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Dance of the Cave Bear: Honouring the Scientific Legacy of Björn Kurtén

Quantitative paleoenvironmental reconstructions based on large mammal communities in Björn Kurtén's work and since then — revising the case of later Late Miocene Old World "*Hipparion* faunas"

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Functional traits of herbivorous mammals provide tools for reconstructing past environments. In 1952, Björn Kurtén used distribution of ecomorphological features in fossil herbivorous mammal communities from Late Miocene "*Hipparion* faunas" of Eurasia to characterize their paleoenvironments as "steppe", "forest" and "mixed" types. We tested Kurtén's results with a revised set of ecometric methods. We used dental ecometric estimates of mean annual temperature and precipitation, net primary productivity, and normalized difference vegetation index to compare Miocene localities with modern biomes, and dental mesowear to estimate woody and grass cover in the paleoenvironments. Our results agree with Kurtén's, indicating steppe-edge environments in northern China, wooded paleoenvironments in Pikermi, Greece, and central Europe, and open woodland-grassland environment in Maragheh, Iran. Our analyses indicate the presence of wooded grassland savanna in Lothagam and tropical forest in Lukeino in East Africa, further demonstrating paleoenvironmental variation and ecological diversity within later Late Miocene "*Hipparion* faunas".

Introduction

Reconstructing past environmental and climatic conditions across the world enables us to understand how the world worked before the current heavy human impact on our ecosystems. Thus, it provides an essential reference point for understanding the pace and magnitude of human influence on the loss of biodiversity and climate change. In other words, one could even say that we need to look into the past to understand how the world "should work" if the human factor is removed.

Reconstructing paleoenvironmental and paleoclimatic conditions from adaptive traits of fossil mammals is a two-part process. On the one hand, we need to understand how functional traits have evolved and what their role is. On the other hand, we need to relate functional traits of mammals with environmental conditions, such as

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climate, primary production, or plant community properties. Here, we discuss Björn Kurtén’s use of mammalian ecomorphology in paleoenvironmental reconstruction, and provide an overview of recent methodological developments in paleoenvironmental reconstruction based on mammalian paleoecology and functional traits. We first look into Björn Kurtén’s work on paleoenvironmental conditions by quantitative assessment of fossil mammal communities. We then review the methods used to reconstruct paleoenvironments based on properties of fossil large mammal communities. These methods include stable isotope analyses, dental ecometrics, dietary analyses based on dental micro- and mesowear, body size variation and distribution within fossil mammal communities, and postcranial ecomorphology of large herbivorous mammals. Finally, we present a case study where new mesowear and dental ecometric data of large herbivorous mammals from later Late Miocene (“Pikermian”, “Turolian” or “Baodean” equivalent) localities are used for testing and revising paleoenvironmental interpretations that Kurtén first suggested in his Master’s thesis *The Chinese Hipparion fauna* (Kurtén 1952).

Björn Kurtén’s work on paleoenvironmental reconstruction based on fossil mammals

Björn Kurtén is perhaps best known for his pioneering work on quantitative analyses of life history aspects of fossil mammals such as their demography, but he also studied the relationships of extinct mammals with their environments. A good example of this is his Master’s thesis (Kurtén 1952), where he looked into differences in the composition of Late Miocene large mammal faunas from China and argued that there was a boundary zone between forest and steppe environments in the region. In particular, he followed Schlosser’s (1903) observation that the presence of two gazelle species differing in their dentition, *Gazella gaudryi* with brachydont (low-crowned) dentition and *G. dorcadoides* with hypsodont (high-crowned) dentition, varied within the region, with “*dorcadoides*” faunas towards the north-west, “*gaudryi*” faunas towards the south-east, and “mixed” faunas in the middle.

At the time when Kurtén wrote his thesis, it was thought that increased hypsodonty in herbivorous mammals is particularly an adaptation to grazing. While this is still understood to be a significant factor, it is now thought that the evolution of hypsodont dentition is typically an adaptation to compensate for the effect of a combination of factors that increase tooth wear rates in dry environments, such as airborne dust and grass phytoliths (Janis & Fortelius 1988, Fortelius *et al.* 2002, Damuth & Janis 2011). Based on the geographic separation of the two species of gazelle and other species of large herbivorous mammals, Kurtén (1952) revised the idea presented originally by Schlosser (1903) that the north-western areas with “*dorcadoides*” faunas represent mammal communities that lived in a steppe environment, while “*gaudryi*” faunas to the south-east were associated with forest environments. The “mixed” faunas in the middle represent a transition zone between the forest and steppe biomes. The age of the Baode fauna was recently determined to represent mammal assemblages of different ages (Kaakinen *et al.* 2013), indicating a local environment change from humid to dry (Eronen *et al.* 2014). However, the geographic division of steppe in north-west and forest in south-east has been supported by more recent work (e.g., Fortelius *et al.* 2002, Liu *et al.* 2023). Finding such associations between quantified properties of fossil mammal assemblages and their environments, and relating them with geographic patterns of biome distribution in the past was relatively new at the time.

Kurtén used the composition of fossil mammal faunas as an indicator of paleoenvironmental conditions in his book *Pleistocene Mammals of Europe* (Kurtén 1968). In the context of Villafranchian (latest Pliocene to earliest Pleistocene) of Europe, Kurtén relied on the ecomorphological similarity of the Pleistocene mammal species to their extant counterparts, dividing the species into “wood”, “steppe” and “amphibious” types. He then used the proportions of “wood” and “steppe” species in the fossil mammal communities to assess whether the paleoenvironments were dominated by closed forest or open steppe habitats. Kurtén’s results mostly agree with more recent interpretations of the paleoenvironments in broad outlines (e.g., Argant 2004, Barbet 2006, Nomade *et al.* 2014, Strani *et al.* 2018), although we now have stratigraphically more high-resolution records that indicate notable fluctuation within the sections, corresponding with more fine-scale glacial-interglacial cyclicity than was known at the time of publication of Kurtén (1968). For example, the strata at Senèze, France, are now understood to have ranged from ca. 2.2 Ma to ca. 1.9 Ma, recording shifts between more wooded interglacial stages and steppe-dominated glacial stages (Roger *et al.* 2000).

Kurtén’s review of the paleoenvironments of the Late Miocene “*Hipparion* faunas” serves as the basis for our case study. The “*Hipparion* faunas” (*sensu* Kurtén 1952) refer to all Late Miocene Old World mammal assemblages, characterized by the widespread presence of hipparionine equids. However, the Chinese “*Hipparion* faunas” of Kurtén (1952) represent later Late Miocene (Turolian equivalent) assemblages, and we have concentrated on large mammal assemblages of that age in our case study. In addition to the Chinese “*Hipparion* fauna” localities, Kurtén presented new interpretations of the paleoenvironments of the classic, broadly contemporaneous Greco-Iranian faunas. He writes (1952: 31): “The Pikermi and Western European fauna was characterized by a number of brachydont, browsing types. Among the giraffes, the browsing *Giraffa* is notable. The gazelles seem mainly to have been brachydont [...] In contrast, Maragha and Samos are dominated by hypsodont types. *Chilotherium* is a common genus. The giraffids are presented by *Palaeotragus*, *Samotherium*, *Helladotherium*, but the browsing *Giraffa* is absent. Deer are rare. Bovids abound; among the gazelles, hypsodont forms seem to predominate”. He then continues: “It is true that Pikermi has been regarded for a long time a typical steppe locality; but this inference seems to rest mainly upon the presence of *Hipparion* and on the the assumption that this horse was an exclusively plains-living form. The untenability of this hypothesis has been demonstrated above” (*ibid*.).

In this study, we tested Kurtén’s (1952) paleoenvironmental interpretations of the classic Turolian (“Pikermian”) “*Hipparion* fauna” localities based on new mammalian ecometric and paleoecological analyses. In addition, we included well-sampled Turolian and Turolian equivalent localities from central Europe and East Africa in order to broaden the geographic range of the analyses. Thus, we could explore whether the mammalian ecometrics capture paleoenvironmental differences in widely separate parts of the Old World, from central Europe in the west to China in the east, and from the tropics in East Africa to the temperate zones in Europe and northern China.

Large mammal-based paleoenvironmental analysis methods since Kurtén

Stable isotope analyses

Several methods for analyzing the connections between fossil large mammals and their environments have been developed since Kurtén’s work on the topic (e.g., Kurtén 1952, 1968). Among the most significant early developments was the use of stable isotope analyses (Lee-Thorp & van der Merwe 1987, Cerling *et al.* 1997), especially in dental enamel, which preserves the isotopic signal during the mineralization of the teeth and is more resistant to diagenetic alteration in the isotope signal than other bone tissues. The use of stable isotope analyses in research on mammalian paleoecology and paleoenvironments is based on understanding of the fractionation of isotopes in biological tissues.

Stable oxygen isotope ratios ($^{16}O/^{18}O$) in the enamel of fossil mammal teeth are fractionated following processes of rainwater re-evaporation and source of drinking water in the environment. Evaporation, which is high in arid environments, is reflected in the stable isotope signal as increased heavy oxygen values ($\delta^{18}O$). On the other hand, herbivorous mammals that receive their water mostly from the vegetation they feed on (typically browsers) also show increased $\delta^{18}O$, compared with mammals that mostly drink meteoric water. Thus, differences in oxygen isotope ratio within the herbivorous mammal community reflect ecological differences between the species (Pedarzani & Britton 2019). There are differences in the sensitivity of different mammal species to evaporation effect on the heavy oxygen isotope (δ^{18}O). For example, Elephantidae, Rhinocerotidae and Hippopotamidae are evaporation-insensitive and their oxygen isotope ratios reflect the isotope ratio of the original source water, whereas the oxygen isotope ratios of evaporation-sensitive mammals such as Giraffidae, Tragelaphini and Hippotragini reflect the isotope ratio of evaporated water (Levin *et al.* 2006, Blumenthal *et al.* 2017). Comparison of δ^{18}O between evaporation-insensitive and evaporation-sensitive mammals is used as an aridity index (Levin *et al.* 2006, Blumenthal *et al.* 2017).

Stable carbon isotope ratios (^{12}C/^{13}C) are widely used in dietary analyses of large herbivorous mammals, as they reflect the proportion of C3, C4 and CAM photosynthesizing plants in their diet (Cerling *et al.* 1997, 1999, Cerling & Harris 1999, Uno *et al.* 2011). Compared to C3 photosynthesis, C4 and CAM photosynthesis results in an increase in δ^{13}C values in plant tissues, and these ratios are transferred into dental enamel and other tissues of herbivorous mammals due to further fractionation processes. On a smaller scale, stable carbon isotope ratios also show a "canopy effect", with more negative δ^{13}C values in closed-canopy environments, and can be used as an indicator of vegetation openness especially outside the range of C4 photosynthesizing plants (Farquhar *et al.* 1989, van der Merwe & Medina 1991). Stable carbon isotope ratios, both from dental enamel of large herbivorous mammals and from soil carbonates, have been used in paleoenvironmental analyses, especially to track the spread of C4 grasses and grasslands during the Cenozoic (Cerling *et al.* 1997, 1999, Cerling & Harris 1999, Kingston & Harrison 2007, Kingston 2011, Uno *et al.* 2011, Manthi *et al*. 2020). The spread of C4 grasses has been much discussed for Africa during the Neogene, often in the context of paleoenvironments associated with hominids and early hominines. Changes in the partial pressure of carbon dioxide in the atmosphere through time have also affected carbon isotope ratios, being another factor to be considered when applying stable carbon isotope analyses in the reconstruction of past herbivore diets and vegetation (Hare *et al.* 2018, Polissar *et al.* 2019).

Stable carbon isotopes were used by Passey *et al.* (2007) to explore the paleoecological patterns of the Chinese "*Hipparion* faunas" suggested by Kurtén (1952). Passey *et al.* (2007) analyzed stable carbon isotope ratios from the species of *Gazella* from the Late Miocene localities of northern China, and found support for Kurtén's (1952) interpretations of their dietary ecology. Their analyses indicated that while the plant communities were C3-dominated, the hypsodont gazelles of the species *Gazella dorcadoides* consumed ca. 20% C4-photosynthesizing vegetation, while the brachydont *G. gaudryi* and the medium-crowned (mesodont) *G. paotehensis* had a purely C3 plant diet. This supports Kurtén's interpretation of a more grazing dietary ecology of *G. dorcadoides* compared with that of the two other species of *Gazella*, as the C4 plants are likely to represent grasses, although this method does not exclude possible consumption of C3 photosynthesizing grasses.

Other stable isotope methods applied to mammalian paleoecological research include analyses of stable nitrogen isotopes, which reflect protein consumption as well as properties of different plants consumed (DeNiro & Epstein 1981, Bocherens 2003, 2015), and strontium isotopes which can reveal migration patterns of large mammals in the past (e.g., Arppe *et al.* 2009, Metcalfe & Longstaffe 2014, Hoppe & Koch 2017, Metcalfe 2017).

Dental ecometrics of large herbivorous mammals and their use in reconstructing past environmental conditions

The basic principles for understanding the relationship of functional adaptations of mammals and their environments in the past started to form long before Kurtén's work. In fact, the use of functional morphology to estimate ecological roles of extinct species goes back in time to the very beginnings of paleontology, with Georges Cuvier's concept of comparative anatomy, whereby the functional anatomy of extinct species could be understood by comparison with the anatomy of extant species that have similar functional traits (Cuvier 1804, Cuvier *et al.* 1834). Cuvier also made some of the earliest remarks on climatic associations of fossil mammals. He noted similarities between the Eocene *Palaeotherium* from the Paris Basin and modern tapirs that are associated with tropical forests, and based on this he argued that climate in France must have been warmer in the distant past (Cuvier 1804). Another example of early ideas about the association of fossil mammals and climate is Edouard Lartet’s observations of the fossil assemblage of mammals from Sansan, France (now understood to be Middle Miocene in age). It seemed to include species that have living analogues today both in hotter and colder climates, but mostly in the temperate climate zone similar to that region today (Lartet 1851).

Paleontological discoveries later in the 19th century laid the foundation for understanding long-term evolution of functional traits of mammals and other organisms. For example, the discovery of evolutionary series of horses (Equidae) in the Cenozoic record in North America revealed an evolutionary trend through time. Several equid genera adapted to increasingly open environments by evolving increasingly running-adapted limbs for efficient movement in open landscape, and increasingly high-crowned dentition with more complex enamel patterns for feeding on tough open-habitat grasses (Marsh 1879, Matthew 1903, Simpson 1951). This classic evolutionary scenario has more recently been revised, revealing a more complex pattern of evolution within several branching lineages, although the basic trend still broadly holds for the big picture of horse evolution (e.g., Cantalapiedra *et al.* 2017, Janis & Bernor 2019, Cirilli *et al.* 2022).

The mammal community structure analysis of Kurtén (1952) brought paleontology closer to modern ecology by providing a quantitative analysis of the distribution of ecomorphological properties within primary consumer communities (fossil herbivorous mammal assemblages) to estimate properties of primary producer communities in the past (categorization of “steppe” *vs*. “forest” environments). Kurtén based his ecological characterization of the herbivorous mammals as “steppe”- and “forest”-adapted species mainly on one key trait, tooth crown height (hypsodonty), which at the time was mostly understood to be an adaptation to feeding on tough grasses in open grassland environments (e.g., Matthew 1903, Simpson, 1944, 1951). Since then, several authors have conceptualized the role of hypsodonty as an adaptive trait to increase functional durability of teeth under conditions that increase tooth wear rate, including grass phytoliths and exogenous mineral particles present in the environment where the animals feed (e.g., Fortelius 1985, Janis & Fortelius 1988, Fortelius *et al.* 2002, Strömberg 2003, 2006, Damuth and Janis 2011, Kaiser *et al.* 2013, Strömberg *et al.* 2013, Madden 2015, Saarinen & Lister 2023).

From this background of understanding the functional role of dental adaptations, such as hypsodonty, in large herbivorous mammals, a methodological framework called “dental ecometrics” has been developed, largely at the University of Helsinki during the last two decades. Ecometrics refers to functional traits of mammals (or other organisms) that are, on the one hand, “taxon-independent”. In other words, they are shared as a common adaptive response across wide taxonomic groups, and hence are not limited by phylogenetic position of the individual species, although relying on adaptations of species that are shared with a wide range of other species and have a similar functional relationship with the environment. On the other hand, these functional traits have a direct quantifiable relationship with properties of their environment, such as climate and vegetation, and thus when averaged at community-level give a quantitative estimate of such properties (Eronen *et al.* 2010a, Polly *et al.* 2011, Polly & Head 2015, Vermillion *et al.* 2018). Hypsodonty can be considered the first dental ecometric trait to be used as a quantitative proxy of mean annual precipitation in terrestrial environments (Fortelius *et al.* 2002). The selection pressure for hypsodont dentition in large herbivorous mammals is driven by a set of factors that cause increased tooth wear rates and are increasingly present in progressively dryer environments. Such factors include phytolith-rich grasses and the accumulation of aeolian mineral dust on plants in dry environments. Thus, when hypsodonty is averaged across the community of herbivorous mammal species, it can be used for estimating mean annual precipitation in terrestrial environments (Fortelius *et al.* 2002). Fortelius *et al.* (2002) introduced the use of ordinated hypsodonty values, where species with brachydont (low-crowned) molars are given value 1, mesodont (medium-crowned) species are given value 2 and hypsodont (high-crowned) species are given value 3. When these ordinated hypsodonty values are averaged across the large herbivorous mammal communities to calculate mean ordinated hypsodonty for fossil localities or modern ecosystems, they can be used to estimate mean annual precipitation. This has become the standard procedure in the use of hypsodonty as a dental ecometric trait, and hypsodonty has been demonstrated to reflect precipitation with a high accuracy in present environments in most parts of the world (Eronen *et al.* 2010a, Liu *et al.* 2012).

Further dental ecometric traits (of large mammal species, averaged over communities) have been used since the original method of using mean ordinated hypsodonty (HYP) of large mammal communities as a proxy of precipitation. These are all functional traits that are related to either durability or cutting, grinding and shearing properties of molar teeth, and their distribution within communities of herbivorous mammals reflects various aspects of the environment via an adaptive link of dental morphology and the vegetation the mammals consume. They are as follows:

1. Longitudinal loph count (LOP). This is the amount of elongate cutting or shearing ridges on the occlusal surface of the molars, with a primary orientation parallel to the main axis of the tooth row (Liu *et al.* 2012). This trait is related to the functional ability of teeth to cut tough plant parts such as branches, and high proportion of LOP is associated with seasonally cool environments where plants drop their leaves during cold seasons. Thus it broadly correlates with mean annual temperature (Liu *et al.* 2012, Oksanen *et al.* 2019). Together with mean ordinated hypsodonty, this trait can be used to estimate net primary productivity (NPP) and approximate biome boundaries in terrestrial environments (Liu *et al.* 2012).
2. Presence (1) or absence (0) of acute lophs (AL). Acute lophs are elongate ridges (spanning more than half the length or width of the tooth crown) that maintain a sharp, cutting edge when worn. We use here the original definition where any sharp-edged lophs with clear facet development are counted as acute, as opposed to obtuse lophs, which are basin-like when worn, with rounded enamel edges (Žliobaitė *et al.* 2016, 2018, Oksanen *et al.* 2019, Saarinen *et al.* 2021a). The functional role of acute lophs is somewhat similar to the longitudinal lophs, with a stronger emphasis on the cutting function needed for breaking tough browse items such as branches. High proportions of acute lophs in large mammal communities have been associated with low mean annual temperatures, as they are a common functional response to browsing on deciduous woody plants (Oksanen *et al.* 2019, Saarinen *et al.* 2021a). Presence of acute lophs has also been used as a covariate in estimating normalized difference vegetation index (NDVI, a measure of green vegetation in terrestrial environments), with which it has a positive relationship based on training data from Kenyan national parks (Žliobaitė *et al.* 2016).
3. Presence (1) or absence (0) of obtuse lophs (OL). Obtuse lophs maintain basin-like profile without sharp enamel edges or facets when worn. A high proportion of obtuse lophs within large herbivorous mammal communities indicates prevalence of shearing (rather than cutting) function in feeding, and it has a negative relationship with precipitation and NDVI, but a positive relationship with temperature in models based on training data from Kenyan national parks (Žliobaitė *et al.* 2016).
4. Presence (1) or absence (0) of structural fortification (SF). Structural fortification refers to structures of molar teeth (usually thickened enamel edges in parts of the occlusal surface) that support the maintaining of relief in the cusps on the occlusal surface in worn molar teeth (Žliobaitė *et al.* 2016, 2018, Oksanen *et al.* 2019, Saarinen *et al.* 2021a). The most typical example of this is thickening of the lingual enamel wall of buccal cusps in the selenodont molars of ruminants, which makes the buccal cusps stand high compared to other surface features in worn molars, although "furchen" (furrowing of enamel) in

bunodont molars was also counted as fortification according to the original definition. This trait is characteristic of mixed-feeders that feed on grasses, fruit and browse in tropical forest understory, forest edge ecotones and wetlands (Žliobaitė *et al.* 2016, 2018, Saarinen *et al.* 2021a). This trait has been mostly used in the context of sub-Saharan Africa, where it correlates positively with precipitation, NPP and NDVI, and negatively with temperature (Žliobaitė *et al.* 2016), and high proportion of species with SF separates evergreen forests from grasslands in Africa (Žliobaitė *et al.* 2018).

