



Ralf-Dietrich Kahlke (Ed.)

The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany)

Part 4

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Zentrum
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Römisch-Germanisches Zentralmuseum
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und
Senckenberg
Research Station of Quaternary Palaeontology Weimar

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Ralf-Dietrich Kahlke (Ed.)

**THE PLEISTOCENE OF UNTERMASFELD
NEAR MEININGEN (THÜRINGEN, GERMANY)**

PART 4

Mit Beiträgen von

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Römisch-Germanisches
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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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CONTENTS

<i>Sabine Gaudzinski-Windheuser</i> Foreword	IX
<i>Ralf-Dietrich Kahlke</i> Preface	XI
<i>Ralf-Dietrich Kahlke</i> Excavation progress and research at the Early Pleistocene site of Untermassfeld during the years 1997–2015	1031
<i>Ralf-Dietrich Kahlke · Ulf Linnemann · Andreas Gärtner</i> New results on the origin and geological history of the Early Pleistocene site of Untermassfeld	1079
<i>Axel Gerdes · Andreas Gärtner · Ulf Linnemann · Ralf-Dietrich Kahlke</i> In situ U-Pb geochronology of re-deposited travertine from the Early Pleistocene site of Untermassfeld	1105
<i>John-Albrecht Keiler · Mark Benecke · Jonas Keiler</i> Bone modifications by insects from the Early Pleistocene site of Untermassfeld	1117
<i>Madelaine Böhme</i> New results on fishes from the Early Pleistocene site of Untermassfeld	1133
<i>Madelaine Böhme</i> New results on amphibians and reptiles from the Early Pleistocene site of Untermassfeld – Bioclimatic analysis of the herpetofauna	1141
<i>Albrecht Manegold</i> New results on birds from the Early Pleistocene site of Untermassfeld	1159
<i>Maia Bukhsianidze</i> New results on bovids from the Early Pleistocene site of Untermassfeld	1169
<i>Marzia Breda · Ralf-Dietrich Kahlke · Adrian M. Lister</i> New results on cervids from the Early Pleistocene site of Untermassfeld	1197
<i>Uwe Kierdorf · Ralf-Dietrich Kahlke</i> Pathological findings on remains of hippopotamids from the Early Pleistocene site of Untermassfeld	1251

<i>Adam Kotowski · Krzysztof Stefaniak · Ralf-Dietrich Kahlke</i> A rhinocerotid skull from the Early Pleistocene site of Untermassfeld	1273
<i>Véra Eisenmann · Nicolas Boulbes</i> New results on equids from the Early Pleistocene site of Untermassfeld	1295
List of contributors	1323
Foldout I	

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), micro-mammals (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.

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Sabine Gaudzinski-Windheuser

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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

NEW RESULTS ON AMPHIBIANS AND REPTILES FROM THE EARLY PLEISTOCENE SITE OF UNTERMASFELD – BIOCLIMATIC ANALYSIS OF THE HERPETOFAUNA

Abstract	1141	3.3. Minimum number of individuals (MNI)	1154
1. Introduction	1141	3.4. Humidity inferences	1154
2. Material and methods	1142	4. Discussion	1155
3. Results	1145	Acknowledgements	1157
3.1. Description	1145	References	1157
3.2. The presence of pond turtles in Untermassfeld	1153		

Abstract

Herpetological remains are not numerous in the late Early Pleistocene (Epivillafranchian) of Untermassfeld. Nonetheless, with 16 species a high diversity is documented: two species of newts (*Lissotriton vulgaris*, *Triturus* cf. *crystatus*), seven species of frogs (*Rana temporaria*, *R. arvalis*, *R. dalmatina*, *Pelophylax ridibundus* vel *esculentus*, *Bufo bufo*, *Bufo viridis*, *Hyla arborea*), three species of lizards (*Anguis fragilis*, aff. *Ophisops elegans*, *Lacerta* sp.), and four snake species (*Eryx* sp., *Elaphe* sp., cf. *Coronella* sp., *Natrix* sp.). *Rana temporaria* and *Pelophylax ridibundus* vel *esculentus* as well as all the reptile taxa are new for the locality. The records of pond turtle, skink and gekko could not be confirmed, but higher squamate diversity cannot be excluded, since the taphocoenosis is biased against reptiles. The most surprising reptile taxon from Untermassfeld is the Sand Boa *Eryx*, which is the first Pleistocene record of this group from Central Europe. Compared to today, the Epivillafranchian climate at Untermassfeld was significantly warmer and less humid. Bioclimatic analysis and the documented thermophilous reptiles suggest five degrees higher mean annual temperature (MAT 13 °C), with mild winters (CMT 2–3 °C) and hot summers (WMT 24 °C), and slightly lower rainfall (MAP ≤ 620 mm). Habitat structure was comparable to present day, except the larger extent of dry and open habitats.

1. Introduction

Amphibians and reptiles represent an important component of terrestrial biodiversity and over 230 extant species are known from the European continent, the majority of them are endemic (Temple and Cox 2009). In recent years, fossil herpetofaunas have attracted greater interest in European Pleistocene palaeontology, also because of their potential for environmental and climate reconstructions (Delfino 2002; Ivanov 2007; Blain 2009).

A key locality of the European Early Pleistocene is the Epivillafranchian site of Untermassfeld (Kahlke 2006), from which herpetofaunas are still only partially known. G. Böhme (1997) gave an initial description of amphibians from Untermassfeld. Based on 151 skeletal remains, recovered during excavation campaigns from 1979–1987, he identified seven species. Two species of tailed amphibians (*Triturus* cf. *crystatus*, *Lissotriton*

cf. *vulgaris*) and five species of frogs (*Bufo* cf. *bufo*, *Bufo* cf. *viridis*, *Hyla* cf. *arborea*, *Rana* cf. *arvalis*, *R.* cf. *dalmatina*). Maul (1997) described a hyoid bone, which he compared to pond turtles (Emydini). Other reptilian groups, such as the squamates remained unstudied, although Sher (1986) mentioned finds of the skink *Chalcides* and the gecko *Eublepharis* identified by L.P. Tatarinov (Moscow).

Here I provide a study of new amphibian remains recovered since 1987 and a description of squamate fossils from Untermassfeld. I further re-evaluate the hyoid bone proposed to derive from a turtle. In addition to the taxonomic evaluation, I investigate the meaning of the herpetofauna for environmental and climatic reconstructions of the Untermassfeld site.

2. Material and methods

The studied fossils are deposited in the collection of the Senckenberg Research Station of Quaternary Palaeontology, Weimar (acronym IQW). They comprise of one articulated frog skeleton and 102 isolated bones, of which 74 belong to amphibians and 28 to squamates (Table 1). The anuran osteologic nomenclature follows G. Böhme (1977) and Bailon (1999). Snake vertebra nomenclature follows Auffenberg (1963), with measurements centrum length (CL) and neural arch width (NAW). All measurements have been taken from photographs. Comparative osteological materials of living amphibian and reptile species are deposited in the Palaeontological collection of Tübingen University (GPIT uncatalogued) and the Museum für Tierkunde, Senckenberg Dresden (MTD). Climatic data have been assessed from online data-bases (Deutscher Wetterdienst, Climate-Data.org by AM Online Projects).

