Ralf-Dietrich Kahlke (Ed.)

The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany)

Part 4

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Ralf-Dietrich Kahlke (Ed.)

THE PLEISTOCENE OF UNTERMASSFELD NEAR MEININGEN (THÜRINGEN, GERMANY)

PART 4

Mit Beiträgen von

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Quaternary Palaeontology Weimar – Skull of an approximately two-year-old *Eucladoceros giulii* (1/3 natural size) from Untermassfeld and
detail of the excavated area (1979–2015 field seasons)

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Dedicated to our esteemed colleague and friend of many years

Helmut Hemmer

on the occasion of his 80th birthday.

FOREWORD

Untermassfeld – A scientific treasure trove for generations to come

As archaeologists we want to comprehend how we became human and to do so, we must look back at the beginning of our species, to understand the ecological niche hominins occupied when they first entered Europe, the niche that formed them and that they in turn influenced. We need contexts that enable us to evaluate the environment encountered by these hominin ancestors.

For these discussions, the site of Untermassfeld is key. Untermassfeld represents a unique archive that offers a wealth of data for the reconstruction of past habitats and landscapes before hominins arrived in Europe. For us, as archaeologists, it provides specific insights into predator-prey relationships that help us to evaluate hominins' position in the food web. With the preservation of a wide variety of remains of a biocoenosis that had fallen victim to a catastrophic flooding episode around one million years ago, Untermassfeld allows the reconstruction of such a food web into which hominins were later to intrude.

Against this background it is astonishing that Untermassfeld still awaits discovery as a crucial source for model building concerning early hominins in archaeology and palaeoanthropology and this is exactly where the Römisch-Germanisches Zentralmuseum, Leibniz-Research Institute for Archaeology (RGZM) comes in. Untermassfeld is a purely palaeontological record; hominins are not a variable at the site. So how is it that already during the 1990s the RGZM Publishing House invested in ensuring the publication of the first three principal volumes about the site (Kahlke 1997a; 2001a; 2001b)? The answer is easy: during our excavations at the beginning of the 1990s at the 1.8 Mio year old Georgian site of Dmanisi, a site that up till now still represents the earliest evidence for hominins outside of Africa, we together with our Georgian colleagues unearthed a well preserved thanatocoenosis including hominin fossils. With its scarcity of lithic tools and lack of evidence for active hominin interaction with the fauna these discoveries illustrated once more hominin interlacement in past habitats and it became apparent once again that we must make an effort to understand these habitats as prerequisite for the evaluation of the role hominins played in them. This was the context for the publication of the first Untermassfeld volumes and we are proud that with the publication of the current volume on Untermassfeld, we could once more contribute to this decade-long achievement, the results of which will remain a treasure trove for generations to come.

Having said all this, the potential of Untermassfeld to benefit archaeological research has not yet been exhausted. Untermassfeld helps us to understand the taphonomic chain of bone loss at both archaeological and palaeontological sites. In unique case studies, data on modification by hyenas (in volume 5), micromammals (Maul 2001), herbivores (Kahlke 2001c) as well as insects (Keiler et al. in this volume) enable the qualitative and quantitative assessment of these biotic agents in a given biocoenosis/thanatocoenosis. Pre- and postburial mechanisms and their consequences for the fossil record can be studied meticulously in settings known in detail and difficult to replicate in controlled experimental setups (Kahlke 1997b). Moreover, Untermassfeld allows an evaluation and interpretation of age profiles used in the zooarchaeological methodological apparatus (Kahlke and Gaudzinski 2005), to mention just a few relevant studies.

Recent publications since 2013 (Garcia et al. 2013; Landeck and Garcia Garriga 2016; 2017) have claimed that Untermassfeld provides the earliest evidence for human occupation of Europe. Particular controversy arose when Landeck and Garcia Garriga (2016) published supposedly anthropogenic cut-marked animal bones, on a sample that proved to be fraudulent (Callaway 2017; Roebroeks et al. 2018). This notorious case had juridical consequences for the first author of the paper, and editors of the journals in which the authors had published about Untermassfeld later expressed their concerns, with consequences for the journals' policy on handling research data. If we review palaeontological and / or archaeological sites throughout human history, not many of them can claim to have been the subject of fraud, which perhaps illustrates perfectly that Untermassfeld is to be counted among the very few that »made it to the top«.

The picture I draw here is from a purely archaeological perspective, which should however not diminish the importance for palaeontology of this well-preserved and species-rich fossil deposit that was exhumed over 127 months of active field work to the exacting standards of archaeological excavation which now make the site so important for our understanding of taphonomic processes.

The Untermassfeld site will forever be linked to the name of Ralf-Dietrich Kahlke, whose unrelenting commitment and passion first helped to establish the scientific value of the site, and with whom we at MONREPOS are proud to collaborate since the 1990's. With this volume and volume 5 including the complete excavation plans, he brings the Untermassfeld project to its preliminary finish, although essential sites such as Untermassfeld will always remain at the focus of scientific interest.

References

Callaway, E., 2017. Archaeologists say human-evolution study used stolen bone. Nature 551, 279–280.

Garcia, J., Landeck, G., Martínez, K., Carbonell, E., 2013. Hominin dispersals from the Jaramillo subchron in central and south-western Europe: Untermassfeld (Germany) and Vallparadís (Spain). Quaternary International 316, 73–93.

