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# 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

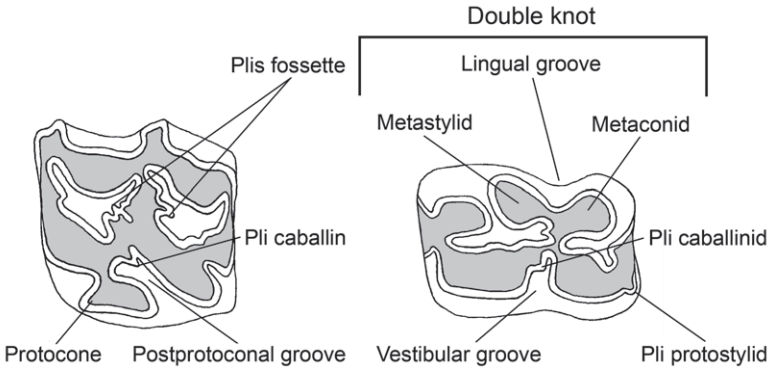


**Fig. 1** Left upper premolar and right lower premolar of *Equus*.

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.

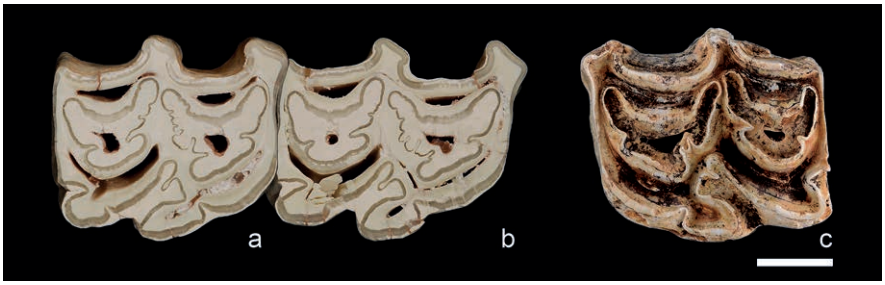


**Fig. 3** *Equus* (*Sussemionus*) *wuesti* Musil, Untermassfeld. – **a–b** Right $P^3$-$P^4$ IQW 2010/31 393 (Mei. 30 555), occlusal view. – **c** Left $P^3$ IQW 1999/26 560 (Mei. 26 089), occlusal views. – Scale: 10 mm.

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: 30 mm.

| | 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**.

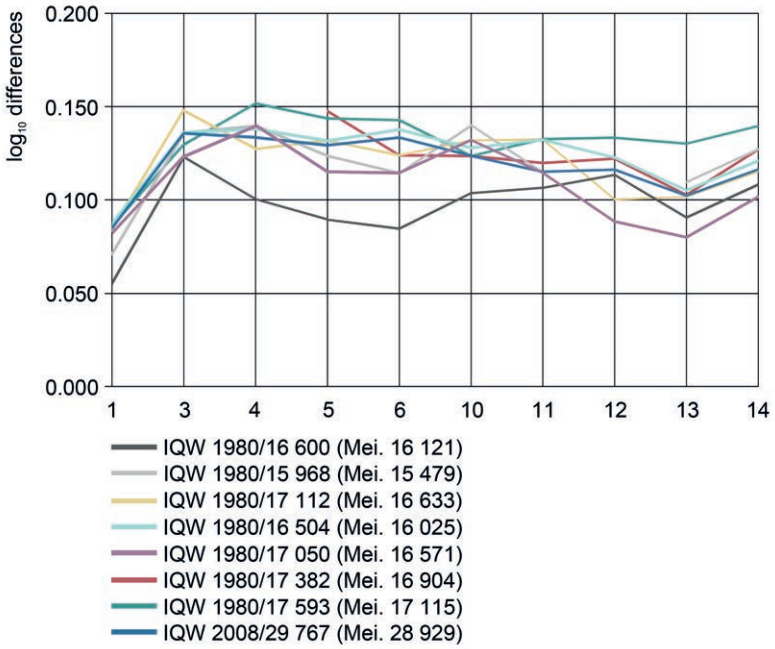


**Fig. 5** *Equus* (*Sussemionus*) *wuesti* Musil, Untermassfeld. Log10 differences of Mt III characters 1, 3–6, 10–14 (explanation of numbers see **Table 5**) between extant *Equus hemionus* Pallas as reference.

