

A Synthesis of the Paleocology of the Ach Valley during the Middle to Upper Paleolithic Transition

With an expanded discussion of the small mammal record from Hohle Fels and Geißenklösterle Caves

Eine Synthese der Paläoökologie des Achtals am Übergang vom Mittel- zum Jungpaläolithikum

Mit einer ausführlichen Diskussion des Befundes der Kleinsäuger aus dem Hohle Fels und dem Geißenklösterle

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Abstract: *The Swabian Jura is one of the most important regions documenting the Middle to Upper Paleolithic transition in Central Europe. The early arrival of anatomically modern humans, coupled with the enigmatic and ephemeral occupation of many cave sites in the region by Neanderthal populations has inspired over 100 years of archaeological investigation. Understanding the climatic context of the final Neanderthal occupation of the Swabian river valleys, which include the Ach, Lone, and Lauchert Valleys, is important to furthering our knowledge of Neanderthal lifeways and adaptations to the changing OIS 3 landscape. This paper summarizes the most recent paleoecological research undertaken in the Ach Valley, with particular emphasis on the small mammal (rodent, insectivore, and bat) record of Hohle Fels and Geißenklösterle caves. A broad picture of the shifts in the landscape composition and climate during the final Middle Paleolithic and earliest Aurignacian periods is presented and contextualized within other terrestrial paleoenvironmental archives of Central and Southern Europe. The applicability of climatically driven hypotheses for the loss of Neanderthal groups in the Ach Valley are tested in light of this new paleoecological record and climatic change is shown to have played a minimal role in this regional extinction event. Instead, a multi-faceted explanatory model is presented taking into account documented low genetic diversity within Neanderthal groups, evidence for increasing niche fragmentation, and the low group sizes and high mobility suggested by the Swabian Middle Paleolithic record.*

Keywords: *Paleoecology, Neanderthal, Hohle Fels, Geißenklösterle, microfauna, rodents, human evolution*

Zusammenfassung: Die Schwäbische Alb ist eine der wichtigsten Regionen Mitteleuropas, die den Übergang vom Mittel- zum Jungpaläolithikum dokumentieren. Die frühe Ankunft anatomisch moderner Menschen in Verbindung mit der meist nur sporadischen und kurzzeitigen Besiedlung vieler Höhlen in der Region durch die Neandertaler hat die Forschung über mehr als hundert Jahre beschäftigt. Das Verständnis des klimatischen Kontextes der Besiedlung der schwäbischen Flusstäler, einschließlich der Täler von Ach, Lone und Lauchert, durch die letzten Neandertaler ist wichtig, um unser Wissen über die Lebensweisen und Anpassungen der Neandertaler an die sich wandelnde Landschaft im Sauerstoffisotopen-Stadium 3 (OIS 3) zu vertiefen. Der vorliegende Beitrag fasst die jüngsten paläoökologischen Untersuchungen im Achtal zusammen, wobei der Schwerpunkt auf den Befunden von Kleinsäufern (Nagetiere, Insektenfresser und Fledermäuse) in den Höhlenfundstellen Hohle Fels und Geißenklösterle liegt. Es wird ein umfassendes Bild der Veränderungen der Landschaftszusammensetzung und des Klimas während des spätesten Mittelpaläolithikums und der frühesten Phasen des Aurignacien präsentiert und in einen Zusammenhang mit anderen terrestrischen Paläoumweltarchiven Mittel- und Südeuropas gestellt. Die Anwendbarkeit von Hypothesen für ein klimatisch bedingtes Verschwinden von Neandertalern im Achtal wird vor dem Hintergrund dieses neuen paläoökologischen Befundes geprüft, und es hat sich gezeigt, dass der Klimawandel bei diesem regionalen Aussterben eine minimale Rolle gespielt hat. Statt-

dessen wird ein facettenreiches Erklärungsmodell vorgestellt, das die nachgewiesene geringe genetische Vielfalt innerhalb der Neandertalergruppen und Hinweise auf eine zunehmende Nischenfragmentierung ebenso berücksichtigt wie die geringen Gruppengrößen und die hohe Mobilität, die sich für das schwäbische Mittelpaläolithikum erschließen lassen.

Schlagwörter: Paläoökologie, Neandertaler, Hohle Fels, Geißenklösterle, Mikrofauna, Nagetiere, menschliche Evolution

Introduction

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 played by interspecies competition, genetic interbreeding, and the climatic instability of Oxygen Isotope Stage 3 (OIS 3) 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 (Schmidt 1912; Conard and Bolus 2003; Conard et al. 2009, 2013; Bolus 2015a, b; Miller 2015). In particular, chronological and stratigraphic records indicating that Neanderthals and anatomically modern humans occupied the valley with little to no overlap or interaction (Schmidt 1912; Hahn 1988; Conard and Bolus 2003; Higham et al. 2010; Conard 2011), as well as the exceptional record of early Aurignacian technological innovation and complex symbolic expression (Conard 2009; Conard et al. 2009; Wolf 2015; Dutkiewicz et al. 2018; Velliky et al. 2018), make this an important region for our understanding of human cultural and biological evolution during this time.

This paper compares the high-resolution and taphonomically robust terrestrial paleoenvironmental record derived from small mammal material recovered from Hohle Fels (Rhodes et al. 2019) and Geißenklösterle caves (Rhodes et al. 2018), located in the Ach Valley, to the long history of archaeological research in the Swabian Jura. The effect of the high amplitude stadial-interstadial oscillations recognizable in the Greenland ice core records (Rasmussen et al. 2014) on local vegetation patterns is also 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 (Chaline 1972; Avery 2007). 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 (López-García et al. 2015, 2017a, b, c). 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 behavior and post-depositional destruction (Andrews 1990; Fernandez-Jalvo and Andrews 1992).

The small mammal record suggests 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 (Rhodes et al. 2018, 2019). Overall, this 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 Greenland stadials 12–9 recognized elsewhere in Western and Central Europe (López-García et al. 2015; Staubwasser et al. 2018). Furthermore, 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 specific stadial-interstadial cycles. Lastly, concurrent vegetative signals from high resolution loess and botanical records from Central and Southwestern Europe are compared with the paleoecological record of the Ach Valley and the validity of ice core and marine proxy records to predict past terrestrial ecological variability is explored.

The lack of a clear signal for dramatic climatic change around the time of Neanderthal abandonment of the valley (Miller 2015; Rhodes et al. 2018, 2019) suggests that deteriorating environmental conditions, and the resultant decrease in resource availability, was not the decisive factor in the loss of Neanderthal groups in the Swabian Jura (Rhodes 2019; Rhodes et al. 2019). 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 (Rhodes 2019).

