orange-yellow pigment described by Repenning (1967). Three specimens are identified as *C. leucodon* based on the presence of a uni-cusped incisor (Repenning, 1967)] the location of the mental foramen below the m1, and an overall mandibular robusticity exceeding that of *C. suaveolens* (Heinrich, 1983). Images of these specimens were shared with L. Maul, at Senckenberg in Weimar, who supports this determination. To our knowledge, this is the first record of the bicolored white toothed shrew in the Swabian Jura.

The few specimens from both Hohle Fels and Geißenklösterle attributed to *Spermophilus* exhibit the brachydont, high cusps of *Sciuridae* and the triangular high-crowned form of *Spermophlius* (Hilson, 1986). Similar to *Marmota* in overall appearance, the upper molars have four transverse ridges extending from low lingual cusps and higher buccal cusps. These specimens are identified to genera *Spermophilius* sp. while the lower basin shaped molars included many characteristic accessory cusps of *S. superciliosus* (following Popova, 2016). The most reliable method for identification of the extinct ground squirrel relies on the use of discriminate analysis to compare the relationship between accessory cusp occurrences within a large sample size (Popova, 2016), which was not possible with the small number of specimens recovered from the Ach Valley. However, both the width and length of our specimens exceeds the reported ranges for *Citellus major* and *S. vulgaris* (Cubuk et al., 1977; Heinrich, 1983) and modern examples of *S. vulgaris* housed at the University of Tübingen. Considering the large overall size of the specimens, the chronological period from which these specimens derive (the Upper Pleistocene) and the prevalence of the large-sized *S. superciliosus* elsewhere in southern Germany in this period (Heinrich, 1969; Cubuk et al., 1977), it is likely that they represent the grassland steppe adapted species *S. superciliosus.*

No bat remains were found within the material sampled from Geißenklösterle, and only 5 specimens could be attributed to the family Chiroptera from the Hohle Fels material. Two of these specimens, a distal humerus fragment and a toothless yet otherwise complete mandible, could be further identified to *Myotis* sp. based on the alveolar pattern, which includes a single rooted p3, double rooted p4, m1, and m2, and an m3 with fused roots, and the general morphology of the trochanter and ulnar protuberance. However, without dental elements, which are the most reliable morphological determinants of bat genera or species (Ziegler, 2000), these identifications should be considered preliminary.

Similarly, *Talpa* sp. is only recognized from the Hohle Fels cave material in this study, despite previous reports from the Ach Valley (Ziegler, 2019). Seven specimens were identified to this genus including an isolated m2, an ulna, tibia, femur, two phalanges, and a highly diagnostic distal humeral fragment. With the exception of the humerus, mole post-crania are not diagnostic to species level (Ziegler, pers. comm.) and the distal fragment analyzed here was left at the general level as the epiphyseal breadth (8 mm) falls within the range of *T. europaea* (von Koenigswald, 1985; van Kolfschoten, 2014) and at the lower boundary of *T.*

magna (Storch, 1974; Hahn, and von Koenigswald, 1977). The isolated m2 proved too fragmented for comparative measurements, however the dilambdodont tooth pattern is clearly visible in the two V's of the tooth and the overall robusticity of the specimen sets it apart from the other dilambdodont insectivores identified herein, specifically Soricidae.

3.3 Taphonomic identifications

Equifinality of the modifications produced by different taphonomic agents necessitates a detailed taphonomic analysis to answer questions related to assemblage accumulation (Lyman, 2004). As such, full taphonomic analysis of the cranial and post-cranial material from Geißenklösterle and Hohle Fels including documentation of nine taphonomic modifications was conducted. Each specimen was examined under 10x – 100x magnification using a desktop Euromax microscope. Modifications documented include: fragmentation of the remains, surface cracking, edge rounding, root etching, abrasion, weathering, thermal discolouration, oxide staining, and digestive corrosion following Andrews (1990), Fernandez-Jalvo and Andrews (1992), Stiner et al. (1995), and Madgwick (2014), among others.

The presence/absence and categorical data produced was then used for intra- and inter-assemblage comparison through the application of several indices and measures. The relative abundance of each skeletal element by GH was calculated using the formula $R = N_i/(MNI \times E_i)$ with N_i indicating the number of elements i identified within the GH and E_i indicating the number of elements i expected in a single skeleton. Minimum number of individuals (MNI) was calculated based on the most abundant skeletal element within each GH's assemblage. In this way, the relative abundance data does not incorporate the taxonomic diversity of the material, simply the preservation of different skeletal elements. This weighted abundance is then compared with the similar data from actualistic prey assemblages (Andrews, 1990) using a correlation coefficient (Kendall's Tau) where highly correlating assemblages ($\tau > 6.000$, $p = < 0.005$) are plotted as a line chart (Appendix 1.1, Rhodes et al., 2018: Fig. 6 and 7; Rhodes et al., 2019: Fig. 3).

The non-modern breakage of the skeletal, cranial and dental elements is reported as both tallies (NISP) and abundance data (%) for long bones (humerus, ulna, femur, and tibia) and maxillae and mandibles following Andrews (1990) categories (Appendix 1.1, Rhodes et al., 2018: Table 9 and 12; Appendix 1.2, Rhodes et al. 2019: Table 4 and 5). The ratio of humerus, radius, ulna, femur and tibia fragments (post-crania) is compared to the mandibles, maxillae, and isolated molars (crania) to indicate preferential loss of either skeletal category, as is the ratio of robust long bones (humeri and femora) to robust cranial elements (mandibles and maxillae) (Appendix 1.1, Rhodes et al., 2018: Table 13; Appendix 1.2, Rhodes et al., 2019: Table 5). Comparison of the distal limb elements (tibia and radius) with proximal limb elements (femur and humerus) is also included alongside the proportion of isolated teeth calculated by dividing the number of expected teeth based on identified empty alveolar spaces against the number of identified isolated teeth. This value was calculated separately for incisors and molars.

Molars identified as having been exposed to the effect of digestive acid during predation are quantified along a categorical ranking from light to extreme modification following Andrews (1990) (Appendix 1.1, Rhodes et al., 2018: Table 15; Appendix 1.2, Rhodes et al., 2019: Table 8 and 9). Only arvicolidae (*Lemmus, Dicrostonyx, Microtus, Chionomys,* and *Arvicola*) specimens are reported to control for the effect of different tooth morphology and mineralization level on the degree of digestive etching expression. Unidentifiable molars exhibiting the *Microtus* pattern are included, as well, to account for differential identifiability between taxonomic groups (e.g. all molars and premolars of *Dicrostonyx* are identifiable by the lack of cementum, whereas only the m1 is identifiable in most *Microtus* species). Evidence of digestive etching documented on the proximal tips and enamel surfaces of all incisors is also reported and compared between sites and against actualistic data (Andrews, 1990) (Appendix 1.1, Rhodes et al., 2018: Table 16; Appendix 1.2, Rhodes et al., 2019: Table 7). Increased porosity and destruction of the trabecular bone of proximal femora and distal humeri is also documented and reported from the Hohle Fels assemblage following the categorical ranking from light to extreme defined by Andrews (1990) (Appendix 1.2, Rhodes et al., 2019: Table 10 and 11). The other taxonomic families (Talapidae, Chiroptera, Gliridae) had no specimens exhibiting the effects of exposure to digestive acids.

3.4 Diversity measures

To compare the taxonomic composition of the two sites measures of richness (NTAXA), heterogeneity (reciprocal of Simpson's index) and evenness (Simpson's evenness) were calculated. NTAXA is calculated as a tally of the present species and genera (when species level determinations were not possible). The reciprocal of Simpson's index is calculated as

$$1/D = \Sigma p_i{}^2$$

where p_i is the abundance of taxon I and the measure is expressed as 1/D so that greater homogeneity is indicated by a higher number. 1/D can be converted to a direct measure of taxonomic evenness using the following formula:

$$E_{1/D} = (1/D)/S$$

This produces a range from 1/S to 1, with 1 indicating perfect evenness. Additionally, the correlation between sample size (NISP) and NTAXA was compared to discern if the sample size is driving the measures of species richness (Appendix 1.1, Rhodes et al., 2018). A rarefaction analysis was run on the NTAXA measures from Hohle Fels using the statistical software PAST version 3.14 to identify the degree of sampling bias and its effect on the representation of rare species (Appendix 1.2, Rhodes et al., 2019).

3.5 Paleoenvironmental reconstructive methods

3.5.1 Modified Indicator Species Method

A modified version of the indicator species method was applied to the taxonomic data collected from both Hohle Fels and Geißenklösterle to produced broad estimates of the vegetative composition and climate around the sites in the past. The indicator species method uses the identification of one or more species with narrow ecological tolerances to infer the environment or climate at a site in the distant past (Lyman, 2016). Also referred to as the taxonomic abundance method (Lyman, 2016), the modified indicator species method assigns each taxon to a vegetative and climatic niche based on modern analogues or, in the case of extinct taxa, inferred habitat preferences from paleontological studies. For this study, modern ecological distribution data from Mitchell-Jones et al. (1999) and Niethammer and Krapp (1978) were used. The abundance of individuals allocated to each ecological niche is then compared to identify shifts in the climate and vegetation around the site through time. While this method is straightforward and produces results which are easy to interpret, in most cases it can only be applied to the portion of the assemblage identifiable to species level, as genera and family groups often contain species with disparate habitat requirements. Description of the ecological niches of the various species identified in the Ach Valley assemblage can be found in Appendix 1.1, Rhodes et al., 2018: section 3.2 and Appendix 1.2, Rhodes et al., 2019: Table 1.

3.5.2 Habitat Weighing Method

To address the shortcomings of the modified indicator species method mentioned above, the habitat weighting method (Evans et al., 1981; Andrews, 1996) was applied to the Hohle Fels data, as well. Originally designed to maximize paleoecological interpretations from Miocene faunal assemblages with low numbers of species level determinations, this method allocates a weight of 1.0 to each taxonomic group which is distributed across all habitat types (i.e. ecological niches) occupied by modern analogue populations, therefore allowing for the inclusion of species, genera, and family level designations. For example, the *Microtus arvalis/agrestis* group is distributed across four habitat types (Open Dry, Open Humid, Open Woodland, and Woodland) in this study, each with a weight of 0.25, based on differences in the ecological distribution of modern *Microtus arvalis* and *Microtus agrestis* groups in Central Europe (following Mitchell-Jones et al., 1999). When including higher level taxonomic groups, such as Muridae, the weight for each habitat type is calculated based on the number of species within the family which occupy that environment in Central Europe; in this case, 60% of wild Muridae species occupy open woodland environments, 20% closed woodland environments, and 20% steppe environments, resulting in a weight of 0.6, 0.2, and 0.2, respectively. In the case of commensal species, such as mice and rats, and taxa with geographic ranges known to have been affected by urban development, only the habitat ranges of unaffected wild populations are considered. The total weight for each habitat type within a horizon is then added and converted to a percentage out of all habitat types represented. Similar to the modified indicator species method, shifts in the proportion of habitat types through time are compared to identify shifts in the ecology of the landscape from which the assemblage derives. Increasing use of this method within European Paleolithic contexts (López-García et al., 2015; López-García et al., 2017c, 2017b) also provides the opportunity to compare the results of Ach Valley analysis with an increasing number of paleoecological reconstructions from neighboring regions.

4.0 Results

The results of the taxonomic, taphonomic, and paleoenvironmental analyses are described in detail in Rhodes et al., 2018 (Appendix 1.1) and Rhodes et al., 2019 (Appendix 1.2). Overall, there are five main conclusions:

1) The small mammal material accumulated in both caves as the result of predation by owls, raptors or small carnivores.
2) The Middle Paleolithic in the Ach Valley was primarily temperate in terms of climate with a mosaic landscape. However, cold and arid periods are indicated in the Geißenklösterle record, with a gradual increase in tundra adapted species observed at both sites.
3) Both hiatus periods were temperate and moist with increasing cold tundra landscapes in comparison to the Middle Paleolithic.
4) There is no evidence for a drastic cold period (i.e. a 'cold snap') coinciding with or following the final Neanderthal occupation at either site.
5) The earliest Aurignacian occupations occur under substantially colder and drier climatic conditions than earlier periods, indicating increased tundra and wooded steppe areas on the landscape.

These conclusions and details of the small mammal derived paleoenvironmental record will be explored in more detail below. Contextualization of this new paleoenvironmental record within our existing picture of the paleoecology of the Ach Valley region is discussed in Chapter 5.

4.1 Taphonomic results

The results of the taphonomic study strongly indicate that the material from both Geißenklösterle and Hohle Fels was accumulated as the result of predation by animals that used the caves as roosting or denning sites. Weathering damage and rounding of the bone surface and fracture edges is minimal throughout both assemblages (Appendix 1.1, Rhodes et al., 2018: Table 9; Appendix 1.2, Rhodes et al., 2019: Table 3), suggesting the bones were not transported to the site via water or sediment movement and were quickly buried once deposited. Evidence of root etching (concave depressions made on the bone surface by the acids released by mineral seeking plant roots) and soil corrosion of the bone surface (often resulting from long-term deposition in highly acidic sediments due to the decay of organic matter and/or shifting pH balances in the percolating water table) is also minimal (Appendix 1.1, Rhodes et al., 2018: Table 9; Appendix 1.2, Rhodes et al., 2019: Table 3), indicating that the cave floors were relatively devoid of growing plant life when the bones were deposited and shortly thereafter, and the effect of highly phosphatic coprolites and/or decomposing plant matter on the skeletal material was minimal throughout both sequences. These interpretations are, of course, spatially restricted to the excavation areas examined, and it remains possible that other areas of the caves included highly acidic sediments or heavy vegetation cover in the past. One exception to this pattern is the proportion of root etched specimens (15%) identified from the hiatus horizon at Geißenklösterle which, as the highest occurrence of this modification, may indicate increased vegetation cover when the cave was unoccupied by human groups.

Conversely, a large proportion of dental elements from both caves exhibit evidence of corrosion resulting from exposure to digestive acids. This type of modification is taphonomically unique (Fernández-Jalvo and Andrews, 2016), meaning the morphology of the effect of digestive acid exposure on enamel and dentine is unlikely to be misidentified as resulting from any other taphonomic agent. At Geißenklösterle, 37.5% of all arvicolid molars and 42.8% of all incisors exhibit digestive corrosion (Appendix 1.1, Rhodes et al., 2018: Table15). When compared with Andrews' (1990) actualistic data, this suggests a Category 2-3 predator, such as the Eurasian eagle owl, kestrel, or little owl, was active at the site in all studied periods. At Hohle Fels the number of dental specimens exhibiting digestive corrosion is substantially lower, with 10.3% of all arvicolid molars and 14.2% of all incisors exhibiting this modification (Appendix 1.2, Rhodes et al., 2019: Table 7, 8, and 9). Additionally, 20.3% of all femurs and 11.4% of all humeri examined from the Hohle Fels sample showed increased porosity of the epiphysial portions and/or destruction of the trabecular bone consistent with digestive acid destruction (Appendix 1.2, Rhodes et al., 2019: Table 10). These proportions are consistent with what Andrews (1990) defines as a category 1-2 predator assemblage produced by a snowy owl, short-eared owl, or European eagle owl.

Skeletal element representation and breakage provides a less clear picture from both cave assemblages. The exceptionally low number of complete elements, particularly crania and long bones, preserved at either site is most likely due to trampling and sediment compression during periods of high site occupation. However, the overall pattern of element preservation follows closely with actualistic assemblages described by Andrews (1990) and this, combined with the evidence for digestive acid exposure, confirms predation as a major accumulating agent of both samples. At Geißenklösterle, the skeletal element abundance within most GHs was strongly correlated ($\tau > 0.600$) with actualistic assemblages produced by the Eurasian eagle owl, kestrel, little owl, and red fox (Appendix 1.1, Rhodes et al., 2018: Table 11, Fig. 7). Andrews (1990) notes that these predators produce a pattern of destruction of weaker skeletal elements and jaws which cannot be distinguished from each other using skeletal element representation alone. At Hohle Fels, all GHs examined revealed similarly high correlations with the pattern of skeletal destruction produced by these same predators, along with less destructive predators such as the great grey owl and short-eared owl (Appendix 1.2, Rhodes et al., 2019: Fig. 3, Table 6). The near ubiquitous pattern of destruction of structurally weak and/or low density skeletal elements at both sites through all time periods suggests that post-depositional destruction (i.e. trampling and/or sediment compression) may have played a significant role in producing these patterns. This interpretation is further supported by the low number of specimens exhibiting rounding of fracture edges (Appendix 1.1, Rhodes et al., 2018: Table 9; Appendix 1.2, Rhodes et al., 2019: Table 3), which suggests that breakage happened after the specimens were exposed to digestive enzymes.

Using both the correlation between the skeletal element preservation by horizon and Andrews' (1990) actualistic patterns, combined with the proportion and intensity of digestive etching on molars and incisors, the possible predatory agents responsible for the material can be narrowed to the Eurasian eagle owl and kestrel at Geißenklösterle, and the Great grey owl, snowy owl, and Eurasian eagle owl at Hohle Fels. The presence of heavily modified arvicolid molars suggests some input by a mammalian predator, such as the red or arctic fox, in several horizons at both sites. Although indicated by both measures as contributing some material to the assemblages, the little owl is excluded from consideration as its size and related small diet would make its contribution at both sites minimal. These results are also broadly consistent with the breakage indices calculated (Appendix 1.1, Rhodes et al., 2018: Table 13; Appendix 1.2, Rhodes et al., 2019: Table 5).

4.2 Taxonomic results

A total of 1694 taxonomically identifiable specimens were recovered from Geißenklösterle and 6165 from Hohle Fels (Appendix 1.1, Rhodes et al., 2018: Table 2; Appendix 1.2, Rhodes et al., 2019: Table 14). This disparity in sample size is only moderately reflected in the taxonomic diversity at the two sites, with the assemblage from Geißenklösterle including 14 unique species and the assemblage from Hohle Fels including 17 unique species (which increases to 19 if each Muridae and Gliridae specimen is included). Overall, both assemblages are dominated by voles including *Microtus gregalis, Chionomys nivalis, Microtus oeconomus,* and the *Microtus arvalis/agrestis* group. Lemmings are the second most numerous taxonomic group, consisting of *Lemmus lemmus* and *Dicrostonyx gulielmi*. This dominance of voles and lemmings is common in Pleistocene small mammal assemblages from Central

Europe. Of the individuals (MNI) represented, the Hohle Fels assemblage, includes nearly twice as many (MNI = 1206) as the Geißenklösterle assemblage (MNI = 670).

The reciprocal of Simpson's (1/D) results suggest that both assemblages have low taxonomic evenness, with 3 - 5 dominant species contributing the majority of the osseous material. A positive correlation between NISP and NTAXA at Geißenklösterle ($\tau = 0.602$, $p < 0.05$) suggests that sample size is driving the diversity of taxa represented within the assemblage. Rarefaction analysis suggests a similar pattern at Hohle Fels, with a variation of between 2 and 3 taxonomic designations suggested (at the 95% confidence level) for all horizons except GH 12 (Appendix 1.2, Rhodes et al., 2019: Fig.6). However, the relative proportion of different species does not appear to be strongly affected by sample size, as suggested by the similarity in NTAXA between sites and a weak negative correlation ($\tau = 0.472$, $p < 0.05$) between NISP and taxonomic evenness (E) at Geißenklösterle. As such, it is highly likely that the small mammal assemblages from these two sites accurately reflect the relative proportion of different species on the Ach Valley landscape in the past.

In terms of community structure, it is important to note that all horizons analyzed at both Geißenklösterle and Hohle Fels present a non-analogous species composition. The presence of grassland, tundra, and rocky/mountainous adapted taxa within the same small mammal community is a composition not seen on modern landscapes. Although this can be caused by mixing of material from different depositional contexts, the ubiquity of the non-analogue pattern throughout both small mammal records, as well as the high level of stratigraphic integrity at both sites (Miller, 2015) makes this unlikely. Furthermore, while the large hunting ranges of the Eurasian eagle owl and kestrel, which span 10 km on average, may have produced this community pattern, we must also consider the phenomenon of progressive deviation from modern analogues with increasing age documented elsewhere (Stewart, 2008) as a possible explanation for this unique community structure. The presence of the mammoth steppe, the most well-known non-analogue ecological biome, throughout Central Europe during this time (Guthrie, 2013) supports this interpretation.

4.3 Paleoenvironmental results

4.3.1 Predator hunting behaviours and habitat preferences

The results of the taphonomic analysis clearly indicate that the small mammal material from both Geißenklösterle and Hohle Fels was accumulated by birds of prey and/or small carnivores. At Geißenklösterle, the most likely predators responsible for the small mammal material are the Eurasian eagle owl and the common kestrel. Both avian predators are opportunistic hunters, meaning they take their prey in relative proportion to their encounter rates within their hunting ranges. However, Andrews (1990) notes that the Eurasian eagle owl prefers the large-bodied water vole (*Arvicola terrestris*) and that both birds of prey produce assemblages dominated by various vole species. The red or arctic fox is also indicated at Geißenklösterle by the presence of heavily digested molars in GH 14, 15, 18, and 22. Both species are known to prefer easily caught and readily available (i.e. nocturnal and non-burrowing) prey, with some selection for lemmings indicated in the diet of the arctic fox (however this is likely the result of higher presence of these species in arctic environments). All three predators are known to inhabit diverse landscapes, particularly open, sparsely wooded environments, and to roost and/or den within small caves or crevices on rocky surfaces (BirdLife International, 2016, 2017; Hoffmann & Sillero-Zubiri, 2016). The Eurasian eagle owl is also known to return to roosting sites over multiple years (BirdLife International, 2016) producing large accumulations of pellets.

Additionally, the snowy owl and great grey owl are potential accumulating agents of the Hohle Fels small mammal material, particularly in GH 9, 11 and 12. Similar to the Eurasian eagle owl, these large-bodied owls are primarily arvicolid hunters, specifically *Lemmus*, *Dicrostonyx*, and *Microtus* species (Andrews, 1990; IUCN, 2016) with the remainder of their diet (~50%) comprised of small birds, murids, hares, and shrews. All their prey are taken on encounter and therefore accurately reflect the relative abundance of prey species on the landscape However, some studies indicate that the snowy owl may select against shew and murid species, likely due to their small body size, whereas the grey owl may preferentially select for shrews and water voles and against arboreal squirrels (Mitchell-Jones et al., 1999). Therefore, shrews may have been more numerous in the Ach Valley during the time that GH 7 and 9 were deposited. The snowy owl breeds on open grasslands and tundra areas close to the tree-line, and nests on the ground, usually at an elevated location (BirdLife International, 2017). The great grey owl is primarily a boreal and/or coniferous forest inhabitant however it prefers areas with forest openings such as pine and fir forests adjacent to montane meadows (BirdLife International, 2015). It is also found in shrublands and subarctic grasslands and, like all avian predators mentioned herein, can be found in wetlands and bog environments (Birdlife International, 2015).

While the little owl is also indicated as a potential accumulating agent at both Geißenklösterle and Hohle Fels, Andrews (1990) notes that this species produces very small accumulations of pellets which contain primarily insect remains and small murid elements. The near lack of murid species in both assemblages, as well as the high number of skeletal elements recovered from both cave sites, suggests this predator was not a major contributing agent.

4.3.2 Modified indicator species method

The results of the modified indicator species method are summarized in Figure 9 (Appendix 1.1; Rhodes et al., 2018) and Figure 7 (Appendix 1.2; Rhodes et al., 2019). In both there is a clear pattern of increasing cold tundra and wooded steppe adapted species through time, with the lowest proportions of both found in the early Middle Paleolithic (GH 22 and 20 at Geißenklösterle and GH 11 at Hohle Fels). This increase in cold, wooded tundra environments within the Ach Valley continues through the cultural hiatus periods of GH 17 at Geißenklösterle and GH 8 at Hohle Fels. Otherwise, the Middle Paleolithic of the Ach Valley included substantial open forest environments, indicated by the presence of cool-adapted *Crocidura leucodon/russula* and warm-adapted Soricinae species (*Sorex araneus, Neomys anomalus, Neomys fodiens*). Boreal forest adapted species (*Microtus oeconomus*) are present from the earliest Middle Paleolithic deposits at both sites, constituting between 7.5% and 11.0% of the assemblage at Hohle Fels and between 5.2% and 7.2% at Geißenklösterle. In the mid- Middle Paleolithic record, forest adapted species exceed cold tundra adapted taxa by 15.7% at Hohle Fels (GH 11) and 6.6% at Geißenklösterle (GH 20). These horizons are marked by both a decrease in tundra environments compared to earlier periods and an increase in the presence of forest patches, including a nearly 3-fold increase (10% to 28%) in forest adapted species at Hohle Fels between GH 12 and 11. The Middle Paleolithic record from both sites also includes the now extinct ground squirrel, *Spermophilus superciliosus*, indicating the presence of steppe grasslands nearby.

Rather than presenting as a particularly cold and inhospitable period, the cultural hiatus horizons reveal a warm and moist climatic signature, particularly at Geißenklösterle where forest adapted species account for 22.3% of the assemblage. Additionally, the proportion of cold tundra with wooded steppe-adapted *Microtus gregalis* individuals increases from 9.3% in GH 18 to 15.6% in GH 17, suggesting a similar increase in the presence of woody patches on the landscape surrounding Geißenklösterle. At Hohle Fels, the forest-adapted component of the material record decreases from 18.0% in GH 9 to 15.0% in GH 8, however the nature of the cultural hiatus deposits (which constitute the lower half of GH 8 only) make it difficult to discern if this shift occurred during the hiatus or afterwards. A minor decrease in the presence of *M. gregalis* from 19.4% in GH 9 to 17.1% in GH 8 may also signal the loss of some woodland/forest patches around Hohle Fels cave. However, it is important to note that the digestive evidence suggests that a snowy owl may have been active in the cave during the hiatus period, and therefore forest dwelling insectivores may be underrepresented within GH 8. As such, the loss of forest environments between the final Middle Paleolithic and the cultural hiatus may have been less pronounced than these results indicate. Furthermore, the single specimen of *S. superciliosus* from this horizon suggests a second expansion of arid grasslands into the Ach Valley (the first taking place in GH 12). The specific habitat requirements of this species, which include short-grass steppes with well-drained soils (allowing for the excavation of expansive underground burrows) indicates that a more temperate climate prevailed at some point during the deposition of this horizon. Overall, there is no evidence for a dramatic cold period directly preceding or during the cultural hiatus at either site.

The clearest evidence for a dramatic shift in the presence of cold tundra across the landscape is found in the early Upper Paleolithic signal at Geißenklösterle. In GH 15/16 the proportion of arctic adapted lemmings (*Lemmus lemmus* and *Dicrostonyx guliumi*) increases from 15.6% to 20.4%, whereas the more boreal *M. gregalis* decreases from 15.6% to 6.0%, alongside a decrease in all forest adapted species from 22.3% to 16.3%. This suggests a substantial increase in the presence of cold tundra biomes within the valley, and a related loss of woody/forest patches. This pattern continues in GH 14, with cold tundra adapted species maintaining their dominance in the assemblage, and appears to reach its apex in GH 13 however this dramatic shift is more likely due to the small sample size of this horizon (MNI = 18).

At Hohle Fels the signal is less clear, again due primarily to the nature of the hiatus and earliest Upper Paleolithic deposits. However, GH 7a/7aa does document a 2.9% increase in cold tundra adapted species alongside an increase in the boreal forest adapted *M. oeconomus* of 6.3%. The sample size of this horizon (NISP = 269; MNI = 70) is large enough that this pattern likely reflects the continued expansion of tundra landscapes, possibly in response to the onset of a stadial period (H4?) in the region, alongside an interstadial-related forest expansion (e.g. GIS 9 or 8). The proportion of species with indeterminate (i.e. variable) habitat preferences drops by 10.8% between GH 8 and GH 7a/7aa, suggesting the landscape around Hohle Fels became more homogeneous during this period, as well. Unfortunately, the same cannot be said for the small mammal material from GH 7, which most likely suffers from sample size bias (NISP = 67; MNI = 26).

In summary, the results of the modified indicator species method suggest that the Ach Valley was primarily temperate in climate with a mosaic landscape of dry tundra and woody/forested patches throughout the Middle Paleolithic. Periodic expansions of nearby grassland environments as well as evidence of substantial forest expansion during the Middle Paleolithic at Geißenklösterle suggest that some dramatic climatic oscillations can be recognized in the Ach Valley environmental record. However, there is no clear indication of a cold period directly preceding or during the cultural hiatus in this valley; instead, the coldest and least hospitable period recognizable in this climatic archive occurred during the initial Upper Paleolithic.

4.3.3 Habitat weighting method

The results of the application of the habitat weighting method to the small mammal taxonomic record from Hohle Fels (Appendix 1.2; Rhodes et al., 2019, Fig. 8) reveals a very similar climatic signal to that observed in the modified indicator species results. This method was applied in an effort to derive a more nuanced picture of any climatic fluctuations which may have been diminished by assigning each species to a single climatic and vegetative biome. There is a stronger indication of woodland environments during the basal Middle Paleolithic horizons using this method, however tundra environments still dominate the record with a clear increase in the presence of these habitats starting in GH 10 and extending through to GH 7. The increase in woodland environments during GH 11 suggested by the modified indicator species results is recognizable in the habitat weighing method as an increase in open, humid meadow environments, mature woodlands and an increase in the presence of waterways on the landscape. As such, this shift is likely driven by increased precipitation and humidity during an interstadial period. A moderate decrease in open meadow areas is also recognizable and coincides with the first presence of temperate grasslands in GH 9. The intensification of cold tundra landscapes recognizable in GH 7a/7aa is more pronounced in the habitat weighting results than elsewhere, with an increase of 16.4% between GH 10 and GH 7a/7aa. Woodland adapted species also decrease by 5.7% between GH 8 and GH 7a/7aa. Again, there is some indication of a return to temperate forested environments in GH 7, however this is likely driven by the small sample size of this assemblage.

Overall, the habitat weighting method confirms the previously recognized signal of a particularly warm and moist period in the mid- Middle Paleolithic record, as well as increasing cold and dry environments beginning in the late Middle Paleolithic and extending through to the early Upper Paleolithic. However, additional climatic oscillations, as suggested by the paleoenvironmental record at Geißenklösterle, are not recognizable in these results. There is broad agreement between the two paleo-reconstructive methods applied to the Hohle Fels small mammal material, suggesting that, in this case, the modified indicator species method was not significantly biased by the exclusion of rare and climatically indeterminate taxa.

5.0 Discussion

5.1 Correlations with the Ach Valley record

Overall, this new paleoenvironmental record fits well with past studies of the paleoecology of the Ach Valley. Miller's (2015) characterization of the Middle Paleolithic at Geißenklösterle as a series of cold climate deposits phosphatized and bioturbated during sequential warmer periods reflects the sequence of moderate forest expansion and retraction indicated in the small mammal record. He also characterizes the Middle Paleolithic of the Ach Valley as more hydraulically active and temperate (reflected in the degree of bioturbation and the lack of loess deposition during the early and mid- Middle Paleolithic), which fits well with the signal of a mosaic wooded-steppe landscape reflected in both previous small mammal studies (Ziegler, 2019) and this new record. Indications for the presence of extensive humid meadows and waterways during this period also fit with this general ecological picture.

During the hiatus, the mixed tundra and forest signal at both sites may be reflecting the quick succession of cold-to-warm periods indicated in the micromorphological record (Miller, 2015). Additionally, the relatively high proportion (15%) of root etched postcranial remains from the hiatus at Geißenklösterle likely indicates increased vegetation coverage accompanying increased humidity and warmth around the time of the erosional event at the top of GH 17 (Miller, 2015). None of the paleoenvironmental proxy records analyzed from Geißenklösterle or Hohle Fels indicate increased climatic instability or the presence of a dramatic cold or dry shift or 'snap' leading up to or during the cultural hiatus. Instead, most signals indicate that the decreasing temperatures and extending tundra landscapes were gradual processes that began earlier in the paleoenvironmental record.

The Aurignacian climatic signal is more variable between proxy records. As described in Chapter 4, the small mammal record suggests that the early Upper Paleolithic was colder than preceding periods, as dry tundra continued to expand and boreal forests retracted. This is reflected in the degree of phosphatization present at the contact of GH 8 and GH 7 at Hohle Fels (Miller, 2015), as well as the shift from mild and humid conditions to colder temperatures documented within GH 15/16 at Geißenklösterle by Laville and Hahn (1981). The botanical records from both sites suggest a mosaic of forest-steppe and extending tundra landscapes throughout the Ach Valley during this period (Hahn et al., 1977; Riehl et al., 2015). Previous small mammal studies from this site also document either low counts of boreal species during the Aurignacian (Hahn et al., 1977; Münzel et al., 1994) or a clear decrease in their presence through time (Ziegler, 2019). This pattern is not as clear in the new small mammal record, however the increasing dominance of cold tundra adapted species reflects similar processes.

In the current study, an increase in both cold tundra and boreal forest components is documented in GH 7a/7aa, the latter of which may indicate a period of warming temperatures and increasing precipitation. This is further suggested by the change in site-formation processes indicated by the discontinuity of the sedimentary deposits of GH 7a and 7aa (Miller, 2015). At Geißenklösterle, Laville and Hahn (1981) suggest that GH 13 and 14 may have been deposited during a warm period that was followed by lowering temperatures in GH 12, a pattern which the new small mammal record contradicts. However, as the sample sizes available from these horizons are particularly low, and Campen's (1990) and Millers (2015) findings were broadly similar, this may be a case of sample size affecting the small mammal environmental signal. Similarly, Miller (2015) reports that GH 7 at Hohle Fels was laid down during a particularly cold period relative to earlier deposits. This is also suggested in the paleobotanical record (Riehl et al., 2015) which contradicts the increase in boreal environments and decrease in steppe-tundra areas signaled by the small mammal record. However, this incongruity is also likely the result of sample size bias.

The large faunal record from the Ach Valley Aurignacian also documents an overall trend towards colder and dryer environments, reflected by an increase in the relative proportion of reindeer to other cervids (Starkovich et al., in press). Similarly, shifts in the ratio of elk to antelope may indicate the spread of steppe landscapes (Münzel et al., 1994). The increased presence of small game, fish, and particularly birds, in the faunal assemblages from the early Aurignacian has been attributed to increasing diet breadth to accommodate higher population densities (Conard et al., 2013; Bertacchi, 2017), but could also be explained by decreasing biomass availability due to the deteriorating climatic conditions suggested in the paleoenvironmental record. The presence of ground squirrels alongside high relative proportions of both the collared and Norwegian lemming in the final Aurignacian deposits at Brillenhöhle (Storch, 1973a) suggests that the pattern of repeated extending grassland and concurrent retracting forest environments seen in the Middle Paleolithic and hiatus records at Geißenklösterle and Hohle Fels continued into the late Aurignacian in the Ach Valley.

5.2 Correlations with the Greenland stadial/interstadials

The paleoenvironmental records described in Rhodes et al., 2018 (Appendix 1.1) and Rhodes et al., 2019 (Appendix 1.2) reveal patterns of both climatic change and relative stasis. With few exceptions, only moderate shifts in the proportion of different small mammal species are recorded between geological horizons, with a greater number of shifts documented in the Geißenklösterle record compared to that from Hohle Fels. These changes can be broadly correlated with stadial and interstadial periods recognized in the Greenland ice core records utilizing the calibrated ^{14}C chronologies from Geißenklösterle (Higham et al., 2012) and Hohle Fels (Bataille and Conard, 2018). However, without more refined dating of the Middle Paleolithic sequence, and a clear picture of the rate of sediment accumulation at both sites, these chronological correlations remain tentative.

In the Middle Paleolithic, climatic shifts occur during GH 22 and 20 at Geißenklösterle and GH 11 at Hohle Fels, where the presence of forest patches increases concurrent with a retraction of cold tundra environments. Recently calibrated radiocarbon dates from Hohle Fels (Bataille and Conard, 2018) place this shift around the time of GIS 11 and 12. Higham et al.'s (2012) ages for the final Middle Paleolithic at Geißenklösterle also suggest that these shifts likely occurred before GIS 11, around the time of GIS 12 or 13 or earlier. The increase in forest-adapted species during the cultural hiatus at Geißenklösterle and, to a lesser extent, at Hohle Fels, may suggest that these deposits were also laid down during an interstadial period, most likely GIS 10 at Geißenklösterle and GIS 10 or 9 at Hohle Fels. The increase in tundra landscapes during the basal Aurignacian layers at Geißenklösterle (GH 15/16) may indicate the onset of a stadial period (perhaps following GIS 10). The most recent radiocarbon dating at the site (Higham et al., 2012) suggests that this shift does not reflect the onset of the Heinrich 4 event. Instead, this chronology would place the Heinrich 4 event around the transition from GH 13 to 12, which appears to be represented in the small mammal record, however the small sample sizes from these horizons make this correlation highly questionable. The mixed forest and tundra signal of GH 7a/7aa at Hohle Fels falls within the span of GIS 9 and the Heinrich 4 event following Bataille and Conard's (2018) ages. A maximum mean age of 39,000 cal BP for GH 7 at Hohle Fels (Bataille and Conard, 2018) also places this horizon within the range of the Heinrich 4 event, which fits well with indications from the botanical record that these deposits were laid down during a cold phase.

There is no doubt that the small mammal assemblages from the various geological horizons at both sites represent an averaged paleoenvironment signal over multiple seasons, decades, and even centuries. A difference in the speed of deposition between the two sites, as hypothesized by Miller (2015), could also explain the greater number of climatic oscillations indicated throughout the Geißenklösterle record relative to that from Hohle Fels. Still, it is likely that the most striking climatic pattern recognized in the small mammal record of the Ach Valley - the gradual cooling beginning in the Middle Paleolithic and extending into the early Upper Paleolithic - can be confidently attributed to the cooling trend spanning D-O oscillations 12 – 9 seen elsewhere in Western Europe (Staubwasser et al., 2018).

