Dietary traits of the late Early Pleistocene *Bison menneri* (Bovidae, Mammalia) from its type site Untermassfeld (Central Germany) and the problem of Pleistocene 'wood bison'

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Highlights

- Bison radiation in Pleistocene Eurasia coincided with the opening up of habitats
- *Bison menneri* from Untermassfeld and *B. priscus* from Taubach were mixed feeders
- *Bison schoetensacki* from Voigtstedt and Süssenborn were grazers
- None of the fossil and extant bison species studied were true browsers
- The current concept of 'wood bison' is problematic

Abstract

Over the course of the Early and early Middle Pleistocene, a climatic cooling trend led to the partial opening up of landscapes in the western Palaearctic. This led to a gradual resplacement of browsers by grazers, whilst some herbivore species shifted their diet towards including more grass. Wear patterns of herbivore cheek teeth can inform our understanding of the timing and extent of this change and indicate levels of dietary plasticity. One of the indicator species of the faunal turnover is the first large-sized form of bison in the Palaearctic, *Bison menneri*. The dental mesowear of the palaeopopulation from the species' late Early Pleistocene type site of Untermassfeld in Central Germany and the Late Pleistocene *B. priscus* from Taubach, both from habitat mosaics of forested habitats and more open landscapes, have a mixed feeder profile similar to that of North American wood bison, which has a distinct preference for open habitats but occasionally consumes a high amount of browse as a fall-back food. In contrast, the grazer

mesowear signature of early Middle Pleistocene *B. schoetensacki voigtstedtensis* from Voigtstedt indicates these animals likely did not regularly feed in the densely forested area around the site. The mesowear of *B. schoetensacki* from Süssenborn, in a more open environment, is similar to that of extant European bison. Both Pleistocene and extant bison are grazers to mixed feeders with relatively high tolerance of a suboptimal browsing diet. None of these species can be regarded as true 'wood bison'.

1. Introduction

The Early Pleistocene was a period of perceptible global cooling. During the 2.6-1.8 Ma interval, characterised by a fairly regular 41 ka climatic periodicity (Lisiecki and Raymo, 2005), landscapes in the western Palaearctic partially opened up, which is clearly reflected in the fossil mammal record. Thermophile species characteristic of humid forest habitats were replaced by forest-steppe to steppe dwellers (Kahlke et al., 2011). A decrease in global temperatures over the subsequent 1.8-1.2 Ma timespan, still governed by the 41 ka cyclicity, led to an increased specialisation of species and faunas. Such differentiation resulted, especially in the western part of the Palearctic, in an ongoing alternation of faunal communities, caused by the interplay of oceanic (Atlanto-Mediterranean) and continental (central Eurasian) climatic influences (Kahlke et al., 2011). The following 1.2-0.9 Ma interval of the late Early Pleistocene, which linked the 41 ka with the following 100 ka periodicity (Lisiecki and Raymo, 2005), was a more unstable transitional time (Kahlke, 2007). Its climatic variability created a renewed variety of habitats in most of Europe, producing ecological niches which new species could exploit (Kahlke et al., 2011).

Whilst the Middle and Late Villafranchian (2.6-1.2 Ma BP) environments in Europe generally supported a large number of browsers, which had their roots in forested habitats of the Pliocene, over the course of the Pleistocene the rise of predominantly open habitats allowed grazers to expand (e.g. Kahlke, 1999, 2014). Moreover, the number of herbivore species which shifted their diets towards including more grass increased. Such dietary adaptations can be expressed by large-scale evolutionary shifts in body morphology and proportions (e.g. Lister et al., 2005; Kahlke and Lacombat, 2008) and / or in dental evolution (e.g. Jernvall and Fortelius, 2002; Fortelius et al., 2002; Liu et al., 2012; Rivals et al., 2012; Lister and Sher, 2015). However, within individual evolutionary lineages such trends can be subtle and lag changes in dietary behaviour. Wear characteristics of herbivore cheek teeth provide additional information about the spatiotemporal frame of functional changes within the dentition, as well as levels of dietary

plasticity given a certain morphological adaptation (e.g. Feranec, 2007; Rivals et al., 2007a, 2009; Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015).

One of the indicator species of the western Palaearctic Epivillafranchian (1.2-0.9 Ma BP) faunal turnover is the newcomer *Bison menneri*, eponym for the corresponding *Bison menneri-Eucladoceros giulii*-assemblage chron (Kahlke, 2007; upgraded by Bellucci et al., 2015). It represents the first large-sized form of bison in the Palaearctic (Sher, 1997). The Middle and Late Pleistocene diversity of *Bison* species probably emerged from this group of bovids. A series of adaptive radiations enabled their wide distribution in the Northern Hemisphere (Kahlke, 1999; Shapiro et al., 2004). If geographical distribution can be taken as a measure of success, large-sized bison represents the most successful group of herbivores in Holarctic Pleistocene faunas. In this context of environmental change and evolutionary adaptation, the dental wear of the *B. menneri* palaeopopulation from the species' late Early Pleistocene type site of Untermassfeld in Central Germany, marking the initial stage of the very successful bison spread, is of particular interest.

2. Fossil bison and the origin of *Bison menneri*

During the Villafranchian (c. 3.5-1.2 Ma BP), the large mammal faunas of Eurasia's mid-latitudes were characterised by a high diversity of bovids of small to medium size classes (Duvernois and Guérin, 1989; Brugal and Croitor, 2007; Crégut-Bonnoure, 2006; and references therein). As heavier bovini, a number of species of the genus *Leptobos* were distributed from East and South Asia to Western Europe (Duvernois, 1992; Bukhsiandize, 2005; Mead et al., 2014). From this group primitive forms of moderately large bison emerged, which have been described in the literature under several specific and generic names (see summaries in Dubrovo and Buchak-Abramovich, 1986; Kahlke, 1999: 57-58; Bukhsianidze, 2005). Based on Flerov (1972, 1975, 1979), at present early bison are mostly referred to the subgenus *Bison* (*Eobison*) (e.g. Sala, 1987; Kostopoulos, 1997; Masini and Sala, 2007; this paper) or to a distinct genus *Eobison* (e.g. De Giuli et al., 1987; Sher, 1997; Kostopoulos, 2006; Croitor and Brugal, 2007). Whereas there has long been consensus about the origin of the genus *Bison* or the *Eobison* group in southern or middle latitudes of Asia (e.g. Flerov, 1979; Sala, 1987; Kahlke, 1999), views about the chronology of its emergence changed recently. Bukhsianidze (2005) underlined the monophyletic character of the bison group and postulated its origin at around 2.5-2.3 Ma BP. Meanwhile, Akhbar Khan et al. (2010) reported fossil remains ascribed to *B.* cf. *sivalensis* from deposits of the Upper Siwaliks in northern Pakistan dated between 3.3 and 2.6 Ma BP.

The phylogeny of Western Palaearctic early bison is still poorly understood (Sher, 1997; Maniakas and Kostopoulos, 2017). The c. 1.77 Ma old Transcaucasian fauna from Dmanisi (Georgia; Lordkipanidze et al., 2007) includes a gracile, long-horned early form, *B*. (*E.*) *georgicus* (Burchak-Abramovich and Vekua, 1994; Bukhsianidze, 2005). The first populations of bison occupied Europe between 1.5 and 1.3 Ma BP, when open grasslands expanded in the Western Palaearctic (Kahlke et al., 2011). The correspondingly oldest known forms are *B*. (*E.*) sp. from Venta Micena (Orce) in Spain (Martinez-Navarro el al., 2011) and *B*. (*E.*) *degiulii* from Pirro Nord (Apricena) in Italy (De Giuli et al., 1987; Masini, 1989; Bukhsianidze, 2005), both of them relatively small in size. A slightly younger palaeopopulation, still with small stature but more evolved than *B. degiulii*, is recorded from the 1.2-1.0 Ma old Epivillafranchian site of Apollonia-1 (Mygdonia basin) in Greece (Kostopoulos, 1997; Maniakas and Kostopoulos, 2017).

Extensive bovid material excavated at Untermassfeld (Thuringia) in Germany (Sher, 1997; Kahlke, 2006; Kierdorf et al., 2012) (Fig. 1) potentially represents a second evolutionary line of Epivillafranchian bison (Maniakas et al., 2014), whose ancestry is not clear so far. A detailed revision of its phylogenetic position is in progress (M. Bukhsianidze, Tbilisi). These extremely tall and slender animals were characterized by exceptionally long metapodials and correspondingly elongated longbones, which are among the largest known bovids. Their heads were relatively small with short horns (Fig. 2). The skeletal reconstruction, produced on the basis of individually related finds, shows a long-legged animal with a high hump (Fig. 3). Based on the Untermassfeld fossil material, Sher (1997) described a new species, *B. menneri*, which is distinguished from the *Eobison* group by its advanced morphology.

Due to the general rarity of Epivillafranchian faunal sites in the Western Palearctic (Kahlke et al., 2011), we have limited knowledge of the spatio-temporal distribution of *B. menneri*. Nevertheless, the species represents an early stage of the successful spread and evolution of the genus *Bison* in the northern hemisphere. Furthermore, the site produced Eurasia's most comprehensive series of fossil bison finds from one single palaeopopulation (cf. Hoffecker et al., 1991; Gaudzinski, 1992; Martínez-Navarro et al., 2011; Baygusheva et al., 2014) and one of the largest series of fossil bison discoveries overall (see section 3.1.).

From the early Middle Pleistocene, *B*. (*B.*) *schoetensacki*, a more advanced, medium-sized species of bison with short or moderately long horn cores, spread in most of Europe and as far as eastern Siberia (Flerov, 1975, 1979). So far it is unclear whether the larger *B*. (*B.*) *priscus* co-occurred with late *schoetensacki* forms in Europe or immigrated later from Asia. During the late Middle Pleistocene, long-horned early forms of the large *B*. (*B.*) *priscus* ranged from

Eastern Asia to Western Europe. The Late Pleistocene produced a patchwork of widespread, not always neatly separable priscoid bison populations with many transitional forms (compilation and map in Kahlke, 1999). In the present study dietary traits obtained from dental series from palaeopopulations of both *B. schoetensacki* and *B. priscus*, as well as several (sub)species of modern bison, are compared with those of the Untermassfeld bison (see section 3.2.).

3. Material and methods

3.1. The Untermassfeld *Bison* material and its palaeobiological context

The Untermassfeld fossil material, continuously excavated since 1978 (Fig. 1, right), comprises 14,224 preparations of large mammal remains (as of January 2017). The material is stored at the Senckenberg Research Station of Quaternary Palaeontology in Weimar (IQW). The unusually high concentration of fossil vertebrate remains recovered at this fluviatile site is the result of a succession of high flood events, which accumulated skeletal material under the lee of a clastic mudflow fan near to the right bank of the river Werra (Ellenberg and Kahlke, 1997). The fossil record includes fossil remains both of direct victims of the floods and of leftovers of predator and scavenger activities, particularly of hyenas, swept away from areas upstream of the site (Kahlke, 1997b, 2006, 2009; Hemmer, 2001; Kahlke and Gaudzinski, 2005).

The faunal assemblage, dated to slightly older than one million years, is one of the most complete mammal assemblages from the 1.2-0.9 Ma BP (Epivillafranchian) interval (Kahlke, 1997a, 2001a, 2001b with studies of numerous authors). Typical elements of the Untermassfeld fauna include *Capreolus cusanoides*, *Cervalces carnutorum*, *Pseudodama vallonnetensis*, *Eucladoceros giulii*, *Hippopotamus antiquus*, *Stephanorhinus hundsheimensis*, *Panthera onca gombaszoegensis*, *Acinonyx pardinensis pleistocaenicus*, *Puma pardoides*, *Megantereon cultridens adroveri*, *Homotherium crenatidens*, *Pachycrocuta brevirostris*, *Ursus* cf. *dolinensis, Xenocyon lycaonoides* and *Canis mosbachensis.* The composition of the Untermassfeld fauna indicates a temperate climate with warmer summers than occur in the region today and mild winters with minimum air temperatures of a few degrees below zero (Kahlke, 2001c, 2006). These parameters are supported by oxygen isotope data of horse bones from the site (Stephan et al., 2001).

Bison menneri is the most common faunal element in the Untermassfeld mammal record. Up to and including the discoveries of the 2014 field season, 2323 identified specimen (NISP count by J. Arnold, Weimar, July 2016) represent a minimum number (MNI) of 50 individuals (Kahlke, 2006 and new discoveries) including bulls, cows and juveniles. The sample is

morphologically homogenous, although its postcranial elements are markedly sexually dimorphic (Sher, 1997). The teeth, however, do not show significant sexual dimorphism. The bison's mortality profile roughly reflects a normal herd structure (Sher, 1997; Kahlke and Gaudzinski, 2005 and new discoveries). In relation to the NISP, dental remains, especially those of the upper jaws, are somewhat underrepresented, caused by a separation of skeletal elements in the water flow. Obstructive skeletal elements, like for example hippopotamus mandibles or skulls, complete antlers attached to cervid skulls and bovid skulls with horn cores that jut out, remain rare or missing in the Untermassfeld fossil record. Such parts of carcasses or skeletons became entangled upstream in comparatively large numbers and were embedded or destroyed outside the limits of the present site (Kahlke 2001c, 2006). Likewise, relatively small bones are clearly underrepresented in the total volume of material. Such elements from the skeletal units disintegrating within the area of the site were carried away in significant quantities.