5. Flat (1) or non-flat (0) occlusal topography (OT). Flat occlusal surface is a condition where worn molars maintain an occlusal surface shape that, parallel to main chewing direction, practically has no other topography than somewhat elevated enamel ridges (enamel being harder than other dental tissues). Flat occlusal surface is a special adaptation of grazers, indicating occlusion that is heavily dominated by horizontal shearing function. Because of its association with specialized open-habitat grazers, a high proportion of flat occlusal surfaces is related to open, dry environments and relatively low NPP and NDVI. In models based on training data from Kenyan national parks, OT is positively related to temperature and negatively related to precipitation, NPP, and NDVI (Žliobaitė *et al.* 2016).
6. Presence (1) or absence (0) of coronal cement (CM). This trait is related to maintaining structural integrity of molars that have complex, folded, narrow and/or high loph structures, and it is often (but not always) associated with flat occlusal surfaces. The ecometric use of this trait has been limited, perhaps because it is a secondary trait for maintaining functional integrity rather than having a more direct functional role in feeding. Nonetheless, Žliobaitė *et al.* (2016) found a negative relationship of this trait with precipitation and NPP.
7. Horizodonty (HOD), with categories 1 (two cusp rows), 2 (three cusp rows) and 3 (more than 3 cusp rows). This trait is an alternative way to increase the durability and/or functional efficiency of molars by multiplying the amount of transverse cusp pairs or lophs on the tooth surface beyond the usual two of most large herbivorous mammals. Ecometric use of this trait has been limited, although it shows a positive relationship with precipitation in East African models (Žliobaitė *et al.* 2016). However, this pattern may be related to the presence of bunodonty, as most horizodont species today are bunodont suids. Increased horizodonty is taxonomically limited, occurring almost exclusively among suids and proboscideans. In proboscideans, horizodonty was a key dental specialization to increase shearing efficiency and functional durability, and it evolved as an evolutionary response primarily to climatic aridification and to some degree to grazing, especially during the last 10 million years among Elephantidae (Cantalapiedra *et al.* 2021, Saarinen & Lister 2023).
8. Presence (1) or absence (0) of bunodonty (BUN). Bunodont molars lack lophs (elongate cutting or shearing ridges) and are typical for omnivorous and frugivorous large mammals that mostly feed in forest environments; however, some highly specialized grazing ungulates such as warthogs have retained bunodont molar morphology (although in a highly modified, multi-cusped and high-crowned form). A high proportion of bunodont species in large herbivorous mammal communities is associated with warm (low-seasonality) environments (e.g., Saarinen *et al.* 2021a, Liu *et al.* 2023), and recent ecometric models show an association of high bunodonty values with the climatically warm southern part of Asia today (Liu *et al.* 2023).
9. Presence (1) or absence (0) of plain selenodonty (PS) (Saarinen *et al.* 2021a), or molars with exclusively obtuse lophs (OO) (Liu *et al.* 2023). This trait is typical of selenodont ungulates adapted to seasonally harsh (dry or cool) environments (Saarinen *et al.* 2021a), sometimes informally called "goat"-type dentition (Liu *et al.* 2023). In Asia, the cool and dry northern part of the continent (north of Tibetan Plateau) is typified by high proportion of OO as compared to the warm and more humid southern part (Liu *et al.* 2023).

Dental ecometric analyses are a powerful tool for reconstructing climatic properties, primary production and biome distribution in terrestrial paleoenvironments. Development of the global fossil mammal database, the NOW Database of fossil mammals (https://doi.org/10.5281/zenodo.4268068, Žliobaite *et al*. 2023) maintained by the University of Helsinki, has enabled geographically large-scale, temporally extensive ecometric analyses to be performed (Casanovas-Vilar *et al.* 2023). Examples include the use of hypsodonty to track changes in precipitation across Eurasia (Fortelius *et al.* 2002, 2006, Eronen *et al.* 2010b) and in the Turkana Basin, East Africa (Fortelius *et al.* 2016) during the Neogene; the discovery of biome shifts in Eurasia from the Middle to Late Miocene (Liu *et al.* 2012); differential patterns of aridification of North American and Eurasian continents during the Cenozoic (Eronen *et al.* 2012, 2015); and changes in early human environments when humans dispersed outside Africa during the Early Pleistocene (Oksanen *et al.* 2019, Saarinen *et al.* 2021a). The most typical use of dental ecometrics has been to retrodict climatic properties (precipitation and temperature) and primary productivity (which relates to broad patterns of biome distribution) based on training data from modern ecosystems. However, other properties of paleoenvironments such as more fine-scale differences between vegetation type in past environments have also been explored (Žliobaitė *et al.* 2018, Saarinen *et al.* 2021a).

While dental ecometric modeling has mostly been based on multiple regression models, new data analysis methods such as redescription mining have brought new approaches to dental ecometric analyses (Galbrun *et al.* 2018, Liu *et al.* 2023). The current dental ecometric models are mostly based on modern training data from present-day ecosystems in Eurasia and Africa, which may limit their use in non-analogue cases, especially the further back in time they are applied. For example, the most commonly used dental ecometric trait, hypsodonty, evolved in most herbivorous mammal lineages during the Miocene, so its use in ecometric estimates in more distant times than the Miocene is not possible. Furthermore, hypsodont dentitions never evolved in endemic Australian large herbivorous mammals, while South American large mammal faunas show particularly high hypsodonty values during most of the Cenozoic, possibly driven by high levels of volcanic ash deposition (Strömberg *et al.* 2013). Such non-analogue cases call for continent-specific models as well as models based on direct proxy comparisons for deep-time paleoenvironmental reconstructions based on dental ecometrics (*see* Wilson & Saarinen 2024).

Dental wear analyses and their paleoenvironmental implications

Dental wear analyses (mesowear and microwear) are a versatile tool for analyzing dietary composition of fossil herbivorous mammals at the level of local populations. They record a more direct response of herbivorous mammals to their environment (via the connection of available vegetation) in the past than the dental functional traits that reflect evolutionary adaptations of species to feeding in different environmental conditions. Thus, dental wear signal from herbivorous mammal assemblages has a high potential for reconstructing vegetation structure in terrestrial paleoenvironments.

Microwear analysis is the first proxy method for reconstructing diets of fossil mammals based on tooth wear (Walker *et al.* 1978). It is based on counting the abundance of microscopic wear marks, such as scratches and pits on tooth enamel caused by chewing on different dietary items. The hypothesis behind this method is that abrasive plant materials, such as grass phytoliths, cause long scratches on the worn enamel facets of the teeth, whereas browsing causes a more pit-dominated microwear pattern. The benefit of this method is that it is applicable to virtually all kinds of teeth and it should give consistent results for mammals with very different tooth morphologies. However, microwear analysis only reveals the last few meals of the animal instead of a long-term average dietary signal (e.g., Rivals *et al.* 2010). Furthermore, it has been suggested that other factors than diet, such as external soil material from the environment, may obscure the dietary signal provided by microwear analysis (Rivals *et al.* 2010). On the other hand, microwear can detect dietary details which other proxy methods do not pick up. For example, characteristic large-sized pits in microwear can reveal feeding on hard seeds (Rivals *et al.* 2012). Ungar *et al.* (2003) developed a new method called dental microwear texture analysis, for analyzing microwear surface textures by combining confocal microscopy with scale-sensitive fractal analysis (Scott *et al.* 2005). Such methodological improvements have made dietary analyses based on microscopic tooth wear patterns more objective compared to the original method based on visual counting of scratches and pits under a microscope.

The use of microwear analyses as paleoenvironmental proxy has been limited, probably largely due to the comparatively laborious data collecting procedure, which may limit community-wide analyses. Another challenge is the lack of extensive dental samples across herbivorous mammal communities associated with present environments, which means that models for estimating environmental variables from community-wide microwear signals based on modern mammal communities are practically lacking. Nonetheless, some studies have linked dental microwear patterns from fossil mammal populations with their paleoenvironments. For example, Rivals *et al.* (2015) showed that the dietary signal both from southern mammoth (*Mammuthus meridionalis*) and the last European gomphothere *Anancus arvernensis* from Early Pleistocene European localities varied in a way that reflects feeding in different environments, with more grass-dominated microwear signals associated with cool-stage "steppe" localities. Community-wide microwear analyses (usually in combination with mesowear, *see* below) have occasionally also been performed and used as paleoenvironmental indicators, such as in the case of Pleistocene localities from the UK (Rivals & Lister 2016), and Late Miocene of Rudabánya, Hungary (Merceron *et al.* 2007), and Nikiti, Greece (Merceron *et al.* 2016a).

Dental mesowear analysis (Fortelius & Solounias 2000, Mihlbachler *et al.* 2011, Solounias *et al.* 2014, Saarinen *et al.* 2015; for a recent review, *see* Ackermans 2020) is a promising ecometric method for estimating vegetation structure in past terrestrial environments. As a fast and inexpensive method it allows large amounts of dietary data from a wide range of fossil mammals to be obtained, and it provides a robust signal of lifetime dietary composition in the browsing-grazing (or attrition-dominated–abrasion-dominated) spectrum. Mesowear reflects the abrasiveness of plant foods consumed by herbivorous mammals, and it is based on observing the macroscopic wear-induced shape of the occlusal surface of herbivorous mammals' molar teeth. The basic principle is simple: progressively more abrasive diet makes tooth cusps increasingly lower in relief and increasingly rounded or blunted, with heavy-abrasion diets causing low relief and blunt cusps. The abrasion, as captured by mesowear, mostly comes from feeding on grasses and possibly other phytolith-rich monocots (Fortelius & Solounias 2000, Kaiser *et al.* 2013, Merceron *et al.* 2016b). It has been suggested that abrasive exogenous mineral particles, such as aeolian dust in dry environments, have an additional effect. However, several studies have indicated that although exogenous particles accelerate overall tooth wear rate, such particles do not have a major effect on the mesowear signal, which is mostly affected by the amount of grass in diet (e.g., Kaiser *et al.* 2013, Kubo & Yamada 2014, Merceron *et al.* 2016b, Saarinen & Lister 2016, 2023). This is probably due to a difference in particle size (larger in phytoliths than in mineral dust), or a "sandpaper effect", where grass phytoliths grind down the surface features of teeth because they are firmly attached in the tough leaves, whereas mineral dust can move freely between the teeth.

The original mesowear method introduced by Fortelius and Solounias (2000) is based on visual observation of the relief and shape of cusps in selenodont, ectolophodont and plagiolophodont ungulate molars (found today in ruminants, camels, horses, rhinoceroses and hyracoids), where a continuous buccal edge ("ectoloph") enables consistent observation of the effect of wear on cusp shape. Fortelius and Solounias (2000) coded the relief of the cusps as high or low (with thresholds between high and low relief for different ungulate groups based on observations from modern ungulates with known diets), and the cusp shape as sharp, rounded, or blunt. Mesowear signal dominated by high relief and sharp cusps indicates attrition-dominated wear and browsing diet, whereas mesowear dominated by low relief and blunt cusps indicates abrasive diet (grazing). Intermediate categories (from predominantly high relief and rounded cusps to predominantly low and rounded) represent a dietary spectrum towards increasing abrasiveness (from browse-dominated to increasingly grass-dominated mixed diets). However, this is a simplification, and in reality, cusp shape and relief can vary separately: low relief can be associated with sharp cusps (resulting from high-pressure but low-abrasion chewing on dietary items such as tough, dry browse). Even a combination of high relief cusps that are blunt at the tip is possible, and can occur in fresh grass grazers such as bovines.

The bivariate mesowear scores of cusp shape and relief can be averaged for extant ungulate species and compared using hierarchical clustering analyses, which demonstrate that mesowear accurately detects dietary differences on a browse-graze continuum in most extant large herbivorous mammal species (Fortelius & Solounias 2000). Several revisions of the original mesowear method have been made to improve its accuracy in dietary analysis, to transform the mesowear relief and shape scores into a single univariate mesowear score for analytical purposes, or to expand the mesowear method beyond the originally limited group of dental morphologies. Mihlbachler *et al.* (2011) used a “mesowear ruler” approach where they use a spectrum of mesowear scores based on combinations of cusp relief and shape changing progressively from high relief and sharp cusp (0) to completely flat, blunt cusp (6). Similar univariate mesowear scores, derived from a combination of cusp shape and relief, have been used by other authors, such as the simplified scores of Rivals and Semprebon (2006) and Rivals *et al.* (2009) on a scale from 1 (high and sharp) to 3 (low and blunt), and Fraser *et al.* (2014) on a scale from 1 (high and sharp) to 5 (low and blunt). While these scoring methods are mostly adequate in representing a spectrum of increasing dietary abrasiveness, they are based on an assumption that progressively changing cusp shape due to abrasion is related to progressively lower reliefs, which is not always the case, as discussed above. Thus, Saarinen *et al.* (2016) introduced an alternative method of calculating a univariate mesowear score on a scale from 1 to 3 as an average of ordinated values of cusp shape (1 = sharp, 2 = rounded, 3 = blunt) and relief (1 = high, 3 = low).

The ”traditional” mesowear methods (mesowear 1 and 2, *sensu* Ackermans (2020)) based on observation of cusp relief and shape have been expanded to cover additional mammal groups, including South American endemic ungulates (Croft & Weinstein 2008), rodents (Ulbricht *et al.* 2015, Kropacheva *et al.* 2017), lagomorphs (Fraser & Theodor 2010), and marsupials (Butler *et al.* 2014). However, such methods are not applicable to dental morphologies that do not have separate cusp apices for which the worn shape could be observed, such as the lamellar molars of elephants. As a solution, Saarinen *et al.* (2015) introduced a method called mesowear angle analyses, which is based on measuring the relief of enamel ridges on a worn occlusal surface of molars as angles measured from the bottom of dentine valleys between the enamel ridges. This method quantifies the amount of abrasion from diet (mainly from feeding on grasses) on the enamel ridges. An increasing amount of abrasive plants in diet has the strongest effect on the top of the enamel ridges on the tooth surface, bringing the relief of the enamel ridges lower in relation to the bottom of the softer dentine valleys between the enamel ridges.

For species with dominant facet development rather than development of basin-like dentine valleys at medium-levels of tooth wear, mesowear angles can alternatively be calculated from slopes of the primary wear facets, and they have been shown to broadly correspond with mesowear angles measured from dentine valleys in deinotheres and other proboscideans (Saarinen & Lister 2023). Mesowear angles have been shown to correlate with stable carbon isotope values in low-latitude proboscidean populations (Saarinen *et al.* 2015) and microwear in several proboscidean paleopopulations (unpublished data), demonstrating that they quantitatively reflect dietary composition in a continuum from browsing to grazing. Moreover, mesowear angles of elephantoid proboscideans have been shown to correlate with the proportion of grass in local environments, rather than with other environmental elements such as aridity and openness, as demonstrated by comparisons of paleobotanical and paleoclimatic records and proboscidean mesowear (Saarinen & Lister 2016, 2023). As very large, ecologically versatile megaherbivores, proboscideans (except for the exclusively browsing deinotheres) tend to be non-selective feeders, which probably explains why their dietary signal tracks local vegetation composition particularly well. The association between elephant dietary composition and vegetation structure has been confirmed for extant African and Asian savanna and forest elephant populations (Cerling *et al.* 1999, Xafis *et al.* 2020, Saarinen & Lister 2023). Thus, proboscidean mesowear patterns alone can be used as an ecometric variable to estimate grass cover (or proportion of grass from total vegetation) in past environments (Saarinen & Lister 2016, 2023). The mesowear angle method has also been applied to xenarthrans (Saarinen & Karme 2017) and facet angles of the lower molars to rhinoceroses (Hernesniemi *et al.* 2011). The benefit of mesowear angle analysis compared to other mesowear analyses is that it is less constrained by differences in primary morphology of the molars, and may work as a basis for universally comparable mesowear analysis, regardless of differences in tooth morphology.

Integrating evidence from paleobotanical analyses and mesowear analyses from fossil mammal assemblages indicates that mesowear can be used as an ecometric method to estimate vegetation structure in past environments. Saarinen *et al.* (2016) found a correlation between non-arboreal pollen percentages (proxy of vegetation openness) and averaged ungulate mesowear scores from Middle and Late Pleistocene localities from central and north-western Europe. Merceron *et al.* (2007) performed dental mesowear and microwear analyses of fossil herbivorous mammals from the Late Miocene locality of Rudabánya, Hungary, and noted that the characteristic browse-dominated dietary spectrum is consistent with closed-canopy forest environment. Belmaker and O’Brien (2018) noted a correlation between ungulate mesowear scores and proportion of grass in vegetation (grass%) of environments, while a more robust correlation was found between proboscidean mesowear angles and grass percentage for the Pleistocene of Britain (Saarinen & Lister 2016) and the Neogene of East Africa (Saarinen & Lister 2023). Ungulate mesowear patterns have revealed (in concert with other paleoecological evidence) that the paleoenvironments in the earliest sites occupied by humans outside Africa, such as Dmanisi in Georgia, Ubeidiya in Israel, and Orce in Spain, were different from East African savanna environments. For example, they were less dominated by grassy undergrowth (Belmaker & O’Brien 2018, Saarinen *et al.* 2021a, Bakhia 2023). These patterns make sense from an ecological perspective, as mesowear reflects the proportion of grass in the diet. While differences in dietary adaptations can obscure the use of the dietary signals of single taxa as a proxy of vegetation properties, when averaged across large herbivorous mammal communities, or concentrating on non-selective and ecologically versatile megaherbivores such as proboscideans, mesowear analyses provide a robust signal of local vegetation (especially proportion of grasses from total available vegetation). Thus, while the mesowear signal of large mammal communities and megaherbivores has been shown to correlate with general vegetation openness (and conversely, cover of woody vegetation) (Saarinen *et al.* 2016, Saarinen & Lister 2016), it is primarily a proxy of grass cover (Saarinen & Lister 2016, 2023).

Mammalian body size as a paleoenvironmental and paleoclimatic indicator

Body size is a trait that is connected with most aspects of the physiology, ecology and environmental adaptations of mammals and organisms in general. Thus, understanding the relationships between mammalian body size and their environments can be used in paleoenvironmental reconstruction, although complexity of the factors affecting body size has to be taken into account. Metabolic rates of mammals follow an approximately 3/4 positive allometry, which means that while larger mammals have higher energetic needs, they need less energy per unit of their mass, following an approximately 1/4 negative allometry (Hemmingsen 1960, West *et al.* 1997, 2002). For this reason, larger size increases fasting endurance (Lindstedt & Boyce 1985), while large body volume (or mass) in relation to body surface reduces loss of water from the body (Peters 1983). Consequently, increasing body size is beneficial for large mammals (species with a body mass of more than 10 kg) in seasonally harsh (cold or dry) environments, where large size helps survive through seasonal shortage of resources, and/or to migrate more efficiently in search of resources (Peters 1983).