5.3 Correlation with other faunal paleoecological signals

The small mammal record from the Lone Valley has not been looked at as intensively in recently years as its equivalent in the Ach Valley, however ongoing analysis of recently excavated material from Langmaldhalde (Wong et al., 2017) will contribute to our picture of Late Pleistocene and Holocene community structure. Preliminary results suggest that the Late Pleistocene (Magdalenian) may have been substantially colder and dryer than the Holocene, a shift indicated by both the loss of lemmings (*Dicrostonyx*) and an increase in the presence of forest adapted shrews (*Sorex/Neomys*) within Holocene deposits. This interpretation is supported by the large faunal record, as well. A similar pattern has been described by Koken (Schmidt, 1912; Hahn, and von Koenigswald, 1977) and Soergel-Rieth (2011) at Klein Scheuer am Hohlenstein. However, the small sample sizes reported by Koken (in Hahn, and von Koenigswald, 1977) and the near-complete lack of *Microtus arvalis/agrestis* throughout the assemblage, a species which is dominant in most OIS 3 and 2 assemblages, suggests that the material may have been biased by a particularly selective predator. Still, these studies suggest that the general pattern of increasing presence of cold and dry tundra environments described here for the Middle and Upper Paleolithic continues throughout the Late Upper Paleolithic in this region.

The large fauna record from the Lone Valley also supports the general pattern of climatic variability described in Chapter 4. At Bockstein, Hohlenstein-Stadel, and Vogelherd, the Middle Paleolithic fauna is dominated by horse, reindeer, mammoth and woolly rhinoceros (Niven, 2006, 2007; Krönneck, 2012; Kitagawa, 2014), with a clear increase in the percentage of reindeer in the Aurignacian at all three sites (Starkovich et al., in press). Rathgeber (2004) summarizes the Paleolithic and Holocene faunal records from six caves and rock-shelters in the Lauchert Valley. Overall, there is a similar taxonomic spectrum as in the Ach and Lone valleys, both in terms of large and small mammals, and there appears to be general continuity in the species representation between the Middle and Upper Paleolithic (Rathgeber, 2004). The results of Toniato's (in prep) analysis of the faunal material from previous and renewed excavations at Schaftstall should provide a more nuanced picture of the faunal record through time in this valley.

The Ach Valley record also shares distinct taxonomic similarities with other long-duration regional small mammal records, such as that from Sesselfelsgrotte (van Kolfschoten, 2014) and Weinberghöhle (von Koenigswald, 1974). The most obvious correlation is in the dominance of the *M. arvalis/agrestis* group, which has been recorded elsewhere in Europe (Kowalski, 1977; van Kolfschoten, 1985; López-García et al., 2015, 2017). von Koenigswald's (1974) work at Weinberghohle documents a lack of soricid remains from the lower most layers at this site, and the presence of various forest-adapted species (such as *Apodemus, Glis,* and *Crocidura)* in the uppermost horizons. This is broadly similar to the pattern seen in the Ach Valley record, and also supports claims by Uthmeier and Richter (Kot and Richter, 2012) that the material dates to OIS 3 rather than OIS 8 or 4, as suggested by von Koenigswald & Müller-Beck (1974). That the material from Weinberghöhle accumulated during a glacial period, like that from Hohle Fels and Geißenklösterle, is undeniable and is also reflected in the low pollen counts from the site (von Koenigswald, 1974).

Outside of Germany, small mammal records from Belgium (López-García et al., 2017b, 2017a), Italy (López-García et al., 2015; Berto et al., 2017, 2018; López-García et al., 2017c), and Poland (Socha, 2014) also document successive oscillations between warmer and moister interstadial periods and cold and dry stadial periods, although to varying degrees and over different periods in the OIS 3 chronology. López-García et al.'s (2015) work at Fumane cave is arguably the most relevant to this thesis, as it covers broadly the same time period as the Ach Valley record and includes at least 5 periods of vegetative and climatic change which may represent 1) the cooling of the H5 event at the very end of the Mousterian, 2) the onset of GIS 12 at the Mousterian to Uluzzian transition, 3) a drop in temperature around the Uluzzian to Aurignacian transition which may correspond to the H4 event, and 4) a shift which likely indicates the end of an interstadial (GIS 8-5) and the onset of the H3 event around the time of the transition from the Aurignacian to Gravettian. These climatic events are recognized in the small mammal records as moderate (5-10%) shifts in the relative proportion of woodland vs. open and dry habitats correlated with shifts of between 2 – 3°C and/or 500 – 1000 mm in measures of past temperature and precipitation. These meteorological variables are derived using the Bioclimatic Model (Fernández and Peláez-Campomanes, 2003), a method which has also been applied to the small mammal record from Hohle Fels (Rhodes and Conard, in prep) and produced similar results. Although less pronounced than model simulations of continental climatic response to the GS 15 to GIS 14 transition (Van Meerbeeck et al., 2011), similarities in the degree of biotic response to D-O oscillations between the Fumane and Ach Valley small mammal records lends significant support to our interpretations in section 5.2.

5.4 Correlation with other paleoecological archives

The presence of potential Löhne Boden deposits at Hohle Fels (GH 6a.-3db) and Geißenklösterle (GH 10) (Miller, 2015) provides the opportunity to correlate the small mammal record with the comprehensive and detailed terrestrial paleoenvironmental record derived from loess paleosol archives (Fitzsimmons et al., 2012). The Great European Plain Loess Belt represents the most continuous terrestrial record of Quaternary environmental change (Gocke et al., 2014; Antoine et al., 2016). However, even in ideal circumstances these climatic archives contain numerous hiatuses, often spanning several thousands of years (Antoine et al., 2016). Many loess-paleosol sequences along the Danube in Germany (e.g Dattahausen) do not preserve or did not record deposits from the period of 60,000 – 30,000 BP (Sauer et al., 2016). However, a few coeval paleosol records have been described which can be broadly correlated with the Ach Valley record.

The loess record from Serbia (Fitzsimmons et al., 2012) suggests that the Middle Paleolithic in the region saw relatively wetter and milder conditions, indicated by decreased weathering of the deposits compared to earlier horizons and greater evidence of pedogenic processes (i.e. soil formation) compared to later periods. The Saxonian loess record (Meszner et al., 2013) contains cambisol deposits dated to ~60,000 BP, indicating a temperate and humid period predating a depositional hiatus that extends to ~30,000 BP. Recent work on the Nusslock loess sequence (Gocke et al., 2014; Prud'Homme et al., 2016), located near Heidelberg, also suggests that the early Lower Pleniglacial (~63,000 – 50,000 BP) saw moist and warm environments, and that the degree of soil formation decreased steadily through time. Löhne Boden deposits are documented in the Middle Pleniglacial deposits of the Dolní Věstonice loess record, in the Czech Republic, as a sequence of boreal and/or arctic soil horizons interstratified with clayey beds of reworked soils and light grey calcareous silts indicative of freeze-thaw processes (Antoine et al., 2013). Associated malacological records suggest the soil horizons occurred during warm, humic, and herbaceous steppe environments (Antoine et al., 2013) and OSL dates bookending these horizons suggest that this brown soil complex records the period spanning GIS 14 – 12, although the potential for hiatuses within the complex make direct temporal correlations tenuous.

The Saxonian record also includes a tundra gley soil dated to ~30,000 BP indicating higher soil moisture and increasing temperatures during summer months, and generally cold winters with low rates of evaporation (Meszner et al., 2013). Similarly, the Nusslock sequence records a cambisol which recent reviews of the ^{14}C and TL dates place between GIS 7 and 5 (Kadereit et al., 2015), postdating the arrival of Aurignacian groups in Germany (Higham et al., 2012; Bataille and Conard, 2018). In the Czech Republic, the site of Dolní Věstonice records Löhne Boden deposits within a brown soil complex including evidence for sequential boreal and arctic soil horizons, supported by a warm, humid, herbaceous steppe signal in the associated malacological record (Antoine et al., 2013). As such, the Ach Valley paleoecological record fits well with indications from the loess paleosol record of Central and Western Europe which suggest the Middle Paleolithic saw a more temperate and moist environment with greater boreal components than later periods.

Pollen records, recovered from lake and sediment cores are another source of high-resolution paleoecological data, as vegetative response to rapid climatic oscillations can occur on a decadal scale (Müller et al., 2003). However, pollen archives from Central and Northern Europe also contain evidence of erosional events and unconformities, due primarily to unfavorable conditions for pollen preservation during the periglacial period (Van Andel and Tzedakis, 1996). The Alps may also restrict the migration of plant taxa from Mediterranean glacial refugia, resulting in a delayed or complete lack of response by Central European vegetation to short-term ameliorative climatic events (Müller et al., 2003). Keeping these complicating factors in mind, a number of paleobotanical records from Germany and the surrounding area are nevertheless informative as to the vegetative characteristics and meteorological variable of OIS 3 landscape.

The pollen record from the Nochten open-cast mine in eastern Germany records a tree-less, tundra environment throughout the Middle and Late Pleniglacial (Bos et al., 2001) with summer temperatures between 10°C and 15°C. Oscillations in the summer temperatures of between 4°C and 6°C may also register the effect of D-O oscillations (Bos et al., 2001). Pollen preserved in sedimentary cores of the Füramoos site in southwest Germany also records three stadial/interstadial oscillations, registered as shifting *Betula* and *Pinus* proportions and in the presence or absence of *Juniperus,* tentatively correlated with D-O events 14 – 11 (Müller et al., 2003). The short duration of earlier D-O events, and the time necessary for reimmigration of arboreal taxa from refugia areas south of the Alps, are suggested explanations for the lack of evidence for D-O events 19 – 16 (Müller et al., 2003). A time-lag of this magnitude may also explain the lack of arboreal elements in the more northerly Nochten records. Evidence of reforestation in the paleobotanical record from Neiderweningen, near Zürich, Switzerland during OIS 3 interstadials (Drescher-Schneider et al., 2007) also supports this interpretation.

Fletcher et al.'s (2010) synthesis of marine and terrestrial pollen records reveals a regional signal of low arboreal pollen counts during stadial periods, and related low proportions of forest-adapted small mammals, and greater forest development during D-O event 14 and 12 than earlier (D-O 16 – 170 and later (D-O 8) periods. This is due partly to a latitudinal pattern in forest extension, with sites located above 40°N (which would include those in the Ach Valley) exhibiting increasing and decreasing forest expansion in response to the amplitude of climatic change (Fletcher et al., 2010). They also note a latitudinal limit at 44°N separating predominantly temperate from mixed temperate and boreal elements, which may explain the strong response of boreal-adapted small mammals (i.e. *M. oeconomus* and *M. gregalis*) throughout the Ach Valley record described in section 5.2.

Finally, Müller et al. (2011) suggest, based on pollen records from northeastern Greece, that the Heinrich 5 event preceding GIS 12 resulted in abrupt cold and dry conditions across Central and Western Europe. They suggest that this dramatic climatic shift may have resulted in decreased population sizes among Western and Central European Neanderthal groups, opening up the landscape for migrating AMHs during the following interstadial. Fletcher et al. (2010) note that local temperate forest taxa are maintained above 40°N only during non-Heinrich stadials, suggesting that the amplitude of amelioration during the interstadials following Heinrich events was insufficient to allow reforestation. This may have affected the density or presence of Neanderthal groups within these northern regions, including the Ach Valley. However, there is minimal evidence of an intense cold peak in the middle and lower Danubian loess record (Fitzsimmons et al., 2012) which questions the extent to which the H5 event affected Central and Eastern European landscapes. As mentioned above, this stadial period is recognizable in the small mammal record at Fumane Cave as a marked decrease in woodland adapted taxa and concurrent lowering of both annual temperatures and precipitation amounts coinciding with the final Mousterian period (López-García et al., 2015). With continued excavation of the early Middle Paleolithic deposits at Hohle Fels, it may be possible to test the role that the H5 event had on the small mammal and hominin populations in the Ach Valley using similar methods in the near future.

6.0 Conclusions

The broad agreement between different paleoecological records from the Ach Valley and elsewhere in Central and Eastern Europe described in Chapter 5 permits the construction of a generalized picture of the climate and landscape in the Ach Valley during the Middle to Upper Paleolithic transition. In comparison with later periods, the Middle Paleolithic appears to have seen moderate forest growth and grassland steppe extension within what was otherwise a mosaic landscape of moist meadows and increasingly dominant cold tundra and wooded steppe areas. These periods likely reflect the onset and duration of D-O cycles 12 – 10, during which the climate became more temperate and moisture availability increased throughout the region. During this time, Neanderthal populations inhabited the cave sites of the Ach and Lone valleys for short periods or as small groups, leaving ephemeral and low-density material records (Conard, 2006; Miller, 2015). Sometime around 44,000 – 42,000 BP (Higham et al., 2012; Bataille and Conard, 2018) they abandoned the region all together, an event which was not coeval with any strong climatic signal but rather occurred midway through a sequence of increasing cold dry tundra landscapes. There are some indications that the climate may have ameliorated during this culturally near-sterile period (Miller, 2015; Rhodes et al., 2018), however, evidence suggests that stadial conditions had returned to the Swabian Jura by the time AMH groups arrived.

The earliest AMH populations in the Swabian Jura would have found the region empty of other human groups, and the landscape a mosaic of cold, dry tundra and wooded steppes. Reindeer and horse were the most numerous large prey species available (Starkovich et al.,in press), however these groups also exploited small game, birds, and fish as they were available (Conard et al., 2013; Bertacchi, 2017). Although small sample sizes limit our ability to determine the landscape composition of the Ach Valley during the Aurignacian using either botanical or small mammal material, a possible stadial/interstadial cycle is suggested in these material records from GH 7a/7aa at Hohle Fels. Based on the evidence available, it seems likely that AMH groups must have been well adapted to cold tundra landscapes and the relatively low resource availability and harsh climatic conditions of such environments. The fact that these early AMHs arrived in the region with a fully-formed Aurignacian culture (Conard and Bolus, 2003b; Conard, 2011), including a diverse technological toolkit and a complex system of symbolic expression, may have bestowed some advantage in coping with the less-than-ideal local environment.

Overall, the high-resolution of the Ach Valley small mammal record is attested by the sequence of D-O oscillations recognizable in the Geißenklösterle and, to a lesser extent, Hohle Fels records. The lack of a clear signal for dramatic climatic change around the time of

Neanderthal abandonment of the river valley suggests that deteriorating environmental conditions, and the resultant decrease in resource availability which likely accompanied the increase in tundra and steppe landscapes, was not the decisive factor in this demographic shift. The fact that this new paleoenvironmental record does not include clear signals for the dramatically cold Heinrich 4 event, despite recording earlier D-O events, may be due to the palimpsest nature of the small mammal assemblage. However it more likely signifies a localized response mediated by differences in the amplitude of climatic change and the ability of the local ecology to respond. Discamps and Royer (2017) have suggested that the OIS 3 climatic cycles had more substantial effect on the presence of cold climate adapted small mammals in southern France, and a similar pattern could be seen in the Swabian Jura record. Furthermore, the Ach Valley arboreal vegetation may have been restricted in its response to interstadial amelioration due to the presence of the Alps to the south (Müller et al., 2003; Fletcher et al., 2010), resulting in limited local woodland environments during warm periods and a low-to-moderate signal of forest loss during cold stadials.

With regards to the models put forth to explain the cultural fluorescence of the Swabian Jura Upper Paleolithic, the ^{14}C chronology and the paleoenvironmental record from the Ach Valley suggest the H4 event was not the cause of the loss of Neanderthal populations in the region, as suggested by the original *Population Vacuum model* (Conard and Bolus, 2006; Conard, 2011). While the Swabian Jura was most likely devoid of hominin groups when early Aurignacian populations arrived, the results of this thesis suggest that climatic deterioration, in the form of a discrete cold period, was not the driving force behind this population vacuum.

Increasing cold and dry landscapes beginning in the Middle Paleolithic may have driven Central and Eastern European Neanderthals to adopt a social and cultural pattern including highly mobile small group sizes (Floss, 1990; Conard, 2006, 2011; Hublin and Roebroeks, 2009; Bradtmöller et al., 2012; Roebroeks and Soressi, 2016), resulting in extended periods of regional depopulation by Neanderthals, during which AMH groups colonized various regions, including the Swabian Jura. Marine records suggesting that stadial periods would have evolved on a decadal scale (Bradtmöller et al., 2012), a timeframe which would have allowed generational recognition of the changing landscapes and resources across southern Germany. Still, further evidence is needed to directly tie the common cooling trend of D-O oscillations 12 – 9 with Neanderthal settlement dynamics (however see Feurdean et al., 2014; Staubwasser et al., 2018).

Alternatively, a near-extinction event during the early part of OIS 3, as suggested by genetic studies (Dalen et al., 2012) may have restricted Neanderthals to small, relatively isolated social groups. As some extinction models have suggested (Zubrow, 1989; Roebroeks and Tuffreau, 1999; Hublin and Roebroeks, 2009; Green et al., 2010; Fu et al., 2016; Hajdinjak et al., 2018), a decrease in genetic variability within Neanderthal groups could have resulted in multiple localized extinction events. Müller et al (2011) suggest that the abrupt cold of the H5 event, dated to ~46,000 B.P., strongly influenced the entire European continent as far as the eastern Mediterranean, and may have led to decreased population sizes among Neanderthal groups. However, the lack of evidence for this climatic event in the lower Danubian loess record (Fitzsimmons et al., 2012) and the moderate response of small mammal groups in southern Europe (López-García et al., 2015) and elsewhere (Belmaker and Hovers, 2011) , challenges this scenario. Ongoing excavation at Hohle Fels cave may reveal deposits dating to this period in the OIS 3 chronology, allowing us to test this hypothesis with locally derived environmental proxy data. Even without this data, it is possible that the loss of Neanderthal groups in the Swabian Jura is the result of a later local extinction, however more regional skeletal remains with preserved aDNA would be necessary to explore this hypothesis further.

Turning to the *Kulturpumpe model*, the presence of cultural hiatus periods interstratified between the Middle Paleolithic and Aurignacian deposits at many Swabian sites has effectively disproven the hypothesis that interspecies competition drove cultural development among AMHs groups. However, the possibility that climatic stress and/or social-cultural and demographic changes pushed Aurignacian populations to develop increasingly complex and innovative technological and symbolic systems remains tenable in light of the evidence presented herein. Multiple material records suggest that the early Upper Paleolithic of the Swabian Jura was particularly colder and dryer than preceding periods, and this may have diminished the available biomass within local large ungulate populations (Kitagawa et al., in press). This resource stress, along with the large group sizes of early AMH populations, suggested by the density of archaeological finds in the region (Conard, 2011), may have driven the rapid development and adoption of innovative technologies and complex communication systems among these groups.

Growing evidence that Neanderthals may have been better adapted to temperate and forested environments (Serangeli and Bolus, 2008; Wißing et al., 2016, 2019; Benito et al., 2017), including local isotopic evidence (Posth et al., 2017) suggests that landscape fragmentation due to climatic instability was also a contributing factor in the extinction of Neanderthals across Europe. Competition with AMH groups for access to resources (Shea, 2003; Bocherens and Drucker, 2006; Banks et al., 2008) or as part of complex inter-species interaction, acculturation, and/or assimilation (Hublin et al., 1996; d'Errico et al., 1998;

Mellars, 1999; d'Errico, 2003; Green et al., 2010; Flas, 2014; Pääbo, 2014) was undeniably a factor in regions where these two groups coexisted. However, a singular cause for Neanderthal extinction, even one as broadly defined as 'the arrival of anatomically modern humans' cannot be sustained in light of contradictory records from regions without evidence of inter-species interaction (Staubwasser et al., 2018), such as the Swabian Jura. As the results of this thesis show, we cannot invoke 'climatic instability during OIS 3' as a singular cause for the extinction of Neanderthal groups in the Ach Valley, either.

The temporal correlation between the gradual extinction of Neanderthal groups and climatic instability recognizable in the Greenland isotopic records has resulted in a revival of paleoclimatic and paleoenvironmental research among Paleolithic archaeologists. There is a continued need for high-resolution, multi-scale terrestrial paleoecological records that emphasize local variation, particularly with the growing evidence that ice core records are inadequate for predicting environmental change on a finer scale (Discamps and Royer, 2017). This thesis describes the creation of a high resolution small mammal-based paleoenvironmental record spanning the Middle Paleolithic and earliest Upper Paleolithic of the Ach Valley, and its integration with existing local and regional paleoecological signals. The results of this project will undoubtedly contribute to the ongoing efforts to discern the variables involved in the Neanderthal depopulation of the Swabian Jura. Ultimately, the loss of Neanderthal groups across Europe may appear stochastic in nature (Stringer et al., 2003) due to the wide variety of locally mediated factors involved. As such, local, high-resolution cultural, paleoanthropological, paleogenetic, and paleoecological records may prove vital in furthering our understanding of the mosaic nature of the loss of Neanderthal groups throughout Europe.

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Appendix

The accepted publications are listed in this appendix following the order in III List of Publications.

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Appendix 1.1

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Small mammal taxonomy, taphonomy, and the paleoenvironmental record during the Middle and Upper Paleolithic at Geißenklösterle Cave (Ach Valley, southwestern Germany)

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ABSTRACT

Geißenklösterle Cave, located in the Ach Valley of the Swabian Alb and one of six Swabian cave sites recently named as a UNESCO World Heritage site, has a long history of archaeological research resulting in a detailed record of human occupation. Sometime around 45,000 years ago Neanderthals seemingly vanished from the Swabian landscape, and after a period of mostly geogenic deposit at Geißenklösterle Cave we find deposits containing characteristically Aurignacian artifacts dating to as early as 42,500 years ago. These Aurignacian groups brought with them complex symbolic expression and communication including bone and ivory beads, musical instruments, and animal and human figurines. This study examines the climatic context of this depopulation through a taxonomic and taphonomic analysis of the rodent and insectivore remains associated with these periods and provides a relatively unbiased climatic record for the period of ~45,000–36,000 years ago in this region. Taphonomic analysis indicates that primarily the European eagle owl (*Bubo bubo*) and the kestrel (*Falco tinnunculus*) were responsible for accumulating the material, and allows us to quantify the potential taxonomic bias resulting from predator behaviour which includes a preference for voles, particularly the water vole (*Arvicola terrestris*). Additionally, rare taxa (which include species of murids and soricids) may have been present in greater quantities than our sample implies. The assemblage from Geißenklösterle Cave is dominated by the field and common vole (*Microtus arvalis/agrestis*), the narrow-headed vole (*Microtus gregalis*), and the root/tundra vole (*Microtus oeconomus*). Overall, the Middle Paleolithic landscape included significant woodland and forested areas while a high proportion of species restricted to cold tundra environments likely indicate punctuated cold and arid periods. The signal from the nearly geogenic layer overlying the Middle Paleolithic material includes a moderate shift in the proportion of cold tundra adapted species, suggesting that the tundra expanded leading up to the Neanderthal depopulation, but no period of drastic climatic change is recognizable. The Aurignacian was significantly colder and drier than the preceding period, with cold tundra expansion reaching its apex (for the time period studied). Based on these results the Swabian landscape first encountered by Aurignacian groups was significantly less hospitable than that known to the earlier Middle Paleolithic populations. These results correlate well with past paleoenvironmental reconstructions based on sedimentary, botanical, and faunal assemblages. There is no evidence in the small mammal record that climatic pressure drove Neanderthals from the Ach Valley, instead it seems likely they enjoyed a more temperate environment than later Aurignacian groups. Ongoing work focused on greater resolution of these climatic oscillations at similarly well-dated Swabian sites will shed further light on the timing and speed of this climatic shift and the response of the biological communities affected, including early human groups.

1. Introduction

A long tradition of research on the Paleolithic of the Swabian

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Jura of Southwestern Germany (Conard, 2011) has resulted in a detailed record of the past in the Ach and Lone valleys (Fig. 1). One of the most thoroughly documented sites in this region is Geißenklösterle Cave, which was first excavated by Eberhard Wagner in 1973 with continued fieldwork lead by Joachim Hahn from 1974 to 1991 (Hahn, 1988) and Nicholas Conard from 2000–2002 (Conard and Malina, 2002). From the resulting research we know that Neanderthals, the assumed makers of the Swabian Mousterian, occupied Geißenklösterle Cave intermittently during the first half of the late Pleistocene exploiting local raw material sources to manufacture lithic artifacts (Conard et al., 2012) while hunting reindeer, horse and ibex and occasionally small game (Conard et al., 2013). About 45,000 years ago Neanderthals seemingly vanished from the Swabian landscape, and after a period of mostly geogenic deposits at Geißenklösterle Cave, we find deposits containing characteristically Aurignacian artifacts documenting the arrival of early humans and dating to as early as 42,500 cal BP (Higham et al., 2012). These Aurignacian groups practiced complex symbolic expression and communication using bone and ivory beads, musical instruments, and animal and human figurines (Wolf, 2013; Conard et al., 2009) and used a wide range of innovative lithic & osseous technologies. Identifying the catalyst, or combination thereof, driving this regional Neanderthal de-population is a major research goal of the ongoing Swabian projects and has inspired two hypothetical models: the Danube corridor model, which suggests this region was a gateway for early human groups to the rest of Europe and which has been substantiated by radiocarbon dates placing the Swabian Aurignacian earlier than elsewhere in Europe (Conard and Bolus, 2003; Higham et al., 2012), and the *Kulturpumpe* model, which considers the active drivers behind the demographic shift from Neanderthal to early human regional occupation. Both models assume an early presence of Aurignacian populations in the region and a subsequent early spread of modern behaviours and cultural expression, and the *Kulturpumpe* model posits competing non-mutually exclusive hypotheses for the development of said cultural and technological innovation focused on inter-taxa competition, climatic variability, and demographic changes within the Aurignacian populations (Conard and Bolus, 2003). The presence of nearly culturally sterile deposits at Geißenklösterle Cave separating the final Middle Paleolithic from the early Aurignacian suggests direct competition between these two groups did not occur locally. The *Kulturpumpe* model also posits that demographic pressures and or climatic stress may have driven Neanderthals from the region. During the Middle Paleolithic, the presence of Neanderthals in the Ach and Lone valleys was in typically low densities with evidence of high group mobility (Conard et al., 2012). As well, the OIS 3 period is known for its climatic volatility as documented in both marine (Dansgaard et al., 1993; Heinrich, 1988) and terrestrial (Boettger et al., 2009) records. Therefore, it is important that we account for the effect of these external agents on the Swabian landscape and its people to better understand the role of social development and symbolic expression during this dramatic cultural shift.

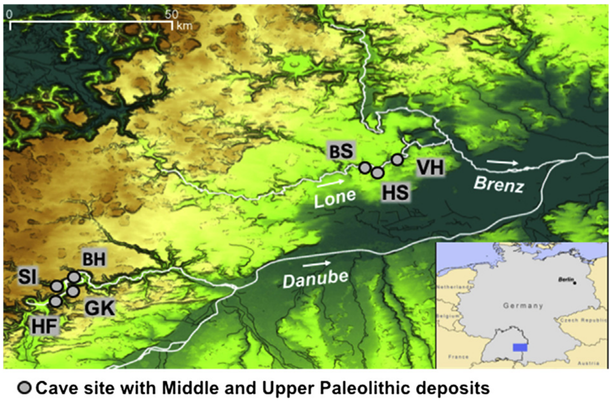

Fig. 1. Map of Swabian Alb showing all well documented Paleolithic cave sites. HF - Hohle fels; SI = Sirgenstein; GK = Geißenklösterle; BH = Brillenhöhle; BS = Bockstein; HS = Hohlesteinstadle; VH = Vogelherd (contribution by A. Barbieri).

Our current picture of the environment in the Ach Valley during the Late Pleistocene is one of climatic fluctuations of moist and temperate periods of intermixed steppe and woodland landscapes with cold and dry periods of extended tundra (Miller, 2015; Riehl et al., 2015; Ziegler, 2000; Storch, 1974; von Koenigswald, 1974a, b). The broad agreement between different material records, sedimentary, botanical, and small mammal, indicating a general trend of increasing cool and dry environments suggests a consistant paleoecological signal from this region. A lack of taphonomic consideration in the small mammal studies, however, does raise some concern. The work described herein was designed to augment previous studies (Ziegler, in press) and to contribute a small mammal paleoenvironmental signal incorporating any taphonomic bias from the regionally important Geißenklösterle Cave to the larger picture. The goals of this project are therfore twofold and include identifying meaningful patterns in small mammal taxonomic composition from the Middle Paleolithic to late Aurignacian deposits at the site and providing a detailed taphonomic analysis of the accummulation and modification of the small mammal assemblage to confirm its value as a record of the ecology and climate of the past. Although there is a long history in Germany of small mammal based paleoenvironmental interpretation in prehistoric studies [e.g. Schmidt, 1912] this is the first detailed taphonomic study from a German late Pleistocene locality. The precise habitat requirements, rapid turn-over rates, and small home ranges of most small mammal species make them outstanding paleoenvironmental indicators (Avery, 2007) and quantifying the potential biases introduced by the mode of death (via avian, mammalian, human predation or natural means) and by post-depositional taphonomic agents ensures these assemblages provide representative reflections of biotic communities in the distant past.

2. Material and methods

The material analyzed in this study was recovered within three 1 × 1 meter excavation quadrants (Qu. 56, 66, and 58) chosen for their uninterrupted stratigraphic deposit spanning the Aurignacian and Middle Paleolithic cultural periods (Fig. 2). The stratigraphic record at Geißenklösterle Cave is divided into geological horizons (GH) indicated by Arabic numerals and archaeological horizons (AH) indicated by Roman numerals and letter subdivisions, which often, but not always, correspond to one another (Table 1). The Aurignacian period, which includes the earliest Upper Paleolithic deposits, spans GH 11 through 15 and AH's IIn - IIIb. Geological horizon 10 is considered a transitional layer between the Aurignacian and Gravettian. The Middle Paleolithic period includes deposits from GH 18 to 23 and AH IV–VIII. These two cultural periods are separated by the nearly culturally sterile geogenic deposits in GH 17. For this study, all the small mammal material from GH 11 to 23 and AH Ic - VIII has been analyzed, including that from GH 17. Only dental specimens from GH 10 providing taxonomic information have been included. Some GH's are missing from each excavation quadrant, largely from the upper Aurignacian deposits, and the density of finds is far from even throughout time, yet when combined the assemblage represents an uninterrupted record of small mammal remains dating from ~48,000 - 33,000 kya BP

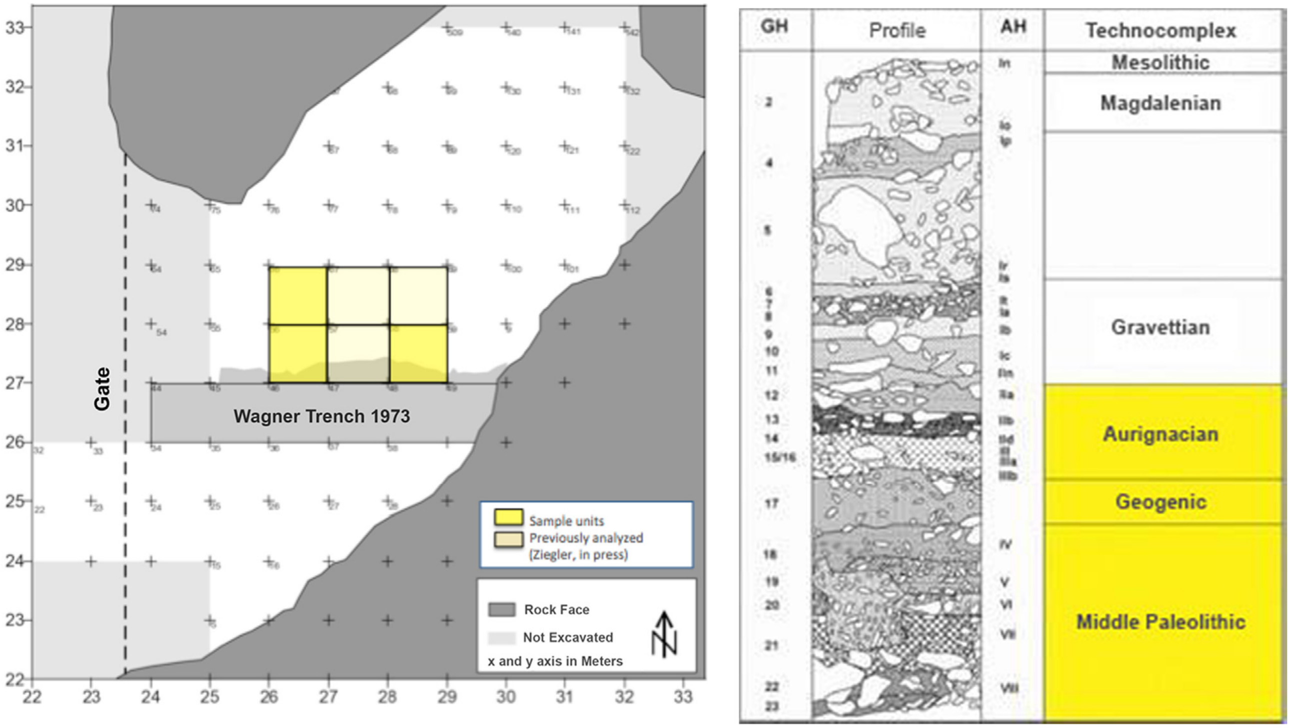

Fig. 2. Geißenklösterle Cave excavation grid including the three sampled quadrants, stratigraphic profile and associated cultural periods.

(Higham et al., 2012).

The fossil remains were collected by water-screening during the 1973–1983 and 1986 - 1993 excavation seasons lead by Joachim Hahn (Hahn, 1988) and the 2001 - 2002 campaigns lead by Nicholas Conard (Conard and Malina, 2003), and were processed and sorted both in the field and later in the lab. Taxonomic identifications were completed primarily on isolated dental elements (mandibles, maxillae, and molars) while taphonomic modifications were documented from both cranial and post-cranial elements. The taxonomically identifiable assemblage included a total of 1694 specimens which correspond to a minimum number of 670 individuals and 14 different species. The number of specimens identified to a taxonomic category are listed in Table 2 by geological horizon, along with the relative proportion and minimum number of individuals (MNI) for each species. All species determinations follow commonly accepted morphological criteria as laid out in Niethammer and Krapp (1978, 1982, 1990 Hrsg.), von Koenigswald (1974a,b), Agadjanian and von Koenigswald (1977), van Kolfschoten (1985, 1990) and Ziegler (in press). The few metric measures described follow Niethammer and Krapp (1978, 1982, 1990 Hrsg.), Storch (1973), von Koenigswald (1985), Ziegler (2000), and van Kolfschoten (1994, 2014). Measures of taxonomic diversity including richness (NTAXA), heterogeneity (reciprocal of Simpson's index 1/D) and evenness (Simpson's evenness E) are included at the bottom of the table. The taxonomic richness varies between geological horizons, with an average of 6.9 taxa in the Aurignacian levels and 9.3 in the Middle Paleolithic. The reciprocal of Simpson's index (1/D) is calculated as

$$1/D = \Sigma p_i^s$$

where p_i is the proportional abundance of taxon I and is expressed here as the reciprocal of Simpson's Index $(1/D)$ so greater evenness is indicated by a larger value. Although this measure is technically a heterogeneity index (and therefore measures both evenness and richness), it is relatively insensitive to the effect of rare taxa, and therefore more applicable to assemblages that may suffer from sampling bias (Faith and Du, 2017). It can be converted into a direct measure of taxonomic evenness (E) using the following

$$E_{1/D} = (1/D)/S$$

and ranges from $1/S$ to 1 for measures of perfect evenness (Faith and Du, 2017). This measure is considered one of absolute evenness, compared to the relative evenness measured by Shannon's E, as the minimum for any taxon is not 0. Our interpretations of these different indices (focused mainly on Simpson's reciprocal) will follow the taphonomic analysis as part of the paleoenvironmental interpretations detailed below.

To address the possibility that sample size (NISP) may be driving differences in species richness (NTAXA) between geological horizons Kendall's Tau b was run to gauge the strength of the relationship between the two variables. This non-parametric test is most applicable as it works well with small sample sizes ($n = 14$), allows outliers, and does not require normality [NISP failed the test of normality (Shapiro-Wilk $p = 0.009$)]. A result of >0.600 with $p < 0.005$ is considered a strong correlation herein. Statistical tests were run and graphs were created using both SPSS version 24 and JMP version 13.0.0.

We conducted a full taphonomic analysis to assess the mode of accumulation of the specimens and to quantify the effect of any post-depositional agents on the assemblage. The cranial and post-cranial elements identified as part of the taphonomic analysis, total 5151 specimens and are listed in Table 9. We documented the presence, absence, or degree of pronouncement of different bone surface modifications, indicated as a categorical ranking, including bone surface cracking, edge rounding, root etching, abrasion, thermal discolouration, oxide staining, and digestive corrosion. Taphonomic modifications were identified following morphological descriptions in Andrews (1990), Fernández-Jalvo and Andrews

Table 1
Lithologic description of the deposits at Geißenklösterle Cave including the geological horizon (GH), archaeological horizon (AH), and associated tool industry (adapted from Goldberg et al., in press).