Kahlke, R.-D. (Ed.), 1997a. Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 1. Monographien des Römisch-Germanischen Zentralmuseums 40, 1, I–VI, 1–418, pls. 1–67.

1997b. Bisheriger Gesamtbefund zur Geologie, Paläozoologie, Taphonomie, Ökologie und Stratigraphie der unterpleistozänen Komplexfundstelle Untermaßfeld. In: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 1. Monographien des Römisch-Germanischen Zentralmuseums 40, 1, 385–418.

(Ed.), 2001a. Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 2. Monographien des Römisch-Germanischen Zentralmuseums 40, 2, I–VIII, 419–698, pls. 68–131, suppl. 1.

(Ed.), 2001b. Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 3. Monographien des Römisch-Germanischen Zentralmuseums 40, 3, I–VI, 699–1030, pls. 132–151, suppl. 1–15.

2001c. Ein Hinweis auf Herbivoren-Osteophagie aus dem Unterpleistozän von Untermaßfeld sowie Bemerkungen zur Gabelbildung an Knochenenden. In: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 3. Monographien des Römisch-Germanischen Zentralmuseums 40, 3, 897–903, pl. 147.

Kahlke, R.-D., Gaudzinski, S., 2005. The blessing of a great flood: differentiation of mortality patterns in the large mammal record of the Lower Pleistocene fluvial site of Untermassfeld (Germany) and its relevance for the interpretation of faunal assemblages from archaeological sites. Journal of Archaeological Science 32, 1202–1222.

Keiler, J.-A., Benecke, M., Keiler, J., in this volume. Bone modifications by insects from the Early Pleistocene site of Untermassfeld, 1117–1132.

Landeck, G., Garcia Garriga, J., 2016. The oldest hominin butchery in European mid-latitudes at the Jaramillo site of Untermassfeld (Thuringia, Germany). Journal of Human Evolution 94, 53–71.

2017. New taphonomic data of the 1 Myr hominin butchery at Untermassfeld (Thuringia, Germany). Quaternary International 436, 138–161.

Maul, L., 2001. Nagespuren von Kleinsäugern an Knochenmaterial aus dem Unterpleistozän von Untermaßfeld. In: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 3. Monographien des Römisch-Germanischen Zentralmuseums 40, 3, 905–916, pls. 148–151.

Roebroeks, W., Gaudzinski-Windheuser, S., Baales, M., Kahlke, R.-D., 2018. Uneven Data Quality and the Earliest Occupation of Europe – the Case of Untermassfeld (Germany). Journal of Paleolithic Archaeology 1, 5–31.

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PREFACE

The extraordinary find- and species-rich Early Pleistocene fossil deposit of Untermassfeld near Meiningen has been the focus of systematic excavation and documentation since it was discovered in January 1978. Until 1992, the work was carried out by the Institute of Quaternary Palaeontology, Weimar, which then became the Weimar-based Quaternary Palaeontology Group of the Institute of Geosciences at the Friedrich Schiller University, Jena, and since 2000, the Senckenberg Research Station of Quaternary Palaeontology. Taking place nearly every year from 1979 onwards, the duration of the field seasons totals 127 months of active field work. During this time, more than 18,000 palaeontological finds were recovered. Over four decades, these finds have been prepared, conserved and stored together in one Untermassfeld collection in their own custom-made cabinets. The excavation work ended during the summer of 2019 and in agreement with the responsible monument protection authorities specially marked reserved areas have been left untouched for future investigations. The status of the entire site as a protected ground monument of the Free State of Thuringia remains unchanged.

From 1997 to 2019, the field and conservation work was mainly supported and financed by the Senckenberg Research Institute and the Free State of Thuringia, annually approved by the Thuringian State Office for Heritage and Archaeology, the City of Meiningen and the District of Schmalkalden-Meiningen. For the many years of successful collaboration we would like to thank State Archaeologist Sven Ostritz (Erfurt, Weimar) and his team, City Treasurer Klaus-Dieter Schmidt (Meiningen), the Heads of the Department of Budget, Tax and Social Issues of the municipality of Meiningen Börje Scholz and David Kempf, the Mayors of the City of Meiningen Reinhard Kupietz (until 2012) and Fabian Giesder (from 2012), and the District Office of Schmalkalden-Meiningen (Monument Protection Authority) represented by Karin Ganß.

Organization of the field season work and site protection lay in the capable hands of John-Albrecht Keiler (Weimar). Accounting support was provided by Regina Langner (until 2009) and Sabine Schneider (from 2009, both Weimar). We thank Tiefbau Schliewe Untermassfeld for the precise implementation of excavation work requiring heavy technical equipment as well as for the annual use of cranes to open and close active excavation areas. Thanks go to our friend Roland Werner † (Jüchsen) as well as the Heimatverein Jüchsen e. V. for technical assistance in the day-to-day running of the field work and for protection and monitoring of the site during excavation-free periods. For their valuable support in protecting the site against repeated thefts and damage, we would like to thank the Schmalkalden-Meiningen Police Service and the Suhl Criminal Investigation Department.