On the other hand, high primary production and low plant defense mechanisms during growing season may enable mammals to attain large size in seasonally harsh climatic conditions (*see* Saarinen 2014 and references therein). Thus, "Bergmann's rule" (Bergmann 1847), which states that mammalian body sizes are larger under colder climatic conditions because of benefits for heat conservation, is in fact more likely explained by seasonally harsh climatic conditions with fluctuations between scarcity of resources and periodic abundance of high-quality resources (Geist 1987, McNab 2010). Ultimately, most patterns of inter- and intraspecific body size variation in large mammals are related to resource availability and quality, a phenomenon dubbed "the resource rule" (McNab 2010, Saarinen 2014). However, growing large in harsh environments is not the only possible survival strategy. Several species of small mammals (< 1 kg body mass) are able to avoid exposure to seasonally harsh conditions by burrowing and hibernating. Alroy (1998) demonstrated a macroecological pattern in mammalian evolution, where small mammals (< 1 kg body mass) remained diverse throughout the Cenozoic, while large mammals (> 10 kg body mass) on average increased in body size. Medium-sized mammals (between 1 and 10 kg in body mass) in turn became less diverse, creating a "body size gap" in the mid-size range. Alroy (1998) related this phenomenon to the climatic cooling and harshening during the Cenozoic, as small mammals could survive due to sleep-or-hide (SLOH) strategies, such as burrowing and hibernating, and several large mammal lineages adapted by evolving larger sizes, while middle-sized mammals suffered most from the changing conditions.

Body size distributions within mammalian communities were first used as an environmental indicator by Legendre (1986), who introduced a method called cenogram analysis. Cenograms are diagrams that show all mammal species, apart from carnivores, ranked by their body size on the x-axis, and their body masses on the y-axis. Originally, the cenogram analysis was based on observations of the shape of mammalian body size distribution, with continuous distribution from small to large species indicating humid and closed environments, an abrupt steepening of the slope of the body size distribution in the large-sized end of the spectrum (few large-sized species) indicating arid environments, and a gap in medium-sized species (between 500 and 8000 g) indicating open environments (Legendre 1986). Cenogram analyses have been used in paleoenvironmental reconstructions, for example to argue for an environmental change in Europe during the Oligocene, where conditions in southern Europe changed from humid and forested in the Eocene to more open and dryer in the Oligocene, reversing back to more humid and closed during the Early Miocene (Escarguel *et al.* 2008). While the cenogram analysis in its original form is based on qualitative observation of the shape of the body size distribution, more quantitative statistical analyses of mammalian body size distributions and their use as an ecometric method to calculate quantitative estimates of climate and properties of plant communities in paleoenvironments have been developed. Alroy (2000) used statistics such as skewness and curtosis for analyses of mammalian body size distributions. Recently, Wilson and Parker (2023) applied a generalized linear latent variable model-based analysis of body size distribution and dietary guild structure of mammal communities in South America for estimating climatic variables (temperature and precipitation), NPP and tree cover. They used this model to retrodict the environmental conditions in the Middle Miocene fossil locality of La Venta from Colombia, South America, with promising results.

Besides body size distributions within communities, body size variation within mammal lineages and species can also be informative of environmental conditions. Smith *et al.* (2010) noted that maximum body size of terrestrial mammals increased exponentially during the Early Cenozoic, following the extinction of non-avian dinosaurs, but levelled off since the Middle Eocene and started following fluctuations in global climate, with peaks of larger maximum size corresponding with events of global cooling during the Oligocene, the Late Miocene and the Pleistocene. Saarinen *et al.* (2014) discovered that maximum body size frequency (the proportion of terrestrial mammal orders reaching their largest body size) was related to cooling events, with a particularly high maximum size frequency during the Pleistocene ice ages. Huang *et al.* (2023) noted a similar pattern for proboscideans, where their body size followed the global oxygen isotope curve both in Eurasia and Africa during the Neogene, with increase in mean and maximum size during periods of cooling (e.g., Late Miocene and Pleistocene), and smallest mean and maximum sizes occurred during the particularly warm Middle Miocene climatic optimum. While these studies show a relationship of body size with global climate change within large taxonomic groups of mammals, an interpretation of a simple effect of cooling on increase in body size of mammals should be avoided. The global cooling has had different effects in different parts of the world, causing cooling in high latitudes, drying in mid-latitudes and increased seasonality in most parts of the world. Global climate change had a drastically different effect on environments in Europe and North America during the Neogene, with dry, open habitats becoming more prominent earlier during the Miocene in North America, and this is reflected in differential patterns of ungulate (artiodactyl and perissodactyl) body size changes on those continents (Huang *et al.* 2022). These observations have led to the interpretation that increased average body size in large mammal groups is typically associated with increased seasonality and "harshness" of climate, which have affected mammal body size through connections with resource availability and quality, rather than decreasing temperature as such (Saarinen 2014, Huang *et al.* 2023).

Saarinen *et al.* (2016) noted that intraspecific body size variation of several Pleistocene European ungulate species was associated with habitat openness, but the association was different in species with different ecological roles and social structures. Woodland species with moderate group sizes, such as red deer (*Cervus elaphus*), tend to be larger in open environments. This agrees with expectations of benefits of large size in coping with seasonal variation in resource availability and efficient movement in open landscape. In contrast, open-landscape adapted bulk feeders and grazers that form large social groups, such as wild horses (*Equus ferus*), tend to have smaller body size in open environments (Saarinen *et al.* 2016). This reflects a pattern observed in extant ungulates under high population densities, where intraspecific resource competition can limit resource availability to individuals, which is compensated by smaller individual body size (Skogland 1983, Choquenot 1991, Toïgo *et al.* 2006, Wolverton *et al.* 2009). Further studies (Bernor *et al.* 2021, Saarinen *et al.* 2021b, Cirilli *et al.* 2022, 2023, 2024) supported a pattern where small-sized equine horses (Equidae, Equinae) tend to be associated with open, grassland-dominated habitats, have heavily grass-dominated diets, and be abundant in the fossil record (suggesting high population densities in open habitats). Large-sized equines tend in turn to be associated with more wooded paleoenvironments, have more mixed-feeding diets, and be less abundant in the fossil record (suggesting smaller population densities). The general relationship of equine body size and ecology is paralleled in intraspecific body size patterns of Pleistocene equine species, with larger sizes associated with more mixed diets and higher productivity of paleoenvironments, and smaller sizes associated with more grass-dominated diets and smaller estimated productivity of paleoenvironments (Cirilli *et al.* 2022). These patterns suggest that equine body size could be used in an ecometric sense as an indicator of habitat openness and vegetation type past environments, with predominantly small-sized species indicating more open, less productive environments, and predominantly large species or populations with large mean body size indicating more closed and productive paleoenvironments. While this pattern is particularly clear in Pleistocene *Equus* (Saarinen *et al.* 2021b, Cirilli *et al.* 2022, 2023, 2024), it can also be seen in hipparionine horses (Bernor *et al.* 2021). For example, in the Turolian "*Hipparion* fauna" localities of this study, such as Maragheh, the small-sized species such as as *Cremohipparion matthewi* tend to have more grazing mesowear signal than medium- and large-sized species, although some large hipparionines, especially in Africa, were also grazers (Bernor *et al.* 2021).

Postcranial ecometrics of mammals

Postcranial (especially limb bone) proportions of terrestrial mammals are associated with various aspects of their environment, as they are adaptations to moving and feeding in environments with different vegetation cover. Polly (2010) noted a relationship of average “calcaneum gear ratio” (ratio of calcaneum tuberosity length to total length of calcaneum) within carnivoran mammal communities with ecological province, mean annual temperature and vegetation cover in present-day North America. Limb ecomorphology of large herbivorous mammals also reflects adaptations to moving in various vegetation cover from closed forests to open, barren landscapes, and their distribution within communities, especially those of ruminants, has been used as an ecometric variable to estimate vegetation cover in Neogene paleoenvironments (e.g., Kovarovic & Andrews 2007, Plummer *et al*. 2008, Barr 2014, 2017, Gruwier & Kovarovic 2022). Besides carnivorans and artiodactyls, limb proportions of equids have been used as paleoenvironmental indicators. For example, Uzunidis (2021) noted that robustness of metapodials is related to humidity of the paleoenvironment, while width of third phalanx is related to patterns of snow cover in Middle Pleistocene European *Equus*.

Case study — revising Kurtén’s interpretation of later Late Miocene Old World paleoenvironments based on new ecometric analyses

Material and methods

Material

We used molars of large herbivorous mammals for the mesowear analysis in this study. These molars are kept in the following museum collections: the Natural History Museum of London (NHMUK), Naturhistorisches Museum Wien (NHMW), the paleontological collections of the University of Vienna, Muséum national d’histoire naturelle, Paris (MNHN), Senckenberg Museum, Frankfurt (SMF), Bayerische Staatssamlung für Paläontologie, Munich (BSP), and National Museums of Kenya, Nairobi (KNM). Most measurements were taken by J. Saarinen. Mesowear data of ungulates from the Chinese “*Hipparion* fauna” localities were obtained from Eronen *et al.* (2014), omitting data for localities that had only ruminant mesowear data, or mesowear data for fewer than three ungulate species. Mesowear data for ungulates from Maragheh were complemented with the data from Bernor *et al.* (2014) and Jokela (2015). Mesowear data of proboscideans from Maragheh were complemented with data from Loponen (2020).

Dental ecometric data for species from the Late Miocene localities, as well as locality minimum and maximum ages were taken from the NOW Database of fossil mammals (https://doi.org/10.5281/zenodo.4268068, Žliobaite *et al*. 2023), and those for species from present-day national parks and nature reserves used in comparative dental ecometric analyses were taken from the IUCN and other sources (*see* footnote to Table 1). The present-day national parks and nature reserves were selected to represent a wide range of modern biomes and are arguably relatively moderately altered by humans as far as herbivore–environment interactions are concerned. An important criterion in this regard was the presence of diverse large herbivorous mammal communities. These can be argued to be as little affected by megafauna loss due to human activities as possible in the present-day situation; for example, they include large mammal species from several families and megaherbivores such as elephants and rhinos in the tropical environments where those taxa are still present. Arjinshan and Dunhuang Xihu National Nature Reserves from China, and a steppe site from Sarisy, Kazakhstan, were chosen to represent Asian steppe environments. Białowieża Forest (Poland–Belarus) and IUCN site 126218 from British Columbia, Canada, were chosen to represent temperate to boreal forests, because of their relatively diverse large mammal communities. Meru National Park, Samburu Hills and Serengeti were chosen to represent dryer, shrubland to grassland-dominated East African savanna ecosystems, while Aberdare National Park represents a more humid, higher altitude forest-savanna mosaic from East Africa. Nouabale Ndoki National Park from Democratic Republic of Congo represents the central African lowland tropical rainforest biome. Bukit Barisan Selatan National Park, Sumatra, was chosen to represent Southeast Asian tropical rainforest with a diverse large mammal community. Kaziranga National Park, India, represents a southern Asian humid forest-grassland mosaic. Finally, Ranth-

Table 1. Dental ecometric traits of large herbivorous mammal communities in the Late Miocene localities and present-day national parks included in this study. MAX_AGE = maximum age, MIN_AGE = minimum age, HYP = hypsodonty, LOP = longitudinal loph count, AL = acute lophs, OL = obtuse lophs, SF = structural fortification, OT = occlusal topography, BUN = bunodonty, HOD = horizodonty.

Locality	MAX_AGE	MIN_AGE	HYP	LOP	AL	OL	SF	OT	BUN	HOD
Pao-Te-Loc.30*	5.8	5.5	2.13	1.80	0.27	0.73	0	0.20	0.07	1.06
Pao-Te-Loc.31*	7.1	6.9	2.00	1.80	0.40	0.70	0	0.10	0	1.00
Pao-Te-Loc.43*	7.1	6.9	1.88	1.63	0.31	0.75	0	0.13	0.06	1.18
Pao-Te-Loc.49*	7.1	6.9	1.53	1.47	0.35	0.71	0	0.06	0.12	1.22
Pao-Te-Loc.108*	6.6	6.4	1.78	1.89	0.44	0.67	0	0.11	0	1.00
Pao-Te-Loc.109*	7.2	5.3	1.88	1.75	0.25	0.63	0	0.13	0.13	1.11
Yushe-hounao*	7.1	5.3	1.33	1.33	0.67	0.17	0	0.17	0.17	1.50
Qingyang-Loc.115*	7.1	5.3	1.89	1.70	0.44	0.56	0	0.11	0.11	1.10
Qingyang-Loc.116*	7.1	5.3	2.00	2.00	0.30	0.70	0	0.10	0.00	1.00
Wu-Hsiang-Loc.73*	7.1	5.3	1.50	1.63	0.38	0.63	0	0.13	0.13	1.13
Pikermi*	7.5	7.2	1.57	1.43	0.64	0.54	0	0.11	0.07	1.25
Maragheh*	7.6	7.1	1.97	1.58	0.52	0.70	0	0.21	0.06	1.15
Mt. Luberon*	7.6	7.1	1.50	1.50	0.67	0.50	0	0.17	0.17	1.17
Dorn-Dürkheim 1*	8.9	7.6	1.28	1.00	0.67	0.50	0	0.11	0.06	1.39
Kohfidisch*	8.9	7.6	1.50	1.79	0.79	0.43	0	0.07	0	1.00
Lothagam (Lower Nawata)*	7.4	6.5	1.95	1.10	0.24	0.66	0.14	0.17	0.28	1.38
Lukeino*	6.6	5.7	1.57	0.91	0.39	0.65	0.09	0.09	0.17	1.39
Aberdare National Park**	recent	recent	2.17	1.17	0.13	0.78	0.26	0.13	0.13	1.22
Kakamega Forest**	recent	recent	1.59	0.82	0.12	0.53	0.29	0.06	0.35	1.18
Meru National Park**	recent	recent	2.24	1.26	0.12	0.76	0.21	0.24	0.18	1.24
Samburu Hills**	recent	recent	2.27	1.42	0.12	0.81	0.15	0.19	0.15	1.19
Ranthambore National Park**	recent	recent	2.21	1.50	0.21	0.79	0.43	0.07	0.14	1.14
Kaziranga National Park**	recent	recent	1.77	1.00	0.31	0.54	0.31	0.08	0.38	1.15
Tropical rainforest, Bukit Barisan Selatan NP, Sumatra***	recent	recent	1.38	0.69	0.38	0.31	0.15	0.08	0.46	1.15
Tropical rainforest, Nouabale-Ndoki NP**	recent	recent	1.48	0.80	0.20	0.48	0.32	0.04	0.40	1.08
Serengeti (INCN site 98913)**	recent	recent	2.36	1.39	0.11	0.75	0.21	0.21	0.21	1.14
Dry steppe, Dunhuang Xihu NNR, China****	recent	recent	2.67	2.00	0.22	1.00	0	0.33	0	1.00
Białowieża (IUCN site 13410)**	recent	recent	1.50	1.67	0.67	0.83	0.33	0	0.17	1.00
Arjinshan National Nature Reserve, China****	recent	recent	2.75	2.00	0.25	1.00	0.13	0.13	0	1.00
Steppe, Sarisy, Kazakhstan (IUCN site 133019)**	recent	recent	2.50	2.00	0.25	1.00	0	0.25	0	1.00
Boreal forest, British Columbia (IUCN site 126218)**	recent	recent	1.83	2.00	0.83	1.00	0	0	0	1.00

Data sources: *https://doi.org/10.5281/zenodo.4268068.
**https://www.iucnredlist.org/resources/spatial-data-download.
***O’Brien & Kinnaird 1996.
****https://www.cms.int/sites/default/files/document/Annex%20Protected%20Areas%20and%20Priority%20Sites.pdf, Otaishi & Gao1990, Kaji *et al.* 1989.

ambore National Park from India was chosen to represent a dryer, more open south Asian shrubland-grassland "savanna" environment. Dental ecometric data for the localities were compiled by the authors of this study (*see* Table 1, and Appendixes 1 and 2).

Dental ecometric estimates of climate, primary production and normalized difference vegetation index

We analyzed dental ecometrics of large herbivorous mammal paleocommunities from some of the "classic" later Late Miocene (broadly equivalent of Turolian mammal age in Europe) "*Hipparion* fauna" localities of the Old World. We estimated mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), net primary production per annum (NPP, $g(C)/m^2/a$) and normalized difference vegetation index (NDVI) of their paleoenvironments. This was used to test Kurtén's interpretations of the steppe, forest and mixed environments of the Chinese "*Hipparion* faunas", as well as the notion that in the Mediterranean region the fauna from the classic Greek locality Pikermi reflects a more wooded paleoenvironment than the locality of Maragheh in Iran (Kurtén 1952). In addition to these "classic" cases, for comparison we included a couple of well-sampled central European Turolian localities, Dorn-Dürkheim 1 (Germany) and Kohfidisch (Austria), as well as the Lower Nawata Formation of Lothagam (West Turkana, Kenya) and Lukeino (Tugen Hills, Kenya) to represent geographically and presumably climatically widely separate regions.

For dental ecometric estimates of paleoclimatic and plant community properties in the paleoenvironments, we used the equations from Liu *et al.* (2012) and Oksanen *et al.* (2019) that relate hypsodonty (HYP), longitudinal loph count (LOP) and presence of acute lophs (AL) with climatic variables. We chose these models because they are based on training data from a wide range of extant biomes globally. These equations are:

$$\mathrm{MAT} = 27 - 28.5 \times \mathrm{AL}$$
$$\mathrm{MAP} = 2.491 - 289 \times \mathrm{HYP} - 841 \times \mathrm{LOP}$$
$$\mathrm{NPP} = 2601 - 144 \times \mathrm{HYP} - 935 \times \mathrm{LOP}$$

In addition, we estimated NDVI using the equation from Žliobaitė (2016): $\mathrm{NDVI} = 0.337 + 1.429 \times \mathrm{AL} + 0.879 \times \mathrm{SF} - 0.374 \times \mathrm{OT}$. It should be noted that this equation is based on training data from East African national parks, which might limit its applicability outside that region. However, compared to for example mean annual temperature, NDVI may be assumed to be a more globally consistent variable. Nonetheless, we considered the NDVI estimates to be meaningful only in relative terms (in relation to the modern East African model), rather than reflecting realistic NDVI values. We consider this approach justified in terms of analytical integrity, as we use estimated rather than measured values for the recent reference localities as well.

We performed a hierarchical clustering using Ward's method to explore associations between the Late Miocene "*Hipparion* fauna" localities and present-day national parks based on the MAP, MAT, NPP and NDVI estimated from dental ecometric traits. We discuss modern biome analogues for the Late Miocene localities based on their clustering with the present-day national parks. In addition, we performed a principal component analysis (PCA) to further explore associations between the modern and Miocene localities based on the estimated MAP, MAT, NPP and NDVI values.

Estimates of dietary variation and local vegetation structure based on mesowear analyses

We performed mesowear analysis following the methodology introduced by Fortelius and Solounias (2000) for the selenodont and ectolophodont ungulates from the Late Miocene localities. The mesowear scorings were then used to calculate univariate mesowear values for the ungulate species following the methodology of Saarinen *et al.* (2016). We analyzed dietary associations of the fossil ungulates with extant ungulates for which dietary composition is known using hierarchical clustering based on percentage of high cusps, percentage of sharp cusps and percentage of blunt cusps, following the methodology introduced by Fortelius and Solounias (2000).

Mean mesowear values averaged over ungulate communities were used for broadly estimating the proportion of arboreal plant taxa (~estimate of woody plant cover). This was done by first estimating relative vegetation openness using the following least squares linear regression between mean ungulate mesowear value and percentage of non-arboreal pollen (NAP%, proxy for non-arboreal plant cover) in palynological records associated with European Pleistocene mammal localities (Saarinen *et al.* 2016): NAP% = 108.94791 × MW – 104.8073 ($R^2 = 0.60$, $p = 0.005$), where MW is the mean mesowear score of the ungulate species in a locality. Next, we calculated arboreal pollen percentages (AP%, proxy for arboreal (woody) plant cover) for the localities by subtracting NAP% from 100%. Note that both trees and shrubs were counted as arboreal ("woody") taxa in Saarinen *et al.* (2016). This approach has its challenges. For example, NAP percentages have their own sources of error and their direct association with the mammalian paleocommunities can be uncertain in some cases. However, there are a couple of reasons for using such a Pleistocene-based method for estimating vegetation structure for the Late Miocene localities, rather than basing it on a relationship between mesowear of ungulates and tree cover in present environments. First, the Pleistocene was the last time before the drastic effect of modern human activities on global environments. For example, the role of megaherbivores in interacting with their environments, and their dietary signal reflecting the environment (Saarinen & Lister 2016, 2023), were important before the end-Pleistocene megafauna extinctions. The loss of diverse large mammal communities since the Pleistocene was well known to Kurtén himself, and the magnitude and mechanisms of megafauna extinctions in different parts of the world at the end of the Pleistocene have recently been under extensive revisions (e.g., Barnosky *et al.* 2004, Koch & Barnosky 2006, Stuart 2014, Metcalf *et al.* 2016, van der Kaars *et al.* 2017). Second, detailed mesowear analyses of recent ungulate communities associated with a particular area and environment today are lacking. This is due to the difficulty of sampling mesowear from "complete" extant ungulate communities, partly because of the lack of collections of dental specimens and partly because human influence has rendered extant mammal communities incomplete. Whereas fossil collections include extensive samples of craniodental material of ungulates from fossil localities, in the context of modern-day ungulate communities there are rarely comprehensive molar teeth collections available.

