Ralf-Dietrich Kahlke (Ed.)

The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany)

Part 4

SENCKENBERG

Römisch-Germanisches Zentralmuseum
Leibniz-Forschungsinstitut für Archäologie

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Römisch-Germanisches Zentralmuseum
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Ralf-Dietrich Kahlke (Ed.)

THE PLEISTOCENE OF UNTERMASSFELD NEAR MEININGEN (THÜRINGEN, GERMANY)

PART 4

Mit Beiträgen von

Mark Benecke · Madelaine Böhme · Nicolas Boulbes · Marzia Breda
Maia Bukhsianidze · Véra Eisenmann · Andreas Gärtner · Axel Gerdes
Ralf-Dietrich Kahlke · John-Albrecht Keiler · Jonas Keiler · Uwe Kierdorf
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Foldout I

Dedicated to our esteemed colleague and friend of many years

Helmut Hemmer

on the occasion of his 80^{th} 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.

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Sabine Gaudzinski-Windheuser

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und

Museum für menschliche Verhaltensevolution,

Römisch-Germanisches Zentralmuseum,

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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*

VÉRA EISENMANN · NICOLAS BOULBES

NEW RESULTS ON EQUIDS FROM THE EARLY PLEISTOCENE SITE OF UNTERMASSFELD

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Abstract

New and ancient material of *Equus* (*Sussemionus*) *wuesti* Musil, 2001 from the Epivillafranchian site of Untermassfeld is described and compared with other middle-sized species between 1.5 and 0.6 Ma BP. Results of this analysis show that *Equus* (*S.*) *wuesti* represents another species inside the Sussemione group close to but different from the equids of Venta Micena (Spain) and Akhalkalaki (Georgia). Both by its age and geographical localization, *E.* (*S.*) *wuesti* fits perfectly inside the range of Sussemiones and represents an important link between the older and western Venta Micena and the younger and eastern Akhalkalaki. A second species at Untermassfeld identified from a radius too large for *Equus* (*S.*) *wuesti* could belong to the large sized members of the same group described at Süssenborn, Akhalkalaki, and NE Siberia. As well as several other sites about the same age, the site of Untermassfeld documents a case of sympatry of two equids species of different size.
However, the Untermassfeld equid remains are different from *Equus apolloniensis* from the Greek locality of Apollonia, which in turn has affinities with the extant wild ass *Equus africanus* and could represent a step within the lineage of asses soon after their differentiation.

1. Introduction

Most equid fossils from Untermassfeld site were already described by Musil (2001) who found that they possessed both primitive and derived characters and referred them to a new species, *Equus wuesti* Musil, 2001, close to, but different from, *Equus altidens* von Reichenau, 1915. At that time, however, the upper dentition was represented only by decidual teeth and the lower dentition only by very worn series.
During following excavations (Kahlke in this volume), more fossils were found, including more cheek teeth and one large radius, too large for the middle-sized dominant species. Finding two *Equus* species at the same locality does not necessarily point to a mixing of fossils from different stratigraphical levels; they may

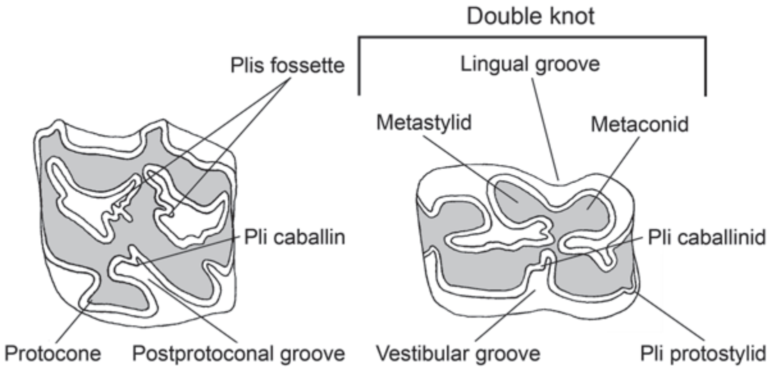

Fig. 1 Left upper premolar and right lower premolar of *Equus*.

have cohabited. Indeed, in East Africa, the ranges of extant *E. grevyi* Oustalet, 1882, and *E. burchelli* Boddaert, 1785, overlap though they do not share the same ecological niche. Occurrence of two fossil *Equus* is possible too: *E*. cf. *suessenbornensis* Wüst, 1900, and *E*. *hipparionides* Vekua, 1960, at Akhalkalaki (Georgia) is a good example.

At Süssenborn (Germany) where deposits span a long time, the coexistence of *E*. *suessenbornensis*, *E*. *altidens* von Reichenau, 1915, and *E*. *marxi* von Reichenau, 1915 (these species will be discussed below) is less certain.

The last mentioned five forms were referred to the new subgenus *Sussemionus* (Eisenmann 2010) defined by dental characters (Eisenmann 2006), in particular the occurrence of plis protostylid and/or elongated and bilobated metaconids on lower teeth, very short protocones and deep postprotoconal grooves on uppers (**Fig. 1**). These characters, however, are not constant, even inside the same series. In consequence their presence is a good indication, their absence is not. *Allohippus* »stenonine« patterns may occur in Sussemiones.

Sussemiones had vast geographical and chronological ranges. Their origin is North-American but they spanned through Asia and Europe and even reached Africa (Eisenmann 2006). In time they persisted 2 My at least and were still present 40,000 BP in Southwestern Siberia (Eisenmann and Vasiliev 2011).

The fossiliferous sands of Untermassfeld are positioned around the onset of the Jaramillo polarity subzone, with an age of approximately 1.07 Ma BP (Ellenberg and Kahlke 1997; Kahlke 2000; Kahlke and Gaudzinski 2005; Kahlke 2006). We will compare the equid fossils from Untermassfeld first with fossils of about the same age, mainly Appollonia (Greece), Vallonnet (France), and Tour de Grimaldi (Italy), then with some other fossils, mainly Venta Micena (Spain), Süssenborn (Germany), and Akhalkalaki (Georgia). Unfortunately our knowledge and understanding of Early/Middle Pleistocene *Equus* are still poor and uncertain. This is especially the case of *E. altidens*. In our captions we prefer to give names of localities and avoid the use specific names unless the species had been described in them.

2. Material and methods

The equid remains are not very numerous but well preserved. They include fragmentary maxillaries and mandibles, upper and lower cheek teeth, and limb bones. Measurements and photographs as well as comparisons using Simpson's diagrams (1941) will be used for their description. The technique of measurement is described in Eisenmann (2009). However, it may be useful to add a figure here to explicit the morphological observations on cheek teeth (**Fig. 1**).

The fossils of Untermassfeld are labelled Mei. for Meiningen and preserved at the IQW collection of Senckenberg Research Station of Quaternary Palaeontology Weimar. AKHA is the abbreviation for Akhalkalaki and

Fig. 2 *Equus* (*Sussemionus*) *wuesti* Musil, Untermassfeld. – Maxillary fragment with left P^3-M^3 and right P^1-M^3 tooth rows IQW 2010/31 393 (Mei. 30 555), occlusal view. – Scale: 30 mm.

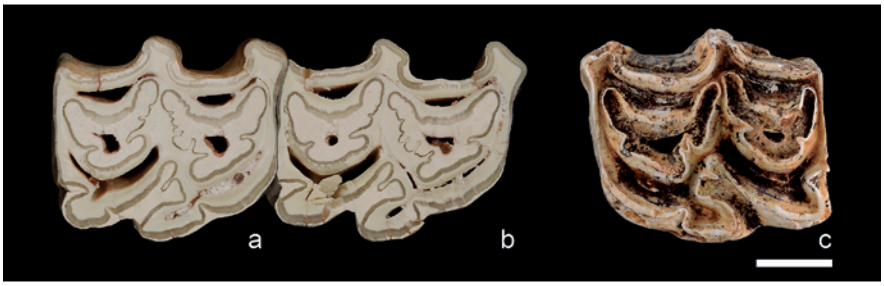

Fig. 3 *Equus* (*Sussemionus*) *wuesti* Musil, Untermassfeld. – **a–b** Right P^3-P^4 IQW 2010/31 393 (Mei. 30 555), occlusal view. – **c** Left P^3 IQW 1999/26 560 (Mei. 26 089), occlusal views. – Scale: 10 mm.

label for fossils preserved in the collections of the Institute of Paleobiology at Tbilisi. APL is the abbreviation for Apollonia and label for fossils preserved at the University of Thessaloniki. DA is the abbreviation for Denizli and label for fossils in the Pamukkale University, Denizli. Fossils from Le Vallonet and La Tour de Grimaldi are preserved in the Regional Prehistoric Museum of Menton. NHM is the abbreviation of the Naturhistorisches Museum Basel. The material of Venta Micena (VM) is stored at the Institut Paleontologic Dr M. Crusafont, in Sabadell (Barcelona), and at the Museo de Prehistoria J. Gibert, in Orce (Granada). ZIN refers to the collection of the Zoological Institute of the Russian Academy of Sciences in St Petersburg.

3. Description of new finds of *Equus* (*Sussemionus*) *wuesti* Musil, 2001 from Untermassfeld

3.1. Upper cheek teeth

IQW 2010/31 393 (Mei. 30 555) is a newly found subadult fragmentary maxillary (**Fig. 2**).
The P^3 and P^4 were sectioned in order to better show the enamel pattern. Protocones are short, postprotoconal grooves are not very deep, plis caballins are normally developed, and fossettes are plicated (**Fig. 3a–b**). Another P^3, IQW 1999/26 560 (Mei. 26 089), although very worn, shows the same aspect (**Fig. 3c**). Measurements are given in **Table 1**.