Background

Climate as a factor in Neanderthal extinction scenarios

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. 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 references therein). This leads to increased focus on cultural adaptation and the role of human agency in navigating external (particularly environmental) forces, beginning with the work of Boas (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). This suggested 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 recognized 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; Dalén 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; Stewart et al. 2003a, b; 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 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.

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 naïve to expect temporally disparate groups, even of the same species, to have similar responses to similar climatic events outside of the laboratory setting. In an effort to explain this anomalous response to previously encountered climatic variability, 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. That AMH groups would have needed different adaptive strategies (potentially including cultural buffering of resource depletion) may explain their success while subjected to the same degree of 'climatic stress' (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. 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, these studies suggest 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. (2003a, 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. Taken to its most extreme, Stewart (2005) suggests that the non-analogue nature of the European landscape during this time, characterized as a mosaic of temperate, boreal, and steppic regions, indicates that any recreation of the Neanderthal ecological niche based on the principle of uniformitarianism would be inherently flawed.

However, the growing consensus that Neanderthal extinction was a *process* which took place over multiple millennia across a vast geographic area, coupled with the stochastic nature of the evidence for the role and influence that various factors (such as inter-species competition, genetic diversity, climate, etc.) had in different regions, suggests that accepting any singular cause for the extinction of Neanderthal groups 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 Middle and Upper Paleolithic archaeology of the Swabian Jura

The Swabian Jura (German: *Schwäbische Alb*) is located in the modern state of Baden-Württemberg in southwestern Germany, and is roughly 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 Valleys. 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. 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 2015b; Conard 2015; Bolus and Conard 2019). As the focus of this paper is on Hohle Fels and Geißenklösterle caves, a short review of the history of work at these sites follows.

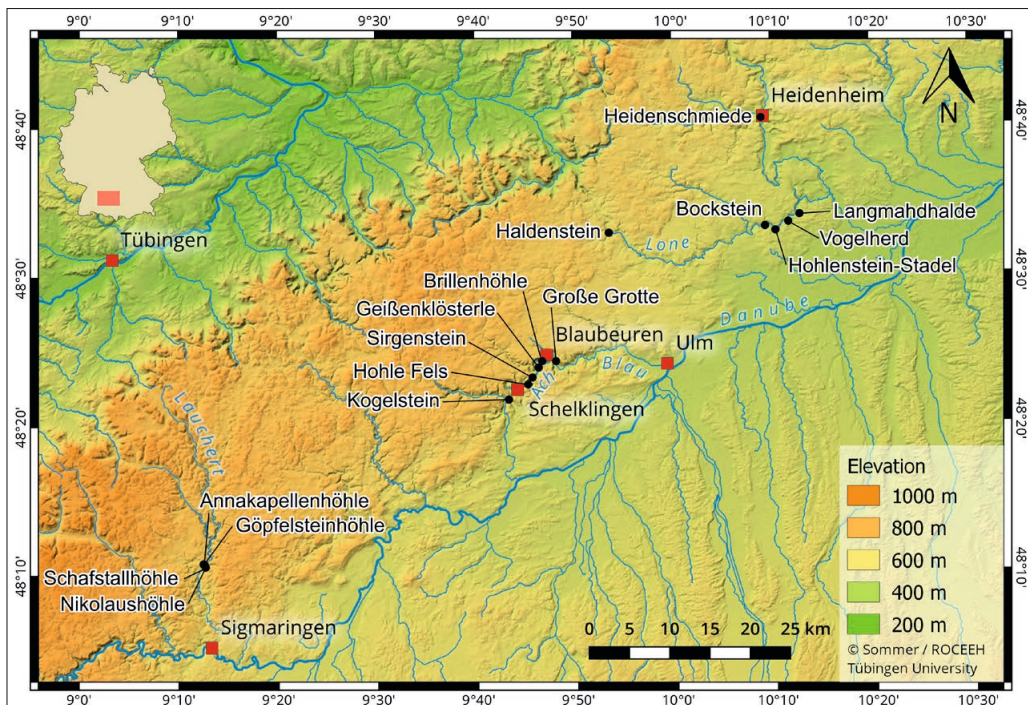


Fig. 1: Map of the Swabian Jura with all important Paleolithic cave sites from the Ach, Lone, and Lauchert Valleys indicated. Map provided by Christian Sommer / ROCEEH (2019): A map collection of the Paleolithic of the Swabian Jura (Version 1.0.0) [Data set]. <http://doi.org/10.5281/zenodo.3460301>.

Abb. 1: Karte der Schwäbischen Alb mit allen wichtigen paläolithischen Höhlenfundstellen aus dem Achtal, dem Lonetal und dem Laucherttal. Karte zur Verfügung gestellt von Christian Sommer / ROCEEH (2019): A map collection of the Paleolithic of the Swabian Jura (Version 1.0.0) [Datensatz]. <http://doi.org/10.5281/zenodo.3460301>.

Hohle Fels Cave

The Ach Valley likely formed during the early Pleistocene along the path of the Paleodanube, 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 2015b; 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 m³ 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 m² 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. J. 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). Horizons 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 three Gravettian horizons, one Magdalenian horizon, a period of mixed Magdalenian and Holocene materials, and finally purely Holocene deposits (Fig. 2).

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).