	Grid square	Find depth below site 0-level	Material
IQW 2004/28 750 (Mei. 27 912)	Q 310–312	n. s.	<i>Lissotriton vulgaris</i> , trunk vertebra
IQW 2004/28 724 (Mei. 27 886)	Q 157, 158	2.0–1.5	<i>Lissotriton vulgaris</i> , trunk vertebra
IQW 2018/45 377 (Mei. 50 686)	Q 156	1.8	<i>Lissotriton vulgaris</i> , caudal vertebra
IQW 2004/28 726 (Mei. 27 888)	Q 49	2.0–1.5	<i>Lissotriton vulgaris</i> , humerus
IQW 2004/28 730 (Mei. 27 892)	Q 156	1.8–1.6	<i>Rana temporaria</i> , left ilium
IQW 2004/28 737 (Mei. 27 899)	Q 48	2.0–1.5	<i>Rana temporaria</i> , left ilium
IQW 2015/41 963 (Mei. 47 272)	Q 156	n. s.	<i>Rana temporaria</i> , left ilium
IQW 2015/41 959 (Mei. 47 268)	Q 41	n. s.	<i>Rana temporaria</i> , right ilium
IQW 2004/28 740 (Mei. 27 902)	Q 156	n. s.	<i>Rana temporaria</i> , left scapula
IQW 2018/45 375 (Mei. 50 684)	Q 156	1.8	<i>Rana arvalis</i> , left ilium
IQW 2004/28 743 (Mei. 27 905)	Q 156	1.75–1.59	<i>Rana arvalis</i> , left and right ilium
IQW 2010/30 892 (Mei. 30 054)	n. s.	n. s.	<i>Rana dalmatina</i> , articulated skeleton
IQW 2004/28 721 (Mei. 27 883)	Q 156	1.8	<i>Rana dalmatina</i> , left ilium, right scapula
IQW 2004/28 734 (Mei. 27 896)	Q 156	n. s.	<i>Rana dalmatina</i> , right scapula
IQW 2018/45 395 (Mei. 50 704)	Q 501–504	n. s.	<i>Rana dalmatina</i> , left scapula

Table 1 Herpetofaunal remains from Untermassfeld described in this study. n. s. – not specified.

	Grid square	Find depth below site 0-level	Material
IQW 2015/41960 (Mei. 47269)	Q 47	n. s.	<i>Rana</i> sp., left ilium
IQW 2004/28759 (Mei. 27921)	Q 512/22	n. s.	<i>Rana</i> sp., juvenile left ilium
IQW 2018/45381 (Mei. 50690)	n. s.	n. s.	<i>Rana</i> sp., juvenile left ilium, articular, radioulna, humerus
IQW 1984/20330 (Mei. 19850)	n. s.	n. s.	<i>Rana</i> sp., ilium fragment, ischium, neural spine
IQW 2018/45382 (Mei. 50691)	Q 39	n. s.	<i>Rana</i> sp., two humeri
IQW 2014/41852 (Mei. 47161)	Q 627	2.64	<i>Rana</i> sp., tibia
IQW 1984/20327 (Mei. 19847)	n. s.	n. s.	<i>Rana</i> sp., sacral vertebra
IQW 2018/45372 (Mei. 50681)	Q 148, 149, 185, 186	n. s.	<i>Rana</i> sp., sacral vertebra, neural arch
IQW 2018/45389 (Mei. 50698)	Q 156	1.75–1.59	<i>Rana</i> sp., radioulna, urostyl, two maxillae, two tarsals
IQW 2018/45390 (Mei. 50699)	Q 156	1.8	<i>Rana</i> sp., radioulna, maxilla, scapula, articular
IQW 2018/45391 (Mei. 50700)	Q 156	n. s.	<i>Rana</i> sp., radioulna
IQW 2018/45394 (Mei. 50703)	Q 50	1.48–1.43	<i>Rana</i> sp., maxilla
IQW 2004/28725 (Mei. 27887)	Q 157, 158	2.0–1.5	<i>Pelophylax ridibundus</i> vel <i>esculentus</i> , left ilium
IQW 2004/28744 (Mei. 27906)	Q 50	1.43–1.34	Bufonidae indet., right humerus
IQW 2018/45374 (Mei. 50683)	Q 49	2.0–1.5	Bufonidae indet., humerus fragment
IQW 2004/28745 (Mei. 27907)	Q 156	1.48	Bufonidae indet., urostyl
IQW 2018/45384 (Mei. 50693)	n. s.	n. s.	Bufonidae indet., articular
IQW 1988/22551 (Mei. 22070)	n. s.	n. s.	<i>Hyla arborea</i> , left juvenile ilium
IQW 2004/28761 (Mei. 27923)	n. s.	n. s.	<i>Hyla arborea</i> , right ilium
IQW 2004/28741 (Mei. 27903)	Q 156	1.4–1.2	<i>Hyla arborea</i> , right ilium
IQW 2018/45383 (Mei. 50692)	n. s.	n. s.	<i>Hyla arborea</i> , right juvenile ilium
IQW 2015/41962 (Mei. 47271)	Q 39	n. s.	<i>Hyla arborea</i> , humerus
IQW 2018/45385 (Mei. 50694)	Q 313	n. s.	<i>Hyla arborea</i> , humerus
IQW 2018/45371 (Mei. 50680)	n. s.	n. s.	Anura indet., neural arch
IQW 2004/28728 (Mei. 27890)	Q 49	1.96–1.94	Anura indet., radioulna
IQW 2004/28729 (Mei. 27891)	Q 157	2.0–1.5	Anura indet., radioulna
IQW 2004/28739 (Mei. 27901)	Q 156	1.45	Anura indet., radioulna
IQW 2015/41975 (Mei. 47284)	Q 560	n. s.	Anura indet., tibiofibula
IQW 2004/28749 (Mei. 27911)	Q 688–690, 705–707	n. s.	Anura indet., tibiotarsus
IQW 2004/28751 (Mei. 27913)	n. s.	n. s.	Anura indet., vertebra centrum, articular, squamosal, radioulna, tibiotarsus
IQW 2004/28746 (Mei. 27908)	n. s.	n. s.	Anura indet., vertebra, articular, radioulna
IQW 2018/45387 (Mei. 50696)	Q 48	2.0–1.5	Anura indet., tarsal bone

Table 1 (continued)