GH	AH	Industry	Description
1	I	Mesolithic	Very loose silt with mica, little limestone sand; 10 YR 7/3 very pale brown; weak humus and roots throughout; horizontal, sharp-edged, limestone debris with surface lightly etched.
2			Relatively loose silt with little coarse limestone sand, roots throughout; 10 YR 7/4 very pale brown; few small to middle-sized, limestone debris with rounded edges that are often inclined to vertical.
3			Compact silt with little coarse limestone sand, roots throughout; 10 YR 7/4 very pale brown; little middle-sized, smaller sharp-edged limestone debris, irregularly bedded, but with some vertically oriented stones.
4			Very loose silt with mica and little limestone sand; 10 YR 7/3 very pale brown; medium-sized, mostly frost-cracked limestone debris.
5			Compact silt with coarse limestone sand, roots throughout; 10 YR 8/4 very pale brown; medium-sized limestone debris with edges partly rounded; irregularly bedded, large limestone blocks.
6	Is	Gravettian	Loose silt with fine and coarse limestone sand, rooting; 10 YR 8/3 very pale brown; little middle-sized and many small-sized limestone debris with slightly rounded edges, more or less horizontally bedded.
7	It	Gravettian	Loose silt with medium-sized and coarse limestone sand, roots throughout; 10 YR 7/3 very pale brown; much medium- and small-sized limestone debris, often flat and horizontally layered; also rounded limestone pebbles.
8	Ia	Gravettian	Loose silt with middle-sized and coarse limestone sand; 10 YR 7/3 very pale brown; higher amount of partly frost-cracked limestone boulders; limestone debris mostly medium-sized with sharp edges and irregularly layered.
9	Ib	Gravettian	Loose, slightly clayey silt with little medium-sized limestone sand; 10 YR 6/4 light yellowish-brown; coarse, sharp-edges, mostly horizontally layered limestone debris.
10	Ic	Gravettian	Loose clayey silt with little medium-sized limestone sand; 10 YR 6/8 brownish-yellow; smaller and medium-sized, irregularly layered limestone debris.
11	IIn	Aurignacian	Loose clayey silt with very little limestone sand; 10 YR 5/6 yellowish-brown; much medium-sized limestone debris, and boulders with rounded edges.
11a		Aurignacian	little clayey silt with mica and fine limestone sand; very loose; 10 YR 6/4 light yellowish-brown; much flat, sharp-edged, horizontally layered limestone debris (= wall facies from 11 in squares 58/59).
12	IIa	Aurignacian	Loose clayey silt with more limestone sand; 10 YR yellowish-brown; many limestone boulders and limestone blocks, as well as coarse, irregularly layered limestone debris with rounded edges and partly dissolved.
13	IIb	Aurignacian	Loose clayey silt with much limestone sand; 10 YR 4/4 dark yellowish-brown; medium-sized rounded limestone debris and limestone boulders; ash layer.
14	IId	Aurignacian	Loose clayey silt with little limestone sand; 10 YR 4/4 dark yellowish-brown; smaller and medium-sized, rounded limestone debris.
15	III and IIIa	Aurignacian	Compact clayey silt; 5 YR 4/6 yellowish-red; medium-sized and fewer smaller, rounded, irregularly layered limestone debris.
16	IIIb	Aurignacian	Compact clayey silt with coarse limestone sand; 7.5 YR brown; medium-sized rounded limestone debris, irregularly layered.
17a		Geogenic deposits	Silty compact clay with mica; 5 YR 4/4 reddish-brown, middle-sized, heavily rounded, partially frost-cracked limestone debris, partially vertical.
17b		Geogenic deposits	Compact silty clay with limestone sand; 5 YR 4/6 yellowish-red, medium-sized, heavily rounded, irregularly layered limestone debris.
18a		Middle Palaeolithic	Compact, clayey silt with coarse limestone sand; 7.5 YR 5/6 very brown; layered flakey small limestone debris and phosphate balls.
18b		Middle Paleolithic	Loose silt; 5 YR 3/4 dark reddish-brown; medium-sized, heavily rounded, irregularly layered limestone debris.
19	IV	Middle Paleolithic	Silty limestone sand with little clay; 10 YR yellowish-brown, medium-sized, heavily rounded, partially rolled limestone debris, more or less horizontally deposited; in Square 46 there is no interstitial sediment.
20		Middle Paleolithic	Dark yellowish-brown (10YR4/6) loamy silt, with mica and coarse limestone sand; irregularly scattered limestone from 5-10 cm, with rounded edges and no systematic orientations. Locally, calcareous sand, and micaceous in the darker areas. It is darker in the northern portion; further south, it is dark yellowish-brown with dark brown flecks.
21		Middle Paleolithic	Dark yellow-brown (10YR4/6) loamy silt; high content of limestone sand (sand up to 10 mm); firmer than GH 20. Limestone between 5 and 12 cm and in upper portion, highly rounded and vertically orientated; in the lower portion, more angular and with somewhat greater horizontal orientation.
22		Middle Paleolithic	Yellow-brown (10YR5/4) silt with some clay, and fine limestone sand. Massive limestone blocks >20 cm and up to 50 cm.

(2016), Madgwick (2014), Marín-Arroyo et al. (2008), and Stiner et al. (1995). Additionally, fragmentation of the assemblage was documented following Andrews (1990) and Fernández-Jalvo (1995). Specimens were examined under a binocular microscope at x10 to x100 magnification.

Lastly, each identified taxon was assigned to a preferred vegetative niche based on published modern analogues (Niethammer and Krapp, 1982, 1978, 1990) following past studies using the indicator species method (von Koenigswald, 1974a,b; van Kolfschoten, 1985, 2014; Ziegler, 2000). Section 3.2 below includes a detailed discussion of the ecological niche of each species identified in this study. The number of individuals (based on MNI calculated in Table 2) assigned to each niche was then plotted as a proportion of the total vegetative signal for each geological horizon (see Fig. 8). The results of this method, which allows for easy recognition of shifts in the cold/warm or dry/wet adapted species, are discussed in section 3.1.

3. Results

3.1. Taxonomic composition of the Geißenklösterle Cave small mammal assemblage

A large difference in the number of identifiable specimens between geological horizons is immediately evident. This is not entirely unexpected for two reasons. First, there are many lines of evidence suggesting that there was significantly higher site occupation in the Swabian Jura during the Aurignacian period compared to the Middle Paleolithic (Conard, 2011). This would result in an inverse pattern in small mammal remains as birds of prey and mammalian predators would have greater access to the site during the Middle Paleolithic. This is indeed the pattern broadly seen in Table 2. Secondly, since the relationship between rate of sediment deposit and time is not clear (Conard, 2011), it is possible that the greater depth of deposits during the Middle Paleolithic at Geißenklösterle Cave reflects a longer time span. However, as the

Table 2
Number of specimens, relative abundance (%), and minimum number of individuals (MNI) by taxonomic determination and geologic horizon at Geißenklösterle.

Geological Horizon	10			11			12			13			14			15			16		
Quadrants	56, 66			66			56			56, 58, 66			58, 66			56, 58, 66			58		
Species	N	%	MNI	N	%	MNI	N	%	MNI	N	%	MNI	N	%	MNI	N	%	MNI	N	%	MNI
Insectivora																					
Soricidae																					
Sorex/Neomys sp.	3	4.8%	1							3	5.2%	1				9	2.8%	3			
Sorex araneus													1	1.3%	1	2	0.6%	2			
Sorex minutus																					
Sorex sp.													1	1.3%	1	2	0.6%	1			
Neomys fodiens																					
Rodentia																					
Sciuridae																					
Spermophilus superciliosus																					
Cricetidae																					
Arvicolinae																					
Arvicola terrestris							1	4.2%	1				1	1.3%	1	2	0.6%	1			
Lemmus lemmus	11	17.7%	3	4	5.2%	2	2	8.3%	1	6	10.3%	2	11	14.7%	4	37	11.7%	9	1	5.0%	1
Dicrostonyx gulielmi	3	4.8%	2				2	8.3%	1	7	12.1%	6	12	16.0%	4	21	6.6%	5	1	5.0%	1
Microtus sp.	24	38.7%	17	57	74.0%	18	11	45.8%	5	25	43.1%	9	35	46.7%	13	147	46.5%	56	17	85.0%	4
Microtus gregalis	2	3.2%	2	1	1.3%	1	3	12.5%	3	9	15.5%	4	3	4.0%	3	10	3.2%	6			
Chionomy nivalis	2	3.2%	2	1	1.3%	1	1	4.2%	1							8	2.5%	4			
Microtus oeconomus	2	3.2%	2	4	5.2%	2	2	8.3%	1				3	4.0%	3	10	3.2%	6			
Myodes glareolus																1	0.3%	1			
Pitymys cf. *subterraneus*																					
Microtus arvalis/agrestis	15	24.2%	7	10	13.0%	7	2	8.3%	1	8	13.8%	5	7	9.3%	8	67	21.2%	42	1	5.0%	1
Microtus arvalis																					
Microtus agrestis													1	1.3%	1						
Grand Total	62	100.0%		77	100.0%		24	100.0%		58	100.0%		75	100.0%		316	100.0%		20	100.0%	
NTAXA (richness)		6			5			7			4			8			9			3	
Reciprocal of Simpson index (1/D)		3.840			2.985			6.259			4.556			4.762			4.290			3.000	
Simpson's evenness (E)		0.640			0.597			0.894			1.139			0.595			0.476			1.000	

Geological Horizon	17			18			19			20			21			22			23			Grand Total		
Quadrants	56, 58, 66			56, 58, 66			56, 58, 66			56, 58, 66			56, 58, 66			56, 58, 66			56, 58			56, 58, 66		
Species	N	%	MNI	N	%	MNI	N	%	MNI	N	%	MNI	N	%	MNI	N	%	MNI	N	%	MNI	N	%	MNI
Insectivora																								
Soricidae																								
Sorex/Neomys sp.	2	1.4%	2	3	1.0%	2	1	0.4%	1	2	1.5%	1	1	1.6%	1							24	1.4%	7
Sorex araneus				2	0.6%	2	2	0.8%	1	1	0.7%	1				2	1.7%	2				10	0.6%	6
Sorex minutus										1	0.7%	1							1	2.4%	1	2	0.1%	2
Sorex sp.				2	0.6%	1				2	1.5%	2										7	0.4%	2
Neomys fodiens	2	1.4%	2				2	0.8%	1	1	0.7%	1										5	0.3%	3
Rodentia																								
Sciuridae																								
Spermophilus superciliosus				1	0.3%	1										2	1.7%	1				3	0.2%	1
Cricetidae																								
Arvicolidae																								
Arvicola terrestris	7	5.0%	4	6	1.9%	3	9	3.6%	3	2	1.5%	1	2	3.3%	1	4	3.4%	1	3	7.1%	1	37	2.2%	11
Lemmus lemmus	13	9.2%	3	57	18.2%	14	59	23.3%	12	5	3.7%	2	2	3.3%	2	4	3.4%	1	4	9.5%	2	216	12.8%	54
Dicrostonyx gulielmi	5	3.5%	2	15	4.8%	4	12	4.7%	2	7	5.2%	1	2	3.3%	2	8	6.8%	2	4	9.5%	1	99	5.8%	30
Microtus sp.	65	46.1%	24	89	28.3%	65	80	31.6%	45	48	35.1%	28	22	36.1%	21	45	38.5%	25	11	26.2%	8	675	39.8%	253
Microtus gregalis	7	5.0%	6	18	5.7%	9	4	1.6%	2	4	3.0%	3	4	6.6%	3	10	8.5%	4	3	7.1%	3	78	4.6%	35
Chionomy nivalis	3	2.1%	2	5	1.6%	3	6	2.4%	5	6	4.5%	4	4	6.6%	3	3	2.6%	1	1	2.4%	1	40	2.4%	19
Microtus oeconomus	5	3.5%	3	7	2.2%	5	9	3.6%	5	7	5.2%	4	2	3.3%	2				1	2.4%	1	52	3.1%	30
Myodes glareolus																						1	0.1%	1
Pitymys cf. *subterraneus*							1	0.4%	1													1	0.1%	1
Microtus arvalis/agrestis	31	22.0%	18	106	33.8%	51	67	26.5%	35	48	35.8%	20	22	36.1%	14	39	33.3%	18	14	33.3%	8	437	25.8%	213
Microtus arvalis	1	0.7%	1				1	0.4%	1													2	0.1%	1
Microtus agrestis				3	1.0%					1	0.7%	1										5	0.3%	1
Grand Total	141	100.0%		314	100.0%		253	100.0%		135	100.0%		61	100.0%		117	100.0%		42	100.0%		1694	100.0%	670
NTAXA (richness)		9			10			11			11			8			8			8			13	
Reciprocal of Simpson index (1/D)		4.46			3.34			3.59			3.03			2.85			2.99			3.86			3.99	
Simpson's evenness (E)		0.50			0.33			0.33			0.28			0.36			0.37			0.45			0.31	

assemblage examined comes from only three of the 42 excavation units it is also possible that the difference in specimen number is the result of sampling bias. The results of Kendall's Tau b test indicate a strong positive correlation between NISP and NTAXA ($\pi = 0.602$, $p < 0.05$). This suggests that as sample size increases, so does species richness. This is not surprising as the effect of sample size on the representation of rare taxa is well documented (Lyman, 2008). This does suggest, however, that we cannot assume that rare taxa which are missing from the current assemblage were also missing in the death and/or life assemblages. To gauge if the relative proportions of different species are also strongly affected by sample size, we compared the sample size (NISP) with taxonomic evenness (E). The results indicate a weak negative correlation ($\pi = -0.472$, $p < 0.05$), suggesting that as sample size increases the evenness decreases and dominant species become more dominant. This would suggest that predominance of a species in our samples correctly reflects their predominance in the death assemblage. Whether the death assemblage correctly reflects the taxonomic diversity of the landscape surrounding the site at any given time is a factor of the taphonomic history of the assemblage, as well, and is discussed in more detail in section 3.3.

3.2. Ecology of the small mammal species

3.2.1. Cold tundra species

3.2.1.1. Lemmus lemmus Linnaeus 1758. **Norway lemming** - European *Lemmus* species date to the Late Pliocene in Poland (Kowalski, 1977) and Hungary (Kowalski, 1995). Specimens of the Norway lemming are identified at Geißenklösterle Cave based on the occlusal pattern of the molars, specifically the lack of enamel along the salient edges and the presence of cementum in re-entrant angles, a feature missing in *Dicrostonyx* molars. The length of the lower first molar material from Geißenklösterle Cave (Table 3) excludes *Lemmus schisticolor* (previously known as *Myopus schisticolor* Lilljeborg, 1844) from consideration and instead falls within the range of *Lemmus lemmus* reported from Weinberghöhle (von Koenigswald, 1974a,b). The Norway lemming is known from Middle and Late Pleistocene records, including Maastricht-Belvédère (van Kolfschoten, 1985) and is a typical inhabitant of the cold tundra, moving seasonally from rocky snowy peaks in winter to moist tundra in the summer (Niethammer and Krapp, 1982). *L. lemmus* is a characteristic indicator species for glacial conditions and is often absent from records during warmer periods (Niethammer and Krapp, 1982).

3.2.1.2. Dicrostonyx gulielmi Sanford 1870. **Collard lemming** - *Dicrostonyx* molar morphology is similar to the Norway lemming apart from a complete lack of cementum in all re-entrant angles. *Dicrostonyx* is known from Central and Western Europe since the Early Pleistocene (Kowalski, 1995*)*. During the Late Pleistocene two species are known, *D. gulielmi* and *D. henseli* which differ in the upper dentition morphology (van Kolfschoten, 2014) and may be more correctly considered as subspecies (Agadjanian and von Koenigswald, 1977). The two-subspecies known from the last glacial, *D. gulielmi rotundus* and *D. gulielmi hensli* are differentiated based on the frequency of morphological characteristics of the upper M1 and M2 (Agadjanian and von Koenigswald, 1977). The material from Geißenklösterle Cave most likely includes only the expected anaglacial *D. gulielmi rotundus*, as has been shown in other samples from the site (Ziegler, in press). The average length of the lower m1 listed in Table 4 is smaller than expected, yet the range of lengths falls within that seen at similarly dated sites including Weinberghöhle (von Koenigswald, 1974a,b) and Kogelstein (Ziegler, 2000). All modern species of collared lemming live in the circumpolar arctic tundra and its presence among Late Pleistocene Kaltsteppe communities has led to its use as a glacial indicator species, like the Norway lemming.

3.2.2. Inhabitants of cold tundra with wooded steppes environments

3.2.2.1. Microtus gregalis Pallas 1798. **Narrow-headed vole** - The narrow-skulled vole is identifiable by its lower m1 morphology only, like most members of the *Microtus* genus, which consists of five non-confluent triangles and an anterioconid complex (ACC) with an under developed sixth triangle and related buccal re-entrant angle. Nadachowski (1982) described several morphotypes which can be used to define variation in the morphology of the *M. gregalis* ACC from a typical ‘gregalid’ pattern to an ‘arvalid’ pattern which is like that seen in *Microtus arvalis/agrestis*. However, this method was not used for the Geißenklösterle Cave material. Instead, all specimens with an under-developed sixth triangle re-entrant angle devoid of cementum build-up were designated *M. gregalis* and those with cementum were designated *M. arvalis/agrestis*, following Ziegler (in press). This means that the number of *M. gregalis* individuals may be underestimated throughout the Geißenklösterle Cave assemblage and the (already dominant) *M. arvalis/agrestis* may be over-represented. The likelihood that this methodological choice greatly affected the relative proportions of these two species is low, as frequency of the ‘arvalid’ morphotype is believed to have been significantly lower during the Late Pleistocene than in recent populations (van Kolfschoten, 2014). The ‘Pitymys’ morphotype variation described from Pleistocene deposits in Poland (Nadachowski, 1982) was not found in the Geißenklösterle Cave assemblage. Previous studies of material from Geißenklösterle Cave found that the *M. gregalis* material varied in

Table 3
Length (mm) of the inferior m1 of *Lemmus lemmus* from Geißenklösterle Cave compared to other Pleistocene localities and recent populations (van Kolfschoten, 2014; Ziegler, 2000; von Koenigswald, 1974a,b, 1985; Storch, 1973).

Lemmus lemmus			
Locality	Nm1	Range	Mean
Geißenklösterle - Aurignacian	8	2.64–3.54	3.2
Geißenklösterle - Sterile	2	3.07–3.14	3.1
Geißenklösterle - Middle Paleolithic	18	2.33–4.14	3.21
Weinberghöhle C - E, H	54	2.70–3.60	3.13
Brillenhöhle V	10	3.00–3.80	3.32
Brillenhöhle VI	6	2.90–3.50	3.16
Brillenhöhle VII	55	3.00–4.10	3.36
Kogelstein	7	3.07–3.54	3.33
Villa Seckendorff	17	2.60–3.48	3.14
Sesselfelsgrotte E	1		3.25
Recent population Finland, Norway, Sweden	35	2.70–3.70	3.20

Table 4
Length (mm) of the inferior m1 of *Dicrostonyx gulielmi* from Geißenklösterle compared to other Pleistocene localities (van Kolfschoten, 2014; Ziegler, 2000; von Koenigswald, 1974a,b, 1985; Storch, 1973).

Dicrostonyx gulielmi			
Locality	Nm1	Range	Mean
Geißenklösterle - Aurignacian	8	3.21–3.54	3.31
Geißenklösterle - Middle Paleolithic	8	2.52–3.55	3.2
Gönnersdorf	35	3.23–4.03	3.61
Weinberghöhle C - E	73	2.90–3.90	3.43
Brillenhöhle V	23	3.20–3.90	3.56
Brillenhöhle VI	13	3.00–3.90	3.58
Brillenhöhle VII	15	3.00–4.10	3.56
Kogelstein	16	3.28–3.80	3.48
Villa Seckendorff	11	3.20–3.60	3.4
Sesselfelsgrotte D, E, G, and K	9	3.31–3.82	3.47

length without a recognizable trend (Ziegler, in press) and this is also seen in the current sample (Table 5).

The narrow-headed vole is another well-known Late glacial fauna, although modern populations are found in a variety of different environments (van Kolfschoten, 2014). Primarily, it is found in the northern arctic and forest tundra, and believed to indicate a particularly dry environment (von Koenigswald, 1985).

3.2.3. Inhabitants of cold tundra environments with rocky formations

3.2.3.1. Chionomys nivalis Martins 1842. **Snow vole** - The snow vole is another cold tundra indicator species often recovered alongside *M. gregalis*, *L. lemmus* and *D. gulielmi* (Kowalski, 2001). Restricted to mountainous regions by preference, modern *C. nivalis* has been shown to inhabit rocky patches with a scarcity of vegetation (Luque-Larena et al., 2002). The lower first molar morphology of the snow vole is like that of *Microtus oeconomus* (described below) but differs in the presence of a fifth closed triangle and the degree to which the forth salient angle is oriented posteriorly. Common ancestry between the two species has been claimed (Chaline, 1972), although recent studies have called this into question (Nadachowski, 1991). No transitional forms were identified in the Geißenklösterle Cave material, a divergence from the record at Brillenhöhle (Storch, 1973; Table 6).

3.2.4. Stepped grasslands species

3.2.4.1. Spermophilus superciliosus Kaup 1839. **European ground squirrel/European souslik** - The large souslik *Spermophilus superciliosus* is the dominant ground squirrel of the Weichselian (van Kolfschoten, 2014) and has been recognized in assemblages from Geißenklösterle Cave during past analyses (Ziegler, in press). The three specimens discussed here all come from Middle Paleolithic deposits and include a left lower p4 (with a length and width of 3.26 and 2.76 mm, respectively), a left upper M2 (with a length and width of 2.09 and 2.55 mm, respectively) and a molar fragment. Smaller ground squirrels are known to prefer warm stepped environments, but this large species is mostly found in open dry areas lacking in dense forest coverage (van Kolfschoten, 2014).

3.2.5. Inhabitants of the boreal forest belt

3.2.5.1. Microtus oeconomus Pallas 1776. **Root vole/tundra vole** - The root vole, also known as the tundra vole, is identified by the confluent fifth triangle and ACC of the first lower molars. All *M. oeconomus* specimens from Geißenklösterle Cave fall within Nadachowski (1982) morphotypes A – D. The 'nivalis'-like morphotype noted by Storch (1973) at Brillenhöhle was not seen within the Geißenklösterle assemblage. The average length of the lower first molar falls well within the range seen in other assemblages of similar age (Table 7). Modern populations of the root vole are known to inhabit humid areas of the cold tundra and taiga zone of Western and Central Europe (van Kolfschoten, 2014), and although this species is often found in association with glacial fauna it is not a direct indicator of glacial climates (von Koenigswald, 1985) (see Table 8).

Table 5
Length (mm) of m1 of *Microtus gregalis* from Geißenklösterle Cave compared with other Pleistocene localities (van Kolfschoten, 2014; Ziegler, 2000; von Koenigswald, 1974a,b; 1985; Storch, 1973).

Microtus gregalis			
Locality	Nm1	Range	Mean
Geißenklösterle - Aurignacian	15	2.54–2.92	2.68
Geißenklösterle - Sterile	4	2.44–2.9	2.64
Geißenklösterle - Middle Paleolithic	35	2.42–3.10	2.42
Gönnersdorf	154	2.26–3.24	2.82
Weinberghöhle C–F	123	2.40–3.10	2.8
Brillenhöhle VI	9	2.50–2.90	2.73
Brillenhöhle VII	10	2.40–3.00	2.75
Kogelstein	83	2.42–3.15	2.77
Villa Seckendorff	82	2.24–3.00	2.65
Burgtonna - SK	61	2.25–2.88	2.53
Sesselfelsgrotte H ″Unten″	7	2.51–2.82	2.64
Sesselfelsgrotte I	27	2.41–2.96	2.63
Sesselfelsgrotte K	74	2.37–2.95	2.6
Sesselfelsgrotte L	4	2.53–2.89	2.69

Table 6
Length (mm) of inferior m1 of *Chionomys nivalis* from Geißenklösterle compared with other Pleistocene localities (van Kolfschoten, 2014; Ziegler, 2000; von Koenigswald, 1974a,b; von Koenigswald, 1985; Storch, 1973).

Chionomys nivalis			
Locality	Nm1	Range	Mean
Geißenklösterle - Aurignacian	8	2.66–3.05	2.85
Geißenklösterle - Sterile	2	2.72–3.21	2.96
Geißenklösterle - Middle Paleolithic	22	2.63–3.07	2.86
Weinberghöhle C - E	29	2.60–3.10	2.82
Brillenhöhle VI, VII, VII	12	2.40–3.00	2.8
Kogelstein	85	2.43–3.15	2.88
Villa Seckendorff	2	2.88–3.16	3.02
Sesselfelsgrotte Layer K	4	2.57–3.01	2.76

3.2.6. Inhabitants of forests and lake margin environments

3.2.6.1. Arvicola terrestris Linnaeus 1758. **Water vole** - The water vole is an important indicator species found at several German sites of Weichselian age (Fig. 3) as either *Arvicola terrestris* or *Arvicola antiquus* (Storch, 1974). Archaeologically it is difficult to differentiate between these two species using dental metrics only (Ziegler, in press) and some have questioned the legitimacy of a species level distinction considering recent observed variation in *A. terrestris* first molar length (van Kolfschoten, 2014). The material from Geißenklösterle Cave falls within the range of both species but, arguably, closer to *A. terrestris* and is therefore designated as such. The morphology of the ACC further supports this determination. The frequency of this species is dependent on the occurrence of open water but it is also a regular occurrence in drier (Kurtén, 2009) and even cold stepped environments (Ziegler, in press). It should be noted that the water vole is a preferred prey species of the European eagle owl and therefore may be over represented in some assemblages.

Table 7
Length (mm) of inferior m1 of *Microtus oeconomus* from Geißenklösterle Cave compared with other Pleistocene localities (van Kolfschoten, 2014; Ziegler, 2000; von Koenigswald, 1974a,b; von Koenigswald, 1985; Storch, 1973).

Microtus oeconomus			
Locality	Nm1	Range	Mean
Geißenklösterle - Aurignacian	20	2.32–3.03	2.62
Geißenklösterle - Sterile	4	2.42–2.76	2.64
Geißenklösterle - Middle Paleolithic	23	2.34–2.91	2.6
Gönnersdorf	12	2.32–32.80	2.61
Weinberghöhle C - E	58	2.40–3.10	2.72
Brillenhöhle VI	6	2.50–2.80	2.6
Brillenhöhle VII	3	2.40–280	2.67
Brillenhöhle XV	6	2.60–2.70	2.67
Kogelstein	13	2.40–2.94	2.66
Villa Seckendorff	12	2.40–2.68	2.51
Sesselfelsgrotte Layer H ″unten″ - K	18	2.4–2.81	2.62
Maastricht-Belvédère 5	14	2.5–3.13	2.78

Table 8
Length (mm) of inferior m1 of *Microtus arvalis* and/or *agrestis* of Geißenklösterle Cave compared with other Pleistocene localities (van Kolfschoten, 2014; Ziegler, 2000; von Koenigswald, 1974a,b, 1985; Storch, 1973).

Microtus arvalis/agrestis			
Locality	Nm1	Range	Mean
Geißenklösterle - Aurignacian	83	2.27–3.07	2.66
Geißenklösterle - Sterile	17	2.48–3.01	2.78
Geißenklösterle - Middle Paleolithic	257	2.30–3.20	2.53
Sesselfelsgrotte H/I	19	2.36–2.97	2.62
Sesselfelsgrotte I	18	2.25–2.89	2.58
Sesselfelsgrotte K	16	2.28–2.98	2.51
Sesselfelsgrotte L	20	2.34–2.80	2.57
Maastricht-Belvédère fauna 3	3	2.37–2.91	2.61
Maastricht-Belvédère fauna 4	16	2.25–3.04	2.54
Gönnersdorf	110		2.73
Burgtonna			2.5
Villa Seckendorff	52		2.6

3.2.7. *Inhabitants of open forests with cool and moist environments*

3.2.7.1. Sorex minutus Linnaeus 1758. **Lesser shrew** - The small size of this insectivorous shrew, as shown in the condylar height (HC) and width of the lower condylar facet (LLF) in Fig. 4, is well documented and useful in differentiating this species from *Sorex coronatus* and *Sorex araneus*. The fact that *Sorex minutus* is found in only two geologic horizons at Geißenklösterle Cave (GH 20 and 23) both dating to the Middle Paleolithic period, and despite the occurrence of other *Sorex* species at later time periods, is likely an artifact of sampling as this species is known across Eurasia and well into the polar region (van Kolfschoten, 2014). Like the other *Sorex* and *Neomys* species identified herein, the lesser shrew prefers localities with dense vegetative ground cover and open water (Niethammer and Krapp, 1982).

3.2.7.2. Sorex araneus Linnaeus 1758. **Common shrew** - Like *S. minutus*, the common shrew has a tricuspulate incisor and a wide condylar facet when compared to *Neomys*. Fig. 4 compares the condylar height and lower facet width of the Geißenklösterle Cave Soricidae and those described by van Kolfschoten (2014) from various levels at Sesselfelsgrotte. Interestingly, some of the Geißenklösterle Cave *S. araneus* material exceeds the lower facet width seen in the Sesselfelsgrotte specimens, which falls within modern ranges in southern Germany (van Kolfschoten, 2014). This comparison also reveals that all *S. araneus* specimens exceed the lower facet width of *Sorex tundrensis*. This, combined with the lack of second incisors in the Geißenklösterle material, excludes the tundra shrew from consideration. The common shrew is known from deciduous woodland and wetlands with heavy vegetation (van Kolfschoten, 2014).

3.2.7.3. Neomys fodiens Schreber 1777. **Eurasian water shrew** - The Eurasian water shrew inhabits similar landscapes to the other Soricidae species detailed here, with a distinct preference for live water and/or swiftly flowing streams in the vicinity (van Kolfschoten, 2014). Morphologically, it can be identified by the presence of a unicusped lower incisor alongside red pigmented dentition and a very narrow mandibular inter-condylar space when viewed posteriorly. The condylar height and lower facet lengths are also distinct from the three *Sorex* species described above (Fig. 4).

3.2.7.4. Myodes glareolus Schreber 1780. **Bank vole** - *Myodes glareolus* (previously known as *Clethrionomys glareolus*) is easily identified as it is the only Arvicolidae in the Geißenklösterle Cave material to exhibit tooth roots. The morphology of the single lower first molar recovered in geological horizon 15 is alike that described by van Kolfschoten (2014) and Ziegler (in press) including the diagnostic deep posterior anticline of the ACC creating a cap-shape to the anterior tooth. Like the *Sorex* and *Neomys* species, the bank vole prefers dense vegetation within a generally moist forest environment.

3.2.8. *Species with indeterminate ecological niches*

3.2.8.1. Pitymys cf. *subterraneus Schrank 1798.* **European pine vole** - Only a single specimen of the pine vole is found in the Geißenklösterle Cave sample, recognizable by the *Pitymys*-rhombus, a

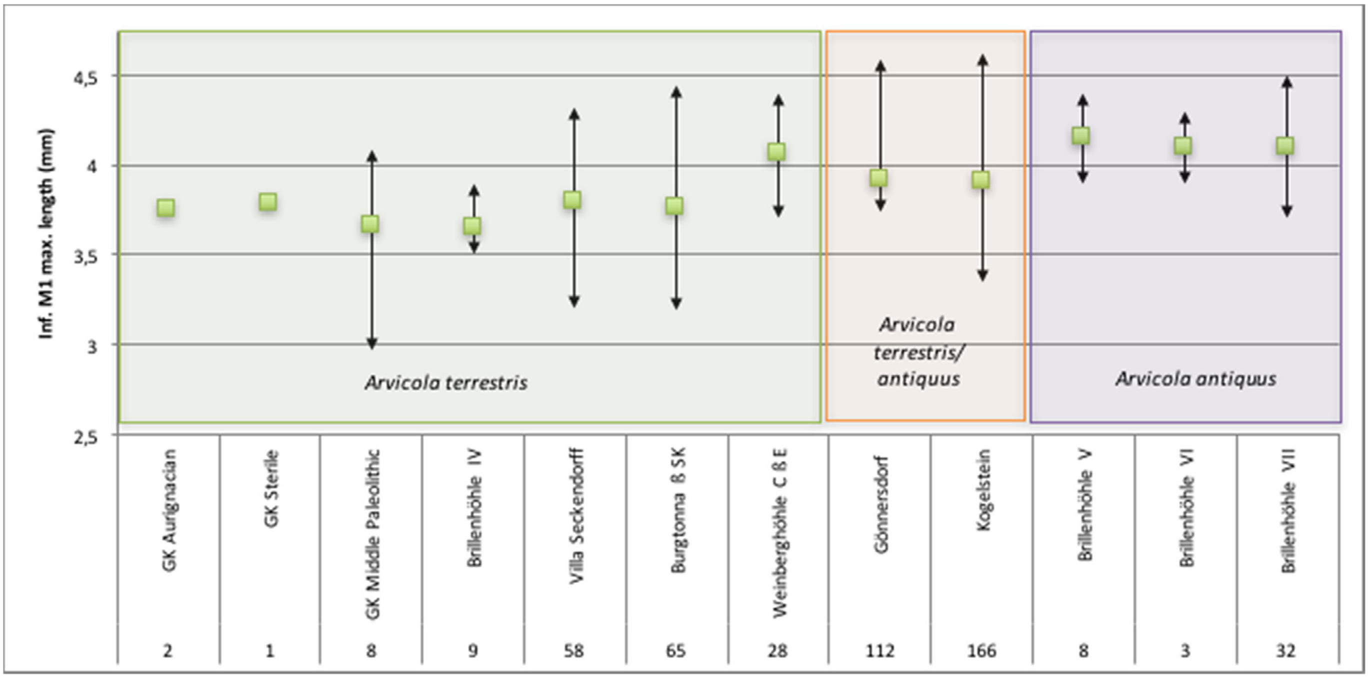

Fig. 3. Inferior m1 length of different *Arvicola* species from key sites (measurements from Ziegler, 2000).

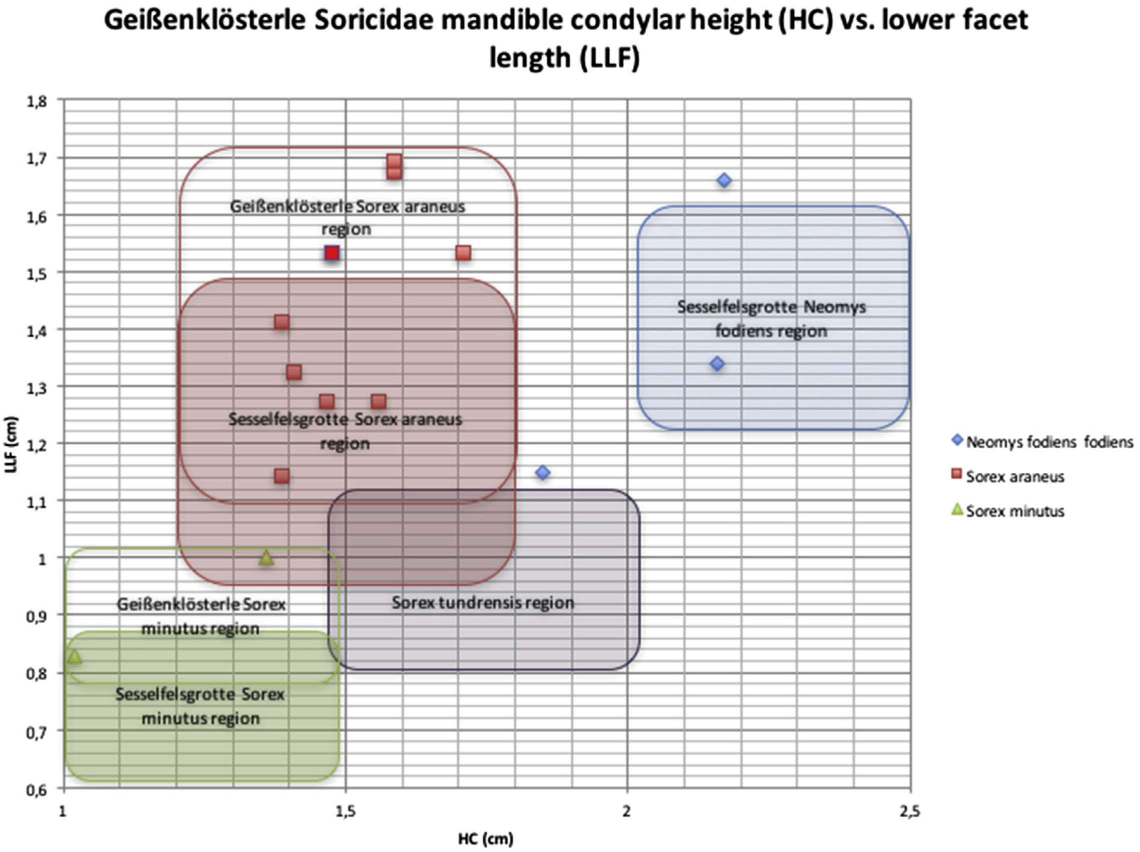

Fig. 4. Soricidae mandibular condylar height (HC) compared to lower facet length (LLF) from both Geißenklösterle Cave and Sesseslfelsgrotte (van Kolfschoten, 2014). Open boxes indicate the size range from Geißenklösterle Cave (excluding the variable Neomys fodiens specimens) and closed boxes indicate the range documented at Sesselfelsgrotte.

confluence of the fourth and fifth triangles of the lower first molar. However, Brunet-Lecomte et al. (1996) note that some individuals within modern French and Polish populations of *Microtus arvalis* and *Microtus agrestis* also exhibit this confluence, raising the possibility that our specimen reflects a morphological variation in the large *M. arvalis/agrestis* sample recovered from Geißenklösterle Cave.

3.2.8.2. Microtus arvalis and/or Microtus agrestis Pallas 1779. **Common vole and/or field vole** - Like many OIS 3 assemblages the common vole and/or field vole dominate the Geißenklösterle Cave record. The occlusal morphology of the lower first molar in both *M. arvalis* and *M. agrestis* is so similar as to be indistinguishable and includes five closed triangles and an anteroconid complex with two additional well-developed triangles (van Kolfschoten, 1990). Despite the many morphotypes described by both Nadachowski (1982) and van Kolfschoten (1990) a rather homogeneous morphology was recognized within the Geißenklösterle Cave material and all specimens with seven well developed closed triangles with cementum present in the re-entrant angles were assigned to *M. arvalis/agrestis* (see the description of *M. gregalis* specimens for comparison). The few specimens identified to specifically *M. arvalis* or *M. agrestis* were recognized by morphology of the upper M3 following Niethammer and Krapp (1982). Furthermore, the mean max. length of the lower first molars overlaps with records for these species from Sesselfelsgrotte (van Kolfschoten, 1990), Maastricht-Belvédère (van Kolfschoten, 1985), Gönnersdorf and Burgtonna (Ziegler, 2000). Modern populations of the common vole and field vole inhabit a wide variety of open and moist environments (van Kolfschoten, 2014).