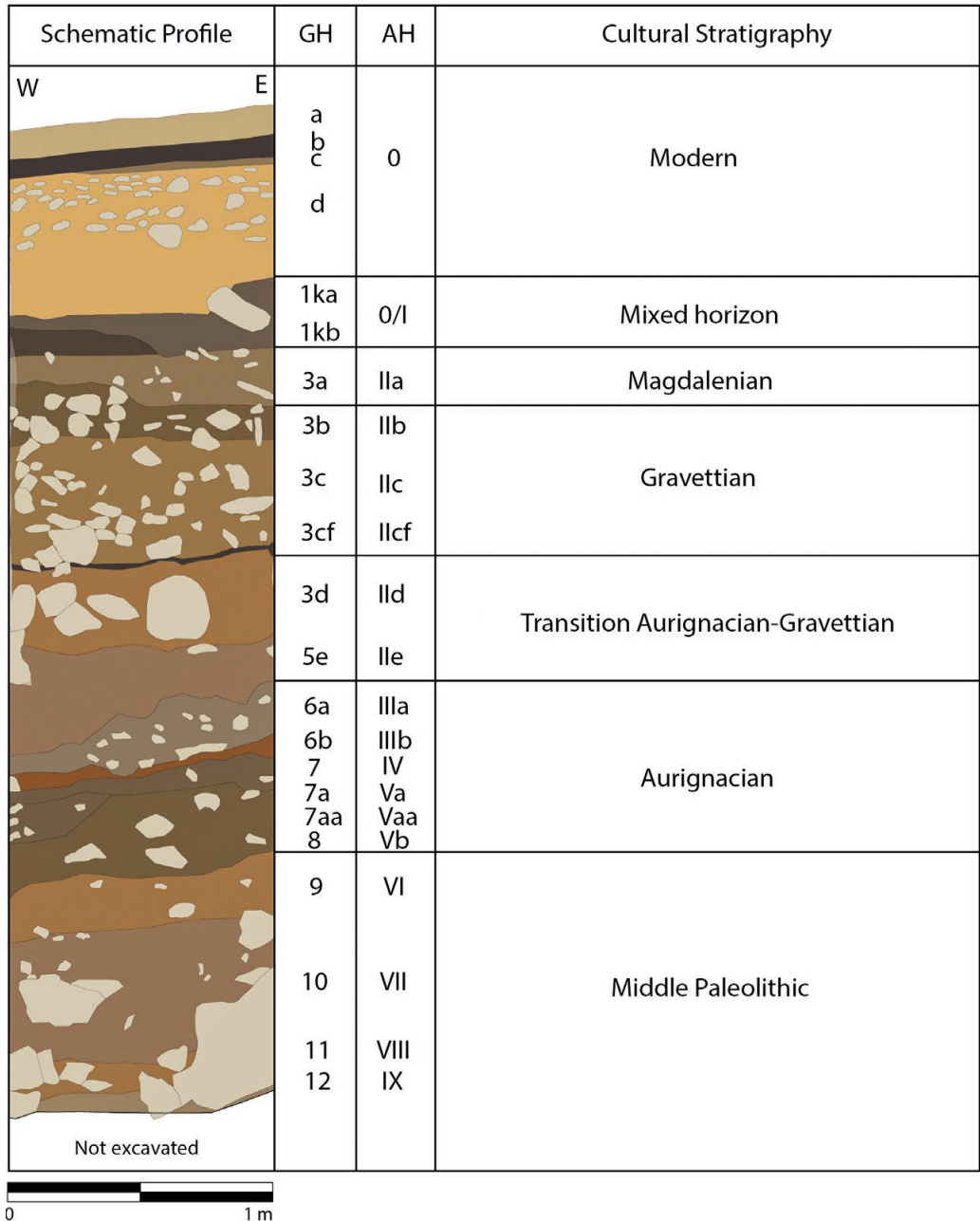


Fig. 2: Schematic profile of the stratigraphy at Hohle Fels and cultural associations. (modified after Rhodes et al. 2019, illustration produced by Maria Malina).

Abb. 2: Schematische Schichtenfolge am Hohle Fels mit Angabe der kulturellen Einheiten (verändert nach Rhodes et al. 2019, Abbildung erstellt von Maria Malina).

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) and another edited collection focused on the faunal and floral records from the site was recently published (Conard et al. 2019). The results of the research included in this new edited volume, as well as that from recent small mammal studies (Rhodes et al. 2018), is discussed in more detail below.

Geißenklösterle contains deposits attributed to the Middle Paleolithic, Aurignacian, Magdalenian, and Mesolithic as well as younger Holocene periods (Fig. 3). 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, IIc, 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 IIc, III, IIIa, and IIIb (Hahn 1988; Teyssandier et al. 2006) which Hahn (1993) later 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). Using the ultrafiltration pre-treatment method which may 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 ¹⁴C dates and fit well with the stratigraphic sequence of the site (Higham et al. 2012). These results suggest that the early Aurignacian (Level III) dates to ~43,000–41,000 cal BP, overlapping slightly with the Aurignacian of 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 ¹⁴C date of 48,600 ± 3200 BP (OxA-21741) for the Middle Paleolithic at Geißenklösterle. Recent ESR dating done by Richard (2019) has suggested that the mid-Middle Paleolithic may date to as early as OIS 5.

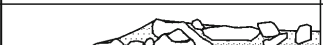


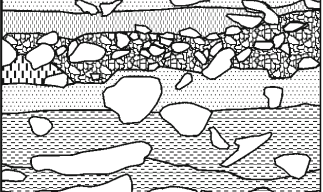













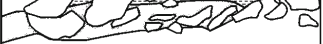

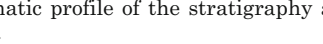
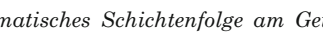

GH	Profilausschnitt	AH	Technokomplex
		In	Mesolithikum
2		Io	Magdalénien
4		Ip	
5		Ir	
6		Is	
7		It	
8		Ia	
9		Ib	Gravettien
10		Ic	
11		IIIn	
12		IIa	
13		IIb	
14		IIId	Aurignacien
15/16		III	
		IIIa	
17		IIIb	
18		IV	
19		V	
20		VI	
21		VII	Mittelpaläolithikum
22		VIII	
23			

Fig. 3: Schematic profile of the stratigraphy at Geißenklösterle and cultural associations (taken from Conard 2019).

Abb. 3: Schematisches Schichtenfolge am Geißenklösterle mit Angabe der kulturellen Einheiten (aus Conard 2019).

The Upper Paleolithic Cultural Fluorescence

The early Aurignacian dates from Geißenklösterle 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 technocomplex is the fact that it appears with what has been termed the ‘full package of early Upper Paleolithic innovations’. 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 2003).

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 2015), with double perforated beads, a characteristically Swabian form, being found throughout the entire sequence of Aurignacian deposits at Hohle Fels and within the earliest Upper Paleolithic deposits at Geißenklösterle (Wolf et al. 2013; Bolus 2015b; Wolf 2015). The presence of bone and ivory flutes at Geißenklösterle, Hohle Fels, and Vogelherd, the earliest dated to ca. 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 Swabia 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, 2008). 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). 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 Keilberg-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 2003, 2008; 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' developed within Swabia (Hussain and Floss, 2016, 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 florescence leading to the dramatic increase in symbolic expression and technological advancement is the direct result of the competition between archaic (Neanderthals) and modern humans following the initial colonization 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 Middle Paleolithic and Upper Paleolithic 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 Vacuum 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 Heinrich 4 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.

The Ach Valley paleoecological record

The Middle Paleolithic

Miller's (2015) micromorphological work at Geißenklösterle and Hohle Fels documents a number of cold/warm oscillations 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, 155). Furthermore, excavation at Hohle Fels has yet to reach bedrock. Campen's (1990) sedimentary analysis suggests a moderately cool event beginning during the deposition 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 solifluction (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, 140). Campen (1990) characterizes the hiatus period at Geißenklösterle (GH 17) as colder and damper than preceding 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, 157). An erosional event is documented at the very top of GH 17 at Geißenklösterle (Conard et al. 2003; Dippon 2003; Miller 2015; Goldberg 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 prevailed 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.), woolly 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 isotope analysis of horse tooth carbonates from Sirgenstein suggests 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*,

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.).