### 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 1980/15438 (Mei. 14950) | IQW 1980/15452 (Mei. 14964) | IQW 1980/15987 (Mei. 15498) | IQW 1980/16199 (Mei. 15710) | IQW 1980/16585 (Mei. 16106) | IQW 1980/16883–4 (Mei. 16404–5) | IQW 1980/16942 (Mei. 16463) | IQW 1980/17011 (Mei. 16532) | IQW 1980/17188 (Mei. 16710) | IQW 1980/17589 (Mei. 17111) | IQW 1984/20272 (Mei. 19792) | IQW 1986/21670 (Mei. 21189) | IQW 1989/23311 (Mei. 22830) | IQW 1998/26413 (Mei. 25942) | IQW 1980/17439 (Mei. 16961) 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 1980/15968 (Mei. 15479) | IQW 1980/16504 (Mei. 16025) | IQW 1980/16543 (Mei. 16064) | IQW 1980/16600 (Mei. 16121) | IQW 1980/17050 (Mei. 16571) | IQW 1980/17112 (Mei. 16633) | IQW 1980/17382 (Mei. 16904) | IQW 1980/17593 (Mei. 17115) | IQW 2008/29767 (Mei. 28929) | IQW 1980/15610 (Mei. 15122) juv | IQW 1980/16953 (Mei. 16474) 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 1980/15397 (Mei. 14909) | IQW 1980/16965 (Mei. 16486) | IQW 1980/17384 (Mei. 16906) | IQW 1980/17395 (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 1980/15453 (Mei. 14965) | IQW 1980/15910 (Mei. 15421) | IQW 1980/16506 (Mei. 16027) | IQW 1980/17047 (Mei. 16568) | IQW 1980/17083 (Mei. 16604) | IQW 1980/17377 (Mei. 16899) | IQW 1981/17698 (Mei. 17220) | IQW 1984/20087 (Mei. 19607) | IQW 2016/43779 (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

| | Ph2 | ant<br>IQW 1980/15752 (Mei. 15264) | ant<br>IQW 1980/16549 (Mei. 16070) | post<br>IQW 1980/15832 (Mei. 15343) | post<br>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 |

| | Ph3 | ant<br>IQW 1980/16771 (Mei. 16292) | post?<br>IQW 1980/15447 (Mei. 14959) | post<br>IQW 1980/15884 (Mei. 15395) | post<br>IQW 1980/16056 (Mei. 15567) | post<br>IQW 1980/17101 (Mei. 16622) | post?<br>IQW 1980/17400 (Mei. 16922) | post<br>IQW 1980/17495 (Mei. 17017) | ?<br>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.

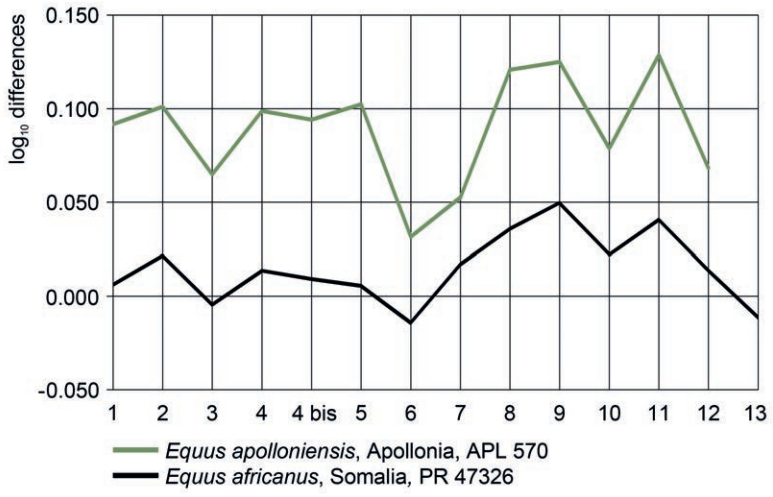


**Fig. 7** Log10 differences of mandible characters 1–13 (explanation of numbers see **Table 2**) between extant *Equus hemionus* Pallas as reference, and *Equus africanus* (Heuglin et Fitzinger) and *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou.

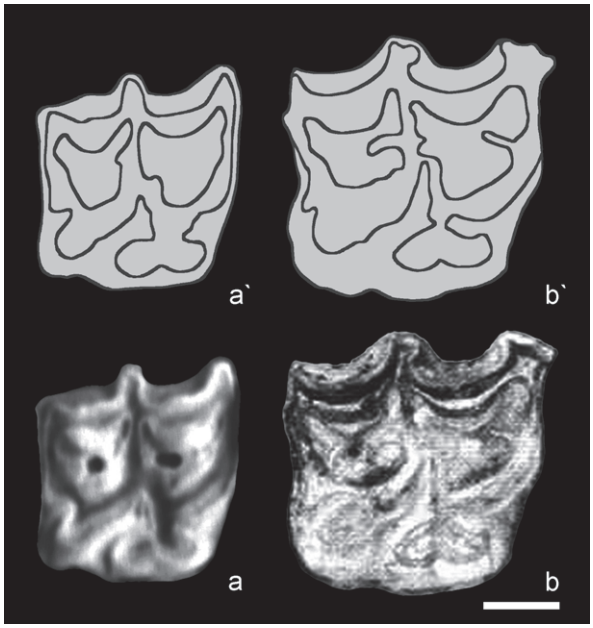


**Fig. 8.** *Equus africanus* (Heuglin et Fitzinger), Somali. – **a–a'** Left $P^4$ (inverted) Basel NHM 3267, occlusal views. | *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou, Apollonia. – **b–b'** Right $P^4$ APL 148, occlusal views. – Scale: 10 mm.

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**).