All excavation work was carried out by the staff of the Senckenberg Research Station of Quaternary Palaeontology, Weimar, with the occasional involvement of student assistants. Conservation of the finds recovered from the year 2000 onwards was the responsibility of Dennis Rössler, Michael Stache (until 2011) and Rebecca Wunder (from 2011). Parallel to the preparation progress, Evelin Haase (Weimar) managed the collection catalogue and created the excavation plans. Management of the collection itself was carried out by Gerald Utschig with the support of Jessica Arnold (both Weimar).

Evaluation of the finds and records from Untermassfeld was conducted by various groups of specialists. Results were published in 1997 and 2001 in three volumes of the monograph series of the Römisch-Germanisches Zentralmuseum, Mainz, as well as in 2006 in an English language summary detailing the knowledge acquired at the time of publication. The present fourth volume of the Untermassfeld monograph contains numerous new findings on site genesis and absolute age, along with bone modifications, as well as ichthyo-, herpeto- and avifauna. Substantial new find of dental and skeletal elements of hitherto little-known artiodactyls and perissodactyls of the western Palaearctic are extensively discussed. The photographs contained in this volume were mainly produced by Thomas Korn (until 2015) and Susann Döring (from 2016) (both Weimar). Evelin Haase created all graphics and arranged the photographs within the figures. Christina Nielsen-Marsh (Leipzig) translated or edited the majority of the English texts and Bärbel Fiedler (Weimar) was responsible for the editorial finishing of the manuscripts. We thank Stefan Flohr (Hildesheim), Matthias Hartmann (Erfurt), Lutz Katzschmann (Jena), John-Albrecht Keiler (Weimar), Dimitris S. Kostopoulos (Thessaloniki), Lutz Christian Maul (Weimar), Gerald Mayr (Frankfurt/M.), Paul P. A. Mazza (Firenze), Richard Albert Roper (Frankfurt/M.), Davit Vasilyan (Fribourg), and one anonymous reviewer for reviewing one or more of the contributions in this volume.

We are grateful to Sabine Gaudzinski-Windheuser (Mainz, Neuwied), who for many years was our cooperation partner within the Römisch-Germanisches Zentralmuseum, which ensured the smooth-running of the printing of the fourth volume of the Untermassfeld monograph, and we thank Claudia Nickel (Mainz) for her help, and attention to detail in publishing this volume. Our heartfelt thanks go last, but not least, to all of our esteemed colleagues for their many years of tireless work and service to the Untermassfeld project.

Weimar, January 2020 *Ralf-Dietrich Kahlke*

MADELAINE BÖHME

NEW RESULTS ON FISHES FROM THE EARLY PLEISTOCENE SITE OF UNTERMASSFELD

Abstract

The study of published and new fish remains from Untermassfeld reveals two species for the Epivillafranchian (late Early Pleistocene) Werra River: the anadromous Atlantic salmon (*Salmo* cf. *salar*), documented by at least six individuals, and the rare cyprinid (*Gobio* sp.). Both fishes characterize the hyporhithral (greyling zone) of European rivers. The salmonid record represents the first non-archaelogical fossils of *Salmo salar*. Their taphonomy suggests that remains derived from carnivore prey, deposited in digested and undigested conditions. These observations point to an important role of salmonids for food webs and nutrient cycles in the Untermassfeld ecosystem.

1. Introduction

Freshwater fishes represent an important component of continental biodiversity. Only 1 % of the present-day earth's surface is covered by lakes and rivers, but freshwater fish diversity exceeds 13,000 species (Lévêque et al. 2008). Their high diversity is attributable to accelerated speciation rates in their comparatively unstable habitats and their ability to adapt to various physical environments. This makes freshwater fishes a useful tool for ecological, environmental, and even climatic reconstruction (Böhme 2004; 2010a; 2010b). Despite their importance, our knowledge of deep-time freshwater fish diversity and biogeography is limited, especially for the Quaternary.

The famous late Early Pleistocene (Epivillafranchian) site of Untermassfeld (Thuringia, Germany) is of utmost significance for our knowledge of fauna and ecology in Eurasia about one million years ago (Kahlke 1997a; 2001a; 2001b; 2006). Its exceptionally rich and well-preserved mammalian record, accompanied by continuous and remarkable skilful excavations and documentation, contribute to its enormous scientific importance. Although freshwater fishes represent only a minor component of the recovered fauna, they may contribute to the palaeoenvironmental picture of the Early Pleistocene Werra River at Untermassfeld.

A first description of fish remains from Untermassfeld was provided by Rutte (1997). He identified three species: *Esox lucius* (pike), *Tinca* sp. (tench), and *Leuciscus* sp. (dace). Here I review previous taxonomic results and describe new fish fossils excavated during the last 20 years.

2. Material and methods

Fossil fish material (**Table 1**) is deposited in the collection of the Senckenberg Research Station of Quaternary Palaeontology, Weimar (acronym IQW). Recent comparative materials used come from the Palaeontological collection, Tübingen. Measurements were taken with an analog calliper with a precision of 0.1 mm.