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 accumulation and a more detailed picture of the landscape cannot be derived from the faunal record. The small mammal material from Kogelstein (Ziegler 2000a), 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 terrestis*. However, the lack of taphonomic consideration in this study leaves open the possibility that the small mammal material was accumulated by a selective predator, such as the European eagle owl which is known to have a preference for the large-bodied water vole (Andrews 1990). As such, the signal for open forests and waterways from Kogelstein should be considered cautiously until substantiating evidence is found. Ziegler (2000a) attributes this material to an interstadial period between Greenland Interstadial (GIS) 13 and 16 based on the biostratigraphic small mammal record.

The Aurignacian

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, 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 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, 20). These include a warm and dry period in GH 14 and 13 followed by lowering temperatures in GH 12, then evidence of increased moisture during a warm period in GH 11 and 10, and finally an oscillation between cool and warmer temperatures in a broadly humid context between GH 9/8 and GH 7 (summarized by Miller 2015, 20). Campen's (1990) and Miller's (2015, 155) climatic records for this period at Geißenklösterle are broadly similar.

The stratigraphic sequence of the 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, 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, 108). The overlying laterally discontinuous 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, 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, 108-109). High proportions of *éboulis* within GH 5 have been interpreted as indicative of a colder climate (Campen 1990; Laville et al. 1980 cited in Miller 2015), however Miller points out that a lack of fine sediment (e.g., loess) deposition during this time would give the same indication, while actually resulting from warmer and wetter conditions (Miller 2015, 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, 26).

Botanical remains, including pollen and wood charcoal, 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 Aurignacian 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 behaviors 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 records from Geißenklösterle (Böhme 2019) 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).

A new small mammal record of the Ach Valley

A new high-resolution small mammal-based paleoenvironmental record spanning the Middle Paleolithic and earliest Upper Paleolithic can now be added to this robust paleoecological picture of the Ach Valley (Rhodes et al. 2018, 2019; Rhodes 2019). Derived from material collected by the Hahn and Conard excavations at Hohle Fels and Geißenklösterle Caves, the results of this research project are designed to be integrated with other existing and future paleoecological data to explore the context of the Neanderthal depopulation of the Swabian Jura. Importantly, this project includes a detailed taphonomic analysis of the small mammal material to ensure the quality of the paleoenvironmental record in representing past climate and landscape patterns. Despite a long history of small mammal research throughout Germany (Schmidt 1912; Storch 1973, 1974; Storch et al. 1973; von Koenigswald 1974; Hahn and von Koenigswald 1977; van Kolfschoten 1990, 1994, 2014; Ziegler 2000a, 2019; Maul 2002; Maul et al. 2013; von Koenigswald and Heinrich 2007), the study of the accumulation of microvertebrate remains within German Paleolithic contexts and the inherent biases introduced by such processes has been absent prior to this study. The overarching goal of the study also involves reassessing the applicability of the environmentally driven explanations for the depopulation of the Ach Valley by Neanderthal groups in the *Kulturpumpe* and *Population Vacuum* hypotheses, allowing the newly produced paleoecological data to be assessed within our current understanding of Neanderthal behavior, population dynamics, and mobility at the end of OIS 3 (~60,000–35,000 cal BP). 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 cave 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)?

Additionally, a number of metric analyses were applied to the small mammal dental specimens to illicit new information on population structure and provide comparative datasets for future small mammal research on Central European Paleolithic contexts. The methods employed to address these questions briefly covered in Rhodes et al. (2018, 2019) are described in more detail below.

Methods

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 *Institut für Naturwissenschaftliche Archäologie* at the University of 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) 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 (Fig. 4). 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).

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.

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 and von Koenigswald 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 the chapter '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 (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 1973), Kogelstein (Ziegler 2000a), and Weinberghöhlen (von Koenigswald 1974; Rhodes et al. 2019).

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 1973) and the more recent *M. rufocanus* and *M. rutilus* (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; Rhodes et al. 2018).

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 1973], 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 Kolf-schoten (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 Jura 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 nivalis 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.

Metric identification

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 von Koenigswald (1973). SDQ is calculated using the following formula:

$$SDQ = TE \times \frac{100}{LE}$$

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 (von Koenigswald and van Kolfschoten 1996). Chaline and Sevilla (1990) have shown that the reduction of root development in arvicolidids, which likely developed independently among a number of lineages, is due to ‘a heterochronic shift of different phases in ontogeny’ (Chaline and Sevilla 1990; von Koenigswald and van 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 (von Koenigswald and van 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 1 (see Supplementary Online Material); the material from Geißenklösterle proved too fragmented to produce comparable SDQ measures.

Additional measurements were taken on all *Lemmus*, *Dicrostonyx*, *Arvicola*, *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. 5). 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 triangles 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 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

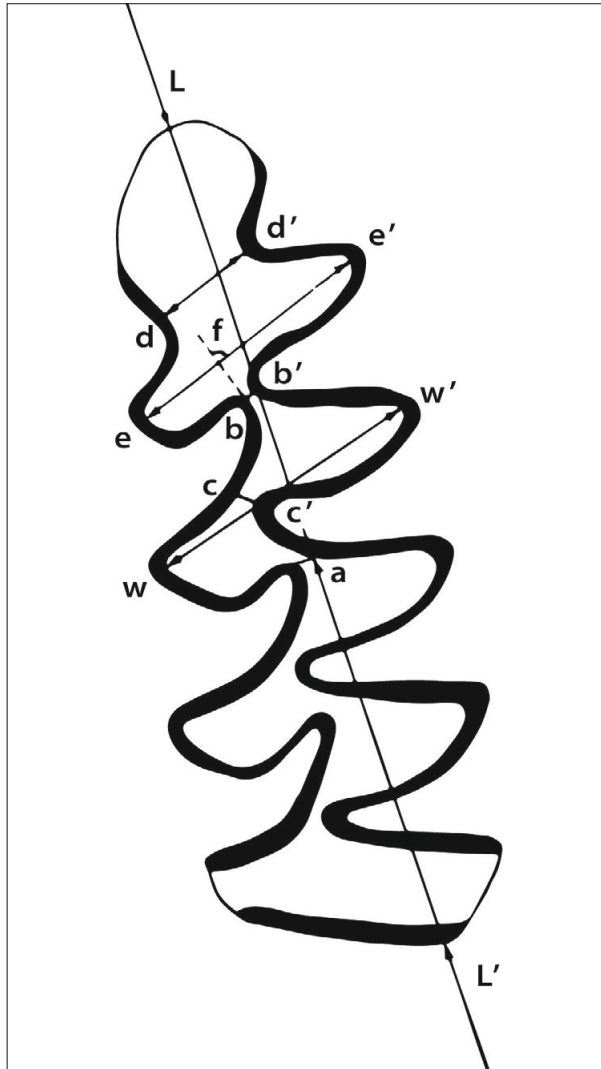


Fig. 5: Occlusal surface of the left m1 of *Microtus* illustrating the parameters measured (adapted from van Kolfschoten 2014). See text for description.