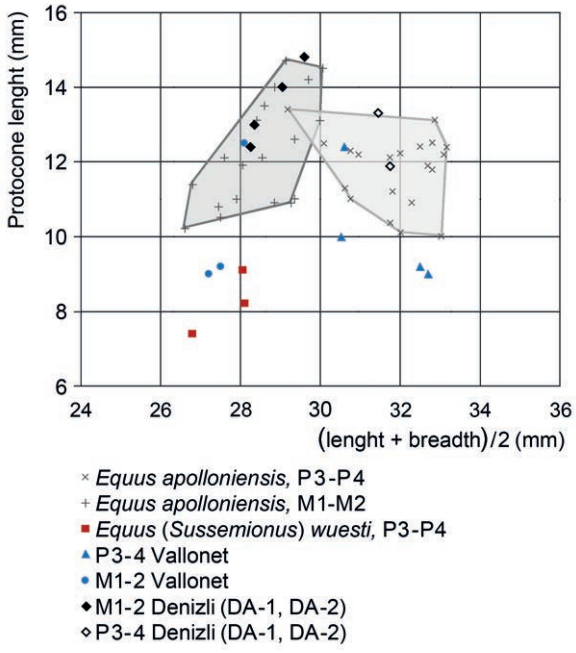


**Fig. 9** Scatter diagram of average occlusal diameter (length + breadth)/2 of $P^3$-$P^4$ and $M^1$-$M^2$. Data from Apollonia *E. apolloniensis* (pers. comm. G.D. Koufos) and Denizli *E.* cf. *apolloniensis* (Boulbes et al. 2014).

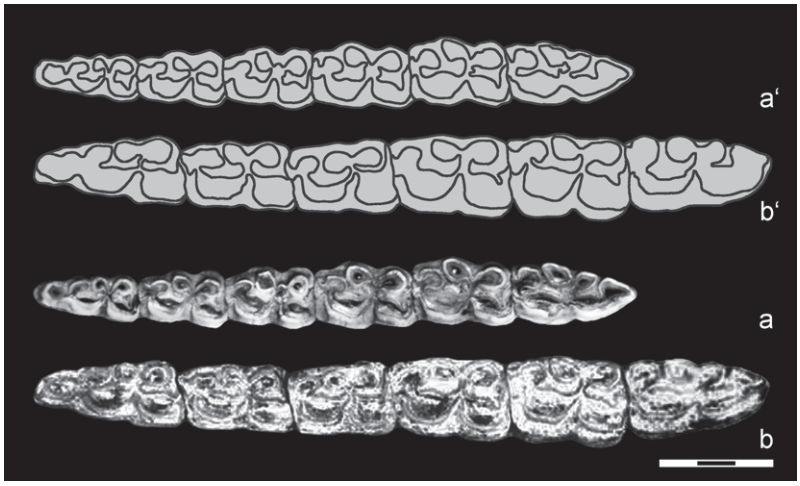


**Fig. 10** *Equus africanus* (Heuglin et Fitzinger), Somalia. – **a–a'** Right $P_2$-$M_3$ ZIN 7204, occlusal views. | *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou, Apollonia. – **b–b'** Right $P_2$-$M_3$ APL 147, occlusal views. – Scale: 30 mm.

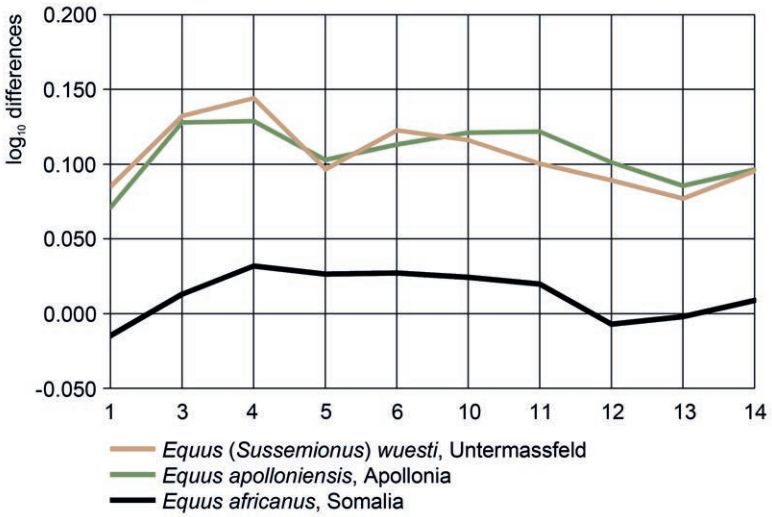


**Fig. 11** Log10 differences of Mc III characters 1–14 (explanation of numbers see **Table 4**) between extant *Equus hemionus* Pallas as reference, *Equus africanus* (Heuglin et Fitzinger), and *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou.

