



# Aquatic resources exploitation during the Palaeolithic in the Swabian Jura based on fish remains from Hohlenstein-Stadel Cave

*Die Nutzung aquatischer Ressourcen während des Paläolithikums auf der Schwäbischen Alb: Fischreste aus der Stadel-Höhle im Hohlenstein*

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**ABSTRACT** - Large game has generally biased our interpretations about Palaeolithic subsistence practices. Studies based on small game and birds point to their exploitation by archaic and modern humans in Central Europe, but studies of aquatic resources and, more specifically, of fish remains are still scarce. Hohlenstein-Stadel in the Swabian Jura represents a well-documented Palaeolithic cave for studying diverse food resources that were available and potentially exploited by humans. The site is also notable for its early Upper Palaeolithic mobiliary art, a prominent example being the Lion Man ivory figurine.

Our study focuses on the fish remains that were collected by water-screening during 2009-2013 excavations and sheds light on aspects such as taxonomy, taphonomy and paleoecology. These remains were found in the Middle Palaeolithic layers, with an age between 45 ka calBP and 42 ka calBP, and the Aurignacian layers, with an age between 35 and 40 ka calBP. The taxonomic study of the fish remains help us characterize the freshwater palaeoenvironment in this region as well as the relationship, including fishing strategies, between humans and fish. The identified species belong to European grayling (*Thymallus thymallus*), burbot (*Lota lota*), and European bullhead (*Cottus gobio*), which are all common species that inhabit cold waters. Only one cyprinid is recovered in the assemblage, corresponding to the chub (*Squalius cf. cephalus*). The remains also demonstrate diversified subsistence strategies with a significant contribution of small game during the Middle Palaeolithic and Aurignacian in Europe.

**ZUSAMMENFASSUNG** - Großwild hat im Allgemeinen unsere Interpretationen zu paläolithischen Subsistenzpraktiken bestimmt. Studien zu Kleinwild und Vögeln weisen auf ihre Ausbeutung durch den archaischen und modernen Menschen in Mitteleuropa hin, Studien zu aquatischen Ressourcen und insbesondere zu Fischresten sind jedoch noch selten. Der Hohlenstein-Stadel auf der Schwäbischen Alb stellt eine gut dokumentierte altsteinzeitliche Höhle zur Erforschung verschiedener verfügbarer und potenziell nutzbarer Nahrungsressourcen dar. Die Stätte ist auch für ihre frühe jungpaläolithische mobile Kunst bekannt, ein prominentes Beispiel ist die Elfenbeinfigur des Löwenmenschen. Unsere Studie konzentriert sich auf die Fischreste, die während der Ausgrabungen 2009-2013 durch Schlämmen gesammelt wurden, und beleuchtet Aspekte wie Taxonomie, Taphonomie und Paläoökologie. Diese Überreste wurden in den mittelpaläolithischen Schichten mit einem Alter zwischen 45 ka calBP und 42 ka calBP und in den Aurignacian-Schichten mit einem Alter zwischen 35 und 40 ka calBP gefunden. Die taxonomische Untersuchung der Fischreste hilft uns, die Süßwasser-Paläoumgebung in dieser Region sowie die Beziehung zwischen Mensch und Fisch, einschließlich der Fangstrategien, zu charakterisieren. Die identifizierten Arten gehören zur Europäischen Äsche (*Thymallus thymallus*), zur Quappe (*Lota lota*) und zur Europäischen Groppe (*Cottus gobio*), alles Arten, die kalte Gewässer bewohnen. Nur ein Cyprinide wurde in den Proben gefunden, der dem Döbel entspricht (*Squalius cf. cephalus*). Die Überreste zeigen auch diversifizierte Subsistenzstrategien mit einem signifikanten Beitrag von Kleintieren während des Mittelpaläolithikums und Aurignacian in Europa.

**KEYWORDS** - Hohlenstein-Stadel, Middle Palaeolithic, Aurignacian, freshwater fish, Seasonality, Swabian Jura  
*Hohlenstein-Stadel, Mittelpaläolithikum, Aurignacien, Süßwasserfisch, Saisonalität, Schwäbischen Alb*

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## Introduction

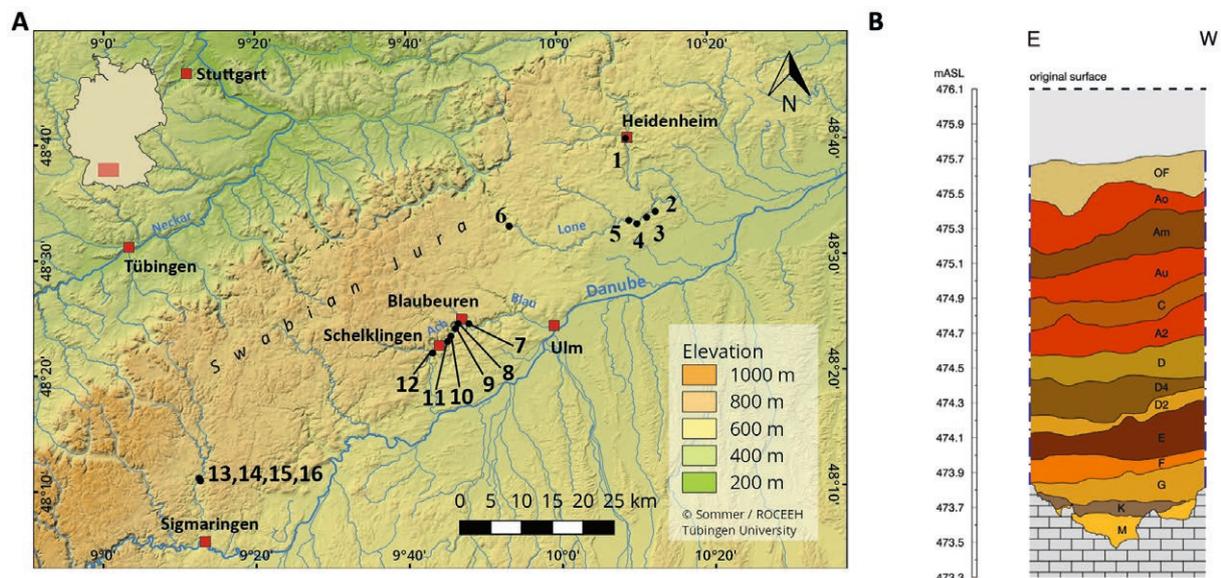
The Swabian Jura in southwestern Germany plays a special role in our understanding of Neanderthal and modern human occupations during the Palaeolithic in Central Europe. Although multiple sites with amazing finds have been discovered, four cave sites are especially important due to their find richness: Geißenklösterle (Conard et al. 2019; Hahn 1988) and Hohle Fels (Conard 2009), in the Ach Valley; and Vogelherd (Niven 2006; Riek 1934) and Hohlenstein-Stadel (Wetzel 1961; Kind 2019) (Fig. 1: A), in the Lone Valley. All four caves are also listed as UNESCO World Heritage Sites (Heidenreich & Meister 2019).