We used a least squares linear regression between elephantoid proboscidean mean mesowear angle (averaged over all species of elephantoids per a locality) and estimated proportion of grasses in Neogene East Africa (Saarinen & Lister 2023) to estimate a difference in the proportion of grasses in the vegetation in the Turolian "*Hipparion* fauna" localities. For this we used an ordinary least squares regression model based on the data presented in Saarinen and Lister (2023: extended data fig. 3): grass% = 2.4131744 × MWA – 230.9144 ($R^2 = 0.70$, $p < 0.0001$), where MWA is the mean mesowear angle of elephantoid proboscidean species in the locality.

To visualize the geographic variation in the dental ecometrics and mesowear, we present color-interpolated maps of mean ordinated hypsodonty (HYP) and mean mesowear score (MW), using grid interpolation with the following settings: 26 km grid size, 400 km search radius, 600 km grid border. For the interpolation method, we used an inverse distance weighted algorithm (IDW). Both hypsodonty and mesowear were color-coded from lowest values (blue) to highest values (red) with intermediate values represented by a range from blue to green to yellow to red, following the color coding convention introduced by Fortelius *et al.* (2002) for hypsodonty maps.

Results

The data used for dental ecometric and mesowear analyses are summarized in Tables 1–3, and estimates of MAP, MAT, NPP, NDVI and grass% (in vegetation) for the later Late Miocene localities and present-day national parks used in this study are presented in Table 4.

Hierarchical clustering of the later Late Miocene localities with present-day national parks

Table 2. Mesowear scores of species from the Late Miocene localities included in this study. We followed the original mesowear method of Fortelius and Solounias (2000), with univariate mesowear scores (MW score) calculated using the method of Saarinen *et al.* (2016). *n* = number of specimens studied; %HIGH, %LOW, %SHARP, %ROUND and %BLUNT are percentages of high, low, sharp, round and blunt cusps.

Locality	Family	Species	*n*	%HIGH	%LOW	%SHARP	%ROUND	%BLUNT	MW score
Dorn-Dürkheim 1	Chalicotheriidae	*Anisodon* indet.	4	100	0	50	50	0	1.25
Dorn-Dürkheim 1	Equidae	*Hippotherium primigenium*	12	75	25	66.7	33.3	0	1.42
Dorn-Dürkheim 1	Equidae	*Hippotherium kammerschmittae*	2	100	0	100	0	0	1.00
Dorn-Dürkheim 1	Cervidae	Cervidae, large (cf. *Procapreolus*/ Muntiacinae indet.)	17	100	0	59	41	0	1.21
Dorn-Dürkheim 1	Cervidae	Cervidae, small (cf. *Cervavitulus minimus*)	5	100	0	80	20	0	1.10
Dorn-Dürkheim 1	Moschidae	*Micromeryx* indet.	3	100	0	100	0	0	1.00
Dorn-Dürkheim 1	Bovidae	*Miotragocerus* indet.	7	100	0	57	43	0	1.21
Kohfidisch	Rhinocerotidae	*Aceratherium*? indet.	1	100	0	100	0	0	1.00
Kohfidisch	Equidae	*Hippotherium* indet.	5	100	0	60	40	0	1.20
Kohfidisch	Cervidae	*Cervavitus* indet.	7	100	0	100	0	0	1.00
Kohfidisch	Cervidae	*Euprox* indet.	3	100	0	66.7	33.3	0	1.17
Kohfidisch	Cervidae	*Procapreolus* aff. *lockzyi*	7	100	0	85.7	14.3	0	1.07
Kohfidisch	Moschidae	*Micromeryx* sp.	5	100	0	100	0	0	1.00
Kohfidisch	Bovidae	Caprinae indet. indet.	4	100	0	100	0	0	1.00
Kohfidisch	Bovidae	*Gazella* aff. *pilgrimi*	9	100	0	55.6	44.4	0	1.22
Kohfidisch	Bovidae	*Miotragocerus* indet.	2	100	0	50	50	0	1.25
Kohfidisch	Bovidae	*Orygotherium heinzi*	2	100	0	100	0	0	1.00
Kohfidisch	Bovidae	*Palaeoryx* indet.	6	100	0	83.3	16.7	0	1.08
Kohfidisch	Bovidae	*Protoryx* indet.	5	100	0	60	40	0	1.20
Kohfidisch	Bovidae	*Tragoportax gaudryi*	6	100	0	83.3	16.7	0	1.08
Maragheh	Chalicotheriidae	*Ancylotherium pentelici*	1	100	0	100	0	0	1.00
Maragheh	Rhinocerotidae	*Iranotherium morgani*	3	33.3	66.7	0	66.7	33.3	2.33
Maragheh	Rhinocerotidae	*Miodiceros neumayri*	2	100	0	0	100	0	1.50
Maragheh	Rhinocerotidae	*Chilotherium persiae*	8	100	0	62.5	37.5	0	1.19
Maragheh	Equidae	*Cremohipparion matthewi*	1	0	100	0	100	0	2.50
Maragheh	Equidae	*Cremohipparion moldavicum*	7	71.4	28.6	42.9	57.1	0	1.57
Maragheh	Equidae	*Cremohipparion* aff. *moldavicum*	6	33.3	66.7	50	50	0	1.92
Maragheh	Equidae	*Hipparion campbelli*	3	66.7	33.3	0	100	0	1.83
Maragheh	Equidae	*Hippotherium brachypus*	5	60	40	0	100	0	1.90
Maragheh	Giraffidae	*Bohlinia attica*	2	100	0	100	0	0	1.00
Maragheh	Giraffidae	*Honanotherium bernori*	2	100	0	50	50	0	1.25
Maragheh	Giraffidae	*Helladotherium duvernoyi*	2	100	0	0	100	0	1.50
Maragheh	Giraffidae	*Palaeotragus coelophryes*	1	100	0	100	0	0	1.00
Maragheh	Giraffidae	*Samotherium neumayri*	5	100	0	20	80	0	1.40
Maragheh	Bovidae	*Tragoportax amalthea*	11	100	0	0	100	0	1.50
Maragheh	Bovidae	*Urmiatherium polaki*	4	50	50	25	75	0	1.88
Maragheh	Bovidae	*Gazella* sp.	9	66.7	33.3	22.2	77.8	0	1.72
Maragheh	Bovidae	*Criotherium argaloides*	1	100	0	100	0	0	1.00
Maragheh	Bovidae	*Miotragocerus* indet.	1	100	0	100	0	0	1.00
Maragheh	Bovidae	*Oioceros atropatenes*	5	100	0	80	20	0	1.10
Maragheh	Bovidae	*Palaeoreas* sp.	8	62.5	37.5	12.5	87.5	0	1.81
Maragheh	Bovidae	*Protoryx carolinae*	1	100	0	0	100	0	1.50
Maragheh	Bovidae	*Protragelaphus skouzesi*	3	66.7	33.3	0	100	0	1.83
Maragheh	Bovidae	*Samoceros minotaurus*	1	100	0	0	100	0	1.50
Mt. Luberon	Equidae	*Hipparion prostylum*	11	9.1	90.9	27.3	63.6	9.1	2.32
Mt. Luberon	Cervidae	*Pliocervus matheronis*	2	100	0	50	50	0	1.25
Mt. Luberon	Bovidae	*Tragoportax amalthea*	3	100	0	33.3	66.7	0	1.33

continued

Table 2. Continued.

Locality	Family	Species	*n*	%HIGH	%LOW	%SHARP	%ROUND	%BLUNT	MW score
Mt. Luberon	Bovidae	*Gazella deperdita*	5	100	0	60	40	0	1.20
Pikermi	Chalicotheriidae	*Ancylotherium pentelici*	2	100	0	100	0	0	1.00
Pikermi	Rhinocerotidae	*Acerorhinus neleus*	1	100	0	100	0	0	1.00
Pikermi	Rhinocerotidae	*Miodiceros neumayri*	7	100	0	42.9	57.1	0	1.29
Pikermi	Rhinocerotidae	*Dihoplus pikermiensis*	7	100	0	85.7	14.3	0	1.07
Pikermi	Equidae	*Cremohipparion mediterraneum*	10	30	70	80	20	0	1.80
Pikermi	Equidae	*Hippotherium brachypus*	8	75	25	37.5	62.5	0	1.56
Pikermi	Giraffidae	*Bohlinia attica*	3	100	0	100	0	0	1.00
Pikermi	Giraffidae	*Helladotherium duvernoyi*	2	100	0	100	0	0	1.00
Pikermi	Giraffidae	*Palaeotragus rouenii*	3	100	0	100	0	0	1.00
Pikermi	Cervidae	*Pliocervus pentelici*	1	100	0	100	0	0	1.00
Pikermi	Bovidae	*Gazella capricornis*	5	100	0	60	40	0	1.20
Pikermi	Bovidae	*Miotragocerus valenciennesi*	7	100	0	85.7	14.3	0	1.07
Pikermi	Bovidae	*Oioceros rothii*	4	100	0	75	25	0	1.13
Pikermi	Bovidae	*Palaeoreas lindermayeri*	7	100	0	85.7	14.3	0	1.07
Pikermi	Bovidae	*Palaeoryx pallasi*	4	100	0	75	25	0	1.13
Pikermi	Bovidae	*Protoryx carolinae*	2	100	0	50	50	0	1.25
Pikermi	Bovidae	*Prostrepsiceros rotundicornis*	1	100	0	0	100	0	1.50
Pikermi	Bovidae	*Protragelaphus skouzesi*	2	100	0	100	0	0	1.00
Pikermi	Bovidae	*Sporadotragus parvidens*	2	100	0	50	50	0	1.25
Pikermi	Bovidae	*Tragoportax amalthea*	11	100	0	54.5	45.5	0	1.23
Pao-Te-Loc.30	Rhinocerotidae	*Chilotherium*-30 indet. (not specified)	6	100	0	16	83	0	1.42
Pao-Te-Loc.30	Bovidae	*Gazella*-30 indet. (not specified)	26	100	0	69	30	0	1.15
Pao-Te-Loc.30	Equidae	*Hipparion*-30 indet. (not specified)	17	64	35	35	64	0	1.68
Pao-Te-Loc.30	Giraffidae	*Palaeotragus*-30 indet. (not specified)	2	100	0	50	50	0	1.25
Pao-Te-Loc.30	Giraffidae	*Samotherium*-30 indet. (not specified)	17	88	11	5	94	0	1.59
Pao-Te-Loc.30	Bovidae	*Sinotragus*-30 indet. (not specified)	10	90	10	70	30	0	1.25
Pao-Te-Loc.30	Bovidae	*Tragoreas* (*Dorcadoryx*)-30 indet. (not specified)	2	100	0	0	100	0	1.50
Pao-Te-Loc.30	Bovidae	*Urmiatherium*-30 indet. (not specified)	31	83	16	25	74	0	1.53
Pao-Te-Loc.31	Rhinocerotidae	*Chilotherium*-31 indet. (not specified)	3	66	33	0	100	0	1.83
Pao-Te-Loc.31	Equidae	*Hipparion*-31 indet. (not specified)	2	100	0	0	100	0	1.50
Pao-Te-Loc.31	Rhinocerotidae	*Sinotherium*-31 indet. (not specified)	2	0	100	100	0	0	2.00
Pao-Te-Loc.31	Bovidae	*Tragoreas* (*Dorcadoryx*)-31 indet. (not specified)	2	100	0	100	0	0	1.00
Pao-Te-Loc.43	Rhinocerotidae	*Chilotherium*-43 indet. (not specified)	5	80	20	20	80	0	1.60
Pao-Te-Loc.43	Bovidae	*Gazella*-43 indet. (not specified)	3	0	100	33	0	66	2.67
Pao-Te-Loc.43	Equidae	*Hipparion*-43 indet. (not specified)	12	100	0	66	33	0	1.17
Pao-Te-Loc.43	Giraffidae	*Palaeotragus*-43 indet. (not specified)	3	100	0	0	100	0	1.50

continued

Table 2. Continued.

Locality	Family	Species	*n*	%HIGH	%LOW	%SHARP	%ROUND	%BLUNT	MW score
Pao-Te-Loc.43	Giraffidae	*Samotherium*-43 indet. (not specified)	2	50	50	0	100	0	2.00
Pao-Te-Loc.43	Bovidae	*Urmiatherium*-43 indet. (not specified)	2	50	50	0	100	0	2.00
Pao-Te-Loc.49	Rhinocerotidae	*Acerorhinus*-49 indet. (not specified)	2	100	0	100	0	0	1.00
Pao-Te-Loc.49	Cervidae	*Cervavitus*-49 indet. (not specified)	2	100	0	50	50	0	1.25
Pao-Te-Loc.49	Bovidae	*Gazella*-49 indet. (not specified)	10	100	0	90	10	0	1.05
Pao-Te-Loc.49	Bovidae	*Urmiatherium*-49 indet. (not specified)	5	80	20	40	60	0	1.5
Pao-Te-Loc.49	Giraffidae	*Honanotherium*-49 indet. (not specified)	2	100	0	0	100	0	1.5
Pao-Te-Loc.49	Giraffidae	*Palaeotragus*-49 indet. (not specified)	3	100	0	33	66	0	1.33
Pao-Te-Loc.49	Equidae	*Hipparion*-49 indet. (not specified)	3	100	0	66	33	0	1.17
Wu-Hsiang-Loc.73	Cervidae	*Cervavitus*-73 indet. (not specified)	16	100	0	62	37	0	1.19
Wu-Hsiang-Loc.73	Bovidae	*Gazella*-73 indet. (not specified)	7	100	0	28	71	0	1.36
Wu-Hsiang-Loc.73	Equidae	*Hipparion*-73 indet. (not specified)	5	100	0	40	60	0	1.30
Lukeino	Equidae	Hipparionini indet.	2	50	50	50	50	0	1.75
Lukeino	Bovidae	*Tragelaphus spekei*?	2	100	0	50	50	0	1.25
Lukeino	Bovidae	Bovidae indet. indet. (large, hypsodont)	1	100	0	100	0	0	1.00
Lothagam (Nawata)	Bovidae	Alcelaphini indet. indet.	3	33.3	66.7	0	33.3	66.7	2.50
Lothagam (Nawata)	Bovidae	*Aepyceros praemelampus*	1	100	0	100	0	0	1.00
Lothagam (Nawata)	Bovidae	*Madoqua* indet.	1	100	0	100	0	0	1.00
Lothagam (Nawata)	Bovidae	Boselaphini indet. indet.	5	100	0	40	60	0	1.30
Lothagam (Nawata)	Bovidae	Tragelaphini indet. indet. (*T. kyaloae*?)	1	100	0	100	0	0	1.00
Lothagam (Nawata)	Bovidae	Bovini indet. indet.	2	100	0	0	100	0	1.50
Lothagam (Nawata)	Giraffidae	*Palaeotragus germaini*	1	100	0	100	0	0	1.00
Lothagam (Nawata)	Equidae	*Sivalhippus turkanense*	3	66.7	33.3	66.7	0	33.3	1.67
Lothagam (Nawata)	Equidae	*Eurygnathohippus feibeli*	4	0	100	0	100	0	2.50
Lothagam (Nawata)	Rhinocerotidae	*Brachypotherium lewisi*	3	100	0	0	66.7	33.3	1.67

Table 3. Elephantoid proboscidean mesowear angles from the Late Miocene localities included in this study. Data collected by J. Saarinen, with data for Maragheh partly obtained from Loponen (2020). MW = mesowear.

Locality	Species	Specimen	Mean MW angle
Dorn-Dürkheim 1	*Anancus lehmanni*	SMF-DD3142	103.07
Dorn-Dürkheim 1	*Anancus lehmanni*	SMF-DD5362a	108.60
Dorn-Dürkheim 1	*Anancus lehmanni*	SMF-DD5377	106.00
Dorn-Dürkheim 1	*Anancus lehmanni*	SMF-DD3167	114.40
Dorn-Dürkheim 1	*Anancus lehmanni*	SMF-DD E1:6G, 16.7.89	108.90
Dorn-Dürkheim 1	*Anancus lehmanni*	SMF-DD zahn 65 Mastodon, F6	108.70
Dorn-Dürkheim 1	*Tetralophodon longirostris*	SMF-DD3163	103.50
Lothagam	*Anancus kenyensis*	KNM-LT 361	116.40
Lothagam	*Anancus kenyensis*	KNM-LT 437	112.40
Lothagam	*Anancus kenyensis*	KNM-LT-361	120.00
Lothagam	*Primelephas korotorensis*	KNM-LT 23783 (type)	110.90
Lothagam	*Primelephas korotorensis*	KNM-LT 23783 (type)	111.75

continued

Table 3. Continued.