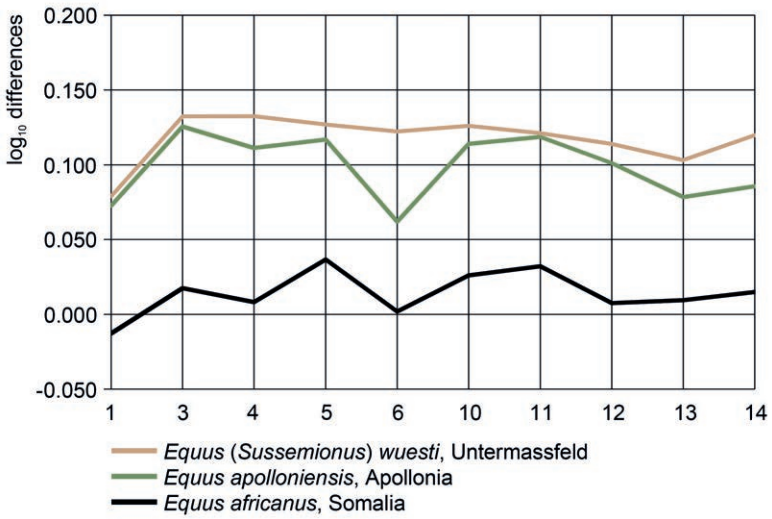


**Fig. 12** Log10 differences of Mt III characters 1–14 (explanation of numbers see **Table 5**) between extant *Equus hemionus* Pallas as reference, *Equus africanus* (Heuglin et Fitzinger) and *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou.

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).

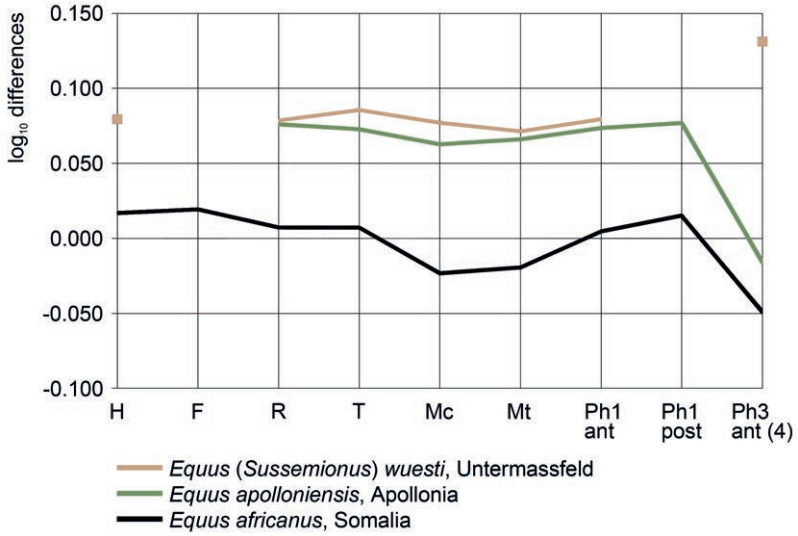


**Fig. 13** Log10 differences of limb bone lengths between extant *Equus hemionus* Pallas as reference, *Equus africanus* (Heuglin et Fitzinger) and *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou. Lengths of humerus (H), femur (F), radius (R), tibia (T), metacarpus (Mc), metatarsus (Mt), anterior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

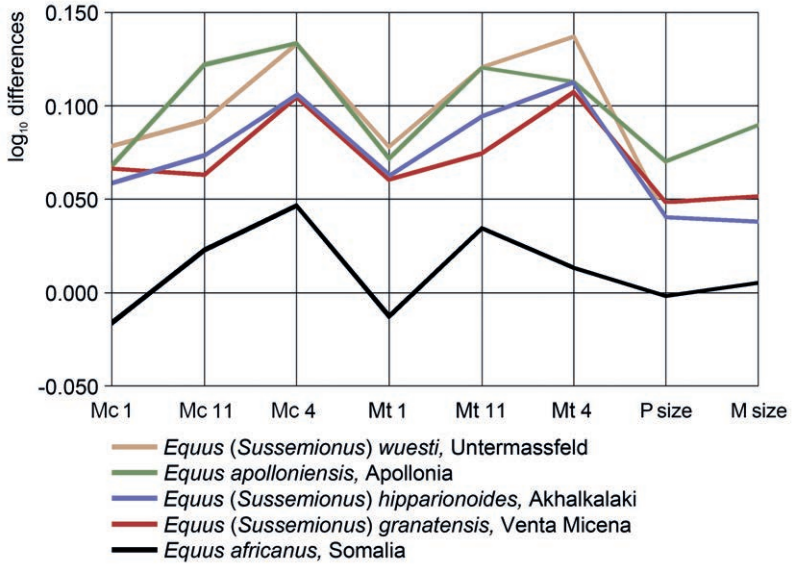


**Fig. 14** Comparison between teeth and metapodial sizes in *Equus africanus* (Heuglin et Fitzinger) and *Equus apolloniensis* Koufos, Kostopoulos et Sylvestrou with *E.* (*Sussemionus*) *wuesti*, *E.* (*Sussemionus*) *granatensis*, and *E.* (*Sussemionus*) *hipparionoides*.