The Hohlenstein site complex (48°32'57"N 10°10'21"E) (Fig. 1: A) is a large rocky massif located at the southern rim of the Lonetal (Lone Valley) in the Swabian Jura (Baden-Württemberg, Germany), about 25 km northeast of the city of Ulm. This massif has yielded at least three Palaeolithic cave sites. Bärenhöhle, in the western part of the massif, has mostly yielded Middle and Upper Palaeolithic finds. Kleine Scheuer, to the east of Bärenhöhle, is a rockshelter where Late Upper Palaeolithic artefacts were discovered. Hohlenstein-Stadel, the focus of this study, is located in the eastern part of the massif

and is beyond doubt the most important of the three sites (Kind et al. 2014). Hohlenstein-Stadel shows an impressive Late Pleistocene stratigraphy with layers dating from the Middle Palaeolithic to the Magdalenian (Wetzel 1961). Excavations took place from 1935 to 1939 and from 1956 to 1961, under the direction of Robert Wetzel, as well as between 2008 and 2013, by the State Office for Cultural Heritage Baden-Württemberg (Kind 2019).

Our analysis consists of fish remains that were recovered from a small sondage (11 m<sup>2</sup>) 25-30 m from the cave entrance during the 2009-2013 excavations, which were conducted by the State Office for Cultural Heritage Baden-Württemberg. Kind (2019) described 17 layers in total and an excavation area with 11 quadrants. The basal layer, Layer M, is archaeologically sterile but the subsequent twelve layers (K-M to C) belong to the Middle Palaeolithic.

Barbieri and Miller (2019), in their geoarchaeological studies, note that the lowest layer, K-M, is characterized by a rich presence of bone, tooth and coprolite material signifying the use of the cave by various animals. In this layer, a few charcoal fragments and lithic artefacts represent the evidence of human activity. Layer K appears to contain more fragments of burnt bones than Layer K-M, a fact that could be



**Fig. 1. A:** General location of the Hohlenstein-Stadel Complex and the Swabian Jura sites: 1. Heidenschmiede, 2. Langmahdhalde, 3. Vogelherd, 4. Hohlenstein site complex: Stadel, Bärenhöhle and Kleine Scheuer, 5. Bockstein, 6. Haldenstein, 7. Große Grotte, 8. Brillenhöhle, 9. Geißenklösterle, 10. Sirgenstein, 11. Hohle Fels, 12. Kogelstein, 13. Annakapelielhöhle, 14. Göpfelsteinhöhle, 15. Schafstallhöhle, 16. Nikolaushöhle. Modified from © Sommer/ROCEEH Universität Tübingen. **B:** Hohlenstein-Stadel Cave. Idealized stratigraphic sequence of the new excavations from 2009-2013. The layers K-M (not pictured in the figure, Layer K-M existed in addition to those in this idealized profile) to C belong to the Middle Palaeolithic, the layers Au, Am, and Ao to the Aurignacian. Layer M is archaeologically sterile, layer OF is a surface with sediment mixing. © State Office for Cultural Heritage Baden-Württemberg. Modified from Kind et al. 2014.

**Abb. 1. A:** Lage des Hohlenstein-Stadel Komplex und verschiedener Fundstellen auf der Schwäbischen Alb: 1. Heidenschmiede, 2. Langmahdhalde, 3. Vogelherd, 4. Hohlenstein: Stadel, Bärenhöhle und Kleine Scheuer, 5. Bockstein, 6. Haldenstein, 7. Große Grotte, 8. Brillenhöhle, 9. Geißenklösterle, 10. Sirgenstein, 11. Hohle Fels, 12. Kogelstein, 13. Annakapelielhöhle, 14. Göpfelsteinhöhle, 15. Schafstallhöhle, 16. Nikolaushöhle. Geändert nach © Sommer/ROCEEH Universität Tübingen. **B:** Hohlenstein-Stadel-Höhle. Idealierte stratigraphische Abfolge der neuen Ausgrabungen von 2009-2013. Die Schichten K-M (in dieser Abb. nicht dargestellt) bis C gehören zum Mittelpaläolithikum, die Schichten Au, Am und Ao zum Aurignacian. Schicht M ist archäologisch steril, Schicht OF stellt eine Sedimentmischung an der Oberfläche dar. © Landesamt für Denkmalpflege Baden-Württemberg. Modifiziert nach Kind et al. 2014.

associated with increased human presence. Few intense erosional events were present in Layer G, and Layer F is characterized by a higher frequency of coprolite fragments and phosphate loess. No further changes were observed throughout layers D2 and D4 where the pieces of bone are particularly well preserved. Layer D lacks phosphate minerals, bones, and charcoal, which suggests that humans and animals were not present in the cave during the accumulation of these sediments. Layer A2, which also contains numerous coprolites, bone and tooth fragments, shows no significant changes when compared to the other Middle Palaeolithic layers of the sequence. Layer C shows a slight but significant decrease in the proportion of coprolites, phosphate crusts, weathered bones, and splinters of teeth. In conclusion, Barbieri and Miller (2019) demonstrate the continuous presence of large carnivore activity (except for layer D), such as hyenas, during the Middle Palaeolithic as well as occasional human activities, which is indicated by the fragments of burnt bone.

Kind (2019) studied the lithic artefacts (N = 631) proving that the lithic raw materials from this site as others in the Swabian Jura are dominated by local Jurassic cherts ca. 3 km of the sites (Conard et al. 2012; Çep, 2013). Although all levels except layer M testify to human occupation in Hohlenstein-Stadel, the majority of the lithic material is recovered from Layer A2 (N = 96), D (N = 210) and K-M (N = 113) and only partial reduction sequences can be reconstructed within the assemblage, characterized by the low presence of blades, cores and tools (Tab. 1). The low frequency of lithic artifacts, appear to reveal characteristics typical of many layers from caves in southwestern Germany during the same period (Conard et al. 2012; Kind 2019). Previous research has demonstrated that the Middle Palaeolithic assemblages

resulted from short and sparse Neanderthal occupations (Beck 1999; Kitagawa 2014; Kind 2019), which has been documented at other sites in the Swabian Jura (e.g., Conard et al. 2012; Böttcher et al. 2001). Hohlenstein-Stadel has also yielded a Neanderthal remain, which corresponds to a right femur shaft from a male individual (Kunter & Wahl 1992) and has been analyzed for paleogenetics (Posth et al. 2017).

On the top of the stratigraphic sequence of the recent excavations, three Aurignacian layers (35,361-40,421 calBP) (Au-Ao) (Tab. 2) were characterized by an extremely low density of lithic artefacts (N = 18) (Tab. 1). Animal remains were, however, common in these layers. Geoarchaeological studies show that, in comparison to the Middle Palaeolithic sequence, the phosphatic proportions in the Aurignacian layers are lower and there is evidence of a change in the sedimentation which favored the preservation of calcite. This change could indicate several scenarios such as lower availability of water from the karst landscape or lower acidity, which resulted from fewer animals in the cave (Barbieri & Miller 2019). Organic tools, such as projectile points, awls and retouchers, made from bone, antler and ivory, were recovered from these Aurignacian layers in both the recent excavations and the earlier excavations of Wetzel (Wetzel 1961; Hahn 1989). Similar artefacts were also recovered from the Aurignacian horizons in Hohle Fels and Geißenklösterle (Wolf 2015; Kitagawa & Conard 2020). In addition, the new excavations in Hohlenstein-Stadel revealed perforated personal ornaments including fox canines/incisors, wolf incisors, reindeer canine as well as an ivory pendant, adding to the handful of personal ornaments which were found in the earlier excavations of Wetzel (Beutelspacher et al. 2011; Hahn 1988; Kind et al. 2014; Kind 2019). Two human teeth (an unerupted lower left third premolar and an unerupted