Locality	Species	Specimen	Mean MW angle
Lothagam	*Primelephas korotorensis*	KNM-LT 358	121.30
Lothagam	*Primelephas korotorensis*	KNM-LT 375	118.00
Lothagam	*Primelephas korotorensis*	KNM-LT 351 (holotype)	116.00
Lothagam	*Stegotetrabelodon orbus*	KNM-LT 23791	115.83
Lothagam	*Stegotetrabelodon orbus*	KNM-LT 347	110.00
Lothagam	*Stegotetrabelodon orbus*	KNM-LT-26318	121.90
Lothagam	*Stegotetrabelodon orbus*	KNM-LT-26319	119.90
Lothagam	*Stegotetrabelodon orbus*	KNM-LT-26319	117.00
Lothagam	*Stegotetrabelodon orbus*	KNM-LT-349	121.20
Lothagam	*Stegotetrabelodon orbus*	KNM-LT-366	121.47
Lothagam	*Stegotetrabelodon orbus*	KNM-LT-367	112.75
Lothagam	*Stegotetrabelodon orbus*	KNM-LT-434	122.60
Lothagam	*Stegotetrabelodon orbus*	KNM-LT 354 (holotype)	108.93
Lukeino	*Anancus kenyensis*	KNM-LU 1023	93.75
Lukeino	*Anancus kenyensis*	KNM-LU 1024	121.80
Lukeino	*Anancus kenyensis*	KNM-LU 525	102.10
Lukeino	*Anancus kenyensis*	KNM-LU 57	98.20
Lukeino	*Anancus kenyensis*	KNM-LU 57	121.25
Lukeino	*Anancus kenyensis*	KNM-LU 57	113.70
Lukeino	*Anancus kenyensis*	KNM-LU 65	104.60
Lukeino	*Anancus kenyensis*	KNM-LU 763	104.90
Lukeino	*Anancus kenyensis*	KNM-LU 975	101.87
Lukeino	*Anancus kenyensis*	KNM-TH 37045	108.95
Lukeino	*Loxodonta cookei*	KNM-LU 526	90.50
Lukeino	*Loxodonta cookei*	KNM-LU 67	101.15
Lukeino	*Loxodonta cookei*	KNM-TH 37521	92.43
Lukeino	*Loxodonta cookei*	KNM-LU 916	105.80
Lukeino	*Mammuthus subplanifrons*	KNM-LU 7597	99.25
Lukeino	*Primelephas korotorensis*	KNM-LU 58	110.10
Lukeino	*Primelephas korotorensis*	KNM-LU 59	121.60
Lukeino	*Primelephas korotorensis*	KNM-TH 15581	98.50
Lukeino	*Primelephas korotorensis*	KNM-TH 15581	102.70
Lukeino	*Primelephas korotorensis*	KNM-TH 32836	99.80
Lukeino	*Primelephas korotorensis*	KNM-LU 1025	97.10
Lukeino	*Primelephas korotorensis*	KNM-LU 522	104.30
Maragheh	*Choerolophodon pentelici*	NHMUK-PV-M7422	126.35
Maragheh	*Choerolophodon pentelici*	NHMUK-PV-M3957	126.60
Maragheh	*Choerolophodon pentelici*	NHMUK-PV-M361	123.20
Maragheh	*Choerolophodon pentelici*	NHMW-Mar-2379 (A 4826)	118.10
Maragheh	*Choerolophodon pentelici*	NHMW-Mar-2392 (A 4831)	127.50
Maragheh	*Choerolophodon pentelici*	NHMW-Mar-2382 (A 4825)	128.40
Maragheh	*Choerolophodon pentelici*	NHMW-Mar-2391	114.85
Maragheh	*Choerolophodon pentelici*	NHMW A 4809	127.95
Maragheh	*Choerolophodon pentelici*	NHMW-Mar-2371 (A 4868)	126.80
Maragheh	*Choerolophodon pentelici*	NHMW-Mar-2377 (A 4807)	120.40
Maragheh	*Choerolophodon pentelici*	NHMW-Mar-2447A	133.70
Maragheh	*Choerolophodon pentelici*	NHMW-Mar-2369A (4868 A)	127.93
Maragheh	*Choerolophodon pentelici*	NHMW-Mar-2447B	123.00
Maragheh	*Choerolophodon pentelici*	NHMW-Mar-2369A (4868 B)	126.40
Maragheh	*Konobelodon atticus*	NHMW Mar 2395	90.40
Maragheh	*Konobelodon atticus*	NHMW Mar 2380	99.60
Pikermi	*Choerolophodon pentelici*	MNHN.Pik-1705	118.90
Pikermi	*Konobelodon atticus*	BSP AS II 182 (type of “*Tetralophodon*” *atticus*)	97.20
Pikermi	*Konobelodon atticus*	MNHN.Pik-3674	104.95
Pikermi	*Konobelodon atticus*	MNHN.Pik-1704a	103.30
Pikermi	*Mammut* indet.	NHMUK-PV-M10104	96.60

based on MAT, MAP, NPP and NDVI estimated from dental traits clustered present-day national parks into groups that reflect similar biomes, and revealed broad similarities of the fossil localities to modern biomes (Fig. 1A). Pao-Te localities 30 and 109 and Qingyang locality 116 clustered with modern central Asian steppe reserves. Pao-Te localities 31, 43, 49 and 108, Qingyang locality 115, Wu-Hsiang locality 73 and Maragheh clustered together, with Ranthambore National Park, India (dry deciduous woodland–grassland mosaic), representing the closest modern analogue. In contrast, Yushe-hounao, Pikermi and Mt. Luberon clustered together, next to Dorn-Dürkheim 1 and Kohfidisch, with Kohfidisch clustering closest to modern Białowieża Forest (temperate forest). The East African localities clustered together with modern African environments, Lothagam with various extant “savanna” national parks of Kenya, and Lukeino with extant African tropical forest reserves, although being ecometrically most closely associated with Kaziranga National Park, India. PCA performed on the estimated MAT, MAP, NPP and NDVI values mirrored the hierarchical clustering results, and it shows that the associations between the fossil localities and present-day national parks are not driven by geographic proximity. For example, tropical rainforests of Africa and Asia are separated from both African and Asian steppes/savannas, and both European and East Asian localities were clustered close to extant temperate forests (Fig. 1B). PC1 explained 52.2% of the variation and was driven by MAP and NPP and to a lesser degree by NDVI, as shown in the loading matrix. PC2 explained 45.9% of variation and was driven principally by MAT and to a lesser degree by NPP and MAP (Fig 1B).

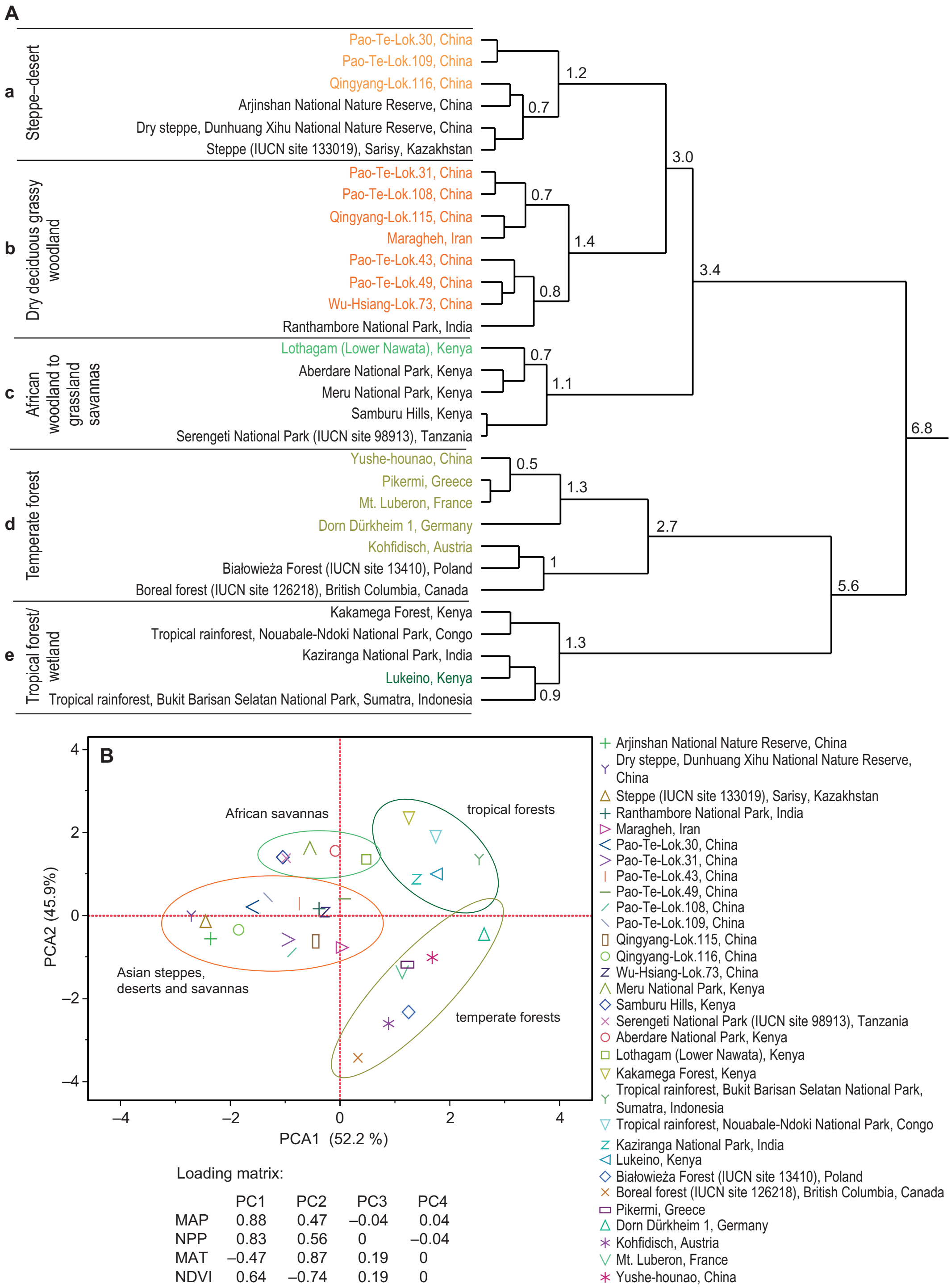
Mean mesowear scores (calculated using the method of Saarinen *et al.* 2016) provided tree cover estimates (equivalent to AP% estimates from Pleistocene European palynological records) for the later Late Miocene “*Hipparion* fauna” localities (Table 4). They mostly agreed with the dental ecometrics-based biome estimates, with Pikermi, Dorn-Dürkheim 1, Kohfidisch and Lukeino showing values higher than 75%, suggesting heavily wooded environments, and Maragheh and Lothagam (Lower Nawata) showing values close to 40%, corresponding with more open “savanna” environments. Of the northern Chinese localities, only Pao-Te-Loc.43 showed very a low AP% estimate (6.3%) consistent with a fully open steppe, while the Pao-Te-Loc.30 and 31 showed intermediate AP% estimates (50% and 32%, respectively), perhaps indicating “mixed” environments at a steppe edge (*sensu* Kurtén 1952). In contrast, Pao-Te-Loc.49 and Wu-Hsiang-Loc.73 had higher estimated woody plant cover (between 65% and 70%), based on mesowear (Table 4). Grass% estimates based on proboscidean mesowear indicated less than 25% grass (of local vegetation) in Dorn-Dürkheim 1, Pikermi and Lukeino, ca. 35% grass in Maragheh and ca. 50% grass in Lower Nawata Formation in Lothagam (Table 4).

The differences in the community-level mesowear signals between the Late Miocene localities were also reflected in the mesowear signal of key taxonomic groups of large herbivorous mammals. Mesowear angle data from proboscideans is mostly too scarce for intra-specific comparisons, but some genus-level patterns can be noted. *Anancus* had browse-dominated mesowear in Dorn-Dürkheim 1 and Lukeino, as opposed to Lothagam, where it showed grass-dominated mesowear (Table 3). Similarly, *Primelephas* showed browse-dominated mesowear in Lukeino, but grass-dominated mesowear in Lothagam (Table 3).

Mesowear analysis using hierarchical clustering based on percentage of high cusps, sharp cusps and blunt cusps (Fig. 2) further demonstrated dietary differences of ungulates from the Late Miocene localities included in this study (excluding the Chinese localities; discussed in Eronen *et al.* 2014). Several species from most of the localities clustered with extant pure browsers such as *Alces alces* and *Rhinoceros sondaicus*. However, these species were often represented by only one specimen, so their dietary interpretation should be considered tentative, and they are shown here because they are included in the community-level mesowear analyses. Most species from Dorn-Dürkheim 1, Kohfidisch and Pikermi cluster with extant browsers and browse-dominated feeders, such as *Okapia johnstoni*, *Odocoileus virginianus*, *Antilocapra* *americana*, *Antidorcas marsupialis*, *Capreolus capreolus*, *Giraffa camelopardalis*, *Dicerorhinus sumatrensis* and *Rhinoceros unicornis*, or the browse-dominated mixed-feeders *Cervus*

Table 4. Mean annual precipitation (MAP, mm), mean anual temperature (MAT, °C), net primary productivity (NPP) and normalized difference vegetation index (NDVI) estimated from large mammal dental ecometrics (Liu *et al.* 2012, Oksanen *et al.* 2019), grass% (percentage of grass in vegetation) estimated from proboscidean mesowear (Saarinen & Lister 2023), and arboreal pollen percentage (AP%, proxy for arboreal (woody) plant cover) estimated from mean mesowear scores of ungulates (Saarinen *et al.* 2016) from later Late Miocene “*Hipparion* fauna” localities and present-day national parks. Note that the NDVI estimate is based on training data from present-day Kenyan national parks (Žliobaitė *et al.* 2016) and should be considered a relative value compared to the East Afican model, rather than “actual” NDVI (thus values above 1 are present in some cases). Minimum and maximum age (MIN_AGE and MAX_AGE, respectively, millions of years) are given for the Miocene localities.

Locality	MAX_AGE	MIN_AGE	NDVI (relative to East African model)	MAP	NPP	MAT	Grass% (estimated from proboscidean mesowear)	AP% (estimated from MW score)
Late Miocene ”*Hipparion* fauna” localities								
Pao-Te-Loc.30	5.8	5.5	0.64	361	611	19		50
Pao-Te-Loc.31	7.1	6.9	0.87	399	630	16		32.3
Pao-Te-Loc.43	7.1	6.9	0.74	583	812	18		6.3
Pao-Te-Loc.49	7.1	6.9	0.82	812	1006	17		67.8
Pao-Te-Loc.108	6.6	6.4	0.93	389	579	14		
Pao-Te-Loc.109	7.2	5.3	0.65	477	695	20		
Yushe-hounao	7.1	5.3	1.23	984	1162	8		
Qingyang-Loc.115	7.1	5.3	0.93	515	739	14		
Qingyang-Loc.116	7.1	5.3	0.73	231	443	18		
Wu-Hsiang-Loc.73	7.1	5.3	0.83	691	866	16		65.2
Pikermi	7.5	7.2	1.22	835	1039	9	24.3	76.6
Maragheh	7.6	7.1	0.99	597	844	12	34.6	38
Mt. Luberon	7.6	7.1	1.23	796	983	8		38.6
Dorn-Dürkheim 1	8.9	7.6	1.25	1281	1482	8	24.6	77.4
Kohfidisch	8.9	7.6	1.43	556	715	5		85.2
Lothagam (Lower Nawata)	7.4	6.5	0.74	1000	1289	20	49.8	39.9
Lukeino	6.6	5.7	0.94	1271	1522	16	15.7	59.5
Present-day national parks								
Aberdare National Park	recent	recent	0.7	875	1190	23		
Kakamega Forest	recent	recent	0.74	1339	1602	24		
Meru National Park	recent	recent	0.6	781	1097	24		
Samburu Hills	recent	recent	0.57	638	944	24		
Ranthambore National Park	recent	recent	0.99	590	880	21		
Kaziranga National Park	recent	recent	1.02	1139	1411	18		
Tropical rainforest, Bukit Barisan Selatan NP	recent	recent	0.99	1509	1754	16		
Tropical rainforest, Nouabale-Ndoki NP	recent	recent	0.89	1390	1640	21		
Serengeti (INCN site 98913)	recent	recent	0.6	638	959	24		
Dry steppe, Dunhuang Xihu NNR, China	recent	recent	0.53	38	347	21		
Białowieża (IUCN site 13410)	recent	recent	1.58	656	827	8		
Arjinshan National Nature Reserve, China	recent	recent	0.76	14	335	20		
Steppe, Sarisy, Kazakhstan (IUCN site 133019)	recent	recent	0.6	87	371	20		
Boreal forest, British Columbia (IUCN site 126218)	recent	recent	1.53	279	467	3		



Loading matrix:

	PC1	PC2	PC3	PC4
MAP	0.88	0.47	–0.04	0.04
NPP	0.83	0.56	0	–0.04
MAT	–0.47	0.87	0.19	0
NDVI	0.64	–0.74	0.19	0

Fig. 1. — **A**: Hierarchical clustering (Ward’s method) of later Late Miocene localities (colored) and present-day national parks (black) based on MAP, MAT, NPP and NDVI (relative to East African model) estimated from dental ecometric traits. Half square Euclidean distances are indicated for 17 selected clusters. Letters **a**–**e** mark clusters that broadly correspond with specified extant biomes. — **B**: PCA results for later Late Miocene localities and present-day national parks performed on MAP, MAT, NPP and NDVI. The ellipses indicate broad biome associations. Colors of the ellipses same as those used for the main clusters in Fig. 1A.

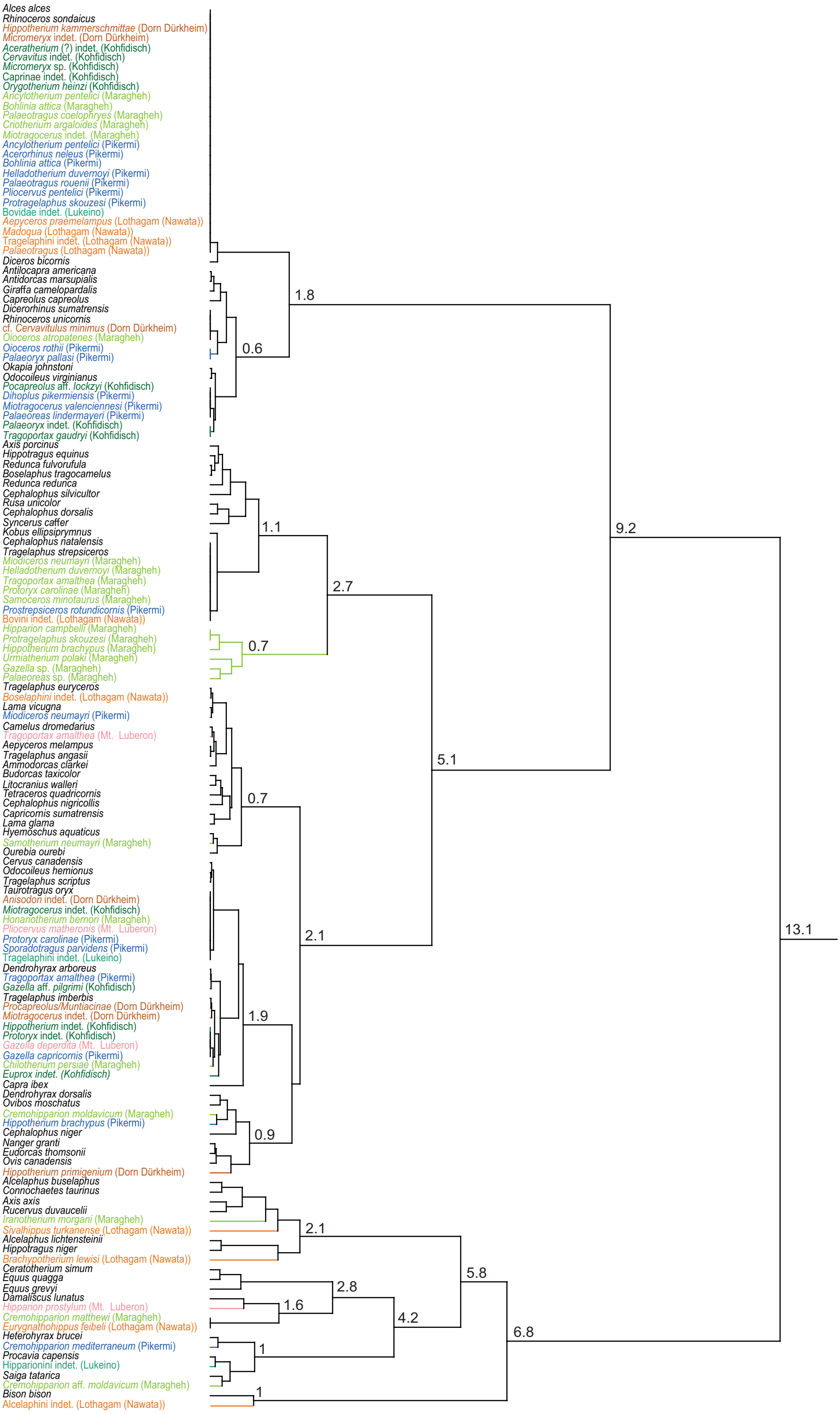


Fig. 2. Hierarchical clustering (Ward's method) of mesowear of ungulates from Pikermi, Maragheh, Dorn-Dürkheim 1, Kohfidisch, Mt. Luberon, Lothagam (Lower Nawata) and Lukeino with extant ungulate species (black) based on percentage of high relief, sharp cusps and blunt cusps. Half square Euclidean distances are indicated for 19 selected clusters. Miocene ungulate paleopopulations are marked with colors according to their localities.

canadensis, *Odocoileus hemionus*, *Tragelaphus scriptus*, *Taurotragus oryx* and *Tragelaphus imberbis* (Fig. 2). *Hippotherium primigenium* from Dorn-Dürkheim 1 and *H. brachypus* from Pikermi clustered with the extant mixed-feeders *Eudorcas thomsonii*, *Nanger granti* and *Ovis canadensis*. *Cremohipparion mediterraneum* from Pikermi clustered with extant *Heterohyrax brucei*. In contrast, the ungulates from Maragheh, Mt. Luberon and Lothagam (Lower Nawata) showed a wider dietary spectrum, including grazers. *Iranotherium morgani* from Maragheh and *Sivalhippus turkanense* from Lothagam clustered with the extant grazers *Alcelaphus buselaphus*, *Connochaetes taurinus*, *Axis axis* and *Rucervus duvaucelii*, and *Brachypotherium lewisi* from Lothagam with *Alcelaphus lichtensteinii* and *Hippotragus niger*. Furthermore, *Cremohipparion matthewi* from Maragheh, *Hipparion prostylum* from Mt. Luberon and *Eurygnathohippus feibeli* from Lothagam clustered with extant *Ceratotherium simum*, *Equus quagga*, *E. grevyi* and *Damaliscus lunatus*, and Alcelaphini indet. from Lothagam with extant *Bison bison*, all of which are pure grazers. Most of the ungulates from Maragheh clustered with a diverse group of extant mixed-feeders, including several grass-dominated feeders, such as *Hippotragus equinus*, *Redunca redunca*, *R. fulvorufula*, *Rusa unicolor*, *Syncerus caffer* and *Kobus ellipsiprymnus*. The ungulate sample from Lukeino was too small for comprehensive interpretation, but they clustered with extant browse-dominated feeders (*Tragelaphus* with extant *Taurotragus oryx* and the hipparionine with extant *Procavia capensis*). In our data, none of the small-sized ungulates from the Miocene localities clustered specifically with the extant "minute abraded brachydont" ("mabra") species such as duikers and hyraxes, which are thought to show cusp tip crushing due to frugivory (Fortelius & Solounias 2000). Thus, we do not expect the "mabra effect" to significantly affect our dietary interpretations within the browse-to-graze spectrum.