At the time of the formation of the site, most of the wide and flat valley of the river Werra was covered by diverse deciduous riparian forest (Kahlke, 2001c, 2006). Permanently humid locations showed softwood stands. Due to the duration of floods and the intervals between them, trees in areas endangered by high water were regularly damaged and hence largely low-growing. Sparse mixed woodland with tall trees and less undergrowth extended across more stable and relatively dry locations in the floodplain. Lush herbaceous vegetation grew on its often loose soils. Besides biotopes with woodland and shrub vegetation poor in species, the rocky slopes near the site also included open areas. Outside the Werra valley, park-like landscapes and sparsely wooded to open biotopes extended over large distances. All in all, a wide range of foodstuffs would have been available to the Untermassfeld bison.

3.2. Comparative fossil *Bison* material

The dietary traits of the Untermassfeld *B. menneri* series were compared with those of three *B.* (*Bison*) palaeopopulations of known stratigraphic position, which inhabited the same region, Central Germany, under various palaeoenvironmental conditions. Voigtstedt, the type locality of *B. schoetensacki voigtstedtensis*, produced a small sample. The Voigtstedt fauna reflects a warm period of the early Middle Pleistocene, most probably MIS 17 (Maul et al., 2007). Its fossil assemblage, with an age of about 0.7 Ma, reflects a landscape dominated by forest (Kahlke, 1965; Kahlke and Kaiser, 2011). A more extended series of *B. schoetensacki* dental remains comes from the slightly younger early Middle Pleistocene site of Süssenborn, most likely accumulated during MIS 16, with an age of c. 0.65 Ma (Kahlke et al., 2011). Although several climatic oscillations are represented in the Süssenborn sequence, its faunal list (Kahlke,

1969) and the feeding traits of the frequently recorded rhinoceros *Stephanorhinus hundsheimensis* (Kahlke and Kaiser, 2011) indicate a long-lasting dominance of open, continentally-influenced conditions. Finally, a sample from a population of large-bodied, robust *B. priscus* from the Late Pleistocene site of Taubach (Kahlke, 1977; Heinrich, 2003; Van Asperen and Kahlke, 2015), confidently assigned to MIS 5e, i.e. the Eemian interglacial (ca. 130-115 ka BP), is also taken into account. The Taubach deposits represent fully developed interglacial conditions (Kahlke, 1977).

Summary statistics for the datasets of the mentioned sites can be found in Tab. 1. The full dataset is provided in the Supplementary Information.

3.3. Methods

The position of the upper molars was determined following Gentry (1999). Wear stages were documented after Grant (1982) and Jones and Sadler (2012) for the mandibular dentition, and after Skinner and Kaisen (1947) for the maxillary dentition. Occlusal length (L) and greatest breadth (W), as well as a number of crown heights (mandibular teeth: H of protoconid, metaconid and entoconid above enamel-cement junction, H of valley above alveolus; maxillary teeth: H of mesostyle and paracone above enamel-cement junction) were measured. MNI values were calculated using numbers of left and right specimens, combined with age determinations and measurements of crown height. Below, the maxillary dentition will be indicated as P2-4 and M1-3 and the mandibular dentition as p2-4 and m1-3.

3.3.1. Mesowear analysis

Mesowear analysis is a well-validated method that indicates wear patterns over a large part of the lifespan of an individual animal (Fortelius and Solounias, 2000; Rivals et al., 2007b). Cusp shape and occlusal relief are correlated with diet in extant herbivores (Fortelius and Solounias, 2000). Tooth wear in browsers, which consume mainly low-abrasive foodstuffs, is dominated by sharp cusps and high relief. In contrast, grazers consume more grasses, often with a higher amount of grit, both of which contribute to an abrasion-dominated wear pattern with round or blunt cusps with low relief (Williams and Kay, 2001). Relatively small samples (n > 10) give reliable and significant results (Fortelius and Solounias, 2000).

Originally, the mesowear method was applied to the M2 only (Fortelius and Solounias, 2000). With the aim of increasing sample sizes for often small fossil assemblages, the method has since been successfully extended for certain taxonomic groups to include a wider range of dental elements (e.g. equids; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003). For bovids,

Franz-Odendaal and Kaiser (2003) tested two sets of scores for browsers (*Giraffa camelopardalis*) and mixed feeders (*Ovibos moschatus*, *Ourebia ourebi*), a four-tooth model including P4-M1-M2-M3, and a two tooth model including M2-M3, and compared these with an M2-only model. Unfortunately, they did not include grazing bovids in their analysis. They conclude that it is likely that the four-tooth model does not result in a consistent classification as compared with the M2-only model, especially in browsers. In contrast, the two-tooth model gave results that are consistent with the M2-only model. Similarly, Louys et al. (2011) found that in African antelopes, within the same trophic category mesowear scores tend to be different between the molars (M1-M2-M3). This is probably due to the larger degree of heterodonty in Artiodactyla than in Perissodactyla, as well as to the different timing of eruption across the dental elements.

Mandibular teeth are usually not included in mesowear analyses. However, Franz-Odendaal and Kaiser (2003) tested for significant differences in mesowear scores between M2 and m2 in browsing and mixed feeding bovids. Occlusal relief variables are not different in upper and lower second molars, but lower teeth tend to be more rounded than upper teeth. As a result, the wear differences between upper and lower teeth are more pronounced in mixed feeders than in browsers and grazers. In contrast, Louys et al. (2011) found few differences between upper and lower molars in the same tooth position in antelopes. Furthermore, they also found that mesowear scores for different lower molars were more similar than for the upper molars.

In these studies, mesowear on the lower molars was scored on the buccal side of the protoconid or hypoconid (whichever is sharper in a particular specimen) of p4-m3, since mesowear on the upper teeth is scored on the buccal side of the tooth. However, in terms of the direction of the chewing stroke, the upper buccal cusps are analogous to the lower lingual cusps. For this reason, Fraser et al. (2014) developed a mesowear scoring system for the lingual cusps of the lower second molars. They found few differences between mesowear scores for buccal upper and lingual lower second molar cusps, but lower molars were generally less rounded and could not differentiate reliably between browsers and mixed feeders. After addition of an extra category, high relief with highly rounded cusps, the correlation between the scores for the upper and lower second molars was stronger and differentiation improved.

In this study, mesowear was scored on the buccal cusps of P4 and M1-M3, and on both the buccal and the lingual cusps of p4 and m1-m3. The occlusal relief was scored as either high or low. Cusp shape was scored on the sharpest cusp as sharp, round or blunt. Teeth of very young and very old individuals, which tend to be characterised by more sharp and more blunt cusps respectively (wear stage IS and S4 of Skinner and Kaisen, 1947) were excluded to prevent any

influence extreme wear stages may have on the classification (Fortelius and Solounias, 2000; Rivals et al., 2007b). Scores for relief and cusp shape were combined into three overall mesowear scores for the upper molars (see Tab. 2): MWCS1 (Rivals et al., 2007b), MWCS2 (Kaiser et al., 2009) and MWCS3 (Fraser et al., 2014). For the lower molars, only MWCS1 and MWCS3 were computed.

3.3.2. Statistical analysis

The homogeneity of the samples was investigated using coefficients of variation (CVs, standard deviation / mean * 100) and Shapiro-Wilk normality tests of the lengths and widths of the teeth. Mann-Witney U tests were used to analyze differences in mesowear scores between different tooth positions and combinations of tooth positions, both within and between the upper and lower tooth rows. Due to the heterodont character of the cheek tooth row, only molars were tested. Specimens of the same individual (i.e. more or less complete maxillary tooth rows) were excluded. The Kruskal-Wallis test was used to analyse differences in mesowear scores between the samples. For those analyses where the Kruskal-Wallis test showed a significant difference, Mann-Whitney U-tests were used to investigate which samples had significantly different mesowear scores.

Using the comparative dataset for 64 extant ungulates, compiled by Fortelius and Solounias (2000), as a training set, a stepwise discriminant function analysis using Wilk's lambda was carried out with the Pleistocene bison samples as ungrouped specimens. Mesowear data for M2s of extant American wood bison (*B. bison athabascae*; Rivals et al., 2007a) and European bison (*B. bonasus*; Rivals, 2012) were also included as ungrouped specimens. Mesowear scores for the fossil assemblages can be found in Tab. 3. Because the mesowear scores are not independent (teeth with blunt cusps nearly always have low relief), variables entered in the analysis were % of teeth with high relief, % of teeth with sharp cusps and % of teeth with round cusps. Species with problematic dietary data (the 'mabra' species of Fortelius and Solounias, 2000) were left out of further analyses (cf. Kaiser and Solounias, 2003), and the conservative dietary classification of Fortelius and Solounias (2000) was used. The accuracy and robusticity of the differentiation between the dietary categories was investigated with jackknifed cross-validation models, using a single species as ungrouped case while using the other species in the original dataset as a generator set for calculating discriminant functions.

Hierarchical cluster analysis with complete linkage (furthest neighbour, squared Euclidean distance) was carried out on the same dataset to investigate which extant species are the most similar in their mesowear signature to the Pleistocene bison. All statistical analyses were

performed with the Statistical Package for the Social Sciences (SPSS) version 23. Information on the diet and preferred habitats of the comparative species were compiled from the IUCN red list website (http://www.iucnredlist.org/) and references listed there.

4. Results

Yablokov (1974) found that measurements of mammalian teeth are relatively variable, with CVs of 5 to 10. However, he notes that 'considerable deviations are possible' (Yablokov, 1974: 42). CVs are relatively high for the Untermassfeld *B. menneri* teeth, especially widths (Tab. 1). In addition, the M1 length (n=16, p=0.006; somewhat bimodal distribution), M2 width (n=17, p=0.034; somewhat bimodal distribution), and m2 length (n=25, p=0.023; one outlier) are not normally distributed. In contrast, most CVs for the Voigtstedt, Süssenborn and Taubach samples have CVs below 10, and only a single measurement, Taubach m2 length (n=20, p=0.007, somewhat bimodal distribution), is not normally distributed. However, on closer inspection, these bimodal distributions are primarily due to the relatively small dimensions of the teeth of younger individuals (wear stage AS after Skinner and Kaisen, 1947), especially at the occlusal surface.

Mann-Whitney U tests showed that mesowear scores (MWCS1, MWCS2 and MWCS3) are not significantly different between the different upper molar positions and between combinations of 2 or 3 upper molars positions for the fossil assemblages (see supplementary information). Likewise, lingual MWCS1 and MWCS3 were consistent between the different lower molar positions and combinations of 2 or 3 lower molar positions. Mesowear scores on the buccal side of the lower teeth were slightly less consistent. However, comparisons of the maxillary scores with the buccal mandibular scores show many significant differences. The maxillary scores are somewhat more consistent with the lingual mandibular scores, especially on MWCS1, but there are still many discrepancies, especially for multi-tooth combinations. Therefore we here use MWCS1 for M1, M2 and M3 combined to increase sample size.

The Voigtstedt sample was too small (n=4) to be included in the Kruskal-Wallis test. The significant result of the Kruskal-Wallis test (chi-square=16.018, p>0.000) showed the mesowear scores of two or more of the three assemblages differ significantly from each other. Subsequent Mann-Whitney U tests showed that the Süssenborn mesowear scores are significantly different from both the Untermassfeld (U=1259.0, p=0.001) and Taubach (U=990.0, p=0.002) samples, whereas the latter two samples are not significantly different.

The DFA (Fig. 4) has an overall correct reclassification rate of 75.0% (cross-validation: 75.0%). The samples from Untermassfeld (Figs. 3 and 6) and Taubach (Fig. 10) are classified as mixed

feeders, whilst the Voigtstedt (Fig. 7) and Süssenborn (Figs. 8 and 9) samples are classified as grazers. The position of the Untermassfeld sample is very similar to that of American wood bison and the four-horned antelope (*Tetracerus quadricornis*). The Taubach sample is located close to these, as well as to *Ourebia ourebi* and *Cervus unicolor*. The sample from Süssenborn falls very close to extant European bison. The sample from Voigtstedt clusters closely with nilgai (*Boselaphus tragocamelus*), roan antelope (*Hippotragus equines*), sable antelope (*H. niger*), mountain reedbuck (*Redunca fulvorufula*) and Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*). American plains bison, in contrast, is in the 'extreme grazer' part of the distribution.

In the cluster analysis (Fig. 5), the Untermassfeld and Taubach samples similarly fall in the same cluster as extant American woodland bison. The oribi (*Ourebia ourebi*), four-horned antelope (*Tetracerus quadricornis*) and sambar deer (*Cervus unicolor*) also fall in this cluster, as well as a range of other bovids and two camelids. The samples from Voigtstedt and Süssenborn cluster with extant European bison, as well as a similar range of bovids and cervids as in the DFA.

