



Paleoclimatic and paleoenvironmental reconstructions based on the small vertebrates from the Middle Paleolithic of Hohle Fels Cave, SW Germany

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Abstract

In this paper, we analyse the fish and small mammal assemblages from the Middle Paleolithic horizons of Hohle Fels Cave to reconstruct the paleoclimatic and paleoenvironmental conditions faced by the Neanderthal groups who occupied the site. The fish assemblage indicates that the freshwater ecosystem around this site was characterized by a pre-mountain river system with the presence of permanent, oxygen-rich, and cold running waters. The results of the Habitat Weighting Method and the Bioclimatic Model applied to the small mammal assemblage, coupled with the new dates obtained for the Archaeological Horizon (AH) IX, allow us to identify two different climatic phases. One phase (AH X-XII) is more temperate possibly corresponding to the end of Marine Isotope Stage (MIS) 5; the other (AH VI-IX) is colder and more arid corresponding to the end of MIS 4 through the beginning of MIS 3. Open environments with a relatively stable forest component dominated the landscape during this part of the Middle Paleolithic. These two climatic phases appear to correspond to different levels of occupational intensity by Neanderthals, with higher occupational intensity during mild climatic periods and lower intensity during cold, arid periods. Our climatic reconstruction and recent absolute dating, together with the recovery of a complete leaf point near the top of AH X, have important implications for the cultural stratigraphy and cultural chronology of the region. Archaeologists have traditionally viewed leaf points as key artefacts of the *Blattspitzengruppe*, a cultural complex attributed to the end of Middle Paleolithic; however, this stratigraphic, climatic, and chronological context indicates the need to revise this interpretation.

Keywords Small mammals · Fish · Habitat Weighting · Bioclimatic Model · Late Pleistocene · Swabian Jura

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Introduction

The Swabian Jura (South-western Germany) is a key region for Paleolithic studies, in particular of the transition between the Middle and Upper Paleolithic and the evolution of the Upper Paleolithic industries (Aurignacian, Gravettian, Magdalenian). The caves in this region (Fig. 1) have been the subject of intensive research for the last 150 years and produced an astonishing archaeological record that helped develop and improve our understanding of past lifeways, subsistence strategies, and technologies of both Neanderthal and modern human groups. The Ach and the Lone Valleys are located along two tributaries of the Danube in the Swabian Jura. The caves and shelters that can be found along these valleys, such as in Hohle Fels, Geißenklösterle, Vogelherd, and Hohlenstein-Stadel (Conard et al. 2009; Conard and Kind 2017), are renowned for the musical instruments and the ivory figurines that have been recovered there. The

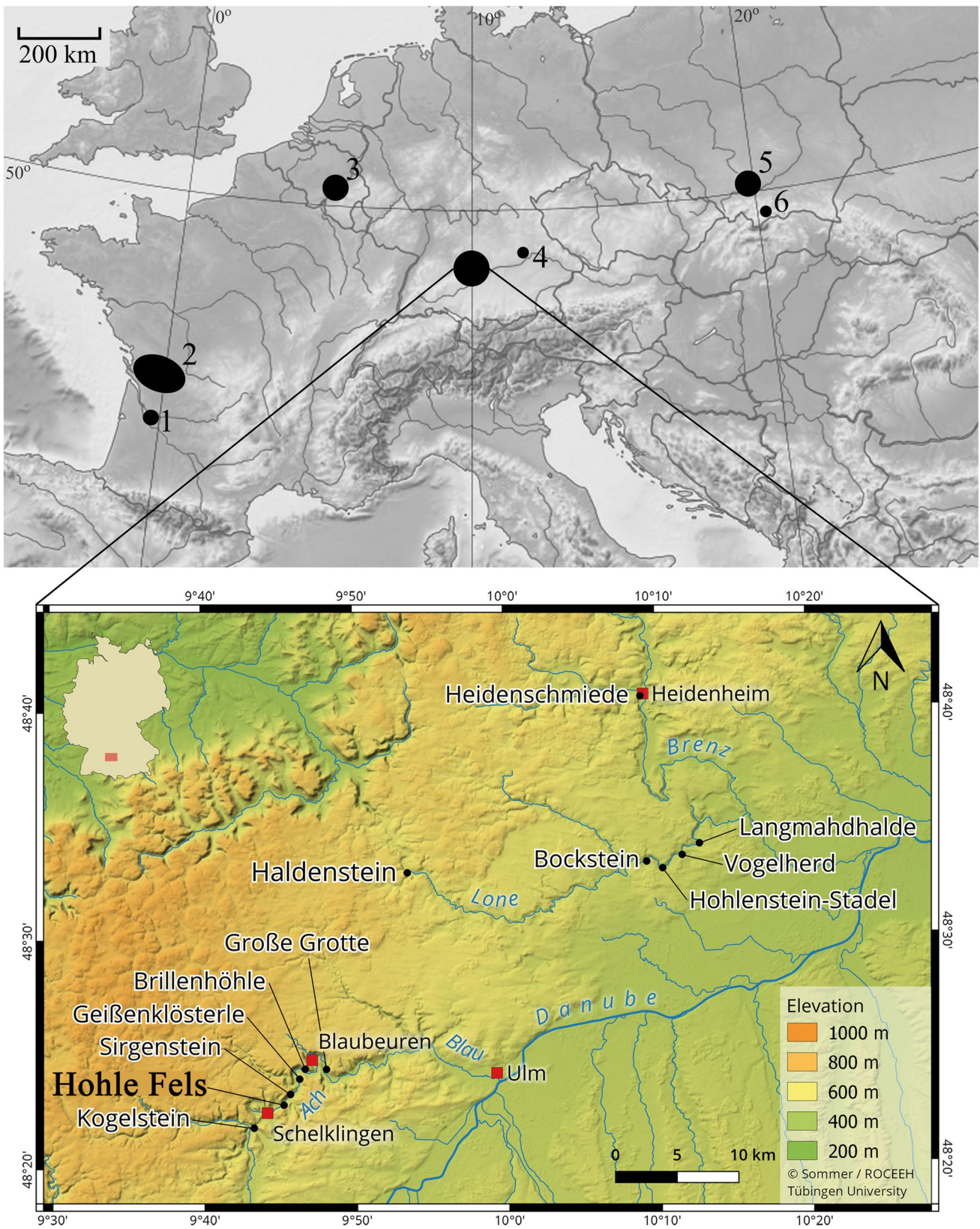


Fig. 1 Location of Hohle Fels Cave and other sites mentioned in the discussion. 1, Gironde; 2, Charente-Maritimes and Charente; 3, Scladina and Marie-Jeanne Caves; 4, Sesselfelsgrötte; 5, Bišník and

Koziarnia Caves; 6, Oblazowa Cave. Detailed map of the Swabian Jura modified after Sommer 2019

study of subsistence strategies during the Middle and Upper Paleolithic provides useful insights into the behaviour of human groups (Barth et al. 2009; Conard et al. 2013; Kitagawa 2014; Wong et al. 2020b; Bertacchi et al. 2021, among others) and recently the potential of small vertebrate studies for the reconstruction of the climatic and environmental conditions faced by those groups was highlighted by the publications of the small mammal assemblage at Hohle Fels (Rhodes et al. 2019), Geißenklösterle (Rhodes et al. 2018), and Langmahdhalde (Wong et al. 2020a).

In this paper, we propose a new climatic and environmental reconstruction of the conditions faced by Neanderthal groups during their occupations of Hohle Fels Cave and try to understand how these conditions might have influenced their strategies and occupation patterns.

The site

Hohle Fels Cave (48° 22' 45" N; E9° 45' 14" E) is located in the Ach River valley (Fig. 1), at 564 m a.s.l. and ca. 7 m above the current floor of the valley. The first scientific investigation of the cave led by Fraas and Hartmann started in 1870–1871 and yielded faunal remains (mostly cave bears), lithic tools, and bone and antler artifacts (Hahn

1978). After that, Schmidt (1912) published the results of his research conducted in 1906 in the book *Die Diluviale Vorzeit Deutschland*. Between 1958 and 1960, further excavations were carried out by Matschak and Riek, and between 1977 and 1979 by Hahn (Hahn 1978, 1979). This last effort provided proof of a well-preserved stratigraphy and an abundance of artifacts (Hahn 1979). Systematic investigation of Hohle Fels started in 1988 under the direction of Hahn (until his death in 1997) and has continued every year from 1997 until the present under the direction of Conard. The excavations exposed a ca 5.5 m-thick sequence, spanning from the Middle Paleolithic to the Magdalenian (Fig. 2). In the past 25 years of researches, the site yielded abundant lithic and faunal remains, but it is especially renowned for the symbolic artifacts including ivory animal and human figurines, personal ornaments, and musical instruments recovered in the Aurignacian levels (Conard 2009; Conard et al. 2009; Wolf and Conard. 2015; Velliky et al. 2021, among others). The material analysed in this study is derived from the horizons assigned to Middle Paleolithic, i.e., Archeological Horizons (AH) VI to XII, which correspond to Geological Horizons (GH) 9–15, excavated between 2014 and 2021 (Fig. 2). The description of the GHs follows Miller (2015) and the field notes from the excavation campaigns.