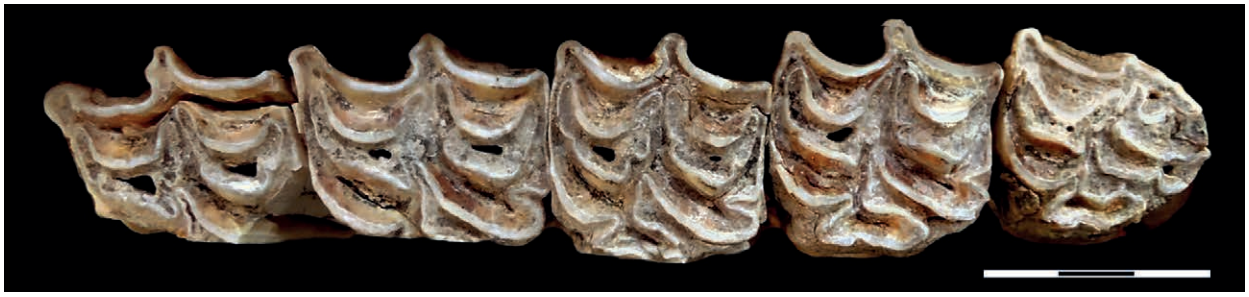

**Fig. 15** *Equus* cf. *apolloniensis*, Denizli. – Left $P^2$-$M^3$ DA-1, occlusal view. – Scale: 30 mm.

*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

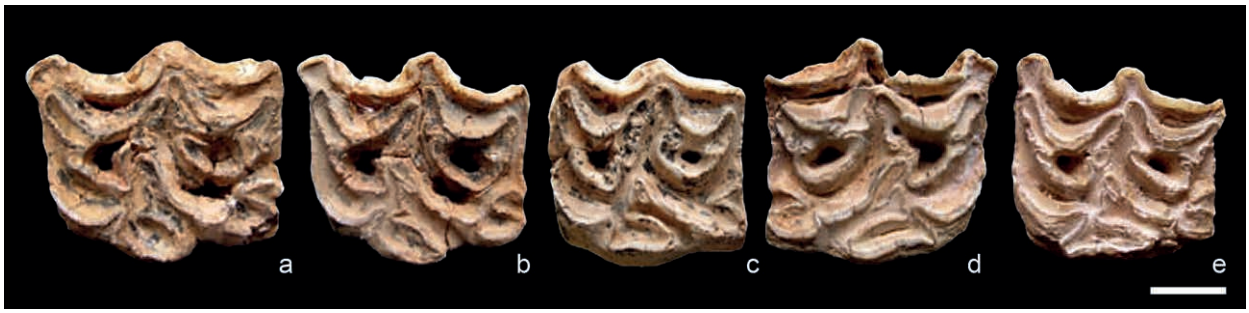


**Fig. 16** Le Vallonnet. – **a** Left $P^3$ A9.AJ54, occlusal view. – **b** Left $P^4$ A9.AJ5.95, occlusal view. – **c** Left $M^1$ B9.BJ16.953, occlusal view. – **d** Right $P^4$ B6.C.3237, occlusal view. – **e** Left $M^2$ B7.288, occlusal view. – Scale: 10 mm.

**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.

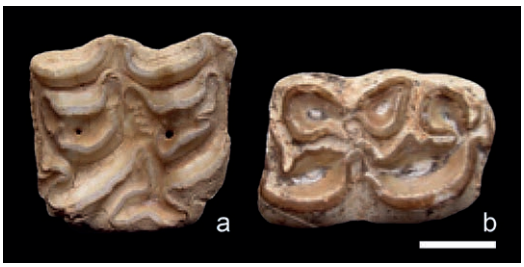


**Fig. 18** Tour Grimaldi. – **a** Right $P^4$ 13692, occlusal view. – **b** Left $P_4$ 13680, occlusal view. – Scale: 10 mm.

## 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.

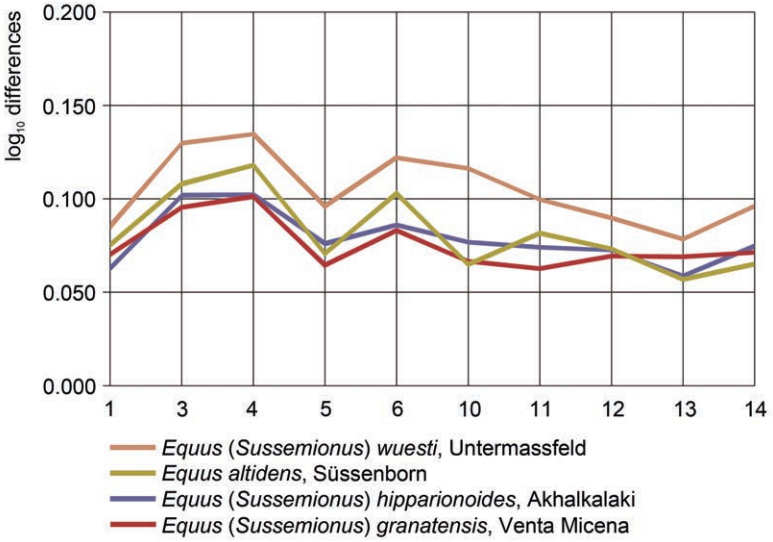


**Fig. 20** Log10 differences of Mc III characters 1–14 (explanation of numbers see **Table 4**) between extant *Equus hemionus* Pallas as reference, *E.* (*Sussemionus*) *wuesti*, *E. altidens*, *E.* (*Sussemionus*) *granatensis* and *E.* (*Sussemionus*) *hipparionoides*.