5. Discussion

5.1. Dietary spectrum of the Untermassfeld *Bison*

In accordance with some environmental indicators from the site (see section 3.1), Sher (1997) proposed that the Untermassfeld bison was a forest dweller, mainly based on the characteristics of its long legs (cf. Fig. 3). However, this is problematic, since the MNI of 50 (Kahlke, 2006 and new discoveries) represented in the Untermassfeld bison material seems to be too high to be accommodated in the spatially limited riparian forest near the site, especially since all these animals are thought to have died in a small number of flood events of relatively short duration or were killed by predators within the river valley (Kahlke 2001c, 2006; Kahlke and Gaudzinski, 2005).

If the Untermassfeld bison was a forest animal indeed, it can be expected to have incorporated a relatively high amount of browse in its diet. In bovids, a higher amount of browse in the diet tends to correlate with smaller body size, as well as lower degrees of sexual dimorphism (Bro-Jørgensen, 2008). However, besides being tall, the postcranial skeleton of the Untermassfeld bison is also markedly sexually dimorphic (Sher, 1997). Furthermore, in contrast to the characteristics of the horn cores and the extremities, the mandibular proportions of the Untermassfeld bison are similar to those of *B. priscus* from Siberia (Sher, 1997), pointing

towards grazer adaptations in the feeding apparatus (Flerov, 1979). Sher (1997) therefore questioned the validity of these mandibular features as ecological indicators.

Since extant bison range across a number of different habitats, including both open plains and closed habitats (see below), it is instructive to review modern bison diets. North American plains bison (*B. bison bison*) are predominantly grazers in all seasons. Grasses can account for 85-95% of the diet, especially in winter, while in summer, sedge intake increases. This is the case in shortgrass (e.g. Peden, 1976; Peden et al., 1974; Schwartz and Ellis, 1981), mixed-grass (e.g. Wydeven and Dahlgren, 1985; Plumb and Dodd, 1993) as well as tallgrass prairie (e.g. Coppedge et al., 1998; Kagima and Fairbanks, 2013). Although forbs and woody plants generally represent only a small part of the diet of modern plains bison, they provide important nutrients and may have been more important in the diet of fossil bison (Bergmann et al., 2015). Wood bison (*B. bison athabascae*), as well as plains bison and mixed herds living in the boreal zone, include a higher proportion of sedges in their diet, particularly in winter (42->95%, Reynolds et al., 1978; Campbell and Hinkes, 1983; Larter and Gates, 1991). In summer, the diet of some wood bison populations includes a larger proportion of browse, particularly willow (up to 95%; Waggoner and Hinkes, 1986; Larter and Gates, 1991). Lichen can also form an important part of the diet in autumn (up to 40%, Larter and Gates, 1991). This reflects the character of the available habitats, which consist of meadows interspersed with shrubs, mainly willow, and boreal forest (Reynolds et al., 1978; Waggoner and Hinkes, 1986). However, Larter and Gates (1991) argue that willow browsing is an opportunistic behaviour in which the bison engage only when their preferred food sources are in short supply.

It is unclear to what degree modern North American bison are able to survive in closed forests, and whether they would choose to occupy such a habitat if not forced by human factors, although use of open woodland is more common (Meagher, 1986). Prehistoric North American bison ranged from Alaska to southern Mexico, inhabiting habitats from semidesert to boreal forest (McDonald, 1981; Jiménez-Hidalgo et al., 2013).

The European bison or wisent (*B. bonasus*) was widely distributed in Europe during the Middle and Late Holocene (< 9.500 BP), covering a range of habitats including dense and open deciduous forest, open coniferous forest and forest steppe (Benecke, 2005). The species became extinct in the wild in 1926-1927 (Heptner et al., 1966; Pucek, 2004). A reintroduction programme, started in the 1950s, led to the establishment of 33 populations in Eastern Europe (Pucek, 2004; Kerley et al., 2012). Although these are presently confined to forested areas, and generally regarded as a forest species, there are indications that these forests represent a suboptimal habitat (Kerley et al., 2012).

Borowski et al. (1967: 368) summarised dietary information available on European bison from Russia and Poland (*B. bonasus bonasus*), stating that forbs make up 50-80% of the diet, with woody species providing 20-50%. Later studies on the population in Białowieża Primeval Forest showed that woody materials make up 6.7-13% of the diet of European bison, while forbs, grasses and sedges account for 85-95% (Gębczyńska et al., 1991: 309; Krasińska and Krasiński, 2007). Similar ratios were observed in the last wild Caucasus wisents (*B. bonasus caucasicus*) (Heptner et al., 1966). In the case of reintroduced Caucasus wisents, the intake of dwarf shrubs and forbs decreases with increasing snow thickness from 59% to 6% (Nemzev et al., 2003). While during the first half of winter 15% of their diet consists of bark and shoots, this increases to up to 79% during the second half. The Białowieża population, like most other populations of European bison, receive supplementary feeding in winter, consisting mainly of grasses. The winter diet of herds that have access to this supplementary fodder is dominated by forbs, grasses and sedges (82%), with woody vegetation making up 16% of the diet (Kowalczyk et al., 2011: 824). In contrast, Białowieża bison that have no access to supplementary fodder consume more woody material (up to 65%), with forbs, grasses and sedges accounting for 32% of the diet. Whilst these bison are able to survive on a diet with a high browse content, they show their preference for grazing by seeking out supplementary fodder, hay and crops from agricultural fields surrounding the forest (Kowalczyk et al., 2011).

Modern North American plains bison teeth have very low relief, with a very high average mesowear score of 2.73 and the highest proportion of blunt cusps in any modern grazer (Rivals et al., 2007a, Tab. 3). As expected from their dietary composition, this is one of the most extreme grazer signatures among modern ungulates. In contrast, modern wood bison teeth from Alberta (Canada) have an average mesowear score of 1.00 (Rivals et al., 2007a). This is the lowest mesowear score observed in any modern grazer.

Teeth from the Late Pleistocene *B. priscus*, *B. antiquus* and *Bison* sp. from North America have high relief and rounded cusps, with average mesowear scores around 1.05-1.31, which places them at the lower end of the grazing spectrum and the upper end of the mixed feeder and fruit browser spectrum (Rivals et al. 2007a). In comparison with modern wood bison teeth, the Late Pleistocene assemblages have considerably lower numbers of specimens with sharp cusps. The low mesowear scores of these fossil samples could indicate a highly varied diet with relatively high browse content, or to a low level of ingestion of abrasive dust particles, which could be related to wet environments or to feeding at a higher substrate level. Several studies suggest that these low mesowear scores are more likely due to high browse content in the diet than to low dust levels (Kaiser et al., 2013; Kubo and Yamada, 2014; Saarinen and Lister, 2016). A

population of plains bison from Big Bone Lick (northern Kentucky, USA), dated to around 1300-1650 AD, is characterised by higher occlusal relief than modern plains bison (Widga, 2006). Their dental wear is more similar to that of browsing animals, in accordance with the forested character of the site at that time.

For extant European bison, an average mesowear score of 1.55 was found, again pointing to a diet rich in browse (data modified after Rivals, 2012). Microwear analysis, another dietary indicator which reflects the food eaten over the last days to a few weeks, indicates that extant European bison is a mixed feeder, with dietary similarities to sympatric red deer (*Cervus elaphus*; Merceron et al., 2014). Seasonal variation in the availability of foodstuffs and supplementary hay feeding is reflected in variation in the microwear signature, ranging from browsing-dominated to grazing-dominated.

The mesowear of the Untermassfeld bison palaeopopulation has a mixed feeder profile that is very similar to that of North American wood bison (Tab. 3, Figs. 2 and 6), both in terms of the overall mesowear score and in the proportion of teeth with high vs. low relief and sharp, round and blunt cusps. Its diet was therefore less abrasive than that of modern European bison and much less abrasive than that of the American plains bison. In the DFA and cluster analysis, the Untermassfeld sample is also similar to the four-horned antelope (*Tetracerus quadricornis*), like wood bison a mixed feeder, in open woodland in South Asia.

5.2. Trends in western Palaearctic *Bison* feeding adaptation

The fact that the radiation and success of bison in the Pleistocene of Eurasia coincided with the opening up of forested habitats (Sher, 1997; Kahlke, 1999; Shapiro et al., 2004; Kahlke et al., 2011) and the development of extensive forest-steppe and steppe habitats (Guthrie, 1990; Kahlke, 1999), has, combined with their large body size and hypsodont teeth, been taken to indicate that in most types of bison a grazing lifestyle became an increasing part of their subsistence strategy (Flerov, 1979; Sala, 1987). Nevertheless, our study shows that one of the earliest and morphologically best known populations, *B. menneri* from Untermassfeld (1.05 Ma BP; Kahlke, 1997b, 2001c, 2006), was consuming a mixed feeder diet. Furthermore, the most recent of the palaeopopulations considered in this study, the one from Taubach (c. 130-115 ka BP), also consisted of mixed feeders (Tab. 3, Fig. 10). The Taubach mesowear signature is characterised by a slightly higher proportion of teeth with high relief and a slightly lower proportion of teeth with sharp cusps than that of Untermassfeld. It is close to the oribi (*Ourebia ourebi*), a mixed feeder in African grasslands, and the Asian sambar deer (*Cervus unicolor*), a browse-dominated mixed feeder in hillside forests. A number of other species in the same

cluster in the cluster analysis (*Ammodorcas clarkei, Camelus dromedarius, Lama glama, Litocranius walleri* and *Tragelaphus angasi*) are browsers or mixed feeders in relatively dry environments. Whilst *B. priscus* was a typical component of the steppe faunas of the later Pleistocene glacials, this species also thrived in the interglacial environments of the river valley at Taubach, characterised by numerous tectonic springs, supporting dense forest. As at Untermassfeld (see section 3.1), the water-permeable limestone subsoils of Middle Triassic age present outside the river valley at Taubach are thought to have been characterised by open landscapes.

In contrast, the Voigtstedt (c. 0.7 Ma BP) and Süssenborn (c. 0.65 Ma BP) bison consumed more grass (Tab. 3, Figs. 7-9). For Süssenborn, this was to be expected, given the open character of the environment at the site (Kahlke, 1969; Kahlke and Kaiser, 2011). The environment at Voigtstedt, however, is described as predominantly forested (Kahlke, 1965; Kahlke and Kaiser, 2011). The mesowear signatures of the Voigtstedt and Süssenborn samples are very similar, the main difference being a slightly higher proportion of teeth with rounded cusps in the Voigtstedt sample. The Voigtstedt sample clusters closely with a number of extant bovids. The nilgai (*Boselaphus tragocamelus*) is a mixed feeder in dry environments in India and incorporates a significant amount of browse in the diet. The mixed feeding mountain reedbuck (*Redunca fulvorufula*) and the grazers Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*), roan antelope (*Hippotragus equinus*) and sable antelope (*H. niger*) inhabit savannah habitats in Africa. It should be kept in mind that the Voigtstedt sample is very small (n=4), limiting the conclusions that can be drawn from the data. It is unusual to find such small numbers of bison remains (Kahlke, 1965) in a faunal assemblage of this age, which may indicate that these animals utilised the forest habitat around the site only occasionally and spent most of their time in more open habitats. The position of the Süssenborn sample is almost identical to that of extant European bison, indicating a preference for grazing but with a potentially significant role for browse in the diet.

So far, no mesowear data are available for other herbivore species from Untermassfeld. Data for Voigtstedt, Süssenborn and Taubach from Saarinen et al. (2016) are not comparable to our data due to a different method of calculating overall mesowear scores. However, it is clear from Saarinen et al. (2016) that on average, the same species have slightly lower mesowear scores at Voigtstedt than at Süssenborn. Rivals et al. (2009) obtained mesowear data for the Taubach bison using the same method as we did, and the overall mesowear scores for *B. priscus* are closely similar (our data: 0.90, Rivals et al. 2009: 1.00). Mesowear scores for other herbivore species from Taubach are relatively low (Rivals et al., 2009), reflecting a mostly closed

environment. Mesowear scores for the rhinoceros species from these three sites indicate a browser (Voigtstedt) to mixed feeder diet (Süssenborn and Taubach; Van Asperen and Kahlke, 2015). In each case, the rhinoceros species has a lower overall mesowear score than the bison species.

6. Conclusions

Although most herbivores prefer a diet with specific abrasive characteristics, most species have maintained considerable dietary flexibility and are able to survive on suboptimal diets if their preferred foodstuffs are not available in sufficient quantities. This has been observed in a range of fossils species, such as Neogene equids (Kaiser, 2003; Tütken et al., 2013) and bovids (Solounias and Hayek, 1993; Kostopoulos and Karakütük, 2015), and Pleistocene rhinocerotids (Van Asperen and Kahlke, 2015). Hypsodont artiodactyl genera such as *Bison*, in particular, to a degree are ecological generalists, able to survive on a wide range of diets (Feranec, 2007).

The general trend within the bison group appears to be in the direction of increased adaptation to open landscapes. Observations on Last Glacial bison population dynamics (Shapiro et al., 2004), with a decrease in population size detected for the warmer, more forested phase of MIS 3, support the conclusion that an increase in forest cover poses a disadvantage for bison nutrition. None of the palaeopopulations studied here can be regarded as true browsers. However, depending on the prevailing environmental conditions, browsing is to varying degrees part of the subsistence strategy of the considered fossil and extant populations.