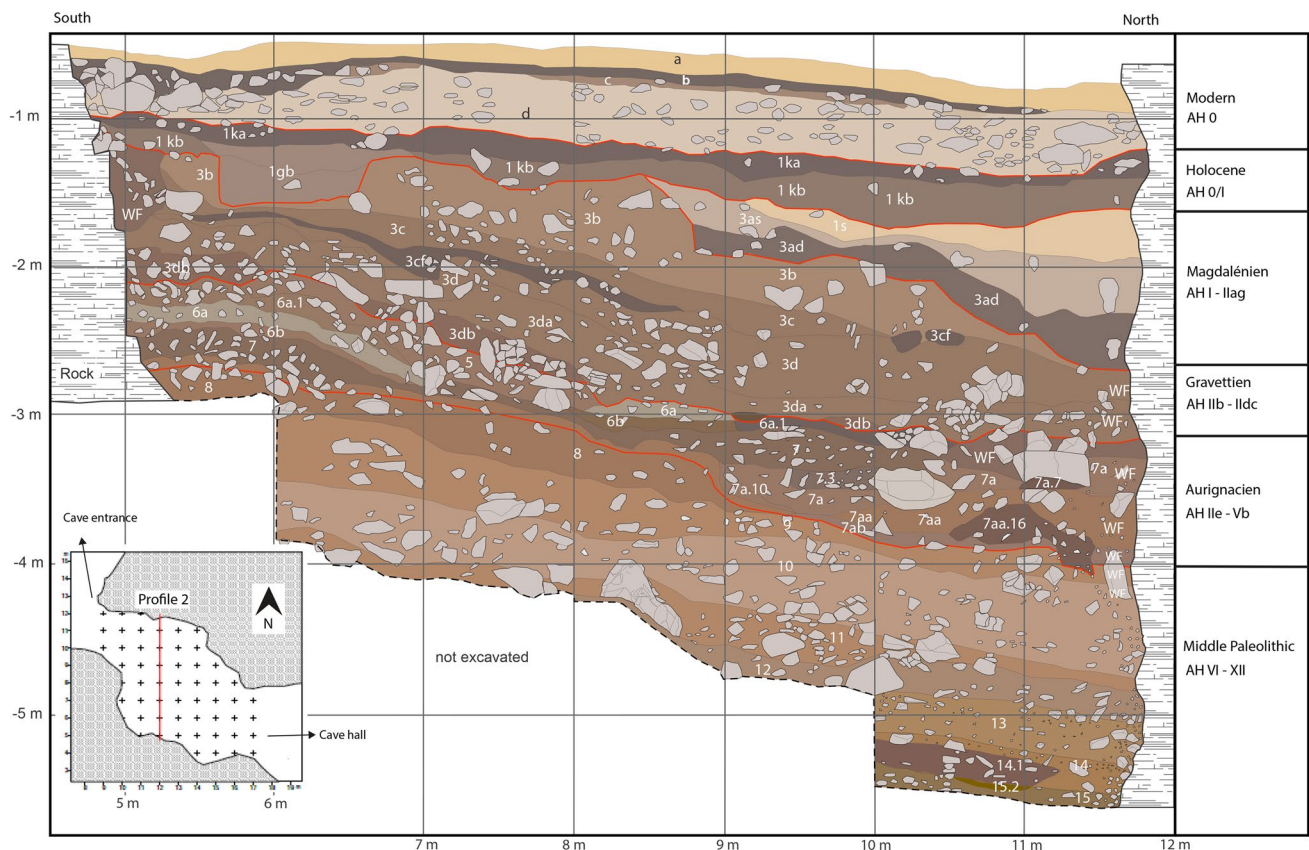


Fig. 2 Profile 2 of Hohle Fels cave, modified after Conard and Janas 2021. Graphic by A. Janas

- GH 9: ca. 30 cm thick. The sediment is brown (7.5 YR 5/6) with yellowish-brown layers alternating with reddish-brown layers. It is composed of silt, with little clay and some lime sand. Limestone blocks make up 20–30% of the units, are sub-rounded, and range in size between 8 and 25 cm. The transition to GH 10 appears gradually over 4 cm.
- GH 10: ca. 30 cm thick. The sediment is brown (7.5 YR 6/4–5/4), has a relatively high proportion of calcite sand and is composed mostly of silt. Limestone blocks are less present than in GH 9 and are angular to slightly rounded. The passage to GH 11 is clear in the east part, over 2 cm, and more gradual in the west part, over 4 cm.
- GH 11: ca. 10–20 cm. The sediment is yellowish-brown (7.5 YR 6/4–5/6) and composed of silty clay. Limestone blocks are smaller, 2–15 cm in size. Gradual transition to GH 12.
- GH 12: the sediment is greenish-brown (10 YR 5/4), composed of clayey silt with a high proportion of coarse limestone sand. Limestone blocks are small, 2–8 cm in size.
- GH 13: the sediment is yellow–brown, darker, and almost reddish in the lower part (10 YR 5/8 upper, 10 YR 4/6 lower). It is composed of silty clay with a relatively high proportion of coarse and fine lime sand. Irregular limestone rubbles up to 20 cm. Transition to GH 14 is gradual but visible.
- GH 14: The sediment is yellow–brown, almost reddish (10 YR 4/6). It is composed of silty clay with a lot of coarse and fine limestone sand. In its lower portion, the sediment is yellowish-brown (10YR 5/6) and composed of clayey silt. Limestone blocks up to 30 cm. GH 14.1 is a feature characterized by grey-brown sediment (10YR 5/4) and unusually high find density. Transition to GH 15 is very clear, sometimes over a few millimetres.
- GH 15: the sediment is yellowish-brown (10 YR 5/4), lighter colour in the northern Sect. (10 YR 5/6). It is composed of clayey silt with a high proportion of limestone sand. High amount of limestone clasts, 50–80%. GH 15.2 is a feature at the contact with GH 14.1 that presents lighter colour (10 YR 5/6) and a high density of bones and small mammal bones.

GH 9 to 11 are dated between 35 and 40 ka years BP, corresponding to ~39–44 ka cal BP (OxCal 4.4, IntCal 20, Bronk Ramsey 2009) and clearly represent minimum ages (Conard and Bolus 2008; Conard 2009; Higham et al. 2012), while new ESR dates for GH 12 put it at 62 ± 4 ka (Conard et al. 2021).

One previous study explored the presence of fish remains in Hohle Fels from the Middle Paleolithic layers and indicated the presence of burbot (*Lota lota*), grayling (*Thymallus thymallus*), and unidentifiable cyprinids, all of which correspond to species of fish commonly found in the Danube and its tributaries such as the Ach River (Conard et al. 2013). In

this study, the authors reported the common presence of fish bones and scales in the Aurignacian and Gravettian deposits but suggested this presence to be only sporadic in the Middle Paleolithic layers. In the present paper, the sample was enlarged to more than 3400 remains in contrast to the original study that included only 19 specimens from the upper portion of the Middle Paleolithic deposits. Additionally, we present a detailed paleoenvironmental study based on the fish species recovered from the site.

Recent studies (Rhodes et al. 2019; Rhodes and Conard 2021) analysed the small mammal assemblages from the Middle Paleolithic GHs available at the time (GH 9–12) and compared them to the early Upper Paleolithic (i.e. Aurignacian) in order to explore the climatic and environmental changes during the Middle to Upper Paleolithic transition. The paleoclimatic reconstruction based on the rodent assemblage describes GH 12 as the less cold and arid layer in the Middle Paleolithic sequence and indicates a decrease in temperature and precipitation in GH 9–11 (Rhodes and Conard 2021). The landscape surrounding the site was a mosaic of arctic tundra and boreal and deciduous forests, with a steppe component always present but fluctuating through time (Rhodes 2019; Rhodes et al. 2019). In this study, we increased the samples for the Middle Paleolithic GHs already published and add samples from the new Middle Paleolithic GHs 13, 14, and 15 excavated in 2020 and 2021.

Material and methods

Small vertebrate material was recovered through water screening using 0.5-mm sieves. The material analysed comes from one square meter excavation units 11, 25, 26, 27, and 28. These are the squares that currently present the whole Middle Paleolithic sequence, going from GH 9 to 15 (Fig. 2). For each GH, we present the number of identified specimens (NISP) and the minimum number of individuals (MNI).

Fishes

We analysed this assemblage using a Zeiss Stemi 305 stereomicroscope and photographed the material using a Dino-Lite Edge Digital Microscope. Anatomical and taxonomical classifications were done by comparison method of external characteristics of those remains using the reference collection hosted in Senckenberg Centre for Human Evolution and Palaeoenvironment (University of Tübingen) and several osteological atlases (Lepiksaar 1994; Watt et al. 1997; Conroy et al. 2005). The taxonomic nomenclature used has been extracted from Cannon (1987) and Wheeler and Jones (2009). In

Small mammals

The identification of the small mammal was based on the best diagnostic elements available: for lagomorphs and rodents, mandibles, maxilla, and isolated teeth; for shrews, mandibles, and maxilla; for moles and bats, mandibles, maxilla, isolated teeth, and postcranial bones were analysed. The criteria for the identification of the material, the nomenclature for morphological descriptions, and the measurements taken follow Niethammer and Krapp (1978; 1982), Nadachowski (1982), and Borodin and Markova (2015) for Rodentia; Laplana et al. (2015) for Lagomorpha; and Niethammer and Krapp (1990) for Eulipothyphla; Sevilla García (1988) for Chiroptera. Comparison of the fossil specimens to the osteological collection of the University of Tübingen was also crucial for the identification. Taxonomic nomenclature follows Wilson and Reeder (2005), except for *Clethrionomys glareolus* (see Tesakov et al., 2010; Kryštufek et al., 2019), *Alexandromys oconomus* (Lissovsky et al. 2018, among others), and *Lasiopodomys anglicus* (see Petrova et al., 2015; Baca et al., 2019). Photos of the material have been taken using a Zeiss Stereo Discovery V8.

Morphometric analysis has been conducted on complete first lower molars of adult specimens of *Arvicola amphibius*. The Schmelzband-Differenzierung-Quotient or SDQ index (Heinrich 1978) quantifies the difference in enamel thickness between the anterior and the posterior wall of each triangle of the tooth (Fig. 3).

$$SDQ_T = \frac{ssp}{ssa} * 100$$

To calculate the SDQ value of a population, it is necessary to obtain the mean SDQ for each m1 (comprehending all the triangles (T1 to T5) and the two sides of PL)

$$SDQ_{m1} = \frac{\sum SDQ_T}{7}$$

and then the mean of the SDQ of all (n) m1 taken into account

$$SDQ_{pop} = \frac{\sum SDQ_{m1}}{n}$$

Photos of the specimens have been taken using a Leica EZ4HD microscope. Measurements have been taken on the photos using ImageJ software. Data have been analysed using PAST software (Hammer et al. 2001).