		Pli cab.	Plis fossette	Length	Protocone	Width	Height	Protostyl
dP^2	IQW 1983/19264 (Mei. 18784)	+	5	44	6	23	20	
dP^3	IQW 1983/19264 (Mei. 18784)	+	1	31	9	24	c. 20	
dP^4	IQW 1983/19264 (Mei. 18784)		1	34	11	22	20	
P^2	IQW 1980/16993 (Mei. 16514)			38*	c. 6.5*	25*	62	unworn
P^3	IQW 2010/31393 (Mei. 30555)	+	9	30.3*	8.2*	25.9*		
P^4	IQW 2010/31393 (Mei. 30555)	+	11	29.4*	9.1*	26.7*		
P^3	IQW 1999/26560 (Mei. 26089)	+	5	28.5	7.4	25.1	37.6	

Table 1 Upper cheek teeth of Untermassfeld *Equus* (*Sussemionus*) *wuesti*. Measures in mm. * – at mid-height or section.

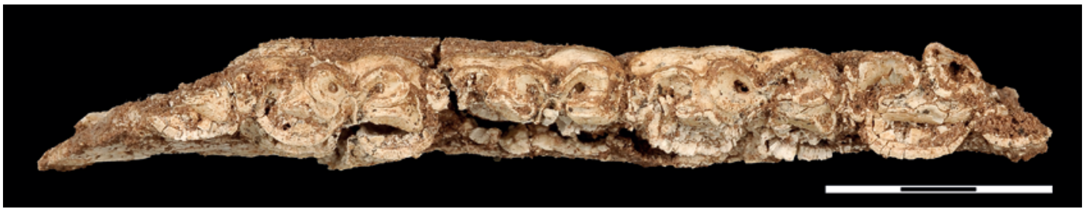

Fig. 4 *Equus* (*Sussemionus*) *wuesti* Musil, Untermassfeld. – Right mandibular fragment IQW 1998/26401 (Mei. 25930) with P_3-M_2, occlusal view. – Scale: 30mm.

	Character	Male, very old IQW 1981/17619 (Mei. 17141)	<1 year IQW 1980/16092 (Mei. 15603)
Diastema	3	96	74
Length of P_2-P_4	4	86	104
Length of M_1-M_3	4 bis	82	
Length of P_2-M_3	5	170	
Symphysis length	6	92	65
Breadth at posterior borders of I_3	7	54	48
Height in front of dP_2	9		51.5
Height behind dP_4	10		58
Least symphysis breadth	12	44	33.1
Canine length	13	16.5	

Table 2 Mandibles of Untermassfeld *Equus* (*Sussemionus*) *wuesti*. Measures in mm.

		Length	Postflexid	LDKnot	Width	Pli caballinid	Height	Protostylid
P_2	IQW 1980/17 067 (Mei. 16 588)	30			16.5			0
P_3	IQW 1980/17 067 (Mei. 16 588)	27.5		16.8	16		c. 30	
P_4	IQW 1980/17 067 (Mei. 16 588)	27		15.1	17		34	
M_1	IQW 1980/17 067 (Mei. 16 588)	22			16			
M_2	IQW 1980/17 067 (Mei. 16 588)	26			15			
M_3	IQW 1980/17 067 (Mei. 16 588)	33			13		23	
P_3	IQW 1998/26 401 (Mei. 25 930)		14.2				c. 34	
P_4	IQW 1998/26 401 (Mei. 25 930)	30	15	17				
M_1	IQW 1998/26 401 (Mei. 25 930)	25		13				
M_2	IQW 1998/26 401 (Mei. 25 930)	27	8	14		0		
P_2	IQW 1989/23 133 (Mei. 22 652)	33*			15*		59	unworn
P	IQW 1989/23 121 (Mei. 22 640)	29*	13*	17*		0		
M_1	IQW 1989/23 094 (Mei. 22 613)	26	9	15		0		
M_2	IQW 1980/17 388 (Mei. 16 910)	c. 27*		13*		0		

Table 3 Lower cheek teeth of Untermassfeld *Equus* (*Sussemionus*) *wuesti*. Measures in mm. * – at mid-height or section. LDKnot – length of the double knot.

3.2. Mandibles and lower cheek teeth

Several fragmentary mandibles were illustrated and measured by Musil (2001). Most specimens were either juvenile or very worn. One new specimen brings some additional information. IQW 1998/26 401 (Mei. 25 930) is a fragmentary tooth row (P_3-M_2); the metastylid is pointed on the P_3, rounded in the other teeth, the vestibular groove is deep on the molars; the pattern is stenonine (**Fig. 4**). Measurements are given in **Tables 2–3**.

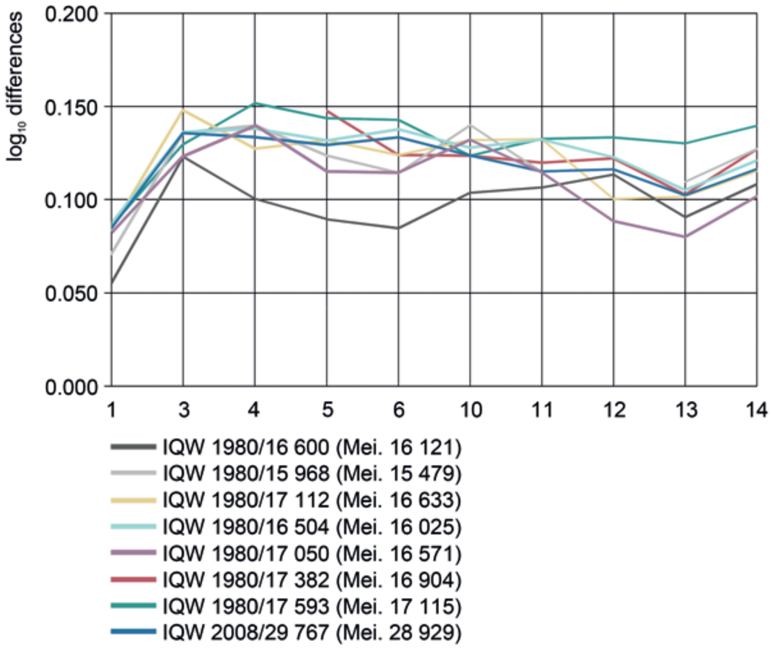

Fig. 5 *Equus* (*Sussemionus*) *wuesti* Musil, Untermassfeld. Log10 differences of Mt III characters 1, 3–6, 10–14 (explanation of numbers see **Table 5**) between extant *Equus hemionus* Pallas as reference.

3.3. Third metacarpals (Mc III) and metatarsals (Mt III)

Most are slender and deep in the diaphysis (**Tables 4–5**). While the Mc III sample appears homogeneous, the Mt III is not. One Mt III, IQW 1980/16600 (Mei. 16121), is notably shorter and smaller by most its dimensions (**Fig. 5**).

3.4. Anterior first phalanges (Ph1 ant)

Beside the specimen illustrated by Musil (2001), there are three Ph1 ant (**Fig. 6**, **Table 4**).

Fig. 6 *Equus* (*Sussemionus*) *wuesti* Musil, Untermassfeld. Anterior first phalanges. – **a–b** IQW 1980/17109 (Mei. 16630), anterior, posterior views. – **c–d** IQW 1980/17464 (Mei. 16986), anterior, posterior views. – **e–f** IQW 1986/21294 (Mei. 20813), anterior, posterior views. – Scale: 30mm.

3.5. Other limb bones

Their measurements are given in **Tables 4–8**.

	Mc III	IQW 1980/15 438 (Mei. 14 950)	IQW 1980/15 452 (Mei. 14 964)	IQW 1980/15 987 (Mei. 15 498)	IQW 1980/16 199 (Mei. 15 710)	IQW 1980/16 585 (Mei. 16 106)	IQW 1980/16 883–4 (Mei. 16 404–5)	IQW 1980/16 942 (Mei. 16 463)	IQW 1980/17 011 (Mei. 16 532)	IQW 1980/17 188 (Mei. 16 710)	IQW 1980/17 589 (Mei. 17 111)	IQW 1984/20 272 (Mei. 19 792)	IQW 1986/21 670 (Mei. 21 189)	IQW 1989/23 311 (Mei. 22 830)	IQW 1998/26 413 (Mei. 25 942)	IQW 1980/17 439 (Mei. 16 961) juv
Greatest length	1	255	255	258	263		258	256	253	243	258		260			
Medial length	2	248	247	249	256			244		235	252		250			
Smallest breadth	3	35	36.2	37.7	36	34	38	36	34.5	34.1	35.5	35	36	36.5	36	
Smallest depth	4		30.7	30.2	31.5	27	29	29	28	29.2	30	27	29	30.5	27	
Proximal breadth	5	54	54	52.5	56		53.5	52	52	50	52		55	53.2	52.5	
Proximal depth	6	36.5	35	37.7	39	36.5	35.5	36	34	35	34		35	33.5	34.1	
Diameter of facet for os carpale III	7	44	44	45	45.5		43	43	42	42	42		45	43	43.5	
Diameter of facet for os carpale IV	8	19	17	16	19	16	17	17	18	16	16		17.5	17	15.7	
Diameter of facet for os carpale IV	8 bis	12	9	12.5	11.5		10.5	10	10	10	10		9.5	10.1		
Diameter of facet for os carpale II	9	c. 3	0 or 6	6	0		0		1		0		3	7.3		
Distal supra-articular breadth	10	53	50.7	52	52		49	50		48.3	50	51	50.5			46
Distal articular breadth	11	50	49	48.5	50.2		49	48		45	48	48	49.2			44
Depth of the sagittal crest	12	37	37	36.1	39		37.2	36.2		34	36	36.8	34.5			34
Least depth of medial condyle	13	30	29.7	29	30.5		29.5	28.4		26.5	28	29.8	27.6			27
Greatest depth of medial condyle	14	34	33	32	34		32.3	31		29.5	31.7	32.7	32			30
Least depth of lateral condyle	13 bis	29.5	28.5	28.2	30		28.3	28.1		26	28	29.1	26.9			26.9

Mc III	n	x	min	max	s	v
1	10	255.9	243	263	5.34	2.09
3	14	35.8	34	38	1.19	3.33
4	13	29.1	27	31.5	1.49	5.14
5	12	53.1	50	56	1.59	2.99
6	13	35.5	33.5	39	1.60	4.49
10	10	50.7	48.3	53	1.43	2.82

Table 4 Third metacarpals (Mc III) and first anterior phalanges (Ph1 ant) of Untermassfeld *Equus* (*Sussemionus*) *wuesti*. Measures in mm and statistics (*associated specimens).