	Grid square	Find depth below site 0-level	Material
IQW 2018/45388 (Mei. 50697)	Q 156	n. s.	Anura indet., tarsal bone
IQW 2018/45392 (Mei. 50701)	Q 156	1.4–1.2	Anura indet., tarsal bone
IQW 2018/45393 (Mei. 50702)	Q 157, 158	2.0–1.5	Anura indet., tarsal bone
IQW 2004/28727 (Mei. 27889)	Q 157	2.0–1.5	Anura indet., tarsal bone
IQW 2004/28738 (Mei. 27900)	Q 156	1.8–1.4	Anura indet., tarsal bone
IQW 2004/28760 (Mei. 27922)	Q 313	n. s.	<i>Anguis fragilis</i> , osteoderm
IQW 2004/28736 (Mei. 27898)	Q 156	2.0–1.5	<i>Anguis fragilis</i> , osteoderm
IQW 2004/28748 (Mei. 27910)	n. s.	n. s.	<i>Anguis fragilis</i> , osteoderm
IQW 2004/28753 (Mei. 27915)	Q 148, 149, 156, 185	n. s.	<i>Anguis fragilis</i> , osteoderm
IQW 2015/41964 (Mei. 47273)	Q 46	n. s.	<i>Anguis fragilis</i> , osteoderm
IQW 2004/28752 (Mei. 27914)	Q 155, 156	n. s.	<i>Anguis fragilis</i> , trunk vertebra
IQW 2018/45378 (Mei. 50687)	Q 156	1.8	<i>Anguis fragilis</i> , trunk vertebra
IQW 2004/28731 (Mei. 27893)	Q 158	1.4–1.14	<i>Anguis fragilis</i> , trunk vertebra
IQW 2018/45368 (Mei. 50677)	Q 156	1.75–1.59	<i>Anguis fragilis</i> , trunk vertebra
IQW 2018/45370 (Mei. 50679)	Q 313	n. s.	<i>Anguis fragilis</i> , sacral vertebra
IQW 2004/28732 (Mei. 27894)	Q 157, 158	2.0–1.5	<i>Anguis fragilis</i> , caudal vertebra
IQW 2004/28733 (Mei. 27895)	Q 157	2.0–1.5	<i>Anguis fragilis</i> , caudal vertebra
IQW 2018/45380 (Mei. 50689)	Q 157, 158	2.0–1.5	<i>Anguis fragilis</i> , caudal vertebra
IQW 2018/45376 (Mei. 50685)	Q 41	n. s.	<i>Anguis fragilis</i> , caudal vertebra
IQW 2018/45369 (Mei. 50678)	n. s.	n. s.	<i>Anguis fragilis</i> , caudal vertebra
IQW 1987/21828 (Mei. 21347)	n. s.	n. s.	aff. <i>Ophisops elegans</i> , right dental
IQW 1987/21829 (Mei. 21348)	Q 313	n. s.	<i>Lacerta</i> sp., right maxilla
IQW 2004/28722 (Mei. 27884)	Q 48	n. s.	<i>Lacerta</i> sp., cranial osteoderm
IQW 2018/45365 (Mei. 50674)	Q 156	1.8	<i>Eryx</i> sp., trunk vertebra
IQW 2004/28755 (Mei. 27917)	Q 228	n. s.	<i>Eryx</i> sp., juvenile trunk vertebra
IQW 2004/28742 (Mei. 27904)	Q 50	1.48–1.43	<i>Elaphe</i> sp., cervical vertebra
IQW 2018/45366 (Mei. 50675)	Q 313	n. s.	<i>Elaphe</i> sp., trunk vertebra
IQW 2018/45367 (Mei. 50676)	Q 156	1.75–1.59	cf. <i>Coronella</i> sp., trunk vertebra
IQW 1987/21824 (Mei. 21343)	n. s.	n. s.	<i>Natrix</i> sp., cervical vertebra
IQW 1984/20329 (Mei. 19849)	n. s.	n. s.	<i>Natrix</i> sp., trunk vertebra
IQW 2004/28754 (Mei. 27916)	n. s.	n. s.	<i>Natrix</i> sp., trunk vertebra fragment
IQW 2015/41958 (Mei. 47267)	Q 41	n. s.	<i>Natrix</i> sp., trunk vertebra fragment
IQW 2018/45367 (Mei. 50676)	Q 148, 149, 185, 186	n. s.	Serpentes indet.

Table 1 (continued)

3. Results

3.1. Description

Caudata Scopoli, 1777

Salamandridae Goldfuss, 1820

Lissotriton Bell, 1839

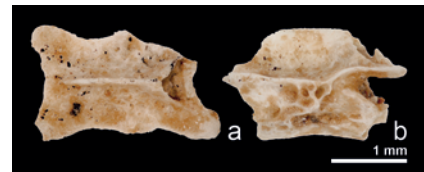
Lissotriton vulgaris (Linnaeus, 1758)

Studied material: trunk vertebra IQW 2004/28 750 (Mei. 27 912), trunk vertebra IQW 2004/28 724 (Mei. 27 886), caudal vertebra IQW 2018/45 377 (Mei. 50 686), humerus fragment IQW 2004/28 726 (Mei. 27 888).

The trunk vertebra is fragmentary with broken condyle and posterior neural arch (Fig. 1). The reconstructed centrum length is 1.8 mm. This small specimen shows diagnostic features of the genus *Lissotriton* (Haller-Probst and Schleich 1994): a moderately tall neural spine with a nearly horizontal dorsal margin, anteriorly vaulted neural arch (cranial view) and distally only slightly elevated neural arch (lateral view). It is very similar to *L. vulgaris* and differs from *L. boscai* and *L. helveticus* by the ridge-like neural spine (wedge shaped in dorsal view in *L. boscai*) and less elevated neural arch (taller in *L. helveticus*).

While the caudal vertebra has no taxonomic value, the attribution of the trunk vertebra to *L. vulgaris*, the most widespread species of *Lissotriton*, is quite confident. However, the genus *Lissotriton* has seven additional species, for which comparative material was not available. These species have restricted distribution outside Central Europe and are native to Southern Europe, the Carpathians, the Balkans, Anatolia and the Caucasus.

Fig. 1 *Lissotriton vulgaris* (Linnaeus, 1758), Untermassfeld. – **a–b** Trunk vertebra IQW 2004/28 750 (Mei. 27 912), dorsal, lateral views.



Anura Rafinesque, 1815

Ranidae Batsch, 1796

Rana Linnaeus, 1758

Rana temporaria Linnaeus, 1758

Studied material: left ilium IQW 2004/28 730 (Mei. 27 892), left ilium IQW 2004/28 737 (Mei. 27 899), left ilium IQW 2015/41 963 (Mei. 47 272), right ilium IQW 2015/41 959 (Mei. 47 268), left scapula IQW 2004/28 740 (Mei. 27 902).

The ilia are broken to various degree, but show all characteristic features of the grass frog (G. Böhme 1977) (Fig. 2a–b): tuber superior is high and bulges laterally as well as dorsally; the vexillum is low (lower than

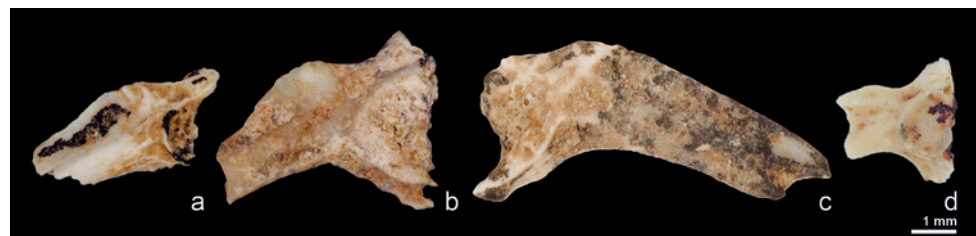


Fig. 2 *Rana temporaria* Linnaeus, 1758, Untermassfeld. – **a** Left ilium IQW 2004/28 730 (Mei. 27 892), lateral view. – **b** Left ilium IQW 2004/28 737 (Mei. 27 899), lateral view. | *Rana arvalis* Nilsson, 1842, Untermassfeld. – **c** Right ilium IQW 2004/28 743 (Mei. 27 905), lateral view. – **d** Left ilium IQW 2018/45 375 (Mei. 50 684), lateral view.

the ala) and decreases in dorsal height directly distal to the tuber where it is medially inclined. A supraacetabular fossa is lacking. The internal crest of the robust scapula is strong, long and curves caudally. The material differs from the morphologically similar *R. arvalis* in its dominant tuber superior, the lack the iliac supraacetabular fossa (see below) and the strong internal crest on scapula.

Rana arvalis Nilsson, 1842

Studied material: left ilium IQW 2018/45375 (Mei. 50684), left and right ilium IQW 2004/28743 (Mei. 27905). The ilia referable to the moor frog have a well-developed supraacetabular fossa, a dorsally and laterally less bulging tuber superior, and a less abrupt decrease of the vexillum than in the grass frog (G. Böhme 1977) (Fig. 2c–d). G. Böhme (1997) identified 10 ilia, which tentatively belong to the moor frog. Some of these fragmentary bones may instead belong to the grass frog, which he does not identify in his materials.

Rana dalmatina Fitzinger in Bonaparte, 1839

Studied material: articulated skeleton IQW 2010/30892 (Mei. 30054), right ilium and right scapula IQW 2004/28721 (Mei. 27883), right scapula IQW 2004/28734 (Mei. 27896), left scapula IQW 2018/45395 (Mei. 50704). The single ilium is fragmentary. It shows a proximally high vexillum and a ventrally less defined tuber superior, leaving no depression between its ventral border and the ala. The internal crest on scapula is well developed, but shorter and less caudally curved than in *R. temporaria*. IQW 2010/30892 (Mei. 30054) is an articulated skeleton of medium-sized ranid, which is seen in ventral view in Fig. 3. Despite its articulated condition, it lacks the skull and the vertebral column, but the pelvic region and extremities are in nearly life position. The proximal ilium is crushed, but this skeleton can nonetheless be referred to *R. dalmatina*.