In some populations, browsing was clearly an established part of the diet. While some aspects of the skeletal morphology of the Untermassfeld bison have been interpreted as reflecting a forest habitat, other characteristics of this assemblage do not fit with this picture (Sher, 1997; Kahlke, 2001c, 2006; Kahlke and Gaudzinski, 2005). The mesowear signature of the Untermassfeld bison is consistent with a varied diet that contained both a relatively large amount of browse and more abrasive foodstuffs. The Untermassfeld *B. menneri* herds will therefore have made use of the full range of environments near the site, from the more open parklands to the more densely vegetated patches. Since mesowear reflects average dietary abrasiveness over a period of months to years (Fortelius and Solounias, 2000; Rivals et al., 2007b), it is possible that certain habitats were more heavily used at certain times of the year, and that some of the mesowear signature is due to the use of less-desirable fall-back foods.

The mesowear pattern of the Untermassfeld bison palaoepolulation is very similar to that of extant American wood bison, which is a mixed feeder whose occasional high browse content is due to suboptimal food availability (Larter and Gates, 1991). Regardless of their low

mesowear score, American wood bison have a distinct preference for open habitats, and cannot be regarded as a true woodland species. Moreover, even *B. priscus*, often regarded as a typical steppe-adapted species thrived as a mixed feeder in the forested interglacial environment at Taubach. Several authors (e.g. Flerov, 1977) assign it to a distinct Late Pleistocene subspecies, *B. priscus mediator*, regarded as typical of European and Western Siberian temperate habitats (Kahlke, 1999). It is interesting to note that the Untermassfeld, Taubach and American wood bison are all relatively large representatives of the genus *Bison*, be it with different body proportions. Saarinen et al. (2016) suggest that lower population densities in closed environments could also lead to decreased intraspecific competition, allowing these animals to grow to larger size. However, this disregards the presence of and competition with other large herbivores. Rather, the large body size in these populations could indicate that a moderate amount of browse in the diet could benefit these ruminants by providing them with a wider range of dietary components and more stable year-round food availability.

In contrast, the grazer mesowear signature of the Voigtstedt bison indicates these animals likely did not regularly feed in the densely forested area around the site. Similarly, although the extant European bison typically occurs in forested areas, this is increasingly regarded as a refugee species inhabiting a suboptimal habitat (Kerley et al., 2012). This is reflected in the fact that its dental wear signature is characteristic for a mixed feeder to grazer (Rivals, 2012; Merceron et al., 2014), and in its behaviour, seeking out the forest edges, supplementary fodder and surrounding agricultural fields (Kowalczyk et al., 2011). It seems, therefore, that bison can adapt their diet to a certain extent to the habitats they live in, but will not become full-fledged browsers.

Neither the bison palaeopopulations from the late Early Pleistocene of Untermassfeld (*B. menneri*), from the early Middle Pleistocene of Voigtstedt (*B. schoetensacki* group) and from the Late Pleistocene of Taubach (*B. priscus* group), nor the extant American wood bison (*B. bison athabascae*) or the European bison (*B. bonasus*) are characterized by purely browsing subsistence strategies. Certain other Pleistocene large mammals, such as rhinos of the genus *Stephanorhinus*, were capable of covering the entire dietary range from browser to grazer without significant changes in hypsodonty (Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015). Whereas the generally highly hypsodont members of the bison group were more restricted in their dietary spectra, they retained sufficient flexibility to survive in a range of habitats throughout the Pleistocene and up to the present. All alleged 'wood bison' investigated here were clearly mixed feeders with relatively high tolerance (for the bison group) of a

suboptimal browsing diet. As far as we can tell, based on dietary traits there are no true 'wood bison', whether in the Pleistocene or in the present.

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References

Akbar Khan, M., Kostopoulos, D.S., Akhtar, M., Nazir, M., 2010. Bison remains from the Upper Siwaliks of Pakistan. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 258, 121-128.

Baygusheva, V.S., Titov, V.V., Timonina, G.I., Simakova, A.N., Tesakov, A.S., Van der Plicht, J., 2014. Mass Burial of Late Pleistocene Bisons in the Northeastern Part of the Sea of Azov Area (Port Katon, Rostov Region). Doklady Earth Sciences 454, 140-142.

Bellucci, L., Sardella, R., Rook, L., 2015. Large mammal biochronology framework in Europe at Jaramillo: The Epivillafranchian as a formal biochron. Quaternary International 389, 84-89.

Benecke, N., 2005. The Holocene distribution of European bison – the archaeozoological record. Munibe (Antropologia-Arkeologia) 57, 421-428.

Bergmann, G.T., Craine, J.M., Robeson II, M.S., Fierer, N., 2015. Seasonal shifts in diet and gut microbiota of the American bison (*Bison bison*). PLoS ONE 10, e0142409.

Borowski, S., Krasiński, Z., Miłkowski, L., 1967. Food and role of the European bison in forest ecosystems. Acta Theriologica 12, 367-376.

Bro-Jørgensen, J., 2008. Dense habitats selecting for small body size: a comparative study on bovids. Oikos 117, 729-737.

Brugal, J.-P., Croitor, R., 2007. Evolution, ecology and biochronology of herbivore associations in Europe during the last 3 million years. Quaternaire 18, 129-152.

Bukhsianidze, M., 2005. The fossil Bovidae of Dmanisi. Ph.D. Thesis, International Doctorate "Environmental, Humans and Compartmental Dynamics", Universitá degli Studi di Ferrara, Italy.

Burchak-Abramovich, N.I., Vekua, A.K., 1994. Novyj predstavitel pleistocennovych bykov iz vostochnoj Gruzii. Voprosy Teriologii, Paleoteriologija, 253-261. (n.v.; in Russian)

Campbell, B.H., Hinkes, M., 1983. Winter diets and habitat use of Alaska bison after wildfire. Wildlife Society Bulletin 11, 16-21.

Coppedge, B.R., Leslie Jr., D.M., Shaw, J.H., 1998. Botanical composition of bison diets on tallgrass prairie in Oklahoma. Journal of Range Management 51, 379-382.

Crégut-Bonnoure, E., 2006. European Ovibovini, Ovini and Caprini (Caprinae, Mammalia) from the Plio-Pleistocene: new interpretations, in: Kahlke, R.-D., Maul, L. C., Mazza, P. (Eds.), Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations. Volume I. Proceedings of the 18th International Senckenberg Conference (VI International Palaeontological Colloquium in Weimar). Courier Forschungsinstitut Senckenberg 256, 139-158.

Croitor, R., Brugal, J.-P., 2007. New insights concerning Early Pleistocene cervids and bovids in Europe: dispersal and correlation, in: Kahlke, R.-D., Maul, L. C., Mazza, P. (Eds.), Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations. Volume II. Proceedings of the 18th International Senckenberg Conference (VI

International Palaeontological Colloquium in Weimar). Courier Forschungsinstitut Senckenberg 259, 47-59.

De Giuli, C., Masini, F., Torre, D., 1987. The Latest Villafranchian Faunas in Italy: the Pirro Nord Fauna. Palaeontographia Italica 74, 51-62.

Dubrovo, I.A., Burchak-Abramovich, N.I., 1986. New Data on the Evolution of Bovine of the Tribe Bovini. Quartärpaläontologie 6, 13-21.

Duvernois, M.-P., 1992. Mise au point sur le genre *Leptobos* (Mammalia, Artiodactyla, Bovidae); Implications biostratigraphiques et phylogénétiques. Geobios 25, 155-166.

Duvernois, M.-P., Guérin, C., 1989. Les Bovidae (Mammalia, Artiodactyla) du Villafranchien supérieur d'Europe occidentale. Geobios 22, 339-379.

Ellenberg, J., Kahlke, R.-D., 1997. Die quartärgeologische Entwicklung des mittleren Werratals und der Bau der unterpleistozänen Komplexfundstelle Untermaßfeld, in: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen), Teil 1. Monographien des Römisch-Germanischen Zentralmuseums Mainz 40, 29-62.

Feranec, R.S., 2007. Ecological generalization during adaptive radiation: evidence from Neogene mammals. Evolutionary Ecology Research 9, 555-577.

Flerov, K.K., 1972. Drevnejshie predstaviteli i istorija roda *Bison*. Nauka, Novosibirsk. (in Russian)

Flerov, C.C., 1975. Die *Bison*-Reste aus den Travertinen von Weimar-Ehringsdorf. Abhandlungen des Zentralen geologischen Instituts, Paläontologische Abhandlungen 23, 163-200.

Flerov, C.C., 1977. Die fossilen Bisonreste von Taubach und ihre Stellung in der Entwicklungsgeschichte der Gattung *Bison* in Europa. Quartärpaläontologie 2, 179-208, pls. XI-XV.

Flerov, C.C., 1979. Sistemaika i evoljuzija, in: Sokolov, V.E. (Ed.): Zubr. Morfologija, sistematika, evoljuzija. Nauka, Moskva, pp. 9-127. (in Russian).

Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. American Museum Novitates 3301, 1-36.

Fortelius, M., Eronen, J., Jernvall, J., Liu, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z., Zhou, L., 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. Evolutionary Ecology Research 4, 1005-1016.

Franz-Odendaal, T.A., Kaiser, T.M., 2003. Differential mesowear in the maxillary and mandibular cheek dentition of some ruminants (Artiodactyla). Annales Zoologici Fennici 40, 395-410.

Fraser, D., Zybutz, T., Lightner, E., Theodor, J.M., 2014. Ruminant mandibular tooth mesowear: a new scheme for increasing paleoecological sample sizes. Journal of Zoology 294, 41-48.

Gaudzinski, S., 1992. Wisentjäger in Wallertheim. Zur Taphonomie einer mittelpaläolithischen Freilandfundstelle in Rheinhessen. Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz 39, 245-423.

Gębczyńska, Z., Gębczyński, M., Martynowicz, E., 1991. Food eaten by the free-living European bison in Białowieża Forest. Acta Theriologica 36, 307-313.

Gentry, A.W., 1999. Fossil ruminants (Mammalia, Artiodactyla) from Westbury Cave, in: Andrews, P., Cook, J., Currant, A., Stringer, C. (Eds.), Westbury Cave: the Natural History Museum excavations 1976-1984. Bristol, Western Academic and Specialist Press, 139-174.

Grant, A., 1982. The use of tooth wear as a guide to the age of domestic ungulates, in: Wilson, R., Grigson, C., Payne, S. (Eds.), Ageing and sexing animal bones from archaeological sites. British Archaeology Reports, British Series 109, 91-108.

Guthrie, R.D., 1990. Frozen fauna of the mammoth steppe, the story of Blue Babe. Chicago, University of Chicago Press.

Heinrich, W.-D., 2003. Rodentier-Biostratigraphie und Altersstellung pleistozäner Säugetier-Fundstätten Mitteldeutschlands, in: Burdukiewicz, J.M., Fiedler, L., Heinrich, W.-D., Justus, A., Brühl, E. (Eds.), Erkenntnisjäger. Kultur und Umwelt des frühen Menschen. Festschrift für Dietrich Mania. Veröffentlichungen des Landesmuseums für Archäologie Sachsen-Anhalt 57/I, 237-245.

Hemmer, H., 2001. Die Feliden aus dem Epivillafranchium von Untermaßfeld, in: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen), Teil 3. Monographien des Römisch-Germanischen Zentralmuseums Mainz 40, 699-782.

Heptner, V.G., Nasimovič, A.A., Bannikov, A.G., 1966. Die Säugetiere der Sowjetunion. Band I: Paarhufer und Unpaarhufer. Gustav Fischer, Jena.

Hoffecker, J.F., Baryshnikov, G., Potapova, O., 1991. Vertebrate remains from the Mousterian Site of Il'skaya I (Northern Caucasus, U.S.S.R.): New Analysis and Interpretation. Journal of Archaeological Science 18, 113-147.

Jernvall, J., Fortelius, M., 2002. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. Nature 417, 538-540.

Jiménez-Hidalgo, E., Cabrera-Pérez, L., MacFadden, B.J., Guerrero-Arenas, R., 2013. First record of *Bison antiquus* from the Late Pleistocene of southern Mexico. Journal of South American Earth Sciences 42, 83-90.

Jones, G.G., Sadler, P., 2012. A review of published sources for age at death in cattle. Environmental Archaeology 17, 1-10.

Kagima, B., Fairbanks, W.S., 2013. Habitat selection and diet composition of reintroduced native ungulates in a fire-managed tallgrass prairie reconstruction. Ecological Restoration 31, 79-88.

Kahlke, H.-D. (Ed.), 1965. Das Pleistozän von Voigtstedt. Paläontologische Abhandlungen A II, 221-692.

Kahlke, H.-D. (Ed.), 1969. Das Pleistozän von Süßenborn. Paläontologische Abhandlungen A III, 367-788.

Kahlke, H.-D. (Ed.), 1977. Das Pleistozän von Taubach bei Weimar. Quartärpaläontologie 2, 1-509.

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

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

Kahlke, R.-D., 1999. The History of the Origin, Evolution and Dispersal of the Late Pleistocene Mammuthus-Coelodonta Faunal Complex in Eurasia (Large Mammals). Fenske Companies, Rapid City.

Kahlke, R.-D. (Ed.), 2001a. Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 2. Monographien des Römisch-Germanischen Zentralmuseums Mainz 40, I-VIII, 419-698.