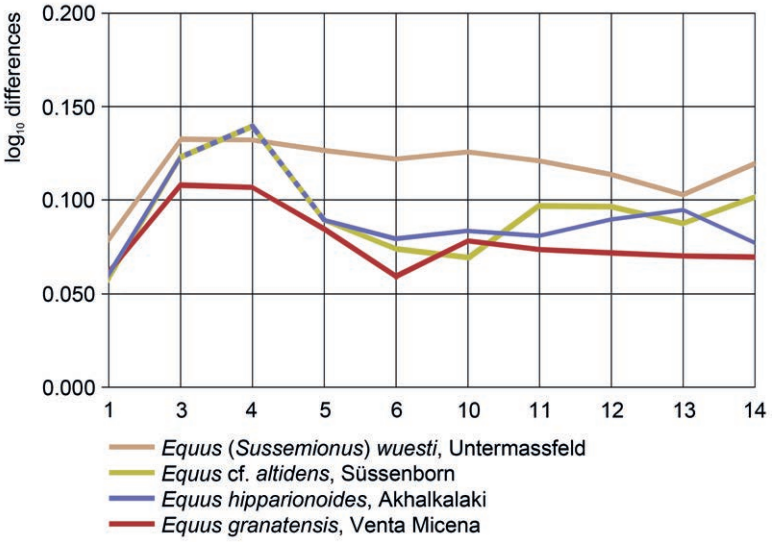


**Fig. 21** Log10 differences of Mt III characters 1–14 (explanation of numbers see **Table 5**) between extant *Equus hemionus* Pallas as reference, *E. altidens*, *E.* (*Sussemionus*) *hipparionoides* and *E.* (*Sussemionus*) *granatensis*.

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.

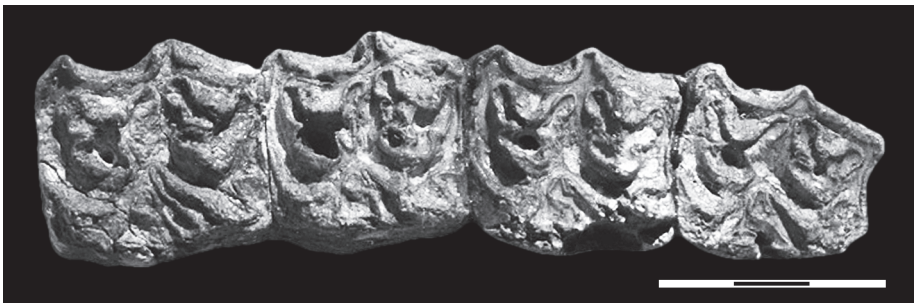

**Fig. 23** *Equus* (*Sussemionus*) *hipparionoides* Vekua, Akhalkalaki. – Left $P^4$-$M^3$ AKHA 100, occlusal view. – Scale: 30 mm.

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).

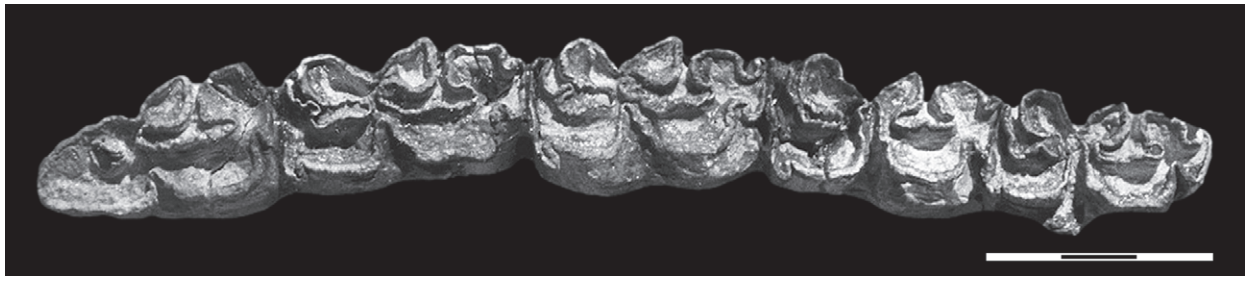

**Fig. 24** *Equus* (*Sussemionus*) *hipparionoides* Vekua, Akhalkalaki. – Right $P_2$-$M_3$ AKHA 9, occlusal view. – Scale: 30 mm.