Paleoenvironmental reconstruction

The habitat weighting method (Evans et al. 1981; Andrews 2006) based on small mammals has been applied in order

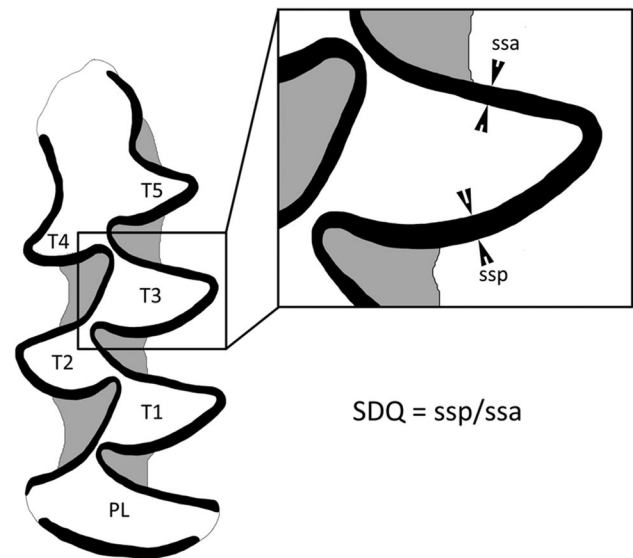


Fig. 3 Scheme for the measurement of the Schmelzband-Differenzierung-Quotient (SDQ) index in first lower molar of *Arvicola amphibius*

to obtain a reconstruction of the landscape and environment surrounding the site. Each mammal species has been assigned to the habitat(s) where it can be currently found. We decided to use two different sets of values, one based on ecological preferences (Suppl. Material 1), and one based on habitat suitability (Suppl. Material 2).

For ecological preferences, six categories have been identified (following López-García et al. 2014, 2017a, 2017b): open dry grassland and steppe (OD), open humid evergreen meadows (OH), open woodland with moderate ground cover, woodland margins, and forest patches (OW), woodland, or mature forest (Wo), rocky environment (R), and water-related environments (Wa).

For habitat suitability, we follow the attributions of the IUNC Red List (IUCN 2021): “forest” including forested and wooded areas, and forest margins; “shrubland” intended as shrubs, bushland and thickets; “grassland,” characterized by grasses and broadleaf herbaceous plants with sparsely distributed or absent woody plants; “wetland”; and “desert.” Since most of the species are no longer present in Southern Germany, we use the attribution(s) given in the global distribution for each species.

We use *Spermophilus citellus* as current reference for *S. superciliosus* and *Cricetulus migratorius* as current reference for *Allocricetus* vel *Cricetulus* sp.

Paleoclimatic reconstruction

Paleoclimatic data have been calculated for each GH based on the insectivore and rodent assemblage, using the Bioclimatic model described in Hernández Fernández (2001,

2005) and recently updated by Royer et al. (2020). The insectivores and rodents' assemblages have been analysed using the Climatic Restriction Index ($CRI_i = 1/n$, where "n" is the number of climatic zones where the species are represented and "i" is the climatic zone where the species appears). Starting from the CRI, the Bioclimatic Component has been calculated (BC; representation by the level of each of the available climatic zones): $BC_i = (\sum CRI_i) \times 100/S$ (where S is the number of species per GH). From the BC, it was possible to estimate climatic parameters by means of multiple linear regression method (Hernández Fernández and Peláez-Campomanes 2005; Royer et al. 2020), using the R script file published by Royer et al. (2020). For this study, the mean annual temperature (MAT expressed in °C) and mean annual precipitations (P expressed in mm) are calculated. Current data for the town of Schelklingen (Fig. 1) show a MAT of 8.3°C and P of 1059 mm (climate-data.org). *Talpa* sp. has been considered as *T. europaea*, being the only species for this genus present at Hohle Fels. *Sorex* sp., *Neomys* sp., and *Sicista* sp. have not been included in the calculation. As for the environmental reconstructions, we use *Spermophilus citellus* as current reference for *S. superciliosus* and *Cricetulus migratorius* as current reference for *Allocricetus* vel *Cricetulus* sp.

Results and discussion

Taphonomic analysis: preliminary results

Fishes

Anthropogenic marks such as burned bones or cut marks and non-anthropogenic damage indicators on the bone surface of the fish that remain such as digestion marks, compression, uniaxial mechanical deformation, or bite marks were analysed. Previous studies have distinguished several categories of digestion marks, depending on the intensity of digestion (Andrews 1990; Guillaud et al. 2018; Frontini et al. 2021; Blanco-Lapaz et al. 2021). The presence of bite marks or crushed bones can give us insight into the gnawing activities carried out by terrestrial carnivores such as foxes or wolves (Nicholson 1993) while digestive marks are indicative of other carnivorous birds (Andrews 1990).

Taphonomic analysis of the fish assemblage from the Middle Paleolithic horizons of Hohle Fels indicates no damages such as mechanical deformation, rounding, or polishing due to compression during the digestion process (Frontini et al. 2021; Blanco-Lapaz et al. 2021). Bite marks, crush marks, or digestive marks were absent from all the fish remains, which means that carnivores and birds can be ruled out as accumulating

agents (Nicholson 1993). No direct anthropogenic marks that indicate burning or butchery activities were documented.

The lack of carnivore modifications on fish bones likely indicates that carnivores, which visited the cave, including red/arctic foxes, wolf, cave/brown bears, hyenas, and birds of prey (Conard et al. 2013; Rhodes et al. 2019; Baumann et al. 2020; Beattie et al. 2021), were not the primary agents of accumulation for the fish remains, leaving humans as most probable accumulation agents. On the other hand, we cannot yet definitively prove that the fish remains were accumulated by humans since there is no direct evidence of anthropogenic modifications such as cut marks or burned bones on the assemblage. Further, more detailed taphonomic studies (ongoing) might provide more data and help identify the main agent of the fish accumulation during the Middle Paleolithic at Hohle Fels.

Small mammals

A comprehensive taphonomic analysis of small mammals from GH 9 to 12 has been published by Rhodes et al. (2019) and suggests that the small mammal material was most likely accumulated by the snowy owl *Bubo scandiacus*, the Eurasian eagle-owl *Bubo bubo*, and/or the great grey owl *Strix nebulosa*, with a limited contribution by foxes. As these predators are mostly generalist hunters, the composition of the assemblages should accurately reflect the diversity of the small mammal community on the landscape at the time of the accumulation.

In this study, a total of 2093 first lower molars of Arvicolids from GH 13 to 15 have been analysed according to the criteria described in Fernández-Jalvo et al. (2016), observing the degree and frequency of digestion signs, in order to determine the principal agents of the small mammal accumulation (Table 1). Due to the high percentage of teeth with absent to moderate modifications, this preliminary study indicates that predators of category 1 or 2 are most likely responsible for the accumulation. Nocturnal birds of prey, such as *Tyto alba*, *Asio flammeus*, and *Asio otus* (cat. 1) or *Bubo scandiacus* and *Strix nebulosa* (cat.2) are listed as possible accumulators (Fernández-Jalvo et al. 2016). Nevertheless, the low percentage of teeth with heavy or extreme digestion signs might indicate that small carnivores (e.g., *Mustela* spp. or *Vulpes* spp.) or diurnal birds of prey (such as *Falco* spp.) also played a role in the formation of the small mammal assemblages. An ongoing study regarding the bird assemblage of Hohle Fels already identified four species of birds of prey from GH 13: *Falco tinnunculus*, *Corvus corax*, *Asio flammeus*, and *Bubo bubo* (Beattie et al. 2021). These preliminary results confirm that opportunistic hunters (Andrews 1990) are the principal responsible for the small mammal accumulation that should therefore accurately reflect the composition of the small mammal community on the landscape surrounding the site.

Table 1 First lower molars of arvicolids with signs of digestion for the geological horizons (GH) excavated during 2020–2021 campaigns

		<i>Alexandromys oeconomus</i>	<i>Arvicola amphibius</i>	<i>Chionomys nivalis</i>	<i>Dicrostonyx torquatus</i>	<i>Lasiopodomys anglicus</i>	<i>Lemmus lemmus</i>	<i>Microtus arvalis</i>	Arvicoli- dae indet	%
GH 13	Absent	55	17	18	6	361	33	82	13	93.75
	Light	1	0	0	0	5	1	1	0	1.28
	Moderate	3	0	1	1	9	0	0	2	2.56
	Heavy	2	0	0	1	1	0	3	4	1.76
	Extreme	0	0	0	0	0	0	0	4	0.64
GH 14	Absent	47	15	9	5	276	7	54	22	91.39
	Light	3	0	0	0	13	0	2	0	3.78
	Moderate	2	0	1	1	8	0	0	1	2.73
	Heavy	1	0	0	0	1	1	0	4	1.47
	Extreme	0	0	0	0	1	0	0	2	0.63
GH 15	Absent	84	17	12	52	653	60	59	25	96.40
	Light	2	0	0	1	8	0	3	0	1.40
	Moderate	1	0	0	1	11	0	0	5	1.80
	Heavy	0	0	0	1	0	1	0	2	0.40
	Extreme	0	0	0	0	0	0	0	0	0.00

Paleoclimatic and paleoenvironmental reconstructions for Neanderthal occupations at Hohle Fels Cave

Fishes

A total of 3482 fish remains, belonging to 8 species, were analysed (Table 2, Fig. 4). The Middle Paleolithic fish assemblage from Hohle Fels comprises five families: Salmonidae, Lotidae, Cyprinidae, Cottidae, and Esocidae. The predominant family recovered is Salmonidae, represented by three species, the European grayling (*Thymallus thymallus*, NISP=1381, MNI=15), the brown trout (*Salmo trutta*, NISP=3, MNI=2), and the Danubian trout (*Hucho hucho*,

NISP=2, MNI=1). Lotidae, represented by the burbot (*Lota lota*, NISP=1112, MNI=11), is the second most common family in the assemblage. The third most represented family is Cottidae, with one species, the bullhead (*Cottus gobio*, NISP=73, MNI=10). Two species belonging to the carp family, Cyprinidae, have been identified: the common chub (*Leuciscus cephalus*, NISP=6, NMI=5) and the common nase (*Chondrostoma nasus*, NISP=2, NMI=1). Esocidae is the least represented family classified in the assemblage with one specimen identified as the northern pike (*Esox lucius*, NISP=1, MNI=1).