Abb. 5: Okklusale Oberfläche des linken m1 von *Microtus*, an dem die gemessenen Parameter veranschaulicht werden (basierend auf van Kolfschoten 2014). Für die Beschreibung siehe Text.

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. 6 and Fig. 7 and the raw data is included in Tables 2-14 (Supplementary Online Material).

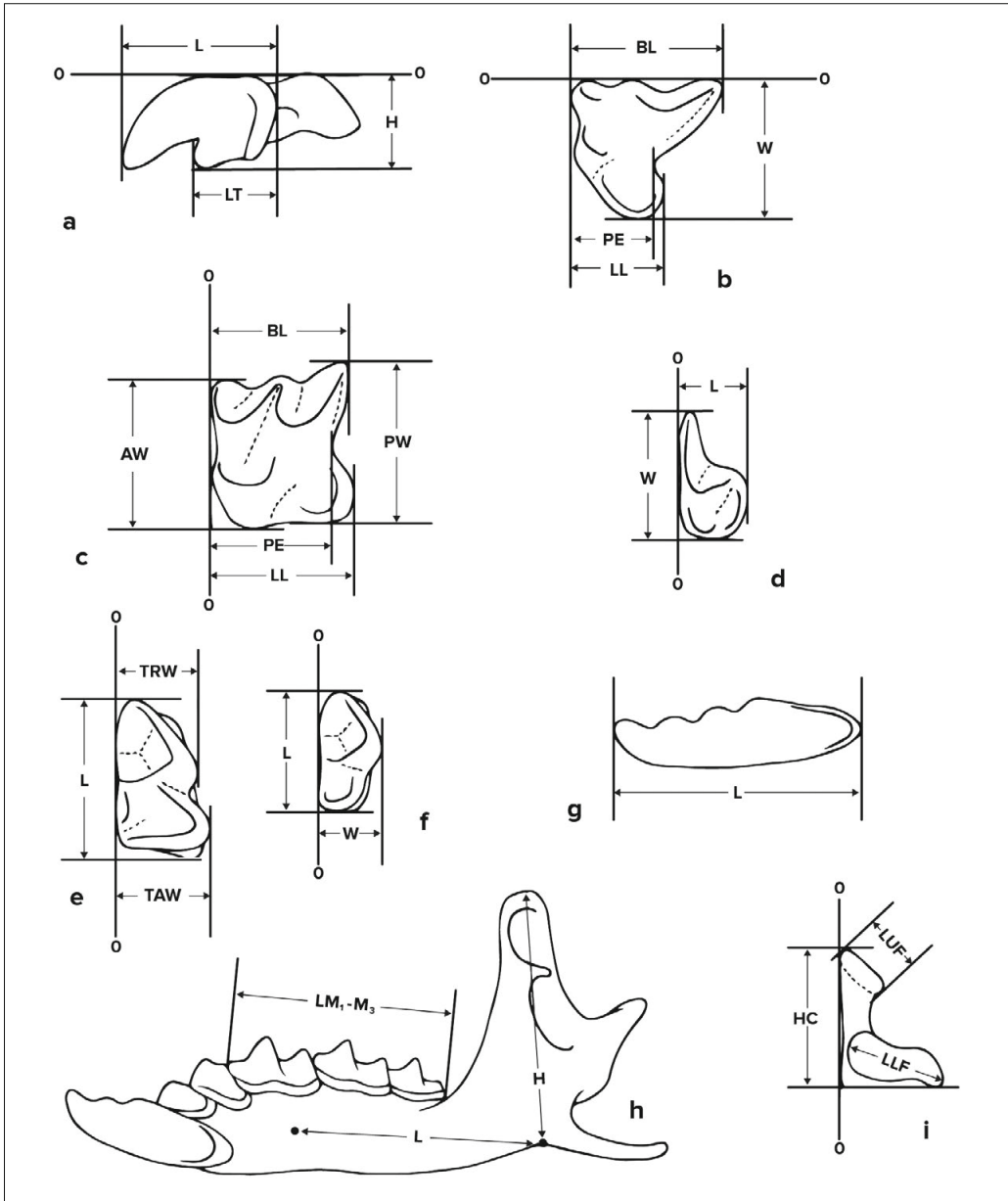


Fig. 6: Measurements taken on Soricidae dentition and mandibles. a) upper incisor, b) P4, c) M1 and M2, d) M3, e) m1 and m2, f) m3, g) lower incisor, h) left mandible, i) mandibular condyle (posterior view). See text for abbreviations (adapted from Reumer 1984).

Abb. 6: Maße, die an der Bezahnung und den Unterkiefern der Soricidae genommen wurden. a) oberer Schneidezahn, b) P4, c) M1 und M2, d) M3, e) m1 und m2, f) m3, g) unterer Schneidezahn, h) linker Unterkiefer, i) mandibularer Condylus (Rückansicht). Für die Abkürzungen siehe Text (basierend auf Reumer 1984).