Kahlke, R.-D. (Ed.), 2001b. Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Teil 3. Monographien des Römisch-Germanischen Zentralmuseums Mainz 40, I-VI, 699-1030.

Kahlke, R.-D., 2001c. Die unterpleistozäne Komplexfundstelle Untermaßfeld – Zusammenfassung des Kenntnisstandes sowie synthetische Betrachtungen zu Genesemodell, Paläoökologie und Stratigraphie, in: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen), Teil 3. Monographien des Römisch-Germanischen Zentralmuseums Mainz 40, 931-1030.

Kahlke, R.-D., 2006. Untermassfeld - A late Early Pleistocene (Epivillafranchian) fossil site near Meiningen (Thuringia, Germany) and its position in the development of the European mammal fauna. British Archaeological Reports, International Series 1578, 1-141.

Kahlke, R.-D., 2007. Late Early Pleistocene European large mammals and the concept of an Epivillafranchian biochron, in: Kahlke, R.-D., Maul, L. C., Mazza, P. (Eds.), Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations. Volume II. Proceedings of the 18th International Senckenberg Conference (VI International Palaeontological Colloquium in Weimar). Courier Forschungsinstitut Senckenberg 259, 265-278.

Kahlke, R.-D., 2009. Das Leichenfeld im Werratal. Europäischer Faunenwandel vor einer Million Jahren. Natur und Museum 139, 146-159.

Kahlke, R.-D., 2014. The origin of Eurasian Mammoth Faunas (*Mammuthus-Coelodonta* Faunal Complex). Quaternary Science Reviews 96, 32-49.

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

Kahlke, R.-D., Kaiser, T.M., 2011. Generalism as a subsistence strategy: advantages and limitations of the highly flexible feeding traits of Pleistocene *Stephanorhinus hundsheimensis* (Rhinocerotidae, Mammalia). Quaternary Science Reviews 30, 2250-2261.

Kahlke, R.-D., Lacombat, F., 2008. The earliest immigration of woolly rhinoceros (*Coelodonta tologoijensis*, Rhinocerotidae, Mammalia) into Europe and its adaptive evolution in Palaearctic cold stage mammal faunas. Quaternary Science Reviews 27, 1951-1961.

Kahlke, R.-D., García, N., Kostopoulos, D.S., Lacombat, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. Quaternary Science Reviews 30, 1368-1395.

Kaiser, T.M., 2003. The dietary regimes of two contemporaneous populations of *Hippotherium primigenium* (Perissodactyla, Equidae) from the Vallesian (Upper Miocene) of Southern Germany. Palaeogeography, Palaeoclimatology, Palaeoecology 1998, 381-402.

Kaiser, T. M., Fortelius, M., 2003. Differential mesowear in occluding upper and lower molars: opening mesowear analysis for lower molars and premolars in hypsodont horses. Journal of Morphology 258, 67-83.

Kaiser, T. M., Solounias, N., 2003. Extending the tooth mesowear method to extinct and extant equids. Geodiversitas 25, 321-345.

Kaiser, T. M., Brasch, J., Castell, J.C., Schulz, E., Clauss, M., 2009. Tooth wear in captive wild ruminant species differs from that of free-ranging conspecifics. Mammalian Biology 74, 425-437.

Kaiser, T.M., Müller, D.W.H., Fortelius, M., Schulz, E., Codron, D., Clauss, M., 2013. Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. Mammal Review 43, 34-46.

Kerley, G.I.H., Kowalczyk, R., Cromsigt, J.P.G.M., 2012. Conservation implications of the refugee species concept and the European bison: king of the forest of refugee in a marginal habitat? Ecography 35, 519-529.

Kierdorf U., Kahlke, R.-D., Flohr, S., 2012. Healed fracture of the tibia in a bison (*Bison menneri* Sher, 1997) from the late Early Pleistocene site of Untermassfeld (Thuringia, Germany). International Journal of Paleopathology 2, 19-24.

Kostopoulos, D.S., 1997. The Plio-Pleistocene artidactyls (Vertebrata, Mammalia) of Macedonia. 1. The fossiliferous site Apollonia-1, Mygdonia basin of Greece. Geodiversitas 19, 845-875.

Kostopoulos, D.S., 2006. Greek bovids through time. Hellenic Journal of Geosciences 41, 141-152.

Kostopoulos, D.S., Karakütük, S., 2015. Late Miocene bovids from Şerefköy-2 (SW Turkey) and their position within the sub-Paratethyan biogeographic province. Acta Palaeontologica Polonica 60, 49-66.

Kowalczyk, R., Taberlet, P., Coissac, E., Valentini, A., Miquel, C., Kamiński, T., Wójcik, J.M., 2011. Influence of management practices on large herbivore diet – Case of European bison in Białowieża Primeval Forest (Poland). Forest Ecology and Management 261, 821-828.

Krasińska, M., Krasiński, Z.A., 2007. European bison, The nature monograph. Mammal Research Institute, Polish Academy of Sciences, Białowieża.

Kubo, M.O., Yamada, E., 2014. The inter-relationship between dietary and environmental properties and tooth wear: comparisons of mesowear, molar wear rate, and hypsodonty index of extant sika deer populations. PLoS ONE 9, e90745.

Larter, N.C., Gates, C.C., 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. Canadian Journal of Zoology 69, 2677-2685.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta18O$ records. Paleoceanography 20, PA1003.

Lister, A.M., 2004. The impact of Quaternary Ice Ages on mammalian evolution. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 359, 221-241.

Lister, A.M., Sher, A.V., 2015. Evolution and dispersal of mammoths across the Northern Hemisphere. Science 350, 805-809.

Lister, A.M., Sher, A.V., van Essen, H., Wei, G., 2005. The pattern and process of mammoth evolution in Eurasia. Quaternary International 126-128, 49-64.

Liu, L., Puolamäki, K., Eronen, J.T., Ataabadi, M.M., Hernesniemi, E., Fortelius, M., 2012. Dental functional traits of mammals resolve productivity in terrestrial ecosystems past and present. Proceedings of the Royal Society B, Biological Sciences 279, 2793-2799.

Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C.P.E., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, G., Martinez-Navarro, B., Mouskhelishvili, A., Nioradze, M., Rook, L., 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. Nature 449, 305-310.

Louys, J., Meloro, C., Elton, S., Ditchfield, P., Bishop, L.C., 2011. Mesowear as a means of determining diets in African antelopes. Journal of Archaeological Science 38, 1485-1495.

Maniakas, I., Kostopoulos, D.S., 2017. Morphometric-palaeoecological discrimination between *Bison* populations of the Western Palaearctic. Geobios 50, 155-171.

Maniakas, I., Kahlke, R.-D., Kostopoulos, D.S., 2014. Morphometric-palaeoecological discrimination between two Epivillafranchian *Bison* populations of the Western Palaearctic, in: Delfino, M., Carnevale, G., Pavia, M. (Eds.), XII Annual Meeting of the European Association of Vertebrate Palaeontologists, Abstract Book and Field Trip Guide, Torino, Italy. Societá Paleontologica Italiana, Torino, p. 101.

Martínez-Navarro, B., Ros-Montoya, S., Espigares, M.P., Palmqvist, P., 2011. Presence of the Asian origin Bovini, *Hemibos* sp. aff. *Hemibos gracilis* and *Bison* sp., at the early Pleistocene site of Venta Micena (Orce, Spain). Quaternary International 243, 54-60.

Masini, F., 1989. I Bovini villafranchiani dell'Italia. Tesi di Dottorato in Palentologia, Università degli Studi di Modena e Reggio Emilia.

Masini, F., Sala, F., 2007. Large- and small-mammal distribution patterns and chronostratigraphic boundaries from the Late Pliocene to the Middle Pleistocene of the Italian peninsula. Quaternary International 160, 43-56.

Maul, L.C., Heinrich, W.-D., Parfitt, S.A., Paunescu, A.-C., 2007. Comment on the correlation between magnetostratigraphy and the evolution of *Microtus* (Arvicolidae, Rodentia, Mammalia) during the Early and early Middle Pleistocene, in: Kahlke, R.-D., Maul, L. C., Mazza, P. (Eds.), Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations. Volume II. Proceedings of the 18th International

Senckenberg Conference (VI International Palaeontological Colloquium in Weimar). Courier Forschungsinstitut Senckenberg 259, 243-263.

McDonald, J. N., 1981. North American bison: their classification and evolution. University of California Press, Berkeley.

Mead, J.I., Jin, C., Wei, G., Sun, C., Wang, X., Swift, S.L., Zheng, L., 2014. New data on *Leptobos crassus* (Artiodactyla, Bovidae) from Renzidong Cave, Early Pleistocene (Nihewanian) of Anhui, China, and an overview of the genus. Quaternary International 354, 139-146.

Meagher, M., 1986. *Bison bison*. Mammalian Species 266.

Merceron, G., Hofman-Kamińska, E., Kowalczyk, R., 2014. 3D dental microwear texture analysis of feeding habits of sympatric ruminants in the Białowieża Primeval Forest, Poland. Forest Ecology and Management 328, 262-269.

Nemzev, A.S., Puzačenko, A.Ju., Rautian, G.S., 2003. Ekologija, in: Nemzev, A.S., Rautian, G.S., Puzačenko, A.Ju., Sipko, T.P., Kalabushkin, B.A., Mironenko, I.V. (Eds.), Zubr na Kavkaze. Majkop, Moskva, pp. 150-213. (in Russian)

Peden, D.G., 1976. Botanical composition of bison diets on shortgrass plains. The American Midland Naturalist 96, 225-229.

Peden, D.G., Van Dyne, G.M., Rice, R.W., Hansen, R.M., 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. Journal of Applied Ecology 11, 489-497.

Plumb, G.E., Dodd, J.L., 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecological Applications 3, 631-643.

Pucek, Z. (ed.), 2004: European bison, Status survey and conservation action plan. IUCN, Cambridge.

Reynolds, H.W., Hansen, R.M., Peden, D.G., 1978. Diets of the Slave River lowland bison herd, Northwest Territories, Canada. Journal of Wildlife Management 42, 581-590.

Rivals, F., 2012. Ungulate feeding ecology and middle Pleistocene paleoenviroments at Hundsheim and Deutsch-Altenburg 1 (eastern Austria). Palaeogeography, Palaeoclimatology, Palaeoecology 317-318, 27-31.

Rivals, F., Solounias, N., Mihlbachler, M.C., 2007a. Evidence for geographic variation in the diets of late Pleistocene and early Holocene *Bison* in North America, and differences from the diets of recent *Bison*. Quaternary Research 68, 338-346.

Rivals, F., Mihlbachler, M.C., Solounias, N., 2007b. Effect of ontogenetic-age distribution in fossil and modern samples on the interpretation of ungulate paleodiets using the mesowear method. Journal of Vertebrate Paleontology 27, 763-767.

Rivals, F., Schulz, E., Kaiser, T.M., 2009. Late and middle Pleistocene ungulate dietary diversity in Western Europe indicate variations of Neanderthal paleoenvironments through time and space. Quaternary Science Reviews 28, 3388-3400.

Rivals, F., Semprebon, G., Lister, A., 2012. An examination of dietary diversity patterns in Pleistocene proboscideans (*Mammuthus*, *Palaeoloxodon*, and *Mammut*) from Europe and North America as revealed by dental microwear. Quaternary International 255, 188-195.

Saarinen, J., Lister, A.M., 2016. Dental mesowear reflects local vegetation and niche separation in Pleistocene proboscideans from Britain. Journal of Quaternary Science 31, 799-808.

Saarinen, J., Eronen, J., Fortelius, M., Seppä, H., Lister, A.M., 2016. Patterns of diet and body mass of large ungulates from the Pleistocene of Western Europe, and their relation to vegetation. Palaeontologia Electronica 19.3.32A.

Sala, B., 1987. *Bison schoetensacki* Freud. from Isernia la Pineta (early Mid-Pleistocene – Italy) and revision of the european species of bison. Palaeontographia Italica 74, 113-170.

Schwartz, C.C., Ellis, J.E., 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. Journal of Applied Ecology 18, 343-353.

Shapiro, B., Drummond, A.J., Rambaut, A., Wilson, M.C., Matheus, P.E., Sher, A.V., Pybus, O.G., Gilbert, M.T.P., Barnes, I., Binladen, J., Willerslev, E., Hansen, A.J., Baryshnikov, G.F., Burns, J.A., Davydov, S., Driver, J.C., Froese, D.G., Harington, C.R., Keddie, G., Kosintsev, P., Kunz, M.L., Martin, L.D., Stephenson, R.O., Storer, J., Tedford, R., Zimov, S., Cooper, A., 2004. Rise and fall of the Beringian steppe bison. Science 306, 1561-1565.

Sher, A.V., 1997. An Early Quaternary Bison population from Untermaßfeld: *Bison menneri* sp. nov., in: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen), Teil 1. Monographien des Römisch-Germanischen Zentralmuseums Mainz 40, 101-180.

Skinner, M.F., Kaisen, O.C., 1947. The fossil *Bison* of Alaska and preliminary revision of the genus. Bulletin of the American Museum of Natural History 89, 123-256.