3.3. *Taphonomy and the accumulating predator*

The taphonomic processes which affect osseous remains in cave deposits and other closed environments are well documented (Fernández-Jalvo and Andrews, 2016; Lyman, 1994) even if, in many cases, equifinality complicates their identification (Lyman, 2004). Since the publication of Andrews' seminal work on micromammal taphonomy (1990) it has become standard practice to include a discussion of the taphonomic nature of any small mammal assemblage under investigation, and detailed reconstructions of the biases introduced by the accumulating predator following his methods continue to grow in ubiquity. Our work at Geißenklösterle Cave is the first to provide such a detailed taphonomic reconstruction to an assemblage from the late Pleistocene of Germany. In assessing the predator responsible for the small mammal assemblage from Geißenklösterle Cave three sources of taphonomic information are used: the representation of skeletal elements, the breakage of skeletal elements, and the degree and frequency of digestive corrosion on both skeletal and dental elements (Andrews, 1990; Fernández-Jalvo, 1995).

3.3.1. *Representation of skeletal elements*

The number of each skeletal element as a raw tally and as a relative proportion based on the MNI by geological horizon is reproduced in Table 9. Immediately apparent is the uneven preservation of the remains, especially the near complete lack of crania. This is not uncommon for assemblages which have endured extensive trampling and/or sediment compression (Andrews, 1990). The high number of molars and incisors present throughout the assemblage suggests that cranial destruction

Table 9
Number of skeletal elements (NISP) and relative abundance (%) by geological horizon at Geißenklösterle Cave. Proportion of post-cranial remains exhibiting various peri- and post-depositional bone surface modifications are included below.

Geological Horizon		11		12		13		14		15 & 16		17		18		19		20		21		22		23		Grand Total
Skeletal Element	E	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	
Mandible	2	3	21.4%	3	37.5%	11	68.8%	5	16.7%	37	38.5%	10	22.7%	55	45.8%	36	52.9%	21	21.0%	5	5.0%	16	36.4%	6	37.5%	208
Maxilla	2	4	28.6%	1	12.5%	2	12.5%	1	3.3%	30	31.3%	4	9.1%	27	22.5%	12	17.6%	10	10.0%	3	3.0%	6	13.6%	3	18.8%	103
Scapula	2	0	0.0%	0	0.0%	1	6.3%		0.0%	6	6.3%	3	6.8%	1	0.8%	3	4.4%	1	1.0%	1	1.0%	3	6.8%	0	0.0%	19
Humerus	2	8	57.1%	4	50.0%	15	93.8%	18	60.0%	80	83.3%	44	100.0%	95	79.2%	47	69.1%	45	45.0%	16	16.0%	42	95.5%	6	37.5%	420
Radius	2	0	0.0%	3	37.5%	1	6.3%	2	6.7%	15	15.6%	6	13.6%	28	23.3%	12	17.6%	2	2.0%	4	4.0%	4	9.1%	2	12.5%	79
Ulna	2	2	14.3%	5	62.5%	10	62.5%	11	36.7%	40	41.7%	8	18.2%	58	48.3%	27	39.7%	25	25.0%	6	6.0%	19	43.2%	5	31.3%	216
Pelvis	2	0	0.0%	0	0.0%	7	43.8%	2	6.7%	19	19.8%	6	13.6%	36	30.0%	21	30.9%	7	7.0%	3	3.0%	14	31.8%	3	18.8%	118
Femur	2	9	64.3%	8	100.0%	10	62.5%	29	96.7%	80	83.3%	24	54.5%	77	64.2%	64	94.1%	29	29.0%	18	18.0%	33	75.0%	16	100.0%	397
Tibia	2	1	7.1%	4	50.0%	8	50.0%	20	66.7%	95	99.0%	24	54.5%	93	77.5%	68	100.0%	37	37.0%	15	15.0%	44	100.0%	13	81.3%	422
Vertebra	36	6	2.4%	1	0.7%	3	1.0%	13	2.4%	42	2.4%	9	1.1%	12	0.6%	17	1.4%	14	14.0%	5	5.0%	13	1.6%	4	1.4%	139
Incisor	4	11	39.3%	11	68.8%	15	46.9%	36	60.0%	171	89.1%	64	72.7%	237	98.8%	136	100.0%	66	66.0%	38	38.0%	84	95.5%	29	90.6%	898
Molar	12	77	91.7%	24	50.0%	58	60.4%	75	41.7%	336	58.3%	141	53.4%	314	43.6%	253	62.0%	135	135.0%	61	61.0%	117	44.3%	42	43.8%	1633
Astragalus/calcaneous	4	0	0.0%	0	0.0%	1	3.1%	8	13.3%	15	7.8%	7	8.0%	5	2.1%	7	5.1%	0	0.0%	2	2.0%	1	1.1%	1	3.1%	47
Rib	24	0	0.0%	0	0.0%	0	0.0%	3	0.8%	3	0.3%	2	0.4%	4	0.3%	6	0.7%	3	3.0%	0	0.0%	2	0.4%	0	0.0%	23
Metapodial	20	2	1.4%	0	0.0%	12	7.5%	12	4.0%	95	9.9%	34	7.7%	33	2.8%	54	7.9%	36	36.0%	17	17.0%	45	10.2%	3	1.9%	343
Phalanx	56	1	0.3%	0	0.0%	2	0.4%	8	1.0%	40	1.5%	12	1.0%	6	0.2%	2	0.1%	6	6.0%	3	3.0%	5	0.4%	1	0.2%	86
Grand Total	174	46		64		156		243		1104		398		1081		765		437		197		448		134		5151
MNI	1	7		4		8		15		48		22		60		34		23		10		22		8		
Cracking (Uneven)		1	2.2%	4	10.3%	2	2.0%	0	0.0%	9	1.2%	8	3.1%	68	8.2%	25	4.6%	12	3.7%	6	4.3%	29	8.3%	9	9.7%	173
Cracking (Even)		9	19.6%	12	30.8%	14	13.9%	20	11.8%	61	7.9%	34	13.4%	128	15.4%	63	11.6%	38	11.8%	20	14.3%	63	18.1%	15	16.1%	477
Rounding		0	0.0%	2	5.1%	4	4.0%	0	0.0%	1	0.1%	3	1.2%	4	0.5%	0	0.0%	0	0.0%	2	1.4%	5	1.4%	0	0.0%	21
Root etching		1	2.2%	2	5.1%	3	3.0%	17	10.1%	61	7.9%	38	15.0%	22	2.7%	15	2.8%	16	5.0%	9	6.4%	22	6.3%	8	8.6%	214
Soil etching		0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	2	0.8%	0	0.0%	0	0.0%	0	0.0%	2	1.4%	1	0.3%	0	0.0%	5
Tooth marks		0	0.0%	0	0.0%	0	0.0%	0	0.0%	1	0.1%	1	0.4%	0	0.0%	1	0.2%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	3

occurred on-site, either pre- or post-depositionally. The concurrent presence of low density elements such as ribs and vertebrae with high density dental elements, combined with the low counts of edge rounding and surface polishing, excludes fluvial transport as a main source of bone accumulation (Korth, 1979). Therefore, the differential preservation of elements is likely the result of destruction during predation or density mediated attrition. While the effect of bone density on preservation has been explored for marmot species (Lyman et al., 1992) and leporids (Pavao and Stahl, 1999), similar studies on the species present in the Geißenklösterle Cave assemblage are lacking. The inherent difficulty in comparing structural density between similarly sized species is well documented (Weissbrod et al., 2005; Pavao and Stahl, 1999) and therefore we consider the element representation at Geißenklösterle Cave in terms of predation breakage only.

Plotting the different proportion of each skeletal element out of the total expected based on the minimum number of individuals (MNI) is a common method used to distinguish between prey accumulations of different predators in both microfaunal (Weissbrod et al., 2005; Fernández-Jalvo, 1995; Andrews, 1990; Andrews and Evans, 1983) and macrofaunal assemblages (Binford, 1978; Stiner, 1991). The formula for this relative abundance is $R = N_i/(MNI\ x\ E_i)$, with E_i being the number of element *i* expected in a single prey skeleton. The relative abundance, by element, is then plotted and compared with modern prey assemblages (particularly Andrews, 1990). Applying a correlation coefficent to the relative abundances takes this comparison one step further. This has been done for the Geißenklösterle Cave data and the results of the Kendall's Tau_B coeffecient are reported in Table 10. This non-parametric test was used as many of both the actualistic prey samples and the element relative proportions calculated proved to be non-normal in their distribution and/or contain outliers.

Fig. 6 plots the R values of geological horizons from Geißenklösterle Cave which proved to have strong correlations ($\pi > 0.710\ p < 0{,}005$) with a small mammal predator assemblage. All 14 geological horizons at Geißenklösterle Cave reveal a strong positive correlation with the relative element proportions produced in red fox assemblages (ranging from $\pi = 0.616 - 0.819$) with the four strongest depicted in Fig. 6. Two geological horizons

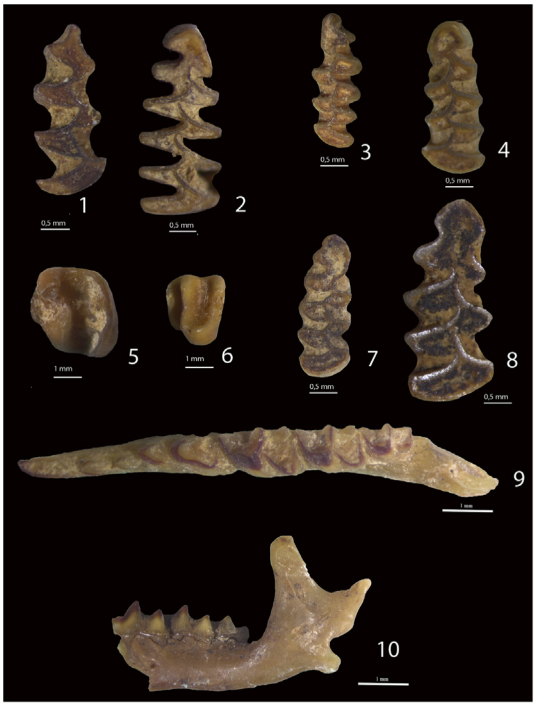

Fig. 5. (Top row) Morphology of the lower first molar of the taxa identified at Geißenklösterle Cave: (1) *Lemmus lemmus* (2) *Dicrostonyx* sp. (3) *Microtus gregalis* (4) *Chionomys nivalis* (5) *Spermophilus superciliosus* lower m1-2 (6) *Spermophilus superciliosus* upper M1-2 (7) *Microtus oeconomus* (8) *Arvicola terrestris* (9) mandibular dentition of *Sorex araneus* and (10) labial view of *Neomys fodiens* manidible with anterior breakage.

Table 10
Kendall's Tau_B Correlation results comparing skeletal element representation by geological horizon at Geißenklösterle Cave with actualistic predator patterns including cranial values.

		GH11	GH12	GH13	GH14	GH15&16	GH17	GH18	GH19	GH20	GH21	GH22	GH23
Red Fox	Correlation Coefficient	0.616**	0.720**	0.724**	0.819**	0.747**	0.802**	0.787**	0.767**	0.718**	0.802**	0.747**	0.814**
	Sig. (2-tailed)	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Barn Owl	Correlation Coefficient	0.070	0.189	0.387*	0.151	0.293	0.269	0.283	0.286	0.350	0.202	0.326	0.245
	Sig. (2-tailed)	0.714	0.329	0.038	0.417	0.115	0.149	0.126	0.125	0.059	0.279	0.079	0.190
Snowy Owl	Correlation Coefficient	−0.211	−0.018	0.034	0.085	0.042	0.068	0.084	0.102	0.084	0.017	0.059	0.060
	Sig. (2-tailed)	0.271	0.926	0.857	0.651	0.821	0.718	0.652	0.588	0.652	0.928	0.752	0.751
European Eagle Owl	Correlation Coefficient	0.446*	0.596**	0.802**	0.582**	0.655**	0.684**	0.644**	0.650**	0.628**	0.658**	0.655**	0.670**
	Sig. (2-tailed)	0.019	0.002	0.000	0.002	0.000	0.000	0.001	0.001	0.001	0.000	0.000	0.000
Long-eared owl	Correlation Coefficient	0.104	0.243	0.403*	0.218	0.310	0.286	0.317	0.353	0.350	0.286	0.360	0.295
	Sig. (2-tailed)	0.583	0.210	0.030	0.241	0.095	0.125	0.087	0.058	0.059	0.125	0.053	0.114
Short-eared owl	Correlation Coefficient	0.244	0.459*	0.605**	0.437*	0.494**	0.571**	0.550**	0.504**	0.517**	0.538**	0.494**	0.481*
	Sig. (2-tailed)	0.200	0.018	0.001	0.019	0.008	0.002	0.003	0.007	0.005	0.004	0.008	0.010
Hen harrier	Correlation Coefficient	0.439*	0.426*	0.576**	0.373*	0.549**	0.559**	0.571**	0.559**	0.538**	0.593**	0.498**	0.502**
	Sig. (2-tailed)	0.022	0.029	0.002	0.047	0.003	0.003	0.002	0.003	0.004	0.002	0.008	0.008
Pine Marten	Correlation Coefficient	0.569**	0.496*	0.609**	0.309	0.479*	0.498**	0.502**	0.438*	0.604**	0.506**	0.547**	0.397*
	Sig. (2-tailed)	0.003	0.012	0.001	0.102	0.011	0.008	0.008	0.021	0.001	0.007	0.004	0.037
Little Owl	Correlation Coefficient	0.451*	0.567**	0.701**	0.667**	0.706**	0.650**	0.695**	0.735**	0.712**	0.641**	0.740**	0.644**
	Sig. (2-tailed)	0.019	0.004	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.001	0.000	0.001
Kestrel	Correlation Coefficient	0.435*	0.531**	0.689**	0.521**	0.611**	0.689**	0.633**	0.588**	0.600**	0.655**	0.611**	0.633**
	Sig. (2-tailed)	0.022	0.006	0.000	0.005	0.001	0.000	0.001	0.002	0.001	0.000	0.001	0.001
Arctic Fox	Correlation Coefficient	0.308	0.065	0.245	0.183	0.139	0.166	0.095	0.096	0.095	0.096	0.104	0.175
	Sig. (2-tailed)	0.115	0.742	0.201	0.338	0.466	0.386	0.616	0.616	0.616	0.616	0.584	0.361
Coyote	Correlation Coefficient	0.483*	0.617**	0.678**	0.610**	0.624**	0.661**	0.639**	0.610**	0.655**	0.669**	0.633**	0.638**
	Sig. (2-tailed)	0.012	0.002	0.000	0.001	0.001	0.000	0.001	0.001	0.000	0.000	0.001	0.001

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

c. Listwise N = 16.

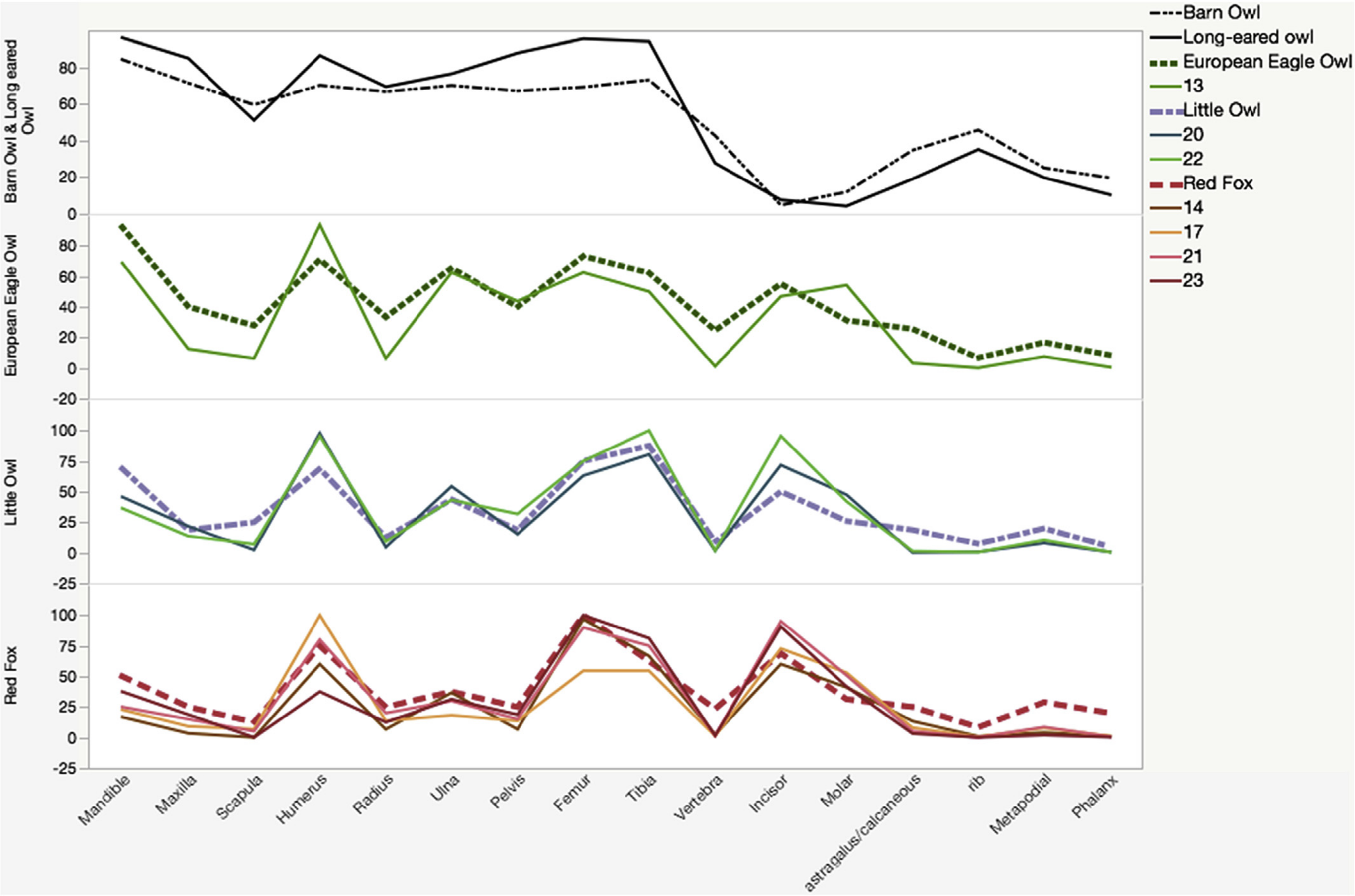

Fig. 6. Skeletal element relative abundance (R) by geological horizon at Geißenklösterle Cave showing strong correlations ($\pi > 0.710$) with modern prey samples (from Andrews, 1990).

containing Middle Paleolithic deposits (GH 20 and 22) correlated strongly with little owl assemblages and a single level of Aurignacian deposits revealed a strong correlation with the European eagle owl actualistic assemblage. These three predators are specifically noted by Andrews' as producing a patterned destruction of weaker skeletal elements and jaws (1990, pp. 45–49). For comparison, the R values of actualistic barn owl and long eared owl prey are included in the top of Fig. 6. These two predators modify the remains of prey the least, and this is clearly seen in the low proportion of isolated molars and incisors and the high proportion of mandibles and maxillae.

To assess the possibility that the selective destruction of mandibles and maxillae (and the subsequent high number of isolated dentition) is disproportionately driving the correlation between the Geißenklösterle Cave material and heavy modifying predator prey assemblages a second set of correlation coefficients was run excluding these elements (Table 11). The results were broadly similar, although stronger correlations were found for many GHs ($\pi > 0.779$ included in Table 11). That the two strongest correlations for each geological horizon remained strongest in both iterations is notable, although they may have swapped ranking, as is the fact that they are always predators with similar levels of element destruction (i.e. little owl and kestrel). Overall, the red fox, European eagle owl, little owl, and kestrel are all strongly correlated with most geological horizons from both the Middle Paleolithic and Aurignacian periods, and as Andrews' found in his actualistic study, it is not possible to distinguish between these predators using element representation alone (Andrews, 1990, p. 49).

3.3.2. *Breakage of skeletal elements*

Each post-cranial specimen examined was assigned a breakage class describing the portion of the bone present. For long bones, crania and mandibles these classes follow Andrews' classification scheme (1990, Figs. 3 and 7, Figs. 3,11 and Fig. 3,12). Quantification of the degree of skeletal breakage throughout the Geißenklösterle Cave sample (Table 12) reveals a similar pattern of high modification as that described above. There are markedly low numbers of complete limb elements throughout the assemblage indicating that the high degree of breakage seen in counts of fragile cranial bones, including the maxillae, is not restricted to those elements. The high proportion of proximal femora and ulnae (relative to distal) and distal humeri (relative to proximal) seen throughout the assemblage suggests selective loss of the less dense distal femora and proximal humeri. This pattern is alike that documented in the prey remains of various diurnal raptors and mammalian predators (Andrews, 1990), however, the high number of distal tibias (particularly in GH 15, 17–23) does not fit this pattern. The proportion of complete femora and humeri also fall in similar ranges to that seen in fox, coyote, and pine martin scat (Andrews, 1990, p. Fig. 3.8). Again, the reported element portions from low breakage prey assemblages, including those produced by barn owls, snowy owls and other common owls, differ greatly from the pattern seen here especially with regards to the number of complete skeletal elements (which ranges from 95% - 100% in barn owl assemblages).

The number of cranial specimens, particularly maxillae, preserved in the Geißenklösterle Cave assemblage is also exceptionally low (Table 13). Breakage of the skulls far exceeds that produced

Table 11
Kendall's Tau_B Correlation results comparing skeletal element representation by geological horizon at Geißenklösterle with actualistic predator patterns excluding cranial values.

		GH 11	GH 12	GH 13	GH 14	GH 15 & 16	GH 17	GH 18	GH 19	GH 20	GH 21	GH 22	GH 23
Red Fox	Correlation Coefficient	0.673**	0.641**	0.772**	0.828**	0.781**	0.787**	0.760**	0.760**	0.667**	0.844**	0.729**	0.844**
	Sig. (2-tailed)	0.004	0.007	0.001	0.000	0.001	0.001	0.001	0.001	0.003	0.000	0.001	0.000
	N	12	12	12	12	12	12	12	12	12	12	12	12
Barn Owl	Correlation Coefficient	0.296	0.557*	0.615**	0.504*	0.687**	0.677**	0.697**	0.697**	0.727**	0.595**	0.727**	0.595**
	Sig. (2-tailed)	0.199	0.018	0.006	0.023	0.002	0.002	0.002	0.002	0.001	0.007	0.001	0.007
	N	12	12	12	12	12	12	12	12	12	12	12	12
Snowy Owl	Correlation Coefficient	0.050	0.158	0.171	0.277	0.308	0.264	0.290	0.351	0.321	0.246	0.260	0.338
	Sig. (2-tailed)	0.830	0.505	0.447	0.215	0.168	0.240	0.192	0.114	0.149	0.270	0.243	0.130
	N	12	12	12	12	12	12	12	12	12	12	12	12
European Eagle Owl	Correlation Coefficient	0.526*	0.696**	0.831**	0.687**	0.779**	0.831**	0.758**	0.758**	0.667**	0.840**	0.727**	0.779**
	Sig. (2-tailed)	0.022	0.003	0.000	0.002	0.000	0.000	0.001	0.001	0.003	0.000	0.001	0.000
	N	12	12	12	12	12	12	12	12	12	12	12	12
Long-eared owl	Correlation Coefficient	0.362	0.592*	0.585**	0.504*	0.657**	0.585**	0.636**	0.697**	0.667**	0.657**	0.667**	0.595**
	Sig. (2-tailed)	0.116	0.012	0.009	0.023	0.003	0.009	0.004	0.002	0.003	0.003	0.003	0.007
	N	12	12	12	12	12	12	12	12	12	12	12	12
Short-eared owl	Correlation Coefficient	0.428	0.661**	0.769**	0.657**	0.748**	0.862**	0.818**	0.758**	0.727**	0.840**	0.727**	0.718**
	Sig. (2-tailed)	0.063	0.005	0.001	0.003	0.001	0.000	0.000	0.001	0.001	0.000	0.001	0.001
	N	12	12	12	12	12	12	12	12	12	12	12	12
Great Grey Owl	Correlation Coefficient	0.329	0.557*	0.615**	0.473*	0.718**	0.646**	0.727**	0.727**	0.758**	0.626**	0.758**	0.565*
	Sig. (2-tailed)	0.153	0.018	0.006	0.033	0.001	0.004	0.001	0.001	0.001	0.005	0.001	0.011
	N	12	12	12	12	12	12	12	12	12	12	12	12
Hen harrier	Correlation Coefficient	0.367	0.495*	0.688**	0.481*	0.636**	0.688**	0.708**	0.646**	0.677**	0.729**	0.615**	0.543*
	Sig. (2-tailed)	0.115	0.038	0.002	0.032	0.005	0.002	0.002	0.004	0.002	0.001	0.006	0.016
	N	12	12	12	12	12	12	12	12	12	12	12	12
Pine Marten	Correlation Coefficient	0.526*	0.431	0.603**	0.221	0.394	0.429	0.406	0.344	0.563*	0.457*	0.500*.500*	0.299
	Sig. (2-tailed)	0.025	0.073	0.008	0.331	0.082	0.060	0.071	0.127	0.013	0.044	0.027	0.187
	N	12	12	12	12	12	12	12	12	12	12	12	12
Little Owl	Correlation Coefficient	0.464*	0.491*	0.698**	0.615**	0.738**	0.636**	0.718**	0.779**	0.687**	0.677**	0.748**	0.615**
	Sig. (2-tailed)	0.045	0.038	0.002	0.006	0.001	0.005	0.001	0.000	0.002	0.002	0.001	0.006
	N	12	12	12	12	12	12	12	12	12	12	12	12
Kestrel	Correlation Coefficient	0.428	0.627**	0.831**	0.718**	0.809**	0.923**	0.818**	0.758**	0.727**	0.901**	0.788**	0.779**
	Sig. (2-tailed)	0.063	0.008	0.000	0.001	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.000
	N	12	12	12	12	12	12	12	12	12	12	12	12
Arctic Fox	Correlation Coefficient	0.342	0.145	0.160	0.349	0.191	0.272	0.205	0.142	0.110	0.191	0.173	0.254
	Sig. (2-tailed)	0.148	0.550	0.485	0.125	0.403	0.235	0.366	0.532	0.627	0.403	0.445	0.265
	N	12	12	12	12	12	12	12	12	12	12	12	12
Coyote	Correlation Coefficient	0.618**	0.689**	0.719**	0.729**	0.744**	0.781**	0.739**	0.708**	0.739**	0.837**	0.739**	0.791**
	Sig. (2-tailed)	0.008	0.004	0.001	0.001	0.001	0.001	0.001	0.002	0.001	0.000	0.001	0.000
	N	12	12	12	12	12	12	12	12	12	12	12	12

**Correlation is significant at the 0.01 level (2-tailed).
*Correlation is significant at the 0.05 level (2-tailed).
c. Listwise N = 16.

during owl predation (which commonly fractures the occipital region) and has resulted in the preservation of maxillary palate fragments exclusively. It should be noted that the few specimens assigned to Andrews' maxillae with zygomatic category (1990, p. 53) exhibited some degree of anterior breakage as well. Only four of the 12 geological horizons examined contained maxilla with *in situ* dentition (GH 14, 18, 19, 20). The fact that three of these are in superposition within the Middle Paleolithic deposits may indicate that deposits from this period were exposed to lower levels of trampling than those laid down during the Aurignacian. This higher degree of bone preservation is also seen in the number and completeness of the mandibular specimens. Overall, the mandibular breakage pattern and the proportion of *in situ* molars follow the pattern produced by the predators mentioned above – the European eagle owl, little owl, kestrel, fox, and pine martin (Andrews, 1990). Exceeding this pattern is the degree of mandibular anterior breakage (in curious similarity to the maxillary specimens) and the low fragmentation of the GH 17 mandibles. The latter may also indicate decreased trampling damage.

The various indices included at the bottom of Table 13 summarize the pattern of breakage and element representation in the assemblage succinctly. When comparing the total post-crania by cranial specimens the results >100 indicate that post-crania is dominant, and to what degree. This is true for all GHs except for GH 11 (from which only dental specimens were recovered). The true dominance of post-crania in the Geißenklösterle Cave assemblage is indicated when isolated molars and incisors are excluded, such as in the femur + humerus/mandible + maxilla index, indicating a significant loss of jaws. This is also apparent, to a lesser degree, in the proportion of isolated molars and incisors throughout the assemblage. Comparing the number of femora and humeri with distal limb elements reveals a loss of the latter throughout the entire deposition sequence. This differential destruction is likely related to bone density and fragility, which may also explain the high number of distal tibia preserved (see Table 12). The complete loss of maxillae and mandibular specimens indicated by the first index is further quantified in the calculation of the proportion of isolated molars and incisors for each GH, where a result >100 indicates the destruction of jaw specimens (conversely, a result <100 would indicate a loss of dentition). This index takes into consideration the *in-situ* dentition noted throughout the assemblage, and therefore the high numbers seen in GH 14, 17, 18, 21 and 22 indicate a much higher number of teeth than would be expected based on the preserved alveolar spaces.

3.3.3. *Digestive corrosion*

It is important to compare skeletal element patterns with digestive corrosion, a predatory modification that is distinctive of

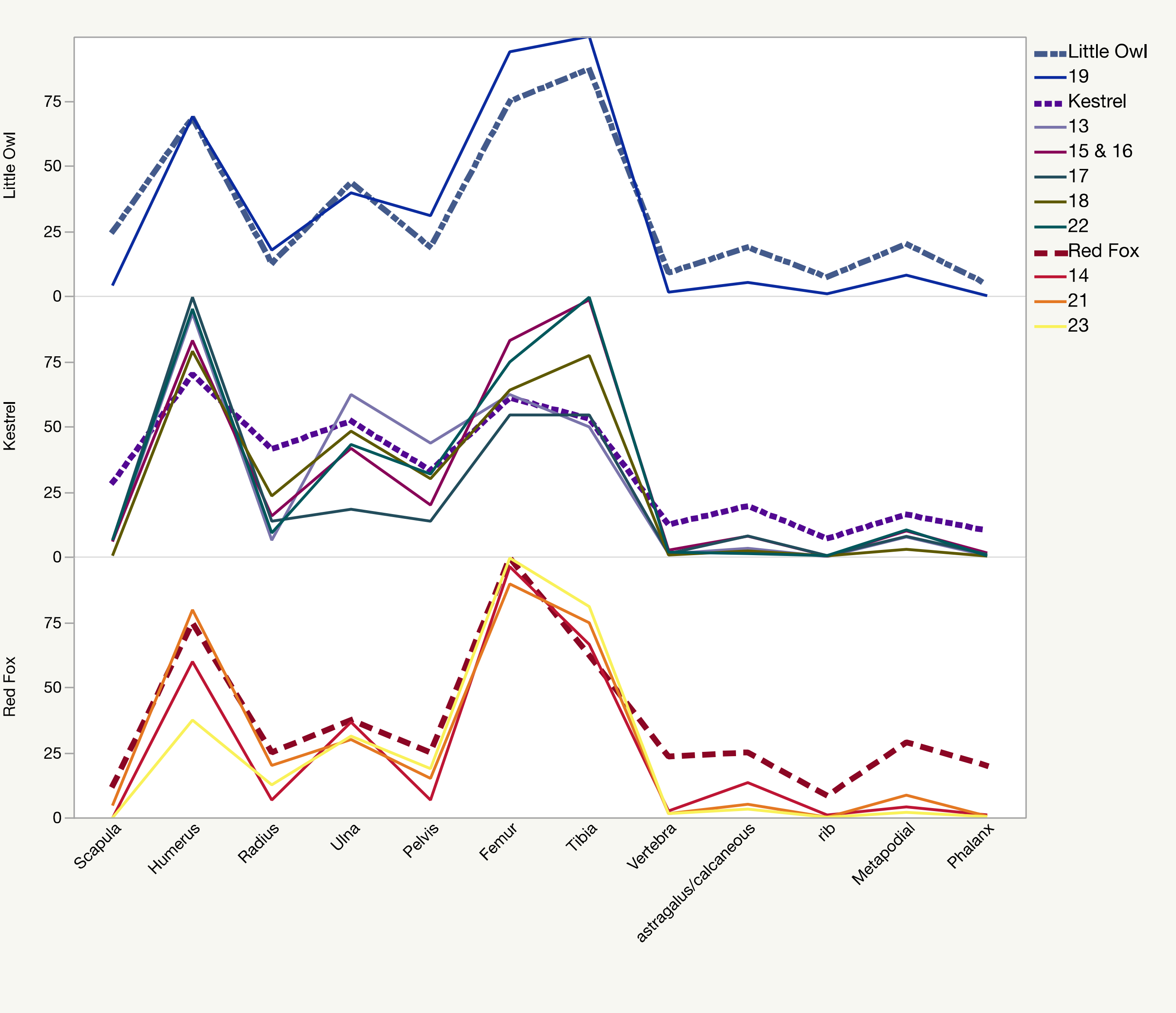

Fig. 7. Skeletal element relative abundance (R) by geological horizon at Geißenklösterle showing strong correlations ($\pi > 0.710$) with modern prey samples (from Andrews, 1990) excluding cranial elements.

Fig. 8. Different degrees of digestion as seen on *Microtus gregalis* inferior m1 including a) no digestive modification b) light digestive corrosion seen as rounding of the salient edges along the occlusal surface, c) moderate etching seen as rounding of the salient edges and retraction of the enamel across 50% of the lingual and buccal lengths and d) heavy modification including greater retraction of the lateral salient edge enamel, penetration of the dentine and overall pitting of the tooth surface.

nearly all other taphonomic modifications (Fernández-Jalvo et al., 2016), as owls, diurnal raptors, and mammalian predators of various sizes are known to inflict trampling damage on prey remains deposited in and around their nest and/or den areas. As trampling experiments have been shown to result in a lack of complete skulls, predominance of isolated dentition, and complete destruction of some or all mandibles (Andrews, 1990, p. 8), this is particularly true for the Geißenklösterle Cave material which exhibits a pattern quite like that described. The proportion of teeth affected by digestive corrosion has been found to be a reliable indicator of predator type from various geographic regions (Fernández et al., 2017; Fernández-Jalvo and Andrews, 2016; Weissbrod et al., 2005). The well known predator categories described by Andrews (1990; Table 3.14) are reproduced in Table 14. Each predator is assigned a category based on both the proportion of teeth modified by exposure to digestive acid enzymes and the greatest degree of modification along a scale of light to extreme modification. There are a number of variables which may influence

Table 12
Number of identified specimens (NISP) and abundance for each paired long bone by geological horizon at Geißenklösterle Cave.

Post-crania Breakage	GH11		GH 12		GH 13		GH 14		GH 15		GH 16	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Humerus												
Complete	0	0.0%	0	0.0%	1	12.5%	0	0.0%	2	3.8%	0	0.0%
Proximal	1	25.0%	0	0.0%	1	12.5%	2	16.7%	5	9.4%	1	50.0%
Shaft	0	0.0%	0	0.0%	3	37.5%	3	25.0%	12	22.6%	0	0.0%
Distal	3	75.0%	4	100.0%	3	37.5%	7	58.3%	34	64.2%	1	50.0%
Ulna												
Complete	1	100.0%	2	40.0%	1	20.0%	0	0.0%	3	10.0%	0	0.0%
Proximal	0	0.0%	3	60.0%	4	80.0%	6	75.0%	19	63.3%	0	0.0%
Shaft	0	0.0%	0	0.0%	0	0.0%	2	25.0%	8	26.7%	0	0.0%
Distal	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
Femur												
Complete	0	0.0%	0	0.0%	0	0.0%	0	0.0%	1	1.9%	0	0.0%
Proximal	2	50.0%	5	83.3%	4	57.1%	8	40.0%	24	45.3%	1	50.0%
Shaft	1	25.0%	1	16.7%	0	0.0%	6	30.0%	14	26.4%	1	50.0%
Distal	1	25.0%	0	0.0%	3	42.9%	6	30.0%	14	26.4%	0	0.0%
Tibia												
Complete	0	0.0%	0	0.0%	0	0.0%	0	0.0%	1	1.5%	0	0.0%
Proximal	1	100.0%	0	0.0%	2	28.6%	3	25.0%	12	18.5%	0	0.0%
Shaft	0	0.0%	2	50.0%	2	28.6%	5	41.7%	17	26.2%	0	0.0%
Distal	0	0.0%	2	50.0%	3	42.9%	4	33.3%	35	53.8%	1	100.0%

Post-crania Breakage	GH 17		GH 18		GH 19		GH 20		GH 21		GH 22		GH 23	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Humerus														
Complete	1	3.6%	8	19.0%	3	12.5%	3	12.0%	0	0.0%	0	0.0%	0	0.0%
Proximal	2	7.1%	5	11.9%	2	8.3%	6	24.0%	1	8.3%	4	14.8%	0	0.0%
Shaft	7	25.0%	7	16.7%	7	29.2%	6	24.0%	1	8.3%	7	25.9%	1	20.0%
Distal	18	64.3%	22	52.4%	12	50.0%	10	40.0%	10	83.3%	16	59.3%	4	80.0%
Ulna														
Complete	0	0.0%	8	25.0%	1	5.6%	3	18.8%	1	16.7%	0	0.0%	0	0.0%
Proximal	4	50.0%	12	37.5%	15	83.3%	8	50.0%	4	66.7%	11	64.7%	3	60.0%
Shaft	3	37.5%	12	37.5%	2	11.1%	5	31.3%	1	16.7%	6	35.3%	1	20.0%
Distal	1	12.5%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	1	20.0%
Femur														
Complete	0	0.0%	3	7.0%	4	10.3%	4	21.1%	2	12.5%	1	4.3%	1	8.3%
Proximal	14	66.7%	28	65.1%	20	51.3%	9	47.4%	8	50.0%	11	47.8%	6	50.0%
Shaft	6	28.6%	6	14.0%	8	20.5%	1	5.3%	2	12.5%	6	26.1%	1	8.3%
Distal	1	4.8%	6	14.0%	7	17.9%	5	26.3%	4	25.0%	5	21.7%	4	33.3%
Tibia														
Complete	1	4.5%	6	10.9%	3	7.9%	1	3.7%	0	0.0%	0	0.0%	0	0.0%
Proximal	2	9.1%	9	16.4%	10	26.3%	3	11.1%	2	15.4%	6	18.2%	1	9.1%
Shaft	7	31.8%	18	32.7%	11	28.9%	12	44.4%	6	46.2%	17	51.5%	7	63.6%
Distal	12	54.5%	22	40.0%	14	36.8%	11	40.7%	5	38.5%	10	30.3%	3	27.3%

the extent to which dental specimens are modified, both between and within predator species including the extent of jaw destruction (isolated teeth are exposed to greater amounts of digestive acid than *in situ* dentition), the age of the predator (younger owls have stronger digestive tracts), and the season of capture (prey captured in the winter may be more heavily processed due to a relative food shortage). Furthermore, the signs of digestion differ between arvicolids, murids and soricids, due to their different molar occlusal morphology (see Fernández-Jalvo et al., 2016 for a description of each). For the current study these complicating variables have been considered when possible, and to control for differental digestion only arvicolidae dentition will be discussed.