	Grid square	Find depth below site 0-level (m)	Material
IQW 2015/41961 (Mei. 47270)	Q 915	n. s.	Three anterior caudal vertebra, two are broken
IQW 1993/24304 (Mei. 23833)	Q 536	1.50	Anterior caudal vertebra
IQW 1988/22633 (Mei. 22152)	Q 708	1.00–0.75	Proximal fragment of an anterior ray from paired fin
IQW 2009/30155 (Mei. 29317)	Q 30	1.54	Two articulated thoracal vertebra
IQW 2009/30149 (Mei. 29311)	Q 30	1.55	Two thoracal vertebra
IQW 2009/30114 (Mei. 29276)	Q 26	1.86	Fragmented vomer and four isolated teeth
IQW 2007/29537 (Mei. 28699)	Q 25	~ 2.00	Proximal fragment of an anterior ray from paired fin
IQW 2015/41972 (Mei. 47281)	Q 151	n. s.	Proximal fragment of an anterior ray from paired fin
IQW 2015/41973 (Mei. 47282)	Q 190, 191	n. s.	Proximal fragment of an anterior ray from paired fin
IQW 1987/21827 (Mei. 21346)	n. s.	n. s.	Isolate tooth
IQW 2018/45363 (Mei. 50672)	Q 156	1.80	Isolate tooth
IQW 2018/45364 (Mei. 50673)	Q 313	n. s.	Isolate tooth

Table 1 New salmonid (*Salmo* cf. *salar*) remains from Untermassfeld. n. s. – not specified.

3. Results

3.1. Description

Salmoniformes Bleeker, 1859
Salmonidae Jarocki, 1822
Salmo Linnaeus, 1758
Salmo cf. *salar* Linnaeus, 1758

The four available caudal vertebrae are large with a length of 10.3 mm and transverse diameters of 12.0 mm [IQW 2015/41961 (Mei. 47270)] and 11.4 mm [IQW 1993/24304 (Mei. 23833)]. The deeply amphicoelic centra are cylindrical (not waisted), and the notochord perforation is tiny. The bone preservation is good, retaining on the lateral centrum sides the regularly small and very small fenestrae (**Fig. 1b**). Incremental growth rings are hardly visible (**Fig. 1c**). Specimens IQW 2015/41961 (Mei. 47270) may depict three growth zones.

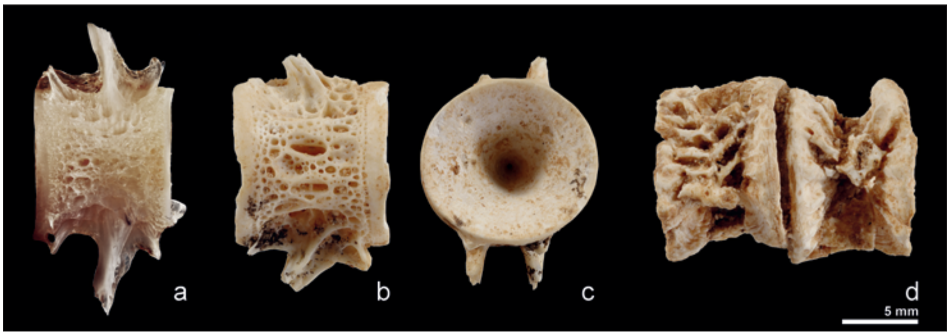

Fig. 1 *Salmo salar* Linnaeus, 1758, recent, GPIT uncatalogued. – **a** Anterior caudal vertebra, lateral view. | *Salmo* cf. *salar*, Untermassfeld. – **b** Anterior caudal vertebra IQW 2015/41 961 (Mei. 47 270), lateral view. – **c** Anterior caudal vertebra IQW 2015/41 961 (Mei. 47 270), cranial view. – **d** Articulated trunk vertebra IQW 2009/30 155 (Mei. 29 317), lateral views.

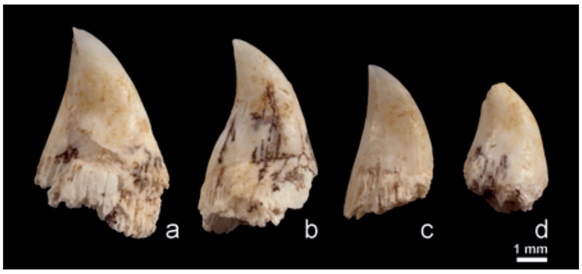

Fig. 2 *Salmo* cf. *salar*, Untermassfeld. – **a–d** Vomerine teeth IQW 2009/30 114 (Mei. 29 276), lateral views.

The individually associated specimen IQW 2009/30 114 (Mei. 29 276) is a totally fragmented, originally elongated, small skull bone with four isolated teeth. The bone was platy at one side and thickened at the other. The thickened bone portion is very spongy. Bone preservation is poor, but two tooth sockets are visible on thickened fragments. The teeth are stout and pointed with round cross section (**Fig. 2**). They are slightly curved and bear indistinct traces of cutting edges on distal tip. The projecting tooth bases are folded. The teeth are of different size: the largest tooth measures 6.5 × 4.4 mm, the smallest 4.3 × 3.0 mm. The curvature of teeth decreases with size. Tooth base and axis form an angle of ~105° in the largest tooth, which declines in smaller teeth. The largest tooth (**Fig. 2a**) bears traces of chemical corrosion on enamel.

The four large-sized vertebra IQW 2009/30 149 (Mei. 29 311) and IQW 2009/30 155 (Mei. 29 317) are poorly preserved in a similar manner to the specimen described before. The bone surface is corroded and deeply etched, and the centra are partially deformed and smashed (**Fig. 1d**). They most probably represent thoracic vertebrae. The only reliable measurement to take is the transverse diameter of 13.1 mm from IQW 2009/30 149 (Mei. 29 311). Incremental growth rings are more clearly visible than in the caudal vertebra, probably because of etching. They correspond to four or five growth zones.