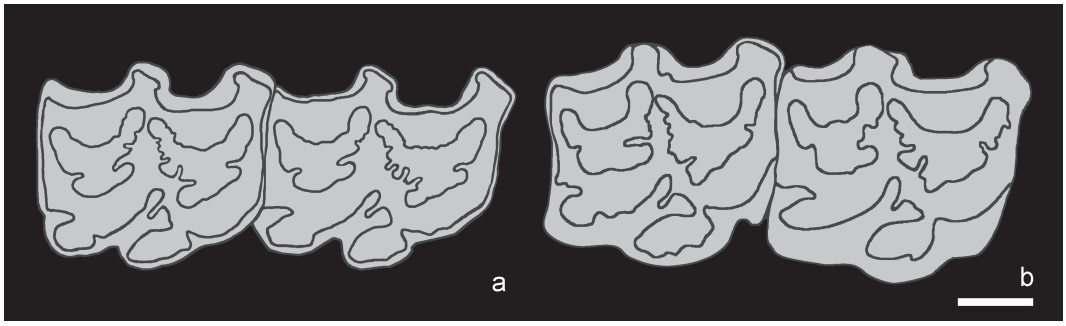


**Fig. 25** *Equus* (*Sussemionus*) *wuesti* Musil, Untermassfeld. – **a** Right $P^3$-$P^4$ IQW 2010/31393 (Mei. 30555), occlusal view. | *Equus* (*Sussemionus*) *granatensis* (Marin), Venta Micena. – **b** Right $P^3$-$P^4$ VM 117–2311, occlusal view. – Scale: 10 mm.

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.

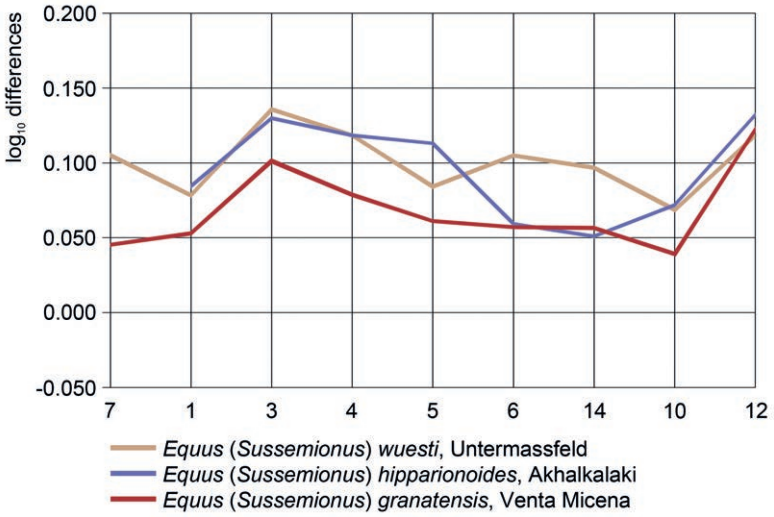


**Fig. 26** Log10 differences of Ph1 ant characters (explanation of numbers see **Table 4**) between extant *Equus hemionus* Pallas as reference, *E.* (*Sussemionus*) *wuesti*, *E.* (*Sussemionus*) *hipparionoides* and *E.* (*Sussemionus*) *granatensis*.

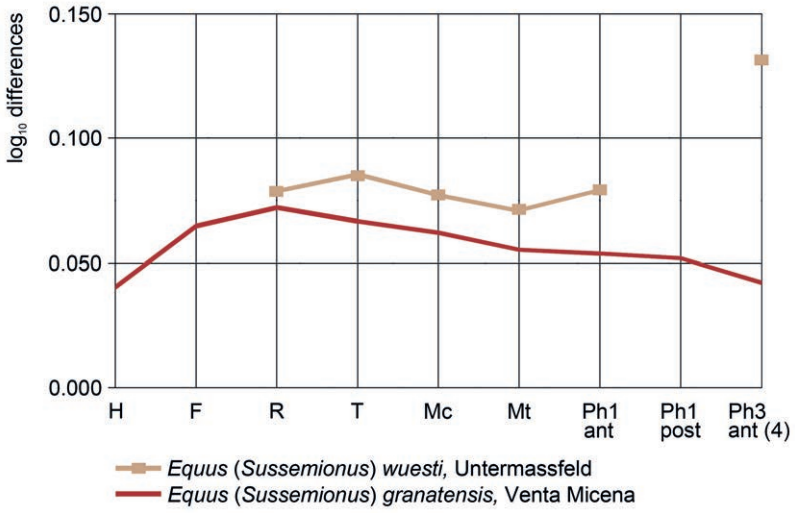


**Fig. 27** Log10 differences of limb bone lengths between extant *Equus hemionus* Pallas as reference, *Equus* (*Sussemionus*) *wuesti* Musil and *Equus* (*Sussemionus*) *granatensis* Marin. Humerus (H), femur (F), radius (R), tibia (T), metacarpus (Mc), metatarsus (Mt), anterior phalanx 1 (Ph1 ant),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

**Fig. 28** *Equus* sp., Untermassfeld. – **a** Right radius IQW 1980/15228 (Mei. 14710), posterior view. | *Equus wuesti* Musil, Untermassfeld. – **b** Right radius IQW 1980/15275 (Mei. 14787), posterior view. – Scale: 30 mm.