Table 15 lists the number and proportion of arvicolidae molars which exhibit digestive etching ranging from light to heavy from the Geißenklösterle Cave material and Fig. 8 includes examples of light, moderate, and heavy digestion. A significant proportion (21.3–66.7%) of molars from each geological horizon exhibit some form of digestive etching. The degree of modification varies between horizons, with light digestive etching present in all periods to between 16.7% and 45.8%. Moderate destruction was also identified in all geological horizons with the highest occurrence noted in GH 12 (12.5%), GH 21 (10%) and GH 23 (11.9%). Heavy destruction was seen on specimens from GH 22, 18, 15 and 14 only.

The overall proportion of modified molars from GH 21 (33.3%) and GH 23 (28.6%) fall between a Category 3 and Category 4 predator, and the degree of modification within these two categories is notably similar (Andrews, 1990 p. 67). Although the skeletal element representation and breakage from these layers suggests a mammalian predator was responsible for these assemblages, specifically the red fox, the degree of digestion on the dental specimens does not support this interepretation. It is more likely that a little owl, kestrel or eagle owl accumulated the remains which were later subjected to trampling resulting in increased breakage. This is further supported by the digestive modification of incisors from these layers (detailed in Table 16) which includes high proportions of tooth surface corrosion (indicitive of greater destruction of the maxilla and anterior mandible during predation) but overall lower total incisor digestion (31% in GH 23 and 42% in GH 21) than would be expected from a category 4 or higher predator. Geological horizon 22 has similar levels of overall molar and incisor digestion (34.5% and 36.9%, respecively) and a single specimen exhibiting heavy destruction (0.9%) suggesting a similar category 3–4 predator, potentially the little owl indicated by the skeletal element R scores. The remaining geological horizons from

Table 13
Breakage of cranial and dental elements and comparative indices by geological horizon at Geißenklösterle Cave.

Breakage of Cranial and Dental Elements	GH 11	GH 12	GH 13	GH 14	GH 15	GH 17	GH 18	GH 19	GH 20	GH 21	GH 22	GH 23
Total Maxillae (N)	3	0	2	1	30	4	27	12	11	3	6	3
% complete	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
% maxillae with zygomatic	0.0%	0.0%	0.0%	100.0%	3.3%	0.0%	4.0%	8.3%	0.0%	0.0%	0.0%	33.3%
% palates	100.0%	0.0%	100.0%	0.0%	96.7%	100.0%	72.0%	83.3%	100.0%	100.0%	66.7%	66.7%
% molars missing	100.0%	0.0%	100.0%	33.3%	100.0%	100.0%	76.0%	88.9%	87.9%	100.0%	100.0%	100.0%
% incisor missing	100.0%	0.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%
Total Mandibles (N)	4	3	11	5	38	10	55	36	21	5	16	6
% complete	0.0%	0.0%	0.0%	20.0%	2.6%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
% anterior break	0.0%	0.0%	54.5%	40.0%	36.8%	20.0%	9.1%	25.0%	28.6%	40.0%	43.8%	16.7%
% inferior border break	25.0%	33.3%	63.6%	40.0%	39.5%	40.0%	36.4%	44.4%	47.6%	20.0%	18.8%	33.3%
% ramus break	75.0%	100.0%	81.8%	40.0%	42.1%	30.0%	60.0%	61.1%	57.1%	60.0%	50.0%	50.0%
% molars missing	58.3%	33.3%	42.4%	53.3%	59.6%	56.7%	47.3%	50.9%	55.6%	53.3%	54.2%	33.3%
% incisor missing	25.0%	33.3%	45.5%	40.0%	89.5%	50.0%	65.5%	38.9%	52.4%	60.0%	43.8%	66.7%
Index												
Postcrania/crania	37.7	104.2	120.7	165.8	166.9	127.0	143.1	129.6	151.9	147.5	192.3	125.6
femur + humerus/mandible + maxilla	242.9	400.0	192.3	783.3	231.3	485.7	212.3	231.3	238.7	425.0	340.9	244.4
tibia + radius/femur + humerus	5.9	58.3	36.0	46.8	70.3	44.1	70.3	72.1	52.7	55.9	64.0	68.2
% Isolated Molars*	422.2	266.7	181.8	475.0	177.1	334.1	173.6	230.3	175.6	295.5	214.8	176.0
% Isolated Incisors**	157.1	366.7	115.4	720.0	267.2	457.1	307.8	323.8	227.6	475.0	400.0	322.2

*calculated by dividing the # isolated molars by the # expected molars (based on 3 per jaw) minus the *in situ* molars.
**calculated by dividing the # isolated incisors by the # expected incisors (based on 1 per jaw) minus the *in situ* incisors.

Table 14
Categories of predators according to digestive modification (modified from Andrews, 1990; reproduced from Rhodes et al., 2016).

Category	Predators	Alterations
1	*Molar digestion:* Barn, Long-eared, Short-eared owl, Verreaux eagle owl, *Incisor digestion*: Barn owl, short-eared owl, snowy owls *Post-cranial digestion*: Barn, snowy, long-eared, short-eared owls, Verreaux eagle owl, great grey owl	Light modification, absent or light digestion Molars: 0–3% Incisors: 8–13%
2	*Molar digestion:* Snowy, spotted eagle, great grey owls *Incisory digestion:* Long-eared owl, Verreaux eagle owl, great grey owl, bat-eared fox *Post-cranial digestion:* European & spotted eagle owls, tawny owl	Little modification, moderate degree of digestion, though enamel is removed from the tips of incisors Molars: 4–6% Incisors: 20–30%
3	*Molar digestion:* European eagle owl, tawny owl, bat-eared fox, mongoose, genet *Incisor digestion:* European & spotted eagle owls, tawny, little owls, pine marten, mongoose, genet *Post-cranial digestion:* Little owl, kestrel, hen harrier	Greater destruction, moderate/heavy digestion over the enamel Molars: 18–22% Incisors 50–70%
4	*Molar digestion:* Little owl, kestrel, pine martin *Incisor digestion:* Kestrel	Heavy/Extreme enamel and dentine corrosion; mustelids produce extreme modification but digested elements appear in low percentages, some of them chewed Molars: 50–70% Incisors: 60–80%
5	*Molar, incisor and post-cranial digestion:* Hen harrier, coyote, red fox, arctic fox, mammalian carnivores.	The most destructive effects (Extreme). Mammalian carnivores produce rounded edges of skeletal elements. Gnaw marks rare, except for some instances of canid predation and of some mustelids Low percentages of digested post-crania and complete lack of cranio-dental elements. Molars: 50–100% Incisors: 100% (dentine corroded)

the Middle Paleolithic deposits (GH 18, 19, and 20) all have similar proportions of digested molars to those described above suggesting that the category of predator (3 and/or 4) throughout the complete span of this cultures deposits. This fits well with most skeletal element correlations (which suggested a little owl and or kestrel in GH 18 and 19) and the incisor digestion (which includes a high degree and proportion of surface damage in GH 18 and 19). The skeletal element representation of GH 20 suggested a great grey owl accumulator which is not upheld by the digestion damage. However, the great grey owl R score pattern is strongly correlated with that of the little owl and kestrel (0.626 and 0.667, $p < 0.005$) which may explain this discrepency to some extent. It is interesting to note that the European eagle owl (a category 3 predator) and the kestrel (a category 4 predator) have strongly corelated skeletal element R scores (0.879, $p < 0.001$), as do most of the other predators from these two categories, suggesting yet another reason that dental digestive corrosion patterns should be considered more decisive than element patterning (Andrews, 1990; Fernández-Jalvo, 1995).

The nearly culturally sterile geological horizon 17 assemblage included both a comparatively high proportion of digested arviolidae molars (41.6%) and a surprisingly low number of digested incisors (35.9%), falling somewhere between a category 2 and category 4 predator when both measures are considered. The skeletal element R score comparison for this horizon returned a strong correlation with the kestrel pattern (0.923, $p < 0.001$); however with such a predator we would expect extreme digestive corrosion to be evident on the assemblage and an overall higher

Table 15
Number and proportion of Arvicolidae molars digested by geological horizon at Geißenklösterle Cave.

Geological Horizon (GH)	*Lemmus lemmus*	*Dicrostonyx gulielmi*	*Microtus gregalis*	*Chionomys nivalis*	*Microtus oeconomus*	*Arvicola terrestris*	*Microtus arvalis*	*Microtus arvalis/ agrestis*		Microtus sp.	Total %
10	11	3	2	2	2	0	0	15	24	59	100.0%
absent	6	3		1	2			7	15	34	57.6%
light	5		2	1				6	8	22	37.3%
Moderate								2	1	3	5.1%
11	4	0	1	1	4	0	0	10	57	77	100.0%
absent	4				3			3	31	41	53.2%
light			1	1	1			5	19	27	35.1%
Light-moderate								2	3	5	6.5%
moderate									3	3	3.9%
Moderate - heavy									1	1	1.3%
12	2	2	3	1	2	1	0	2	11	24	100.0%
absent	1	1	1		1				4	8	33.3%
light	1	1	2	1	1	1		1	5	13	54.2%
Moderate								1	2	3	12.5%
13	6	7	9	0	0	0	0	8	25	55	100.0%
absent	2	3	6					3	16	30	54.5%
light	2	3	2					2	7	16	29.1%
Light-moderate	2		1					3		6	10.9%
Moderate		1							2	3	5.5%
14	11	12	3	0	3	1	0	7	35	72	100.0%
absent	5	3	1		1	1		1	18	30	41.7%
light	4	6	1		2			4	13	30	41.7%
Light-moderate		2	1					1		4	5.6%
Moderate	1							1	4	6	8.3%
Heavy	1	1								2	2.8%
15	38	22	10	8	10	2	0	68	164	322	100.0%
absent	20	12	3	7	9	1		41	105	198	61.5%
light	13	8	5		1	1		16	50	94	29.2%
Light-moderate	1	1						1	4	7	2.2%
Moderate	3	1	1	1				8	5	19	5.9%
Moderate - heavy	1							1		2	0.6%
Heavy			1					1		2	0.6%
16	1	1	0	0	0	0	0	1	17	20	100.0%
absent	1								9	10	50.0%
light		1							5	6	30.0%
light-moderate									2	2	10.0%
Moderate									1	1	5.0%
Moderate - heavy								1		1	5.0%
17	13	5	7	3	5	7	1	31	65	137	100.0%
absent	5	2	3	1	3	5	1	16	44	80	58.4%
light	7	2	2	1	2	2		14	21	51	37.2%
Moderate	1	1	2	1				1		6	4.4%
18	57	15	18	5	7	6	0	106	90	304	100.0%
absent	39	11	8	5	5	5		67	65	205	67.4%
light	15	3	8		2	1		29	23	81	26.6%
Light-moderate			1							1	0.3%
Moderate	2	1	1					10	2	16	5.3%
Heavy	1									1	0.3%
19	59	12	4	6	9	9	1	67	80	247	100.0%
absent	28	7	2	4	7	1		45	57	151	61.1%
light	25	4	2	1	2	7	1	18	21	81	32.8%
Moderate	6	1		1		1		3	2	14	5.7%
Moderate - heavy								1		1	0.4%
20	5	7	4	6	7	2	0	48	48	127	100.0%
absent	5	7	2	4	6	2		36	38	100	78.7%
light			2	2	1			11	8	24	18.9%
Moderate								1	2	3	2.4%
21	2	2	4	4	2	2	0	22	22	60	100.0%

(*continued on next page*)

Table 15 (*continued*)

Geological Horizon (GH)	*Lemmus lemmus*	*Dicrostonyx gulielmi*	*Microtus gregalis*	*Chionomys nivalis*	*Microtus oeconomus*	*Arvicola terrestris*	*Microtus arvalis*	*Microtus arvalis/ agrestis*		*Microtus sp.*	Total %
absent	1	1	1	4	1	1		15	16	40	66.7%
light	1		1		1	1		4	6	14	23.3%
Moderate		1	2					3		6	10.0%
22	4	8	10	3	0	4	0	39	45	113	100.0%
absent	2	5	6	2		3		20	36	74	65.5%
light	2	2	2	1		1		15	8	31	27.4%
Moderate		1	2					3	1	7	6.2%
Heavy								1		1	0.9%
23	4	5	3	1	1	3	0	14	11	42	100.0%
absent	1	5	1	1	1	2		11	8	30	71.4%
light	1					1		3	2	7	16.7%
Moderate	2		2						1	5	11.9%
Grand Total	217	101	78	40	52	37	2	438	694	1659	100.0%
absent total	120	60	34	29	39	21	1	265	462	1031	62.1%
light total	76	30	30	8	13	15	1	128	196	497	30.0%
Light-moderate total	3	3	3	0	0	0	0	7	9	25	1.5%
Moderate total	15	7	10	3	0	1	0	33	26	95	5.7%
Moderate - heavy total	1	0	0	0	0	0	0	3	1	5	0.3%
Heavy total	2	1	1	0	0	0	0	2	0	6	0.4%
absent %	55.3%	59.4%	43.6%	72.5%	75.0%	56.8%	50.0%	60.5%	66.6%		62.1%
light %	35.0%	29.7%	38.5%	20.0%	25.0%	40.5%	50.0%	29.2%	28.2%		30.0%
Light-moderate %	1.4%	3.0%	3.8%	0.0%	0.0%	0.0%	0.0%	1.6%	1.3%		1.5%
Moderate %	6.9%	6.9%	12.8%	7.5%	0.0%	2.7%	0.0%	7.5%	3.7%		5.7%
Moderate - heavy %	0.5%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.7%	0.1%		0.3%
Heavy %	0.9%	1.0%	1.3%	0.0%	0.0%	0.0%	0.0%	0.5%	0.0%		0.4%

Table 16
Number (N) and proportion (%) of digested incisors from Geißenklösterle Cave by geological horizon.

Geological Horizon			Tip						Surface								Total
	Absent		Light		Moderate		Heavy		Light		Moderate		Heavy		Total digested		
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	
11	9	81.8%							2	18.2%					2.0	18.2%	11
12	5	45.5%	1	9.1%					5	45.5%					6.0	54.5%	11
13	9	60.0%	3	20.0%					2	13.3%	1	6.7%			6.0	40.0%	15
14	20	55.6%	11	30.6%	3	8.3%			2	5.6%					16.0	44.4%	36
15	113	66.1%	31	18.1%	9	5.3%	2	1.2%	13	7.6%	1	0.6%	2	1.2%	58.0	33.9%	171
17	41	64.1%	11	17.2%	2	3.1%	2	3.1%	7	10.9%	1	1.6%			23.0	35.9%	64
18	101	42.6%	41	17.3%	25	10.5%	9	3.8%	28	11.8%	27	11.4%	6	2.5%	136.0	57.4%	237
19	76	55.9%	16	11.8%	3	2.2%	2	1.5%	34	25.0%	5	3.7%			60.0	44.1%	136
20	45	68.2%	7	10.6%	2	3.0%			11	16.7%	1	1.5%			21.0	31.8%	66
21	22	57.9%	11	28.9%			1	2.6%	4	10.5%					16.0	42.1%	38
22	53	63.1%	17	20.2%	4	4.8%			10	11.9%					31.0	36.9%	84
23	20	69.0%	3	10.3%					6	20.7%					9.0	31.0%	29
Grand Total	514	57.2%	**152**	16.9%	**48**	5.3%	**16**	**1.8%**	**124**	**13.8%**	**36**	**4.0%**	**8**	**0.9%**	384	42.8%	898

proportion of digested teeth. It is more likely that a less digestively destructive predator with a similar element representation pattern, such as the European eagle owl, is responsible for these remains. The overall proportion of digested molars increases in the Aurignacian deposits, although not equally across all digestive categories. That this increase is not reflected in the proportion of digested incisors is interesting. It is possible that the heavily modified incisor specimens were not identified in the field, and therefore were systematically excluded from collection, but this cannot be confirmed. The skeletal element R score correlation between the material from geological horizons 12 and 13 and a great grey owl predation pattern is therefore substantiated. There is, however, no evidence in the digestive patterning of geological horizon 14 to suggest it differs from the overlying deposits, meaning that differential destruction of the post-crania (likely due to trampling) may have increased the correlation between this horizon's R scores and the highly destructive patterning seen in red fox prey assemblages.

Overall, it would appear that the accumulating predator for both the Aurignacian and Middle Paleotlihic deposits was likely a European eagle owl (*Bubo bubo*), kestrel (*Falco tinnunculus*) or little owl (*Athene noctua*) based on both the skeletal element representation and the degree of digestive corrosion evident on the assemblages. It is also possible that a more destructive predator, such as the red fox, was active in the cave at the same period as the avian predators and contributed to the high proportion of digested molars seen in some geologic horizons (GH 14 and 12, specifically). Andrews suggests that little owls likely contribute few mammal remains to archaeological assemblages due to their small size and related small dietary needs (Andrews, 1990, p. 193), while both European eagle owls and kestrels are known to focus on vole species when available with limited species specific preference (eagle owls are known to hunt a disproportionate number of water voles). Red foxes also focus on easily caught and readily available prey, without any particular preference. This results in a minor bias towards non-burrowing species, such as the field vole, compared to the bank vole and other burrowing rodents. Furthermore, these two avian predators live in open environments with limited forest yet will roost in cliff edges and cracks and even in small caves when necessary. Therefore, the diet and behaviour of these three predators fits well with the taxonomic diversity evident in the small mammal assemblages and the inferred paleoenvironment as discussed in the next section.

4. Discussion

4.1. Paleoenvironment at Geißenklösterle Cave

The ability of any faunal assemblage to accurately represent ecological communities from the distant past is dependent upon various factors such as its mode of accumulation, its taphonomic history, the excavation techniques used and, when applicable, the sampling strategy employed. Although the agents active throughout the accumulation, fossilization and preservation of a faunal assemblage are often viewed as innately destructive, many also add paleoecological or environmental information to our picture of the past (Fernández-Jalvo et al., 2011). Far too often it is assumed that small mammal assemblages from caves are the result of non-destructive owl predation and therefore present an unbiased input into a closed environment. Without thorough taphonomic analysis, including skeletal representation, preservation and, most importantly, consideration of digestive corrosion present in the assemblage, we cannot assume that the taxonomic composition of the assemblage reflects the environment surrounding the site. As we have shown in our analysis of the small mammal remains from Geißenklösterle Cave, interpreting the taphonomic record with the goal of identifying the specific accumulating predator can be a complex process requiring that all lines of evidence be considered together.

We have determined the most likely predators active at Geißenklösterle Cave during the Paleolithic are the European eagle owl (*Bubo bubo*) and the kestrel *(Falco tinnunculus*), with possible contributions by the red fox (*Vulpes vulpes*). Fox remains have been identified from all periods at Geißenklösterle Cave, while owl and/or raptor specimens have been found in the Aurignacian only (Conard et al., 2013), however presence of a predator within the faunal assemblage of any site neither confirms or excludes them as a taphonomic agent. Both the European eagle owl and the kestrel are opportunistic hunters producing accumulations with high species diversity, particularly in palimpsests (Andrews, 1990). The European eagle owl and the red fox are both nocturnal and therefore prey more heavily on animals with a similar activity pattern; however, in northern Europe voles (particularly the water vole) may make up between 30% and 80% of the owls' diet. The kestrel's diet is quite similar, with voles accounting for 50–90% of individuals identified from modern pellets (Andrews, 1990). Shrews, murids, and reptiles appear to contribute substantial proportions to the diets of northern European kestrels only during warm periods (when some vole populations drop) and are almost never found in red fox scats. Modern populations of both avian predators preferentially hunt over open environments and therefore introduce some environmental bias into their prey assemblages (Peterson et al., 2002), while the fox is entirely opportunistic and hunts in open areas and areas of high vegetation cover equally. The European eagle owl has a noted preference for inhabiting wooded habitats, while the kestrel inhabits exclusively the same open spaces it hunts (Peterson et al., 2002). Due to its large size the European eagle owl can travel up to 10 km in search of food; it also inflicts significant breakage on any pellets which fall around its nesting site (Andrews, 1990).

In addition to the predator introduced bias we also know that the assemblage taxonomic richness may be sample size dependent. We have shown that the relative proportions of each species likely reflect that seen on the landscape, however it is possible that rare species are under-represented in some geological horizons. Taking this into consideration, along with the possible over representation of open and moist environments (due to predation patterns) we can interpret the ecology and climate of the landscape surrounding Geißenklösterle Cave in an informed manner. Using the habitat preferences of the various species (as listed in section 2.1) the expression of each preference as a relative proportion of the total for each geological horizon is shown in Fig. 9.

All deposits at Geißenklösterle Cave are dominated by species reported to have indeterminate habitat requirements (the common and field vole, primarily) making up between 33.3% and 58.1% of the identified fauna (the one exception being geological horizon 12 where this category makes up only 9.1% of the sample). Modern populations of common voles and field voles do inhabit a wide variety of environments; however, they are known to prefer open woodland and moist open environments, respectively (van Kolfschoten, 2014). The dominance (or near dominance) of *M. arvalis/agrestis* within Upper Pleistocene small mammal assemblages is common and documented from many central European sites including Sesselfelsgrotte (van Kolfschoten, 2014), Kogelstein (Ziegler, 2000), the Aurignacian deposits at Brillenhöhle (Storch, 1973), Fumane Cave (López-García et al., 2015), and within the OIS 3 deposits at Biśnik Cave (Socha, 2014). This pattern can be partly attributed to higher fecundity, as the field vole produces litters with 2–3 more births than the narrow-headed or water vole, for example, and is prone to substantial population expansion when environmental conditions are favorable (Myllymäki, 1977). Otherwise, the Middle Paleolithic horizons at Geißenklösterle Cave (GH 23–18) include a high proportion of cold tundra adapted species (35.3%–15.9%) and boreal environments (with or without open water) are also well represented (9.7%–22.7%). The open forest adapted shrews in GH 20 total 13.6% of the assemblage, suggesting this horizon may have been deposited during a particularly temperate and moist period. Grassland adapted species are found only in the Middle Paleolithic (within GH 22 and indicated by a nearly imperceptible green bar in Fig. 9); this holds true for both the current assemblage and past studies (Ziegler, in press). In this case only the European ground squirrel belongs to this category, a species which requires rather dry landscapes with short vegetation coverage, and are also found in the Kogelstein (Ziegler, 2000) and Weinberghöhle (von Koenigswald, 1974a,b) deposits. Compared with the early Upper Paleolithic (GH 14 and 15/16) the Middle Paleolithic at Geißenklösterle Cave was likely warmer, with a temperate steppe/forest ecology overall and punctuated cold and arid periods. The rather low proportions of the collared lemming as well as the fact that the narrow-headed vole and the Norwegian lemming have been found within temperate interglacial deposits elsewhere (van Kolfschoten, 2014; Kowalski, 1977) further supports this interpretation. This mosaic environment is similar to that suggested by the Kogelstein small mammals (Ziegler, 2000) and the large mammal assemblage from Bockstein (Krönneck, 2012) and may even represent an extension of the cyclical cool and relatively

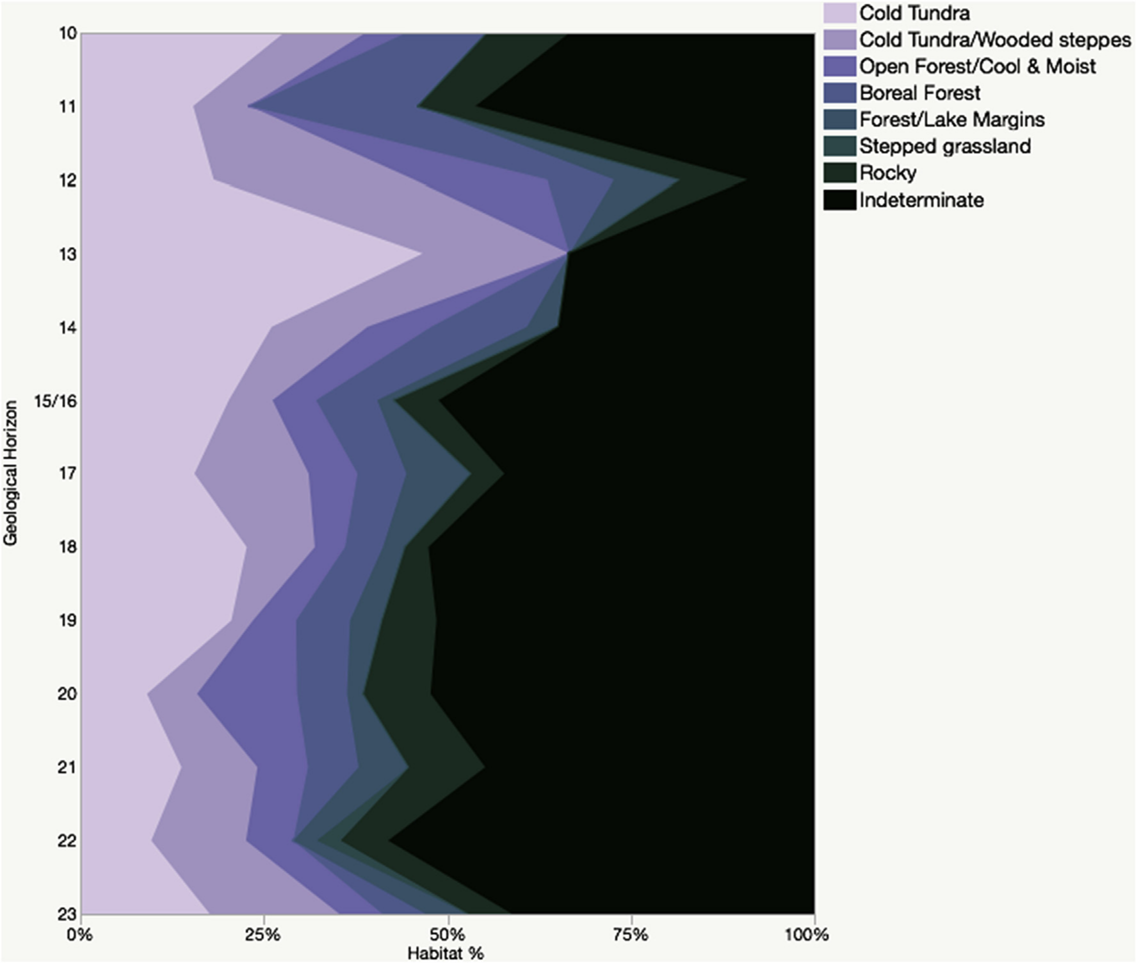

Fig. 9. The relative proportion of each habitat type at Geißenklösterle (based on species frequency) by geological horizon.

warm phases seen in the Sesselfelsgrotte layers L-G (which are broadly correlated to the late OIS4–early OIS3; van Kolfschoten, 2014). In terms of community structure, each GH dated to the Middle Paleolithic contains a non-analogous species composition, particularly in regard to the occurrence of *L. lemmus*, *M. gregalis*, and *M. nivalis*, as stepped, tundra, and mountainous species do not co-occur in modern landscapes. It is unlikely that this results from admixture of the sediments, as this pattern is consistent throughout the Middle Paleolithic at Geißenklösterle Cave and in other regional records. While it is conceivable that the moderately large hunting ranges of the European eagle owl and kestrel, which span 10 km on average, may have produced this community pattern, it is more likely that the phenomenon of progressive deviation from modern analogues with increasing age seen in mammalian community structure elsewhere (Stewart, 2008) due to adaptation to extinct environments and ecologies (i.e. the mammoth steppe) is at play here as well. The reciprocal of Simpson's index results for these layers (Table 2) range from 2.85 to 3.86 which, considering the Middle Paleolithic also has the highest species richness ranging from 8–11, suggests dominance by 3–4 taxa within these levels. More than half of the species contributing to these assemblages are present in much smaller proportions than the others, but are present nonetheless.

The nearly geogenic GH 17 has a similar pattern suggesting a level of environmental continuity with earlier deposits. Despite being nearly culturally sterile this layer does not exhibit the highest volume of microfaunal specimens (Table 17), yet it does have one of the highest species richness values (NTAXA = 9) and reciprocal of Simpson index (1/D = 4.46) suggesting a relatively homogenous species distribution. Based on the proportion of shrews (2.8%) and water voles (5.0%) and the low proportion of collared lemming (3.5%), this period may have been more temperate and moister than the preceding period. The erosional event at the top of GH 17 recognized in the sedimentary record (Miller, 2015) indicating an abrupt increase in aridity and colder temperatures, is not reflected in the small mammal record. Interestingly, 15% of the specimens from this geological horizon exhibit root etching, the highest proportion documented in the collection, suggesting that the erosional event and the subsequent absence of human presence in the cave may be recognizable in the taphonomic record if not in the taxonomic. However, the gradual increase in the proportion of cold tundra species (with a related decrease in boreal species) which begins in GH 19 continues in the GH 17 sample. The immediate affect this gradual increase would have on landscape or human occupation at the site is unknown without finer resolution to our data. However, it does suggest a lack of a drastic climatic shift directly before or during the depopulation of the region by Neanderthal groups.

The Aurignacian period at Geißenklösterle Cave (GH 15–10/11) is defined by a drastic increase in the amount of cold tundra species (ranging from 23.1% to 72.3%) and a decrease in the number of forest and lake-side adapted species. Again, the non-analogous

Table 17
Find densities for the most common material types recovered from Geißenklösterle Cave including microfauna (adapted from Conard et al., 2012).

AH	GH	Cultural Group	excav. Area (m2)	approx. thickness (cm)	lithic artifacts (n)	lithic n/m3	microfauna (n)	microfauna n/m3)[a]	burnt bone (g)	charcoal (n)[b]	modified fauna (n)[b,c]
II	12−14	Aurignacian	43	35	2781	185	466	444	2042	4	618
IIIa,b	15 & 16	Aurignacian	39	20	12856	1648	1105	1105	2019	10	665
IIIc	17	Sterile (artifacts likely from Aurignacian)	13	20	198	76	395	658	37	0	10
IV	18	Middle Paleolithic	13	10	74	57	1144	3813	11	0	11
V	19	Middle Paleolithic	12	10	97	81	794	2647	22	0	4
VI	20	Middle Paleolithic	12	15	196	109	456	1013	25	10	4
VII	21	Middle Paleolithic	9	30	259	96	201	223	65	0	5
VIII	22 & 23	Middle Paleolithic	7	35	39	16	600	571	18	0	9
III - IIIc	12−17	Aurignacian total	95	75	15835	1909	1966	874	4098	14	1293
IV−VIII	18−23	Middle Paleolithic total	53	100	665	359	3195	1065	141	1	33

[a] The calculation of microfauna volume is based on an excavation area of 3 square meters only.
[b] Includes pieces collected with x, y, z coordinates and some collected per sediment unit within a quarter of a meter.
[c] Includes pieces with cutmarks and/or impact scars and debris of artifact production; bone tools are not included.

community structure of GH 10, 12 and 15 may indicate a Pleistocene landscape unknown in modern ecology, or it may represent delayed individualistic species response to gradual climatic change indicated in the taxonomic abundance measures. The sharp increase in glacial species seen at GH 13/14 in Fig. 9 may be due to the small sample size of these two layers, yet this also marks the transition where Soricidae become decidedly rare in the record, suggesting a significant decrease in temperate forested environments. The average proportion of collared and Norwegian lemming (cold tundra species) more than doubles between the Middle Paleolithic (15.6%) and Aurignacian (35.2%) periods. This suggests a shift in the landscape surrounding the site including a decline in open water and forest habitats and extension of the arid tundra steppe. This gradual decline in riverine and forest environments paired with an extension of cold arid tundra fits well with other paleoenvironmental interpretations from this region (Miller, 2015; Kitagawa, 2014; Conard et al., 2013; Krönneck, 2012; Müller, 2001; Ziegler, in press, 2000; Storch, 1973). Higham et al. (2012) suggested that the earliest Aurignacian deposits (GH 15/16) pre-date the Heinrich 4 event by millennia, which leaves open the possibility that the increase in cold tundra species within GH 14 and 13 is related to this cold episode. The spike in GH 13 of cold tundra and cold wooded steppe species mimics the onset of a sudden climatic cooling however it is almost certainly driven by the complete lack of boreal and temperate forest species, which is likely due to the horizons small sample size (NISP = 58). The spike in cold adapted species between GH 11 and 10 is of a similar nature.

Disregarding the sample size issue in the Aurignacian horizons, the overall trend seen in Fig. 9 is one of general cooling towards a dry steppe environment with clear cold and warm oscillations. This pattern is very like that recognized in the sedimentary record from the site (Miller, 2015) and conforms to what we know of the variable OIS 3 climate (Dansgaard et al., 1993). It is possible that the increases in cold tundra species documented at GH 21, 19/18, 15/16, and 13 are the biotic response to the drastic cooling of H6–H4 (Heinrich, 1988) however, greater temporal resolution would be necessary to make a substantiated claim as such. Although small mammal species have short life-spans and quick-reproductive rates, a certain time lag in community response could still be expected (Guthrie and van Kolfschoten, 2000) and it is not impossible to imagine that small mammal assemblages may reflect earlier climatic periods than their stratigraphic position implies. This might explain the lack of a drastic climatic shift in the record at the time of regional depopulation (GH 18–17), but that would be speculative only.

When we consider the artifact density at the site (Table 17) another possibility arises. Overall, the Aurignacian horizons contain a higher density of anthropogenic artifacts than the Middle Paleolithic deposits, suggesting more intense occupation of the site during this time (Conard et al., 2012). We would expect the density of microfauna to follow an inverse pattern, indicating greater occupation of the site by avian predators when the hominin site occupation was lowest. However, this is only seen clearly between GH 22/23 and 21 and between GH 18 and 19. As we mentioned above, the nearly culturally sterile layer GH 17 has a lower microfauna density than both the preceding and overlying deposits. This may suggest that the decrease in occupation intensity at Geißenklösterle Cave began earlier than is reflected in the artifact record; potentially during GH 18 and 19 when a clear cooling trend is seen in the small mammal record. The high small mammal density in GH 15/16 may also indicate that the re-occupation of the site by anatomically modern humans was slower than suggested by their material culture spatial distribution. However, the comparability of the artifact densities is also affected by differences in the excavation techniques between the Hahn and Conard seasons, different lithic reduction sequences (Conard et al., 2012), and the fact that the microfauna density is calculated based on only 3 m^2 excavation areas. Greater resolution in the microvertebrate data and the paleoenvironmental record from the Ach Valley would help clarify these hypotheses and is a major goal of our ongoing research in this region.

4.2. Conclusions and future research

Our detailed analysis of the small mammal assemblage from Geißenklösterle Cave supports past regional paleoenvironmental interpretations based on botanical, faunal and sedimentary records and provides new information regarding the occupation intensity and predatory behaviour taking place at the site from ~48,000–33,000 BP. Demographic shifts in the small mammal communities on the landscape around the site reflect both a general trend towards cold dry steppe environments through time and some of the warm/cool oscillations known to characterize OIS 3 environments in Central Europe. The presence of forest and grassland adapted species in the Middle Paleolithic deposits suggest this period was decidedly warmer and moister than later periods, while the high proportion of species restricted to cold tundra environments (ranging from 15.9% to 31.9%) likely indicate punctuated cold and arid periods, particularly during GH 21 and 19/18. The generally temperate environment is further indicated by the decidedly high taxonomic richness of these deposits. The nearly culturally sterile deposits at the site separating the two cultural periods are useful in addressing the role climate played in the depopulation of the region by Neanderthal groups (following the *Kulturpumpe* model). The small mammal climatic signal from geological horizon 17 suggests a temperate and moist environment overall, potentially more temperate than earlier periods. Other material records have drawn a similar conclusion, suggesting the overall climate during GH 17 was relatively warm and wet (Miller, 2015). The abrupt shift to increased aridity and cold temperatures documented at the boundary of GH 17 and GH 15/16 in the sedimentary records is recognizable only in the taphonomy of the small mammal assemblage. Therefore, the hypothesis that climatic pressure drove Neanderthals from the Swabian region is not substantiated. Recent dating suggests the beginning of Aurignacian occupation of the site predates the Heinrich 4 event (Higham et al., 2012), which also supports the conclusion that Neanderthal abandonment of the region and the resulting population vacuum was not due to a sudden cold period (as suggested in Conard, 2003). However, a gradual shift towards cooler and drier tundra environments can be seen in the small mammal record starting in GH 19/18 and extending throughout the Aurignacian period, albeit with intersperced warm and/or moist periods, suggesting that the Swabian landscape occupied Aurignacian groups was less hospitable than that known to the earlier Middle Paleolithic populations. Ongoing research at similarly well dated Swabian sites, including Hohle Fels Cave, will shed further light on the timing of these climatic shifts and the response time of the biological communities affected, including early human groups.