As mentioned above, the Salmonidae family is represented by three different species. The European grayling (*T. thymallus*), which is present throughout the sequence, is native to

Table 2 Identified taxa of Fish from the Middle Paleolithic Geological Horizons (GH) in Hohle Fels. NISP: number of identified specimens; MNI: minimum number of individuals. 1, Salmonidae; 2, Lotidae; 3, Cottidae; 4, Cyprinidae; 5, Esocidae; 6, Teleostei

		GH 9		GH 10		GH 11		GH 12		GH 13		GH 14		GH 15		Total NISP	Total MNI
		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI		
1	<i>T. thymallus</i>	34	1	13	1	92	1	727	4	119	3	148	2	248	3	1381	15
	<i>S. trutta</i>	1	1					2	1							3	2
	<i>H. hucho</i>			1	1							1	1			2	2
	Unident	1	1			3	1	15	1	1	1	1	1	11	1	32	6
2	<i>L. lota</i>	29	1	12	1	91	1	539	4	156	1	155	1	130	2	1112	11
	3	<i>C. gobio</i>						9	1	14	3	39	4	11	2	73	10
4	<i>L. cephalus</i>							2	2	2	1	2	2			6	5
	<i>C. nassus</i>											2	1			2	1
	Unident	1	1			2	1	8	1	34	1	48	1	1	1	94	6
5	<i>E. lucius</i>													1	1	1	1
6	Unident	20		18		51		281		145		163		98		776	-
Total		86	5	44	3	239	4	1583	14	471	10	559	13	500	10	3482	59

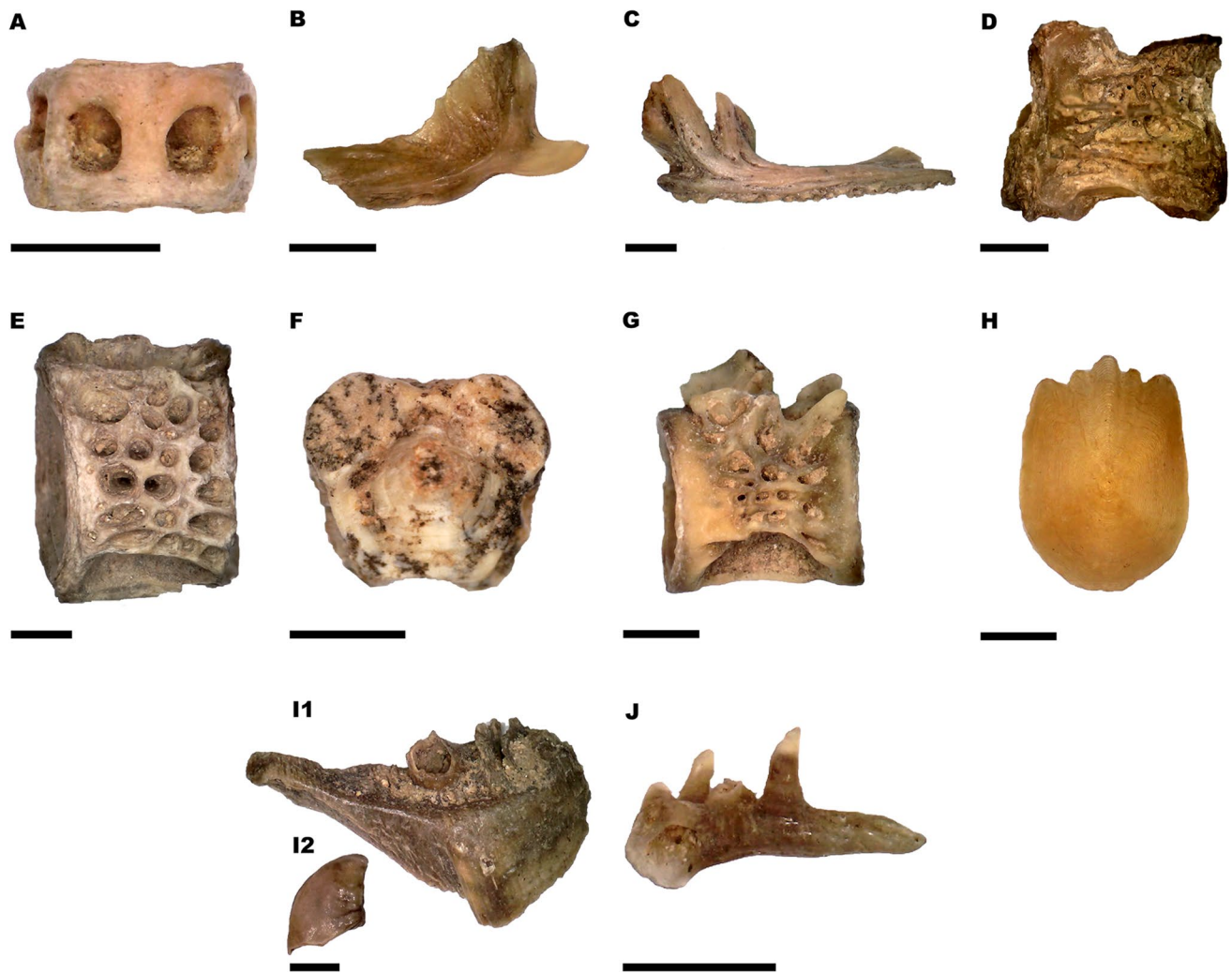


Fig. 4 **A** Precaudal vertebra. Pike (*Esox lucius*), HF21 25 3727 15 XII; **B** Left praeoperculum fragment. Bullhead (*Cottus gobio*), HF21 25 3786.1 15 XII; **C** Left praemaxilar. Burbot (*Lota lota*), HF21 25 3786.2 15 XII; **D** Caudal vertebra. Burbot (*Lota lota*), HF21 25 3786.3 15 XII; **E** Precaudal vertebra. Danubian trout (*Hucho hucho*), HF21 25 3551 14 XI; **F** Precaudal vertebra. Brown trout (*Salmo trutta*), HF17 26 1633 12 IX; **G** Precaudal vertebra. Grayling (*Thymallus thymallus*), HF21 25 3785.1 15 XII; **H** Scale. Grayling (*Thymallus thymallus*), HF21 25 3785.2 15 XII; **I1** Left pharyngeal arch fragment. Common nase (*Chondrostoma nasus*), HF21 25 3316.1 14 XI; **I2** pharyngeal tooth fragment. Common nase (*Chondrostoma nasus*), HF21 25 3316.2 14 XI; **J** Left pharyngeal arch fragment. Common chub (*Leuciscus cephalus*), HF21 11 2411 14 XI. Scale 2 mm

H Scale. Grayling (*Thymallus thymallus*), HF21 25 3785.2 15 XII; **I1** Left pharyngeal arch fragment. Common nase (*Chondrostoma nasus*), HF21 25 3316.1 14 XI; **I2** pharyngeal tooth fragment. Common nase (*Chondrostoma nasus*), HF21 25 3316.2 14 XI; **J** Left pharyngeal arch fragment. Common chub (*Leuciscus cephalus*), HF21 11 2411 14 XI. Scale 2 mm

the northern parts of the Palearctic and Nearctic ecozones, ranging from the UK and northern Europe across Eurasia to Siberia. These fishes require cool, well-oxygenated water, preferably with a swift current; they are found in large, sandy- or gravel-bottomed rivers and lakes, but *T. thymallus* may occasionally be found in brackish conditions. Generally omnivorous, they feed primarily on crustaceans, insects, and zooplankton. As they are highly sensitive to changes in water quality, *Thymallus* fishes may be considered indicator species. This species can reach a maximum weight of 1.5 kg and a maximum size of 50 cm (Füllner et al. 2016). The brown trout (*S. trutta*), which has only been found in layers GH 9 and 12, requires oxygen-rich water and a specific temperature for

hatching and growing. Nowadays, *S. trutta* is usually found in cold running water with temperatures ranging from 0 to 20°C (Jonsson and Jonsson 2009; Elliott and Elliott 2010). The Danubian trout (*H. hucho*), only present in GH 10 and 14, is endemic to the Danube basin in Europe and reaches about 1.5 m in length and more than 50 kg in weight, although the average length is between 60 to 120 cm. This permanent cold-water salmonid spawns in April, when water reaches a temperature of 6 to 9 °C (Füllner et al. 2016).

The burbot (*Lota lota*), the only gadiform (cod-like) freshwater species, is present in the Hohle Fels assemblage throughout the sequence. This species has a circumpolar distribution above 40°N. Populations are continuous from the

British Isles across Europe and Asia to the Bering Strait. Burbot live in large, cold rivers, lakes, and reservoirs, primarily preferring freshwater habitats, but can thrive in brackish environments for spawning. During the summer, they are typically found in the colder water below the thermocline. As benthic fish, they tolerate an array of substrate types, including mud, sand, rubble, boulder, silt, and gravel for feeding. Burbot populations are fluvial during the winter months, and they migrate to near-shore reefs and shoals to spawn on the grounds of sand or gravel. As adults, they are primarily piscivores, preying on lamprey, whitefish, young northern pike, suckers, bullhead, and stickleback. This species can reach a maximum weight of 4 kg and a maximum size of 80 cm (Füllner et al., 2016).