3.2. Comparison

The perforated lateral vertebra wall observed in caudals was called the »honeycomb pattern« by Watt et al. (1997) and is typical for members of the family Salmonidae, especially the genus *Salmo*. Within *Salmo*, species recognition on vertebral morphology alone is impossible, but according to Van Neer et al. (2007) a combination of individual age and size of specimens allows distinction of non-migratory *Salmo* (e.g., *S. trutta fario*, brown trout) from anadromous *Salmo* (e.g., *S. salar*, Atlantic salmon; *S. trutta trutta*, sea trout). Atlantic salmon and sea trout reach large sizes of much over 1 m in a few years (especially the former species), owing to their accelerated growth in the Atlantic (Neresheimer 1937), whereby Atlantic salmon usually grow faster under similar conditions (Turrero et al. 2014). According to Neresheimer (1937) *Salmo salar* gains weight up to over 1 kg per month in the ocean. The caudal vertebra from Untermassfeld therefore point, based on large size (840–960 mm fork length, see below) and young age (probably one freshwater and two marine years, see below) to migratory *Salmo*, either Atlantic salmon or sea trout.

The skull bone, although fragmentary, can be identified as a vomer based on following features: elongate and general plate-like shape; tooth sockets on thickened bone portion; teeth slightly curved; positive correlation of tooth curvature and size; tooth bases of larger teeth not perpendicular to tooth axis, most distinct in largest teeth. Despite their generally very similar osteology, *Salmo salar* and *S. t. trutta* can be distinguished by their vomer bones and teeth (Henking 1929), although with some uncertainty due to frequent tooth loss during preparation (Neresheimer 1937; Witten et al. 2005). The sea trout bears about 11 teeth in a single row along the vomer axis, which do not much differ in size and curvature. In the anterior part this species has four smaller teeth in a transverse row. In contrast, Atlantic salmon shows only four longitudinally arranged teeth, decreasing significantly in size and curving caudad. Its anterior vomer plate is toothless. Accordingly, IQW 2009/30 114 (Mei. 29 276) can be best compared with *Salmo salar*.

Four proximal fragments of well-ossified rays from paired fins [IQW 1988/22 633 (Mei. 22 152), IQW 2007/29 537 (Mei. 28 699), IQW 2015/41 972 (Mei. 47 281), IQW 2015/41 973 (Mei. 47 282)] may also belong to a large salmonid. The morphology of their proximal articulation very much resemples pectoral fin rays of recent *Salmo salar*.

Rutte (1997) described 30 specimens from large fishes from Untermassfeld, which he attributes to *Esox lucius*. The figures he provided from six (purported) dental fragments and one quadrate (no vertebra is figured) definitely contradict this identification. The bones are strongly ornamented with deep sub-parallel furrows, which are never seen in pikes of similar size. They lack an elevated dental shelf. The dentary teeth of *Esox* are very elongated and narrow (acicular) and not stout and massive [even triangular in IQW 1982/18 566 (Mei. 18 086), Rutte 1997, pl. 20, 4]. All these characteristics instead correspond to *Salmo*, so I attribute this material to that genus. The purported dentary bones should instead be attributed to maxillas. The figured isolated tooth IQW 1984/19 789 (Mei. 19 309) (Rutte 1997, pl. 20, 7) is in my opinion not a fish at all.

3.3. Size and age estimates

For fork-size estimation I use the least square linear regression relationships for caudal vertebra length and width of migratory salmon established by Turrero et al. (2014). The vertebra IQW 2015/41 961 (Mei. 47 270) results in 841 ± 58 mm (for caudal length) and 959 ± 58 mm (for caudal width), whereas IQW 1993/24 304 (Mei. 23 833) gives estimates of 841 ± 58 mm and 922 ± 56 mm fork length, respectively. This indicates that both fishes may have reached 90 cm body length. The three growth zones hardly visible on IQW 2015/41 961 (Mei. 47 270) may be translated in one freshwater and two marine years (age class 1.2). The poorly preserved thoracic vertebra IQW 2009/30 149 (Mei. 29 311) point to an even larger size: 1015 ± 88 mm (based on measurable centrum width). If I interpret its incremental growth rings correctly, this fish may have spent three or four years in the ocean (age class 1.3 or 1.4). These young ages and huge sizes may further corroborate the taxonomic attribution of the Untermassfeld salmon to *Salmo salar*, since this species has faster growth rates than *S. trutta,* which rarely exceed 700 mm after four years (Neresheimer 1937; Turrero et al. 2014).