Layers	Flakes	Blades	Chunks	Cores	Chips	Tools	Total
Ao	-	-	-	-	1	-	1
Am	3	3	-	-	2	-	8
Au	1	-	-	-	8	-	9
C	3	-	-	1	8	-	12
A2	21	1	1	2	71	-	96
D	43	-	11	1	151	4	210
D4	4	-	1	-	9	-	14
D2	1	-	2	-	4	-	7
E	-	-	2	-	13	1	16
F	7	-	2	-	24	-	33
G	4	-	-	-	15	-	19
J-L	23	2	7	2	89	1	124
K-M	17	-	6	-	58	1	82
Total	127	6	32	6	453	7	633

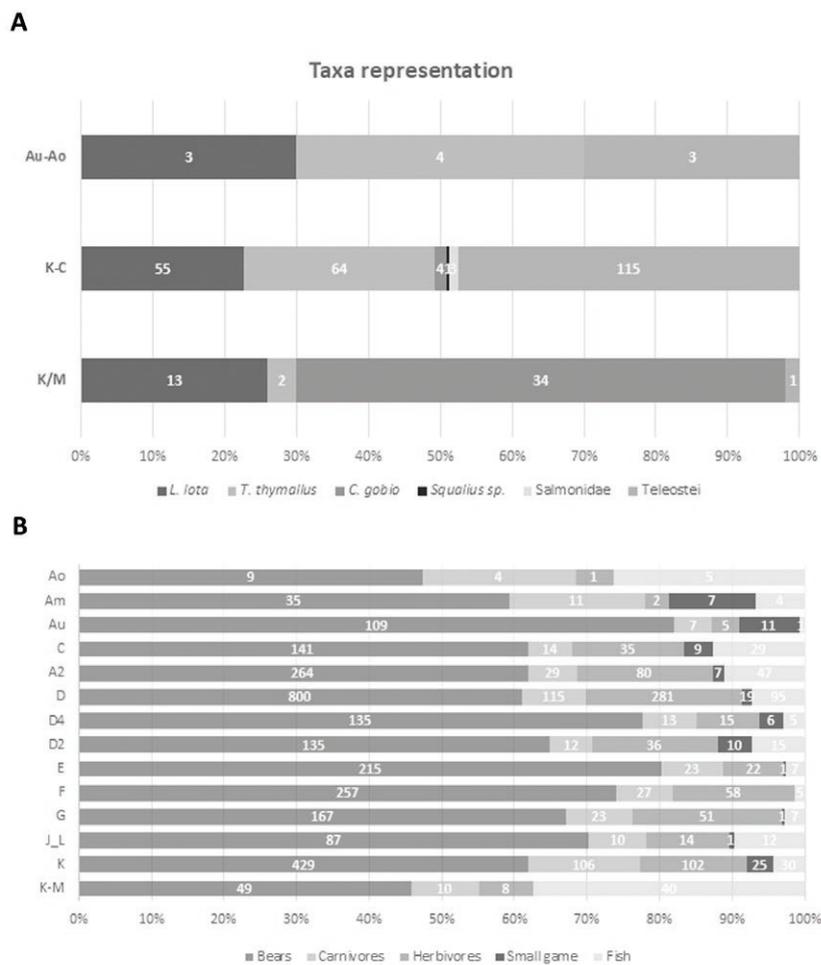
Tab. 1. Hohlenstein-Stadel Cave. Frequencies of lithic artefacts. Modified from Kind 2019.

Tab. 1. Hohlenstein-Stadel Höhle. Häufigkeiten lithischer Artefakte. Modifiziert nach Kind 2019.

Lab-No.	GH	AH	Technocomplex	<sup>14</sup> C BP	δ <sup>13</sup> C (‰)	calBP (Calpal)	calBP (Oxcal)
ETH-41231	Ao	1o	Aurignacian	31,950 ± 210	- 18.5 ± 1.1	36,000 ± 363	35,361-36,310
ETH-41232	Am	1m	Aurignacian	33,390 ± 245	- 21.1 ± 1.1	37,985 ± 740	36,836-38,440
ETH-38797	Au	1u	Aurignacian	35,185 ± 270	- 23.0 ± 1.1	40,165 ± 860	39,046-40,421
ETH-38798	C	3	Middle Palaeolithic	39,805 ± 420	- 22.4 ± 1.1	43,640 ± 607	42,811-44,316
ETH-38799	A2	4	Middle Palaeolithic	41,920 ± 545	- 23.2 ± 1.1	45,364 ± 835	44,361-46,327
ETH-38800	D	5	Middle Palaeolithic	40,560 ± 480	- 22.3 ± 1.1	44,137 ± 771	43,248-45,038
ETH-41234	E	6	Middle Palaeolithic	46,440 ± 1,050	- 21.4 ± 1.1	49,904 ± 2,202	out of range

**Tab. 2.** Hohlenstein-Stadel. Radiocarbon-dates. Calibration with CalPal (U. Danzeglocke/O. Jöris/B. Weninger, CalPal-2007online: <http://www.calpal-online.de>) and Oxcal (IntCal13: Reimer et al. 2009; oxcal v 4.2. Bronk Ramsey 2009). The calibrated data were calculated before 1950. All samples from bone. GH = Geological Horizon, AH = Archaeological Horizon.

**Tab. 2.** Hohlenstein-Stadel. Radiokarbon-Daten. Kalibrierung mit CalPal (U. Danzeglocke/O. Jöris/B. Weninger, CalPal-2007online: <http://www.calpal-online.de>) und Oxcal (IntCal13: Reimer et al. 2009; oxcal v 4.2. Bronk Ramsey 2009). Die kalibrierten Daten wurden vor 1950 berechnet. Alle Proben wurden aus Knochen gewonnen. GH = Geologischer Horizont, AH = Archäologischer Horizont.



**Fig. 2. A:** Representation of percentage by groups of layers and taxa from Hohlenstein-Stadel. K-M, K to C are Middle Palaeolithic layers (large number of remains belong to Teleostei, corresponds to spine and scale fragments); Au-Ao, layers belonging to the Aurignacian. **B:** Faunal representation of percentage in the Middle Palaeolithic Layers K to C, including bear, carnivorous, herbivorous, small game [modified from Kitagawa (2019)] and fish.

**Abb. 2. A:** Prozentuale Darstellung nach Schichtengruppen und Taxa aus Hohlenstein-Stadel. K-M, K bis C sind Mittelpaläolithische Schichten (eine große Anzahl von Überresten gehört zu Teleostei, entspricht Wirbelsäulen- und Schuppenfragmente); Au-Ao, Schichten, die zum Aurignacian gehören. **B:** Faunistische Darstellung des Prozentsatzes in den mittelpaläolithischen Schichten K bis C, einschließlich Bären, Carnivoren, Pflanzenfresser, kleine Tiere [modifiziert von Kitagawa (2019)] und Fisch.

lower left deciduous canine) were also found in the Aurignacian layers during the most recent excavations (2009-2013). Based on their morphology, as well as metric analyses, both teeth can be safely attributed to modern human individuals (El Zaatari & Harvati 2019). The stratigraphy of the recent excavation ends with a surface level revealing mixed finds with Middle and Upper Palaeolithic lithics as well as Holocene material, including ceramics (OF) (Fig. 1: B).