The European bullhead (*C. gobio*) is found in Hohle Fels from GH 12 to 15 and is missing in the rest of the layers (GH 9–11). The European bullhead is a small demersal fish and prefers cold, clear, fast-flowing small streams and middle-sized rivers. It occurs on gravelly shores of cold lakes as well. The diet of this species is typically based on insects, crustaceans, and other invertebrates and it breeds in the spring. Some individuals can measure up to 15 cm although they are usually about 6 cm in length. This species is also a common prey of the burbot and other carnivorous fishes (Füllner et al., 2016).

The two species of cyprinids recovered from Hohle Fels are more typical of temperate waters and live in waters with temperatures between 10 and 25 °C (Doadrio 2002; Tissot and Souchon 2010). In Hohle Fels, the common chub (*L. cephalus*) is present in GH 12–14. This species is distributed throughout most of northern Eurasia, can reach lengths up to 60 cm, can weigh between 2 and 4 kg, and reach ages of 15–16 years (Füllner et al., 2016). The common nase (*C. nasus*) is only present in GH 14 and the individuals of this species are naturally found in drainages of the Black Sea (e.g. Danube), the southern Baltic Sea, and the southern North Sea. They range from 25 to 40 cm in length and weigh about 1 kg (Füllner et al., 2016). Accordingly, cyprinids such as the genus *Leuciscus* or *Chondrostoma* can be found in salmonid zones, as they also thrive in running water. However, cyprinids in general are present in multiple environments and show enormous diversity in their diet, which includes arthropods and other fishes (Doadrio, 2002).

The least represented species classified at Hohle Fels corresponds to the northern pike (*E. lucius*), represented in the assemblage by one caudal vertebra in GH 15. This species is carnivorous and typical of the fresh waters of the Northern Hemisphere. The northern pike has an average length of 50 cm but it can measure up to 150 cm and weigh 25 kg (Füllner et al., 2016).

No relevant environment changes are observed during the Hohle Fels sequence based on the fish remains since the majority of the identified species, such as the European grayling, the brown trout, the Danubian trout, the burbot, the bullhead, and the pike are common cold-water species

(Füllner et al., 2016). The presence of these species characterizes the fish assemblages as belonging to a pre-mountain river system with the presence of permanent, oxygen-rich, and cold running waters. Only the common chub and nase are associated with habitat with temperate water but can also live in cold waters (Doadrio, 2002).

Small mammals

A total of 6538 small mammal remains, corresponding to a MNI of 2310, were identified. Six insectivores, one bat (only identifiable at genus level as *Myotis* sp.), one small lagomorph (*Ochotona pusilla*), and 14 rodents are represented at Hohle Fels (Table 3, Fig. 5). A few taxonomical remarks: the red-toothed shrews, with intermediate size between *Sorex* ex gr. *araneus* and *S. minutus*, a slightly posterior position of the mandibular foramen and a somewhat slender condylar articulation (Fig. 5B) has been assigned to *S. tundrensis*, following van Kolfschoten (2014); *Neomys fodiens* and *N. anomalus* (Fig. 5D and 5E) have been separated following the metric criteria in Popov and Zidarova (2008); *Sicista* cf. *subtilis* and *S. cf. betulina* (Fig. 5T and 5U) have been separated following the morphological and metric criteria of Niethammer and Krapp (1982); the small size hamsters (Fig. 5S) have been assigned to *Allocricetus* vel *Cricetulus* sp. due to the low number of specimens which does not allow the morphological and morphometric population study necessary to discriminate between the two genera (Hir 1993; Cuenca Bescós 2003).

To reconstruct the environment and landscape in the surrounding of the site, we decided to apply the Habitat Weighting Method with two different sets of values, one indicating the ecological preferences of each species, to obtain a general view of the changes in the environment while the other is based on habitat suitability, which allows us to recognize oscillation in the sequence by including different categories and dividing them further into sub-habitats.

We also decided to give particular weight to the changes in the relative frequency of the two lemming species present at Hohle Fels, *Lemmus lemmus* and *Dicrostonyx torquatus*. These two species are in fact strongly linked to subarctic and tundra environments (Wilson et al. 2017; IUCN 2021). They are easily identifiable so that they cannot be confused with other arviculines in the sequence (Nadachowski 1982) and are therefore good indicators of cooling periods. A summary of the results of the environmental analysis is given in Fig. 6.

Based on the percentage of lemmings (Table 3, Fig. 6), GH 14 seems to represent a more temperate period than GH 15. Conditions got slightly cooler and then colder respectively in GH 13 and 12. During GH 11 and 10 it is possible to observe an amelioration but at GH 9 there seems to be a recrudescence of the colder climate. The results of Habitat Weighting based on ecological preferences describe four

Table 3 Identified taxa of small mammals from the Middle Paleolithic Geological Horizons (GH) in Hohle Fels. NISP: number of identified specimens; MNI: minimum number of individuals

	GH 9		GH 10		GH 11		GH 12		GH 13		GH 14		GH 15								
	NISP	% MNI	NISP	% MNI	NISP	% MNI	NISP	% MNI	NISP	% MNI	NISP	% MNI	NISP	% MNI							
<i>Talpa europaea</i>	1	1	1	0.61	2	1	0.22	5	1	0.28	2	1	0.37	10	3	0.55					
<i>Talpa</i> sp.	2		1		2						7			7							
<i>Sorex ex gr. araneus</i>	11	4	1.72	12	9	5.49	18	12	4.14	22	9	2.00	50	30	8.29	18	9	3.35	17	12	2.21
<i>Sorex minutus</i>	1	1	0.61	1	1	0.34				4	2	0.55	3	3	1.12	1	1	0.18			
<i>Sorex tundrensis</i>	1	1	0.43	2	2	1.22	1	1	0.34	7	4	0.89	7	4	1.10	4	3	1.12	19	12	2.21
<i>Sorex</i> sp.	3		5		6		20			42			35			41					
<i>Neomys cf. anomalus</i>	1	1	0.43				2	2	0.45	1	1	0.28	2	1	0.37	4	2	0.37			
<i>Neomys cf. fodiens</i>	1	1	0.43				3	3	0.67	1	1	0.28				5	3	0.55			
<i>Neomys</i> sp.	1		1		4		4			7			3			12					
Soricidae indet	5		11		9		18			112			95			54					
<i>Myotis</i> sp.							1														
<i>Ochotona pusilla</i>																					
<i>Alexandromys oeconomus</i>	28	15	6.47	32	16	9.76	30	16	5.52	41	22	4.90	61	36	9.94	53	29	10.78	87	46	8.46
<i>Arvicola amphibius</i>	15	3	1.29	16	3	1.83	45	6	2.07	27	6	1.34	36	9	2.49	26	10	3.72	65	11	2.02
<i>Chionomys nivalis</i>	4	3	1.29	9	6	3.66	10	7	2.41	10	7	1.56	19	11	3.04	10	6	2.23	12	6	1.10
<i>Clethrionomys glareolus</i>	1	1	0.43																		
<i>Dicrostonyx torquatus</i>	55	9	3.88	32	3	1.83	64	12	4.14	64	11	2.45	46	5	1.38	19	4	1.49	194	31	5.70
<i>Lastopodomys anglicus</i>	244	132	56.90	166	91	55.49	236	130	44.83	367	200	44.54	377	194	53.59	299	161	59.85	672	337	61.95
<i>Lemmus lemmus</i>	198	24	10.34	92	8	4.88	284	32	11.03	335	67	14.92	186	19	5.25	51	5	1.86	254	34	6.25
<i>Microtus arvalis</i>	74	38	16.38	36	23	14.02	182	71	24.48	226	114	25.39	86	45	12.43	56	29	10.78	62	38	6.99
Arvicolidae indet	3		5		16		27			23			29			32					
<i>Allocrietus</i> vel <i>Cricetulus</i> sp.													2	1	0.37	7	3	0.55			
<i>Apodemus cf. sylvaticus</i>													1	1	0.37						
<i>Allactaga cf. major</i>													1	1	0.28	1	1	0.37			
<i>Sicista cf. betulina</i>													1	1	0.28	1	1	0.37			
<i>Sicista cf. subtrilis</i>													1	1	0.22	4	2	0.74	1	1	0.18
<i>Sicista</i> sp.													1			1			2		
<i>Spermophilus superciliosus</i>	1	1	0.43	3	1	0.61	3	2	0.69	5	2	0.45	3	1	0.28	1	1	0.37	7	2	0.37
Total	644	232		426	164		906	290		1185	449		1069	362		727	269		1580	544	

different phases (Table 4). GH 15 to 13 represent a humid phase, with dominating open humid meadows (OH) and water-related environments (Wa). GH 12 and 11 represent a more arid phase, with an increase in open dry grassland (OD) and open woodland (OW) and a decrease in Wa and OH. Elements of mature forest (Wo) slightly decrease in this phase. In these two GHs, the relative percentage of *Microtus arvalis* reached its maximum, alongside a decrease in the proportion of *Lasiopodomys anglicus*, which however remains dominant (Table 3). This indicates a moment in the Late Pleistocene that can be considered relatively less cold than the following GHs, but still colder than the preceding phase when subarctic and tundra elements are less represented. GH 10 represents another relatively humid phase, while GH 9 presents again as cold and relatively dry (Fig. 6).