	11	10	48.5	45	50.2	1.46	3.01
	12	10	36.4	34	39	1.41	3.88
	13	10	28.9	26.5	30.5	1.25	4.33
	14	10	32.2	29.5	34	1.35	4.19
	7	12	43.5	42	45.5	1.22	2.82
	8	13	17	15.7	19	1.12	6.56

	Ph1 ant	IQW 1980/17 068 (Mei. 16 589)	IQW 1980/17 109 (Mei. 16 630)	IQW 1980/17 464 (Mei. 16 986)	IQW 1986/21 294 (Mei. 20 813)
Greatest length	1	94.5	90	90	92.2
Anterior length	2	86	82	80	85
Smallest breadth	3	35	32.7	33	33.7
Proximal breadth	4	55.5	53	54	53
Proximal depth	5	39	37	36.5	38
Distal supra-articular breadth	6	48	43.1	45	46.7
Greatest length of trigonum phalangis	7	60	61.5	61	61
Smallest length of trigonum phalangis	8	54	53	53	53.5
Posterior length	9	84	80	79	82
Medial supratuberosital length	10	71	66	66.5	69
Lateral supratuberosital length	11	70	67	67.5	69
Medial infra-tuberosital length	12	15	15.5	15.5	14
Lateral infra-tuberosital length	13	15	13	14	13.7
Distal articular breadth	14	45.1	41.2	43	44.5
Distal articular depth	15	26	26	25.9	26

Table 4 (continued)

	Mt III	IQW 1980/15 968 (Mei. 15 479)	IQW 1980/16 504 (Mei. 16 025)	IQW 1980/16 543 (Mei. 16 064)	IQW 1980/16 600 (Mei. 16 121)	IQW 1980/17 050 (Mei. 16 571)	IQW 1980/17 112 (Mei. 16 633)	IQW 1980/17 382 (Mei. 16 904)	IQW 1980/17 593 (Mei. 17 115)	IQW 2008/29 767 (Mei. 28 929)	IQW 1980/15 610 (Mei. 15 122) juv	IQW 1980/16 953 (Mei. 16 474) juv
Greatest length	1	290	302		280	298	300	299	300	300	290	
Medial length	2		297		272		291			294		
Smallest breadth	3	35	35	34	34	34	36	35	34.5	35	30	
Smallest depth	4	35	34.9	34	32	35	34		36	34.5	31	
Proximal breadth	5	53	54		49	52	54	56	55.5	53.7		
Proximal depth	6	45	47.5		42	45	46	46	48	47		
Diameter of facet for os tarsale III	7		50		47	47	50	50	51.5	50		
Diameter of facet for os tarsale IV	8		12.5		11.5	12.5	14	15	14	14		
Diameter of facet for os tarsale II	9	7	10		8	7	12	10	9.5			
Distal supra-articular breadth	10	53	51.5		48.7	52	52	51	51	51	49	45
Distal articular breadth	11	49	51		48	48.9	51	49.5	51	49	>46	42
Depth of the sagittal crest	12	c. 39	40		39.2	37	38	40	41	39.4	>36	
Least depth of medial condyle	13	30.5	30.2		29.2	28.5	30	30	32	30		c. 27.5
Greatest depth of medial condyle	14	35	34.5		33.5	33	34	35	36	34.1		
Least depth of lateral condyle	13 bis	30	29.1		28.4	27.5	29	30	30.5			25.5

Mt III	n	x	min	max	s	v
1	8	296.1	280	302	7.45	2.52
3	4	34.7	34	36	0.67	1.92
4	8	34.4	32	36	1.17	3.4
5	8	53.4	49	56	2.19	4.09
6	8	45.8	42	48	1.89	4.12

Table 5 Third metatarsals (Mt III), tali, and calcanei of Untermassfeld *Equus* (*Sussemionus*) *wuesti*. Measures in mm.

	10	8	51.3	48.7	53	1.25	2.44			
	11	8	49.7	48	51	1.17	2.36			
	12	8	39.2	37	41	1.25	3.18			
	13	8	30.1	28.5	32	1.01	3.37			
	14	8	34.4	33	36	0.95	2.76			
	7	7	49.4	47	51.5	1.7	3.45			
	8	7	13.4	11.5	15	1.21	9.1			

	Talus	IQW 1980/15 432 (Mei. 14 944)	IQW 1980/15 974 (Mei. 15 485)	IQW 1980/16 305 (Mei. 15 816)	IQW 1980/16 601 (Mei. 16 122)	IQW 1980/16 987 (Mei. 16 508)	IQW 1980/17 045 (Mei. 16 566)	IQW 1980/17 105 (Mei. 16 626)	IQW 1980/17 588 (Mei. 17 110)	IQW 1984/20 005 (Mei. 19 525)
Greatest length	1	67	69	73	71	68	70	69	71	68
Medial length of trochlea	2	64	68	66	65	64	69	64	67	68
Greatest breadth	3	62	67	66	66	65	67	67	69	64
Trochlear breadth	4	30	31	31	29	30	29	31	30	32.5
Distal articular breadth	5	53	55	56	55	55	57	57	57	55
Distal articular depth	6	40	39	39	40	38	41	40		39
Greatest medial depth	7	55	57	55	56	55	58	55	56	57

	Talus	n	x	min	max	s	v
	1	9	69.6	67	73	1.88	2.7
	2	9	66.1	64	69	1.96	2.97
	3	9	65.9	62	69	2.03	3.08
	4	9	30.4	29	32.5	1.11	3.65
	5	9	55.6	53	57	1.33	2.39
	6	8	39.5	38	41	0.93	2.35
	7	9	56	55	58	1.12	2

Table 5 (continued)

	Calcaneum	IQW 1980/15431 (Mei. 14943)	IQW 1980/15975 (Mei. 15486)	IQW 1980/16597 (Mei. 16118)	IQW 1980/17054 (Mei. 16575)	IQW 1980/17091 (Mei. 16612)	IQW 1980/17365 (Mei. 16887)	IQW 1980/17571 (Mei. 17093)	IQW 1982/18033 (Mei. 17553) juv	IQW 1987/21992 (Mei. 21511)
Greatest length	1	118	123	119	124.5		124			118
Length of proximal part	2	79	84	81	83		81	c. 82		82
Smallest breadth	3	21	23	23.5	21		23		21	21
Proximal breadth	4	38	39.5	37	37	38.5	37.5	39		38.5
Proximal depth	5	52	58	58	54	54	55	55		56
Distal depth	6		58	57			55		54	58
Distal breadth	7	55	62	61	59		60		60	54 sic
Maximal diameter of sustentaculum tali	8	40	43	42	40		40		40	39
Articular diameter of sustentaculum tali	9	37	40	41	37		39		40	38

Calcaneum	n	x	min	max	s	v
1	6	121.1	118	124.5	3.07	2.51
2	7	81.7	79	84	1.6	1.96
3	7	21.9	21	23.5	1.17	5.34
4	8	38.1	37	39.5	0.92	2.4
5	8	55.3	52	58	2.05	3.72
6	5	56.4	54	58	1.82	3.22
7	7	58.7	54	62	3.04	5.18
8	7	40.6	39	43	1.4	3.44
9	7	38.9	37	41	1.57	4.05

Table 5 (continued)

	Humerus	IQW 1980/15900 (Mei. 15411)	IQW 1980/16302 (Mei. 15813)	IQW 1980/16371 (Mei. 15882)	IQW 1980/17448 (Mei. 16970)	IQW 1980/17480 (Mei. 17002)	IQW 1981/17616 (Mei. 17138)
Greatest length	1					c. 290	
Smallest breadth	3	40	39	39		40	40
Depth at same level	4					51.5	49
Distal breadth	7	80	81	77	75	79	80
Distal medial depth	8	88	89	84	82	86.5	87
Height of medial condyle	9	52	55	51	52	51	51
Smallest height of trochlea	10	40	41	40	39	39	40.5
Height of trochlea	11	49	48.5	47	46	46	47
Height of lateral condyle	12	43.5	43.5	41	40.5	41	42.5

	Radius	IQW 1980/15228 (Mei. 14710)	IQW 1980/15275 (Mei. 14787)	IQW 1980/16304 (Mei. 15815)	IQW 1981/17638 (Mei. 17160)	IQW 1980/16550 (Mei. 16071) juv
Greatest length	1	c. 400	348	353	355	
Medial length	2′		333	327	329	
Lateral length	2		329	330	332	
Smallest breadth	3	55	46	47	45	39
Smallest depth	4′	35	31	31.5	31	24.5
Greatest proximal breadth	4		88	89	91	80
Proximal articular proximal breadth	5		79	78	81	77
Proximal articular depth	6		43	42	43	42
Greatest distal breadth	7	98	84	83	80	
Greatest distal breadth	8	c. 83	70	67	67	
Distal articular depth	9	c. 48	40.2	40	41	
Breadth of medial condyle	10	32	27	28	29	
Breadth of lateral condyle	11		19	17	18	

Table 6 Humeri and radii of Untermassfeld *Equus* (*Sussemionus*) *wuesti*, and radius of Untermassfeld *Equus* (?*Sussemionus*) sp. Measures in mm.