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RESEARCH ARTICLE

Did climate determine Late Pleistocene settlement dynamics in the Ach Valley, SW Germany?

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Abstract

The loss of Neanderthal groups across Western and Central Europe during Oxygen Isotope Stage (OIS) 3 has held the attention of archaeologists for decades. The role that climatic change, genetic interbreeding, and interspecies competition played in the extinction of Neanderthal groups is still debated. Hohle Fels is one of several important Middle and Upper Paleolithic sites from the Ach Valley in southwestern Germany which documents the presence of Neanderthals and modern humans in the region. Chronological and stratigraphic records indicate that these two groups occupied the site with little to no overlap or interaction. This provides the opportunity to examine the behavioural variability of Swabian Neanderthal populations without the complication of cross-cultural influence. In this study we contribute a terrestrial paleoenvironmental record derived from the small mammal material from Hohle Fels Cave to the ever-growing archaeological record of this period. By reconstructing the climate and landscape of the Ach Valley during this time we can identify the effect that the OIS 3 environment had on the presence of Neanderthals in the region. Based on indicator taxa and the habitat weighing method, the small mammal record, which includes rodents, insectivores, and bats, from Hohle Fels shows that the earliest Neanderthal occupation took place on a landscape characterized by substantial woodland and forest, rivers and ponds, as well as moist meadows and grasslands. A gradual increase in cold tundra and arctic environments is clear towards the end of the Middle Paleolithic, extending to the end of the early Aurignacian which may correlate with the onset of the Heinrich 4 event (~42,000 kya). Our taphonomic analysis indicates the material was accumulated primarily by opportunistic predators such as the great grey owl, snowy owl, and European eagle owl, and therefore reflects the diversity of landscapes present around the site in the past. Importantly, at the time Neanderthals abandoned the Ach Valley we find no indication for dramatic climatic deterioration. Rather, we find evidence of a gradual cooling of the Swabian landscape which may have pushed Neanderthal groups out of the Ach Valley prior to the arrival of modern human Aurignacian groups.

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Introduction

The climatically unstable oxygen isotope stage (OIS) 3 and the extinction of Neanderthals across most of Western and Central Europe during this period has been an important area of archaeological research throughout the 20th century. The Pleistocene record of central and southern Germany includes both cave and open-air sites from OIS 3, which dates roughly from 60,000 to 20,000 years before present (BP). The nature of the sites (i.e. repeat occupations [1] vs. possible temporary mass hunting camps [2]), as well as the duration of occupation varies through time and space. This variability might reflect demographic changes driven by repeated northern advances and southern retreats, shifting subsistence and/or mobility strategies, or the effects of localized extinctions of Neanderthal groups following shifts in glacial ice coverage and arctic tundra during stadial and interstadial events [3,4]. Although issues of site preservation confound the picture, particularly with regard to open-air sites, the record from the beginning of OIS 3 also includes examples of site clusters within small geographic regions. An iconic example of such a cluster of Middle Paleolithic (MP) sites is found in the Swabian Jura.

The Ach and Lone valleys (Fig 1), located along two tributaries of the Danube in the Swabian Jura, house a number of caves and rock shelters preserving an archaeological record spanning the late MP through to the Neolithic [5]. Many of these sites, such as Geißenklösterle, Vogelherd, and Hohlestein-Stadel are well-known for the spectacular bone and ivory figurines and flutes found in the Aurignacian deposits [6–8]. Others, while lacking such ample evidence for artistic expression, have none-the-less produced important records of both MP and Upper Paleolithic (UP) occupation, including detailed faunal, geoarchaeological, technological and chronological records (i.e. Sirgenstein [5], Große Grotte [9], Kogelstein [10,11], Brillenhöhle [12], and the Bockstein complex [13]). One of the most well-known sites in the Swabian Jura is Hohle Fels, located in the Ach Valley just outside of the town of Schelklingen. Excavations under Nicholas Conard's direction have continued annually for more than 20 years and have produced a rich material record spanning the late MP through to the Mesolithic, including symbolic artifacts such as ivory animal and human figurines [14], musical instruments [6], and one of the oldest phallic representations in the world [15].

Despite clear evidence of occupation by both MP (i.e. Neanderthal) and UP (i.e. anatomically modern human) groups, the chronological and stratigraphic records of many sites from the Ach and Lone valleys strongly suggest that a temporal hiatus separates these occupations [16,17]. The clearest indications of this hiatus is seen in the geogenic deposits that typically separate the final MP and the earliest Aurignacian [5,17]. Where these layers are clearly stratified and easily delineated, as at Geißenklösterle and Hohle Fels, they can be used to test hypotheses related to the depopulation of the region by Neanderthal groups prior to modern human arrival [18].

Numerous hypotheses have been proposed, and in some cases clearly refuted [19], to explain the loss of Neanderthal groups across Europe around the same time the continent was first occupied by modern humans. Some researchers now support a multi-faceted model for Neanderthal extinction, which includes competition [20,21] and interbreeding with modern human groups [22] in combination with dramatic climatic change, small population size, and genetic bottlenecks [19], as key forces driving Neanderthal groups into refugia and triggering population collapse [19,21,23,24]. Understanding why Neanderthals may have chosen to abandon regions they occupied repeatedly over extended periods may provide important insight into the species' adaptive strategies, particularly in relation to group mobility. Areas like the Swabian Jura and elsewhere along the upper and middle Danube [25], where the archaeological record suggests interactions between Neanderthals and modern human groups did not

Fig 1. Map of Swabian Alb showing all Paleolithic cave sites mentioned in the text.

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occur, provide the opportunity to explore Neanderthal mobility and behavioural variability in the absence of cross-cultural influence [alternatively see 26]. Establishing the impact of external forces, such as climatic instability, during the final period of Neanderthal occupation of a region is a key step in this line of inquiry.

To this end, we present here a detailed climatic record derived from our analysis of the small mammal material from Hohle Fels designed to identify periods of dramatic climatic shifts correlating with the final occupation of the Ach Valley by Neanderthal groups. In applying a modified indicator species method [18] and the habitat weighting method [27,28] to material recovered from deposits dating from $\geq$ 44,300 calBP to 39,000 calBP [29], we have identified changes in the vegetation of the Ach Valley landscape and broad shifts in the temperature and humidity of the region. Contextualizing this record within the history of paleoenvironmental research at Hohle Fels and Geißenklösterle allows us to test environmentally driven models for the depopulation of the Ach Valley.

Site description

The Swabian Jura is a karstic plateau formed primarily of Jurassic limestone which ranges from 500 to 1500 m a.s.l. and extends across part of southwestern Germany, with the Neckar Valley to the north and the Danube Valley to the south [30]. The Ach and Lone valleys, formed by tributaries of the Danube River, include a number of important archaeological cave sites with MP and UP deposits. Hohle Fels (48˚22’45”N E9˚45’14”E) sits at 534 m a.s.l. and comprises a 29 meter long corridor and a 23 m long main hall, both of which were filled with sediments deposited primarily through a now closed chimney at the back of the cave [30,31]. The cave entrance opens to the northwest and overlooks the Ach Valley, which is now filled with fluvial sediments and lies 5–10 m higher than in the Late Pleistocene [30]. Archaeological excavation of the cave has been ongoing since 1977 by the University of Tübingen under the

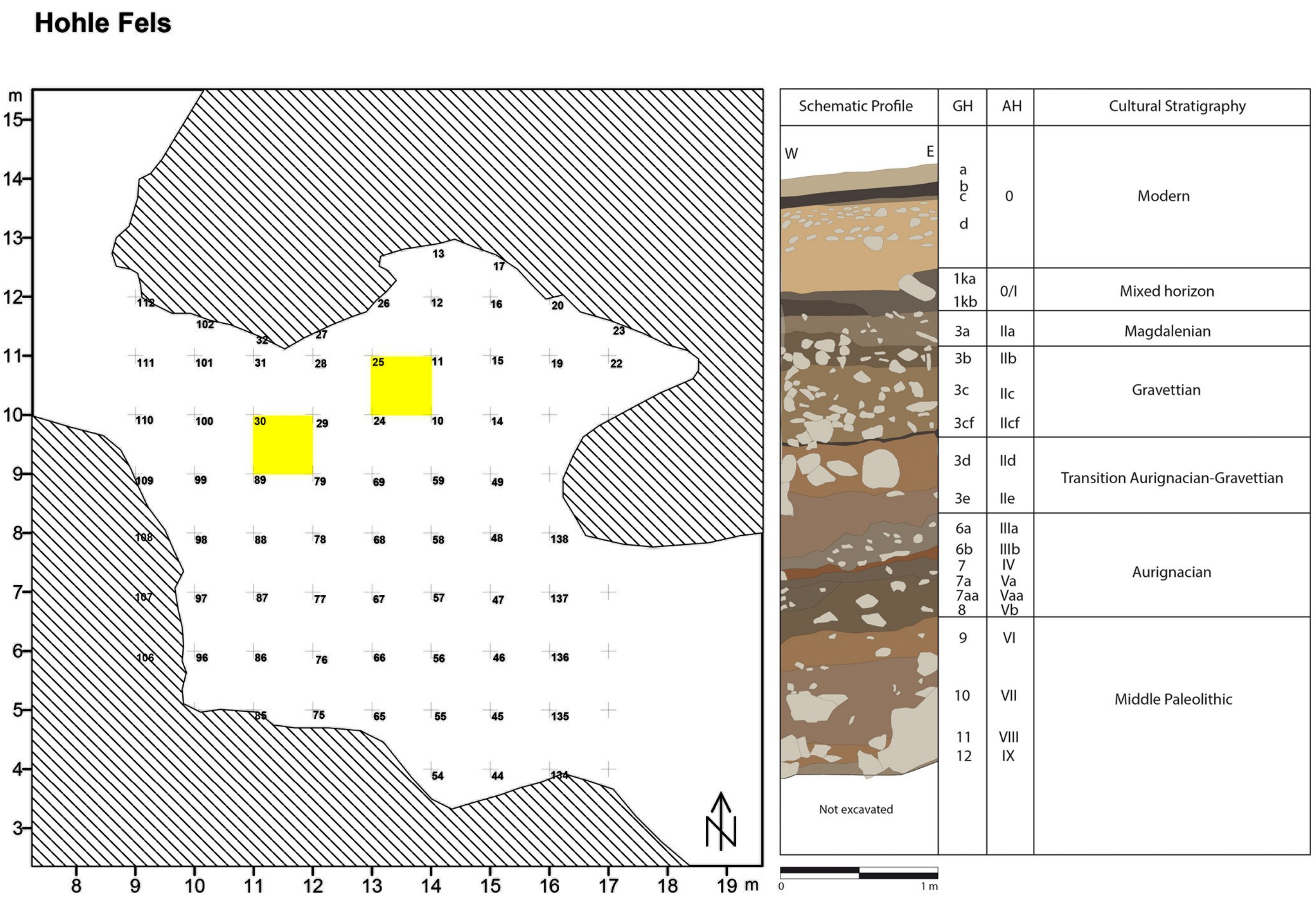

Fig 2. Excavation grid of Hohle Fels (left) with quadrants 30 and 25 highlighted; Stratigraphic profile (right) with correlated geological horizons (GH) and archaeological horizons (AH) and cultural periods.

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direction of Joachim Hahn and subsequently Nicholas Conard. However, the earliest investigations occurred between 1870 and 1871 and were conducted by Oscar Fraas and Theodor J. Hartmann [5]. Gustav Riek also directed excavations from 1958 to 1960, however his results were never published.

The combined excavations by Hahn and Conard have produced a 5-meter-thick stratigraphic sequence spanning the Holocene through to the MP. The stratigraphic record is divided into geological horizons (GHs) indicated by Arabic numerals and archaeological horizons (AHs) indicated by Roman numerals with letter subdivisions which often, but not always, correspond to each other (Fig 2). Aurignacian lithic and symbolic materials are found from GH 6a through GH 8, while MP lithic artifacts occur in much lower densities from GH 9 through GH 12. A possible cultural hiatus has been identified in the lower portion of GH 8, akin to the nearly-culturally sterile horizons separating MP and UP deposits at Geißenklösterle [31], Vogelherd, [31] and Sirgenstein [5] caves.

Materials and methods

Sample selection

The small mammal material from Hohle Fels analyzed for this study derived from two 1 m^2 excavation units (Qu. 30 and 25) and includes GH 7 through 12. Excavation permits were granted by the State Heritage office of Baden-Württemberg (Baden-Württemberg Landsamt für Denkmalpflege) and the specimen collections are accessibly housed at the Universität Tübingen Institut für Naturwissenschaftliche Archaëologie in Tübingen, Germany. No permits were required for the described study.

Due to similarities in the geological substrate of GH 7a and 7aa [31,32], these stratigraphic units have been grouped as 7a/7aa for the current study. Combining these layers also results in a taxonomic sample size large enough to allow statistical analysis, which greatly enhances the informative potential of the material. The exceptional quality and density of anthropogenic finds recovered from Qu. 30 include numerous lithic and bone tools, ivory and bone flute fragments [33] and the Venus figurine [34]. Excavation of Qu. 30 has not yet reached the earliest MP, therefore material from GH 11 and 12 originating in Qu. 25 was also included in this study. Qu. 25 was chosen for its extremely high quantity of small mammal remains and its close proximity to Qu. 30.

Taxonomic methods

At Hohle Fels, sediments are excavated from 25 cm^2 sub-quadrants and water-screened on site using water pumped from the nearby Ach River. The remaining material is then sorted in the field house in Blaubeuren by material type and size. All bones, including fragments, are removed and sorted by either specimen size or broad taxonomic category, which include bird, fish, and microfauna. The small mammal material is then sorted from the amphibian, reptile, and small bird and fish remains in the zooarchaeology lab at the University of Tübingen. A Euromax binocular microscope is used to examine all specimens at 10x – 50x magnification. Our taxonomic identification focused on isolated dental elements (maxillae, mandibles, incisors and molars) and select post-cranial elements via direct comparison with osteological collections at the University of Tübingen and published morphological and metric data including Adadjanian and von Koenigswald [35], van Kolfschoten [36] and Nadachowski [37] for Arvicolidae, Corbet [38] for Gliridae, Ziegler [39] for Talpidae, Popova [40,41] and Cubuk [42] for Sciuridae, Reumer [43] and Heinrich [44] for Soricidae, and Storch [12] and Sevilla [45] for Chiroptera. We identified arvicolid taxa by a combination of lower m1 occlusal morphology and occlusal measurements which follow van Kolfschoten [36]. *Dicrostonyx gulielmi* is the only exception, as these specimens are identified to genus based on the combination of tooth morphology, a lack of enamel along the triangle salient edges, and the lack of cementum in re-entrant angles. Species designations are based on the abundance of Agadjanian & von Koenigswald's [35] morphotype 1 and 2 in the assemblage.

We calculated diversity indices including richness (NTAXA), and heterogeneity (reciprocal of Simpson's Index, 1/D [46]). We measured NTAXA as the total number of taxonomic designations below family level (including genera identifications only when species-level attributions were not possible). The reciprocal of Simpson's Index (1/D) was calculated as

$$1/D = \Sigma p_i^{\,2}$$

Where p is the proportional abundance of taxon i. This measure is expressed here as 1/D so that greater evenness is suggested by a larger value, with the minimum possible value being one and the maximum being the NTAXA in the assemblage. To assess the degree to which the small mammal material from Hohle Fels suffers from a sampling bias limiting the representation of rare species [47], we produced rarefaction curves using NTAXA data for each geological horizon in PAST 3.14.

Taphonomic methods

Conducting detailed taphonomic analyses of all faunal remains recovered from archaeological contexts is an important first step before interpreting evidence of past environments or site specific human behaviours. To this end, we conducted a full taphonomic analysis of both the crania and post-crania of the small mammal material to identify the mode of accumulation and to qualify any related taxonomic bias. We documented the presence, absence, or degree of pronouncement (as a categorical ranking) of bone and tooth modifications including fragmentation, surface cracking, edge rounding, root etching, abrasion, weathering, thermal discolouration, oxide staining, and digestive corrosion. Identification of these modifications was based on Andrews [48], Fernandez-Jalvo & Andrews [49], Madgwick [50], Marín-Arroyo et al. [51], and Stiner et al. [52].

Description of the fragmentation of cranial and post-cranial elements follows Andrews' [48] breakage classes. We calculated relative abundances for each skeletal element by GH using the formula $R = N_i/(MNI \ x \ E_i)$, with E_i being the number of element *i* expected in a single prey skeleton and MNI being the minimum number of individuals based on the most abundant skeletal element within the GH assemblage. This weighted abundance is used to distinguish between predator produced prey accumulations in microfaunal studies [49,53–55]. We applied a correlation coefficient, Kendall's Tau, to compare our relative element abundances with Andrews' [48] actualistic data. The high possibility that the small mammal skeletal remains from Hohle Fels were subjected to substantial post-depositional breakage through non-predator agents such as sediment compression and trampling limits the interpretive potential of the skeletal element representation data. This was noted by Andrews [48] as a complicating factor when studying material from taphonomically complex contexts. To correct for this, we also documented digestive corrosion on incisors, molars and select post-cranial elements throughout the Hohle Fels material and compared this with Andrews' [48] actualistic results.

Digestive corrosion of both mandibular and maxillary incisors presents on either the tip or the anterior surface of the tooth, and we documented the occurrence and intensity of this modification separately for both portions. The progressive nature of digestive destruction also follows tooth shape and therefore presents differently for arvicolid, murid and soricid molar dentition [56]. Only two Soricidae specimens exhibited digestive corrosion, and in each case the modification was of the lowest intensity category (moderate) for these taxa. Therefore, only arvicolid digestive corrosion is reported herein. The categorical ranking of modification intensity is the same as that used for incisors, with progressive enamel damage scaled from light to extreme.

Andrews [48] describes two types of bone modification due to exposure to digestive acids: intrusive digestion on the articular ends and epiphyseal fusion lines and rounding of broken edges and nearby bone surfaces. This second type of bone modification is equifinal with a number of post-depositional processes (such as weathering, soil acid corrosion, sediment abrasion and tumbling damage), and is therefore less informative of predator action and not used in this study. As digestive corrosion is heavier on less mineralized juvenile epiphyses and metaphyses intrusive digestion has been documented on fully fused adult bone, only.

Paleoenvironmental reconstruction methods

We used both the modified indicator taxa method [27] and the Habitat Weighting method [28] to interpret the paleoenvironmental signal of the small mammal material from Hohle Fels. When applying the modified indicator taxa method, we assigned each taxon a vegetative and climatic niche based on the habitat preferences of published modern German analogues

[48,57,58] and those derived from paleontological studies [1,37,59,60]. A list of the species present in the Hohle Fels assemblage and their identified niches is included in Table 1.We then calculated the proportion of individuals allocated to each vegetative/climatic niche out of the total sample for each geological horizon and compared these percentages within and between horizons to identify shifts in the environmental pattern between key archaeological periods and through time generally [18]. Comey et al. [61] have shown that this method, which is also referred to as the taxonomic abundance method [62], is highly informative when the environmental variables considered are those that direct small mammal community structure, particularly local vegetative structure. Additionally, these authors [61] found that predator misidentification lead to erroneous environmental signals in their study of modern small mammal assemblages. This assumedly holds true in archaeological studies, as well, and supports the inclusion of a complete taphonomic analysis in this study.

Additionally, we employed the habitat weighing method [28] which distributes each small mammal species into habitat types based on their modern distributions. Six habitat types were represented in the Hohle Fels small mammal assemblage including open dry meadows (OD), open, humid evergreen meadows with dense pastures (OH), open woodland and forest edges (OW), mature forest woodlands (Wo), rocky areas with stony substratum (Rocky) and areas along streams, lakes and pond edges (Water). We added two additional habitat types as the assemblage includes species found exclusively in or partly within cold, dry treeless landscapes which may have permanently frozen subsoils (Tundra) and temperate grasslands (Steppe). This method differs from the indicator taxa method as it takes into account the fact that some species may inhabit multiple habitat types when available on the landscape. The weighting (1.0) for species with such broad tolerances is distributed across multiple habitat types according to how often they are found within each habitat. For example, *Microtus arvalis* is assigned to 0.5 open dry (OD) and 0.5 woodland (Wo) environments in Belgium [63] and 0.75 OD and 0.25 Wo in Italy [64]. In our current study, the *M. arvalis/agrestis* group weighting is divided over three habitat types (Table 2), as we take into consideration a larger geographic range

Table 1. List of species and primary habitat preference used for the indicator species analysis of the Hohle Fels Cave small mammal assemblage.

Species	Habitat Preference
Insectivora	
Crocidura leucodon/russula	Open forest, warm and dry
Sorex minutus	Open forest, cool and moist
Sorex araneus	Open forest, cool and moist
Neomys fodiens	Open forest, cool and moist
Rodentia	
Sciuridae	
Spermophilus superciliosus	Steppe grassland
Arvicolidae	
Lemmus lemmus	Cold tundra
Dicrostonyx gulielmi	Cold tundra
Microtus gregalis	Cold tundra/wooded steppe
Chionomys nivalis	Rocky
Microtus oeconomus	Boreal forest
Arvicola terrestris/antiquus	Open forest and lake margins
Microtus subterraneus	Indeterminate
Microtus arvalis/agrestis	Indeterminate

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Table 2. List of species identified at Hohle Fels Cave and their weighted habitat preferences.

Species	O. Dry	O. Humid	O. Wood	Woodland	Rocky	Water	Steppe	Tundra
Chiroptera indet.					1			
Myotis sp.			0.2	0.4		0.4		
Talpa sp.		0.4	0.5				0.1	
Crocidura sp.	0.3	0.4					0.3	
Crocidura leucodon/russula		0.5					0.5	
Crocidura leucodon	0.25	0.75						
Sorex sp.		0.25		0.75				
Sorex cf. *araneus*		0.25		0.50		0.25		
Sorex araneus		0.25		0.50		0.25		
Neomys cf. *anomalus*						1		
Neomys fodiens		0.25				0.75		
Spermophilus superciliosus							1	
Spermophilus sp.			0.3				0.7	
Muridae			0.6	0.2			0.2	
Gliridae	0.15			0.85				
Arvicola terrestris/antiquus						1		
Dicrostonyx gulielmi								1
Lemmus lemmus								1
Microtus gregalis			0.25					0.75
Chionomys nivalis					1			
Microtus oeconomus	0.25	0.5				0.25		
Microtus subterraneus	0.25	0.25	0.25	0.25				
Microtus arvalis/agrestis	0.25	0.25	0.25	0.25				

https://doi.org/10.1371/journal.pone.0215172.t002

(which includes most of Central Europe with Austria, Croatia, the Czech Republic, Germany, Hungary, Poland, Slovenia, Switzerland, Belgium, the Netherlands, and Luxembourg). Dividing the weighting of a taxon across multiple habitat types allows the addition of species previously considered as 'indeterminate' indicator species, such as the *Microtus arvalis/agrestis* group. This flexibility also allows the inclusion of family and genus level, or higher, identifications by dividing the weighting across all habitat types populated by the species within the group [27]. For the current study, this was done at the family and genus level for the single Muridae and Gliridae specimens and the *Myotis* sp., *Talpa* sp., *Sorex* sp., and *Crocidura* sp. individuals. For example, the *Sorex* sp. specimens were weighted with 0.75 woodland environments as *S. minutus*, *S. magna*, *S. pinus* and *S. coronatus* occupy woodlands more commonly than *S. anomalus*. Mitchel-Jones et al. [58] was used to determine the habitat distributions of extant species. We estimated the habitat weighing of species currently extinct or extirpated within Central Europe (which includes *Microtus gregalis* and *Spermophilus superciliosus*) from Kurten [60] and van Kolfschoten [1]. A list of the taxa used in this method and their habitat type weighing can be found in Table 2.

Results

General taphonomy

We documented the presence and intensity of nine different taphonomic modifications within the Hohle Fels assemblage. Seven of these modifications are detailed in Table 3 and include evidence of discolouration from burning, the adherence of authigenic oxide minerals to the

Table 3. Skeletal element representation as expected in one small mammal individual (E) and by geological horizon (GH) and the tally of identified taphonomic modifications from Hohle Fels Cave.

Geological Horizon (GH)		**GH 7**		**GH 7a/7aa**		**GH 8**		**GH 9**		**GH 10**		**GH 11**		**GH 12**		**Grand Total**	
Skeletal Element	**E**	**NSP**	**%**	**NSP**	**%**	**NSP**	**%**	**NSP**	**%**	**NSP**	**%**	**NSP**	**%**	**NSP**	**%**	**NSP**	**%**
Mandible	2	25	10.2%	25.00	3.3%	116.00	5.7%	123	3.5%	10.00	2.1%	73.00	5.5%	464.00	5.1%	836	4.8%
Maxilla	2	2	0.8%	19.00	2.5%	49.00	2.4%	80	2.3%	9.00	1.8%	37.00	2.8%	253.00	2.8%	449	2.6%
Scapula	2	0	0.0%	10	1.3%	23	1.1%	51	1.4%	4	0.8%	8	0.6%	126	1.4%	222	1.3%
Humerus	2	24	9.8%	53	7.0%	158	7.7%	227	6.4%	35	7.2%	106	8.0%	677	7.4%	1280	7.3%
Radius	2	4	1.6%	8	1.1%	30	1.5%	93	2.6%	8	1.6%	39	3.0%	204	2.2%	386	2.2%
Ulna	2	10	4.1%	25	3.3%	73	3.6%	150	4.2%	31	6.4%	45	3.4%	385	4.2%	719	4.1%
Pelvis	2	15	6.1%	27	3.6%	57	2.8%	105	3.0%	10	2.1%	36	2.7%	330	3.6%	580	3.3%
Femur	2	32	13.1%	58	7.7%	195	9.5%	224	6.3%	31	6.4%	76	5.8%	682	7.5%	1298	7.4%
Tibia	2	29	11.8%	70	9.3%	183	9.0%	284	8.0%	67	13.8%	143	10.8%	823	9.0%	1599	9.1%
Vertebra	36	4	1.6%	25	3.3%	47	2.3%	161	4.5%	9	1.8%	53	4.0%	477	5.2%	776	4.4%
Incisor	4	38	15.5%	125	16.5%	322	15.8%	440	12.4%	65	13.3%	188	14.3%	1142	12.5%	2320	13.2%
Molar	12	38	15.5%	215	28.4%	559	27.3%	897	25.3%	114	23.4%	318	24.1%	2457	26.9%	4598	26.2%
Premolar	-	1	0.4%	1	0.1%	9	0.4%	7	0.2%	1	0.2%	8	0.6%	27	0.3%	55	0.3%
Astragalus/calcaneus	4	4	1.6%	8	1.1%	16	0.8%	51	1.4%	4	0.8%	10	0.8%	110	1.2%	203	1.2%
Rib	24	1	0.4%	14	1.9%	35	1.7%	112	3.2%	12	2.5%	13	1.0%	166	1.8%	353	2.0%
Metapodial	20	10	4.1%	63	8.3%	157	7.7%	478	13.5%	66	13.6%	146	11.1%	698	7.6%	1618	9.2%
Phalanx	56	8	3.3%	10	1.3%	15	0.7%	69	1.9%	11	2.3%	19	1.4%	122	1.3%	254	1.4%
Grand Total	174	245	100.0%	756	100.0%	2044	100.0%	3552	100.0%	487	100.0%	1318	100.0%	9143	100.0%	17546	100.0%
MNI	1																
Burning		20	12.4%	18	11.2%	39	24.2%	26	16.1%	23	14.3%	18	11.2%	15	9.3%	161	0.9%
Oxide		207	1.4%	718	4.7%	1711	11.2%	3306	21.6%	457	3.0%	1260	8.2%	7640	49.9%	15304	87.2%
Cracking (Uneven)		2	16.7%	2	16.7%	5	41.7%	1	8.3%	5	41.7%	3	25.0%	3	25.0%	12	0.1%
Cracking (Even)		2	1.4%	9	6.4%	42	30.0%	49	35.0%	18	12.9%	11	9.0%	9	6.4%	140	0.8%
Rounding		6	22.2%	4	14.8%	11	40.7%	1	3.7%	5	18.5%	9	33.3%	9	33.3%	27	0.2%
Root etching		2	11.8%	0	0.0%	3	17.6%	1	5.9%	0	0.0%	2	11.8%	9	52.9%	17	0.1%
Weathering		0	0.0%	2	50.0%	0	0.0%	1	25.0%	1	25.0%	0	0.0%	0	0.0%	4	0.0%
Juvenile specimens		5	1.5%	10	3.0%	2	0.6%	54	16.3%	9	2.7%	29	8.8%	222	67.1%	331	1.9%

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bone/tooth surface, occurrences of bone or enamel cracking leading to either perpendicular (even) or jagged (uneven) break edges, rounding of the bone surface and broken edges due to fluvial or sedimentary tumbling, tunneling of the bone surface due to the adherence of mineral seeking plant roots, and weathering of the bone surface due to exposure to wind, rain, and/or sunlight for extended periods.

With the exception of oxide mineral discolouration, all of these taphonomic agents had a very limited effect on the Hohle Fels small mammal sample. The highest proportion of discoloured specimens due to exposure to high or long duration temperatures occurs in GH 7 where 8.2% of all specimens were discoloured. Within all assemblages only 17 specimens were identified to Stiner's 'lightly burnt' code 2. These specimens are also distributed throughout the stratigraphic sequence without any clear temporal relationship. There were no specimens recorded with burning beyond Stiner's code 2. This is surprising considering that GH 7a/7aa contains a number of potentially anthropogenic hearth features. Rhodes et al. [65] have demonstrated that thermal discolouration of small mammal remains can accompany *in situ* combustion events within prehistoric deposits, and therefore a higher proportion of thermally modified specimens would be expected from within the GH 7a/7aa assemblage. As the degree of potential thermal discolouration throughout all assemblages did not warrant examination using more advanced methods, such as scanning electron microscopy or fourier-transform infrared spectroscopy, it remains possible that these specimens are in actuality exhibiting a form of anomalous oxide staining, as these two types of bone discolouration can be quite similar under visual examination [66,67].

The authigenic oxide staining prevalent throughout the Hohle Fels small mammal assemblage was differentiated from thermal discolouration visually based on its characteristic dendritic patterning, exclusive black colour, and metallic shine under high magnification. However, of the 85.7% of the small mammal sample with oxide discolouration, 3.9% had a staining morphology more appropriately described as a 'wash,' in which large continuous portions of the bone or tooth surface were discoloured to a light grey-black colour like that described by Marín-Arroyo et al. [51]. This oxide wash occurs on samples spanning the entire depth of the archaeological sequence included in this study, which suggests the depositional context producing this staining occurred during multiple temporal periods. It is possible that this anomalous staining indicates areas of increased moisture content within the sedimentary matrix or periods of water-logging during which the bones may have soaked in mineral rich water allowing a greater portion of the bone surface to become homogenously discoloured. The majority of specimens exhibiting both dendritic and 'wash' oxide staining exhibited the discolouration over <10% of the bone surface, and those with heavier deposition, either in characteristic dendritic patterning or as a wash, show no clear vertical patterning throughout the depth of deposits.

Although we documented rounding of element break edges on 2.5% of the specimens from GH 7, this modification was found on far fewer specimens throughout the rest of the assemblage (0.1% total). This suggests that despite the potentially high sedimentary moisture content indicated by the oxide staining, the assemblage was not subject to tumbling or sediment abrasion by water movement either pre- or post-depositionally. The high proportion of rounded specimens in GH 7 is more likely a result of the small sample size in this horizon than of any unique accumulation events. The other taphonomic modifications detailed in Table 1 occur in such small amounts as to not warrant further discussion.

The limited evidence of rounding, as well as the lack of articulated specimens and the heterogeneous nature of the taxonomic composition of the assemblage (see below) eliminate fluvial transport and mass death as possible mechanisms of accumulation for the assemblage. Instead, predation by owls, diurnal raptors, or mammalian carnivores remain the most likely methods by which the assemblage was deposited. To determine which small mammal predators were active at the site through time we conducted detailed analyses of the skeletal element representation and fragmentation, and the degree of digestive corrosion on the dental and select post-cranial elements.

Predation related modifications

Skeletal element representation and breakage. We present skeletal element representation in Table 3 and the breakage patterns of certain post-cranial and cranial elements in Table 4 and Table 5, both of which are comparable to actualistic [48] and other archaeological [18,49,54,68–71] studies. However, it is important to be cautious when using skeletal element representation and/or breakage as indicators of assemblage accumulation since studies of small mammal bone density-mediated attrition are rare [54], and generally utilize density measurements of single species [72, 73] making comparison with multi-species assemblages less than ideal [54]. It has also been shown that post-depositional trampling can mimic patterns of bone breakage and loss seen in assemblages produced by moderately destructive predators [18,48]. The high site occupation intensity suggested by the artifact densities of the

Table 4. Number (NSP) and proportion (%) of long bones by geological horizon at Hohle Fels Cave.

Geological Horizon (GH)	GH 7		GH 7a/7aa		GH 8		GH 9		GH 10		GH 11		GH 12		Grand Total	
	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%
Femur																
Complete	3	9.3%	5	8.8%	4	2.1%	16	7.4%	1	3.2%	10	13.3%	66	9.8%	105	8.2%
Proximal	17	53.1%	31	54.4%	94	48.4%	101	46.8%	23	74.2%	34	45.3%	345	51.1%	645	50.4%
Shaft	9	28.1%	13	22.8%	74	38.1%	63	29.2%	6	19.4%	20	26.7%	129	19.1%	314	24.5%
Distal	3	9.4%	8	14.0%	22	11.3%	36	16.7%	1	3.2%	11	14.7%	135	20.0%	216	16.9%
Total	32	100.0%	57	100.0%	194	100.0%	216	100.0%	31	100.0%	75	100.0%	675	100.0%	1280	100.0%
Humerus																
Complete	2	8.3%	5	9.6%	2	1.3%	18	8.0%	1	2.9%	12	11.3%	101	14.9%	141	11.1%
Proximal	0	0.0%	6	11.5%	14	9.4%	36	15.9%	1	2.9%	17	16.0%	167	24.7%	241	19.0%
Shaft	0	0.0%	7	13.5%	22	14.8%	45	19.9%	13	37.1%	18	17.0%	77	11.4%	182	14.4%
Distal	22	91.7%	34	65.4%	111	74.5%	127	56.2%	20	57.1%	59	55.7%	331	49.0%	704	55.5%
Total	24	100.0%	52	100.0%	149	100.0%	226	100.0%	35	100.0%	106	100.0%	676	100.0%	1268	100.0%
Tibia																
Complete	3	10.0%	0	0.0%	1	0.5%	2	0.7%	2	3.0%	3	2.1%	6	0.7%	17	1.1%
Proximal	7	23.3%	14	20.0%	47	25.5%	78	27.5%	15	22.4%	32	22.7%	287	35.7%	480	30.4%
Shaft	9	30.0%	20	28.6%	62	33.7%	91	32.0%	25	37.3%	50	35.5%	234	29.1%	491	31.1%
Distal	11	36.7%	36	51.4%	74	40.2%	113	39.8%	25	37.3%	56	39.7%	276	34.4%	591	37.4%
Total	30	100.0%	70	100.0%	184	100.0%	284	100.0%	67	100.0%	141	100.0%	803	100.0%	1579	100.0%
Ulna																
Complete	0	0.0%	2	7.1%	5	6.9%	14	9.2%	0	0.0%	3	6.7%	34	8.8%	58	8.0%
Proximal	10	100.0%	12	42.9%	41	56.9%	82	53.9%	16	51.6%	26	57.8%	191	49.6%	378	52.3%
Shaft	0	0.0%	14	50.0%	24	33.3%	53	34.9%	11	35.5%	14	31.1%	110	28.6%	226	31.3%
Distal	0	0.0%	0	0.0%	2	2.8%	3	2.0%	4	12.9%	2	4.4%	50	13.0%	61	8.4%
Total	10	100.0%	28	100.0%	72	100.0%	152	100.0%	31	100.0%	45	100.0%	385	100.0%	723	100.0%
Total																
Complete	8	8.3%	12	5.8%	12	2.0%	50	5.7%	4	2.4%	28	7.6%	207	8.2%	321	6.6%
Proximal	34	35.4%	63	30.4%	196	32.7%	297	33.8%	55	33.5%	109	29.7%	990	39.0%	1744	36.0%
Shaft	18	18.8%	54	26.1%	182	30.4%	252	28.7%	55	33.5%	102	27.8%	550	21.7%	1213	25.0%
Distal	36	37.5%	78	37.7%	209	34.9%	279	31.8%	50	30.5%	128	34.9%	792	31.2%	1572	32.4%
Total	96	100.0%	207	100.0%	599	100.0%	878	100.0%	164	100.0%	367	100.0%	2539	100.0%	4850	100.0%

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Aurignacian horizons at Hohle Fels [74], would imply that material deposited before and during the Aurignacian period may have been subject to substantial post-depositional trampling breakage. However, fragmentation data from these horizons are still useful as they can corroborate other lines of evidence related to assemblage accumulation (i.e. digestive etching).

At Hohle Fels the small mammal skeletal element representation is surprisingly uniform through time. Although the sample size between geological horizons varies greatly (from 244 to 9116 specimens), the proportional value of each element is rather homogeneous throughout all deposits, as well as when the assemblages are considered as a whole (Table 3). When the raw data are converted into relative proportions, the overall pattern can be compared to those recovered from actualistic assemblages both visually (Fig 3) and statistically (Table 6). We identified strong correlations ($\tau > 6.000$; Table 6 and Fig 3) between the patterns produced by the little owl (*Athena noctua*), red fox (*Vulpes vulpes*), great grey owl (*Strix nebulosa*), and European eagle owl (*Bubo bubo*) and those identified in the Hohle Fels element abundances from horizons 7 through 12. The ‘zig-zag’ pattern of the relative abundance seen in Fig 3

Table 5. Number (NSP) and proportion (%) of maxillae and mandibles including proportion of specimens exhibiting various breakage categories and comparative breakage indices (both following Andrew, 1990) from Hohle Fels Cave. See the text for interpretation.