The Habitat Weighting based on habitat suitability offers a different perspective and allows us to understand better the changes in the landscape and environmental conditions (Table 5). It is interesting to notice that the forest component seems to be relatively stable throughout the sequence, except for GH 15 and GH 9 that present the lowest percentages. This stability might be linked to the constant presence of water in the Ach River system, as testified by the fish assemblage, that might have been able to support a riparian forest. The relative percentage of wetlands also does not vary much, although it is possible to divide the sequence into two phases: GH 15 to 13 with wetlands at >9%, and GH 12 to 9 with <9%. An interesting result is an increase in shrublands with a general decrease of all the other habitats, i.e. grassland, forest, wetlands, rocky, and desert, in GH 12 and partially in GH 11. This might indicate a process of degradation of the grasslands, possibly brought by the loss of ground-water resources, as indicated by the % of Wa and Wetland. It might also point to a stronger seasonality in precipitations that could generate generally drier conditions and facilitate woody plant encroachment (Archer et al. 2017).

To summarize, the landscape surrounding Hohle Fels during the deposition of the Middle Paleolithic Horizons was dominated by open environments, with forest components always present, due to the influence of the Ach River. GH 15 presents as relatively temperate and humid; GH 14 as more temperate and humid; GH 13 less temperate and humid; GH 12 and 11 cold and arid but relatively more temperate than the following periods; GH 10 is still cold but less arid; GH 9 clearly colder and arid.

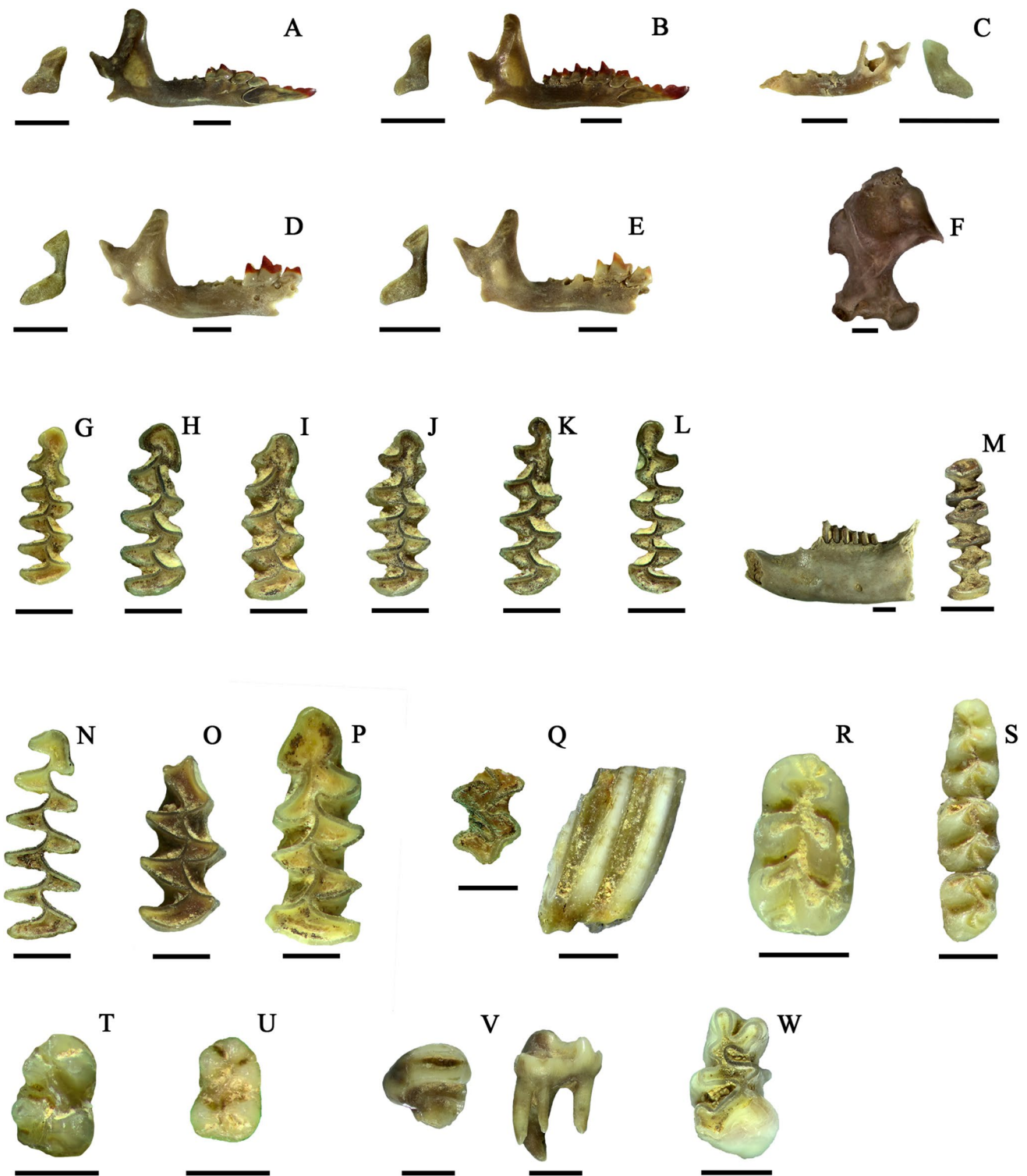
The data from the bioclimatic model are consistent with our environmental reconstruction (Table 6). The MATs inferred for the sequence are always lower than modern temperatures, between 4.2 (GH 14) and 9.48 °C (GH 9) less than the present. Ps are also significantly lower, between 638 (GH13) and 672.73 mm (GH9) less than present mean annual precipitation. After a relatively temperate and humid period (GH 13–15), climatic conditions became increasingly

colder and more arid (GH 9–12). These results confirm the trend already observed by Rhodes and Conard (2021) for GH 9–12. Furthermore, our reconstruction also coincides with the paleoclimatic data obtained from micromorphology analysis of GH 9–12 (Miller 2015), which showed a gradual decrease in temperate and humid conditions throughout the Middle Paleolithic layers excavated at the time.

Based on the limited radiocarbon dates available at the time for the lower GHs, Rhodes (2019) suggested that the shift in climatic conditions between GH 12 and 11 might take place around the time of the Greenland Interstadial (GI) 12, at ca. 47 ka cal BP. Using the new ESR dates available for GH 12 and the radiocarbon dates for the upper Middle Paleolithic Horizons, we can tentatively try to relate the different GHs to the oxygen isotope curve for the Late Pleistocene (Fig. 7). GH 12, dated at 62.5 ± 4 ka (Conard et al. 2021), corresponds to the end of Marine Isotope Stage (MIS) 4—beginning of MIS 3. Given its relatively temperate signal, it might correspond to the GI 18 (ca. 64 ka BP) or to the beginning of MIS 3 (ca. 59–57 ka BP) (after Rasmussen et al. 2014). Consequently, GH 15 to 13 probably correspond to the end of MIS 5 (ca. 87–71 ka BP, after Rasmussen et al. 2014), and we can cautiously assign GH 14, with the highest MAT, to GI 21, 20, or 19, while GH 15 and 13 to the cooling periods preceding and following it (as described in Wohlfarth 2013). GH 11 to 9 show a trend toward colder and more arid conditions, typical of MIS 3, but it is not possible at the time to correlate these GHs to any particular point of the curve.

Small mammals: biochronological inferences

Furthermore, the stage of evolution of the water vole *Arvicola amphibius* as quantified by the Schmelzband-Differenzierungs-Quotient (SDQ) can help with the chronological attribution of the lower Middle Paleolithic Horizons. A general decrease in the value of SDQ index is observed in water vole populations all across Europe during the Middle and Late Pleistocene (Heinrich 1990; van Kolfschoten 1992; Koenigswald von 1994; van Kolfschoten and Turner 1996; Desclaux et al. 2000; Maul et al. 2000; Paunescu et al. 2004; Kalthoff et al. 2007; Cuenca-Bescós et al. 2010). However, this trend is not perfectly smooth through time or synchronous in all regions (Maul and Markova 2007; Maul et al. 2007, 2014; Masini et al. 2020). Hence, criticisms have been made about the use of the SDQ index as a tool for specific determination and/or stratigraphic correlations (Escudé et al. 2008; Martin 2014). The SDQ pattern is in fact influenced by factors including climate, geography, altitude, latitude, and migration (Kratovichil 1981; Röttger 1987; van Kolfschoten 1992; Ruddy 2011) but, even considering its limits, the SDQ index remains a very powerful descriptive tool and, given the amount of study and analysis presented in literature, a solid base for comparison.



Furthermore, once the context is taken into account (i.e., the small mammal assemblage as a whole, the geographic position, the possibility of contact between different populations, and the morphology of the molars), it is possible to use the SDQ index to obtain a reliable biochronological indication for the relative age of a site.