Femur		IQW 1980/15 397 (Mei. 14909)	IQW 1980/16 965 (Mei. 16486)	IQW 1980/17 384 (Mei. 16906)	IQW 1980/17 395 (Mei. 16917)
Smallest breadth	3	c. 45		43	
Depth at same level	4	57		45	
Proximal breadth	5				125
Depth of caput femoris	7		65.5		65.2

Tibia		IQW 1980/15 453 (Mei. 14965)	IQW 1980/15 910 (Mei. 15421)	IQW 1980/16 506 (Mei. 16027)	IQW 1980/17 047 (Mei. 16568)	IQW 1980/17 083 (Mei. 16604)	IQW 1980/17 377 (Mei. 16899)	IQW 1981/17 698 (Mei. 17220)	IQW 1984/20 087 (Mei. 19607)	IQW 2016/43 779 (Mei. 49088)
Greatest length	1			405	380		390	368	365	
Medial length	2′			372	358		368	345	337	
Lateral length	2									
Smallest breadth	3	50	50	47	47		49	48	46	
Smallest depdth	4	32	33	32.5	34		34	32.6	36	
Proximal breadth	5				105		106		110	
Proximal depth	6				96			c. 91		
Distal breadth	7	75	48	78	80	77		80	80	79
Distal depth	8	49	54	52	53	53	51	50	50	
Length of fossa digitalis	9			58	56			54	63	
Breadth of fossa digitalis	10			22	22			25	c. 23	

Table 7 Femora and tibiae of Untermassfeld *Equus* (*Sussemionus*) *wuesti*. Measures in mm.

4. Comparisons with finds from localities of about the same age as Untermassfeld

4.1. Apollonia

Apollonia P-1 belongs to the Platanochori Formation from the Early Pleistocene of Mygdonia Basin (Macedonia, northern Greece). The large mammal assemblage of Apollonia is dated to the beginning of the 1.2–0.9 Ma BP interval (Spassov 2003), and represents the most complete fossil assemblage of the South-Eastern European Epivillafranchian. Equid fossils are very numerous and well preserved. *E. apolloniensis* was described by Koufos et al. (1997). According to the published data, it has many morphological resemblances

		ant	ant	post	post				
	Ph2	IQW 1980/15752 (Mei. 15264)	IQW 1980/16549 (Mei. 16070)	IQW 1980/15832 (Mei. 15343)	IQW 1980/16973 (Mei. 16494)				
Greatest length	1	53	50	49	51				
Anterior length	2	41	40	39					
Smallest breadth	3	46	47	43	42				
Proximal breadth	4	52.5	c. 52	49.7	49				
Proximal depth	5	35	35	33					
Distal breadth	6	50	50.5	47	46				
Distal depth	7	30	32	29	28.5				
		ant	post?	post	post	post	post?	post	?
	Ph3	IQW 1980/16771 (Mei. 16292)	IQW 1980/15447 (Mei. 14959)	IQW 1980/15884 (Mei. 15395)	IQW 1980/16056 (Mei. 15567)	IQW 1980/17101 (Mei. 16622)	IQW 1980/17400 (Mei. 16922)	IQW 1980/17495 (Mei. 17017)	IQW 1989/23122 (Mei. 22641)
Anterior length	1	54	60	58	54		53	55	
Dorsal length	1′	58	61	60.5	58		57	56	
Plantar length	2	67							
Height	3	47	44	45	44			43.5	
Plantar breadth	4	73	c. 65	c. 67	>60			c. 60	
Articular breadth	5	51.5	46	49	c. 47	46		45	c. 47
Articular antero-posterior diameter	6	29	30	30	26.5	31.5	29	28	28
Plantar »circumference«	7	c. 187	c. 160	c. 160					

Table 8 Second (Ph2) and third (Ph3) phalanges of Untermassfeld *Equus* (*Sussemionus*) *wuesti*. Measures in mm.

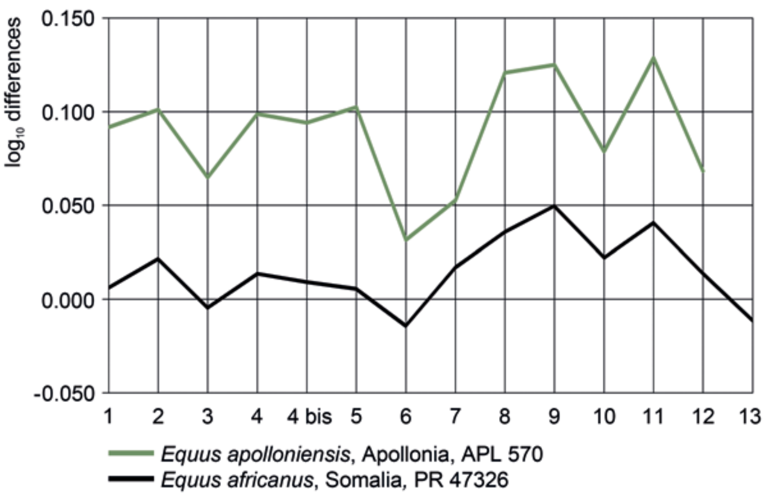

Fig. 7 Log10 differences of mandible characters 1–13 (explanation of numbers see **Table 2**) between extant *Equus hemionus* Pallas as reference, and *Equus africanus* (Heuglin et Fitzinger) and *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou.

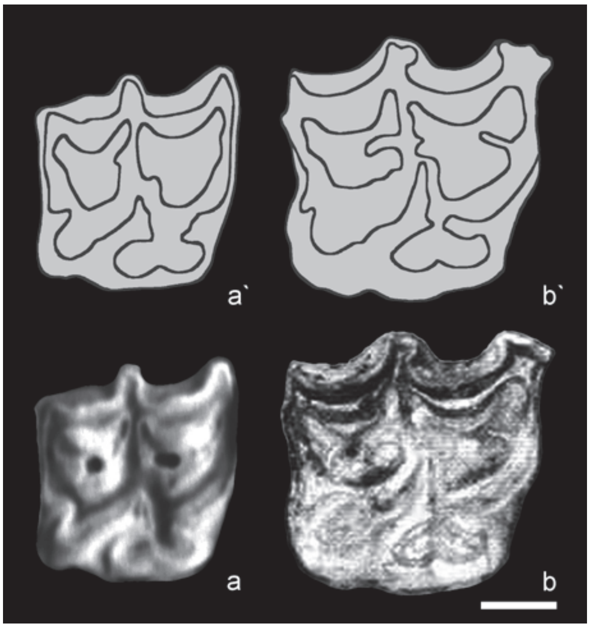

Fig. 8. *Equus africanus* (Heuglin et Fitzinger), Somali. – **a–a'** Left P4 (inverted) Basel NHM 3267, occlusal views. | *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou, Apollonia. – **b–b'** Right P4 APL 148, occlusal views. – Scale: 10 mm.

with the extant Wild Ass, *E. africanus*, although it was much larger. Because of bad preservation skulls are no help but the well-preserved mandible APL 570 is close by its proportions to an extant Somali Ass (**Fig. 7**). There is no mandible from Untermassfeld allowing a comparison.

On upper cheek teeth the short and often grooved protocones are very similar (**Fig. 8**) while they differ from the oblique and not grooved protocones of Untermassfeld; the postprotoconal groove is deep (**Fig. 8**).

Furthermore the premolars of *E.* (*Sussemionus*) *wuesti* are much smaller as indicated by the scatter diagram of the protocone length versus the average occlusal diameter (**Fig. 9**).

On lower cheek teeth double knots are round and vestibular grooves shallow on all teeth like in *E. africanus* (**Fig. 10**) thereby again differing from the deep vestibular grooves on the molars of Untermassfeld (**Fig. 4**).

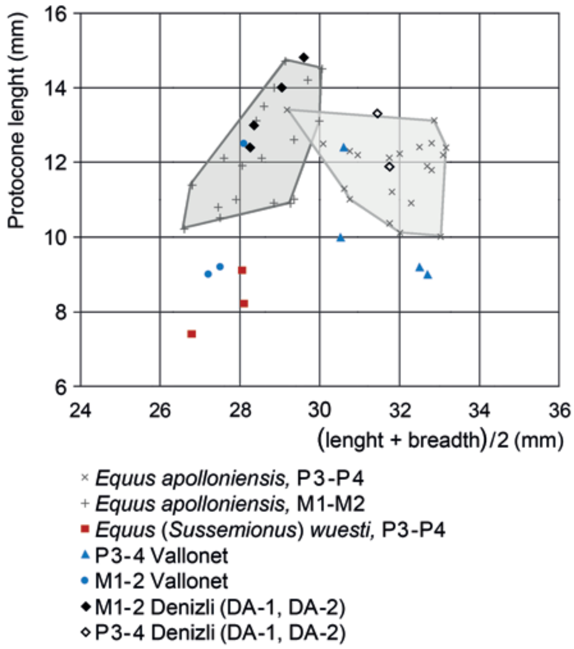

Fig. 9 Scatter diagram of average occlusal diameter (length + breadth)/2 of P^3-P^4 and M^1-M^2. Data from Apollonia *E. apolloniensis* (pers. comm. G.D. Koufos) and Denizli *E.* cf. *apolloniensis* (Boulbes et al. 2014).

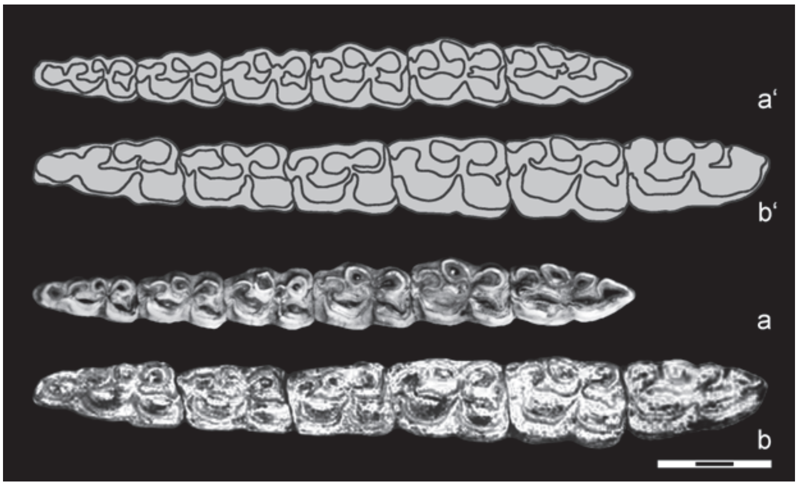

Fig. 10 *Equus africanus* (Heuglin et Fitzinger), Somalia. – **a–a'** Right P_2-M_3 ZIN 7204, occlusal views. | *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou, Apollonia. – **b–b'** Right P_2-M_3 APL 147, occlusal views. – Scale: 30 mm.