The middle to large-sized mammals, which were studied by Kitagawa (2014, 2019) show that both hominins and non-human predators visited the site. During the Middle Palaeolithic, the cave served as a den for hyenas and a short-term Neanderthal occupation site, which is documented by the presence of burnt bones and lithic artefacts. Cave bears dominate the Hohlenstein-Stadel faunal assemblage, that is also observed in other Swabian Jura sites such as Geißenklösterle or Hohle Fels. Kitagawa et al. (2012) concluded that the cave bears often occupied these caves during the winter season, showing accumulated remains by natural causes and predation by hyenas and other large carnivores. During the Middle Palaeolithic in Hohlenstein-Stadel, carnivores are less represented in comparison with herbivores and cave bear (Fig. 2: B), but the assemblage represents one of the richest spectra of large and middle sized carnivores in the Swabian Jura in comparison to Geißenklösterle or Hohle Fels, representing a palimpsest of hominin, cave bear and carnivore activities (Kitagawa et al. 2012; Kitagawa 2014).

In Hohlenstein-Stadel, the proportion of the specimens with anthropogenic modifications (excluding organic artifacts) such as cutmarks, impact fractures or burning is relatively low throughout the sequence, observing a greater number of specimens with impact fractures than those with cutmarks (Kitagawa et al. 2012; Kitagawa 2014, 2019). The majority of the cutmarks are present on herbivore remains but also are present on cave bear remains (Kitagawa 2014). The occasional exploitation of cave bears is also documented in other sites in the Swabian Jura such as Hohle Fels or Geißenklösterle, proving that the Neanderthals often used the same caves that cave bears used (Münzel & Conard 2004a; Conard et al. 2012).

The common prey animals during the Middle Palaeolithic at this site include horses, wholly rhinoceros, reindeer and mammoths as well as aurochs/bison and red deer. Reindeer and horse remains point to summer-fall as the season of the death and presumably the season of Neanderthal occupations (Kitagawa 2014).

The Aurignacian is characterized by relatively few indicators of anthropogenic subsistence activities but, the symbolic activity of the Aurignacian is demonstrated by the Lion Man figurine and the accompanying personal ornaments. While the abundance of carnivores decreases compared to the Middle

Palaeolithic, cave bears remain dominant and there is evidence of their opportunistic exploitation by humans (Kitagawa 2014).

The previous studies of micromammals from the Middle Palaeolithic and Aurignacian layers indicated a spectrum which is dominated (more than 40%) by tundra species, such as arctic and Norway lemming (*Dicrostonyx torquatus* and *Lemmus lemmus*) and narrow-headed voles (*Microtus gregalis*), although steppe species, such as steppe pikas (*Ochotona pusilla*), grey dwarf hamster (*Cricetulus migratorius*), ground squirrel (*Spermophilus superciliosus*), and southern birch mouse (*Sicista subtilis*), were also present in the assemblages (Ziegler 2019). From layer K-M to G, *M. gregalis* is more frequent than *D. torquatus*. From layer E to the Aurignacian layers, the tundra species dominate (more than 40-60%). Only in layer F is there a decrease in tundra species and an increase in generalist species, which is possibly indicative of interstadial conditions. In conclusion, Ziegler (2019) argued that the upper layers (E to Ao) as well as the lower layers (K-M to F) are characterized by a fluctuation between cooler stadial and more temperate interstadial periods. The birds are represented by ptarmigans (*Lagopus* sp.), geese (*Anser* sp.), grouse (*Tetrao/Lyrurus* sp.) and ducks (*Anas* sp.) in the Middle Palaeolithic layers and grouse and ptarmigans in the Aurignacian layers (Krönneck & Kind 2019). The presence of ducks and geese is indicative of water sources near the site (Krönneck et al. 2004; Krönneck 2012).

Previous studies on the Hohlenstein-Stadel fish assemblage are scarce and focus on the taxonomical aspect of the analysis, describing the presence of mainly grayling (*Thymallus thymallus*) and burbot (*Lota lota*) (Blanco-Lapaz 2019).

The nearest aquatic source today is the seasonal Lone River, which is located about 50 m in front of the cave. In the past, the Lone River was one of the major rivers feeding into the Danube River in the Swabian Jura (Strasser et al. 2009). The four taxa recovered in Hohlenstein-Stadel for this study are still present in the rivers and streams of the Swabian Jura today (Leuner & Klein 2000) and, therefore, were likely captured locally.

Other studies on fish from the nearby sites, such as of Geißenklösterle and Hohle Fels, indicate the presence of similar species, such as European bullhead (*Cottus gobio*), common minnow (*Phoxinus phoxinus*), burbot (*Lota lota*) and grayling (*Thymallus thymallus*) (Torke 1981). Böhme (2019) described the accumulation of fish, amphibian, and reptile remains in late Pleistocene deposits of Geißenklösterle from pellets that the birds of prey left in the cave. The fish remains recovered in the Middle Palaeolithic deposits of this site correspond to grayling, burbot and European bullhead. In the Aurignacian layers, the same species are present in the sample in addition to the common minnow. The author also described the presence of

the common frog (*Rana temporaria*), which is the only species that occurs in glacial climate phases that correspond to the Middle Palaeolithic and Aurignacian in Geißenklösterle.

In addition to these studies, Conard et al. (2013) also mentioned the presence of burbot, grayling and cyprinids in the Middle Palaeolithic and Aurignacian layers of Hohle Fels. The authors also described a gradual increase in the exploitation of small game and fish during the Aurignacian. During the Middle Palaeolithic, a marginal fish exploitation was observed; however, the sample size was scarce, with only 19 recovered fish remains. An ivory figurine depicting a fish that resembles a salmonid from Vogelherd also attests to modern humans interaction with, and exploitation of fish in the Upper Palaeolithic (Conard 2009).

## Method and Materials

### Taxonomy

A total of 302 fish remains were collected, by screening, from the archaeological layers of Hohlenstein-Stadel during the 2009-2013 campaigns. Of these, 193 were identified to the species level, 7 to the family level, and 102 as unidentified fish remains. When grouped, 53 remains were recovered from Layer K-M, 239 from Middle Palaeolithic layers K to C, and 10 from the Aurignacian layers Au to Ao (Fig. 2).

During the analysis of this material, a binocular EXACTA OPTECH model LFZ s/n 201030 20W was used. Anatomical and taxonomical classifications were conducted using the modern reference collection at the University of Tübingen and several osteological atlases (Lepiksaar 1994; Watt et al. 1997; Conroy et al. 2005). The taxonomic nomenclature from Cannon (1987) and Wheeler and Jones (2009) was employed and this study refers to the number of identified specimens (NISP) as a standard measure of abundance (Grayson 1984), but indeterminate fragments were also considered in the taphonomic studies. Many fragments were indeterminate due to poor preservation. For this paper, when osteometric models to estimate the fish size were not available, it was visually estimated through direct comparison (Guillaud et al. 2017b; Guillaud et al. 2021) with specimens of known length data from the modern comparative collection (University of Tübingen).

### Taphonomy, element representation and accumulation agents

It is important that fish remains are reliably attributed to human activities before making inferences about human behavior such as seasonality and subsistence strategies (Butler 1990; Russ 2010, 2011; Hardy & Moncel 2011; Guillaud et al. 2018, 2021; Blanco-Lapaz et al. 2021). Several accumulating agents can create assemblages of fish remains at archaeological sites. Humans are not the only agents, and various animals have been investigated as possible agents

of accumulation. Potential non-human accumulators include otters (Nicholson 2000; Guillaud et al. 2017b), bears (Russ & Jones 2011), wolves (Butler & Schroeder 1998) and birds (Russ 2010; Guillaud et al. 2018, 2019; Blanco-Lapaz et al. 2021).