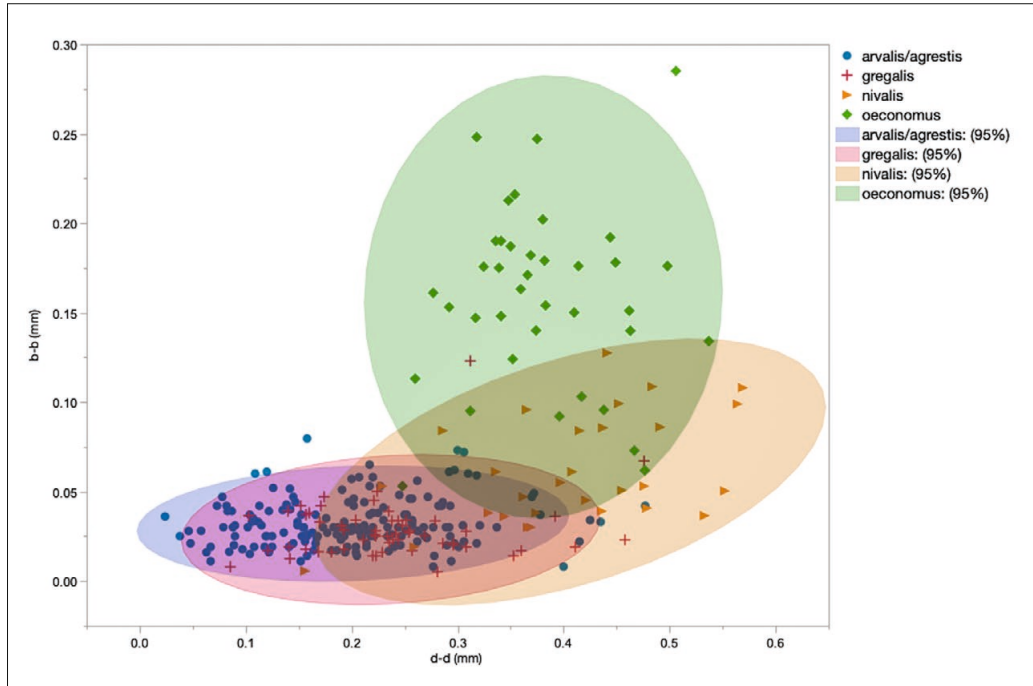


Fig. 7: Scatterplot of the d-value and b-value (in mm) of the m1 of *Microtus arvalis/agrestis*, *Microtus gregalis*, *Microtus nivalis*, and *Microtus oeconomus* from all horizons at Geißenklösterle. Ellipses indicate 95% density.

Abb. 7: Streudiagramm für den d-Wert und den b-Wert (in mm) des m1 von *Microtus arvalis/agrestis*, *Microtus gregalis*, *Microtus nivalis* und *Microtus oeconomus* aus allen Schichten des Geißenklösterle. Die Ellipsen kennzeichnen eine Dichte von 95%.

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 (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 lophys 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 (Heinrich 1983; Reumer 1984; van Kolfschoten 1985, 1994, 2014; Ziegler 2019). These measurements are illustrated in Fig. 8 and the raw data is included in Table 15 (Supplementary Online Material).

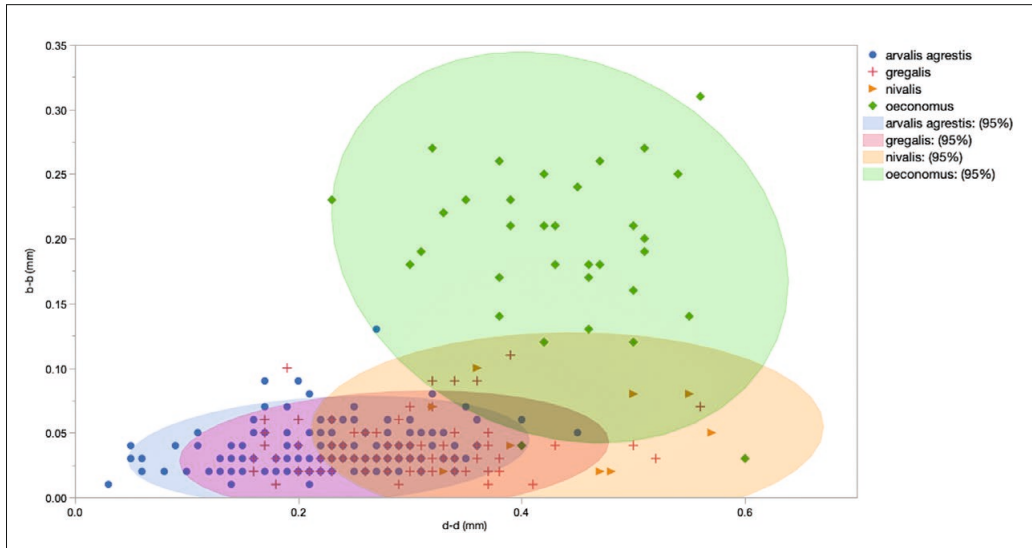


Fig. 8: Scatterplot of the d-value and b-value (in mm) of the m1 of *Microtus arvalis/agrestis*, *Microtus gregalis*, *Microtus nivalis*, and *Microtus oeconomus* from all horizons at Hohle Fels. Ellipses indicate 95% density.

Abb. 8: Streudiagramm für den d-Wert und den b-Wert (in mm) des m1 von *Microtus arvalis/agrestis*, *Microtus gregalis*, *Microtus nivalis* und *Microtus oeconomus* aus allen Schichten des Hohle Fels. Die Ellipsen kennzeichnen eine Dichte von 95%.

The HC and LLF measurements from Geißenklösterle are compared with those reported from Sesselfelsgrötte (van Kolfschoten 2014, 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 exceeded 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 tooth row with *in situ* m2 and m3 was identified as *Neomys* cf. *anomalous* 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 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 1973) is discussed in further detail in Rhodes et al. (2019).

The specimens attributed to *Crociodura 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 *Spermophilus* (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 *Spermophilus* 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. 1980; 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. 1980), 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 five 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 2000b), 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 Kolfshoten 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.

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 discoloration, oxide staining, and digestive corrosion following Andrews (1990), Fernandez-Jalvo and Andrews (1992), Stiner et al. (1995), and Madgwick (2014), among others. Detailed description of the results of this analysis are included in Rhodes et al. (2018) and Rhodes et al. (2019) and therefore will not be reiterated herein. However, an expanded discussion of the paleoecological signals derived from the predators indicated by the taphonomic analysis is included in the 'Results' section.

Paleoenvironmental reconstructive methods

Two methods of paleoenvironmental reconstruction were applied to the taxonomic data collected from both Hohle Fels and Geißenklösterle to produce broad estimates of the vegetative composition and climate around the sites in the past (Rhodes et al. 2018, 2019). 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.

To address the shortcomings of the modified indicator species method, the habitat weighting method (Nesbit Evans et al. 1981; Andrews 1996) was applied to the Hohle Fels data (Rhodes et al. 2019). 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, 2017b, c) also provides the opportunity to compare the results of Ach Valley analysis with an increasing number of paleoecological reconstructions from neighboring regions.

Results

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

- 1) The small mammal material accumulated in both caves is 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.

A total of 1694 taxonomically identifiable specimens were recovered from Geißenklösterle (Rhodes et al. 2018) and 6165 from Hohle Fels (Rhodes et al. 2019). 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).

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.