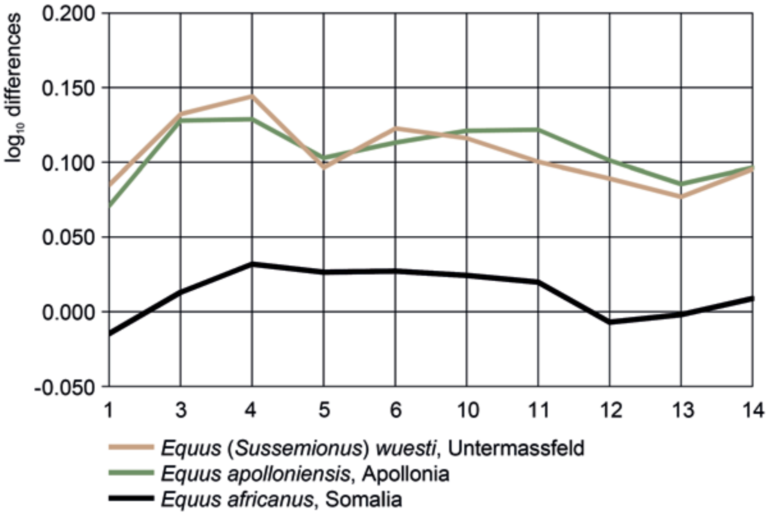

Fig. 11 Log10 differences of Mc III characters 1–14 (explanation of numbers see **Table 4**) between extant *Equus hemionus* Pallas as reference, *Equus africanus* (Heuglin et Fitzinger), and *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou.

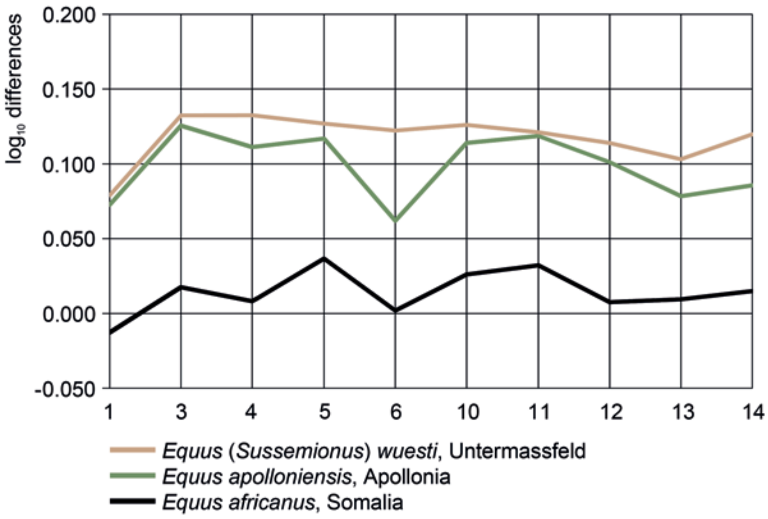

Fig. 12 Log10 differences of Mt III characters 1–14 (explanation of numbers see **Table 5**) between extant *Equus hemionus* Pallas as reference, *Equus africanus* (Heuglin et Fitzinger) and *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou.

The metacarpals are also similar to some African Wild Asses (**Fig. 11**) and slightly differ from *Equus* (*Sussemionus*) *wuesti* by smaller depths of diaphysis and proximal end (measurements 4 and 6).
Metatarsals of Untermassfeld differ also from *E. apolloniensis* and *E. africanus* (**Fig. 12**).
The limb bones proportions of *E. apolloniensis* and *E. africanus* are close (**Fig. 13**). The third anterior phalanx of *E.* (*Sussemionus*) *wuesti* is much wider.
Finally, in *E.* (*Sussemionus*) *wuesti* (**Tables 2–5**) as well as in *E.* (*Sussemionus*) *granatensis* and *E.* (*Sussemionus*) *hipparionoides*, upper cheek teeth are proportionally smaller relative to metapodials than in *E. apolloniensis* and *E. africanus* (**Fig. 14**).
Some other sites have yielded remains referred to *E. apolloniensis*: From the new locality Platanochori-1 of Mygdonia Basin (Macedonia, northern Greece) Konidaris et al. (2015) figured a fragment of *Equus* metacarpal about the size of *E. apolloniensis*. The fauna is indicative of a latest Villafranchian age, similar to that of Apollonia-1 (Konidaris et al. 2015). The published data, however, are not enough for a discussion. Koufos et al. (1997) reported the presence of this species in other Early Pleistocene Greek localities (Alikes, Ionian islands).

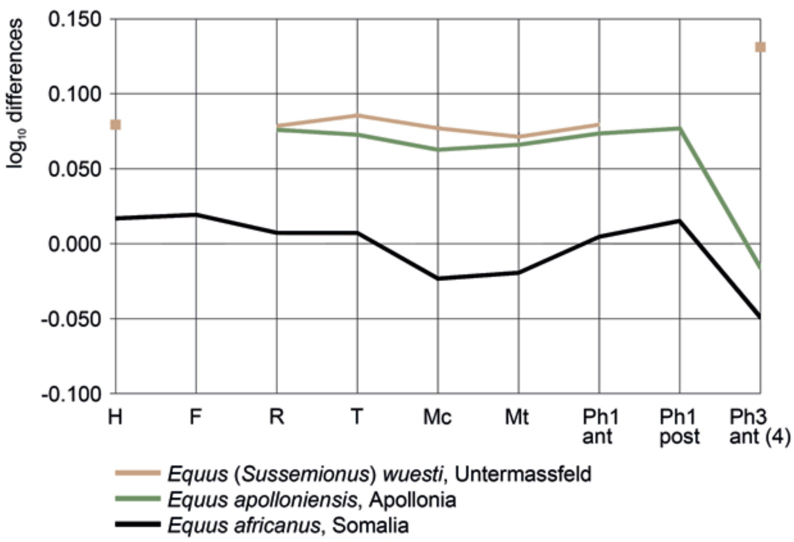

Fig. 13 Log10 differences of limb bone lengths between extant *Equus hemionus* Pallas as reference, *Equus africanus* (Heuglin et Fitzinger) and *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou. Lengths of humerus (H), femur (F), radius (R), tibia (T), metacarpus (Mc), metatarsus (Mt), anterior phalanx 1 (Ph1 ant), posterior phalanx 1 (Ph1 post), maximal breadth of anterior phalanx 3 [Ph3 ant (4)].

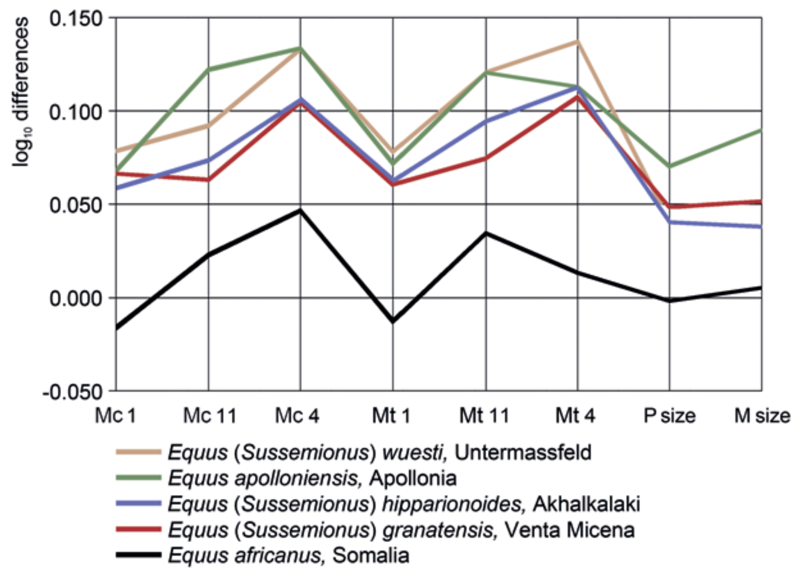

Fig. 14 Comparison between teeth and metapodial sizes in *Equus africanus* (Heuglin et Fitzinger) and *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou with *E.* (*Sussemionus*) *wuesti*, *E.* (*Sussemionus*) *granatensis*, and *E.* (*Sussemionus*) *hipparionoides*.

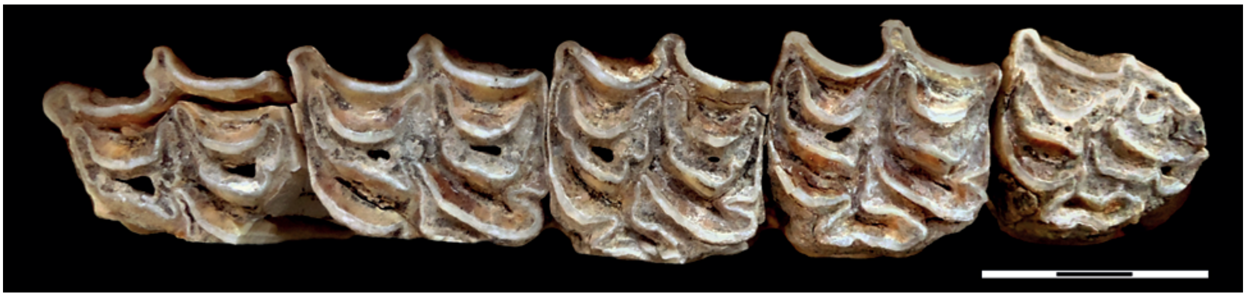

Fig. 15 *Equus* cf. *apolloniensis*, Denizli. – Left P^2-M^3 DA-1, occlusal view. – Scale: 30 mm.

Equus cf. *apolloniensis* seems also be represented in the Denizli Basin (Aegean region, southwestern Turkey). Two upper cheek teeth series show deep post-protoconal grooves and bilobated protocones, like in *E. apolloniensis* (**Fig. 15**). The size of the teeth and the length of the protocone (**Fig. 9**) fit well with *E. apolloniensis* (Boulbes et al. 2014). New dating based on cosmogenic nuclides (26Al/10Be) of conglomerate levels framing the upper fossiliferous travertine unit constrains its deposition between 1.1 and 1.6 Ma BP (Lebatard et al. 2014).