3.4. Minimum number of individuals (MNI)

The poorly preserved four thoracic vertebra IQW 2009/30 149 (Mei. 29 311) and IQW 2009/30 155 (Mei. 29 317) certainly belong to the same individual. The specimens show the same preservation and were found very near together in the same stratum of Q 30, directly below and nearby a *Homotherium* mandible. The vomer IQW 2009/30 114 (Mei. 29 276), as poorly preserved as the vertebra, may also belong to this individual as it was found about four meters next to the vertebra (Q 26) at comparable profile depth (**Table 1**). The well preserved caudal vertebrae IQW 2015/41 961 (Mei. 47 270) and IQW 1993/24 304 (Mei. 23 833) were found widely separated and in different layers, so they must represent two additional individuals of *Salmo*. In addition, the *Salmo* remains from older excavations, mis-identified by Rutte (1997) as *Esox*, can be interpreted as deriving from at least three individuals (three left and three right maxilla fragments). Taking together, the Atlantic salmon is represented in Untermassfeld by at least six individuals. Four of them, the Rutte material and the finds from Q 30 and 26, display etched preservation.

3.5. Cyprinid fishes

Rutte (1997) described two cyprinid pharyngeal teeth, which I had the opportunity to study. The tooth IQW 1987/21 982 (Mei. 21 501), attributed by him as *Tinca*, represents, based on texture (apatite prisms) and morphology, an enamel cup fragment of a mammalian bonodont tooth (probably a tooth germ). The second tooth fragment IQW 1987/21 979 (Mei. 21 498), attributed by Rutte to *Leuciscus*, may indeed belong to a cyprinid, but corresponds rather to a gudgeon (genus *Gobio*) than to a dace (M. Böhme in Kahlke 2006, 19). Furthermore, the presence of *Scardinius* (rudd) is mentioned by G. Böhme (1997), but it is not figured and it remains unclear to which specimen the statement refers.

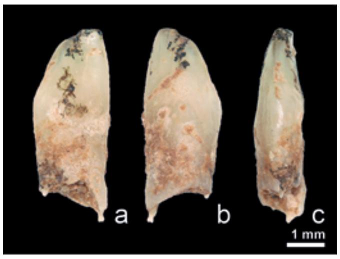

Fig. 3 *Gobio* sp., Untermassfeld. – **a–c** Pharyngeal tooth IQW 2018/45 386 (Mei. 50 695), lateral, medial, posterior view.

Despite extensive excavations during the last 20 years, which include wet screen-washing of 170 metric tons of sediment (Kahlke 1997b; in this volume; Maul 2001), only one single additional cyprinid pharyngeal tooth has been found in the samples. This tooth [IQW 2018/45 386 (Mei. 50 695)] is 5.1 mm tall and the corpus is compressed (**Fig. 3**). The hook is not bended. The tooth base is broken and the surface is corroded, indicating that this tooth was probably ingested as prey. A rather sharp and straight medial crest is well developed, but a lateral crest, and therefore a masticatory area, is missing. This feature points to the cyprinid sub-family Gobioninae (gudgeons). In contrast to leuciscins, which pharyngeal teeth have a masticatory area, Gobionine teeth bear a medial crest only (Böhme 2008). The common European Gudgeon, *Gobio gobio*, is a rather small fish (standard length usually below 20 cm). The Untermassfeld tooth point to a somewhat larger individual (at least 20–25 cm), which is here referred to *Gobio* sp.

4. Discussion

Fossil salmon or trout are very rare in the Eurasian record and so far only known from the Middle Pleistocene onwards (Böhme and Ilg 2003). The oldest non-migratory *Salmo* is described from the Middle Pleistocene fissure filling Gamsenberg near Oppurg, Thuringia / Germany (G. Böhme 2001). Migratory (Atlantic) salmon are so far only recorded from archaeological contexts in Spain and Belgium from Aurignacian onwards (Consuegra et al. 2002; Neer et al. 2007).

The identification of an Atlantic salmon in the late Early Pleistocene site Untermassfeld is an ecologically very interesting and unexpected (albeit not surprising) result. Besides aforementioned size-age relationships, the well-ankylosed and large teeth (**Fig. 2**; Rutte 1997, pl. 20, 1–5) also indicate anadromous lifestyle for Untermassfeld salmonids. During spawning migrations in Atlantic and Pacific salmon, osteologic and odontologic changes take place, especially dentognathic remodelling (Neresheimer 1937; Vladykov 1962; Witten et al. 2005). These changes affect particularly tooth size, shape and attachment. Teeth of spawning individuals returning into freshwater are ankylosed and longer with much larger bases (Vladykov 1962; Witten et al. 2005), usually called »breeding teeth«.

Before industrialization and constructions of damming structures, Atlantic salmon were common in European rivers with Atlantic discharge (Neresheimer 1937). Their upstream migrations start in late summer and reach spawning places in the headwaters (hypo- and metarhithral) of rivers usually during winter. *Salmo salar* was even native in the Werra River at Untermassfeld (between Meiningen and Belrieth) until late 18th century (Anonymous 1835).

Spawning places of *Salmo salar* in the hypo- and metarhithral (greyling to trout zones of rivers) are characterized by shallow, oxygen-rich, and fast-flowing waters with stony bedload. During this time salmon are very vulnerable to predators (Bentley et al. 2014), especially ursids and large canids (Darimont et al. 2008; Matsubayashi et al. 2017).