Fig. 3 *Rana dalmatina* Fitzinger in Bonaparte, 1839, Untermassfeld. – Articulated skeleton IQW 2010/30892 (Mei. 30054), ventral view.

	Radioulna	Scapula	Femur	Tibia	Tibiale	Prox. Phalanx IV
Length	9.3	6.9	25.2	26.7	13.5	10.6

Table 2 *Rana dalmatina*. Measurements (in mm) on the articulated skeleton IQW 2010/30892 (Mei. 30054).

This based on the high and moderately distal shallowing of the vexillum and the relatively gracile scapula in which the internal crest curves less caudally. The medial crest on distal humerus is twice as long as the capitulum. Furthermore, the position of all four legs, the ilia and the scapula indicates that the trunk was not much more than 32 mm long, resulting in a snout-trunk length of about 40 mm. This is short relative to the length of the hind leg (femur + tibia = 52 mm, **Table 2**), which further indicates that the specimen belong to the long legged agile frog *Rana dalmatina* (Günther 1996, fig. 173).

Rana sp.

27 bones (**Table 1**) represent most probably brown frogs. For secure determination, they are too much broken, derive from juvenile individuals, or are undiagnostic elements (maxilla, radioulna, etc.).

Pelophylax Fitzinger, 1843

Pelophylax ridibundus vel *esculentus*

Studied material: left ilium IQW 2004/28725 (Mei. 27887).

A single diagnostic bone documents the water frog. This large ilium (**Fig. 4a**), although broken proximally, shows a dorsally very high vexillum, which is nearly twice as high as the ala. The vexillum reaches its highest point distal to the large tuber superior. The tuber is drop-like with a well-defined ventral border, leaving a depression between tuber and ala. This prominent tuber characterizes *Pelophylax*, in contrast to the quite similar *R. dalmatina* (G. Böhme 1977, Bailon 1999). However, the tuber is not as dominant as in *P. lessonae* and corresponds more to *P. ridibundus* and *P. esculentus* (G. Böhme and Günther 1979). Both latter species can be separated osteologically only with frontoparietals (G. Böhme and Günther 1979), which are not preserved here.



Fig. 4 *Pelophylax* sp., Untermassfeld. – **a** Left ilium IQW 2004/28725 (Mei. 27887), lateral view. | Bufonidae indet., Untermassfeld. – **b** Right humerus IQW 2004/28744 (Mei. 27906), anterior view. | *Hyla arborea* (Linnaeus, 1758), Untermassfeld. – **c** Right ilium IQW 2004/28761 (Mei. 27923), lateral view.

Bufonidae Gray, 1825

Bufonidae indet.

Studied material: right humerus IQW 2004/28744 (Mei. 27906), humerus fragment IQW 2018/45374 (Mei. 50683), urostyl IQW 2004/28745 (Mei. 27907), articular fragment IQW 2018/45384 (Mei. 50693).

The distal humerus fragment (**Fig. 4b**) lacks the condyle. The bone surface shows thin longitudinal furrows and pits, typical for bufonid bones. The humerus has a closed cubital fossa, which also characterize all Bufonidae. Both, crista lateralis and medialis are weakly developed. The small-sized urostyl has two cotyli and shows the same bufonid-type bone sculpturing, as did the articulare. The extant European representatives of toads have recently been classified into three genera: *Bufo*, *Bufotes*, and *Epidalea*. Differentiation of these taxa on humeri may be possible, but only with complete bones and only *Epidalea* show distinct urostyl morphology (Bailon 1999). Differentiation of bufonid species on articular fragments is impossible. G. Böhme (1997) identified from Untermassfeld two bufonids: *Bufo* cf. *bufo* and *Bufotes* cf. *viridis*. He

figured a humerus (Böhme 1997, fig. 4), attributed by him to the latter species, which show stronger development of lateral and medial crests.

Hylidae Rafinesque, 1815

Hyla Laurenti, 1768

Hyla arborea (Linnaeus, 1758)

Studied material: left juvenile ilium IQW 1988/22 551 (Mei. 22 070), right ilium IQW 2004/28 761 (Mei. 27 923), left ilium IQW 2004/28 741 (Mei. 27 903), right juvenile ilium IQW 2018/45 383 (Mei. 50 692), humerus IQW 2015/41 962 (Mei. 47 271), humerus IQW 2018/45 385 (Mei. 50 694).

The four ilia show all characteristics of the common European tree frog *Hyla arborea*: absence of the vexillum (crista dorsalis), cranially expanded pars descendens, triangular acetabulum, lateral projecting and bulbous tuber superior not raised above the corpus, and absence of the supraacetabular fossa (Fig. 4c). Based on the latter two characters, the ilia are distinct from *H. meridionalis* (Holman 1992) and *H. savignyi* (Vasilyan et al. 2017).

Anura indet.

20 frog bones, mostly fragments of radioulnae, vertebrae, or long-bones (Table 1) could not be assigned to a species or genus but only to Anura indet.

Squamata Oppel, 1811

Anguimorpha Fürbinger, 1900

Anguidae Gray, 1825

Anguis Linnaeus, 1758

Anguis fragilis Linnaeus, 1758

Studied material: osteoderm IQW 2004/28 760 (Mei. 27 922), osteoderm IQW 2004/28 736 (Mei. 27 898), osteoderm IQW 2004/28 748 (Mei. 27 910), osteoderm IQW 2004/28 753 (Mei. 27 915), osteoderm IQW 2015/41 964 (Mei. 47 273), trunk vertebra IQW 2004/28 752 (Mei. 27 914), trunk vertebra IQW 2018/45 378 (Mei. 50 687), trunk vertebra IQW 2004/28 731 (Mei. 27 893), trunk vertebra IQW 2018/45 368 (Mei. 50 677), sacral vertebra IQW 2018/45 370 (Mei. 50 679), caudal vertebra IQW 2004/28 732 (Mei. 27 894), caudal vertebra IQW 2004/28 733 (Mei. 27 895), caudal vertebra IQW 2018/45 380 (Mei. 50 689), caudal vertebra IQW 2018/45 376 (Mei. 50 685), caudal vertebra IQW 2018/45 369 (Mei. 50 678).

Anguid lizards are documented by five osteoderms and ten vertebrae, which are attributed to *Anguis fragilis* (Table 1). The *Anguis*-type osteoderms (Fig. 5a–b) are thin and lack the longitudinal ridge characterizing most osteoderms of *Ophisaurus* and *Pseudopus* (Hoffstetter 1962). The trunk vertebra (Fig. 5c–e) show a ventrally smooth centrum, whose lateral walls are parallel (anteriorly divergent in *Ophisaurus* and *Pseudopus*; Roček 1984; Vasilyan et al. 2016) and slightly constricted in the middle. The height of the cotyle is greater than

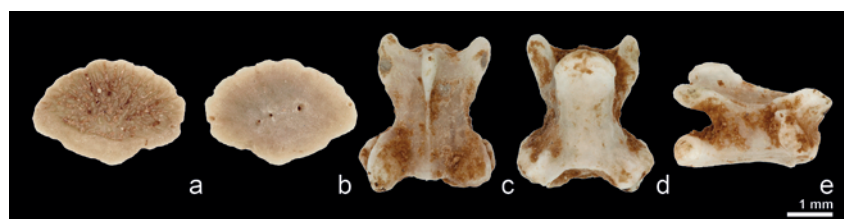
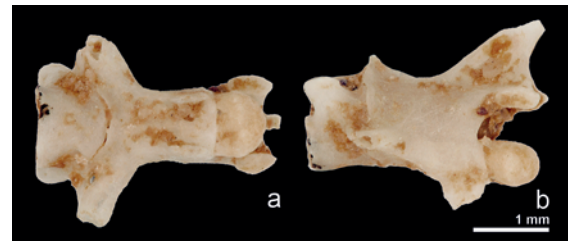


Fig. 5 *Anguis fragilis* Linnaeus, 1758, Untermassfeld. – **a–b** Osteoderm IQW 2004/28 748 (Mei. 27 910), dorsal, ventral views. – **c–e** Trunk vertebra IQW 2018/45 368 (Mei. 50 677), dorsal, ventral, lateral views.