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 2016a, 2017a; Hoffmann and Sillero-Zubiri 2016). The Eurasian eagle owl is also known to return to roosting sites over multiple years (Cantrell 2015; BirdLife International 2017a) 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; Tsytsulina et al. 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 shrew 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 2017b). 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 2016b). 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 2016b). 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

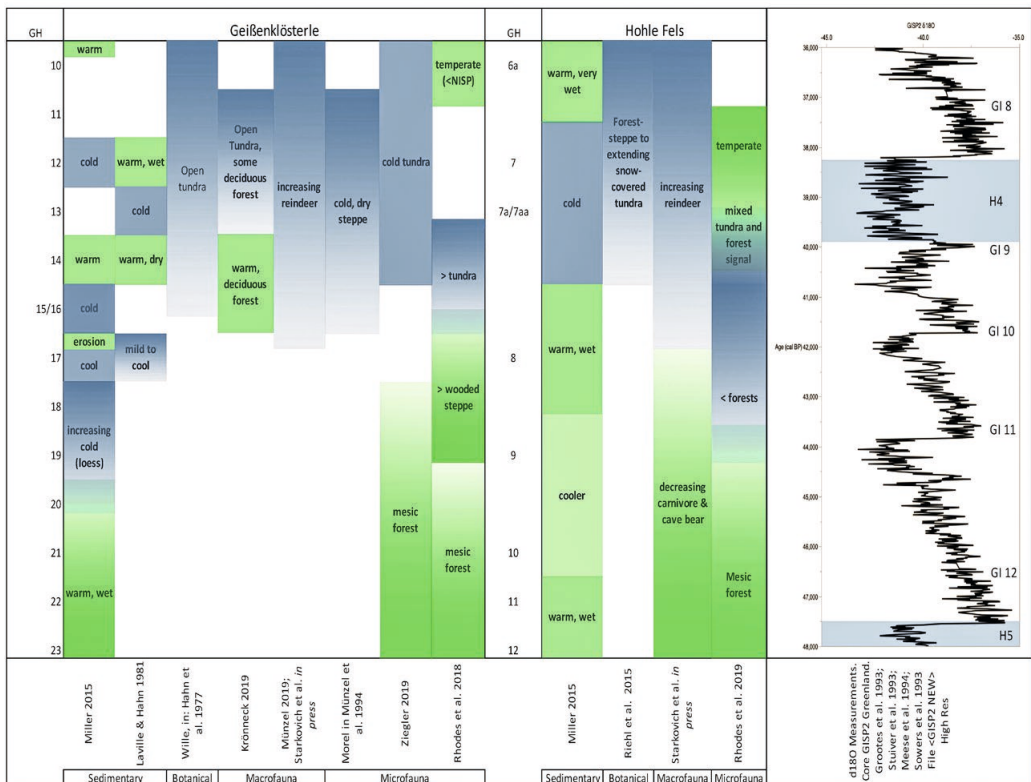


Fig. 9: Schematic of the different paleoenvironmental proxy records from Geißenklösterle and Hohle Fels spanning the Middle to early Upper Paleolithic against the GISP ¹⁸O record (based on dates from Higham et al 2012).

Abb. 9: Schematische Darstellung der verschiedenen Paläoumwelt-Daten für das Mittelpaläolithikum und das frühe Jungpaläolithikum aus dem Geißenklösterle und dem Hohle Fels gegen die GISP ¹⁸O-Kurve (basierend auf Daten von Higham et al. 2012).

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.

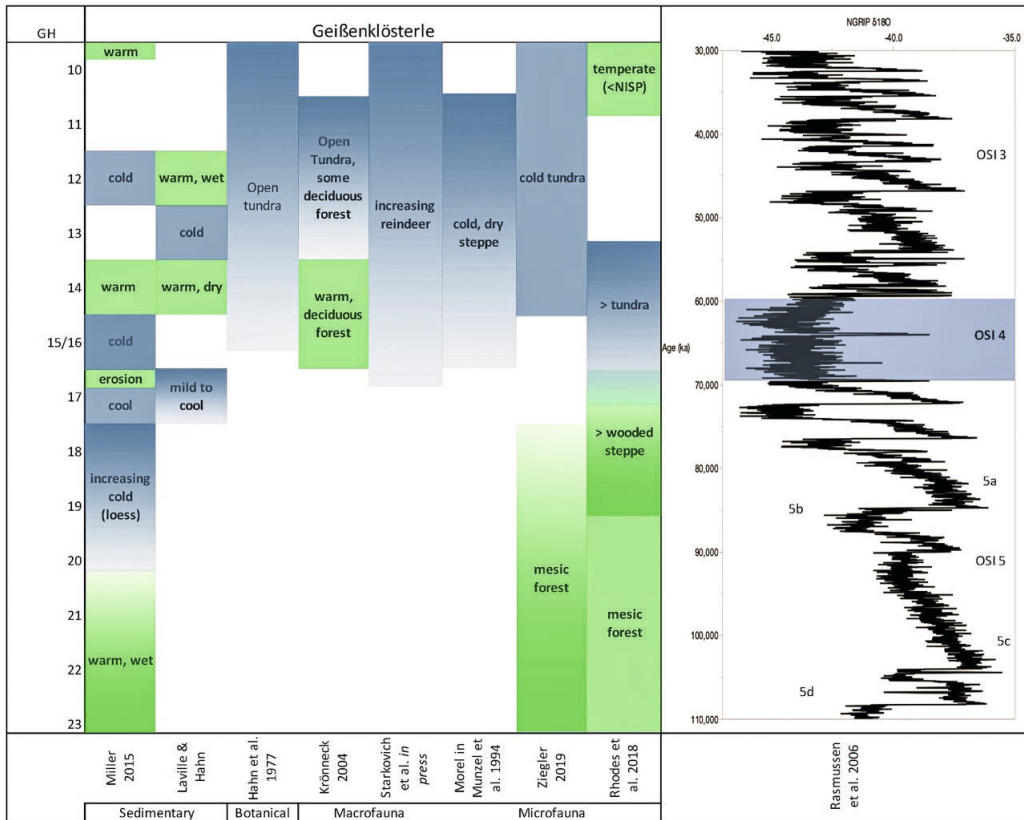


Fig. 10: Schematic of the different paleoenvironmental proxy records from Geißenklösterle spanning the Middle to early Upper Paleolithic against the GISP ¹⁸O record for OIS 5–3 (based on dates from Richard 2019).

Abb. 10: Schematische Darstellung der verschiedenen Paläoumwelt-Daten für das Mittelpaläolithikum und das frühe Jungpaläolithikum aus dem Geißenklösterle gegen die GISP ¹⁸O-Kurve der Phasen OIS 5–3 (basierend auf Daten von Richard 2019).