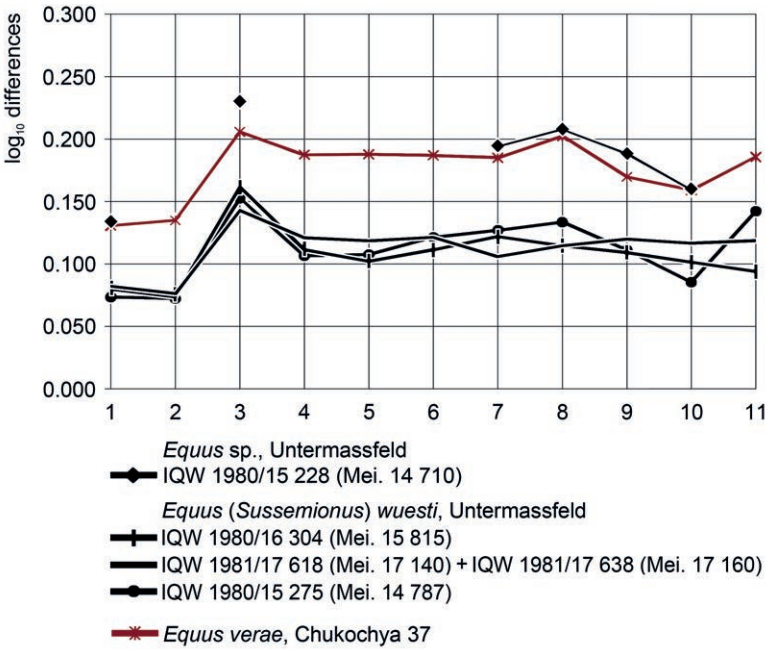


**Fig. 29** Log differences of the radius characters (explanation of numbers see Table 6) between extant *Equus hemionus* Pallas as reference, *E.* (*Sussemionus*) *wuesti*, *Equus* sp. from Untermassfeld, and *E.* (*Sussemionus*) *verae* Sher from Chukochya 37, NE Siberia.

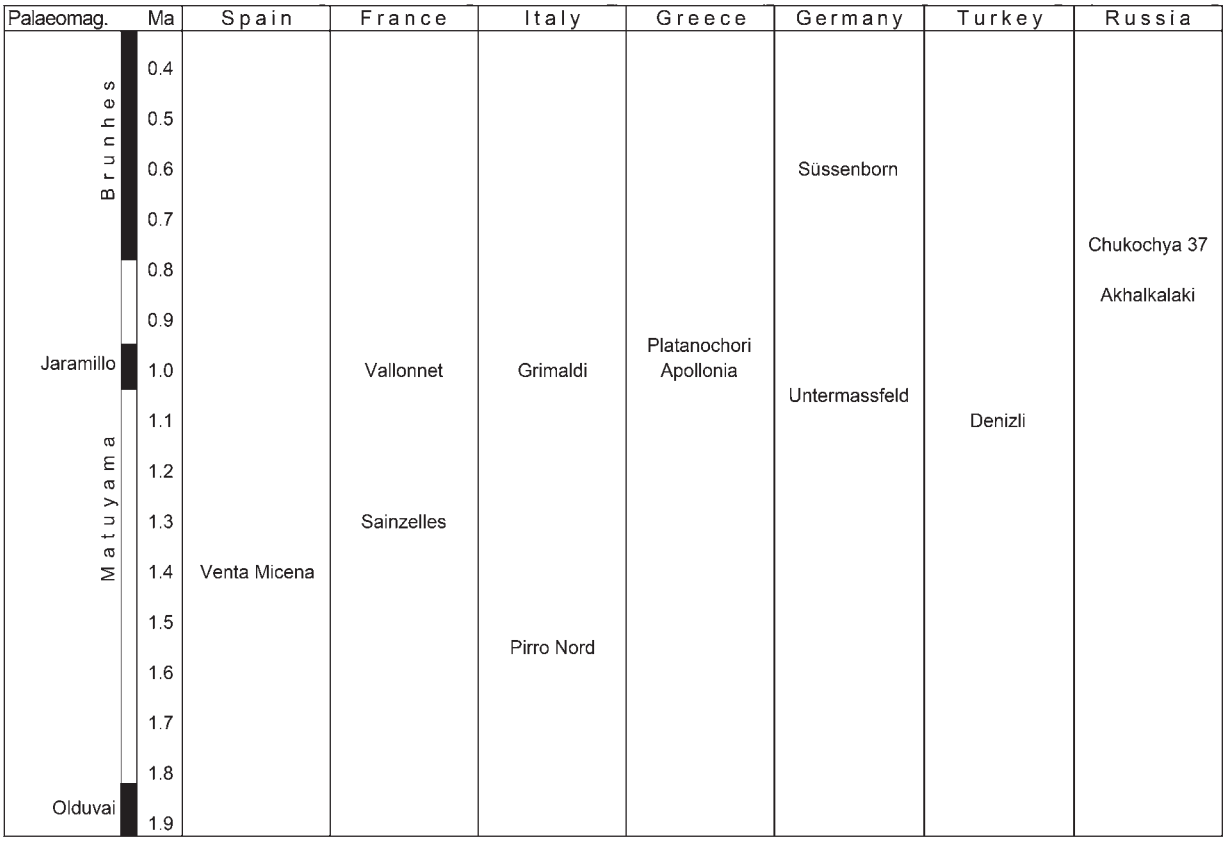


**Fig. 30** Approximate chronology of some localities mentioned in the text.

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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