To determine the main agent responsible for the accumulation of the fish remains, it is necessary to consider different aspects of the fish assemblage, such as the biology (ecology, species diversity and fish size), diversity, taphonomy (element representation, element fragmentation, bone surface modification such as digestion marks and spatial distribution) and species seasonality.

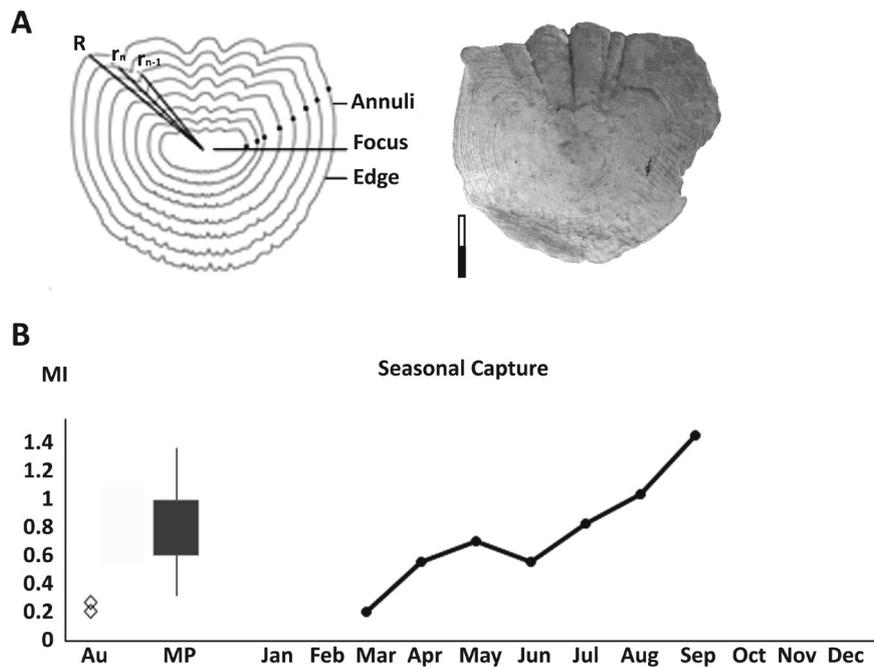
Bone modification, such as digestion marks, compression, mechanical deformation, bite marks, or burning, was analyzed. Previous studies have distinguished several categories of digestion marks depending on the intensity of digestion (Andrews 1990; Guillaud et al. 2018; Blanco-Lapaz et al. 2021; Frontini et al. 2021). This analysis has identified three different categories of digestion marks: null-light (0), moderate (1), and moderate-heavy (1-2) (Blanco-Lapaz et al. 2021) (modified from Andrews 1990; Guillaud et al. 2015). The presence of bite marks or crushed bones can give us insights 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).

### Seasonality

Previous studies indicate that fish remains can serve as an important tool to explore the seasonal occupation of sites or the seasonal exploitation of aquatic resources (e.g., Casteel 1976; Mellars & Wilkinson 1980; Mouini et al. 2010; Guezi & Kara 2015). Several elements such as otoliths, vertebrae, and scales, are commonly used for seasonality studies. In this study, scales were used due to their good preservation. We conducted a sclerochronological analysis on the well-preserved grayling (*T. thymallus*) scales.

This method is based on the study of growth marks (or annuli) which are present on scales. These growth increments were measured from the focus (or center) to the distal margin of the scale, based on the distance between the edge and the last growth ring, as well as the edge and the second to last growth ring (Beamish & McFarlane 1983; Guillaud et al. 2017a). Using published data on the periodicity of the increment formation from modern fish individuals from France, Finland, Switzerland and Sweden (Guillaud et al. 2017a), we can estimate the death of the animal and infer the seasonality of fish exploitation. In Guillaud et al. (2017a), the analysis of marginal increment in growth rings indicates an active period of growth from March to June. The average distance between the last growth ring and the scale edge increases during the growth season.

To estimate the periodicity of the increment formation, marginal increment analysis (MIA, Beamish



**Fig. 3. A:** Schematic description of a typical grayling (*T. thymallus*) scale (left) with the localization of the focus, the edge, the annuli (or growth rings) and the scale radii ( $r_n$  and  $r_{n-1}$ ) (modified from Guillaud et al. 2017a). Example of archaeological grayling scale from Middle Palaeolithic of Hohlenstein-Stadel (ST13\_D2\_193/172\_1073) (right). Size 2 mm. **B:** Monthly Marginal increment (MI) performed on all modern specimens (modified from Guillaud et al. 2017a) (left) in comparison with the archaeological fish remains: Au, Aurignacian fish remains from Hohlenstein-Stadel; MP, Middle Palaeolithic fish remains from Hohlenstein-Stadel (right).

**Abb. 3. A:** Schematische Beschreibung einer typischen Äschenschuppe (*T. thymallus*) (links) mit der Lokalisation des Fokus, des Randes, der Ringe (oder Jahresringe) und der Schuppenradien ( $r_n$  und  $r_{n-1}$ ) (modifiziert nach Guillaud et al. 2017a). Beispiel einer archäologischen Äschenschuppe aus dem Mittelpaläolithikum Hohlenstein-Stadel (ST13\_D2\_193/172\_1073) (rechts). Durchmesser 2 mm. **B:** Monthly Marginal Increment (MI) durchgeführt an allen modernen Exemplaren (modifiziert nach Guillaud et al. 2017a) (links) im Vergleich zu den archäologischen Fischresten: Au, Aurignacien Fischreste aus dem Hohlenstein-Stadel; MP, Mittelpaläolithische Fischreste aus dem Hohlenstein-Stadel (rechts).

Layers	<i>T. thymallus</i> (Grayling)				<i>L. lota</i> (Burbot)				<i>C. gobio</i> (Bullhead)				<i>S. cf. cephalus</i> (Chub)				Total	
	Ce	Cv	Tv	Sc	Ce	Cv	Tv	Sc	Ce	Cv	Tv	Sc	Ce	Cv	Tv	Sc		
Ao	-	-	-	3	-	-	1	-	-	-	-	-	-	-	-	-	-	4
Am	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	2
Au	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
C	-	2	9	5	-	-	2	-	-	-	-	-	-	-	-	-	-	18
A2	-	-	-	6	-	-	3	-	-	-	-	-	-	-	-	-	-	9
D	-	27	6	14	-	5	11	-	-	-	4	-	-	-	-	-	-	67
D4	-	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	4
D2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
E	-	-	1	-	-	2	-	-	-	-	-	-	-	-	1	-	-	4
F	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2
G	-	1	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	4
J_L	-	-	-	1	1	4	1	-	-	-	-	-	-	-	-	-	-	7
K	-	3	1	-	-	12	10	-	-	-	-	-	-	-	-	-	-	26
K-M	-	-	2	-	-	6	10	-	-	34	-	-	-	-	-	-	-	52

**Tab. 3.** NISP of each anatomical element and identified remain to species level recovered in Hohlenstein-Stadel Cave. Ce, Cranial element; Cv, Caudal vertebra; Tv, Thoracic vertebra; Sc, Scale.