Solounias, N., Hayek, L.-A.C., 1993. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. Journal of Zoology 229, 421-445.

Stephan, E., Uerpmann, H.-P., Cramer, B., 2001, Paläotemperaturbestimmungen nach δ^{18}O-Werten von Equiden-Resten aus dem Unterpleistozän von Untermaßfeld, in: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen), Teil 3. Monographien des Römisch-Germanischen Zentralmuseums Mainz 40, 917-930.

Tütken, T., Kaiser, T.M., Vennemann, T., Merceron, G., 2013. Opportunistic feeding strategy for the earliest Old World hypsodont equids: evidence from stable isotope and dental wear proxies. PLoS One 8, e74463.

Van Asperen, E.N., Kahlke, R.-D., 2015. Dietary variation and overlap in Central and Northwest European *Stephanorhinus kirchbergensis* and *S. hemitoechus* (Rhinocerotidae, Mammalia) influenced by habitat diversity. Quaternary Science Reviews 107, 47-61.

Waggoner, V., Hinkes, M., 1986. Summer and fall browse utilization by an Alaskan bison herd. Journal of Wildlife Management 50, 322-324.

Widga, C., 2006. Niche variability in late Holocene bison: a perspective from Big Bone Lick, KY. Journal of Archaeological Science 33, 1237-1255.

Williams, S.H., Kay, R.F., 2001. A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. Journal of Mammalian Evolution 8, 207-229.

Wydeven, A.P., Dahlgren, R.B., 1985. Ungulate habitat relationships in Wind Cave National Park. Journal of Wildlife Management 49, 805-813.

Yablokov, A.V., 1974. Variability of mammals. New Delhi, Amerind.

Table 1. Summary statistics for the *Bison* dental assemblages from Untermassfeld (UM; 1.05 Ma BP), Voigtstedt (VO; c. 0.7 Ma BP), Süssenborn (SU; c. 0.65 Ma BP) and Taubach (TA; c. 130-115 ka BP)

UM	Length				Width				Buccal mesowear				Lingual mesowear		
Element	mean	sd	CV	n	mean	sd	CV	n	MWCS1	MWCS2	MWCS3	n	MWCS1	MWCS3	n
P2	18.1	1.2	6.6	8	13.7	0.5	3.6	7							
P3	18.2	1.6	8.8	10	16.4	2.0	12.2	10							
P4	18.1	2.0	11.0	8	18.7	2.6	13.9	8	1.00	1.00	2.00	5			
M1	26.9	3.1	11.5	16	20.7	2.9	14.0	16	1.07	1.60	2.33	15			
M2	31.2	1.9	6.1	17	20.6	3.2	15.5	17	0.80	0.80	1.87	15			
M3	31.7	1.2	3.8	13	21.0	2.1	10.0	13	0.75	0.88	1.88	8			
p2	12.2	1.0	8.2	14	8.6	1.0	11.6	14							
p3	20.0	1.7	8.5	15	11.0	1.0	9.1	16							
p4	22.2	1.3	5.9	21	12.6	1.0	7.9	21	1.05		2.21	19	1.24	2.53	17
m1	26.7	2.5	9.4	21	15.2	1.8	11.8	23	1.61		3.26	23	1.00	2.05	19
m2	29.3	2.6	8.9	25	16.1	1.6	9.9	25	1.24		2.52	25	1.00	2.14	22
m3	41.4	2.1	5.1	20	16.4	2.6	15.9	23	1.26		2.53	19	1.00	2.00	17
VO	**Length**				**Width**				**Buccal mesowear**				**Lingual mesowear**		
Element	mean	sd	CV	n	mean	sd	CV	n	MWCS1	MWCS2	MWCS3	n	MWCS1	MWCS3	n
P2	18.8	1.5	8.0	2	13.4	0.1	0.7	2							
P3	20.3	3.2	15.8	2	16.6	2.0	12.0	2							
P4	17.6	1.6	9.1	3					1.00	1.00	2.00	2			
M1	27.8	1.4	5.0	2	24.3	4.5	18.5	2	1.50	2.00	3.00	2			
M2	31.2			1	21.3				1.00	1.00	2.00	1			
M3	31.0			1	25.8			1	1.00	1.00	2.00	1			
p2	12.6			1	9.3			1							
p3	18.9	0.1	0.5	2	12.1	0.8	6.6	2							
p4	21.7	1.6	7.4	2	13.4	0.6	4.5	2	1.50		3.00	2	1.00	2.00	1
m1	26.3	2.1	8.0	4	16.5	1.6	9.7	4	1.50		3.25	4	1.00	2.33	3
m2	30.4	1.6	5.3	2	18.0	0.8	4.4	2							
m3	42.7	0.9	2.1	4	16.9	0.8	4.7	4							
SU	**Length**				**Width**				**Buccal mesowear**				**Lingual mesowear**		
Element	mean	sd	CV	n	mean	sd	CV	n	MWCS1	MWCS2	MWCS3	n	MWCS1	MWCS3	n

TA	Length				Width				Buccal mesowear				Lingual mesowear		
Element	mean	sd	CV	n	mean	sd	CV	n	MWCS1	MWCS2	MWCS3	n	MWCS1	MWCS3	n
P2	18.6			1	12.1			1							
P3	18.8	0.6	3.2	4	17.7	1.0	5.6	4							
P4	17.3	1.5	8.7	4	18.6	0.4	2.2	3	1.50	2.00	3.00	4			
M1	30.1	2.0	6.6	28	21.6	2.6	12.0	25	1.32	1.56	2.64	25			
M2	32.1	1.8	5.6	43	22.1	1.9	8.6	37	1.28	1.59	2.69	39			
M3	34.2	2.2	6.4	30	23.6	2.2	9.3	26	1.23	1.43	2.50	30			
p2	12.7			1	9.5			1							
p3	21.0	1.3	6.2	6	11.8	0.9	7.6	6							
p4	23.2	2.0	8.6	2	12.5	0.1	0.8	2	1.50		3.50	2	1.50	3.00	2
m1	26.6	1.0	3.8	8	16.0	1.3	8.1	8	1.67		3.11	9	1.33	2.67	9
m2	31.0	1.9	6.1	30	16.2	1.2	7.4	31	1.94		3.65	31	1.19	2.88	32
m3	43.5	2.4	5.5	17	16.5	1.1	6.7	18	2.11		3.89	18	1.22	2.78	18
TA	Length				Width				Buccal mesowear				Lingual mesowear		
Element	mean	sd	CV	n	mean	sd	CV	n	MWCS1	MWCS2	MWCS3	n	MWCS1	MWCS3	n
P2	22.1	1.5	6.8	4	16.9	1.0	5.9	4							
P3	21.4	1.3	6.1	5	19.0	1.4	7.4	5							
P4	21.9	2.2	10.0	8	22.2	1.8	8.1	7							
M1	33.0	1.5	4.5	15	23.3	2.1	9.0	15	0.93	1.07	2.07	14			
M2	35.9	1.4	3.9	14	25.5	2.4	9.4	14	0.85	0.92	2.00	13			
M3	38.1	1.7	4.5	4	24.2	2.6	10.7	4	1.00	1.00	2.33	3			
p2	13.0			1	9.6			1							
p3	21.3	0.7	3.3	6	12.9	0.9	7.0	6							
p4	24.3	1.2	4.9	7	14.6	1.4	9.6	7	1.14		2.29	7	1.86	3.14	7
m1	29.6	2.1	7.1	15	17.8	1.5	8.4	16	1.50		2.94	16	1.19	2.50	16
m2	34.2	1.2	3.5	20	18.7	1.0	5.3	20	1.40		2.85	20	1.06	2.25	16
m3	48.6	2.8	5.8	18	18.8	1.4	7.4	19	1.21		2.53	19	1.06	2.35	17

Table 2. Overall mesowear scores combining scores for relief and cusp shape

Combined score	Score	Relief	Cusp shape
MWCS1 (Rivals et al. 2007b)	0	High	Sharp
	1	High	Round
	2	Low	Round
	3	Low or negative	Blunt
MWCS2 (Kaiser et al. 2009)	0	High	Sharp
	1	High	Round
	2	Low	Sharp
	3	Low	Round
	4	Low or negative	Blunt
MWCS3 (Fraser et al. 2014)	1	High	Sharp
	2	High	Round
	3	High	Very round
	4	Low	Round
	5	Low or negative	Blunt

Table 3. Overall mesowear scores and mesowear variables for M1-M2-M3 for the fossil assemblages and modern bison populations

Site	MWCS1			Mesowear variables			
	mean	n	MNI	%high	%sharp	%round	n
Untermassfeld	0.90	38	29	82.5	23.1	79.9	40
Voigtstedt	1.25	4	4	75.0	0.0	100.0	4
Süssenborn	1.28	94	22	74.5	1.1	95.7	94
Taubach	0.90[1]	30	8	90.9	20.0	80.0	33
American plains bison[2]	2.73	15	15	0.0	0.0	26.6	15
American wood bison[3]	1.00	11	11	90.9	27.3	72.7	11
European bison[4]	1.55	7	7	71.4	0.0	100.0	7

[1] This is comparable to the findings of Rivals et al., 2009

[2] Data from Fortelius and Solounias, 2000; Rivals et al., 2007a (extant *Bison bison bison*)

[3] Data from Rivals et al., 2007a; Rivals pers. comm. March 2016 (extant *Bison bison athabascae*)

[4] Data from Rivals, 2012; Rivals pers. comm. March 2016 (extant *Bison bonasus*)

Fig. 1. Left: Sites with remains of Pleistocene *Bison* palaeopopulations mentioned in the text. Asterisk: Untermassfeld; 1. Venta Micena; 2. Pirro Nord; 3. Apollonia-1; 4. Dmanisi; 5. Voigtstedt; 6. Süssenborn; 7. Taubach. Right: Untermassfeld, part of the excavation plan of the SW area of the fossil site (squares Q 47-48, Q 157-158, Q 194-195), including a partial skeleton of *B. menneri* with complete skull (see Figure 2) among remains of other species.
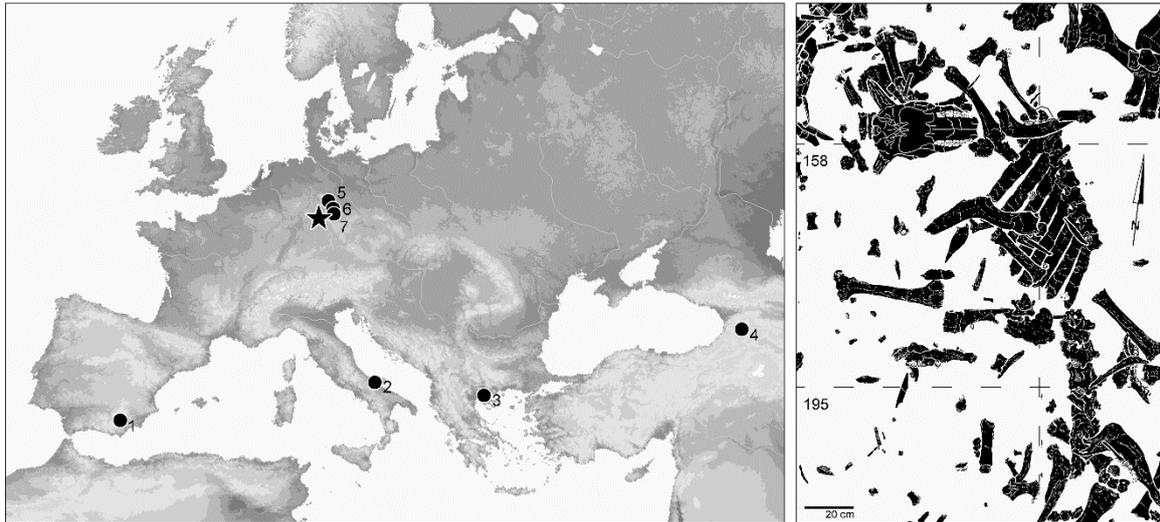
Fig. 2. *Bison menneri* from Untermassfeld, skull of an adult individual (IQW 2003/ 28 250 (Mei. 27 412)); a. palatal view; b-c. right tooth row with P2-M3, buccal and occlusal views; d-e. left tooth row with P2-M3, buccal and occlusal views; scale bar: 3 cm.

Fig. 3. *Bison menneri*, skeletal reconstruction based on individually related finds from Untermassfeld. Elongated longbones and high hump produced a very tall type of bison (implementation R.-D. Kahlke, E. Haase).