Fig. 6 *Anguis fragilis* Linnaeus, 1758, Untermassfeld. – **a–b** Caudal vertebra IQW 2004/28733 (Mei. 27 895), ventral, lateral views.



the neural canal (reverse in *Ophisaurus*; Vasilyan et al. 2016). As is typical for anguids (Etheridge 1967), the caudal vertebrae bear two converging transverse processes encompassing the fracture plane for caudal autotomy (Fig. 6). Based on molecular genetic studies, *Anguis fragilis* has recently be subdivided into three species (*A. fragilis*, *A. colchica*, *A. graeca*; Gvoždik et al. 2010), whose osteological distinctness is currently unknown. Since this species complex had already separated by the Early Pleistocene (Gvoždik et al. 2010), I prefer a taxonomic attribution to the Common European Slow Worm, distributed today in Western and Central Europe.

Lacertibaenia Vidal et Hedges, 2005

Lacertidae Bonaparte, 1831

Ophisops Ménétriés, 1832

Ophisops elegans Ménétriés, 1832

aff. *Ophisops elegans* Ménétriés, 1832

Studied material: right dental IQW 1987/21 828 (Mei. 21 347).

This tiny fragment is of 2.6 mm length and preserve about the anterior third of the dentary (Fig. 7a–b). The bone is broken at the level of the sixth functional tooth position; the ventral lamina is broken between the second and the third teeth. Despite these preservation limitations, the dental corpus can be characterized as elongate. The symphysis is narrow and pointed. The dental shelf is low and its crista has irregular shape. The dental sulcus is very narrow and the horizontal lamina is thin. Its largest thickness, below the third tooth position, the bone equals the diameter of the fifth functional tooth. Every second tooth socket is empty, and the first four functional teeth are broken. The fifth functional tooth is unicuspid with a nearly symmetric cusp. The labial side of the dentary shows five mental foramina at the positions of every tooth.

The combination of small dimensions, elongate dentary, very narrow dental sulcus, low dental shelf, thin horizontal lamina, and unicuspid teeth compared best to the extant species *Ophisops elegans*. Other small-size European lizards differ in two or more features (compare Rauscher 1992, Holman 1998): *Podarcis muralis* (high dental shelf, uni- and bicuspid teeth), *Zootoca vivipara* (deep dental sulcus, tricuspid teeth), *Lacerta agilis* (deep dental sulcus, high dental shelf, uni- and bicuspid teeth). However, the fossil differs from *O. elegans* (Rauscher 1992 and GPIT comparative material) in some details: in *O. elegans* the horizontal lamina is thicker in the symphyseal area and thickest behind the sixth tooth position and the tooth cusps are slightly recurved. Considering these differences of the single specimen, some reservations remain with the taxonomic allocation.



Fig. 7 aff. *Ophisops elegans* Ménétriés, 1832, Untermassfeld. – **a–b** Dental bone IQW 1987/21 828 (Mei. 21 347), medial, lateral views. | *Lacerta* sp., Untermassfeld. – **c–d** Maxilla IQW 1987/21 829 (Mei. 21 348), medial, lateral views.

Lacerta Linnaeus, 1758

Lacerta sp.

Studied material: right maxilla IQW 1987/21829 (Mei. 21348), cranial osteoderm IQW 2004/28722 (Mei. 27884).

The maxilla fragment is 2.7 mm long and preserves the middle part of the bone (~30% of complete bone), with five tooth positions anterior the infraorbital foramen (Fig. 7c–d). The facial process is broken. The buccal side shows two large labial foramina (Fig. 7d). The dental sulcus is relatively wide. The teeth are robust and bicuspid, with blunt main and anterior accessory cusps.

The combination of robust bicuspid teeth, wide dental sulcus, and few large labial foramina is comparable to *Lacerta agilis* (Rauscher 1992). The maxillary teeth of *O. elegans* are gracile with less expressed bicuspid crowns. The specimen therefore documents a second lacertid in Untermassfeld, although a secure specific identification needs more and better-preserved materials.

IQW 2004/28722 (Mei. 27884) is a 2.5 mm large and ~0.4 mm thick cranial osteoderm of a lacertid. The sculpturing is similar to dermal bones of the Eastern Green Lizard *L. viridis*. This type of bone is rarely described in lizard anatomy, and never been used in palaeontology. According to Costantini et al. (2010) its shape and size correspond to a supraocular osteoderm. These authors found that cranial osteoderms are prominent in adult Western Green Lizards, *Lacerta bilineata*, but less extensive in young ontogenetic stages or small-sized species. This Untermassfeld osteoderm indicates at least a larger-size lizard. The questions, whether it can be referred to Green Lizards (*Lacerta viridis* vel *bilineata*) and whether it is conspecific to the maxilla fragment, remains unresolved.

Serpentes Linnaeus, 1758

Boidae Gray, 1825

Erycinae Bonaparte, 1831

Eryx Daudin, 1802

Eryx sp.

Studied material: trunk vertebra IQW 2018/45365 (Mei. 50674), juvenile trunk vertebra IQW 2004/28755 (Mei. 27917).

The trunk vertebra (Fig. 8) is wider (NAW 1.67 mm) than long (CL 1.55 mm; CL/NAW 0.93) and lacks a paracotylar foramen, which indicates a member of Boidae. The small dimensions, the long and slender neural spine, the dorso-ventrally depressed neural arch, the rough and dorsally tilted prezygapophysis, the short prezygapophyseal process, and the weak haemal keel point to the subfamily Erycinae, especially the genus *Eryx* (Rage 1984; Szyndlar 1991). The juvenile trunk vertebra has similar proportions, but is less ossified and adds no further information. Unfortunately, trunk vertebrae of most living members of the genus *Eryx* differ little in morphology (Szyndlar and Schleich 1994), and more diagnostic caudal vertebra are lacking from Untermassfeld.

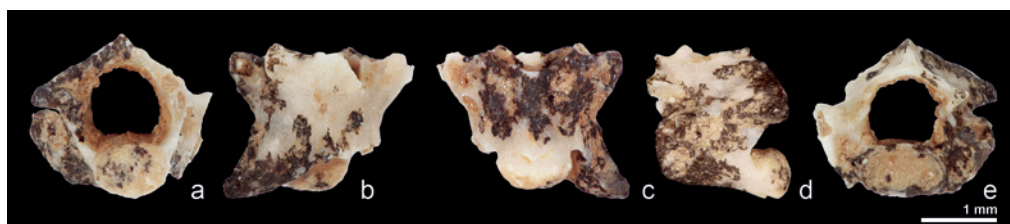


Fig. 8 *Eryx* sp., Untermassfeld. – a–e Trunk vertebra IQW 2018/45365 (Mei. 50674), anterior, dorsal, ventral, lateral, posterior views.

For further taxonomic identification, comparison with two available trunk vertebrae of *E. jaculus* (GPIT) show subtle differences: in both fossils, the haemal keel is a little more pronounced and accompanied by subcentral grooves. These features are found in the African erycine genus *Gongylophis* (*G. conicus*, Hoffstetter and Rage 1972, fig. 4). However, Szyndlar and Schleich (1994, 235) note that haemal keels can also occur in some species of *Eryx* and »that the presence or absence of this structure is subject to intraspecific or allometric variations«. More material, especial caudal vertebrae, are needed for specific identification of this Sand Boa.