**Tab. 3.** NISP von jedem anatomischen Element (auf Artebene), das in der Hohlenstein-Stadel-Höhle gefunden wurde. Ce, Schädelement; Cv, Schwanzwirbel; Tv, Brustwirbel; Sc, Schuppen.

& McFarlane 1983) was carried out on our archaeological scales by calculating the monthly marginal increment (MI) according to the following formula:  $MI = (R - r_n) / (r_n - r_{n-1})$  where  $R$  is the scale radius,  $r_n$  is the distance between the edge and the last growth ring and  $r_{n-1}$  is the distance between the edge and the second last growth ring (Fig. 3: A). In our assemblage, 130 scales were recovered. Of these, 34 scales, securely identified as grayling, were considered because the rest were very fragmentary and impossible to classify. The majority of the identified scales (NISP = 22) come from two squares (193/172 and 194/172) located in the center of the excavation area. However, after the removal of incomplete, fragmented and regenerated scales, only 14 Middle Palaeolithic grayling scales and two Aurignacian grayling scales were considered suitable for the MIA (Fig. 3: B).

## Results and Discussion

### Taxonomy and Ecology

This paper provides the first comprehensive presentation of the freshwater fish assemblage of Hohlenstein-Stadel. It gives insight into the freshwater ecosystem around this site, which was characterized by a pre-mountain river system with the presence of permanent, oxygen-rich and cold running waters. The presence of some micromammals, such as the eulipotyphlan water shrew (*Neomys* sp.) (Ziegler 2019), and birds (ducks and geese) (Krönneck & Kind 2019) also indicates the presence of well-developed local water sources and rivers.

The fish assemblage from the archaeological layers comprises four different taxonomic families: Salmonidae, Lotidae, Cyprinidae and Cottidae (Fig. 2 & Tab. 3). The predominant family recovered in Layer K-M is Cottidae, represented by only one species, the bullhead (*C. gobio*). This species was not recovered in the Aurignacian layers (Fig. 2: A). In layers K-M to C (Middle Palaeolithic), the most common family is Salmonidae (represented by the grayling, *T. thymallus*), followed by Lotidae (represented by the burbot, *L. lota*). In the Aurignacian layers (Au to Ao), the broad pattern remains and *T. thymallus* and *L. lota* are the most represented species in the assemblage (Fig. 2: A).

As mentioned above, the salmonids are represented by the European grayling (*T. thymallus*). The grayling is native to the northern parts of the Palearctic and Nearctic ecozones, ranging across Eurasia from the United Kingdom to northern Europe and Siberia. These fish require cool, well-oxygenated water, preferably with swift currents; they are found in large, sandy- or gravel-bottomed rivers and lakes, but may also occasionally be found in brackish conditions. Generally omnivorous, they feed primarily on crustaceans, insects and zooplanktons. As they are highly sensitive to changes in water quality, graylings may be considered as an 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 majority of the grayling specimens recovered from Hohlenstein-Stadel are ca. 30 cm.

Only one species of Lotidae, the burbot (*L. lota*), is represented in the assemblage of Hohlenstein-Stadel. Burbot is the only gadiform (cod-like) freshwater fish. This species has a circumpolar distribution above 40 °N. Populations are continuous from the British Isles across Europe and Asia to the Bering Strait and Canada. Burbot live in large, cold rivers, lakes, and reservoirs. They primarily prefer freshwater habitats but can thrive in brackish environments for spawning. During summer, they are typically found in colder water below the thermocline. In Lake Superior (Canada), burbot can live at depths below 300 m. As benthic fish, they tolerate an array of substrate types, including mud, sand, rubble, boulder, silt and gravel. Adults construct extensive burrows in the substrate for shelter during the day. Burbot populations are fluvial during the winter months and they migrate to near-shore reefs and shoals to spawn in grounds of sand or gravel. As adults, they are, active crepuscular hunters and their diet is primarily piscivorian, preying on lamprey, whitefish, young northern pike, suckers, bullheads and stickleback. This species can reach a maximum weight of 4 kg and a maximum size of 80 cm (Füllner et al. 2016) although for the Hohlenstein-Stadel specimens range between 20-30 cm.

The European bullhead (*C. gobio*) is the only species recovered in the assemblage from the Cottidae family. The European bullhead is a small demersal fish characteristic of cold, clear, fast-flowing small streams and middle-sized rivers. It also occurs near the gravelly shores of cold lakes. 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. This species is also common prey for the burbot and other carnivorous fish (Füllner et al. 2016). Their body length ranges mostly between 6 and 12 cm in the Hohlenstein-Stadel assemblage.

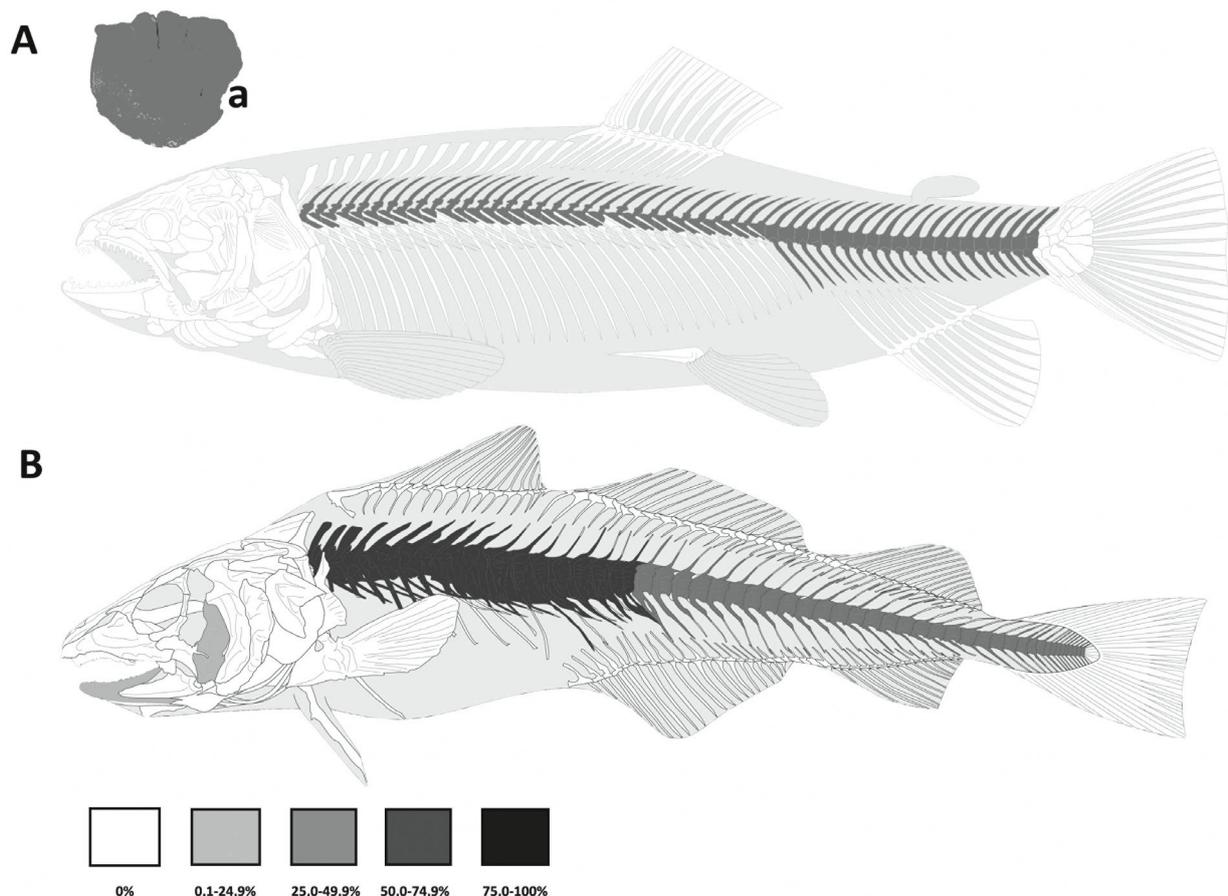
In the assemblage, only two remains were identified to genus level and correspond to branchial arch fragments of a chub (*S. cf. cephalus*). We attribute the remain to *Squalius* because it presents traits that are characteristic of this genus, such as the presence of a second tooth row. Although the only species of this genus present in Germany is *S. cephalus*, we classify this specimen as *S. cf. cephalus* because it was in a fragmentary state. Cyprinids are more typical of temperate waters and live in water temperatures between 10-25 °C (Doadrio et al. 2011; Tissot & Souchon 2010). Accordingly, cyprinids such as the genus *Squalius* can be found in salmonid zones as they also thrive in running water. However, cyprinids in general are present in multiple environments, showing enormous diversity in their diet, which includes arthropods and other fish (Doadrio et al. 2011). The individuals of *S. cephalus* can be measured up to