	GH 7	GH 7a/7aa	GH 8	GH 9	GH 10	GH 11	GH 12
Total Maxillae (NSP)	2	19	49	80	9	37	253
% complete	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
% maxillae with zygomatic	50.0%	0.0%	12.2%	17.5%	22.2%	24.3%	11.4%
% palates	50.0%	100.0%	87.8%	82.5%	77.8%	75.7%	88.6%
Total Mandibles (NSP)	25	25	116	123	10	73	464
% complete	0.0%	0.0%	0.0%	0.8%	2.6%	0.0%	3.0%
% anterior break	68.0%	60.0%	67.2%	82.9%	70.0%	43.8%	29.7%
% inferior border break	40.0%	60.0%	75.9%	67.5%	40.0%	64.4%	30.8%
% ramus break	68.0%	84.0%	91.4%	92.7%	80.0%	86.3%	86.0%
Breakage Index							
post-crania/crania	221.1	122.1	131.0	165.1	171.5	158.9	153.3
femur+humerus/mandible+maxilla	207.4	252.3	213.9	222.2	347.4	165.5	189.5
tibia+radius/femur+humerus	58.9	70.3	60.3	83.6	113.6	100.0	75.6
% isolated molars*	38.8%	115.1%	85.9%	105.6%	137.0%	70.1%	83.0%
% molar occlusal break	18.4%	18.1%	9.8%	12.3%	16.6%	16.9%	12.3%

*calculated by dividing the # isolated molars by the # expected molars (based on 3 per jaw) minus the in situ molars

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indicates preferential preservation of higher density elements [48], specifically the humerus, femur, tibia, and, to a lesser extent, the ulna. The relative amount of isolated dental elements (incisors and molars) is also quite high, ranging from 20% to 80%, (Fig 3) and this is reflected in the low number of maxillae and mandibles present. At the nearby site of Geißenklösterle, archaeological skeletal element abundances were also strongly correlated with the patterns

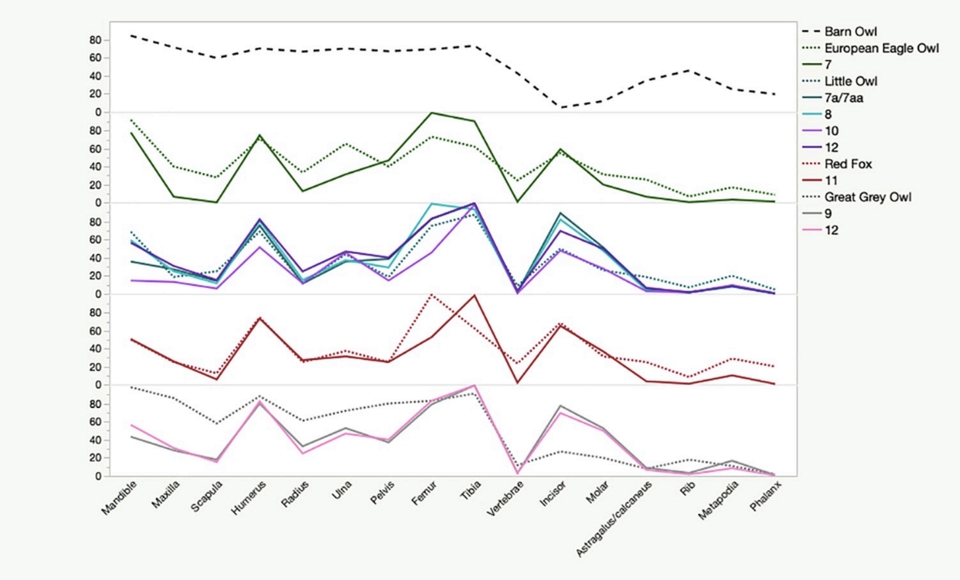

Fig 3. Skeletal element relative abundance (R) by geological horizon at Hohle Fels Cave. Only horizons showing a strong correlation (τ = > 0.600) with modern prey samples (from Andrews, 1990) are included. We include the pattern produced by barn owls (*Tyto alba*) at the top for comparison, as this low modifying predator approximates the pattern expected if perfect preservation of all elements were to occur.

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Table 6. Kendall's Tau (τ) correlation results by geological horizon at Hohle Fels Cave showing all significant correlations > 0.600.

Geological Horizon (GH)	Actualistic predator pattern (adapted from Andrews, 1990)	τ	P score (<0.05 significant)
7	European Eagle Owl	0.7745	<0.0001
	Red Fox	0.7392	0.0001
	Coyote	0.7009	0.0002
	Kestrel	0.6950	0.0002
	Little Owl	0.6466	0.0007
7a/7aa	Little Owl	0.7575	<0.0001
	Red Fox	0.6611	0.0005
	European Eagle Owl	0.6387	0.0006
8	Little Owl	0.7798	<0.0001
	Red Fox	0.7524	<0.0001
	European Eagle Owl	0.7280	<0.0001
	Kestrel	0.6500	0.0004
	Coyote	0.6219	0.0008
9	Little Owl	0.7628	<0.0001
	Red Fox	0.7182	0.0001
	European Eagle Owl	0.6778	0.0003
	Kestrel	0.6333	0.0006
	Coyote	0.6219	0.0008
	Great Grey Owl	0.6000	0.0012
10	Little Owl	0.7351	<0.0001
	Red Fox	0.7070	0.0002
	European Eagle Owl	0.6498	0.0005
	Kestrel	0.6051	0.0012
11	Red Fox	0.7524	<0.0001
	Little Owl	0.7459	<0.0001
	Coyote	0.6891	0.0002
	Kestrel	0.6667	0.0003
	European Eagle Owl	0.6611	0.0004
	Short-eared owl	0.6167	0.0009
	Hen Harrier	0.6051	0.0012
12	Little Owl	0.8306	< .0001
	Red Fox	0.7695	< .0001
	European Eagle Owl	0.7448	< .0001
	Kestrel	0.6667	0.0003
	Coyote	0.6387	0.0006
	Great Grey Owl	0.6000	0.0012

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produced by the European eagle owls, little owls, red foxes, and kestrels (*Falco tinnunculus*), however the relative proportion of isolated dentition was higher (50–100%), suggesting that comparatively the Hohle Fels material was subject to less intensive fragmentation. Few complete specimens were recovered of either post-crania (Table 4) or cranial elements (Table 5), suggesting that none of the assemblages were accumulated by low-modifying owls or raptors. Comparison of the different long bone breakage classes (Table 4) with Andrews' [48] actualistic data suggests that mammalian predators, particularly the red fox, or heavily modifying birds of prey such as the little owl and hen harrier may be responsible for accumulating all the Hohle Fels material.

Similarly, the lack of complete crania in the assemblages and the prevalence of isolated palates and mandibular fragments (Table 5) attests to the high level of overall destruction, also suggesting a mammalian predator as the main accumulator. In geological horizons 10 and 11 the proportion of maxillae and zygomatic specimens reaches similar levels to those seen in short-eared owl assemblages, a predator which was also suggested by the post-cranial skeletal element representation of GH 11 (Table 3). The number of complete mandibles is likewise low, totaling less than 7% of the total assemblage and found only in the MP deposits (GH 9–12). The percent of specimens exhibiting broken rami and/or a break along the inferior border of the corpus falls within ranges produced by the kestrel, hen harrier, mongoose, and other mammalian predators according to Andrews [48: Table 3.7] for all horizons. The high degree of mandibular and maxillae breakage is further indicated in the proportion of isolated molars, presented here as an index which is calculated by dividing the number of isolated molars by the total molars expected based on empty alveolar spaces present in the recovered mandibles and maxillae (Table 5). The results again fall within the range produced by the kestrel, hen harrier, mongoose, and other mammalian predators in geological horizons 7, 8, 11, and 12, whereas results higher than 100%, as in horizons 7a/7aa, 9, and 10, indicate the complete loss of mandibular elements.

Digestive corrosion on dental elements. Due to the distinct possibility that post-depositional trampling and sediment compression has increased the level of skeletal element breakage, we also documented the presence and degree of digestive corrosion on incisors (Table 7), molars (Table 8 and Table 9) and select post-cranial elements (Table 10 and Table 11). Corrosion due to exposure to digestive enzymes is unique in that it can be differentiated from all processes which produce similar alteration of bones and teeth through careful examination of the morphology and extent of the modification.

Following Andrews [48], we documented digestion on both isolated and *in situ* incisors and present them here as combined totals (Table 5). The intensity of the modification on incisors is tallied along a continuous scale from light to extreme. Examples of light and moderate level digestion of incisors can be seen in Fig 4. Overall, the majority of incisors from Hohle Fels (73.7% to 89.9%) show no evidence of digestive corrosion and the highest proportions of specimens with either tip or surface corrosion exhibit only light retraction of the enamel or pockets of enamel loss. None of the specimens exhibit extreme digestion, which presents as a complete loss of the tooth enamel and heavy modification of the dentine core. Only one specimen from GH 7a/7aa and one from GH 12 was categorized as having heavy tip corrosion, in which the enamel was retracted posteriorly and the dentine was eroded and cracked across the body of the tooth. GH 9, and to a lesser extent GH 8, include the highest number of incisors with surface modification, which may indicate that more specimens from these layers were broken from their alveolar socket during predation, as isolated teeth experience greater surface acid exposure. The total amount of both tip and surface digestion fall within Andrews' [48] digestion category 1 (Table 12), in which digestive modification is absent or minimal and is associated with barn owl, short-eared owl, and snowy owl (*Bubo scandiacus*) actualistic assemblages. Although the moderately damaged specimens might indicate the presence of more destructive predators, such as an eagle owl or little owl, there is no clear pattern in the distribution of these more heavily modified specimens across horizons to suggest a particular period of cave occupation by these predators.

A similar pattern is seen when we consider the evidence for digestive corrosion on both isolated and *in situ* molars. The arvicolidae results are presented in Table 8 for isolated molars and Table 9 for *in situ* specimens. In actualistic predator assemblages the proportion of molars exhibiting digestive corrosion is significantly lower than the proportion of incisors [48]. At Hohle Fels, the majority of arvicolid molars have no evidence of digestive modification (86.7%

Table 7. Number (N) and proportion (%) of digested incisors out of all incisors by geological horizon divided by area of modification from Hohle Fels Cave.

Geological Horizon (GH)	Tip Digestion												Total Tip Digested	
	Absent		Light		Light-Moderate		Moderate		Moderate-Heavy		Heavy			
	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%
7	28	73.7%	3	7.9%		0.0%	2	5.3%	1	2.6%		0.0%	6	15.8%
7a/7aa	101	80.8%	6	4.8%	2	1.6%		0.0%		0.0%	1	0.8%	9	7.2%
8	269	83.5%	5	1.5%	3	0.9%		0.0%		0.0%		0.0%	8	2.4%
9	387	88.0%	10	2.3%		0.0%		0.0%		0.0%		0.0%	10	2.3%
10	58	89.2%	3	4.6%	2	3.1%		0.0%		0.0%		0.0%	5	7.7%
11	170	89.9%	4	2.1%	2	1.1%	1	0.5%	1	0.5%		0.0%	8	4.2%
12	1003	87.9%	62	5.4%	4	0.4%	2	0.2%	1	0.1%	1	0.1%	70	6.1%
Grand Total	2016	86.9%	93	4.0%	13	0.6%	5	0.2%	3	0.1%	2	0.1%	116	5.0%

Geological Horizon (GH)	Surface Digestion								Total Surface Digested		Grand Total	
	Light		Light-Moderate		Moderate		Moderate-Heavy					
	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%
7	1	0.0%	2	0.0%	1	2.6%		0.0%	4	10.5%	38	1.6%
7a/7aa	12	9.6%	3	2.4%		0.0%		0.0%	15	12.0%	125	5.4%
8	25	7.8%	19	5.9%	1	0.3%		0.0%	45	13.9%	322	13.9%
9	22	5.0%	16	3.6%	3	0.7%	2	0.5%	43	9.7%	440	19.0%
10	2	3.0%		0.0%		0.0%		0.0%	2	3.0%	65	2.8%
11	8	4.2%	3	1.6%		0.0%		0.0%	11	5.8%	189	8.1%
12	51	4.4%	11	0.9%	5	0.4%	1	0.1%	68	5.9%	1141	49.2%
Grand Total	121	5.2%	54	2.3%	10	0.4%	3	0.1%	188	8.1%	2320	100.0%

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- 96.0%) and only geological horizons 8, 9, and 12 include specimens with heavy to extreme modification (Fig 4). The remaining molars with light to moderate levels of digestive modification account for between 3.5% and 13.3% of the arvicolid teeth in any given horizon (Table 8 and Table 9). It is interesting to note that the specimens exhibiting greater than moderate modification come from two lemming species (*Lemmus lemmus* and *Dicrostonyx* sp.) and two vole species (*Microtus arvalis/agrestis* and *M. gregalis*). Identifying digestive etching on lemming molars is complicated by the natural lack of enamel along the salient edges of the teeth, which may cause low level modification to appear greater in intensity. This distinct tooth morphology also allows identification of all isolated lemming molars to genera level. Conversely, the vole dental pattern is more conservative with only the lower m1 exhibiting enough interspecies variation to allow taxonomic determination. As such, the lemming sample from Hohle Fels is inflated in relation to the vole sample, and the 4 specimens which exhibit heavy or extreme digestive corrosion may have originated from only 3 individuals, whereas the *M. arvalis/agrestis* and *M. gregalis* specimens adds up to at least 6 individuals. Still, the occurrence of digestive damage of greater intensity on just these four taxa from three horizons suggests that a diurnal raptor or mammalian predator with a dietary preference for voles and lemmings was active in the cave during these periods.

The overall proportion of digested isolated arvicolid molars from most geological horizons falls within Andrews' [58] digestion category 2 and indicates the presence of a moderately destructive predator in the cave, such as a snowy owl, European eagle owl, or great grey owl. GH 7a/7aa and GH 10 have total counts that fall between Andrews' category 2 and category 3, which may suggest that a European eagle owl or tawny owl was present when these deposits were accumulated. The proportion of modified *in situ* molars (Table 9) follows this trend, with

Table 8. Digestion of isolated Arvicolid dental elements by geological horizon and etching intensity from Hohle Fels Cave. Includes all molars to allow comparability with Andrews 1990.

Geological Horizon (GH)	*Lemmus lemmus*	*Dicrostonyx gulielmi*	*Microtus gregalis*	*Microtus oeconomus*	*Chionomys nivalis*	*Arvicola terrestris/ antiquus*	*Microtus subterraneous*	*Microtus arvalis/ agrestis*	*Microtus* sp.	Total	%
7	4	2	0	5	0	0	0	8	30	49	
absent	4	2		5				6	30	47	95.9%
light								2		2	4.1%
7a/7aa	34	10	13	9	3	4	0	34	133	240	
absent	31	10	9	7	2	4		26	119	208	86.7%
Light	2		3	2	1			5	10	23	9.6%
Light-moderate								2		2	0.8%
Moderate	1		1					1	4	7	2.9%
8	72	22	36	8	4	5	0	92	421	660	
absent	65	19	30	7	3	5		82	412	623	94.4%
light	5	2	5	1				5	7	25	3.8%
Light-moderate	1		1					1		3	0.5%
Moderate	1	1			1			3	2	8	1.2%
Heavy								1		1	0.2%
9	73	14	48	15	2	5	0	123	761	1041	
absent	65	14	42	12	2	4		101	759	999	96.0%
Light	3		5			1		16	1	26	2.5%
Light-moderate								1		1	0.1%
Moderate	1		1	1				3		6	0.6%
Moderate—heavy	2			2						4	0.4%
Heavy	2							2		4	0.4%
Extreme									1	1	0.1%
10	6	2	3	3	0	1	0	16	95	126	
absent	6	2	2	2		1		12	91	116	92.1%
Light			1	1				4	2	8	6.3%
Moderate									2	2	1.6%
11	19	5	5	11	8	18	0	74	243	383	
absent	18	5	4	9	8	18		57	243	362	94.5%
light	1		1	2				13		17	4.4%
Light-moderate								2		2	0.5%
moderate								2		2	0.5%
12	261	40	90	31	7	13	2	397	2040	2881	
absent	243	38	75	22	6	13	1	321	2040	2759	95.8%
light	4		9	7			1	56		77	2.7%
Light-moderate			1					8		9	0.3%
moderate	11	1	3	1	1			5		22	0.8%
Moderate—heavy	1		1	1				2		5	0.2%
Heavy	1	1						2		4	0.1%
Heavy-extreme	1		1					3		5	0.2%

(*Continued*)

Table 8. (Continued)

Geological Horizon (GH)	*Lemmus lemmus*	*Dicrostonyx gulielmi*	*Microtus gregalis*	*Microtus oeconomus*	*Chionomys nivalis*	*Arvicola terrestris/ antiquus*	*Microtus subterraneous*	*Microtus arvalis/ agrestis*	*Microtus* sp.	Total	%
Isolated total	469	95	195	82	24	46	2	744	3723	5380	
absent total	432	90	162	64	21	45	1	605	3694	5114	95.1%
light total	15	2	24	13	1	1	1	101	20	178	3.3%
Light—Moderate total	1	0	2	0	0	0	0	14	0	17	0.3%
Moderate total	14	2	5	2	2	0	0	14	8	47	0.9%
Moderate—Heavy total	3	0	1	3	0	0	0	2	0	9	0.2%
Heavy total	3	1	0	0	0	0	0	5	0	9	0.2%
Heavy—Extreme total	1	0	1	0	0	0	0	3	0	5	0.1%
Extreme total	0	0	0	0	0	0	0	0	1	1	0.0%
%absent	92.1%	94.7%	83.1%	78.0%	87.5%	97.8%	50.0%	81.3%	99.2%	95.1%	
%light	3.2%	2.1%	12.3%	15.9%	4.2%	2.2%	50.0%	13.6%	0.5%	3.3%	
%light—moderate	0.2%	0.0%	1.0%	0.0%	0.0%	0.0%	0.0%	1.9%	0.0%	0.3%	
%moderate	3.0%	2.1%	2.6%	2.4%	8.3%	0.0%	0.0%	1.9%	0.2%	0.9%	
%moderate—heavy	0.6%	0.0%	0.5%	3.7%	0.0%	0.0%	0.0%	0.3%	0.0%	0.2%	
%heavy	0.6%	1.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.7%	0.0%	0.2%	
%heavy-extreme	0.2%	0.0%	0.5%	0.0%	0.0%	0.0%	0.0%	0.4%	0.0%	0.1%	
%extreme	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	

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most horizons having between 4.2% and 7.5% of the sample exhibit digestive corrosion. Two horizons, GH 7 and GH 10, had no *in situ* molars present, indicating a higher than expected loss of dentition and destruction of jaws. Overall, the proportion of *in situ* dentition ranges from 3.2% to 9.9% of all teeth examined, which suggests that retention of molars within their original alveolar sockets was low throughout all periods.

Digestive corrosion on post-cranial elements. At Hohle Fels, evidence of intrusive digestion is absent on most proximal femora and distal humeri with only 20.3% and 11.4% of all specimens, respectively, showing any level of corrosive modification (Table 10 and Table 11 and see Fig 5). When broken down by geological horizon, the range of digested femora varies from 13.3% to 62.5% throughout the deposits. The amount of digested distal humeri in each geological horizon falls within the range of 6.3% to 33.3%. Exactly why there exists such a discrepancy in the amount of digestion on humeri vs. femora is unclear, although it may relate to the speed of ossification and fusion between elements and species. Distal humeri have been shown to fuse at around three weeks of age in mice [75], whereas both the proximal and distal femur is ossified by the end of the fourth week [76] but only fused by the 13 – 15th postnatal week [75]. Assuming voles and shrews follow a similar fusion pattern, late ossification and fusion rates may have increased the number of femora affected by digestive acid exposure in our sample. If this hypothesis is correct, then the distal humerus would prove a more reliable indicator of the category of accumulative predator than the proximal femur, and so when the two post-cranial records are in disagreement we give greater weight to the signal from the humerus. For example, in geological horizons 7, 7a/7aa, and 8 (the Aurignacian layers), the proportion of digested distal humeri fall within Andrews' [58] low-modifying category 1

Table 9. Digestion of in situ Arvicolid dental elements by geological horizon and etching intensity from Hohle Fels Cave. Includes all molars to allow comparability with Andrews, 1990.

Geological Horizon (GH)	*Lemmus lemmus*	*Dicrostonyx gulielmi*	*Microtus gregalis*	*Microtus oeconomus*	*Chionomys nivalis*	*Arvicola terrestris/ antiquus*	*Microtus arvalis/agrestis*	*Microtus* sp.	Total	%
7a/7aa	2		2		2		5	6	17	
Absent	2		2		2		4	6	16	94.1%
Light									0	0.0%
Moderate							1		1	5.9%
8	4	4	9		3	2	26	17	65	
Absent	4	4	9		3	2	24	16	62	95.4%
Light							2	1	3	4.6%
Moderate									0	0.0%
9	3		11	2	3		6	17	42	
Absent	3		11	2	3		6	17	42	100.0%
11			3				7	14	24	
Absent			3				7	13	23	95.8%
Light								1	1	4.2%
12	46	13	43	3	2	4	108	98	317	
Absent	46	12	37	3	2	4	97	92	293	92.4%
Light			5				9	5	19	6.0%
Light—Moderate							2	1	3	0.9%
Moderate		1	1						2	0.6%
In situ total	55	17	68		10	6	152	152	465	
Absent total	55	16	62		10	6	138	144	436	
Light total	0	0	5		0	0	11	7	23	
Light—Moderate total	0	0	0		0	0	2	1	3	
Moderate total	0	1	1		0	0	1	0	3	
%absent	100.0%	94.1%	91.2%		100.0%	100.0%	90.8%	94.7%	93.8%	
%light	0.0%	0.0%	7.4%		0.0%	0.0%	7.2%	4.6%	4.9%	
%light—moderate	0.0%	0.0%	0.0%		0.0%	0.0%	1.3%	0.7%	0.6%	
%moderate	0.0%	5.9%	1.5%		0.0%	0.0%	0.7%	0.0%	0.6%	

https://doi.org/10.1371/journal.pone.0215172.t009

Table 10. Number and percentage of proximal femurs exhibiting digestive corrosion damage by geological horizon from Hohle Fels cave.

Geological Horizon (GH)	Proximal Femur Digestion								Total Femur Digestion	
	Absent		Light		Light—Moderate		Moderate			
	NSP	%	NSP	%	NSP	%	NSP	%	NSP	%
7	8	40.0%	9	45.0%	1	5.0%	2	10.0%	12	60.0%
7a/7aa	28	77.8%	7	19.4%	1	2.8%		0.0%	8	22.2%
8	85	86.7%	11	11.2%	1	1.0%	1	1.0%	13	13.3%
9	91	77.8%	17	14.5%	7	6.0%	2	1.7%	26	22.2%
10	9	37.5%	7	29.2%	7	29.2%	1	4.2%	15	62.5%
11	27	61.4%	11	25.0%	2	4.5%	4	9.1%	17	38.6%
12	350	85.2%	17	4.1%	18	4.4%	26	6.3%	61	14.8%
Grand Total	598	79.7%	79	10.5%	37	4.9%	36	4.8%	152	20.3%

https://doi.org/10.1371/journal.pone.0215172.t010

Table 11. Number and percentage of distal humeri exhibiting digestive corrosion by geological horizon from Hohle Fels cave.

Geological Horizon (GH)	Distal Humerus Digestion								Total Humerus Digestion	
	Absent		Light		Light—Moderate		Moderate			
	N	%	N	%	N	%	N	%	N	%
7	18	75.0%	6	25.0%		0.0%		0.0%	6	25.0%
7a/7aa	32	82.1%	7	17.9%		0.0%		0.0%	7	17.9%
8	106	93.8%	6	5.3%	1	0.9%		0.0%	7	6.2%
9	122	84.1%	15	10.3%	5	3.4%	3	2.1%	23	15.9%
10	14	66.7%	5	23.8%	2	9.5%		0.0%	7	33.3%
11	54	76.1%	12	16.9%	3	4.2%	2	2.8%	17	23.9%
12	403	93.3%	16	3.7%	12	2.8%	1	0.2%	29	6.7%
Grand Total	749	88.6%	67	7.9%	23	2.7%	6	0.7%	96	11.4%

https://doi.org/10.1371/journal.pone.0215172.t011

predators, including the barn owl, snowy owl, long-eared owl, and great grey owl; whereas the proportion of modified proximal femora suggest a category 2 or 3 predator was active when these deposits were laid down, such as the little owl, hen harrier, European eagle owl, spotted

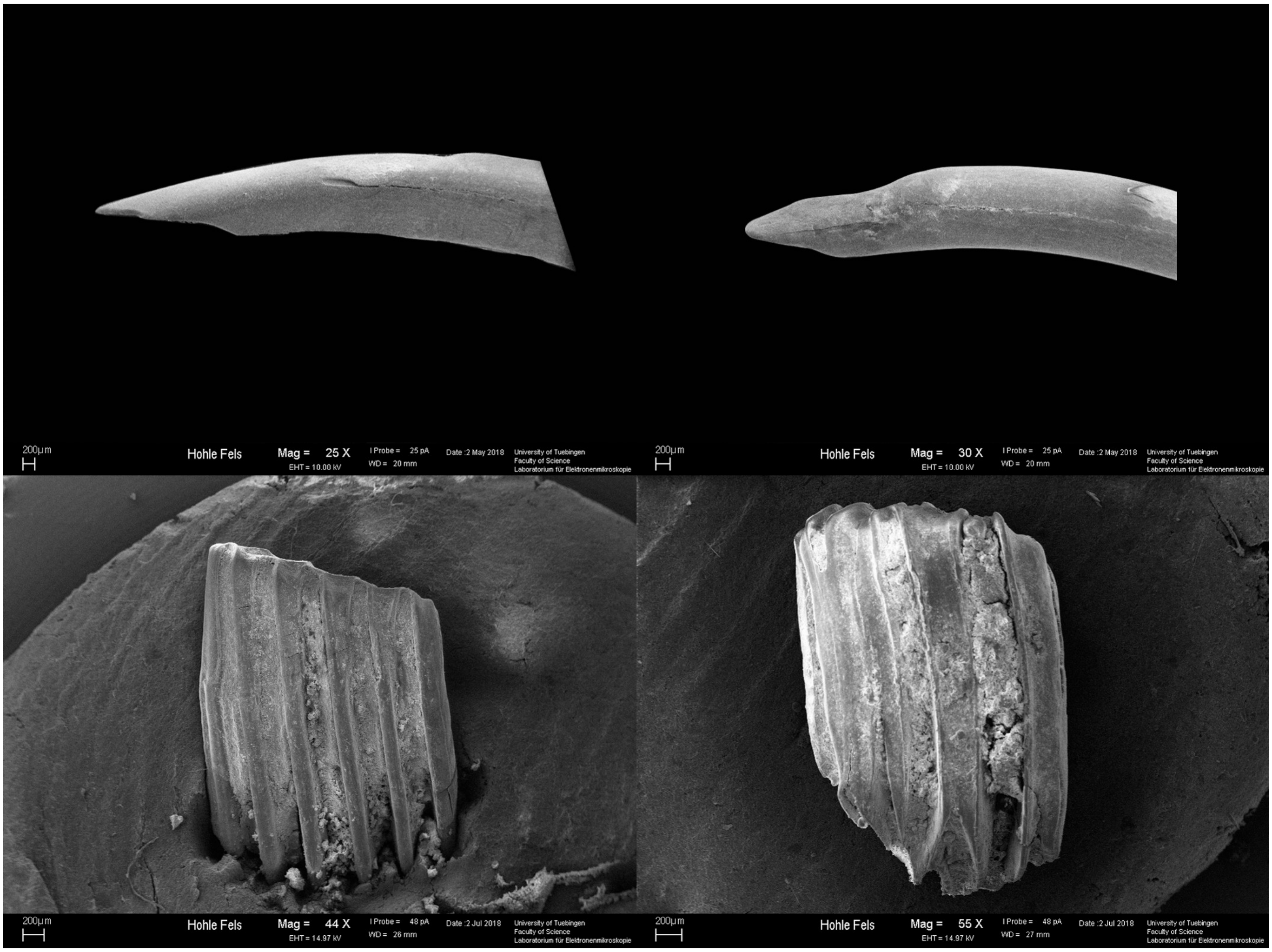

Fig 4. Scanning Electron Microscopy photos of digestive modification on dental elements from Hohle Fels Cave. Top left: lightly digested arvicolid incisor; Top right: moderately digested arvolid incisor; Bottom left: lightly digested arvicolid molar; Bottom right: heavily digested arvicolid molar.

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Table 12. Categories of predators according to digestive modification (modified from Andrews, 1990).

Category	Predators	Alterations
1	*Molar digestion*: Barn, Long-eared, Short-eared owl, Verreaux eagle owl,	Light modification, absent or light digestion Molars: 0–3% Incisors: 8–13% Post-crania: 0–20%
	Incisor digestion: Barn owl, short-eared owl, snowy owls	
	Post-cranial digestion: Barn, snowy, long-eared, short-eared owls, Verreaux eagle owl, great grey owl	
2	*Molar digestion*: Snowy, spotted eagle, great grey owls	Little modification, moderate degree of digestion, though enamel is removed from the tips of incisors Molars: 4–6% Incisors: 20–30% Post-crania: 25–50%
	Incisory digestion: Long-eared owl, Verreaux eagle owl, great grey owl, bat-eared fox	
	Post-cranial digestion: European & spotted eagle owls, tawny owl	
3	*Molar digestion*: European eagle owl, tawny owl, bat-eared fox, mongoose, genet	Greater destruction, moderate/heavy digestion over the enamel Molars: 18–22% Incisors 50–70% Post-crania: 60–100%
	Incisor digestion: European & spotted eagle owls, tawny, little owl, pine marten, mongoose, genet	
	Post-cranial digestion: Little owl, kestrel, hen harrier, peregrine falcon	
4	*Molar digestion*: Little owl, kestrel, pine martin	Heavy/Extreme enamel and dentine corrosion; mustelids produce extreme modification but digested elements appear in low percentages, some of them chewed Molars: 50–70% Incisors: 60–80% Post-crania: ~100%
	Incisor digestion: Kestrel	
	Post-cranial digestion: same as category 5	
5	*Molar, incisor and post-cranial digestion*: Hen harrier, coyote, red fox, arctic fox, mammalian carnivores.	The most destructive effects (extreme). Mammalian carnivores produce rounded edges of skeletal elements. Gnaw marks rare, except for some instances of canid predation and of some mustelids Low percentages of digested post-crania and complete lack of cranio-dental elements. Molars: 50–100% Incisors: 100% (dentine corroded) Post-crania: ~100%

https://doi.org/10.1371/journal.pone.0215172.t012

eagle owl or tawny owl. It is possible that predators from all three categories were active at the same time at the site. However, considering the signal for multiple predation patterns is coming from inter-bone comparisons, rather than inter-specific or relative abundance patterning, a more parsimonious explanation is that a low-modifying predator was active during all three periods and produced higher-than-expected levels of digestive corrosion on femoral heads due to the selective predation of juvenile individuals. The same logic can be applied to the contradictory signals within geological horizon 9, for which humeral proportions suggest a category 1 predator and femoral digestion suggests category 2 predator, and for geological horizon 10 which the post-cranial digestion data suggests may have been accumulated by category 3–5 predators such as the little owl or hen harrier, or by a category 2 predator such as the spotted or tawny owl. Only the two oldest MP horizons, geological horizon 11 and 12, showed agreement in all post-cranial corrosion and were likely accumulated by a category 2 predator (European eagle owl based on femoral digestion) and a category 1 predator, respectively.

Taphonomy: Summary and predator description. Table 13 summarizes the predators indicated by the various taphonomic indices used to evaluate the Hohle Fels small mammal assemblage. With few exceptions, the digestive evidence suggests that a category 1–2 predator

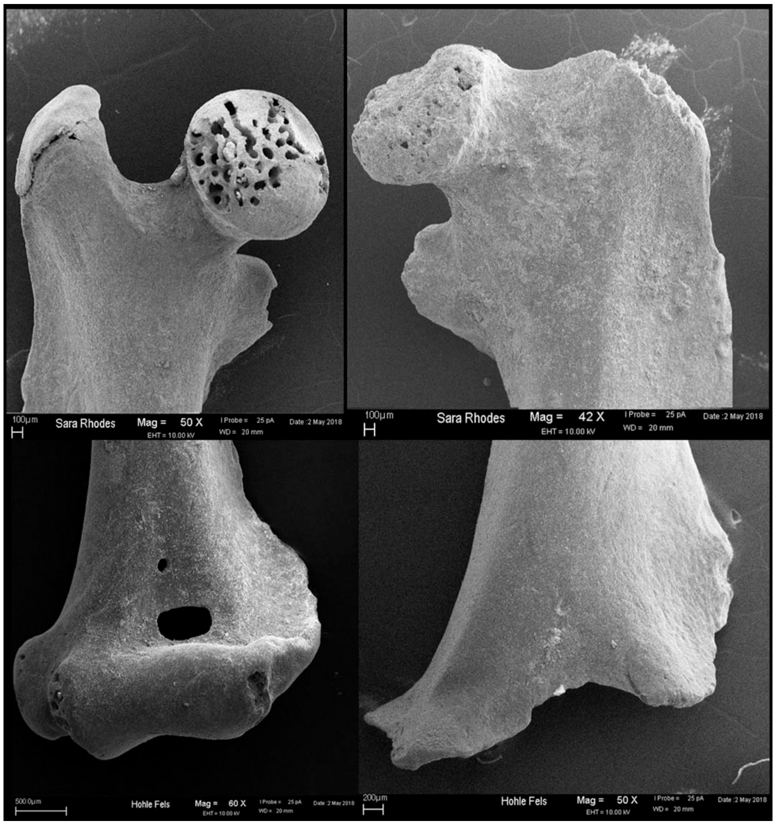

Fig 5. Scanning electron microscopy photographs of digestive modification on post-cranial specimens from Hohle Fels Cave. Top left: lightly digested proximal femur; Top right: heavily digested proximal femur; Bottom left: lightly digested distal humerus; Bottom right: heavily digested distal humerus.

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was active throughout the sequence, while the skeletal element data suggests a category 4 or 5 predator was present in both the MP and Aurignacian. In all cases where the digestion and breakage results were not in agreement, we gave greater weight to the digestive evidence identified on isolated and *in situ* molars. This is most clearly seen with regards to GH 8, 9, and 12, the three largest subsamples of the Hohle Fels small mammal assemblage (Table 1). This also suggests that there may be a relationship between sample size and the presence of rare highly modified dental specimens. The predation signals from the other geological horizons all suggest that category 1–2 predators occupied the site. In the Aurignacian (GH 7 and 7a/7aa), this was likely a snowy owl, although the European eagle owl is also a possible accumulator, particularly in GH 7a/7aa. Regarding the MP, in GH 10 the eagle owl is also indicated in both the evidence of digestive corrosion and the correlation with actualistic skeletal element preservation. In GH 11 tooth digestion suggests either a great grey owl or snowy owl accumulated the small mammal material.

Our taphonomic results support the use of this assemblage for paleoenvironmental reconstruction as the European eagle owl, snowy owl, great grey owl, little owl, and both the red and arctic fox are all mainly non-selective hunters [48,58]. The snowy owl, European eagle owl and great grey owl are specialized hunters of arvicolids, specifically *Microtus*, *Lemmus* and *Dicrostonyx*, which comprise at least 50% of their diet [48,77] and which are taken on encounter and therefore reflect the relative abundance of the prey species on the landscape. However, snowy owl pellet assemblages have been shown to include lower than expected amounts of shew and

Table 13. Small mammal predators indicated by the different taphonomic indices applied to the Hohle Fels cave assemblage divided by geological horizon.