Rather than reiterate these results further, the remainder of this paper will focus on integrating the new small mammal paleoenvironmental signal with the existing picture of the Middle and Upper Paleolithic landscape in the Swabian Jura, and comparison with the Greenland ice core and Central and Western European terrestrial loess-paleosol archives.

Discussion

Correlations with the Ach Valley record

Overall, this new paleoenvironmental record fits well with past studies of the paleoecology of the Ach Valley. The different proxy material records from Geißenklösterle and Hohle Fels are illustrated in Fig. 9 against the OIS 3 GISP ^{18}O signal. Fig. 10 shows the same proxy records from Geißenklösterle against the OIS 5–3 GISP record, to incorporate the new dating suggested by Richard (2019). 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 Rhodes et al. (2018, 2019), 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 small mammal record, 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 Miller's (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 1973) 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.

Correlations with the Greenland stadials/interstadials

The paleoenvironmental records described above 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).

Correlation with other faunal paleoecological signals

The small mammal record from the Lone Valley has not been looked at as intensively in recent years as its equivalent in the Ach Valley, however ongoing analysis of recently excavated material from Langmahdhalde (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 Kleine Scheuer am Hohlenstein. However, the small sample sizes reported by Koken (in Schmidt 1912; see 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, suggest 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 above. 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 Giulia Toniato's (in prep.) analysis of the faunal material from previous and renewed excavations at Schafstall 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 Sesselfelsgrötte (van Kolfschoten 2014) and Weinberghöhlen (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, 2017a, b, c). The work of von Koenigswald (1974) at Weinberghöhlen documents a lack of soricid remains from the lowermost 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 and Müller-Beck (Müller-Beck 1974; von Koenigswald 1974). That the material from Weinberghöhlen 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. 2017 a, b), Italy (López-García et al. 2015, 2017c; Berto et al. 2017, 2018), 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 paper, as it covers broadly the same time period as the Ach Valley record and includes at least five 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 (Hernández 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 Meerbeek 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.

Correlation with other paleoecological archives

The presence of potential Lohner 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., Datthausen) 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 (e.g., 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 Nussloch 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. Lohner 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 Nussloch sequence records a cambisol which recent reviews of the ¹⁴C 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 Lohner 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 Fürmoos 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 re-immigration 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 16–17) 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 this paper.

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.

Conclusions

The broad agreement between different paleoecological records from the Ach Valley and elsewhere in Central and Eastern Europe described above 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 Greenland interstadials 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 2003; 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 stadial/interstadial 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 stadial 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 florescence 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 my thesis (Rhodes 2019) 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 (Dalén 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 Heinrich 5 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 and Neanderthal 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. 2019). 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; Bocherens et al. 2016) or as part of complex inter-species interaction, acculturation, and/or assimilation (Hublin et al. 1996; d'Errico et al. 1998; Mellars et al. 1999; d'Errico 2003; Conard 2008, 2010; 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 my thesis (Rhodes 2019) 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). My thesis (Rhodes 2019) 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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**Supplementary Online Material / *Ergänzendes
Online-Material***
(accessible under / *abrufbar unter*: mgfuopenaccess.org)

Tables / *Tabellen* 1-15

Table 1: *Arvicola* enamel thickness quotient (SDQ) measurements (in mm) from Hohle Fels Cave.

Tabelle 1: *Messwerte (in mm) des Zahnschmelz-Dicken-Quotienten (SDQ) von Arvicola aus dem Hohle Fels.*

Table 2: Measurements (in mm) taken on *Microtus arvalis/agrestis* specimens from Geißenklösterle.

Tabelle 2: *An Exemplaren von Microtus arvalis/agrestis aus dem Geißenklösterle genommene Messwerte (in mm).*

Table 3: Measurements (in mm) taken on *Microtus gregalis* specimens from Geißenklösterle.

Tabelle 3: *An Exemplaren von Microtus gregalis aus dem Geißenklösterle genommene Messwerte (in mm).*

Table 4: Measurements (in mm) taken on *Microtus nivalis* specimens from Geißenklösterle.

Tabelle 4: *An Exemplaren von Microtus nivalis aus dem Geißenklösterle genommene Messwerte (in mm).*

Table 5: Measurements (in mm) taken on *Microtus oeconomus* specimens from Geißenklösterle.

Tabelle 5: *An Exemplaren von Microtus oeconomus aus dem Geißenklösterle genommene Messwerte (in mm).*

Table 6: Measurements (in mm) taken on *Lemmus lemmus* specimens from Geißenklösterle.

Tabelle 6: *An Exemplaren von Lemmus lemmus aus dem Geißenklösterle genommene Messwerte (in mm).*

Table 7: Measurements (in mm) taken on *Dicrostonyx* sp. specimens from Geißenklösterle.

Tabelle 7: *An Exemplaren von Dicrostonyx sp. aus dem Geißenklösterle genommene Messwerte (in mm).*

Table 8: Measurements (in mm) taken on Soricidae specimens from Geißenklösterle.

Tabelle 8: *An Exemplaren von Soricidae aus dem Geißenklösterle genommene Messwerte (in mm).*

Table 9: Measurements (in mm) taken on *Microtus arvalis/agrestis* specimens from Hohle Fels.

Tabelle 9: *An Exemplaren von Microtus arvalis/agrestis aus dem Hohle Fels genommene Messwerte (in mm).*

Table 10: Measurements (in mm) taken on *Microtus gregalis* specimens from Hohle Fels.

Tabelle 10: *An Exemplaren von Microtus gregalis aus dem Hohle Fels genommene Messwerte (in mm).*

Table 11: Measurements (in mm) taken on *Microtus nivalis* specimens from Hohle Fels.

Tabelle 11: *An Exemplaren von Microtus nivalis aus dem Hohle Fels genommene Messwerte (in mm).*

Table 12: Measurements (in mm) taken on *Microtus oeconomus* specimens from Hohle Fels.

Tabelle 12: An Exemplaren von *Microtus oeconomus* aus dem Hohle Fels genommene Messwerte (in mm).

Table 13: Measurements (in mm) taken on *Lemmus lemmus* specimens from Hohle Fels.

Tabelle 13: An Exemplaren von *Lemmus lemmus* aus dem Hohle Fels genommene Messwerte (in mm).

Table 14: Measurements (in mm) taken on *Dicrostonyx* sp. specimens from Hohle Fels.

Tabelle 14: An Exemplaren von *Dicrostonyx* sp. aus dem Hohle Fels genommene Messwerte (in mm).

Table 15: Measurements (in mm) taken on Soricidae specimens from Hohle Fels.

Tabelle 15: An Exemplaren von Soricidae aus dem Hohle Fels genommene Messwerte (in mm).