4.2. Le Vallonnet and La Tour Grimaldi

The large mammals of Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes, France) cave were found inside a level contemporary of Jaramillo event (de Lumley et al. 2009). This age agrees with absolute dating of the stalagmitic floors by the ESR method range between 0.91 and 1.37 Ma BP (Yokoyama et al. 1988). New dating by uranium-lead (U-Pb) method, coupled with palaeomagnetic constraints, wide the age range from 1.2 to 1.1 Ma BP (Michel et al. 2017). Equid fossils are few: several teeth and very rare postcranial elements. The teeth found at Vallonnet were referred to *Equus stenonis* sensu lato (Moullé et al. 2006; Moullé 2012). The upper cheek teeth however resemble Sussemione (Boulbes, unpublished data). Fossettes are plicated, the pli caballin is well developed and sometimes double. On the premolars corresponding to the same individual, the protocone is short, oval and oblique like in the new maxillary of *E.* (*Sussemionus*) *wuesti* from Untermassfeld (**Fig. 16a–b**). The upper teeth of the equid from Le Vallonnet (**Fig. 16**) are, however, much larger than those of *E. wuesti* (**Fig. 9**). Two other teeth, in particular a M^2 have more elongated protocones (**Fig. 16d–e**).
In lower cheek teeth the pattern of the double knot is stenonine (**Fig. 17**). The ectoflexid (vestibular groove) penetrates the isthmus on the molar (**Fig. 17c**) but stay away from the lingual groove. A pli protostylid is present at the occlusal level on the worn premolars (**Fig. 17a–b**) and well developed at mid-level of

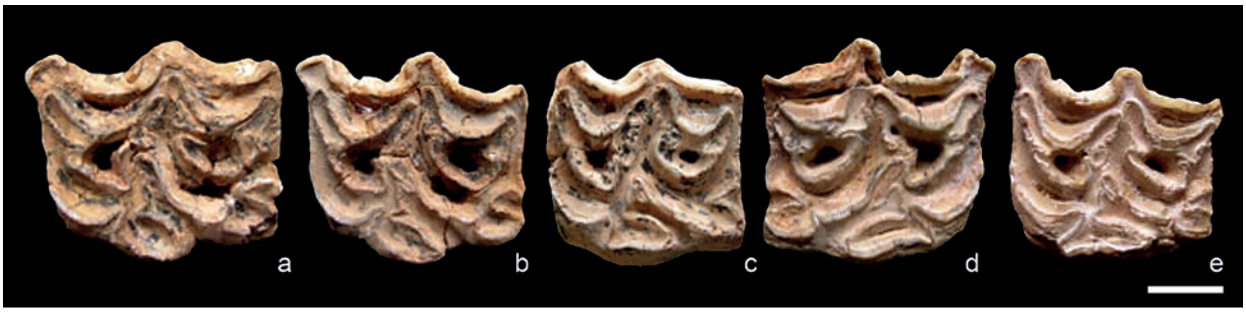

Fig. 16 Le Vallonnet. – **a** Left P^3 A9.AJ54, occlusal view. – **b** Left P^4 A9.AJ5.95, occlusal view. – **c** Left M^1 B9.BJ16.953, occlusal view. – **d** Right P^4 B6.C.3237, occlusal view. – **e** Left M^2 B7.288, occlusal view. – Scale: 10 mm.

Fig. 17 Le Vallonnet. – **a** Left P_3 A6.AG13.8214, occlusal view. – **b** Left P_4 G9.20034, occlusal view. – **c** Left M_2 G9.20033, occlusal view. – Scale: 10 mm.

the crown on the molar. The presence of these plis together with the pattern of the upper left premolars (Fig. 16a–b) strongly suggest that they represent a Sussemione.

Scarce equid remains come from the site of La Tour de Grimaldi (Liguria, Italy) near Le Vallonnet. Geological and paleontological correlations with Vallonnet cave suggest that the site is about the same age (de Lumley 1969; Moullé 1996; Lacombat and Moullé 2005).

An upper premolar has a deep post-protoconal groove and a bilobated protocone like in *E. apolloniensis* (Fig. 18a) but seems too small for this species. The lower P_4 (Fig. 18b) has an asymmetrical double knot: rounded metaconid and pointed or triangular metastylid with an isthmus between them. The pli protostylid is well developed at mid-level of the crown. This lower premolar looks like the ones from Vallonnet.

Fig. 18 Tour Grimaldi. – **a** Right P^4 13692, occlusal view. – **b** Left P_4 13680, occlusal view. – Scale: 10 mm.

5. Comparisons with finds from other localities

5.1. Süssenborn

The fluviatile horizons of the site of Süssenborn (Thuringia, Central Germany) represent a long time interval within the early Brunhes magnetochron and could be associated to MIS 16 (Kahlke et al. 2011). The large and micromammal fauna includes characteristic early Middle Pleistocene elements.

Fig. 19 *Equus altidens* von Reichenau, syntype, Süssenborn. – **a** Right M^1 IQW 1964/1 199 (Süß. 4 433), occlusal view. | *Equus marxi* von Reichenau, holotype, Süssenborn. – **b** Right P^4 IQW H.G. Süß. 1365, occlusal view. – **c** Right M^2 IQW H.G. Süß. 1367, occlusal view. – **d** Left (mirrored) M^1 IQW H.G. Süß. 1366, occlusal view. – Scale: 10 mm.

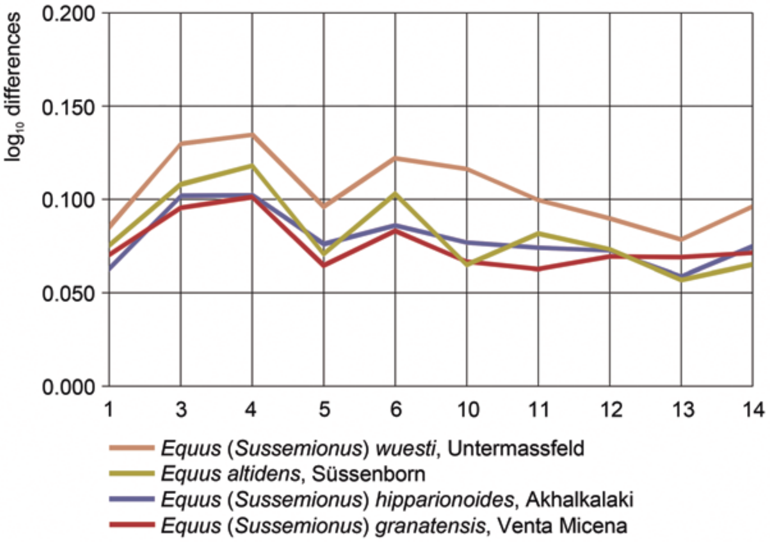

Fig. 20 Log10 differences of Mc III characters 1–14 (explanation of numbers see **Table 4**) between extant *Equus hemionus* Pallas as reference, *E.* (*Sussemionus*) *wuesti*, *E. altidens*, *E.* (*Sussemionus*) *granatensis* and *E.* (*Sussemionus*) *hipparionoides*.

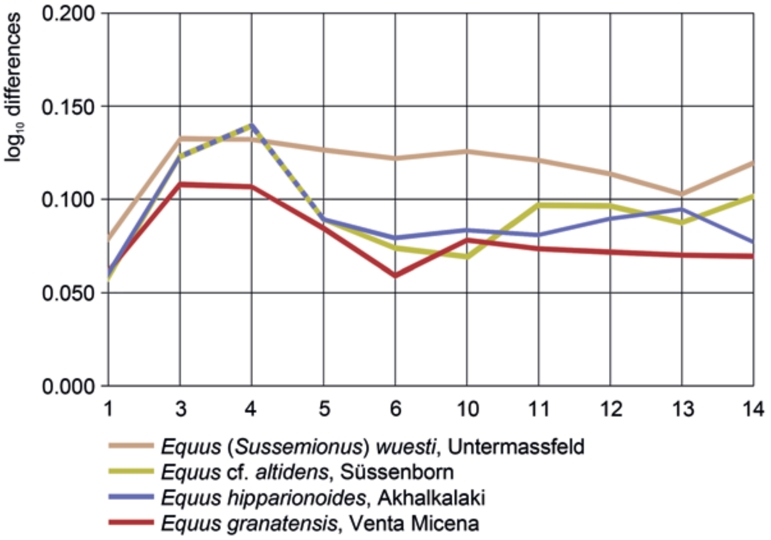

Fig. 21 Log10 differences of Mt III characters 1–14 (explanation of numbers see **Table 5**) between extant *Equus hemionus* Pallas as reference, *E. altidens*, *E.* (*Sussemionus*) *hipparionoides* and *E.* (*Sussemionus*) *granatensis*.

Many European fossils have been compared with, or referred to, *E.* cf. *altidens* or *E. altidens* – a species first described from Süssenborn. But in spite of their number and historic importance the Süssenborn equids are still poorly known and understood, especially *E. altidens* and *E. marxi*.

The type upper molar of *E. altidens* is smaller than the teeth of the type of *E. marxi* (**Fig. 19**). The protocone is medium-sized, the postprotoconal groove is not deep, there is no pli caballin. Some of the small lower teeth from Süssenborn [illustrated in Eisenmann (2008) as belonging to *Equus* sp.] may be referred to *E. altidens*; their pattern is stenonine. Neither upper nor lower are characteristic of Sussemiones.

The only resemblances of *E. altidens* to Sussemiones are provided by one metacarpal (**Fig. 20**) and one metatarsal (**Fig. 21**).

Fig. 22 *Equus marxi* von Reichenau, paratypes, Süssenborn. – **a** Left P_1 IQW H.G. S. 1368, occlusal view. – **b** Left P_2 IQW H.G. S. 1369, occlusal view. – **c** Left M_2 IQW H.G. S. 1370, occlusal view. – Scale: 10 mm.