Geological Horizon (GH)	Barn owl	Short-eared owl	Snowy owl	Long-eared owl	Great grey owl	European eagle owl	Tawny owl	Little owl	Kestrel	Pine martin	Hen harrier	Golden Jackal	Red fox	Arctic fox	Modification type
Predator Category	1,	1	1, 2	1,2	1,2	2,3	2,3	3,4	3,4	3,4	3,5	4,5	4,5	4,5	
7						x		x	x			x	x	x	Skeletal element representation
								x			x		x	x	Skeletal element breakage
									x	x	x	x	x	x	Cranial breakage
		x				x						x			Post-crania to crania index
													x	x	Femur +humerus/ mand+max
									x						Tibia+radius/ femur+humerus
									x	x	x	x	x	x	%isolated molars
															% molar with occlusal breaks
			x		x										Dig. Isolated molars
												x	x	x	Dig. *In situ* molars
	x	x	x												Dig. Incisors
	x	x	x	x	x	x	x	x	x		x				Dig. Post-crania
7a/7aa						x		x					x	x	Skeletal element representation
								x			x		x	x	Skeletal element breakage
									x	x	x	x	x	x	Cranial breakage
															Post-crania to crania index
													x	x	Femur +humerus/ mand+max
						x		x	x				x	x	Tibia+radius/ femur+humerus
												x	x	x	%isolated molars
															% molar with occlusal breaks
						x	x								Dig. Isolated molars
			x		x										Dig. *In situ* molars
	x	x	x												Dig. Incisors
	x	x	x	x	x	x	x	x	x		x				Dig. Post-crania

(*Continued*)

Table 13. (Continued)

Geological Horizon (GH)	Barn owl	Short-eared owl	Snowy owl	Long-eared owl	Great grey owl	European eagle owl	Tawny owl	Little owl	Kestrel	Pine martin	Hen harrier	Golden Jackal	Red fox	Arctic fox	Modification type
Predator Category	**1,**	**1**	**1, 2**	**1,2**	**1,2**	**2,3**	**2,3**	**3,4**	**3,4**	**3,4**	**3,5**	**4,5**	**4,5**	**4,5**	
8						x		x	x			x	x	x	Skeletal element representation
								x			x		x		Skeletal element breakage
									x	x	x	x	x	x	Cranial breakage
															Post-crania to crania index
													x	x	Femur +humerus/ mand+max
											x				Tibia+radius/ femur+humerus
									x	x	x	x	x	x	%isolated molars
											x				% molar with occlusal breaks
					x								x^{**}	x^{**}	Dig. Isolated molars
			x		x										Dig. *In situ* molars
	x	x	x			x		x							Dig. Incisors
	x	x	x	x	x	x	x	x	x		x				Dig. Post-crania
9					x	x		x	x			x	x	x	Skeletal element representation
								x			x		x	x	Skeletal element breakage
									x	x	x	x	x	x	Cranial breakage
															Post-crania to crania index
													x	x	Femur +humerus/ mand+max
		x										x			Tibia+radius/ femur+humerus
												x	x	x	%isolated molars
									x						% molar with occlusal breaks
		x	x										x^{**}	x^{**}	Dig. Isolated molars
			x		x										Dig. *In situ* molars
						x		x							Dig. Incisors
	x	x	x	x	x	x	x	x	x		x				Dig. Post-crania

(*Continued*)

Table 13. (Continued)

Geological Horizon (GH)	Barn owl	Short-eared owl	Snowy owl	Long-eared owl	Great grey owl	European eagle owl	Tawny owl	Little owl	Kestrel	Pine martin	Hen harrier	Golden Jackal	Red fox	Arctic fox	Modification type
Predator Category	1,	1	1, 2	1,2	1,2	2,3	2,3	3,4	3,4	3,4	3,5	4,5	4,5	4,5	
10						x		x	x				x	x	Skeletal element representation
								x			x		x	x	Skeletal element breakage
		x							x	x	x	x	x	x	Cranial breakage
															Post-crania to crania index
													x	x	Femur +humerus/ mand+max
	x														Tibia+radius/ femur+humerus
												x	x	x	%isolated molars
								x							% molar with occlusal breaks
						x									Dig. Isolated molars
												x	x	x	Dig. *In situ* molars
	x	x	x												Dig. Incisors
						x	x	x			x				Dig. Post-crania
11		x				x		x	x		x		x	x	Skeletal element representation
								x			x		x	x	Skeletal element breakage
		x							x	x	x	x	x	x	Cranial breakage
															Post-crania to crania index
								x							Femur +humerus/ mand+max
	x														Tibia+radius/ femur+humerus
									x	x	x	x	x	x	%isolated molars
								x							% molar with occlusal breaks
					x										Dig. Isolated molars
			x		x										Dig. *In situ* molars
	x	x	x												Dig. Incisors
						x	x								Dig. Post-crania

(*Continued*)

Table 13. (Continued)

Geological Horizon (GH)	Barn owl	Short-eared owl	Snowy owl	Long-eared owl	Great grey owl	European eagle owl	Tawny owl	Little owl	Kestrel	Pine martin	Hen harrier	Golden Jackal	Red fox	Arctic fox	Modification type
Predator Category	**1,**	**1**	**1, 2**	**1,2**	**1,2**	**2,3**	**2,3**	**3,4**	**3,4**	**3,4**	**3,5**	**4,5**	**4,5**	**4,5**	
12					x	x		x	x			x	x	x	Skeletal element representation
								x			x		x		Skeletal element breakage
									x	x	x	x	x	x	Cranial breakage
															Post-crania to crania index
								x							Femur +humerus/ mand+max
						x			x				x	x	Tibia+radius/ femur+humerus
									x	x	x	x	x	x	%isolated molars
									x						% molar with occlusal breaks
		x	x										x**	x**	Dig. Isolated molars
			x		x										Dig. *In situ* molars
	x	x	x												Dig. Incisors
	x	x	x	x											Dig. Post-crania

Light grey tallies are based on comparison between taphonomic indices (i.e. lack of *in situ* dentition) or potentially anomalous data (i.e. % digested femoral heads).

** indicates <1% of sample exhibited predator modifications.

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murid taxa, and some studies suggest the great grey owl may select against squirrels and water voles and for shrews in their hunting behaviour [58]. As such, it is possible that more Soricids were present around Hohle Fels during the deposition of GH 7 and GH 9 than the taxonomic composition of these layers suggests. Furthermore, we may expect that GH 8 and GH 11 had a greater presence of grasslands and stream/lake beds around the site than our paleoenvironmental reconstruction indicates. The European eagle owl is known to preferentially hunt water voles, however this is clearly not the case in GH 7a/7aa or GH 10 where this species is found in very small numbers. The varied diet of the little owl, as well as its small size, make it unlikely to have been a major contributor to the Hohle Fels small mammal material [48,78]. However, like the red fox and arctic fox, the little owl hunts opportunistically and would therefore contribute a representative sample of the small mammal taxa present on the landscape surrounding its nest site. A slight selection against burrowing prey, such as the water vole, some murids, and moles can be expected in red fox assemblages, as would be a selection for lemmings by the arctic fox. When doing so will not result in some form of circular reasoning, as with the potential Arctic fox derived material, we also include the habitat preferences and/or requirements of the indicated predator species in our paleoenvironmental reconstruction as an additional source of vegetative and climatic data.

Taxonomic composition

The number of identified specimens (NISP) and minimum number of individuals (MNI) attributed to each taxonomic level are detailed in in Table 14. Seven taxonomic families, including 12 genera and 14 species were identified from the 6165 specimens comprising the Hohle Fels small mammal assemblage. Our rarefaction analysis suggests that the small sample sizes from geological horizons 7, 7a/7aa and 10 likely underrepresent rare taxa. Furthermore, a variation of between 2 and 3 taxonomic designations, at the 95% confidence level, is seen in all but the largest horizons (Fig 6).

Arvicolidae is the most numerous group with 9 species represented, including 7 vole species—the water vole (*Arvicola terrestris/antiquus*), narrow-headed vole (*Microtus gregalis*), snow vole (*Chionomys nivalis*), tundra vole (*Microtus oeconomus*), pine vole (*Microtus subterraneous*), and the common (*Microtus arvalis*) and field vole (*Microtus agrestis*). The common and field vole cannot be differentiated by tooth morphology alone, and therefore are presented as one group *Microtus arvalis/agrestis*. The species designation of the *Arvicola terrestris/antiquus* group is left unclear as the maximum length of the specimens from all cultural periods falls within the range of both *A. terrestris* and *A. antiquus* (S1 Appendix). Ziegler [79] reports a similar pattern in the Geißenklösterle assemblage and distinguishes the two species based on the inferred environment. As the goal of the Hohle Fels analysis is to derive a paleoenvironmental signal from the site, assigning species identifications to these specimens based on assumed climatic conditions would be circular reasoning. Furthermore, the small sample size of *Arvicola* specimens from Hohle Fels (n = 10) leaves open the possibility that the anomalous size is the result of *A. terrestris* population variation. This taxonomic dominance by voles is common in Central European Upper Pleistocene assemblages [10,12,80]. The species richness (NTAXA) ranges from 8 to 14 throughout the horizons and exceeds that found by Rhodes et al. [18] at Geißenklösterle. Both cave assemblages are dominated by between 3 and 5 species, with the reciprocal of Simpson's index (1/D) from the Hohle Fels assemblages ranging from 3.55 to 5.07.

Shrews account for a large proportion of the assemblage from Hohle Fels, even during the Aurignacian when they were rare at Geißenklösterle [18]. This is driven at least in part by the addition of bicolored white-toothed shrews (*Crocidura leucodon* and *C. russula*) which occur

Table 14. Taxonomic list of the small mammals identified in the Hohle Fels Cave assemblage by geological horizon. NISP: number of identified specimens, %: proportion of total material from geological horizon, MNI: minimum number of individuals.

Geological Horizon (GH)		**7**			**7a/7aa**			**8**			**9**			**10**			**11**			**12**			**Grand Total**		
Quadrant		**30**			**30**			**30**			**30**			**30**			**25**			**25**			**30 & 25**		
Taxonomic category	**Common name**	**NISP**	**%**	**MNI**	**NISP**	**%**	**MNI**	**NISP**	**%**	**MNI**	**NISP**	**%**	**MNI**	**NISP**	**%**	**MNI**	**NISP**	**%**	**MNI**	**NISP**	**%**	**MNI**	**NISP**	**%**	**MNI**
Carnivora																									
Mustela erminea	Stoat				1	0.4%	1	6	0.8%	1				1	0.7%	1				1	0.03%	1	9	0.1%	4
Chiroptera																									
Chiroptera indet.		1	1.5%																	1	0.03%	1	2	0.0%	1
Myotis sp.	Mouse-eared bats	1	1.5%	1																1	0.03%	1	2	0.0%	2
Insectivora																									
Talpa sp.	European moles				1	0.4%	1	1	0.1%	1	4	0.4%	1				1	0.2%	1				7	0.1%	4
Soricidae					1	0.4%		3	0.4%		8	0.7%		1	0.7%		9	2.0%		18	0.5%		40	0.6%	
Crocidura sp.											4	0.4%	1										4	0.1%	1
Crocidura leucodon/ russula	Bicolored/Greater white-toothed shrew				5	1.9%	1	6	0.8%	1	8	0.7%	2										19	0.3%	4
Crocidura leucodon	Bicolored shrew				3	1.1%	1																3	0.0%	1
Soricinae								1	0.1%		6	0.5%		6	4.4%		14	3.1%		41	1.2%		68	1.1%	
Sorex sp.								5	0.7%	2	1	0.1%	1										6	0.1%	3
Sorex cf. *araneus*	Common shrew							1	0.1%	1	4	0.4%	1				1	0.2%	1	48	1.4%	9	54	0.9%	12
Sorex araneus	Common shrew	13	19.4%	3	1	0.4%	1	18	2.3%	4	10	0.9%	2	1	0.7%	1	21	4.6%	5	9	0.3%	3	73	1.2%	19
Neomys cf. *anomalus*	Miller's water shrew										3	0.3%	1										3	0.0%	1
Neomys fodiens	Eurasian water shrew	2	3.0%	1							4	0.4%	2	2	1.5%	1	4	0.9%	1	10	0.3%	4	22	0.4%	9
Rodentia																									
Sciuridae																									
Spermophilus sp.																				2	0.1%	1	2	0.0%	1
Spermophilus superciliosus	Ground squirrel							1	0.1%	1										3	0.1%	1	4	0.1%	2
Murinae																				1	0.0%	1	1	0.0%	1
Gliridae		1	1.5%	1																			1	0.0%	1
Arvicolinae																									
Arvicola terrestris/ antiquus	Water vole				4	1.5%	1	7	0.9%	1	5	0.4%	2	1	0.7%	1	18	3.9%	4	17	0.5%	4	52	0.8%	13
Dicrostonyx gulielmi	Collared lemming	2	3.0%	1	10	3.7%	2	26	3.4%	3	14	1.2%	3	2	1.5%	1	5	1.1%	2	53	1.6%	11	112	1.8%	23
Lemmus lemmus	Norwegian lemming	4	6.0%	1	36	13.4%	9	76	9.9%	18	76	6.7%	14	6	4.4%	1	19	4.2%	4	307	9.2%	61	524	8.5%	108
Microtus sp.		30	44.8%	10	139	51.7%	19	438	57.1%	45	778	68.5%	76	95	69.3%	9	257	56.2%	35	2138	64.1%	301	3875	62.9%	495
Microtus gregalis	Narrow-headed vole				15	5.6%	9	45	5.9%	18	59	5.2%	26	3	2.2%	2	8	1.8%	3	133	4.0%	51	263	4.3%	109
Chionomys nivalis	Snow vole				5	1.9%	2	7	0.9%	2	5	0.4%	2				8	1.8%	4	9	0.3%	5	34	0.6%	15
Microtus oeconomus	Tundra vole	5	7.5%	3	9	3.3%	6	8	1.0%	6	17	1.5%	10	3	2.2%	2	11	2.4%	8	34	1.0%	17	87	1.4%	52
Microtus subterraneus	Common pine vole																			2	0.1%	2	2	0.0%	2
Microtus arvalis/agrestis	Common/Field vole	8	11.9%	5	39	14.5%	17	118	15.4%	47	129	11.4%	66	16	11.7%	10	81	17.7%	40	505	15.2%	204	896	14.5%	389
Grand Total		67	100%	26	269	100%	70	767	100%	151	1135	100%	144	137	100%	29	457	100%	108	3333	100%	678	6165	100%	1206
NTAXA (richness)				8			12			13			12			9			10			14			19
Reciprocal of Simpsons (1/D)				4.56			5.07			4.63			4.58			4.02			4.27			3.55			4.14

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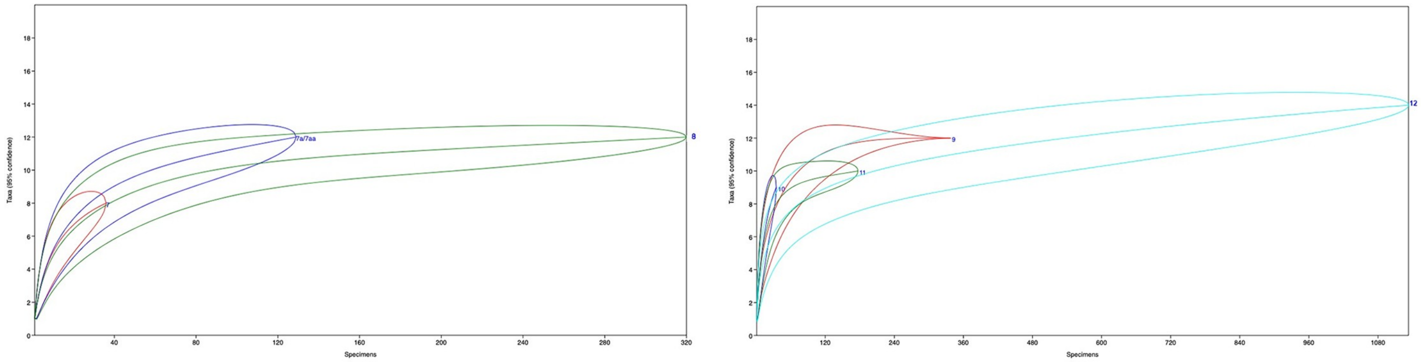

Fig 6. Rarefaction curves of species richness by geological horizon at Hohle Fels cave. Left) the Aurignacian geological horizons 7, 7a/7aa, and 8. Right) the Middle Paleolithic geological horizons 9, 10, 11 and 12.

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only in the latest MP and early Aurignacian deposits (GH 9 through 7a/7aa). To our knowledge, this is the only occurrence of white toothed shrews in the Ach Valley, and their preference for dry steppe and open humid woodland environments differs from other Soricinae species identified at the site. The 54 specimens designated *Sorex* cf. *araneus* exhibit a larger than expected size in the lower condylar facet and condylar height (following [43]) and/or molar length and breadth (following [44]). The morphology of these specimens is typical of Soricini, with the lower m1 and m2 exhibiting an entoconid crest and a broad interarticular area of the condyle without lingual emargination, yet their size falls within published measures of *Neomys* sp. from Sesselfelsgrotte [1], Geißenklösterle [18] and Pisede bei Malchin [81]. Storch [12] reported particularly large shrews from Brillenhöhle designated *Sorex* cf. *araneus* and this, combined with the fact that a small number of the Hohle Fels specimens fall within the range of *Sorex* sp. reported by Reumer [43] guided our classification. Although it has been suggested that the large size of the Brillenhöhle *S.* cf. *araneus* specimens was a climatically driven phenotypic response, Prost et al.'s [82] study of soricids from the Pleistocene-Holocene transition in Austria and Belgium found no clear correlation between climate and increased body size in *S. araneus* groups.

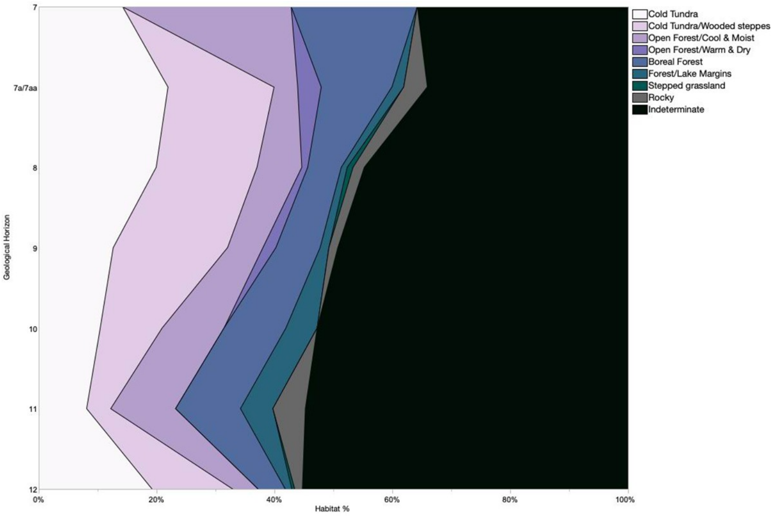

Fig 7. Relative proportion of individuals by habitat types at Hohle Fels Cave by geological horizon.

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In addition to voles and shrews we identified the mouse-eared bat (*Myotis* sp.), mole (*Talpa* sp.), and ground squirrel (*Spermophilus superciliosus*) at Hohle Fels. The same species have been identified at other Swabian sites including Geißenklösterle [18,79], Brillenhöhle [12], Hohlenstein [83] and Kogelstein [10]. The specimens attributed to Murinae and Gliridae are both incomplete maxilla fragments identified based on root pattern morphology, and therefore the determinations are considered provisional. However, *Apodemus* sp. was identified from geological horizon 17 at Geißenklösterle [79] and at the MP site of Kogelstein [10]. The single *Talpa* sp. humerus specimen from horizon 8 is missing the proximal portion and part of the diaphysis, restricting our comparison with *T. europaea* and *T. magna* material to the distal epiphyseal breadth. Based on reports from Villa Seckendorff [84], Hohlenstein [83], and Ochtendung [42] the Hohle Fels specimen falls at the lowest end of the *T. (europaea) magna* range and within the average size range of recent southern German populations [1], and so we restricted our identification of all mole material to *Talpa* sp. and placed it into a temperate open forest, cool & moist habitat category in the indicator species paleoenvironmental reconstruction. In the habitat weighting analysis, 10% of the specimen weighting was attributed to cold steppe environment in recognition of the possibility that some of the material may belong to *T. (e.) magna*.

Paleoenvironmental signal and its context within the Ach Valley

To assess the paleoenvironmental signal from the Hohle Fels small mammal record we applied both a modified indicator species method [18] and the habitat weighing method [27,28]. The benefit of the indicator species method is that it allows comparison with a number of past small mammal paleoenvironmental studies conducted in Germany and parts of Central Europe [10,12,36,42,83,85,86], including our recent study of the MP and UP small mammal assemblage from Geißenklösterle [18]. We present the results from this method for Hohle Fels in Fig 7. Although a number of similarities in the records from Hohle Fels and Geißenklösterle are immediately apparent, we must be cautious when suggesting one-to-one comparisons as differences in sedimentation rate and time averaging cannot be directly quantified [31]. As such, we discuss these two paleoenvironmental records separately here at the end of this section with the goal of identifying climatic shifts which affected the Ach Valley broadly.

The environmental signal of the earliest layers at Hohle Fels is driven by cold tundra adapted lemmings (35.0%) and various forest adapted species (14.5%), with a small yet important grassland component indicated by the presence of *S. superciliosus*. This fits well with the taphonomic data suggesting snowy owls, great grey owls, and European eagle owls accumulated the small mammal material in the early MP, as snowy owls are known to inhabit cold tundra environments and the great grey, European eagle, and snowy owl all hunt within open steppe and forest edge areas [48]. A warm period is indicated by the drop in cold tundra taxa from 33.0% in GH 12 to 12.3% in GH 11, and our results suggest that cold tundra landscapes gradually returned, reaching similar highs only by GH 9 where cold, wooded tundra species account for 32.1% of the assemblage. Our taphonomic analysis suggests that the GH 9 material was likely accumulated by the snowy owl, with inputs from a mammalian predator, likely the arctic fox. This picture of the MP fits well with the micromorphology-based environmental signal from the site, which suggests a warm and wet environment in the lowest most deposits and a decided lack of clearly defined cold stadial/warm interstadial oscillations at Hohle Fels [31]. The ratio of reindeer to other cervids is also at its lowest in the MP of Hohle Fels, suggesting that the environment was warmer and more temperate overall than in the later Aurignacian, with less coniferous forests or stepped environments [87].

At Geißenklösterle, Sirgenstein, and, to a lesser extent, Vogelherd, a hiatus in the occupation of the sites can be clearly seen both stratigraphically [31] and in terms of artifact density. This hiatus is also present at Hohle Fels but is not as clearly defined and constitutes the lower portion of the basal Aurignacian deposits of GH 8 [29,31]. A moderate increase in cold tundra and wooded steppe species can be seen in the Hohle Fels record between GH 9 and GH 8, however, there are no clear indications that a cold snap, a quick and intense cold period, occurred either before, during or directly after the hiatus deposits. Instead, tundra landscapes clearly increase gradually across what is likely a long temporal period. The micromorphological record also suggests that a markedly warm and moist climate defines the lowermost deposits of GH 8, especially when compared to later deposits [31], a signal which may have been obscured in the small mammal record by the occurrence of high proportions of cold adapted taxa in the upper half of GH 8. The presence of the great grey owl, as indicated in the taphonomic record of GH 8, further supports the micromorphological conclusions, as this predator mostly inhabits boreal forest environments and prefers to hunt in open, swampy landscapes [48,88]. The pattern of gradual cooling beginning in GH 9 is also seen in the increasing ratio of reindeer to other cervids in the Hohle Fels faunal record [87] and the increase of willow alongside pine, deciduous birch, and other tundra species in the sites macrobotanical record [89].

The earliest Aurignacian deposits at Hohle Fels includes GH 8 and GH 7, above which the upper Aurignacian (GH 7 – 6a) underlies a phase of mixed Aurignacian and Gravettian deposits [29]. Recently recalibrated ^{14}C dates by Bataille and Conard [29] places the earliest Aurignacian to between 41.7 and 39.0 ka calBP with a possible maximum age of 44.0 ka calBP for GH 8. This places the Hohle Fels Aurignacian prior to Heinrich event 4 and raises the possibility that the markedly cold period recognized in the sedimentary and small mammal material directly following the earliest Aurignacian in GH 7a/7aa reflects the onset of H4 in the region. The effect of this cold event extends through GH 7a/7aa and ends with the onset of a warm phase beginning in GH 7. This warming signal is slightly earlier in the stratigraphic chronology than expected, as sedimentary and C^{14} dating place interstadial 7 at GH 6a (directly overlying GH 7). The increasing warm, open forest component seen in the Hohle Fels record in GH 7a/7aa and extending into GH 7 may be indicative of an even earlier start to this pre-H3 warm phase, however this may also be due to time averaging of the deposits and the small sample size (n = 67) of GH 7. Neither the taphonomic signal of GH 7a/7aa, which suggests the presence of the boreal European eagle owl, nor that of GH 7, which best matches actualistic snowy owl assemblages, fits with the overall climatic signals of these horizons. This may be explained by some form of equifinality and/or multi-predator mixed accumulation, although this is not clear from our analysis.

We applied the habitat weighting method [27,53] to the small mammal record in an effort to derive a more nuanced picture of the climatic fluctuations throughout the MP to UP transition at Hohle Fels. Comparing the results seen in Fig 8 with those derived from the modified indicator species analysis (Fig 7) we can see the same broad trend of increased cooling throughout all deposits, with a sharp decrease in tundra environments at GH 11 and a subsequent increase in GH 7a/7aa, is present in both records. There is a greater indication of woodland environments during the basal MP deposits in the habitat weighting method results, which fits more closely with the sedimentary signal of a warm and temperate environment during this time [31]. The warm MP event in GH 11 appears to be the result of more lakes and rivers on the landscape as well as open and humid meadows and pastures and increased mature woodland elements. This mosaic landscape remains relatively stable throughout the MP, with only moderate decreases in the open meadow areas coinciding with the first presence of temperate grasslands and the gradually extension of cold, dry tundra landscapes, which increased by close to 20% by the end of the MP (GH 9). The aforementioned marked cold

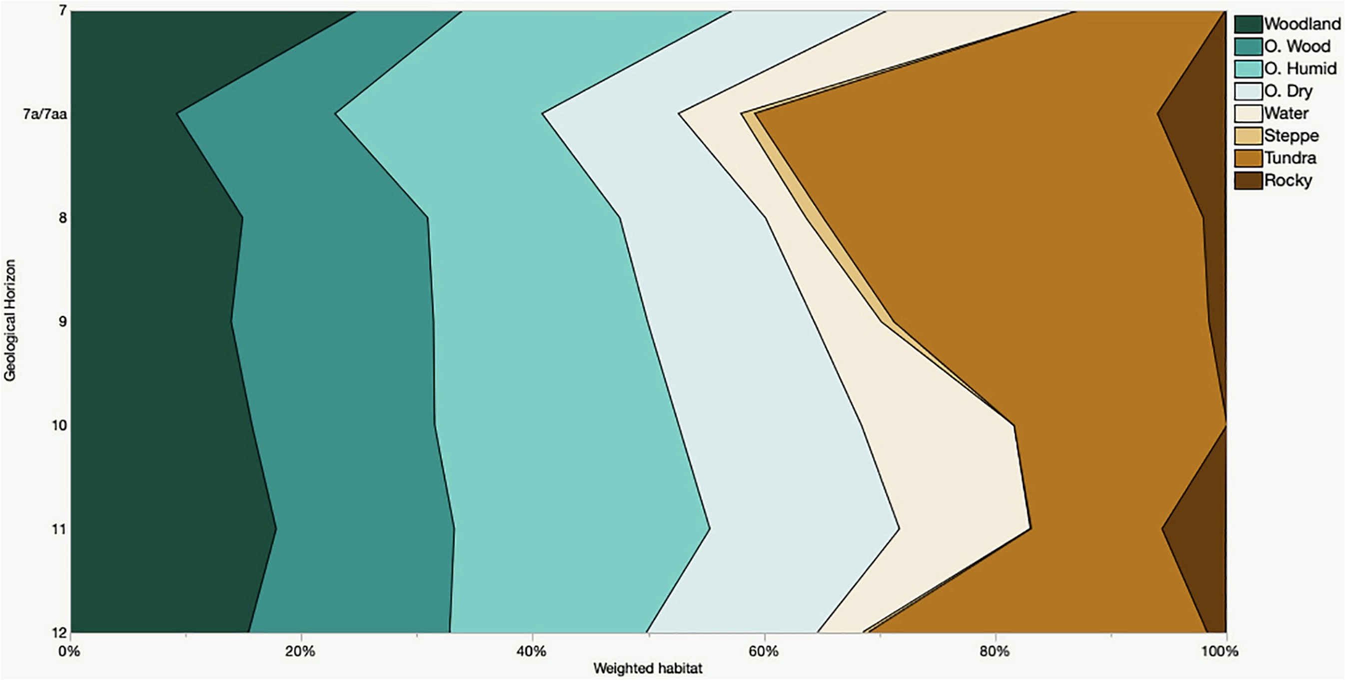

Fig 8. Relative proportion of weighted habitats by geological horizon at Hohle Fels Cave. O. Wood = open wood; O. Humid = open humid; O. Dry = open dry.

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phase of GH 7a/7aa is also clear in the habitat weighing results. That this horizon is defined by the presence of anthropogenic dumped ash features [31] may speak to the increased need for fire for warmth during an extended cold period. A shift back to more temperate conditions is visible in the weighted habitat results of GH 7, with the presence of streams and ponds, humid evergreen meadows, and mature woodlands returning to nearly MP proportions. Overall, the habitat weighting method presents a similar climatic signal to that derived from the modified indicator species analysis, indicating broad agreement between the two paleo-reconstructive methods. This supports our paleoenvironmental reconstruction and suggests that, in this case, the modified indicator species method is not significantly biased by the exclusion of rare and 'indeterminate' taxa.

Comparing the small mammal record from Geißenklösterle [18] with this new record from Hohle Fels we note a number of similarities and differences. In the MP rocky and river/lake-edge species are more prominent at Geißenklösterle, however this likely reflects the fact that this site is located high along a steep-sided wall of the Ach Valley, approximately 60 m above the modern valley floor which has likely risen upwards of 40 m since the Paleolithic [31]. At Geißenklösterle the MP is also marked by two warm/moist and cold/dry oscillations recognizable in the MP deposits (between GH 22 and 21, and GH 20 and 19) [18]; events that were also documented in the micromorphological record from this site, which otherwise suggested the Ach Valley was warm and wet at the beginning of the MP [31]. That these climatic oscillations are not seen in the Hohle Fels record may speak to the degree of time averaging inherent in the MP deposits.

At Geißenklösterle the small mammal signal clearly shows a moderate increase in cold tundra and wooded steppe species at the transition from the hiatus layer (GH 17) to the earliest Aurignacian deposits (GH 15/16) similar to the pattern seen at Hohle Fels between GH 9 and GH 8. Here one should note that in contrast to Hohle Fels, where the stratigraphic record over the shift from the late Middle Paleolithic to the Aurignacian is continuous, there is a stratigraphic unconformity in the Geißenklösterle record between the top of GH 17 and the base of the lower Aurignacian layer [31]. Although the stratigraphic observations tell us little about the duration reflected by the unconformity, radiometric dates from Geißenklösterle suggest a duration on the scale of several hundred to a couple thousand years. This being said, the micromorphological work at Geißenklösterle has ruled out the possibility of mixing between Aurignacian and MP deposits [31]. The micromorphological record also suggests that the occupational hiatuses at both sites had markedly warm and moist climates, especially when compared to later deposits [31].

Like the newly calibrated dates from Hohle Fels, ultra-filtration AMS dates from Geißenklösterle place the earliest Aurignacian before the global timing of the Heinrich 4 event [90], suggesting that a similarly markedly cold event seen in both the sedimentary and small mammal records of GH 13 may reflect the onset of this cold period. This cold event extends through GH 12 and, to a lesser extent, GH 11 however the sample sizes available for the small mammal analysis from these upper Aurignacian horizons were quite small and are likely skewing our picture of this period at Geißenklösterle [18]. Overall, these two sites present broadly similar environmental records for the time periods under examination, with differences possibly attributable to variation in sedimentation rate and the effect of time averaging on fine-scale taxonomic variation. As such, we are able to reconstruct a generalized picture of the environment during the MP and UP in the Ach Valley which can then be used to test hypotheses put forth to explain the cultural and biological turnover recognizable in the archaeological record of this region.

Discussion and conclusions

Based on this analysis of the small mammal material from Hohle Fels we can draw the following conclusions:

1. The small mammal material was most likely accumulated by the snowy owl, European eagle owl, and/or great grey owl, with a limited contribution by foxes. As these predators are mostly generalist hunters, the composition of the assemblages should reflect the diversity of the small mammal community on the landscape at the time.
2. The assemblages are taxonomically rich, comprising 12 genera and 14 distinct species including the first occurrence of the bicolored white-toothed shrew (*Crocidura*) from the Swabian Jura and possible large forms of *Arvicola* and *Talpa*. Rarefaction analysis suggests that only two or three rare species are missing from each GH examined.
3. There is a clear trend of increased cooling and the spread of tundra and steppe environments from the MP through the early Aurignacian, with a warm event in GH 11 and a cold event in GH 7a/7aa suggested by both the modified indicator species and habitat weighting methods.
4. The habitat weighting method indicates that mature woodlands, open meadows, and lakes and rivers were prominent components of the MP landscape.
5. There is no clear signal for drastic climatic change before or during the cultural hiatus. Therefore, climate should not be invoked as the driving force behind the depopulation of the region by Neanderthal groups.

These results echo other paleoenvironmental signals derived from the macrobotanical [89], micromorphological [31], and large fauna [87] records from Hohle Fels and the surrounding sites. By applying two paleoenvironmental-reconstructive methods to the Hohle Fels material, this study follows other recent multi-analytic small mammal studies [80,91] in attempting to minimize the influence of both rare and abundant taxa–each of which affect small mammal reconstructive methods to different degrees [91]. With the incorporation of a taphonomically rigorous small mammal climatic signal, we can confidently surmise that the MP of the Ach Valley was a mosaic of dry tundra and open coniferous and old-growth forests, with rivers and ponds close to the cave. A period of climatic amelioration occurred around the middle of the MP record, allowing the spread of forests, pastures, and grasslands, likely associated with an increase in precipitation and water sources in the valley. Overall, the environmental signal at Hohle Fels suggests a more homogenously temperate climate than that indicated from similar material records at other sites [18].

Importantly, this study further supports the conclusion that the MP to UP transition, including the nearly-culturally sterile 'hiatus' found at Geißenklösterle and Hohle Fels caves, saw a gradual increase in cold and dry arctic environments [18]. This likely correlates with the cooling trend spanning D-O cycles 12–9 seen elsewhere in Western Europe [25]. That the reaction of the Swabian small mammal community to the D-O cycles and related Heinrich events is less pronounced than we would expect suggests that the Ach Valley may have experienced a regionally bound ecological response to these climatic episodes, similar to what has been suggested for the Lower Danube region [92]. As none of the environmental proxies studied in detail (which include the small mammal, botanical, and sedimentary records) have revealed indications of a 'cold snap' or increased climatic instability around the MP to UP transition, the hypothesis that climatic variability lead to the abandonment of the region by Neanderthal groups as put forth in variants of the *Kulturpumpe* and *Population Vacuum* models cannot be substantiated. While the *Kulturpumpe* model also posits that inter-taxa competition and/or internal socio-economic dynamics may have triggered the cultural innovations of the Swabian Aurignacian [93], the presence of 'hiatus' deposits between the two cultural periods in the stratigraphy of many sites in the region, as well as the lack of transitional lithic industries, suggests that inter-taxa competition and/or acculturation were not active factors within the Swabian Jura.

However, the current study does suggest that the earliest Swabian UP groups arrived in the region during a particularly cold and dry period, when the landscape was dominated by cold tundra and wooded steppe landscapes. That these groups remained and flourished in such a challenging environment suggests that UP cultural and symbolic innovations may have arisen in part as a response to the gradual climatic cooling during the early Aurignacian [93,31]. In this context, one should recall that figurative art, musical instruments and personal ornaments are well documented from the basal Aurignacian horizons [6, 14], which suggests that they were part of the behavioral repertoire of the Aurignacian inhabitants of Swabia when they arrived in the region, or that they developed nearly immediately after they entered this region that appears to have been largely void of indigenous Neanderthal populations. One argument for the local evolution of these cultural features is the complete absence of mammoth ivory figurines, bone flutes, three dimensionally formed ivory ornaments and other specific elements of the Swabian Aurignacian lithic and organic technologies in other European regions at this early date.

Concerning the late Middle Paleolithic of the Swabian Jura, a wide range of observations indicate that population densities were typically much lower than during the Aurignacian and that small highly mobile and perhaps demographically isolated groups of Neanderthals occupied the region [74]. In Central Europe as a whole, Neanderthal groups appear to have lived in small and genetically isolated yet self-sufficient and highly mobile populations [94]. Within this framework, Neanderthals may have adapted to climatic shifts by retreating out of and later recolonizing areas affected by stadial and interstadial oscillations [25,95]. Furthermore, it is highly likely that some groups experienced local extinction events in the face of climatic pressures or inter-species competition [3]. Comparison of the density of anthropogenically derived materials, including lithic artifacts, burnt bone, charcoal and modified fauna, through time does suggest that Neanderthals occupied the Swabian sites with lower intensity or for shorter durations than later Aurignacian groups [18,31,74]. The more ephemeral nature of Neanderthal site use in this region may reflect real differences in population size as well as mobility and subsistence strategies, which may have proven detrimental both genetically [95] and in terms of innovative potential [96] in the face of the climatic instability of OIS 3 and the arrival of larger and more socially connected modern human groups. Interbreeding and niche competition with modern humans was clearly a factor in the extinction of Neanderthals across Europe [21], however these inter-species interactions did not contribute to the loss of Neanderthal populations within the Swabian Jura. Furthermore, as this study has shown, dramatic climatic instability did not drive Neanderthal groups from the Ach Valley [18,31]. The gradual decline in the environmental hospitality of the region may help to explain why Neanderthal groups left, as one of possibly many retreats [25] within a cycle of repeated abandonment and recolonization of Northern latitude regions. Isotopic studies have shown that individual Neanderthals travelled upwards of 20 km during their lifetime [97], and evidence for long distance movement of raw materials within the Swabian Jura suggest greater ranges of resource exploitation [98,99]. The stadial periods recognizable in the marine isotopic records would have evolved on a decadal scale [4], allowing for generational recognition of the changing landscapes and resources due to increased aridity and lowering temperatures across southern Germany. Recognition of the gradually declining climatic conditions may have prompted the late MP Swabian Neanderthal groups to abandon the region before facing local extinction. While speculative in nature, new and ongoing studies from within the Ach Valley and nearby areas will hopefully allow for further testing of this hypothesis explaining the decline of Neanderthal populations and the dramatic appearance of modern humans during the early Aurignacian of the Upper Danube region.

Supporting information

S1 Appendix. Table 1 Inferior m1 length of Arvicola from Hohle Fels cave and other key sites; Table 2: Cranial elements by geological horizon and bucket ID number; Table 3: Post-cranial elements and incisors by geological horizon and bucket ID number.
(XLSX)

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Visualization: Sara E. Rhodes.

Writing – original draft: Sara E. Rhodes.

Writing – review & editing: Sara E. Rhodes, Britt M. Starkovich, Nicholas J. Conard.

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