60 cm and it can weigh 2-4 kg when they reach the ages of 15-16 years (Füllner et al. 2016). All the individuals recovered in Hohlenstein-Stadel are smaller than 10 cm. Cyprinids are present exclusively in layers F and E, which points to a more temperate environment (Fig. 2: A). Ziegler (2019) also indicated a relative decrease in the tundra environment in layer F, based on the recovered micromammal species. Although the author noted its small sample size (N = 35), micromammals and cyprinids both point to a likely interstadial condition in the F and E layers.

Three of the four identified fish taxa from Hohlenstein-Stadel (European grayling, burbot and European bullhead) are good indicators of low water temperatures (with average temperature that ranges between 10-12 °C) (Mallet et al. 2011). Only the chub is associated with a habitat with more temperate water but it can also live in cold water (Doadrio et al. 2011). All these fish species have also been recovered in Hohle Fels (Conard et al. 2013), Geißenklösterle (Torke 1981; Böhme 2019), Kogelstein (Böttcher et al. 2000) and Brillenhöhle (Lepiksaar 1973). This corresponds to the spectrum of tundra and steppe mammalian fauna

from the region (Weinstock 1999; Münzel & Conard 2004a, b; Niven 2006; Krönneck 2012; Kitagawa 2012, 2014).

In other Middle Palaeolithic and Aurignacian sites from Central Europe, the presence of grayling (*T. thymallus*), burbot (*L. lota*), bullhead (*C. gobio*), and chub or cyprinids has also been documented. Böhme (2011) described a characteristic salmonid region in association with the Höhlenruine Hunas site in Bavaria with the presence of bullhead, grayling, burbot, common minnow, and brown trout (*S. trutta*) while Böttcher (2014) identified greater fish diversity in Sesselfelsgrotte, with sturgeons (*Acipenser* sp.), pike (*Esox lucius*), Danube salmon (*Hucho hucho*), cisco (*Coregonus* sp.), grayling (*T. thymallus*), burbot (*L. lota*), zingel (*Zingel zingel*), bullhead (*C. gobio*) and the cyprinids: barbel (*Barbus barbus*), nase (*Chondrostoma nasus*), common dace (*Leuciscus leuciscus*), vimba bream (*Vimba vimba*) and stone loach (*Barbatula barbatula*). The high diversity and small size of the Sesselfelsgrotte assemblage, as well as the taphonomy, could indicate the non-anthropogenic origin of the fish accumulation (Böttcher 2014).



**Fig. 4.** Percentage of skeletal element present in Hohlenstein-Stadel Cave. **A:** Salmonid skeleton representing the grayling (*T. thymallus*) including their scale representation on the top left (a). **B:** Gadid skeleton representing the burbot (*L. lota*). Modified from Michel Coutureau & Philippe Béarez (collab.), 2017/ArcheoZoo.org (License CC BY NC SA 4.0 International).

**Abb. 4.** Prozentsatz der Skelelemente aus dem Hohlenstein-Stadel-Höhle. **A:** Salmonidenskelett einer Äsche (*T. thymallus*), einschließlich ihrer Schuppendarstellung oben links (a). **B:** Gadid-Skelett einer Quappe (*L. lota*). Modifiziert von Michel Coutureau & Philippe Béarez (zusammen), 2017/ArcheoZoo.org (Lizenz CC BY NC SA 4.0 International).

Guillaud et al. (2021) analyzed two Belgian Palaeolithic caves, Walou and Marie-Jeanne, both with the presence of bullhead, burbot and grayling. The same authors also analyzed several sites in France (Vaufrey Cave, Baume Moula-Guercy, Barasses II Cave and Abri des Pêcheurs). In all cases, grayling and burbot are the dominant species, representing more than 50 % of the recovered fish remains (Guillaud et al. 2021). In Borsuka Cave (Southern Poland), burbot and cyprinids remains were also recovered, representing more than 71 % of the fish sample (Wilczyński et al. 2012).

We can observe that in all the studied sites from Western-Central Europe, the dominant fish correspond to burbot, grayling and cyprinids, to Hohlenstein-Stadel.

**Taphonomy, fish bone representation, and accumulation agents**

Hohlenstein-Stadel samples are characterized by postcranial elements, namely vertebrae and scales (total NISP = 299; 99 %). Cranial bones (NISP = 2; 1 %) are clearly underrepresented. They are only recovered from the Middle Palaeolithic layers and absent in the Aurignacian layers (Tab. 3 & Fig. 4). The cranial bones correspond to a fragment pharyngeal arch corresponding to *S. cf. cephalus* and a quadrate and a dentary fragment of *L. lota* (Fig. 4: B).

In Hohlenstein-Stadel, the herbivore remains present several carnivore modifications such as gnawing, scoring, pits and punctures, which could correspond to scavenging and predation activities. On the contrary, Fish remains with no carnivore modification are likely an indication that carnivores which visited the cave such as red/arctic foxes, wolves, cave/brown bears and hyenas were not the primary agents of the fish accumulation (Russ 2010; Russ et al. 2011).

Taphonomic analysis indicates no damages such as mechanical deformation, rounding or polishing due to the compression during the digestion process (Blanco-Lapaz et al. 2021; Frontini et al. 2021), which means that birds of prey can also be ruled out as an accumulation agent of fish (Nicholson 1993). Some authors (Andrews 1990; Bennisar-Serra 2010) also that micromammal accumulations produced by birds of prey are located, generally, close to their nests and commonly in adjacent areas to the wall of the caves. In Hohlenstein-Stadel, the fish remains were recovered mainly in the center of the excavation area, excluding birds of prey as the main fish accumulators.