Salmonid materials from Untermassfeld represent isolated finds or a few associated vertebra from same body region (**Table 1**). They occur in two different states of preservation. Besides perfect bone preservation of single and associated caudal vertebra [IQW 1993/24 304 (Mei. 23 833) and IQW 2015/41 961 (Mei. 47 270)] and fin-rays (**Table 1**), attributed to two individuals, most finds (four individuals, see above) display an etched or corroded appearance and some are crushed or deformed (**Fig. 2d**). Such preservation is a strong indication of bone digestion (Jones 1984; Butler and Schroeder 1998; Guillaud et al. 2017) and suggests that these fossils were buried with carnivore faeces. Two potential carnivore predators for large sized salmons (up to 1 meter length and 10 ± 2 kg weight) are known from Untermassfeld: the bear *Ursus* cf. *dolinensis* (García 2004) and the large canid *Canis* (*Xenocyon*) *lycaonoides* (Sotnikova 2001). Moreover, the undigested vertebra can potentially also be associated with carnivore predation, since bears frequently leave behind much of a salmon carcass. Especially during fall months, before hibernation, they prefer the skull (brain), ovaries and dorsal musculature because of their nutritional value (Reimchen 2000). This would exactly fit with anatomical parts of digested (skull bone, thoracal vertebra) and undigested (caudal vertebra, fin rays) bones and coincides well with the winter half-year of site formation (H.-D. Kahlke 2001).

Furthermore, carnivore predation on salmonids is not only crucial to predator nutrition and growth rates (Hilderbrand et al. 1999; 2004), but, importantly, is of great significance for ecosystem nutrient budgets (Semeniuk 2003). Cederholm et al. (1999) have shown that carcasses of salmons left over by bears in riverside forests contribute to nutrient, especially nitrogen, flow across ecosystems. So, carnivore predation on migrating salmons significantly affects net transport of marine-based nitrogen into terrestrial ecosystems, improving their productivity (Cederholm et al. 1999; Hocking and Reynolds 2012).

The common occurrence of Atlantic salmon and the gudgeon in Untermassfeld further indicate that both characteristic fishes of the hyporhitral (greyling zone) occupied this habitat already since more than one million years.

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References

Anonymous, 1835. Chronik der Stadt Meiningen von 1676 bis 1834. Hennebergischer altertumsforschender Verein, Meiningen.

Bentley, K.T., Schindler, D.E., Cline, T.J., Armstrong, J.B., Macias, D., Ciepiela, L.R., Hilborn, R., 2014. Predator avoidance during reproduction: diel movements by spawning sockeye salmon between stream and lake habitats. Journal of Animal Ecology 83, 1478–1489.

Böhme, G., 1997. Fossile Fischfaunen aus dem jüngeren Känozoikum Deutschlands. Quartär 47/48, 113–138.

2001. Eine fossilführende Pleistozäne Schichtenfolge vom Gamsenberg bei Oppurg (Orlagau, Thüringen). Veröffentlichungen des Naturhistorischen Museums Schleusingen 16, 37–51.

Böhme, M., 2004. Migration history of air-breathing fishes reveal Neogene atmospheric circulation pattern. Geology 32, 393–396.

2008. Ectothermic vertebrates (Teleostei, Allocaudata, Urodela, Anura, Testudines, Choristodera, Crocodylia, Squamata) from the Upper Oligocene of Oberleichtersbach (Northern Bavaria, Germany). Courier Forschungsinstitut Senckenberg 260, 161–183.

2010a. Ectothermic vertebrates, climate and environment of the West Runton Freshwater Bed (early Middle Pleistocene, Cromerian). Quaternary International 228, 63–71.

2010b. Ectothermic vertebrates (Actinopterygii, Allocaudata, Urodela, Anura, Crocodylia, Squamata) from the Miocene of Sandelzhausen (Germany, Bavaria) and their implications for environment reconstruction and palaeoclimate. Paläontologische Zeitschrift 84, 3–41.

Böhme, M., Ilg, A., 2003. fosFARbase [Online]. Available: http://www.wahre-staerke.com/. [Accessed 14 August 2017]

Butler, V.L., Schroeder, R.A., 1998. Do Digestive Processes Leave Diagnostic Traces on Fish Bones? Journal of Archaeological Science 25, 957–971.

Cederholm, C.J., Kunze, M.D., Murota, T., Sibatani, A., 1999. Pacific Salmon Carcasses: Essential Contributions of Nutrients and Energy for Aquatic and Terrestrial Ecosystems. Fisheries 24, 6–15.

Consuegra, S., García de Leániz, C., Serdio, A., González Morales, M., Straus, L.G., Knox, D., Verspoor, E., 2002. Mitochondrial DNA variation in Pleistocene and modern Atlantic salmon from the Iberian glacial refugium. Molecular Ecology 11, 2037–2048.

Darimont, C.T., Paquet, P.C., Reimchen, T.E., 2008. Spawning salmon disrupt trophic coupling between wolves and ungulate prey in coastal British Columbia. BMC Ecology 2008, 8:14.

García, N., 2004. New results on the remains of Ursidae from Untermaßfeld: comparisons with *Ursus dolinensis* from Atapuerca and other Early and Middle Pleistocene sites. In: Maul, L.C., Kahlke, R.-D. (Eds.), Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations. 18th International Senckenberg Conference, VI International Palaeontological Colloquium in Weimar, Weimar (Germany), 25th–30th April, 2004, Conference Volume. Terra Nostra, Schriften der Alfred-Wegener-Stiftung 2004/2, 112–113.