1,90 m
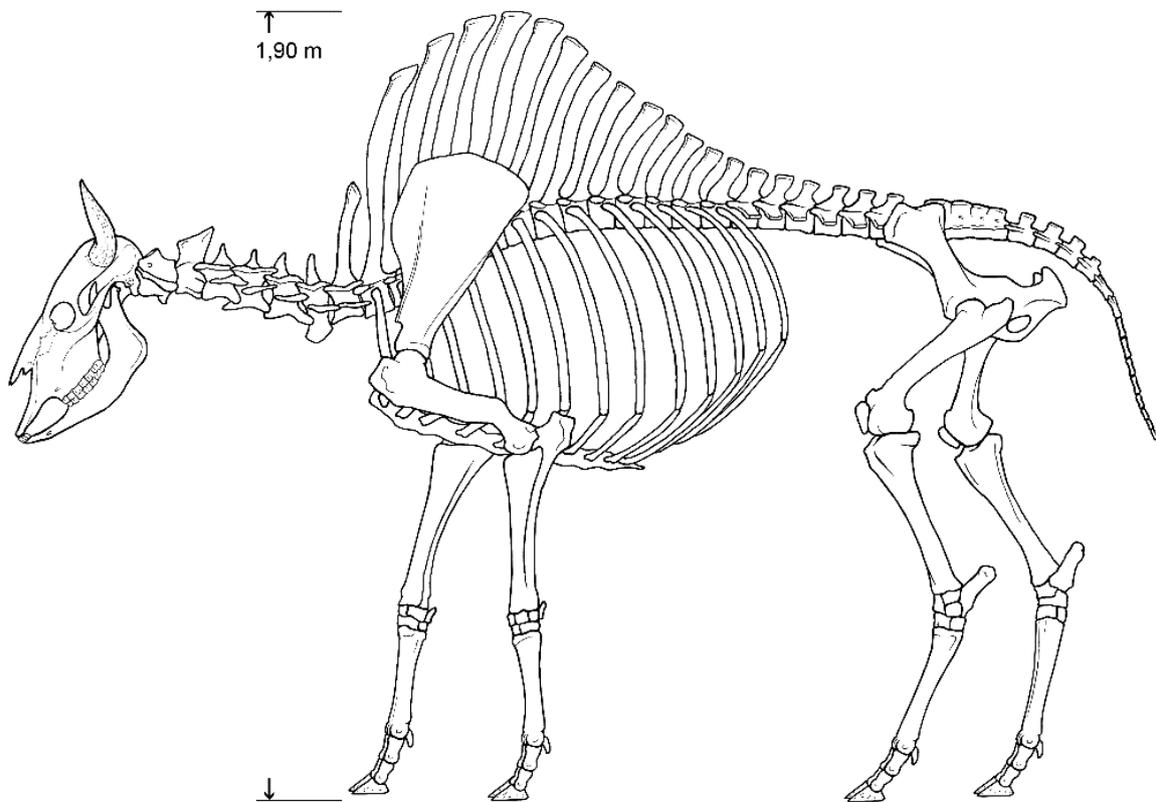
Fig. 4. Plot of scores on DF2 vs. DF1 for a range of extant herbivore species, including bison, and Pleistocene bison assemblages.
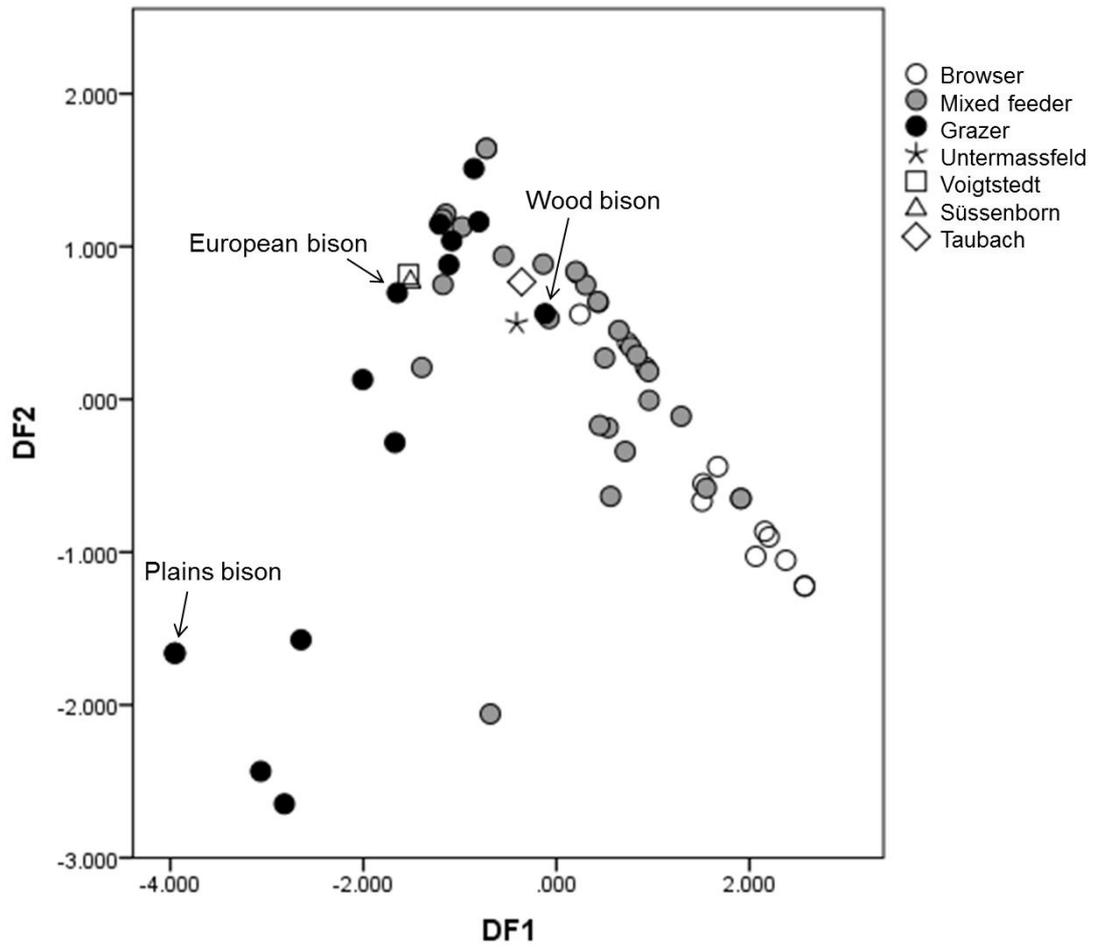
Fig. 5. Cluster diagram using mesowear variables for extant herbivores and European Pleistocene bison assemblages; dots: extant bison species; arrows: Pleistocene samples.
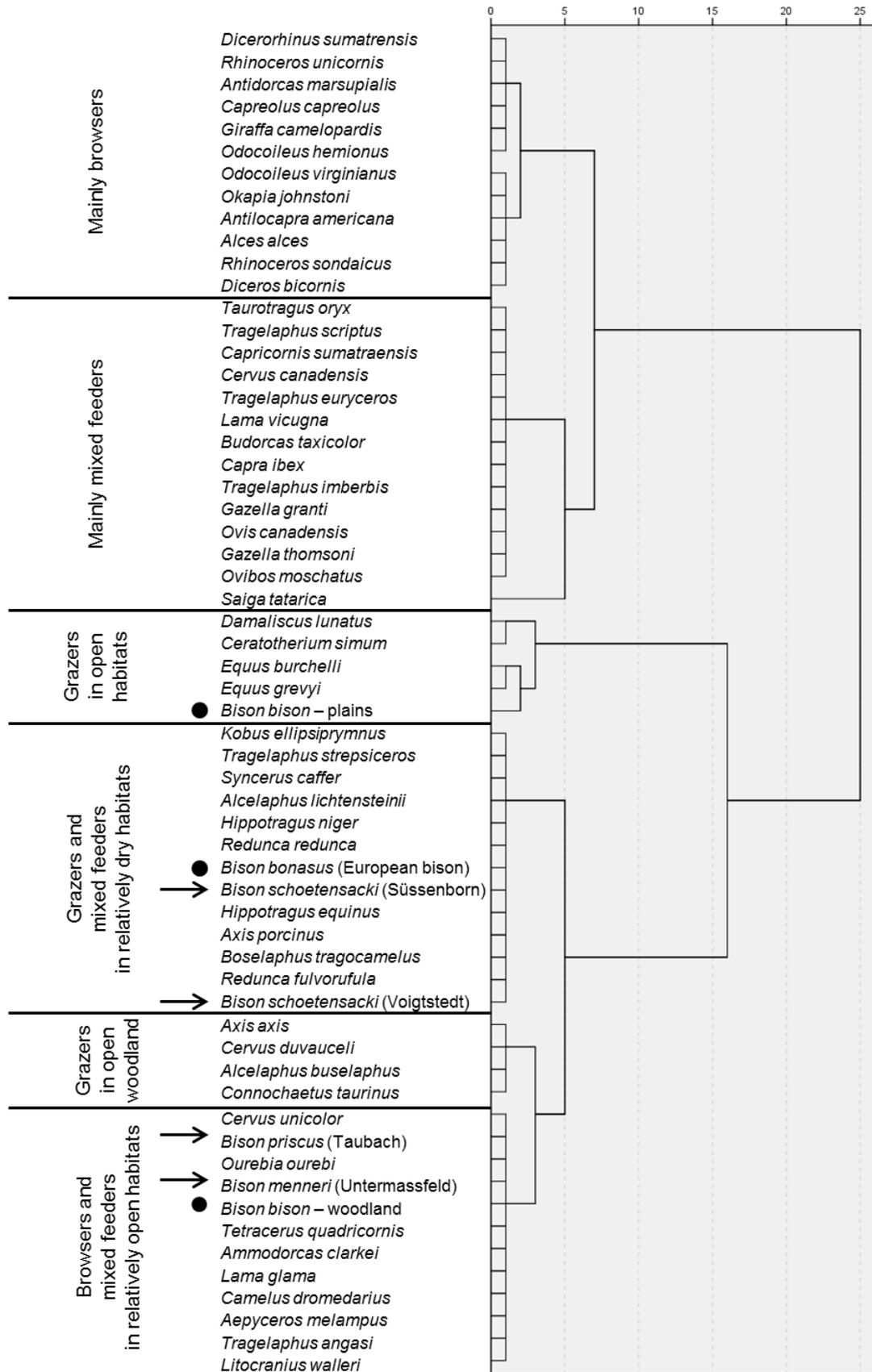
Fig. 6. *Bison menneri* from Untermassfeld, tooth row of an early adolescent individual (IQW 1995/ 24 778 (Mei. 24 307)); a-b. left tooth row with DP3-DP4 and M1-M3, buccal and occlusal views.
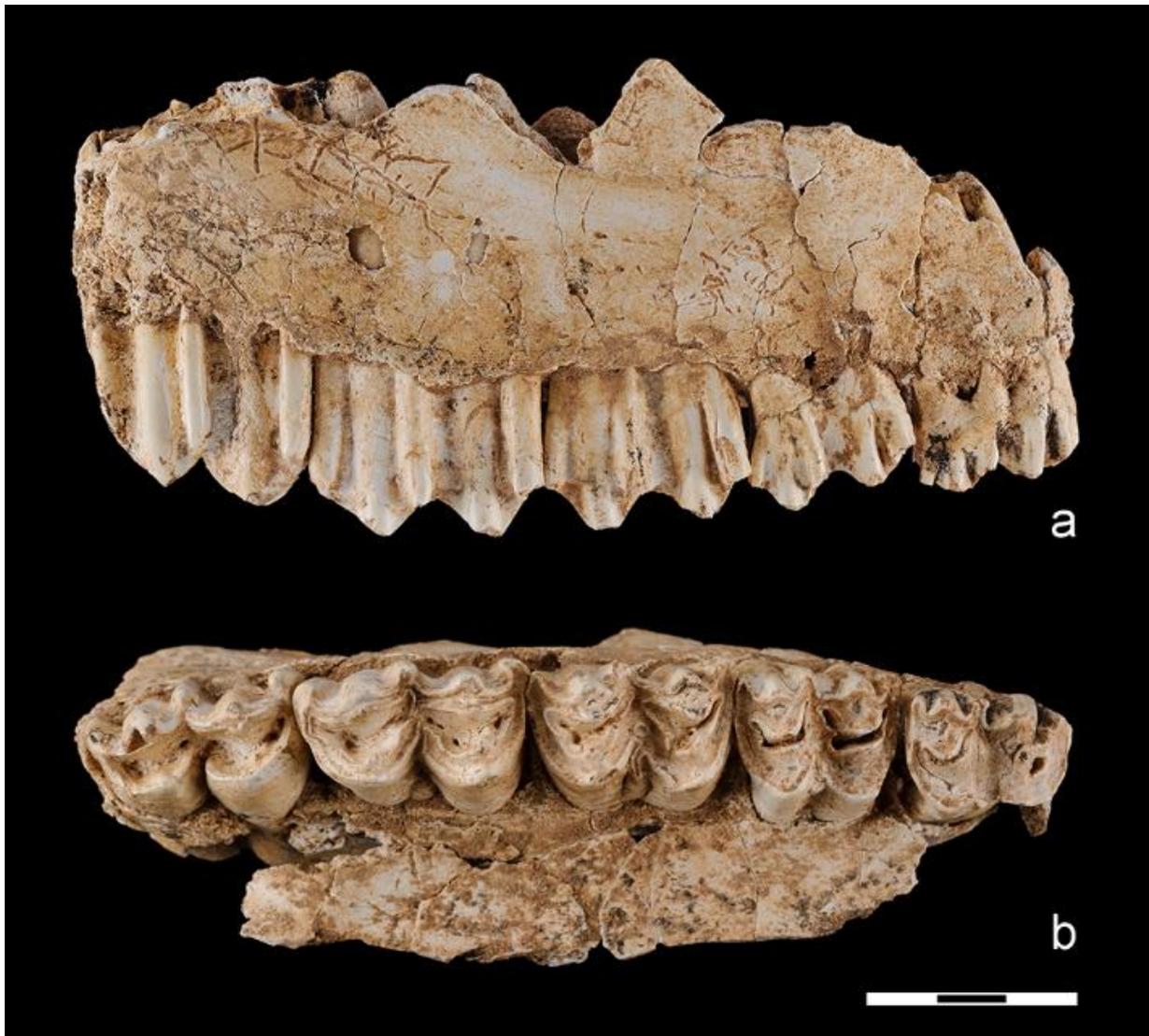
Fig. 7. Buccal and occlusal views of teeth of *Bison schoetensacki voigtstedtensis* from Voigtstedt; a-b. M1 (IQW 1966/5153 (Voi. 1887)); c-d. M2 (IQW 1966/5158 (Voi. 1877)); e-f. M3 (IQW 1966/6669 (Voi. 2395)).