Colubridae Oppel, 1811

Colubrinae Oppel, 1811

Elaphe Wagler, 1833

Elaphe sp.

Studied material: cervical vertebra IQW 2004/28742 (Mei. 27904), trunk vertebra IQW 2018/45366 (Mei. 50675).

The 2.32 mm long cervical vertebra is well-preserved (Fig. 9) and only parts of the neural and hypapophysal spines and the right part of the zygosphene are broken off. The centrum width is 1.76 mm (CL/NAW 1.32). In posterior view (Fig. 9e), the neural arch is tall. The anterior margin of the zygosphene is concave between the well-developed outer lobes. The hypapophysis is postero-ventrally directed. The parapophyseal process is ventrally directed and of moderate length (Fig. 9a). The prezygapophyseal process is moderately long. This specimen differs from cervical vertebrae of *E. longissima* (Ivanov 1997, fig. 6) by the longer prezygapophyseal process, more strongly lobed zygosphenal roof, and smaller size, but as pointed out by Ivanov (1997), the interspecific and ontogenetic variability can be important.

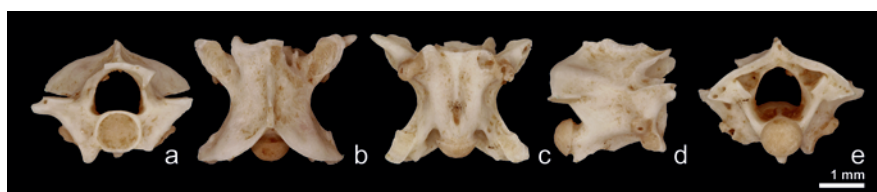


Fig. 9 *Elaphe* sp., Untermassfeld. – a–e Cervical vertebra IQW 1984/20327 (Mei. 19847), anterior, dorsal, ventral, lateral, posterior views.

The trunk vertebra is strongly damaged, viz. the left zygosphene wing and the right postzygapophysis are broken (Fig. 10). The small and robust vertebra (CL 3.26 mm, NAW 2.94 mm, CL/NAW 1.11) lacks a hypapophysis and represent therefore a member of the »small-sized colubrine« group (sensu Szyndlar 1991). The neural arch is vaulted. The haemal keel broadens and flattens posteriorly and is generally less defined (Fig. 10c). The zygosphenal roof shows distinct outer lobes (Fig. 10b). The prezygapophyseal process, although distally broken (Fig. 10b–c), is small. These morphologic features can be best compared with species of the genus *Elaphe*. In contrast to other colubrines, many Rat Snake species (except *Zamenis longissimus*, *Elaphe situla*) have vertebrae of similar robustness (CL/NAW 1.0–1.25; Szyndlar 1981; 1991; Ivanov 1994). However, these species (*E. paralongissima*, *E. quatuorlineata*) usually have larger vertebrae, with CL >4.3 mm. Unfortunately, a better identification of the Untermassfeld Rat Snake is hindered by the badly preserved and limited material.

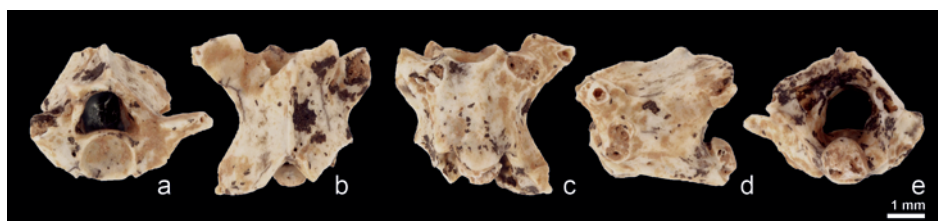


Fig. 10 *Elaphe* sp., Untermassfeld. – a–e Trunk vertebra IQW 2018/45366 (Mei. 50675), anterior, dorsal, ventral, lateral, posterior views.

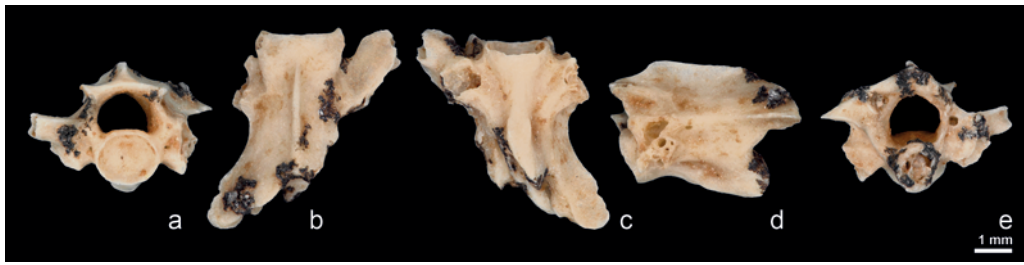


Fig. 11 cf. *Coronella* sp., Unter-massfeld. – **a–e** Trunk vertebra IQW 2018/45367 (Mei. 50676), posterior, dorsal, ventral, lateral, anterior views.

cf. *Coronella* sp.

Studied material: trunk vertebra IQW 2018/45367 (Mei. 50676).

Another »small sized colubrine« is documented by a partly preserved trunk vertebra (**Fig. 11**), which has a broken condyle, left prezygapophysis, right postzygapophysis, paradiapophysis and prezygapophyseal spines. The dimensions are small (CL ~2 mm, NAW ~1.4 mm) and rather elongate (CL/NAW ~1.4). The neural arch is dorso-ventrally depressed, and the haemal keel is distinct but flattened. The roof of the zygosphene shows well-developed outer lobes and a medial tubercle is missing. The neural spine is very low and does not overhang anteriorly or posteriorly. Ivanov (1997) describes similar vertebra, especially regarding the very low neural spine, as cf. *Coronella* sp.

This vertebra differ from material of *Elaphe* sp. described above by their dorso-ventral depression, the very low neural spine, and the elongate dimensions. By these features, they resemble the genus *Coronella* (Szyndlar 1991; Ivanov 1997), but this determination is unconfident.

Natricinae Bonaparte, 1838

Natrix Laurenti, 1768

Natrix sp.

Studied material: cervical vertebra IQW 1987/21824 (Mei. 21343), trunk vertebra IQW 1984/20329 (Mei. 19849), trunk vertebra fragment IQW 2004/28754 (Mei. 27916), trunk vertebra fragment IQW 2015/41958 (Mei. 47267).

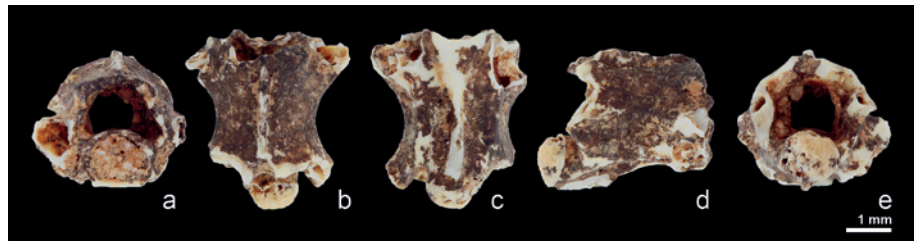
The cervical vertebra (**Fig. 12**) is elongate (CL 3.40, NAW 2.20, CL/NAW 1.54), the neural spine is short and very low, and the neural arch is posteriorly depressed. The anterior margin of the zygosphene is straight with slightly developed outer lobes. The trunk vertebrae are medium size (best preserved specimen CL 3.75 mm, **Fig. 13**) and elongate (NAW 2.22 mm, CL/NAW 1.69), with broken hypapophysis and parapophyseal processes. The neural arch is posteriorly vaulted and both vertebra show small subcotylar tubercles. Specific determination is not possible on these materials.

A single, highly fragmentary snake vertebra IQW 2018/45373 (Mei. 50682) could not be assigned to any group.