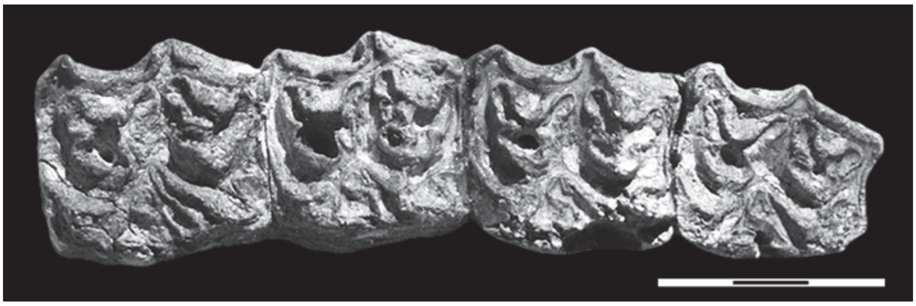

Fig. 23 *Equus* (*Sussemionus*) *hipparionoides* Vekua, Akhalkalaki. – Left P^4-M^3 AKHA 100, occlusal view. – Scale: 30 mm.

The upper cheek teeth of *E. marxi* (**Fig. 19**) have medium to long protocones, deep postprotoconal grooves and no pli caballin. They resemble teeth of extant Hemiones. The lower cheek teeth (**Fig. 22**) are typical for *Sussemionus*; actually, they could be easily referred to *E.* (*Sussemionus*) *suessenbornensis*.

There is no resemblance at all between *Equus* (*Sussemionus*) *wuesti* and the types of *E. altidens* and *E. marxi* neither in the upper cheek teeth pattern (**Figs. 3**, **19**) nor in the lower ones (**Figs. 4**, **22**).

Not a single Mt III of *Equus* (*Sussemionus*) *wuesti* from Untermassfeld resemble slender Sussemiones [*E. altidens, E.* (*Sussemionus*) *hipparionoides, E.* (*Sussemionus*) *granatensis*; see **Figs. 5–21**]. The Mc III, however, are not very different in their proportions although wider at the distal supra-articular tuberosities (**Fig. 20**, measurement 10).

5.2. Akhalkalaki

Faunal correlations and reversed paleomagnetics of Akhalkalaki (Samtskhe-Javakheti, southern Georgia) point to its belonging in the late Matuyama Chron, probably between 0.98 and 0.78 Ma BP (Tappen et al. 2002).

Together with a rich collection of *E*. (*Sussemionus*) cf. *suessenbornenis* bones were found a few remains of another and new species: *E.* (*Sussemionus*) *hipparionoides* (Vekua 1962; 1986). The upper cheek teeth are typical for a small Sussemione (**Fig. 23**). So are the lower ones (**Fig. 24**).

The Mc III (**Fig. 17**) and one Mt III (**Fig. 18**) resemble those referred to *E. altidens*.

5.3. Venta Micena

The combined uranium series-electron spin resonance (US-ESR) dating obtained for the site of Venta Micena (Granada, Guadix-Baza Basin, southeastern Spain) yielded an age about 1.4 Ma BP (Duval et al. 2011).

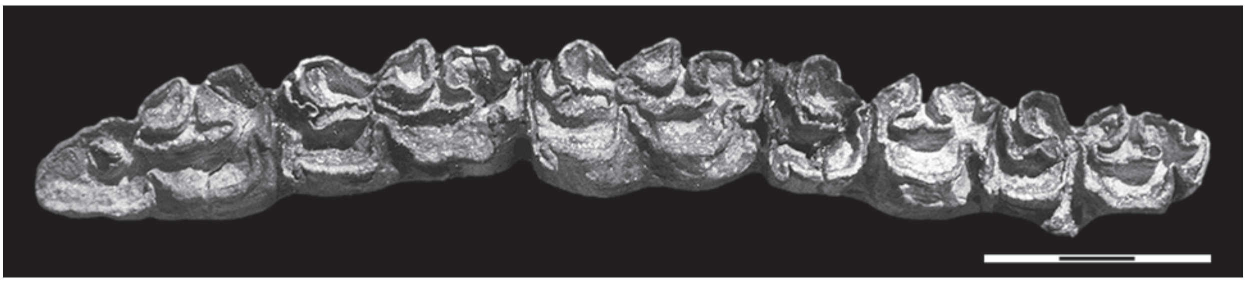

Fig. 24 *Equus* (*Sussemionus*) *hipparionoides* Vekua, Akhalkalaki. – Right P_2-M_3 AKHA 9, occlusal view. – Scale: 30 mm.

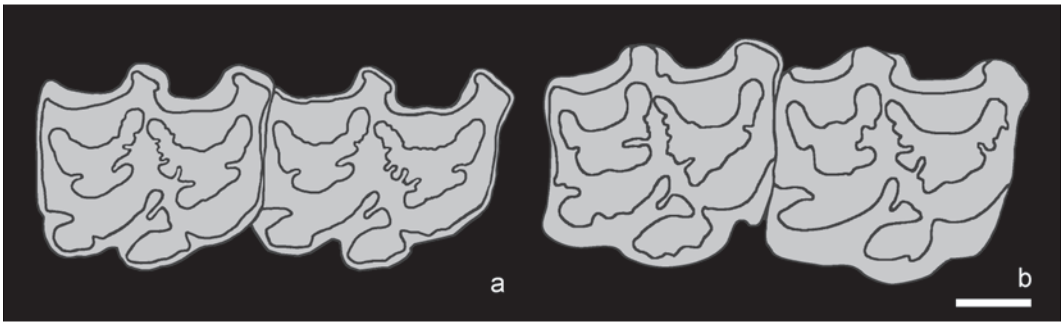

Fig. 25 *Equus* (*Sussemionus*) *wuesti* Musil, Untermassfeld. – **a** Right P3-P4 IQW 2010/31 393 (Mei. 30 555), occlusal view. | *Equus* (*Sussemionus*) *granatensis* (Marin), Venta Micena. – **b** Right P3-P4 VM 117–2311, occlusal view. – Scale: 10 mm.

As can be seen on **Fig. 25**, the resemblance of upper cheek teeeth between E. (*Sussemionus*) *wuesti* and *E.* (*Sussemionus*) *granatensis* (Eisenmann 1999; 2006) of Venta Micena is striking.

We have already noted that the few *E.* (*Sussemionus*) *wuesti* lower cheek teeth from Untermassfeld do not show any of the peculiarities often found in Sussemiones (Eisenmann 2006) but that these peculiarities are not constant and their lack is not very significant.

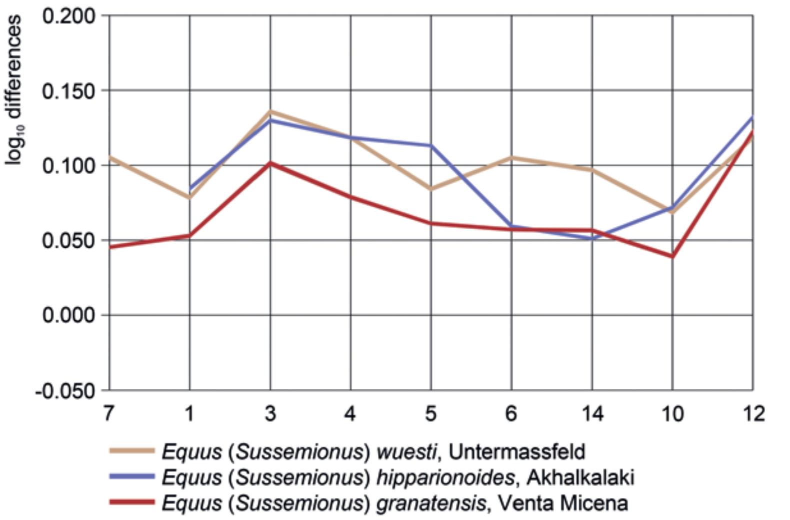

Fig. 26 Log10 differences of Ph1 ant characters (explanation of numbers see **Table 4**) between extant *Equus hemionus* Pallas as reference, *E.* (*Sussemionus*) *wuesti*, *E.* (*Sussemionus*) *hipparionoides* and *E.* (*Sussemionus*) *granatensis*.

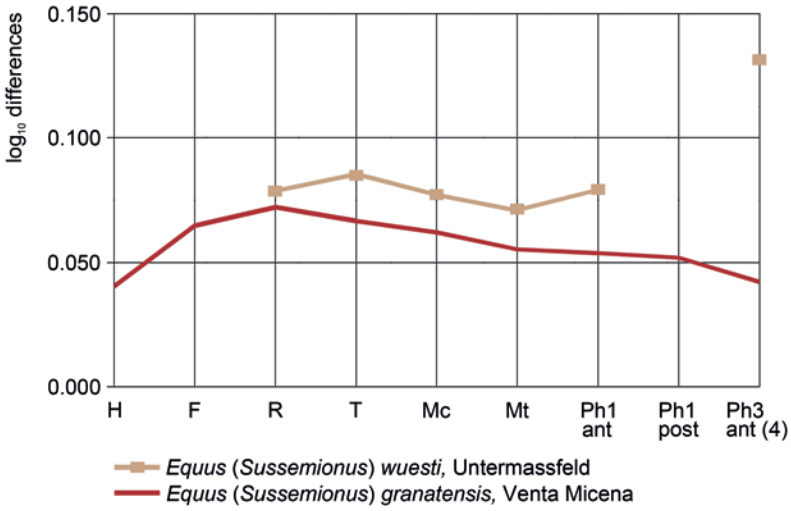

Fig. 27 Log10 differences of limb bone lengths between extant *Equus hemionus* Pallas as reference, *Equus* (*Sussemionus*) *wuesti* Musil and *Equus* (*Sussemionus*) *granatensis* Marin. Humerus (H), femur (F), radius (R), tibia (T), metacarpus (Mc), metatarsus (Mt), anterior phalanx 1 (Ph1 ant), posterior phalanx 1 (Ph1 post), maximal breadth of anterior phalanx 3 [Ph3 ant (4)].