Guillaud, E., Bearez, P., Denys, C., Raimond, S., 2017. New data on fish diet and bone digestion of the Eurasian otter (*Lutra lutra*) (Mammalia: Mustelidae) in central France. The European Zoological Journal 84, 226–237.

Henking, H., 1929. Untersuchungen an Salmoniden: mit besonderer Berücksichtigung der Art- und Rassefragen. Band 1. Rapports et procès-verbaux des réunions 61, 1–99.

Hilderbrand, G.V., Farley, S.D., Schwartz, C.C., Robbins, C.T., 2004. Importance of salmon to wildlife: Implications for integrated management. Ursus 15, 1–9.

Hilderbrand, G.V., Jenkins, S.G., Schwartz, C.C., Hanley, T.A., Robbins, C.T., 1999. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Canadian Journal of Zoology 77, 1623–1630.

Hocking, M.D., Reynolds, J.D., 2012. Nitrogen uptake by plants subsidized by Pacific salmon carcasses: a hierarchical experiment. Canadian Journal of Forest Research 42, 908–917.

Jones, A.K.G., 1984. Some effects of the mammalian digestive system on fish bones. In: Desse-Berset, N. (Ed.), 2nd fish osteoarchaeology meeting. Notes et monographies techniques 16, 61–65.

Kahlke, H.-D., 2001: Neufunde von Cerviden-Resten aus dem Unterpleistozän von Untermassfeld. In: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 2. Monographien des Römisch-Germanischen Zentralmuseums 40, 2, 461–482, pls. 72–76.

Kahlke, R.-D. (Ed.), 1997a. Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 1. Monographien des Römisch-Germanischen Zentralmuseums 40, 1, I–VI, 1–418, pls. 1–67.

1997b. Zur Entdeckungs- und Erforschungsgeschichte der unterpleistozänen Komplexfundstelle Untermassfeld. In: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 1. Monographien des Römisch-Germanischen Zentralmuseums 40, 1, 1–28.

(Ed.), 2001a. Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 2. Monographien des Römisch-Germanischen Zentralmuseums 40, 2, I–VIII, 419–698, pls. 68–131, suppl. 1.

(Ed.), 2001b. Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 3. Monographien des Römisch-Germanischen Zentralmuseums 40, 3, I–VI, 699–1030, pls. 132–151, suppl. 1–15.

2006. Untermassfeld. A late Early Pleistocene (Epivillafranchian) fossil site near Meiningen (Thuringia, Germany) and its position in the development of the European mammal fauna. British Archaeological Reports, International Series 1578. Oxford.

in this volume. Excavation progress and research at the Early Pleistocene site of Untermassfeld during the years 1997–2015. 1031–1078.

Lévêque, C., Oberdorff, T., Paugy, D., Stiassny, M.L.J., Tedesco, P.A., 2008. Global diversity of fish (Pisces) in freshwater. Hydrobiologia 595, 545–567.

Matsubayashi, J., Ohta, T., Takahashi, O., Tayasu, I., 2017. Reconstruction of the extinct Ezo wolf's diet. Journal of Zoology 302, 88–93.

Maul, L., 2001. Die Kleinsäugerreste (Insektivora, Lagomorpha, Rodentia) aus dem Unterpleistozän von Untermassfeld. In: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 2. Monographien des Römisch-Germanischen Zentralmuseums 40, 2, 783–887, pls. 144–145.

Neresheimer, E., 1937. Die Lachsartigen (Salmonidae). I. Teil. In: Demoll, R., Maier, H.N. (Eds.), Handbuch der Binnenfischerei Mitteleuropas. Band III, Lieferung 5. Stuttgart.

Reimchen, T.E., 2000. Some ecological and evolutionary aspects of bear-salmon interactions in coastal British Columbia. Canadian Journal of Zoology 78, 448–457.

Rutte, E., 1997. Die Fischreste aus dem Unterpleistozän von Untermassfeld. In: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 1. Monographien des Römisch-Germanischen Zentralmuseums 40, 1, 77–80, pl. 20.

Semeniuk, R.S., 2003. How bears feed salmon to the forest. Natural History 4, 22–28.

Sotnikova, M.V., 2001. Remains of Canidae from the Lower Pleistocene site of Untermassfeld. In: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 2. Monographien des Römisch-Germanischen Zentralmuseums 40, 2, 607–632, pls. 102–113.

Turrero, P., García-Vázquez, E., Garcia de Leaniz, C., 2014. Shrinking fish: comparisons of prehistoric and contemporary salmonids indicate decreasing size at age across millennia. Royal Society Open Science 1, 140026.

Van Neer, W., Wouters, W., Germonpré, M., 2007. Fish remains from three Upper Palaeolithic cave deposits in southern Belgium. Anthropologica et Praehistorica 118, 5–22.

Vladykov, V.D., 1962. Osteological studies on Pacific salmon of the genus *Oncorhynchus*. Ottawa.

Watt, J., Pierce, G.J., Boyle, P.R., 1997. Guide to the Identification of North Sea Fish Using Premaxillae and Vertebrae. International Council for the Exploration of the Sea (ICES), Cooperative Research Report 220. Copenhagen.

Witten, P.E., Hall, B.K., Huysseune, A., 2005. Are breeding teeth in Atlantic salmon a component of the drastic alterations of the oral facial skeleton? Archives of Oral Biology 50, 213–217.