Fig. 12 *Natrix* sp., Unter-massfeld. – **a–e** Cervical vertebra IQW 1987/21824 (Mei. 21343), anterior, dorsal, ventral, lateral, posterior views.

Fig. 13 *Natrix* sp., Untermassfeld. – **a–e** Trunk vertebra IQW 1984/20329 (Mei. 19849), anterior, dorsal, ventral, lateral, posterior views.



3.2. The presence of pond turtles in Untermassfeld

Maul (1997) described a hyoid bone IQW 1989/23391 (Mei. 22910) (Fig. 14a–c) and attributed it to an emydid turtle. He identified this bone as cornu branchiale II. The relatively straight bone (enclosed angle 170°) has an oval proximal articulation facet and a flattened distal facet. Both articulation facets are rough and the bones proximal and distal ends are expanded, indicating that IQW 1989/23391 (Mei. 22910) intercalated between two cartilaginous elements. A virtual identical bone, although 10% larger and from the opposite side of the body, represent IQW 2004/28756 (Mei. 27918).

In turtles, three paired primary elements comprise the hyoid skeleton (see Heiss et al. 2011): medially the cornu branchiale II, articulating proximally with the corpus hyoidei; laterally the cornu branchiale I, which articulates proximally with the corpus hyoidei and distally with the third primary element the epibranchiale I. In contrast to the cornu branchiale II, the cornu branchiale I has therefore two articulation facets. Besides the lack of a distal articulation, the cornu branchiale II in turtles is distally very broad and flattened. Therefore, if IQW 1989/23391 (Mei. 22910) belongs to a turtle, it should be attributed to cornu branchiale I.

The cornu branchiale I of *Emys orbicularis* (Fig. 14d), *Mauremys leprosa* (MTD 43362), and turtles in general (Maul 1997, figs. 3c-13c; Heiss et al. 2011, fig. 4), is much more angulated (dorsally bent). This dorsal angulation is because the cornu branchiale I needs to curve around the postero-ventral edge of the skull. These observations refute the hypothesis that IQW 1989/23391 (Mei. 22910) and IQW 2004/28756 (Mei. 27918) belong to a turtle. Instead, these bones can potentially be mammalian hyoid bones. In mammals, five paired elements compose the hyoid skeleton (Frey and Riede 2013). Three of them (ceratohyal, epihyal, thyrohyal) are straight bones with both proximal and distal articulation facets.

Fig. 14 Hyoid bone, Untermassfeld. – **a–c** IQW 1989/23391 (Mei. 22910), lateral(?), dorsal(?), ventral(?) views. | *Emys orbicularis*, recent. – **d** GPIT uncatalogued cornu branchiale I, lateral view.



	MNI	Ecophysiologic group	Index
<i>Triturus cf. cristatus</i>	1	Peri-aquatic	0.3918
<i>Lissotriton vulgaris</i>	3	Peri-aquatic	0.3918
<i>Bufo bufo</i>	2	Peri-aquatic	0.3918
<i>Bufotes viridis</i>	2	Heliophile	0
<i>Rana temporaria</i>	3	Peri-aquatic	0.3918
<i>Rana arvalis</i>	8	Semi-aquatic	0.513
<i>Rana dalmatina</i>	4	Peri-aquatic	0.3918
<i>Pelophylax ridibundus</i> vel <i>esculentus</i>	1	Semi-aquatic	0.513
<i>Hyla arborea</i>	4	Peri-aquatic	0.3918
<i>Anguis fragilis</i>	1	Fossorial	0.0917
aff. <i>Ophisops elegans</i>	1	Heliophile	0
<i>Lacerta</i> sp.	1	Heliophile	0
<i>Eryx</i> sp.	2	Fossorial	0.0917
<i>Elaphe</i> sp.	2		
cf. <i>Coronella</i> sp.	1		
<i>Natrix</i> sp.	2		
Ecophysiologic index			0.27386
Mean annual precipitation (mm)			622
95 % prediction interval (mm)			252

Table 3 Amphibians and reptiles from Untermassfeld, supposed minimum number of individuals (MNI), ecophysiological groups, and calculation details for the estimation of palaeoprecipitation (according to Böhme et al. 2006).

3.3. Minimum number of individuals (MNI)

The estimated minimum numbers of individuals (MNI) for the Untermassfeld herpetofauna are summarized in **Table 3**. The estimates for anurans are based on left versus right ilia counts and include the materials published by G. Böhme (1997). The majority of brown frog (*R. temporaria*, *R. arvalis*) ilia (n=22, MNI= 11) could not be referred to one of both species with certainty, so that the individual numbers per species are an approximation. Estimates of MNI for leg-less reptiles (anguines, snakes) are further problematic. For snakes, I count different ontogenetic stages to different individuals, but the 15 bones of *Anguis fragilis*, counted here as one individual, could in fact derive from many more individuals. Given these constraints, the total MNI for herpetofauna is 38, of which 28 belong to amphibians and 10 to reptiles. The most abundant group are the brown frogs *Rana temporaria* and *R. arvalis*, with together 11 individuals. Rare and single finds belong to the Northern Crested Newt (*Triturus cf. cristatus*), the Green Frog (*Pelophylax ridibundus* vel *esculentus*), the potential Smooth Snake (cf. *Coronella* sp.), and both lizards (aff. *Ophisops elegans*, *Lacerta* sp.).

3.4. Humidity inferences

Böhme et al. (2006) introduced the bioclimatic analysis of herpetofaunas to calculate humidity conditions during the Neogene. This method classifies amphibian and reptile (excluding non-fossorial snake) taxa into

eight eco-physiologic categories united into six groups. The diversity distribution of eco-physiologic groups has been found to correlate with present-day mean annual precipitation (MAP) of extra-tropical climates in the Old World. This method gives robust results if 1) the fauna is ecologically cohesive; 2) the assemblage is not significantly biased by taphonomy or collection artefacts; and 3) the assemblage contains at least six to seven taxa. The bioclimatic results for Untermassfeld are summarized in **Table 3**. The estimated MAP is 622 ± 252 mm, which suggest sub-humid conditions.

4. Discussion

The studied amphibian remains belong to seven taxa. *Rana temporaria* and *Pelophylax ridibundus* vel *esculentus* are newly identified frog species for the locality. The material studied by G. Böhme (1997) contains in addition *Triturus* cf. *cristatus* and the two toads *Bufo bufo* and *Bufo viridis* (in the present material only Bufonidae indet.). The Untermassfeld amphibian fauna therefore contains in a total of nine species (**Table 3**), two newts and seven anurans. Within Anura, the brown frogs (genus *Rana*) dominate with respect to diversity (three species) and MNI (58%).

Reptiles have been found to represent seven species: one anguid, two lacertids, and four snakes (**Table 3**), all of them are newly reported for the locality. Neither the record of a pond turtle could be confirmed, nor could the skink and gekkonid taxa mentioned by Sher (1986). Although the Untermassfeld materials returned from loan to Moscow (Kahlke in this volume), neither Scincidae nor Gekkonidae could be identified, which at least allows the possibility that these materials are lost. Sher (1986, citing Tatarinov) mentioned procoelous gekkonid vertebrae (which indeed characterize Eublepharidae – a family without a known fossil record; Böhme and Ilg 2003), leaving the chance of hidden squamate diversity in Untermassfeld.

The most surprising reptile taxon from Untermassfeld is the Sand Boa *Eryx*, which is the first Pleistocene record of this group from Central Europe. Besides several Miocene records, *Eryx* is known from the Pliocene of Spain, Italy, France, Hungary, and Armenia, and from the Pleistocene of Egypt, Israel, Syria, Greece, and the Ukraine (Böhme and Ilg 2003).