Color-interpolated maps (Fig. 3) demonstrate the geographic distribution of mean ordinated hypsodonty and mean mesowear score in the Late Miocene "*Hipparion* fauna" localities. They show a "core area" of the "Old World savannah palaeobiome" (OWSP), *sensu* Kaya *et al.* (2018), including Lothagam, Maragheh, Qingyang localites and some of the Pao-Te localites. Here relatively high hypsodonty and mesowear values indicate relatively dry, open and grassy paleoenvironments, although some other localities considered part of the OWSP, most notably Pikermi, differ from these by having lower mean ordinated hypsodonty and more browse-dominated mesowear signal, indicating a somewhat more humid and less grass-rich paleoenvironment.

Discussion

Our results broadly support Kurtén's (1952) interpretations of a steppe-edge ecotone with steppe, forest and mixed environments in northern China, wooded paleoenvironments in Pikermi and in central Europe, and a more open environment in Maragheh. The northern Chinese localities showed interesting variation in the dental ecometric estimates. Qingyang-Loc.116 (Kurtén's "*dorcadoides*" fauna) and Pao-Te localities 30 and 109 clustered with modern steppe reserves, Yushe-hounao (Kurtén's "*gaudryi*" fauna) clustered close to modern temperate forest (Białowieża Forest), and the rest of the sites (for example most of the Pao-Te localities, considered by Kurtén to mostly represent "mixed" faunas at a steppe edge environment) clustered close to the deciduous woodland-grassland mosaic of present-day Ranthambore National Park. More detailed differences are revealed when the dental ecometric patterns and the ungulate mesowear-based estimates of woody plant cover are compared. Pao-Te localities 31 and 108, and Qinyang-Loc.115 clustered with Maragheh, and are differentiated from Pao-Te localities 43 and 49 and Wu-Hsiang-Loc.73 and Ranthambore National Park mainly because of the lower MAP and NPP estimates. Mesowear indicated very low percentage of woody plant cover for Pao-Te-Loc.43, intermediate woody cover for Pao-Te localities 30 and 31, and relatively high woody cover for Pao-Te-Loc.49 and Wu-Hsiang-Loc.73. These patterns reflect the dental ecometric estimates, which indicate higher precipitation and NPP values for Pao-Te-Loc.49 and Wu-Hsiang-Loc.73 than for the rest of the localities. Unfortunately, mes-

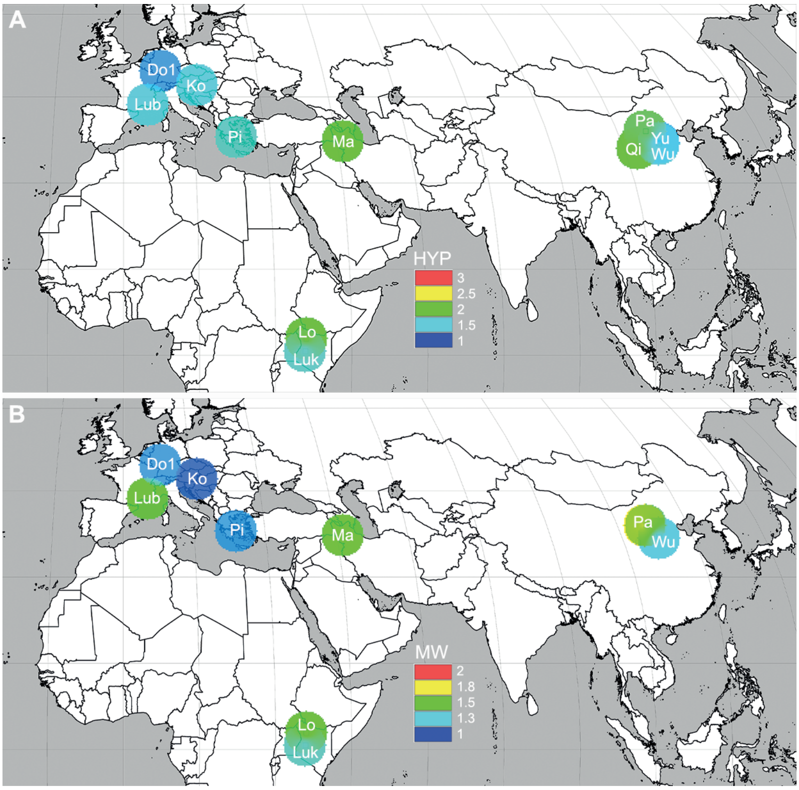


Fig. 3. (**A**) Geographic distribution of the mean ordinated hypsodonty, and (**B**) mean mesowear scores (Saarinen *et al.* 2016) for Late Miocene localities. Do1 = Dorn-Dürkheim 1, Ko = Kohfidisch, Lub = Mt. Luberon, Pi = Pikermi, Ma = Maragheh, Lo = Lothagam (Lower Nawata), Lu = Lukeino, Pa = Pao-Te, Qi = Qingyang, Yu = Yushe-hounao, Wu = Wu-Hsiang.

owear data for the rest of the localities were too scarce to allow for woody cover estimation.

Paleoenvironmental interpretations of the Chinese “*Hipparion* fauna” localities based on dental ecometrics and mesowear can be summarized as follows: (1) Qinyang localities 116 and 115 represent relatively dry and low-productivity, possibly steppe-like environments, in broad agreement with Kurtén’s assessment based on the mostly open-adapted “*dorcadoides*” fauna. (2) Pao-Te localities 30, 31, 43, 108 and 109 are characterized by relatively low MAP and NPP estimates and very low to intermediate estimates of woody cover based on mesowear, thus being in broad agreement with Kurtén’s interpretation of them representing “ecotone” environments at the steppe-forest edge, based on ecomorphologically “mixed” faunas. (3) Pao-Te locality 49 and Wu-Hsiang-Loc.73 are characterized by higher precipitation and NPP estimates and higher woody cover estimates than the previously mentioned sites, while Yushe-hounao has even higher precipitation and NPP estimates, clustering with modern temperate forests. Of these localities, Wu-Hsiang-Loc.73 and Yushe represent Kurtén’s “*gaudryi*” faunas, which he interpreted as being associated with forest environments, while Pao-Te-Loc.49 is more ambiguous in terms of Kurtén’s interpretation, possibly representing a “mixed” faunal assemblage. Thus, our new ecometric estimates broadly correspond with Kurtén’s (1952) interpretations. They suggest a similar environmental gradient from the driest, least productive and most open environments in the north-west (Qinyang localities and some of the Pao-Te localities), to the most humid, productive and wooded environments in the south-east (Wu-Hsiang and Yushe), and intermediate environments in the middle (most of the Pao-Te localities).

Dental ecometric estimates of climatic variables, NPP and NDVI clustered the classic Turolian “*Hipparion* fauna” of Pikermi together with Yushe-hounao and Mt. Luberon, with the closest modern analogue being Białowieża Forest (temperate forest). Mesowear-based estimates indicated relatively high woody plant cover (AP% = 76.6%) and low grass cover (grass% = ca. 24), suggesting a woodland environment with some grassy undergrowth. As with the other Miocene localities, it is important to avoid direct association of Pikermi with modern biomes, such as temperate forest in Białowieża, as the climate and environment in the Late Miocene may not have direct modern analogues, but such comparison serves as a broad approximation. In fact, the cluster containing Pikermi, Yushe-hounao and Mt. Luberon is separated from Dorn-Dürkheim 1 and a cluster containing Kohfidisch and the modern Białowieża Forest, reflecting some differences in the environments, while common features for all these include a combination of relatively low estimated MAT, and relatively high MAP, NPP and NDVI (Fig. 1 and Table 4). It is important to note that some of the ecometric estimates, MAT and NDVI in particular, should be considered only relative and comparable only with other dental ecometrics-based estimates rather than representing "actual" values. While estimates of precipitation and NPP based on dental ecometric estimates tend to correspond with estimated values based on other proxies, temperature estimates from dental ecometrics tend to be less accurate and should be taken to reflect relative differences that are comparable only with other dental ecometrics-based estimates (e.g., Oksanen *et al.* 2019). This is also evident in the case of Pikermi: the MAP estimate based on dental ecometrics is similar to that estimated from associated plant fossil records (800–1000 mm/year; *see* Bruch *et al.* 2006, 2007), while the MAT estimated from plant fossil data is higher and more plausible (17–18 °C; *see* Bruch *et al.* 2006, 2007). It is likely that while dental ecometrics cluster Pikermi with extant temperate forests, this connection reflects similar plant community properties (especially NPP) rather than exact climatic analogue, especially in terms of temperature. Several paleobotanical studies have supported the presence of dry to mesic, temperate to subtropical forest or woodland habitat in Pikermi (Solounias & Dawson-Saunders 1988, Solounias *et al.* 2010, Denk *et al.* 2018).

Our results indicate browse-dominated dietary spectrum of the ungulates and proboscideans in Pikermi. Nearly all ungulates in Pikermi had browsing to browse-dominated mesowear signals, and only two species of hipparionine equids (*Hippotherium brachypus* and *Cremohipparion*) had more grass-dominated mixed-feeding mesowear signals (Table 2). Of the elephantoid proboscideans, *Mammut* indet. and *Konobelodon atticus* had mesowear values indicating browsing diets, with only *Choerolophodon pentelici* showing more grass-dominated mesowear angle (although this is based on only one specimen) (Table 3). Our mesowear-based results of predominantly browse-dominated diets in Pikermi correspond with similar results from other dietary analysis methods, such as microwear analyses (Solounias *et al.* 2010). Furthermore, some faunal elements in Pikermi have been argued to reflect a relatively wooded paleoenvironment, for example the primate *Mesopithecus* and many browse-adapted large herbivorous mammal taxa (Kostopoulos 2009). Since Kurtén (1952), many authors have noted the relatively low percentage of hypsodont large herbivorous mammal species in Pikermi compared to Maragheh (Solounias *et al.* 1999, Ataabadi *et al.* 2013), which we also confirm here (Table 1). These results support Kurtén's original assessment of a wooded paleoenvironment in Pikermi (Kurtén 1952).

In contrast to Pikermi, dental ecometric estimates clustered Maragheh with several of the north Chinese "*Hipparion* fauna" localities, with Ranthambore National Park, India, representing the closest modern analogue. Mesowear-based estimates indicate much lower woody plant cover (AP% = 38%) and higher grass cover (grass% = ca. 35%), further suggesting a "savanna-like" woodland-grassland environment, perhaps something similar to the vegetation type in the Ranthambore National Park today. This interpretation corresponds with Kurtén's (1952) assessment of a more open environment in Maragheh than in Pikermi based on higher proportion of hypsodont ungulates, which has since then been noted by others in more recent revisions (e.g., Ataabadi *et al.* 2013) and confirmed here (Table 1).

Other proxies independent of the mammalian fossil record support a broadly similar paleoenvironmental interpretation. Denk *et al.* (2018) noted based on paleobotanical record an environmental gradient from the wooded environments in the west (Europe) to more open “steppe forest” environments towards the east (Anatolia), which they considered broadly equivalent to Kurtén’s (1952) remarks. Strömberg *et al.* (2007) argued, based on phytolith analysis, a prominent presence of open-habitat grasses in Lower Maragheh (as in Turolian localities from Anatolia). Our results demonstrate a more diverse dietary spectrum of the large herbivorous mammals from Maragheh as compared with those from Pikermi, with the presence of true grazers (e.g., *Cremohipparion matthewi* and *Iranotherium*) in addition to dominant mixed-feeders and grass-dominated feeders (most species of bovids, giraffids and rhinos) and less abundant browsers (*Ancylotherium*, *Bohlinia*, *Palaeotragus*, *Miotragocerus*, *Oioceros* and *Criotherium*) (Table 2). Of the elephantoid proboscideans, *Choerolophodon pentelici* was abundant showing mesowear angles that indicate grazing diet, while browsing *Konobelodon atticus* was present but less abundant (Table 3). In contrast to Pikermi, browsing *Mammut* indet. was absent from Maragheh.

Kurtén argued for forest-dominated environments in central Europe, although the example cases he mentioned are mostly earlier Late Miocene (Vallesian) localites such as Eppelsheim in Germany (Kurtén 1952). In our completely new ecometric analyses of a few key Turolian localities from central and western Europe (Dorn-Dürkheim 1 in Germany, Kohfidisch in Austria, and Mt. Luberon in southern France), those localites clustered together with Pikermi, Yushe-hounao and Białowieża Forest (the closest modern analogue), broadly representing various “temperate forest equivalent” paleoenvironments. However, the mesowear-based estimates of woody plant cover indicated some interesting differences. Wood cover estimates (AP%) for Dorn-Dürkheim 1 and Kohfidisch were high (ca. 77% and ca. 85%, respectively), whereas for Mt. Luberon AP% it was much lower (ca. 39%). The above AP% estimates for Dorn-Dürkheim 1 and Kohfidisch indicate forest-dominated environments, while Mt. Luberon was probably more of an open woodland, shrubland or savanna-like environment. To some extent this may reflect the present-day conditions with southern France differing notably from Germany by having a more Mediterranean climate and predominantly more open environments, although this is not clear from the climatic estimates, and heavy human influence today should be noted.

The climatic and plant community structure estimates for Dorn-Dürkheim 1 were quite similar to those for Pikermi, however with higher precipitation and NPP estimates. They indicate predominantly humid forest or woodland environment, with possibly some more open and grassy areas in Dorn-Dürkheim 1, broadly corresponding with previously published interpretations of the paleoenvironment (Franzen 2013, Costeur *et al*. 2013). Dorn-Dürkheim 1 has been considered unique in being the only Turolian fossil mammal locality in Germany, and “the best known European site of this age that represents a wooded environment” (Franzen 2013: 111). Several features of the mammal fauna indicate a humid, forested paleoenvironment, such as the last records of tapirs (*Tapirus* and *Tapiriscus*) and chalicotheres (*Anisodon*) in the Miocene fossil record from Europe, and abundance of deer (Franzen 1997, 2013). However, Costeur *et al*. (2013) argued for a more open, savanna-like paleoenvironment in Dorn-Dürkheim 1, based on cenogram analysis. Our results indicate a predominantly humid, forested environment, but the mesowear-based woody cover and grass cover estimates indicate presence of some open habitats and grasses as well. Presence of wetland environments in Dorn-Dürkheim 1, supported by high diversity of fossil beavers (Castoridae), has also been discussed (Costeur *et al.* 2013), and it is possible that open, grassy areas at Dorn-Dürkheim 1 represent wetlands rather than dry open habitats. This interpretation is supported by our results indicating a predominantly humid, wooded environment with some open habitats. Mesowear analysis clustered most ungulates from Dorn-Dürkheim 1 with extant browsers, and *Hippotherium primigenium* with extant browse-dominated mixed-feeders. Mesowear angle analysis indicates browse-dominated diets for the elephantoid proboscideans *Anancus lehmanni* and *Tetralophodon longirostris*.

For Kohfidisch we found a combination of highest relative NDVI and AP% estimates, but lower estimated precipitation and NPP than for Dorn-Dürkheim 1 and the lowest annual temperature estimate for the Miocene localities studied here, associating it closest with the extant temperate forest sites (especially Białowieża Forest). However, as discussed above, the temperature estimates for the Miocene European localities based on dental ecometrics are probably underestimates, likely resulting from non-analogue trait-environment associations in the Miocene. Nonetheless, the vegetation type estimates are again generally similar to estimates derived from other proxies. Hofmann and Zetter (2005) presented a detailed paleoenvironmental reconstruction from the geographically adjacent paleobotanical site of Badensdorf, Austria, which they consider contemporaneous with Kohfidisch. Based on the paleobotanical evidence, the local vegetation was dominated by a swamp forest with *Glyptostrobus*, *Nyssa* and other warm temperate to subtropical wetland trees. The swamp forest was surrounded by a more xeric forest, characterized by conifers (e.g., *Sequoia*, *Tsuga*, *Abies*, *Pinus*, *Picea* and *Cedrus*) as well as deciduous angiosperm trees (*Buxus*, *Fagus*, *Castanea*, *Eucommia* and *Tilia*), maidenhair trees (*Gingko*) and smaller amounts of mostly non-grass herbaceous taxa (e.g., *Plantago* and *Artemisia*). A minor element of meadow vegetation (e.g., *Rumex*, *Impatiens*, *Valeriana*, Cyperaceae and Poaceae) was present in the vicinity. These interpretations of the local vegetation community correspond with the estimates for Kohfidisch based on mammalian ecometrics and mesowear, which indicate a closed but not humid temperate forest environment. The mesowear analysis of the ungulates from Kohfidisch clustered all the species with extant browsers, making it the most browser-dominated of all the localities studied here. Perhaps surprisingly, the ungulate fauna is dominated by browsing bovids, although cervids are also diverse. The only proboscidean represented in Kohfidisch is *Deinotherium*. Deinotheres were consistently canopy-level browsers across their temporal and spatial range (e.g., Harris 1975, Markov *et al.* 2001, Calandra *et al.* 2008, Saarinen *et al.* 2015, Xafis *et al.* 2020, Saarinen & Lister 2023).

The dental ecometric estimates from Mt. Luberon, France, indicate a broad association with temperate forests, but the ungulate mesowear signal indicates a relatively high proportion of open, grassy vegetation. This is mostly driven by the abundant hipparionine *Hipparion prostylum*, which shows a grazing mesowear signal in Mt. Luberon. It should be noted that the large herbivorous mammal assemblage from Mt. Luberon is represented by only six species, with mesowear data for only three of them, making the paleoenvironmental interpretation for this locality tentative at best. However, the close association with Pikermi seems plausible.

Finally, the East African example localities, Lothagam (Lower Nawata) and Lukeino show clear differences to the Eurasian Late Miocene localities in terms of dental ecometric estimates (overall higher temperature and NPP estimates, and comparative higher proportion of large herbivorous mammals with structurally fortified and bunodont dentitions). Lothagam (Lower Nawata) clusters ecometrically with extant East African savanna national parks, such as Meru, Samburu Hills, Serengeti and the more wooded Aberdare. The woody cover estimate based on ungulate mesowear (ca. 40% AP) and the very high grass% estimate (ca. 50%) are consistent with an interpretation of a wooded grassland savanna at Lothagam during the Late Miocene. Other paleoenvironmental proxies support this interpretation, for example stable carbon isotope analyses from soil carbonates indicate the presence of 20%–70% (average 48%) C4 vegetation (grasses) at Lower Nawata Formation at Lothagam (Uno *et al.* 2011). The mesowear analyses indicate grazing diets for many of the large herbivorous mammals in Lothagam, including alcelaphine bovids, the rhinoceros *Brachypotherium lewisi*, the hipparionine equids *Eurygnathohippus feibeli* and *Sivalhippus turkanense* and the elephantoid proboscideans (*Primelephas*, *Stegotetrabelodon* and *Anancus*).

