



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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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 replacement 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’.

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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. Thermophilous 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 Palaearctic, 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 Lacombe, 2008) and/or in dental evolution (e.g. Jernvall and

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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 Palaeartic 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 Palaeartic (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; Bukhsianidze, 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, Akbar 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 Palaeartic 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 Palaeartic (Kahlke et al., 2011). The correspondingly oldest known forms are *B. (E.)* sp. from Venta Micena (Orce) in Spain (Martínez-Navarro et 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, which are among the largest known bovids, were characterised by exceptionally long metapodials and correspondingly elongated longbones. 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 Palaeartic (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 fluvial 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,

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