Fig. 28 *Equus* sp., Untermassfeld. – **a** Right radius IQW 1980/15 228 (Mei. 14 710), posterior view. | *Equus wuesti* Musil, Untermassfeld. – **b** Right radius IQW 1980/15 275 (Mei. 14 787), posterior view. – Scale: 30 mm.

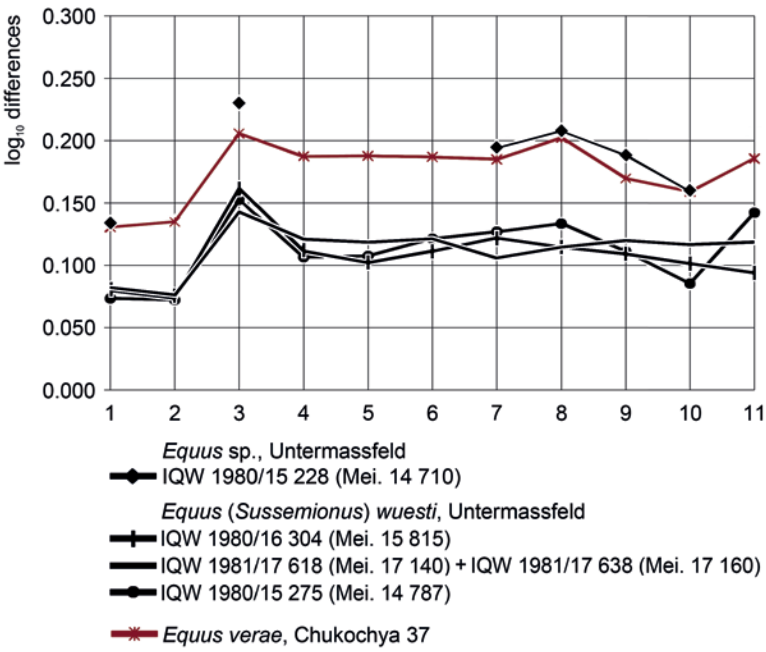

Fig. 29 Log differences of the radius characters (explanation of numbers see **Table 6**) between extant *Equus hemionus* Pallas as reference, *E.* (*Sussemionus*) *wuesti*, *Equus* sp. from Untermassfeld, and *E.* (*Sussemionus*) *verae* Sher from Chukochya 37, NE Siberia.

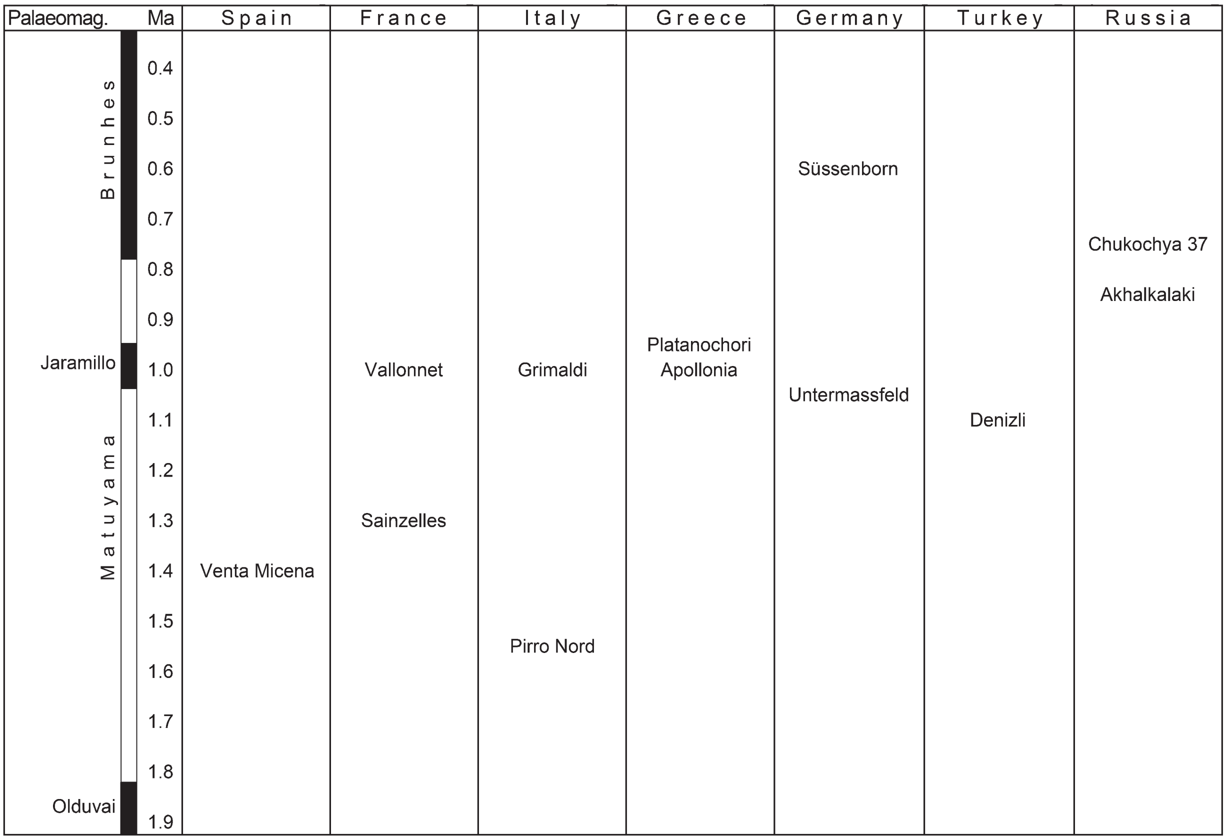

Fig. 30 Approximate chronology of some localities mentioned in the text.

The Mc III (**Fig. 20**) and Mt III (**Fig. 21**) have similar proportions although quite smaller. The first anterior phalanges are quite different (**Fig. 26**). The Untermassfeld limb bone lengths are larger than in *E.* (*Sussemionus*) *granatensis* of Venta Micena, and the width the third anterior phalanx is much wider but other proportions are similar (**Fig. 27**).

5.4. Further sites from Spain, France and Italy

In Spain several Early and Middle Pleistocene localities yielded equids mostly referred to *Equus altidens* and / or *Equus* (*Sussemionus*) *suessenbornensis* (Madurell-Malapeira et al. 2014). In the timing of the deposit of Untermassfeld, i. e., at around 1.0 Ma BP, the two species are in particular present in Cueva Victoria (Murcia, Spain) (Alberdi and Piñero 2014). *Equus altidens* is also well represented in the Epivillafranchian levels of Vallparadis (Barcelona, Spain) (Aurell-Garrido et al. 2010).

In France, *E. altidens* may be present at Sainzelles (Haute-Loire, France). In the South of France the new locality of Bois de Riquet (Hérault, France) yielded numerous remains of equids under study. According to Bourguignon et al. (2016) these also share affinities with *E. altidens* / *E. marxi* and *E.* (*Sussemionus*) *suessenbornensis*.

In Italy De Giuli et al. (1986) and Alberdi and Palombo (2013) referred in particular the slender equid of Pirro Nord (Puglia, Italy) to *E*. *altidens*.

6. *Equus* sp. from Untermassfeld

A fragmentary radius IQW 1980/15 228 (Mei. 14 710) is quite larger than those referred to *E.* (*Sussemionus*) *wuesti* from Untermassfeld (**Figs. 28a**, **29**). As far as can be seen, its proportions are close to that of *E.* (*Sussemionus*) *verae* (**Fig. 29**) from Chukochya locality 37 (Nizhnekolymskij district, NE Siberia) (Sher 1971; 1987) believed to be the same age as Akhalkalaki. Teeth from locality 37 are remarkably similar to those of *E.* (*Sussemionus*) cf. *suesenbornensis* of Akhalkalaki.

7. Conclusions

From the comparisons above, it seems that the best represented and smaller equid of Untermassfeld shares enough teeth and skeletal characters with *E.* (*S.*) *granatensis* of Venta Micena and *E.* (*S.*) *hipparionoides* of Akhalkalaki to be considered as a new species of the Sussemione group: *E.* (*S.*) *wuesti.* It differs from *E.* (*S.*) *granatensis* and *E.* (*S.*) *hipparionoides* by its larger size and the lack of the peculiarities often found in Sussemione lower cheek teeth (Eisenmann 2006); these peculiarities however are not constant and their lack is not significative.

There are not enough data to be certain but it seems probable that the large radius belonged to the same *Sussemionus* group but to the large sized species of Süssenborn, Akhalakalaki, and NE Siberia. If so, at Untermassfeld as well as at Akhalkalaki, two Sussemione species of different size coexisted.

Several other late Early and Middle Pleistocene localities in western Europe yielded two equids of different size mostly referred to *Equus altidens* and *Equus suessenbornensis*, in Spain (Alberdi and Piñero 2015; Piñero and Alberdi 2015 and references therein), in Italy (Alberdi and Palombo 2013), in France (Lacombat 2005; Bourguignon et al. 2016) or in England (Lister et al. 2010). The simplified chronological frame of **Fig. 30** (mostly from Nomade et al. 2013) shows how the discussed localities are chronologically situated in respect to Untermassfeld.

Both by its age and geographical localization, *E.* (*S.*) *wuesti* fits perfectly inside the range of Sussemiones and represents an important link between the older and western Venta Micena and the younger and eastern Akhalkalaki.

As already mentioned, many European fossils have been compared with, or referred to, *E*. cf. *altidens* or *E. altidens* – a species described from Süssenborn. But in spite of their number and historic importance the Süssenborn equids are still poorly known and understood, especially *E. altidens*. It seems better to be careful to refer any fossil to this species nor to *E. marxi*, another poorly defined species of Süssenborn. In the course of this study, many affinities were found between *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou 1997 from the Greek locality of Apollonia and extant wild Ass *Equus africanus*. This species could represent a step within the lineage of asses soon after its differentiation.

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