Burning is the most common form of anthropogenic modification across the sequence for mammalian bones, which are often fragmented and charred (Kitagawa 2012; Kitagawa et al. 2014). Although there is no direct evidence of clear anthropogenic modifications on the fish remains, the lack of carnivore and birds of prey modifications makes humans the most likely accumulating agent for the fish assemblage in Hohlenstein-Stadel.

The abundance of scales (NISP = 130; 43 %) possibly indicates the processing of fish by humans through the

removal of scales for consumption. Although there is no direct evidence of fishing artefacts, such as hooks or harpoons, humans likely used composite tools or fishing traps made of wood or plant fibers, which do not preserve in the wet, humid conditions of the cave. Further analyses would need to be conducted to demonstrate the hunting and processing method of fish at Hohlenstein-Stadel.

**Season of capture and fishing pattern differences**

The MIA study of the Middle Palaeolithic and Aurignacian scales from Hohlenstein-Stadel shows a relatively large growth zone at the edge, which is observed in the majority of the archaeological scales. In the Middle Palaeolithic layers, the MIA analysis indicates that the majority of the scales derive from fish that died during summer or fall (Fig. 3: B & Tab. 4). In layer Au, we observed a fish captured during the first half of the year, possibly in spring, although, the results are not conclusive with two samples (Fig. 3: B & Tab. 4). In both cases, no scales showed capture during winter, the most common season for natural death due to decreased food availability (Barret 1997; Roselló-Izquierdo & Morales-Muñiz 2005; Doadrio et al. 2011).

Studies of seasonality based on fish remains in Western and Central Europe are relevant for understanding the human occupation and subsistence practices during the Middle Palaeolithic and Aurignacian (Le Gall 2000; Roselló-Izquierdo & Morales-Muñiz

Layer	ID	Age (year)	MI (mm)	Season
Ao	ST13_919_	7	0.47	April/June
Ao	ST13_920_	6	0.39	April/June
C	ST13 194/172 167.1	4	1.08	September
C	ST13 194/172 151	5	1.29	September
C	ST13 194/172 167	3	0.75	July/August
C	ST13 194/172 151	5	0.72	July/August
A2	ST13 195/172 144	8	1.20	September
D	ST13 194/172 951	5	1.24	September
D	ST13 194/172 1031	4	0.91	August/September
D	ST13 195/172 367	5	0.61	May/June
D	ST13 195/172 544	4	0.35	March/April
D	ST13 194/172 1136	5	0.95	August/September
D	ST13 194/172 506	4	0.81	July/August
D2	ST13 193/172 1057	3	0.44	April/June
D2	ST13 193/172 997	4	0.63	May/June
D2	ST13 193/172 1073	5	0.42	April/June

**Tab. 4.** Seasonal data from Hohlenstein-Stadel, indicating for each studied grayling scale, the level, the ID number, the MI value and the season of capture/death.

**Tab. 4.** Saisondaten aus dem Hohlenstein-Stadel, die für jede untersuchte Äschenschuppe Schicht, ID Nummer, den MI-Wert und die Fang-/Todessaison angeben.

2005; Guillaud et al. 2017a, 2021) and are particularly important due to the scarce data on aquatic resources (Morales & Roselló 1989). Furthermore, exploring how common fishing was – if it was a casual, opportunistic or systematic activity – can have great implications for understanding what role fishing played in the diets of hunter-gatherers in Western and Central Europe.

Only a few changes have been observed in the subsistence practices of the Middle Palaeolithic and the Aurignacian at Hohlenstein-Stadel (Kitagawa 2014, 2019). Although large game dominated during the Middle Palaeolithic, including horse and reindeer, fish may have complemented the Neanderthal diet during summer and fall. During the Aurignacian, reindeer exploitation increased considerably (Kitagawa 2014, 2019). Again, fish could have been an extra food resource in the diet of modern humans. The exploitation of small game and marine mollusks in several Middle Palaeolithic sites indicates that the Neanderthal diet was diversified, depending on the available resources (Starkovich 2011; Guillaud et al. 2021; Moncel et al. 2021). Seasonal data are extremely rare but point to a preferential capture. In the future, similar studies in other Swabian Jura sites with rich Aurignacian occupations, such as Geißenklösterle or Hohle Fels, will help us consider broader patterns of fishing practices in the region and test whether this seasonal signal is robust.

## Conclusions

Generally, studies of the use and exploitation of aquatic resources during the Middle Palaeolithic and Aurignacian remain rare in Central and Western Europe, making it hard to reconstruct fishing activities by archaic and modern humans (Guillaud et al. 2021; Moncel et al. 2021). In the Swabian Jura, the fish assemblages from some sites have been analyzed (Torke 1981; Böttcher et al. 2001; Conard et al. 2013; Böhme 2019).

Analyses of taphonomy, taxonomy, paleoecology, and seasonality on fish remains from Hohlenstein-Stadel showed that during the Middle Palaeolithic and Aurignacian, Neanderthals and modern humans mostly exploited two species of fish, European grayling (*T. thymallus*) and burbot (*L. lota*). The majority of the 302 (NISP) fish remains are postcranial remains, including vertebrae and scales. All recovered taxa (European grayling, burbot, European bullhead, and common chub) have been documented in other Palaeolithic sites from Southwestern Germany (Torke 1981; Conard et al. 2013; Böhme 2019).

No important ecological changes were observed during the Middle Palaeolithic and Aurignacian in Hohlenstein-Stadel. The grayling and the burbot are present throughout the sequence. The bullhead, which decreased during the Middle Palaeolithic are absent in the Aurignacian layers. Cyprinids, which are only present in layers F and E, could indicate a more temperate environment. This observation is supported by the previous studies on micromammals

(Ziegler 2019) and could be interpreted as an indication for interstadial condition with decreased tundra elements from the landscape during certain phases of the Middle Palaeolithic.

Despite the low density of lithic artefacts and herbivore remains with anthropogenic marks recovered at the site, they are more frequent in layers A2, D and K/K-M. (Kitagawa 2014; Kind 2019). The fish assemblage follows the same and most of the remains are present in those layers as well, which possibly points to sporadic and opportunistic fishing. The cave is narrow and lacks regular exposure to sunlight that likely made this cave unfavorable for long-term occupations (Kitagawa 2014). In general, several arguments support the hypothesis of short-term Neanderthal occupations in Hohlenstein-Stadel such as low density of lithic artefacts and the preference of local raw materials by expedient reduction sequences (Conard et al. 2012; Picin et al. 2020; Moncel et al. 2021), few anthropogenic marks on bones, the narrowness of the cave and the seasonality studies based on the reindeer and horse remains (Kitagawa 2014, 2019). The present seasonality studies based on fish remains complement the previous work based on large game, indicating presumably in both cases, summer-fall as the season of Neanderthal occupations.

Our results indicate that fishing exploitation during the Middle Palaeolithic and Aurignacian in Central Europe was limited but were observed throughout the region and future studies on fish remains are necessary to better understand the local freshwater ecosystems, the taphonomic history of fish accumulation, and the subsistence practices of Palaeolithic hunter-gatherers. Currently, further studies from other Swabian Palaeolithic sites are underway. They could broaden our knowledge and put greater focus on non-mammalian fauna from Palaeolithic sites. Exploring more fish assemblages from Middle Palaeolithic sites could also help to reconsider the assumption that the Neanderthals were unable to use fish as a resource in continental waters. Future studies may also provide evidence that fishing, although limited, was part of Neanderthal subsistence activities and suggest that their dietary patterns were more diverse than commonly assumed.

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