Only GH 15, 14, 13, and 12 at Hohle Fels present complete first lower molars of *A. amphibius* which could be measured (Table 7). Although the number of specimens analysed is limited, it is possible to see that the values for the index in GH 15, 14, and 13 are >90, while the value of the sample from GH 12 is only 84.2. Compared with SDQ values of populations from

Fig. 5 **A** *Sorex* ex gr. *araneus*, condylar process and right mandible, HF_25-GH12-154; **B** *Sorex tundrensis*, condylar process and right mandible, HF_25-GH12-155; **C**: *Sorex minutus*, left mandible and condylar process, HF_28d-GH13-432; **D** *Neomys fodiens*, condylar process and right mandible, HF_28c-GH15-n4001; **E** *Neomys anomalus*, condylar process and right mandible, HF_27a-GH15-n3434; **F** *Talpa europaea*, left humerus, HF_27b-GH15-n3411. Scale 2 mm. **G** *Microtus arvalis*, right m1, HF_27b-GH15-672; **H**: *Chionomys nivalis*, right m1, HF_27b-GH9-345; **I** *Alexandromys oeconomicus*, right m1, HF_26a-GH15-115; **J** *Lasiopodomys anglicus*, right m1, HF_27b-GH9-355; **K** *Lasiopodomys anglicus*, right m1, HF_27b-GH9-356; **L** *Lasiopodomys anglicus*, left m1, HF_27b-GH9-357; **M** *Ochotona pusilla*, left mandible, lateral and occlusal view, HF_26a-GH14-n1887; **N** *Dicrostonyx torquatus*, right m1, HF_26a-GH15-117; **O** *Lemmus lemmus*, right m1, HF_25-GH12-77; **P** *Arvicola amphibius*, left m1, HF_27a-GH15-25; **Q** *Clethrionomys glareolus*, left M2, occlusal and lateral view, HF_27b-GH9-316; **R** *Apodemus* cf. *sylvaticus*, right m1, HF_27a-GH14-505; **S** *Alloricetus* vel *Cricetulus* sp., left m1, m2, m3, HF_25d-GH15-329; **T** *Sicista* cf. *subtilis*, left m1, HF_27a-GH14-506; **U** *Sicista* cf. *betulina*, left m1, HF_28-GH13-446; **V** *Spermophilus* cf. *superciliosus*, right M3, occlusal and lateral view, HF_25d-GH15-42; **W** *Allactaga* cf. *major*, right m1, HF_25c-GH 14.1–187. Scale 1 ms

Central Europe (Heinrich 1990; Kalthoff et al. 2007; Maul et al. 2014), our data suggest that GH 15 to 13 might be related to the Early Weichselian (MIS 5d–5a) while GH 12 belongs to a later period, in accordance with the ESR dates obtained for GH 12 and with our paleo-environmental and -climatic reconstruction.

Were Neanderthal occupations at Hohle Fels influenced by climatic and environmental changes?

Neanderthal subsistence practices in freshwater ecosystems

Several authors presented evidence of aquatic resources exploitation during the Lower Paleolithic in Africa (Brooks et al. 1995; Yellen et al. 1995) and Neanderthal marine coastal adaptation, including fishing activities, in the Iberian Peninsula and the Atlantic coast (e.g., Morales-Muñiz and Roselló-Izquierdo 2005; Stringer et al. 2008; Brown et al. 2011; Zilhão et al. 2020). Nevertheless, the possibility of the exploitation of continental freshwater ecosystems in Western-Central Europe by Neanderthal groups has not often been the subject of systematic research. This is partially due to the lack of well-preserved, abundant assemblages. However, the study of inland fishing activities, occurring close to rivers or lakes, during the Middle Paleolithic has been shown to have great potential by authors who have already analysed this topic with interesting results (e.g., Blanco-Lapaz 2019; Guillaud et al. 2021).

Our analysis shows that the freshwater ecosystem around this site was characterized by a pre-mountain river system with the presence of permanent, oxygen-rich, and cold running waters inhabited by preys suitable to humans, due to their relatively larger size and weight (Morales-Muñiz and Roselló-Izquierdo 2005). Other Middle Pleistocene sites in

Western Europe show smaller fish accumulations, indicating probably that this abundance of fish results from birds of prey or small-medium carnivores (Guillaud et al. 2021). Based on our preliminary results on the Hohle Fels fish remains, we cannot discard fishing as part of the subsistence practices of Paleolithic hunter-gatherers in Central Europe. However, future studies on fish remains would be necessary to better understand the local freshwater ecosystems, the taphonomic history of fish accumulation, and how fish constitute part of the human diet. In an effort to address some of these issues, additional studies from other Swabian Palaeolithic sites are underway. Exploring more fish assemblages from Middle Paleolithic sites could also help to investigate, and possibly refute, the existing paradigm that Neanderthals were unable to use fishes as a resource in continental waters (Morales-Muñiz and Roselló-Izquierdo 2005; Conard et al. 2013; Guillaud et al. 2021; Blanco-Lapaz et al. 2021).

Neanderthal occupations at Hohle Fels Cave

The upper units attributed to the Middle Paleolithic, corresponding to AH VI-IX / GH 9–12, are relatively poor in anthropogenic finds (i.e., lithic industries, burned bones, modified bones) (Conard et al. 2012). Going from bottom to top, the density of the finds decreases and the layer underlying the first Aurignacian proved to be essentially sterile (Conard and Bolus 2008). This led to the hypothesis that the last Neanderthal groups and the first modern human inhabited the cave with little or no overlaps (Conard et al. 2006). The low density of finds in AH VI-IX might indicate frequent moves and few long-term occupations by large groups of Neanderthals and, although well-adapted to the steppe environment, population density also appears to be low (Conard et al. 2012). On the other hand, the new lower Middle Paleolithic units, corresponding to AH X-XI / GH 13–15, present a relatively high finds density, not comparable with the density of the Aurignacian layers, but remarkably higher than those of AH VI-IX (Conard et al. 2021). This increase in anthropogenic findings coincides with the more temperate climatic phase detected by the analysis of the small mammal assemblage. This suggests that Neanderthals used the cave more intensely during periods with less harsh conditions. The increased levels of all classes of anthropogenic materials reflect the presence of larger groups, occupations for longer periods, or both. The archaeological signal might also point to higher population density at the end MIS 5 than during MIS 3. Changes in sedimentation rates and taphonomic factors including biological, geological, and/or anthropogenic influences might also contribute to the differences in anthropogenic signals between AH VI-IX and AH X-XII. Thus, more studies are ongoing to ascertain the characteristics of the newly excavated AHs. Here, it is important to note that the deepest part of the excavation currently corresponds to only 6m², and a far greater sample is needed to confirm or refute these trends.

Fig. 6 Paleoenvironmental reconstruction for the Middle Paleolithic Horizons of Hohle Fels. GH: geological horizons; OD: open dry; OH: open humid; Wa: water-related environment. % of *Lemmus + Dicrostonyx* indicates subarctic and tundra environments

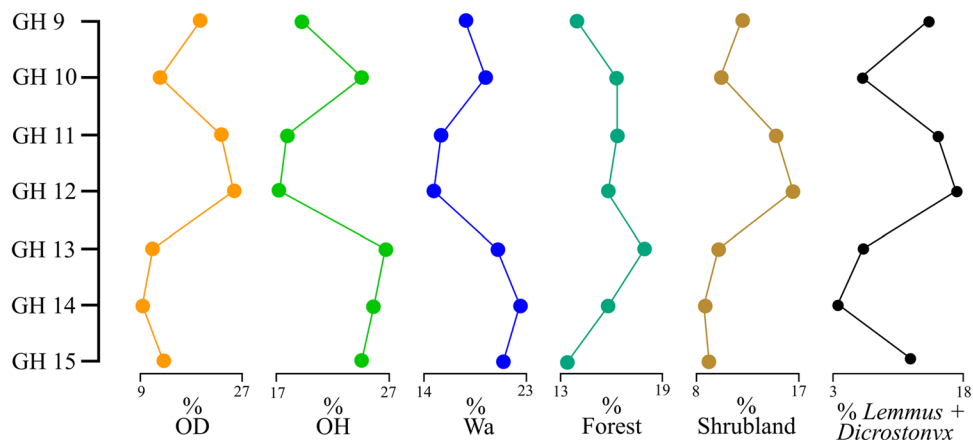


Table 4 Paleoenvironmental reconstruction based on ecological preferences of rodents and insectivores. GH: geological horizons; OD: open dry; OH: open humid; OW: open woodland; Wo: woodland; R: rocky environment; Wa: water-related environment. Values are expressed in percentages

	OD	OH	OW	Wo	R	Wa
GH 9	19.29	19.18	25	3.02	15.52	18
GH 10	12.65	24.24	22.41	3.35	17.53	19.82
GH 11	24.31	17.41	26.21	2.67	13.62	15.78
GH 12	26.17	16.54	27.73	1.84	12.69	15.03
GH 13	11.77	26.18	21.26	3.25	16.48	21.05
GH 14	9.05	25.28	21.46	4.29	17.26	22.67
GH 15	13.42	23.99	20.94	3.69	16.65	21.31

Table 5 Paleoenvironmental reconstruction based on habitat suitability of rodents and insectivores. GH: geological horizons. Values are expressed in percentages

	Forest	Shrubland	Grassland	Wetland	Rocky	Desert
GH 9	14.17	12.14	64.22	8.00	1.29	-
GH 10	16.79	10.25	60.30	8.84	3.66	-
GH 11	16.85	15.07	56.55	8.87	2.41	-
GH 12	15.90	16.50	57.26	8.52	1.56	-
GH 13	17.94	10.16	58.04	10.63	3.05	0.04
GH 14	15.87	8.87	62.95	9.74	2.24	0.21
GH 15	13.50	9.06	65.84	10.17	1.11	0.22

Table 6 Paleoclimatic reconstruction based on the Bioclimatic Model. GH: Geological Horizons; MAT: mean annual temperature (fit); P: mean annual precipitations (fit), with lower (lwr) and upper

(upr) limit values. ΔT : difference between the obtained MAT and the current mean annual temperature. ΔP : difference between the obtained P and the current mean annual precipitation

	MAT (°C)				P (mm)			
	fit	lwr	upr	ΔT	fit	lwr	upr	ΔP
GH 9	-1.18	-7.37	5.02	-9.48	386.27	-177.77	950.33	-672.73
GH 10	1.07	-5.23	7.37	-7.23	403.93	-169.93	977.80	-655.07
GH 11	1.19	-5.12	7.50	-7.11	405.52	-168.67	979.72	-653.48
GH 12	2.49	-3.78	8.76	-5.81	404.74	-166.24	975.74	-654.26
GH 13	3.09	-3.28	9.46	-5.21	421.51	-158.49	1001.52	-637.49
GH 14	4.10	-2.19	10.39	-4.20	417.49	-155.06	990.05	-641.51
GH 15	3.24	-3.04	9.51	-5.06	407.94	-163.06	978.94	-651.06