Today, more than 10 Sand Boa species live in arid and semiarid regions of southern Eurasia and northern Africa. The Western Sand Boa, *E. jaculus*, thrives as a fossorial resident of sandy soils in Mediterranean habitats of North Africa and the Eastern Mediterranean. Its northernmost occurrences are continental steppe habitats in the lower Danube area (Dobruja, 45° N; Sahlean et al. 2015) and to the north of the Caucasus (Kalmykia, 46° N; Stoyanov et al. 2011). At these northern edges of its distribution, the mean annual temperature (MAT) is at least 10 °C and summers (mean warm month temperature, WMT) are very warm (22 °C Dobruja, 25 °C Kalmykia). In these regions, the humidity is low (MAP 400 mm, respectively 250 mm), but evenly distributed through the year without a rainless season. Accepting *Eryx* as a palaeoclimatic index-taxon for Untermassfeld, it suggests warmer climate than today (MAT > 10 °C), warmer summers (WMT > 22 °C), and low but evenly distributed rainfall.

An even more thermophilous species is the Snake-Eyed Lizard *Ophisops elegans*. Based on the single specimen in the Untermassfeld record, the identification of this taxon is ambiguous (aff. *O. elegans*), but it is known from similar-aged levels of Deutsch-Altenburg with more materials and higher confidence (Rauscher 1992). *Ophisops elegans* has an eastern Mediterranean, Turanian and Caucasian distribution, with northern boundaries in the eastern Rhodopes/lower Thrace Basin (41.5° N), respectively Ingushetia/Chetchenia (43.5° N, Stoyanov et al. 2011). The climate at the European northern fringe is: MAT 13 °C, mean cold month temperature (CMT) 2–3 °C, WMT 23–24 °C, with dry summers and MAP 550–600 mm; on the Caucasian side: MAT 11 °C, CMT -3 °C, WMT 24 °C, with dry winters and MAP 460 mm.

According to Kahlke (2006) CMT below 0 °C can be excluded based on the occurrence of hippos. This ruled out the winter-cold, highly continental northern Caucasus as reference climate. The combination of temperature conditions in the northernmost Balkan occurrences of both most thermophilous reptiles from Untermassfeld, *Eryx* sp. and aff. *O. elegans*, will result in warm climate (MAT 13 °C), with mild winters (CMT 2–3 °C) and hot summers (WMT 24 °C). The reconstruction of a much warmer climate with hotter summers (MAT and WMT 5 and 8 °C higher than today, respectively) is in agreement with the correlation of Untermassfeld to the very warm interglacial MIS 31 at the base of the Jaramillo sub-chron before 1.07 Ma BP (Wiegank 1997; Kahlke 2006).

The bio-climatic estimate of MAP for Untermassfeld gives 622 mm, which is about 6 % less than the present day value in this area (Meiningen: MAP 660 mm for 1961–1990; Deutscher Wetterdienst). However, I suppose this MAP value is slightly overestimated, because supposition 2 («the assemblage is not significantly biased by taphonomy», see above) may be not fully achieved. The Untermassfeld herpetofauna is taphonomically biased against reptiles. Of total 252 herpetological specimens (including the materials described by G. Böhme 1997), 28 bones belong to reptiles. Reptiles contribute 11 % of all herpetological bones, but represent 26 % of all individuals (10 out of 38) and 44 % of all taxa (7 out of 16). Indeed, except for *Anguis fragilis*, one to four bones only document each of the remaining reptile species. This bias may overestimate humidity results especially with respect to heliophile lizards. Among the 28 reptile bones, only three lacertid specimens were found, representing a small and a larger species. However, lacertid diversity during the Early Pleistocene in Central Europe is reported to be higher. For insistence, from the late Early Biharian levels of Deutsch-Altenburg 2C1 (~ 1.2 Ma BP, slightly pre-dating Untermassfeld) and Deutsch-Altenburg 4B (~ 0.9 Ma BP, slightly post-dating Untermassfeld), Rauscher (1992) documented four, respectively seven lacertid species. Indeed, the two Untermassfeld bones assigned to *Lacerta* sp., may potentially represent two species (see section 3.1.). The hypothetical addition of two unrecognized lacertids (or scincids, gekkonids) to the Untermassfeld assemblage will reduce MAP by 87 mm, indicating sensitivity of the method to potentially biased squamate diversity in Untermassfeld. The calculated MAP of 622 mm should therefore be accept as an upper limit only.

The reconstruction of a warm and relatively dry climate for the late Early Pleistocene (Epivillafranchian, early Biharian) in Central Europe agrees with similar findings by Ivanov (2007). He deduced from the diverse and abundant records of thermophilous snakes in the early Biharian (Epivillafranchian) of eastern Central Europe and their decrease (or absence) in late Biharian (Galerian) times, that sustained cooling occurred at the Early/Middle Pleistocene transition. An espially warm and relatively dry Epivillafranchian climate can now also confirmed for western Central Europe.

<i>Ichthyosaura alpestris</i>		<i>Pelophylax esculentus</i>	
<i>Triturus cristatus</i>	*	<i>Pelophylax lessonae</i>	
<i>Lissitriton helveticus</i>		<i>Pelophylax ridibundus</i>	*
<i>Lissotriton vulgaris</i>	*	<i>Lacerta agilis</i>	
<i>Bufo bufo</i>	*	<i>Zootoca vivipara</i>	
<i>Bufo viridis</i>	*	<i>Anguis fragilis</i>	*
<i>Hyla arborea</i>	*	<i>Coronella austriaca</i>	*
<i>Rana arvalis</i>	*	<i>Natrix natrix</i>	*
<i>Rana temporaria</i>	*	<i>Vipera berus</i>	

Table 4 Amphibian and reptilian diversity on topographic map Meiningen (TK25 5428). Species occurrence data from Günther (1996). Asterisks indicate fossil representation in the site of Untermassfeld.

Despite the potentially biased reptile diversity, the number of 16 herpetofaunal taxa recorded in Untermassfeld is exceptionally high for the European Pleistocene. To my knowledge (Böhme and Ilg 2003), higher diversities are only documented for the two karstic sites Kozi Grzbiet (19 species, Szyndlar 1981; Sanchiz and Szyndlar 1984) and Pirro Nord (18 species, Delfino and Atzori 2013), although Biharian levels of Deutsch-Altenburg (Rauscher 1992) and the Middle Pleistocene TD10 of Gran Dolina (Blain 2009) may reach comparable diversi-

ties to Untermassfeld. All four localities, however, produce significantly higher MNI and specimen numbers (e. g., > 140.000 in Kozi Grzbiet, Sanchiz and Szyndlar 1984), highlighting that the documented diversity for Untermassfeld is probably underestimated.

The herpetofauna can further provide information to environmental and landscape reconstruction. Given the potential accumulation of herpetological bones by birds of prey, the spatial scale of inferences may be several square kilometres. As the preferred spawning habitats of amphibian species suggest (Günther 1996), several types of water bodies were available around Untermassfeld. Calm areas in rivers (e. g., Werra River) may be used by *Rana temporaria*, whereas the majority of amphibian species spawn in still-water habitats outside the main discharge. The water bodies may be seasonal, but the rare *Triturus cristatus* and *Pelophylax* indicate the existence of some perennial ponds or pools. The articulated skeleton of *Rana dalmatina* shows, that the banks of the Werra River were part of its land habitat. With a high level of certainty, extensive open and dry habitats with sandy and rocky soils must have existed. This is indicated by the presence of the Sand Boa, as well as the Snake-Eyed Lizard *Ophisops elegans* and the Green Toad *Bufo viridis*. A mixture of vegetated and open landscapes best explains the herpetofaunal composition. The present-day diversity of amphibians and reptiles in the area of Untermassfeld (topographic map Meiningen, scale 1:25,000) is 18 species (Table 4). The majority of them, 11 species, have now been documented from the Epivillanfranchian fossil locality. The thermophilous elements are lacking today, but otherwise habitat composition in the area probably did not change dramatically compared to one million years ago.

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