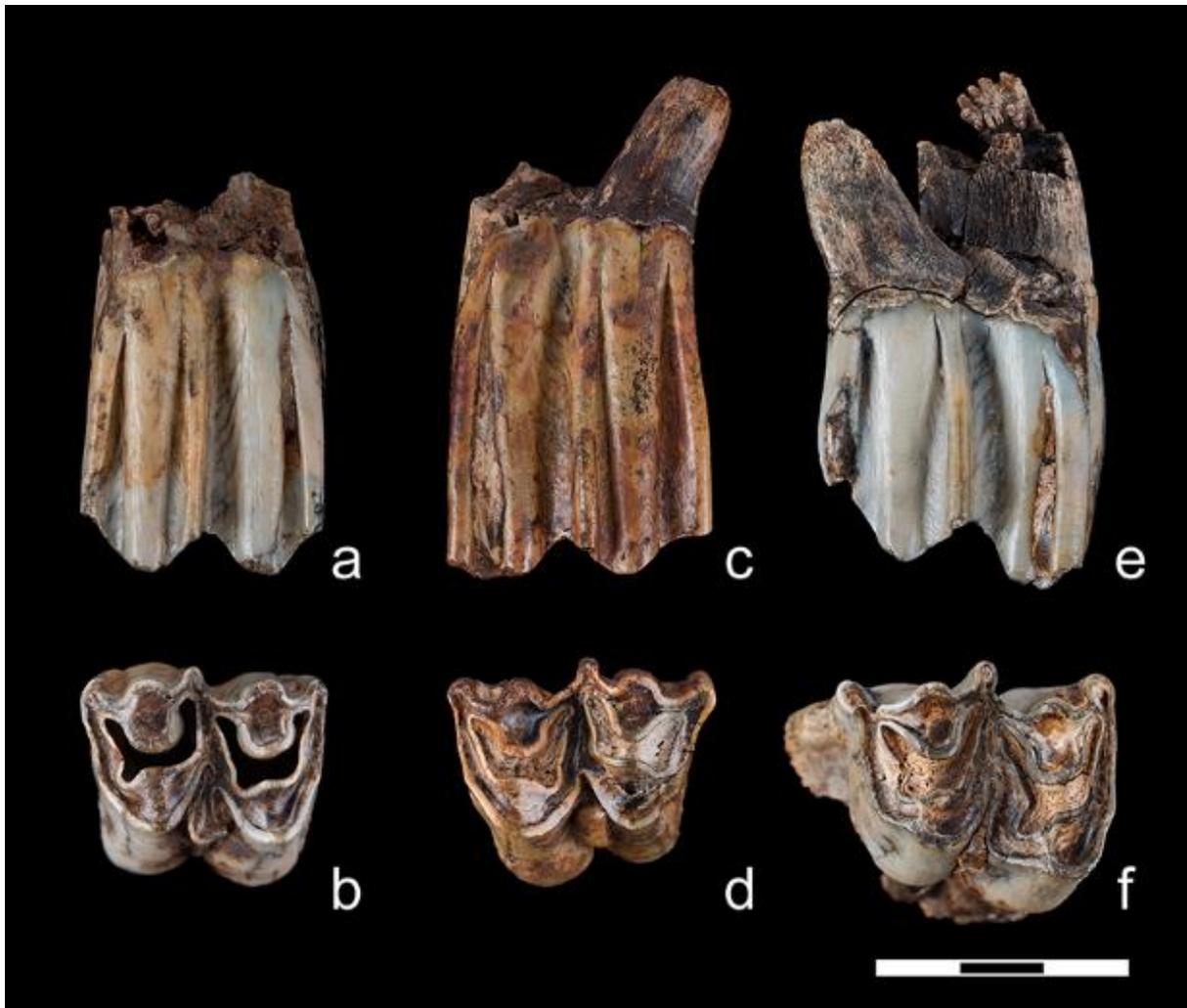
Fig. 8. Buccal and occlusal views of M1 of *Bison schoetensacki* from Süßenborn; a-b. IQW 1964/517 (Süß. 5848); c-d. IQW 1964/496 (Süß. 6626); e-f. IQW 1964/618 (Süß. 4482).
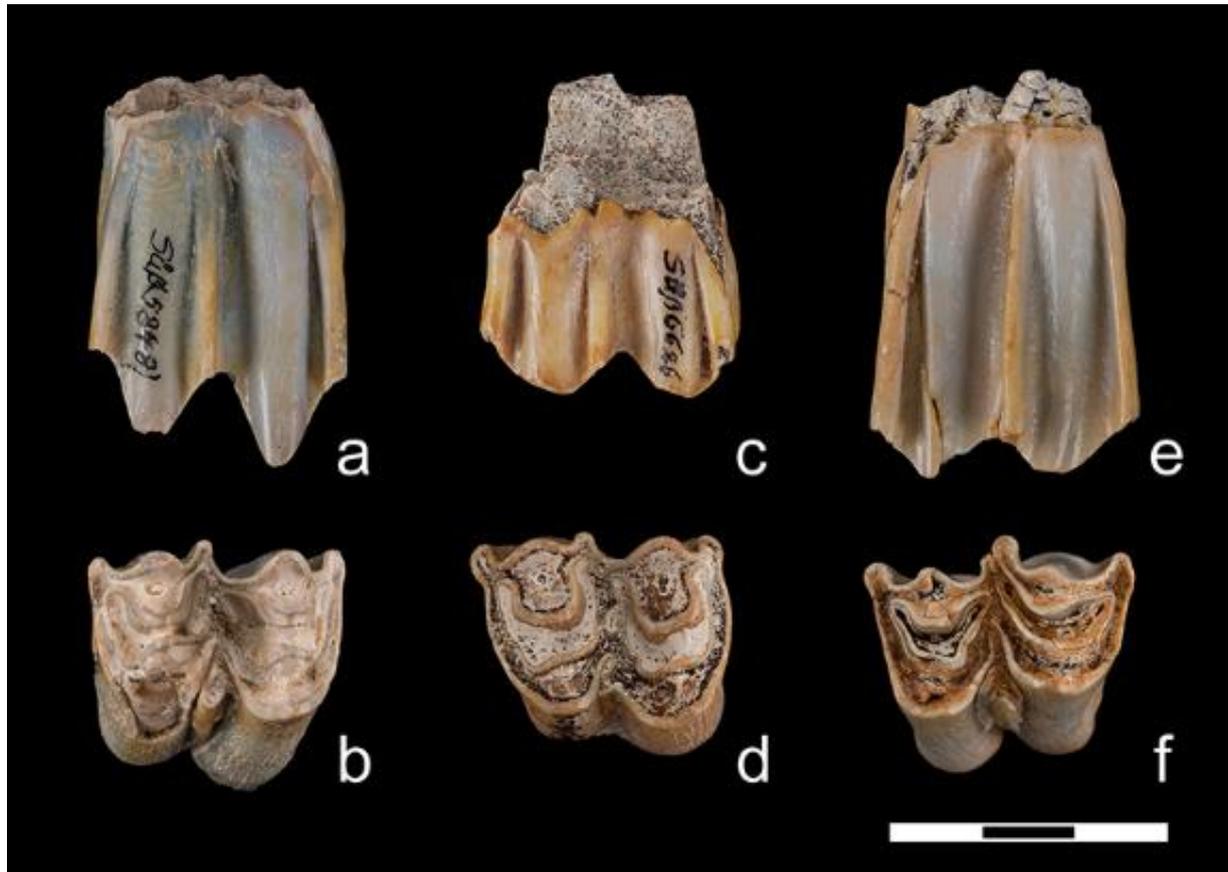
Fig. 9. Buccal and occlusal views of M2 (a-h) and M3 (i-l) of *Bison schoetensacki* from Süßenborn; a-b. IQW 1964/446 (Süß. 5195); c-d. IQW 1964/634 (Süß. 6885); e-f. IQW 1964/542 (Süß. 7374); g-h. IQW 1964/486 (Süß. 5812); i-j. IQW 1964/530 (Süß. 5220); k-l. IQW 1964/474 (Süß. 5563).
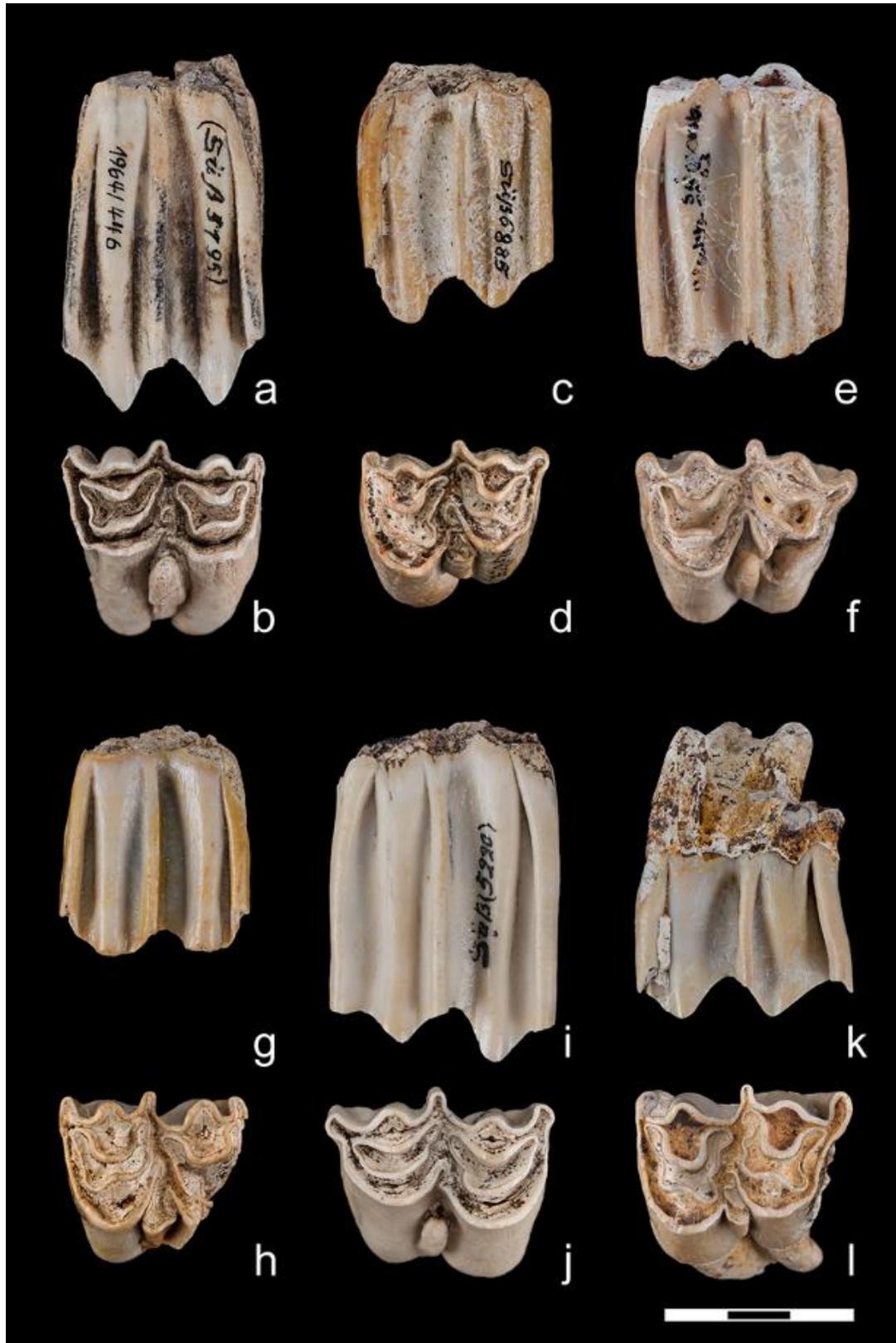
Fig. 10. Buccal and occlusal views of M1 (a-d), M2 (e-j) and M3 (k-l) of *Bison priscus* from Taubach; a-b. IQW 1969/11052 (Taub. 1431); c-d. IQW 1969/11053 (Taub. 1430); e-f. IQW 1969/11065 (Taub. 4129); g-h. IQW 1969/11051 (Taub. 3938); i-j. IQW 1970/12921 (Taub. 13329); k-l. IQW 1969/11793 (Taub. 12639).