In contrast, Lukeino shows higher precipitation and NPP estimates, and lower temperature estimate, clustering it with extant African tropical forests and the tropical forest-wetland mosaic of Kaziranga National Park, India. Mesowear-based estimates indicate a relatively high woody plant cover (ca. 60% AP) and low grass% (ca. 16%), consistent with an overall interpretation of a predominantly wooded environment with some more open, grassy vegetation, which could represent either wetland or dryer open habitats. These interpretations are supported by paleobotanical analyses. Bamford *et al.*'s (2013) analysis of fossil leaves supported the presence of a humid forest or woodland in Lukeino, and stable carbon isotope analyses of Plummer *et al.* (1999) indicated scarcity of C4 plants at that locality. This is further confirmed by the presence of forest-indicating faunal elements, such as chalicotheres and cephalophine bovids in the Lukeino mammal assemblage. The limited mesowear data we had for ungulates from Lukeino clustered with extant browsing and browse-dominated ungulate species. Mesowear angle analyses of elephantoid proboscideans from Lukeino similarly showed browse-dominated dietary signal for all the species, including *Anancus kenyensis*, *Loxodonta cookei* and *Mammuthus subplanifrons*. The mesowear-based interpretations of browse-dominated diets for the large herbivores from Lukeino are supported by stable isotope analyses, which indicate mostly C3-plant based diets (Roche *et al.* 2013).

One "indicator taxon" considered in the context of the paleoenvironmental interpretations could be the deinotheriid proboscideans. Deinotheriids had browsing diets throughout their history, and their ecological role as canopy-level leaf browsers (e.g., Harris 1975, Markov *et al.* 2001, Calandra *et al.* 2008) suggests that they were mostly associated with relatively wooded paleoenvironments. This study suggests that while deinotheres were widely present in the Late Miocene localities (missing only from the Chinese localities in our case), their relative abundance was related to the paleoenvironmental patterns we observed. Deinothere fossils are relatively abundant in the fossil records from the wooded paleoenvironments of Kohfidisch (where they are in fact the only proboscideans) and Dorn-Dürkheim 1, less abundant in Maragheh and Pikermi, and very scarce in Lothagam.

We encountered some challenges in our studies. Our analyses indicated some non-analogue trait–environment associations in the Late Miocene, particularly regarding temperature estimates (for further discussion of non-analogue ecometric associations in the past and on separate continents *see* also Wilson & Saarinen 2024). While mesowear analyses offer a robust method for paleodietary analyses, they ideally require data for several specimens per species or population. Here, however, this was not the case for all the species in the fossil assemblages, as mesowear data for some species were from single specimens. However, we decided to include those data in our community-level mesowear analyses, as long as most of the species from the communities were represented by more than one specimen. Finally, interpretation of the results from the ungulate mesowear-based woody plant cover estimates should be interpreted with care, as browse-dominated diets do not necessarily indicate high tree cover, only lack of grass-dominated vegetation, and thus their interpretation should depend on the context and additional environmental proxies, such as the dental ecometrics-based estimates of plant community properties. It has been argued that the proportion of grazers *vs*. browsers in Africa today does not reflect patterns of tree cover, and grazers can be abundant in environments with high tree cover when there is plenty of grassy undergrowth (Negash & Barr 2023, Sokolowski *et al.* 2023). However, this result is based on broad characterization of species into dietary classes, and does not take into account intraspecific (or intrageneric) dietary variation, which as we demonstrate for the Miocene ungulates, can be considerable, especially among ecologically flexible, dietarily non-selective taxa such as elephantoid proboscideans. Even the dietary signal of equids of the genus *Equus*, one of the most grazing-adapted genera in existence, has been shown to vary considerably in the past, being related to local vegetation patterns (e.g., Rivals *et al.* 2015, Saarinen *et al.* 2021b, Uzunidis 2021, Cirilli *et al.* 2022).

In summary, the new ecometric estimates of later Late Miocene (Turolian and equivalent) localities from Eurasia and Africa reflect a considerable diversity of paleoenviroments and climatic zones from tropical forests and grassland savannas to warm temperate woodlands, temperate woodland–grassland mosaics and dry steppes, thus demonstrating considerable variation in the environmental conditions of the "*Hipparion* faunas". It is interesting to note that while analysis of faunal similarity indicated the presence of a large, more or less uniform biogeographic zone called the "Old World savannah paleobiome" from East Africa to eastern Asia during the Late Miocene (Kaya *et al.* 2018), there was remarkable ecometric, paleoecological and paleonvironmental variation within this realm. This is in agreement with paleoenvironmental inferences from other proxies (e.g., Kurtén 1952, Solounias *et al.* 1999, 2010, Denk *et al.* 2018). This is not to say that the interpretation of Kaya *et al.* (2018) of a coherent Old World savannah paleobiome is wrong, it just refers to an environmentally diverse biogeographic zone with similar faunal elements. Indeed the authors themselves have clarified that the concept of OWSP refers to a diverse set of environments that were "savanna-like" in a very broad sense (Fortelius *et al.* 2019a). While the traits of the herbivorous mammals only reflect the part of the vegetation that the herbivorous mammals consume, thus not providing information on all details of the plant community, averaged trait conditions within the communities reflect broad properties of the plant communities (Fortelius *et al.* 2019b). In fact, we do find differences both in the ecometric trait distribution and dietary signal of the large herbivorous mammals that reflect considerable paleoenvironmental differences between localities considered to be part of the OWSP, such as Pikermi and Maragheh. Indeed, in several genera of large mammals that are present across this vast area, such as bovids of the genera *Tragoportax* and *Gazella*, and proboscideans of the genus *Anancus*, ecometric and mesowear analyses indicate remarkable paleoecological variation between species and populations. For example, mesowear of *Gazella* and *Tragoportax* indicate browse-dominated diets in Pikermi but more grass-dominated mixed-feeding in Maragheh, whereas hipparionine equids were browse-dominated feeders in Dorn-Dürkheim 1, mixed-feeders in Pikermi, more grass-dominated in Maragheh and grazers in Lothagam (Lower Nawata). Some taxa, such as *Gazella*, also show considerable variation in functional traits such as hypsodonty across their range in the Late Miocene, as already noted by Kurtén (1952). The diets of proboscideans, especially elephantoids, are shown to vary a lot according to locally available vegetation, and this is clearly seen in the Late Miocene proboscideans as well. Most strikingly this is demonstrated in East Africa, where the proboscideans show remarkable dietary difference between Lothagam and Lukeino, even intraspecifially with *Primelephas* and *Anancus* being browse-dominated feeders in Lukeino and grass-dominated feeders in Lothagam (Saarinen & Lister 2023, and this study).

Conclusions

Large amounts of paleontological and paleoenvironmental information, based on a wide range of analytical methods, have accumulated since Björn Kurtén published his early work on paleoenvironmental implications of large mammals and their ecomorphological traits (Kurtén 1952, 1968). The mammalian fossil record has provided material and techniques for paleoenvironmental interpretation, including analyses of community structure, stable isotopes, ecomorphology, dental and postcranial functional traits, dental wear as an indicator of diet and environments, and body size variation and body size distribution within mammal communities. As a result, our understanding of interactions and relationships between mammals, vegetation and climate in the present and the past has broadened and provided further understanding of macroevolutionary and macroecological mechanisms, biotic interactions in the absence of human influence on the biosphere and even conditions of human evolution and dispersal history. Challenges for the future include non-analogue trait-environment relationships in the past, which require looking into models based on deep-time proxy comparisons, especially the further back in time the analyses are extended.

On the other hand, many of the basic principles of the relationships between mammals and their environments in the present and in the past were already well known to Kurtén during his career. In this paper, we provided a revision of a few key "*Hipparion* fauna" localities from the later Late Miocene of the Old World based on recently developed dental ecometric and dietary analyses of fossil herbivorous mammal communities. While we present new quantitative estimates of climatic and plant community structure properties in the paleoenvironments, we note that Kurtén was on the right track in the interpretations in his Master's thesis (Kurtén 1952). He suggested a presence of a steppe-forest transition zone in northern China, wooded paleoenvironments in Pikermi and central Europe, and a more open environment in Maragheh during the Late Miocene. Our new results further demonstrate that biomes during the Late Miocene across the Old World were diverse, ranging from tropical forests and savannas in Africa to temperate forests, savannas and steppes in Eurasia.

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Appendix 1. Species-level dental ecometric data. HYP = hypsodonty, LOP = longitudinal loph count, AL = acute loph, OL = obtuse loph, SF = structural fortification, OT = occlusal topography, BUN = bunodonty, HOD = horizodonty.

Locality/species	HYP	LOP	AL	OL	SF	BUN	OT	OO	HOD
Pikermi									
Gazella capricornis	2	2	1	0	0	0	0	0	1
Miotragocerus valenciennesi	1	2	1	1	0	0	0	0	1
Oioceros rothi	2	2	0	1	0	0	0	1	1
Paleoreas lindermayeri	2	2	1	1	0	0	0	0	1
Palaeoryx pallasi	2	2	0	1	0	0	0	1	1
Prostrepsiceros rotundicornis	2	2	0	1	0	0	0	0	1
Protoryx carolinae	1	2	1	1	0	0	0	0	1
Protragelaphus skouzesi	2	2	1	0	0	0	0	0	1
Sporadotragus parvidens	2	2	0	1	0	0	0	1	1
Tragoportax amalthea	2	2	1	1	0	0	0	0	1
Lucentia indet.	1	2	1	0	0	0	0	0	1
Pliocervus pentelici	1	2	1	0	0	0	0	0	1
Bohlinia attica	1	2	1	0	0	0	0	0	1
Helladotherium duvernoyi	2	2	1	0	0	0	0	0	1
Palaeotragus roueni	1	2	1	0	0	0	0	0	1
Hippopotamodon major	1	0	0	0	0	1	0	0	2
Dorcatherium indet.	1	2	1	0	0	0	0	0	1
Ancylotherium pentelicum	1	1	1	0	0	0	0	0	1
Cremohipparion mediterraneum	3	2	0	1	0	0	1	0	1
Hippotherium brachypus	3	2	0	1	0	0	1	0	1
Acerorhinus neleus	1	1	1	1	0	0	0	0	1
Dihoplus pikermiensis	2	1	1	1	0	0	0	0	1
Miodiceros neumayri	2	1	1	1	0	0	0	0	1
Mesopithecus pentelicus	1	0	0	0	0	1	0	0	1
Deinotherium proavum	1	0	1	0	0	0	0	0	1
Konobelodon atticus	1	0	0	1	0	0	0	0	3
Choerolophodon pentelici	2	0	0	1	0	0	1	0	3
Mammut indet.	1	0	1	0	0	0	0	0	3
Maragheh									
Ancylotherium pentelici	1	1	1	0	0	0	0	0	1
Iranotherium morgani	3	1	0	1	0	0	1	0	1
Miodiceros neumayri	2	1	1	1	0	0	0	0	1
Chilotherium persiae	2	1	1	1	0	0	0	0	1

continued

Appendix 1. Continued.

Locality/species	HYP	LOP	AL	OL	SF	BUN	OT	OO	HOD
Maragheh									
Cremohipparion matthewi	3	2	0	1	0	0	1	0	1
Cremohipparion moldavicum	3	2	0	1	0	0	1	0	1
Cremohipparion aff. *moldavicum*	3	2	0	1	0	0	1	0	1
Hipparion campbelli	3	2	0	1	0	0	1	0	1
Hippotherium brachypus	3	2	0	1	0	0	1	0	1
Bohlinia attica	1	2	1	0	0	0	0	0	1
Honanotherium bernori	1	2	1	0	0	0	0	0	1
Helladotherium duvernoyi	2	2	1	0	0	0	0	0	1
Palaeotragus coelophryes	1	2	1	0	0	0	0	0	1
Samotherium neumayri	2	2	1	1	0	0	0	0	1
Tragoportax amalthea	2	2	1	1	0	0	0	0	1
Urmiatherium polaki	3	2	0	1	0	0	0	1	1
Gazella sp.	2	2	1	0	0	0	0	0	1
Criotherium argaloides	3	2	0	1	0	0	0	1	1
Miotragocerus indet.	1	2	1	1	0	0	0	0	1
Oioceros atropatenes	2	2	0	1	0	0	0	1	1
Palaeoreas sp.	2	2	1	1	0	0	0	0	1
Protoryx carolinae	1	2	1	1	0	0	0	0	1
Protragelaphus skouzesi	2	2	1	0	0	0	0	0	1
Hippopotamodon major	1	0	0	0	0	1	0	0	2
Deinotherium proavum	1	0	1	0	0	0	0	0	1
Konobelodon atticus	1	0	0	1	0	0	0	0	3
Choerolophodon pentelici	2	0	0	1	0	0	1	0	3
Skoufotragus laticeps	2	2	1	1	0	0	0	0	1
Prostrepsiceros rotundicornis	2	2	0	1	0	0	0	0	1
Prostrepsiceros vinyaki	3	2	0	1	0	0	0	0	1
Mesopithecus pentelicus	1	0	0	0	0	1	0	0	1
Samoceros minotaurus	2	2	1	1	0	0	0	0	1
Oioceros rothii	2	2	0	1	0	0	0	1	1
Mt. Luberon									
Hipparion prostylum	3	2	0	1	0	0	1	0	1
Pliocervus matheronis	1	2	1	0	0	0	0	0	1
Tragoportax amalthea	2	2	1	1	0	0	0	0	1
Gazella deperdita	1	2	1	0	0	0	0	0	1
Dihoplus schleiermacheri	1	1	1	1	0	0	0	0	1
Microstonyx erymanthius	1	0	0	0	0	1	0	0	2
Dorn-Dürkheim 1									
Anisodon indet.	1	1	1	0	0	0	0	0	1
Hippotherium primigenium	3	2	0	1	0	0	1	0	1
Hippotherium kammerschmittae	3	2	0	1	0	0	1	0	1
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	1	2	1	0	0	0	0	0	1
Cervidae, small (cf. *Cervavitulus minimus*)	1	2	1	0	0	0	0	0	1
Micromeryx indet.	1	2	1	0	0	0	0	0	1
Miotragocerus indet.	1	2	1	1	0	0	0	0	1
Dorcatherium naui	1	2	1	0	0	0	0	0	1
Hippopotamodon major	1	0	0	0	0	1	0	0	2
Aceratherium incisivum	1	1	1	1	0	0	0	0	1
Alicornops alfambrensis	2	1	1	1	0	0	0	0	1
Dihoplus schleiermacheri	1	1	1	1	0	0	0	0	1
Tapiriscus pannonicus	1	0	1	0	0	0	0	0	1
Tapirus priscus	1	0	1	0	0	0	0	0	1
Deinotherium proavum	1	0	1	0	0	0	0	0	1

continued

Appendix 1. Continued.

Locality/species	HYP	LOP	AL	OL	SF	BUN	OT	OO	HOD
Dorn-Dürkheim 1									
Anancus lehmanni	1	0	0	1	0	0	0	0	3
Tetralophodon longirostris	1	0	0	1	0	0	0	0	3
Stegolophodon caementifer	1	0	0	1	0	0	0	0	3
Kohfidisch									
Aceratherium? indet.	1	1	1	1	0	0	0	0	1
Hippotherium indet.	3	2	0	1	0	0	1	0	1
Cervavitus indet.	1	2	1	0	0	0	0	0	1
Euprox indet.	1	2	1	0	0	0	0	0	1
Procapreolus aff. *lockzyi*	1	2	1	0	0	0	0	0	1
Micromeryx sp.	1	2	1	0	0	0	0	0	1
Caprinae indet indet.	2	2	0	1	0	0	0	0	1
Gazella aff. *pilgrimi*	2	2	1	1	0	0	0	0	1
Miotragocerus indet.	1	2	1	0	0	0	0	0	1
Orygotherium heinzi	1	2	1	0	0	0	0	0	1
Palaeoryx indet.	2	2	0	1	0	0	0	0	1
Protoryx indet.	2	2	1	1	0	0	0	0	1
Tragoportax gaudryi	2	2	1	0	0	0	0	0	1
Deinotherium indet.	1	0	1	0	0	0	0	0	1
Lothagam (Lower Nawata)									
Aepyceros praemelampus	3	2	0	1	0	0	0	1	1
Damaliscus sp.	3	2	0	1	0	0	1	1	1
Bovini indet. (cf. *Simatherium*) indet.	3	2	0	1	1	0	0	0	1
Hippotragus indet.	3	2	0	1	1	0	1	1	1
Kobus laticornis	3	2	0	1	1	0	0	0	1
Kobus praesigmoidalis	3	2	0	1	1	0	0	0	1
Menelikia leakeyi	3	2	0	1	0	0	1	1	1
Tragelaphus kyaloae?	2	2	1	1	0	0	0	0	1
Prostrepsiceros indet.	2.5	2	0	1	0	0	0	0	1
Raphicerus indet.	3	2	1	1	0	0	0	0	1
Tragoportax indet.	2	2	1	1	0	0	0	0	1
Palaeotragus germaini	1	2	1	0	0	0	0	0	1
Sivatherium indet.	2	2	0	1	0	0	0	1	1
Archaeopotamus harvardi	1	0	0	0	0	1	0	0	1
Archaeopotamus lothagamensis	1	0	0	0	0	1	0	0	1
Conohyus giganteus	1	0	0	0	0	1	0	0	2
Kubanochoerus indet.	1	0	0	0	0	1	0	0	2
Nyanzachoerus jaegeri/*euilus*	1	0	0	0	0	1	0	0	2
Potamochoerus indet.	1	0	0	0	0	1	0	0	2
Sivachoerus syrticus	1	0	0	0	0	1	0	0	2
Eurygnathohippus feibeli	3	2	0	1	0	0	1	0	1
Sivalhippus turkanense	3	2	0	1	0	0	1	0	1
Brachypotherium lewisi	2	1	1	1	0	0	0	0	1
Ceratotherium praecox	2	1	1	1	0	0	0	0	1
Deinotherium bozasi	1	0	1	0	0	0	0	0	1
Stegotetrabelodon orbus	1	0	0	1	0	0	0	0	3
Primelephas korotorensis	1	0	0	1	0	0	0	0	3
Anancus kenyensis	2	0	0	1	0	0	0	0	3
Parapapio lothagamensis	1	0	0	0	0	1	0	0	1
Lukeino									
Aepyceros indet.	3	2	0	1	0	0	0	1	1
Cephalophus indet.	1	2	0	1	1	0	0	0	1
Gazella indet.	3	2	1	1	0	0	0	0	1
Tragelaphus spekei	1	2	1	1	0	0	0	0	1
Ugandax gautieri	2	2	0	1	1	0	0	0	1

continued

Appendix 1. Continued.

Locality/species	HYP	LOP	AL	OL	SF	BUN	OT	OO	HOD
Lukeino									
Giraffa jumae	1	2	1	0	0	0	0	0	1
Hippopotamus indet.	1	0	0	1	0	0	0	0	1
Cainochoerus africanus	1	0	0	0	0	1	0	0	1
Sivachoerus syrticus	1	0	0	0	0	1	0	0	2
Ancylotherium ceboitense	1	1	1	0	0	0	0	0	1
Chemositia indet.	1	1	1	0	0	0	0	0	1
Sivalhippus turkanense	3	2	0	1	0	0	1	0	1
”*Hipparion*” *sitifense*	3	2	0	1	0	0	1	0	1
Brachypotherium lewisi	2	1	1	1	0	0	0	0	1
Ceratotherium praecox	2	1	1	1	0	0	0	0	1
Diceros bicornis	2	1	1	1	0	0	0	0	1
Colobus indet.	1	0	0	0	0	1	0	0	1
Orrorin tugenensis	1	0	0	0	0	1	0	0	1
Deinotherium bozasi	1	0	1	0	0	0	0	0	1
Stegotetrabelodon orbus	1	0	0	1	0	0	0	0	3
Primelephas korororensis	1	0	0	1	0	0	0	0	3
Anancus kenyensis	2	0	0	1	0	0	0	0	3
Loxodonta cookei	1	0	0	1	0	0	0	0	3
Tropical rainforest, Bukit Barisan Selatan NP									
Elephas maximus	3	0	0	1	0	0	1	0	3
Macaca fascicularis	1	0	0	0	0	1	0	0	1
Presbytis cristata	1	0	0	0	0	1	0	0	1
Presbytis melalophus	1	0	0	0	0	1	0	0	1
Hylobates agilis	1	0	0	0	0	1	0	0	1
Symphalangus syndactylus	1	0	0	0	0	1	0	0	1
Tapirus indicus	1	0	1	0	0	0	0	0	1
Dicerorhinus sumatrensis	1	1	1	1	0	0	0	0	1
Sus scrofa	1	0	0	0	1	1	0	0	1
Tragulus javanicus	1	2	1	0	0	0	0	0	1
Muntiacus muntjak	1	2	1	0	0	0	0	0	1
Rusa unicolor	2	2	1	1	0	0	0	0	1
Bubalus bubalis	3	2	0	1	1	0	0	0	1
Kaziranga National Park									
Elephas maximus	3	0	0	1	0	0	1	0	3
Rhinoceros unicornis	2	1	1	1	0	0	0	0	1
Bubalus arnee	3	2	0	1	1	0	0	0	1
Bos gaurus	3	2	0	1	1	0	0	0	1
Rusa unicolor	2	2	1	1	0	0	0	0	1
Rucervus duvaucelii	2	2	1	1	0	0	0	0	1
Axis porcinus	2	2	0	1	1	0	0	0	1
Muntiacus muntjak	1	2	1	0	0	0	0	0	1
Sus scrofa	1	0	0	0	1	1	0	0	1
Macaca mulatta	1	0	0	0	0	1	0	0	1
Macaca assamensis	1	0	0	0	0	1	0	0	1
Trachypithecus pileatus	1	0	0	0	0	1	0	0	1
Hoolock hoolock	1	0	0	0	0	1	0	0	1
Ranthambore National Park									
Elephas maximus	3	0	0	1	0	0	1	0	3
Bos gaurus	3	2	0	1	1	0	0	0	1
Bubalus arnee	3	2	0	1	1	0	0	0	1
Boselaphus tragocamelus	3	2	0	1	1	0	0	0	1
Antilope cervicapra	2	2	0	1	0	0	0	1	1
Gazella bennettii	3	2	0	1	0	0	0	1	1

continued

Appendix 1. Continued.