Fig. 7 Bioclimatic reconstruction for the Middle Paleolithic Horizons of Hohle Fels with tentative correlation to the Isotope Curve (after Lisiecki and Raymo 2005). MAT: mean annual temperature; P: mean annual precipitations

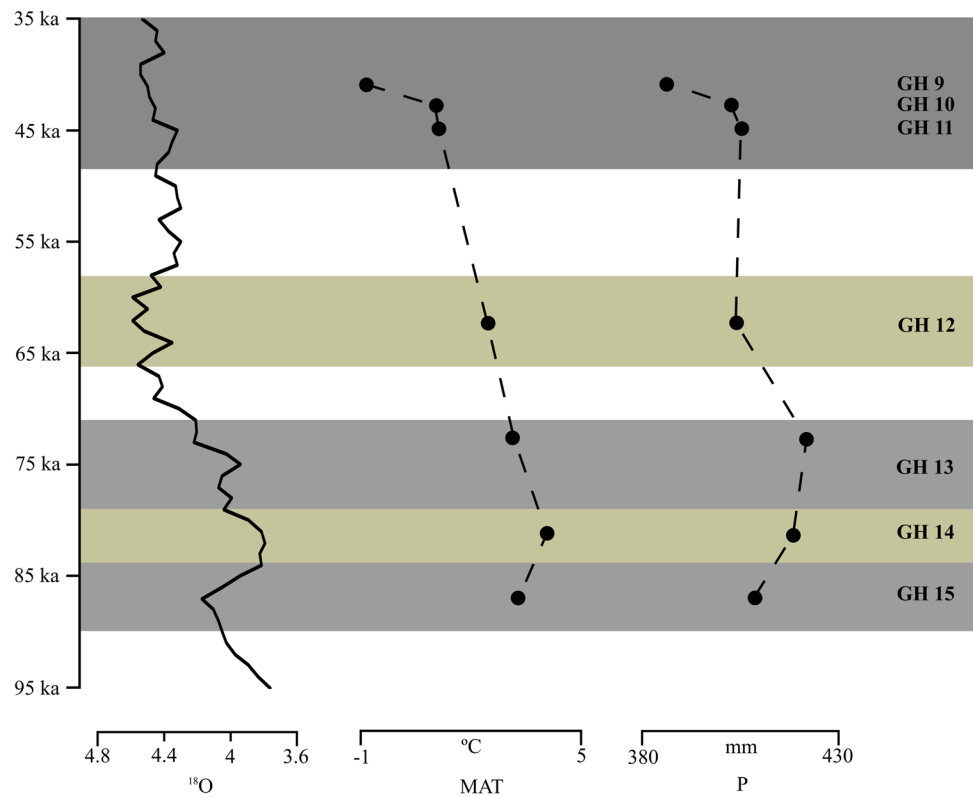


Table 7 SDQ values for *Arvicola amphibius*. GH: geological horizons; n: number of specimens; min: minimum value; max: maximum value; SD: standard deviation

	n	Mean	Median	Min	Max	SD
GH 12	8	84.57	84.2	73.52	92.42	5.81
GH 13	7	88.73	91.13	76.19	97.1	7.39
GH 14	9	97.84	98.03	89.06	105.55	4.51
GH 15	12	90.70	91.6	81.8	100.69	6.23

Among the findings from AH X, the most remarkable is the presence complete leaf point, the first one recovered in situ in the Swabian Jura after the 1936 excavation at Haldenstein (Lone Valley) conducted by Riek (Riek 1938). The leaf point is 7.6 cm long, 4.1 cm wide, 0.9 cm thick, made from locally available, grey Jurassic chert from the Swabian region. It was hafted at the less pointy end, probably used as a projectile during hunting, and discarded after a failed attempt at resharpening (Rots et al. 2021). In Germany, leaf points are referred to as “Blattspitzen” and until now, the Blattspitzengruppe, the cultural unit to which the leaf points belong, has been assigned to the final Middle Paleolithic (Bosinski 1967; Conard and Fischer 2000; Bolus 2004, 2011). The new dates for GH 12, combined with the biostratigraphic signal of *A. amphibius* and the climatic reconstruction here presented, would place the leaf point of Hohle Fels at a much earlier time than expected and thereby questioning the traditional cultural chronology of Swabian Jura. Here, it is important to reiterate that our biostratigraphic arguments are consistent with new

radiometric dates (Conard et al. 2021). A reappraisal of this cultural unit and its chronological attribution is needed to document Middle Paleolithic technology and hunting strategies, as well as to refine our understanding of the circumstances that led to the extinction of Neanderthals. Every indication suggests that the ongoing excavations at Hohle Fels will continue to contribute to these research questions.

Neanderthal occupations at Hohle Fels Cave in the context of Central-Western Europe (Germany, Belgium, Poland, and France)

The small mammal assemblages related to the Middle Paleolithic GHs at Hohle Fels provide a fundamental regional reference for this chronology, for its sample size, and for the reliable dates available for the sequence. The assemblage of Geißenklosterle (GHs 23–18, Ach Valley, Rhodes et al. 2018) is dated to the end of MIS 5 up to MIS 3 (Richard et al. 2019b). It is smaller in size, but consistent in faunal

composition with the Hohle Fels one. The assemblage of Stadel-Höhle at Hohlenstein (Lone Valley, Ziegler 2019) is dated to the MIS 3 (Richard et al. 2019a) and it differs from the Hohle Fels one for the presence, although sporadic, of *Clethrionomys glareolus*, *Glis glis*, *Sciurus vulgaris*, *Apodemus* sp., indicators of woodland and forest patch, and of *Ochotona pusilla* and large- and small-size hamsters, indicators of open and arid environments. These differences might indicate that micro-environmental and micro-climatic conditions were not the same in the two valleys during the last Neandertal occupations.

A recent publication by Rhodes and Conard (2021) suggests that climatic conditions in the Ach Valley were colder and more arid than in other Central European sites with the same chronology as GHs 12–7 of Hohle Fels. The present study confirms these results also for the lower GHs 15–13. The small mammal assemblage from Sesselfelsgrotte (Germany, layers L-G, MIS 4–3; van Kolfschoten 2014) indicates generally more temperate conditions than those registered at Hohle Fels, due to the relative dominance of *M. arvalis/agrestis* over *L. anglicus* (= *Microtus gregalis*) and the presence of *C. glareolus*. Data from small mammal assemblages directly related to Middle Paleolithic occupations at Scladina Cave (MIS 5–3, López-García et al. 2017a, 2017b) and Marie-Jeanne Cave (MIS 3, López-García et al. 2017a), both located in Belgium, indicate more temperate conditions than at Hohle Fels, testified by the presence of *C. glareolus*, *Microtus (Terricola) subterraneus*, *Glis glis*, and *Apodemus* gr. *sylvaticus/flavicollis*. During MIS 5, the landscape at Scladina and Marie-Jeanne Caves was always dominated by woodland, while that at Hohle Fels open environment is always dominant. During both MIS 5 and MIS 3, the mean annual precipitation indicates more humid conditions than at Hohle Fels. Similar comparisons can be drawn between the Hohle Fels assemblage and the assemblage from Biśnik Cave (MIS 5–3, layers 13 to 9; Socha 2014) in Poland. Both faunal composition and bioclimatic reconstructions indicate more temperate and humid conditions than at Hohle Fels. The small mammals from Obłazowa Cave (Poland, early MIS 3; Valde-Nowak and Nadachowski 2014) also indicate more humid conditions, due to the relatively high percentage of *A. oeconomicus*. Another recent study concerning small mammal assemblages in Middle Paleolithic context at Koziarnia Cave (Poland, Berto et al. 2021) indicates a general dominance of the open environment, but the sample size does not allow for further comparisons. According to the environmental reconstructions of Discamps and Royer (2017), the conditions at Hohle Fels seem to be close to those of the sites of the Atlantic region (i.e. Charente-Maritime, Charente, and Gironde, see Fig. 1), with *L. anglicus* dominant over *M. arvalis/agrestis* and generally dry and open landscape, while in the rest of southern France conditions seem more humid and temperate, with a higher component of shrubland and woodland.

In this context, the Middle Paleolithic occupations registered at Hohle Fels both during MIS 5 (GHs 15–13) and MIS4-3 (GHs 12–9) took place in a more arid and colder environmental setting than those registered in Sesselfelsgrotte, Poland, and Belgium. Further studies are needed to clarify if this is a local (Ach Valley) or regional (Swabian Jura) peculiarity.

Conclusions

The joint study of fish and small mammal assemblages from the Middle Paleolithic of Hohle Fels provided insights into the climatic and environmental conditions faced by Neanderthals in the Ach Valley. The freshwater ecosystem around this site was characterized by a pre-mountain river system with the presence of permanent, oxygen-rich, and cold running waters. The landscape was dominated by an open environment, and thanks to the presence of the Ach river, the forest component was always relatively stable throughout the sequence. Our research has identified two major climatic oscillations: one more temperate corresponding to Neandertal occupations of relatively high intensity, the other colder and more arid, presenting a trend toward increasingly harsher conditions, characterized by low-intensity Neandertal occupations. Future studies, including additional material from Aurignacian, Gravettian, and Magdalenian units of Hohle Fels (already ongoing) will provide further knowledge about the changes in climate and environment during the human occupations at Hohle Fels. This ongoing research will document how human groups interacted with and adapted to the different climatic settings and will further illuminate their use of freshwater resources.

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Author contributions E. Luzi and S. Rhodes analysed the small mammal assemblage. Á. Blanco-Lapaz analysed the fish assemblage. N. Conard directs the excavation at Hohle Fels provided archaeological and geological context and funding. The manuscript was written by E. Luzi. All authors contributed to sections of the manuscript. All authors reviewed and approved the manuscript before submission.

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Data availability Raw data are available upon request. Corresponding author contact: elisa.luzi@ifu.uni-tuebingen.de.

Declarations

Competing interests The authors declare no competing interests.

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