Locality/species	HYP	LOP	AL	OL	SF	BUN	OT	OO	HOD
Tetraceros quadricornis	3	2	0	1	1	0	0	0	1
Rusa unicolor	2	2	1	1	0	0	0	0	1
Rucervus duvaucelii	2	2	1	1	0	0	0	0	1
Axis porcinus	2	2	0	1	1	0	0	0	1
Axis axis	2	2	0	1	1	0	0	0	1
Muntiacus muntjak	1	2	1	0	0	0	0	0	1
Semnopithecus dussumieri	1	0	0	0	0	1	0	0	1
Macaca mulatta	1	0	0	0	0	1	0	0	1
Aberdare National Park									
Loxodonta africana	3	0	0	1	0	0	1	0	3
Aepyceros melampus	3	2	0	1	0	0	0	1	1
Cephalophus harveyi	2	2	0	1	1	0	0	0	1
Cephalophus nigrifrons	2	2	0	1	1	0	0	0	1
Kobus ellipsiprymnus	3	2	0	1	1	0	0	0	1
Nanger granti	3	2	0	1	0	0	0	1	1
Neotragus moschatus	2	2	0	1	0	0	0	1	1
Oreotragus oreotragus	3	2	0	1	0	0	0	1	1
Philantomba monticola	1	0	0	1	0	0	0	0	1
Sylvicapra grimmia	2	2	0	1	0	0	0	1	1
Syncerus caffer	3	2	0	1	1	0	0	0	1
Taurotragus oryx	3	2	0	1	0	0	0	1	1
Tragelaphus eurycerus	2	2	0	1	0	0	0	1	1
Tragelaphus scriptus	2	2	0	1	0	0	0	1	1
Hippopotamus amphibius	2	0	0	1	1	0	0	0	1
Hylochoerus meinertzhageni	2	0	0	1	1	0	0	0	2
Phacochoerus africanus	3	0	0	0	0	1	1	0	3
Equus quagga	3	2	0	1	0	0	1	0	1
Diceros bicornis	2	1	1	1	0	0	0	0	1
Cercopithecus mitis	1	0	0	0	0	1	0	0	1
Chlorocebus pygerythrus	1	0	1	0	0	0	0	0	1
Colobus guereza	1	0	1	0	0	0	0	0	1
Papio anubis	1	0	0	0	0	1	0	0	1
Kakamega Forest									
Cephalophus silvicultor	2	2	0	1	1	0	0	0	1
Cephalophus harveyi	2	2	0	1	1	0	0	0	1
Cephalophus weynsi	2	2	0	1	1	0	0	0	1
Neotragus moschatus	2	2	0	1	0	0	0	1	1
Philantomba monticola	1	0	0	1	0	0	0	0	1
Sylvicapra grimmia	2	2	0	1	0	0	0	1	1
Tragelaphus scriptus	2	2	0	1	0	0	0	1	1
Tragelaphus spekii	2	2	0	1	0	0	0	1	1
Hylochoerus meinertzhageni	2	0	0	1	1	0	0	0	2
Phacochoerus africanus	3	0	0	0	0	1	1	0	3
Potamochoerus larvatus	1	0	0	0	1	1	0	0	1
Cercopithecus ascanius	1	0	0	0	0	1	0	0	1
Cercopithecus mitis	1	0	0	0	0	1	0	0	1
Cercopithecus neglectus	1	0	0	0	0	1	0	0	1
Chlorocebus pygerythrus	1	0	1	0	0	0	0	0	1
Colobus guereza	1	0	1	0	0	0	0	0	1
Papio anubis	1	0	0	0	0	1	0	0	1
Meru National Park									
Loxodonta africana	3	0	0	1	0	0	1	0	3
Aepyceros melampus	3	2	0	1	0	0	0	1	1
Alcelaphus buselaphus	3	2	0	1	0	0	1	0	1
Kobus ellipsiprymnus	3	2	0	1	1	0	0	0	1

continued

Appendix 1. Continued.

Locality/species	HYP	LOP	AL	OL	SF	BUN	OT	OO	HOD
Meru National Park									
Litocranius walleri	2	2	0	1	0	0	0	1	1
Madoqua guentheri	2	2	0	1	0	0	0	1	1
Madoqua kirkii	2	2	0	1	0	0	0	1	1
Nanger granti	3	2	0	1	0	0	0	1	1
Oryx beisa	3	2	0	1	1	0	1	0	1
Ourebia ourebi	3	2	0	1	0	0	0	1	1
Philantomba monticola	1	0	0	1	0	0	0	0	1
Raphicerus campestris	3	2	0	1	0	0	0	1	1
Redunca redunca	3	2	0	1	1	0	0	0	1
Sylvicapra grimmia	2	2	0	1	0	0	0	1	1
Syncerus caffer	3	2	0	1	1	0	0	0	1
Taurotragus oryx	3	2	0	1	0	0	0	1	1
Tragelaphus imberbis	2	2	0	1	0	0	0	1	1
Tragelaphus scriptus	2	2	0	1	0	0	0	1	1
Tragelaphus strepsiceros	2	2	0	1	0	0	0	1	1
Giraffa camelopardalis	1	2	1	1	0	0	0	0	1
Hippopotamus amphibius	2	0	0	1	1	0	0	0	2
Hylochoerus meinertzhageni	2	0	0	1	1	0	0	0	2
Phacochoerus aethiopicus	3	0	0	0	0	1	1	0	3
Phacochoerus africanus	3	0	0	0	0	1	1	0	3
Potamochoerus larvatus	1	0	0	0	1	1	0	0	1
Equus quagga	3	2	0	1	0	0	1	0	1
Equus grevyi	3	2	0	1	0	0	1	0	1
Diceros bicornis	2	1	1	1	0	0	0	0	1
Ceratotherium simum	3	2	0	1	0	0	1	0	1
Cercopithecus mitis	1	0	0	0	0	1	0	0	1
Chlorocebus pygerythrus	1	0	1	0	0	0	0	0	1
Colobus guereza	1	0	1	0	0	0	0	0	1
Erythrocebus patas	1	0	0	0	0	1	0	0	1
Papio anubis	1	0	0	0	0	1	0	0	1
Samburu Hills									
Loxodonta africana	3	0	0	1	0	0	1	0	3
Aepyceros melampus	3	2	0	1	0	0	0	1	1
Eudorcas thomsonii	3	2	0	1	0	0	0	1	1
Kobus ellipsiprymnus	3	2	0	1	1	0	0	0	1
Litocranius walleri	2	2	0	1	0	0	0	1	1
Madoqua guentheri	2	2	0	1	0	0	0	1	1
Madoqua kirkii	2	2	0	1	0	0	0	1	1
Nanger granti	3	2	0	1	0	0	0	1	1
Oreotragus oreotragus	3	2	0	1	0	0	0	1	1
Oryx beisa	3	2	0	1	1	0	1	0	1
Sylvicapra grimmia	2	2	0	1	0	0	0	1	1
Syncerus caffer	3	2	0	1	1	0	0	0	1
Taurotragus oryx	3	2	0	1	0	0	0	1	1
Tragelaphus imberbis	2	2	0	1	0	0	0	1	1
Tragelaphus scriptus	2	2	0	1	0	0	0	1	1
Tragelaphus strepsiceros	2	2	0	1	0	0	0	1	1
Giraffa camelopardalis	1	2	1	1	0	0	0	0	1
Hippopotamus amphibius	2	0	0	1	1	0	0	0	2
Phacochoerus africanus	3	0	0	0	0	1	1	0	3
Equus quagga	3	2	0	1	0	0	1	0	1
Equus grevyi	3	2	0	1	0	0	1	0	1
Diceros bicornis	2	1	1	1	0	0	0	0	1
Cercopithecus mitis	1	0	0	0	0	1	0	0	1

continued

Appendix 1. Continued.

Locality/species	HYP	LOP	AL	OL	SF	BUN	OT	OO	HOD
Samburu Hills									
Chlorocebus pygerythrus	1	0	1	0	0	0	0	0	1
Erythrocebus patas	1	0	0	0	0	1	0	0	1
Papio anubis	1	0	0	0	0	1	0	0	1
Tropical rainforest, Nouabale-Ndoki NP									
Arctocebus aureus	1	0	0	0	0	1	0	0	1
Cephalophus callipygus	2	2	0	1	1	0	0	0	1
Cephalophus dorsalis	2	2	0	1	1	0	0	0	1
Cephalophus leucogaster	2	2	0	1	1	0	0	0	1
Cephalophus nigrifrons	2	2	0	1	1	0	0	0	1
Cephalophus ogilbyi	2	2	0	1	1	0	0	0	1
Cephalophus silvicultor	2	2	0	1	1	0	0	0	1
Cercocebus agilis	1	0	0	0	0	1	0	0	1
Cercopithecus cephus	1	0	0	0	0	1	0	0	1
Cercopithecus neglectus	1	0	0	0	0	1	0	0	1
Cercopithecus nictitans	1	0	0	0	0	1	0	0	1
Cercopithecus pogonias	1	0	0	0	0	1	0	0	1
Colobus guereza	1	0	1	0	0	0	0	0	1
Colobus satanas	1	0	1	0	0	0	0	0	1
Euoticus elegantulus	1	0	0	0	0	1	0	0	1
Gorilla gorilla	1	0	0	0	0	1	0	0	1
Hyaemoschus aquaticus	1	2	1	1	0	0	0	0	1
Lophocebus albigena	1	0	1	0	0	1	0	0	1
Loxodonta cyclotis	3	0	0	1	0	0	1	0	3
Mandrillus sphinx	1	0	0	0	0	1	0	0	1
Miopithecus ogouensis	1	0	1	0	0	0	0	0	1
Neotragus batesi	2	2	0	1	0	0	0	1	1
Pan troglodytes	1	0	0	0	0	1	0	0	1
Perodicticus potto	1	0	0	0	0	1	0	0	1
Philantomba monticola	1	0	0	1	0	0	0	0	1
Potamochoerus porcus	1	0	0	0	1	1	0	0	1
Syncerus caffer nanus	3	2	0	1	1	0	0	0	1
Tragelaphus spekei	2	2	0	1	0	0	0	1	1
Serengeti (INCN site 98913)									
Aepyceros melampus	3	2	0	1	0	0	0	1	1
Alcelaphus buselaphus	3	2	0	1	0	0	1	0	1
Chlorocebus pygerythrus	1	0	0	0	0	1	0	0	1
Colobus guereza	1	0	1	0	0	0	0	0	1
Connochaetes taurinus	3	2	0	1	0	0	1	0	1
Damaliscus lunatus	3	2	0	1	0	0	1	0	1
Diceros bicornis	2	1	1	1	0	0	0	0	1
Equus quagga	3	2	0	1	0	0	1	0	1
Eudorcas thomsonii	3	2	0	1	0	0	0	1	1
Giraffa camelopardalis	1	2	1	1	0	0	0	0	1
Hippotragus equinus	3	2	0	1	1	0	0	0	1
Kobus ellipsiprymnus	3	2	0	1	1	0	0	0	1
Loxodonta africana	3	0	0	1	0	0	1	0	3
Madoqua kirkii	2	2	0	1	0	0	0	1	1
Nanger granti	3	2	0	1	0	0	0	1	1
Oreotragus oreotragus	3	2	0	1	0	0	0	1	1
Otolemur crassicaudatus	1	0	0	0	0	1	0	0	1
Ourebia ourebi	3	2	0	1	0	0	0	1	1
Papio anubis	1	0	0	0	0	1	0	0	1
Papio cynocephalus	1	0	0	0	0	1	0	0	1

continued

Appendix 1. Continued.

Locality/species	HYP	LOP	AL	OL	SF	BUN	OT	OO	HOD
Serengeti (INCN site 98913)									
Phacochoerus africanus	3	0	0	0	0	1	1	0	3
Potamochoerus larvatus	1	0	0	0	1	1	0	0	1
Raphicerus campestris	3	2	0	1	0	0	0	1	1
Redunca fulvorufula	3	2	0	1	1	0	0	0	1
Redunca redunca	3	2	0	1	1	0	0	0	1
Sylvicapra grimmia	2	2	0	1	0	0	0	1	1
Syncerus caffer	3	2	0	1	1	0	0	0	1
Tragelaphus scriptus	2	2	0	1	0	0	0	1	1
Białowieża Forest (IUCN site 13410)									
Alces alces	1	2	1	1	0	0	0	0	1
Bison bonasus	3	2	0	1	1	0	0	0	1
Capreolus capreolus	1	2	1	1	0	0	0	0	1
Cervus elaphus	2	2	1	1	0	0	0	0	1
Dama dama	1	2	1	1	0	0	0	0	1
Sus scrofa	1	0	0	0	1	1	0	0	1
Boreal forest, British Columbia (IUCN site 126218)									
Alces americanus	1	2	1	1	0	0	0	0	1
Cervus canadensis	2	2	1	1	0	0	0	0	1
Odocoileus hemionus	1	2	1	1	0	0	0	0	1
Odocoileus virginianus	1	2	1	1	0	0	0	0	1
Oreamnos americanus	3	2	0	1	0	0	0	1	1
Ovis canadensis	3	2	0	1	0	0	0	1	1
Arjinshan National Nature Reserve									
Bos mutus	3	2	0	1	1	0	0	0	1
Camelus bactrianus	3	2	0	1	0	0	0	1	1
Cervus elaphus yarkandensis	2	2	1	1	0	0	0	0	1
Equus kiang	3	2	0	1	0	0	1	0	1
Ovis ammon	3	2	0	1	0	0	0	1	1
Pantholops hogdsoni	3	2	0	1	0	0	0	1	1
Procapra picticaudata	3	2	0	1	0	0	0	1	1
Przewalskium albirostris	2	2	1	1	0	0	0	0	1
Dry steppe, Dunhuang Xihu NNR									
Cervus elaphus kansuensis	2	2	1	1	0	0	0	0	1
Equus hemionus	3	2	0	1	0	0	1	0	1
Equus kiang	3	2	0	1	0	0	1	0	1
Equus przewalskii	3	2	0	1	0	0	1	0	1
Gazella subgutturosa	3	2	0	1	0	0	0	1	1
Moschus chrysogaster	1	2	1	1	0	0	0	0	1
Ovis ammon	3	2	0	1	0	0	0	1	1
Procapra picticaudata	3	2	0	1	0	0	0	1	1
Saiga tatarica	3	2	0	1	0	0	0	1	1
Steppe, Sarisy, Kazakhstan (IUCN site 133019)									
Capreolus pygargus	1	2	1	1	0	0	0	0	1
Equus hemionus	3	2	0	1	0	0	1	0	1
Gazella subgutturosa	3	2	0	1	0	0	0	1	1
Saiga tatarica	3	2	0	1	0	0	0	1	1
Sus scrofa	1	0	0	0	1	1	0	0	1

Appendix 2. Specimen-level mesowear data of ungulates from the Late Miocene localities.

Locality/species	Specimen	High	Low	Sharp	Rounded	Blunt
Dorn-Dürkheim 1						
Anisodon indet.	SMF DD449 (cast)	1			1	
Anisodon indet.	SMF DD no number (cast)	1		1		
Anisodon indet.	SMF DD240	1		1		
Anisodon indet.	SMF DD230	1			1	
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD4626	1		1		
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD4305	1			1	
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD4394	1		1		
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD847	1		1		
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD3854	1		1		
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD4760	1			1	
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD815	1		1		
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD844	1		1		
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD804	1			1	
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD4089	1		1		
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD804	1			1	
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD4081	1			1	
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD4413	1			1	
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD827	1		1		
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD821	1		1		
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD811	1		1		
Cervidae, large (cf. *Procapreolus*/Muntiacinae)	SMF DD843	1			1	
Cervidae, small (cf. *Cervavitulus minimus*)	SMF DD 4100	1		1		
Cervidae, small (cf. *Cervavitulus minimus*)	SMF DD 4729	1		1		
Cervidae, small (cf. *Cervavitulus minimus*)	SMF DD 3807	1		1		
Cervidae, small (cf. *Cervavitulus minimus*)	SMF DD 919	1			1	
Cervidae, small (cf. *Cervavitulus minimus*)	SMF no number	1		1		
Hippotherium primigenium	SMF DD5669	1		1		
Hippotherium primigenium	SMF DD115	1		1		
Hippotherium primigenium	SMF DD3867		1	1		
Hippotherium primigenium	SMF DD3205	1			1	
Hippotherium primigenium	SMF DD3219	1			1	
Hippotherium primigenium	SMF DD113	1		1		
Hippotherium primigenium	SMF DD4300	1		1		
Hippotherium primigenium	SMF DD5722	1		1		
Hippotherium primigenium	SMF DD3788		1		1	
Hippotherium primigenium	SMF DD3204	1		1		
Hippotherium primigenium	SMF DD65	1		1		
Hippotherium primigenium	SMF DD5728		1		1	
Hippotherium kammerschmittae	SMF DD5652	1		1		
Hippotherium kammerschmittae	SMF DD4274	1		1		
Micromeryx sp.	SMF DD4287	1		1		
Micromeryx sp.	SMF DD478	1		1		
Micromeryx sp.	SMF DD306	1		1		
Miotragocerus indet.	SMF DD3940	1		1		
Miotragocerus indet.	SMF DD337	1			1	
Miotragocerus indet.	SMF DD582	1			1	
Miotragocerus indet.	SMF DD574	1		1		
Miotragocerus indet.	SMF DD335	1		1		
Miotragocerus indet.	SMF DD352	1			1	
Miotragocerus indet.	SMF DD3920	1		1		
Kohfidisch						
Aceratherium? indet.	NHMW Koh.1962	1		1		
Caprinae indet. indet.	NHMW 129	1		1		
Caprinae indet. indet.	NHMW 129	1		1		

continued

Appendix 2. Continued.

Locality/species	Specimen	High	Low	Sharp	Rounded	Blunt
Caprinae indet. indet.	NHMW 130	1		1		
Caprinae indet. indet.	NHMW 130	1		1		
Cervavitus sp.	NHMW 33 (1958)	1		1		
Cervavitus sp.	NHMW 32 (1958)	1		1		
Cervavitus sp.	NHMW 32 (1958)	1		1		
Cervavitus sp.	NHMW 32 (1958)	1		1		
Cervavitus sp.	NHMW 32 (1958)	1		1		
Cervavitus sp.	NHMW IV/1 (1962)	1		1		
Cervavitus sp.	NHMW 38 (1957)	1		1		
Euprox sp.	NHMW 54 (1963 / III)	1		1		
Euprox sp.	NHMW 59	1		1		
Euprox sp.	NHMW 58 (1961, II, 2)	1			1	
Gazella aff. *pilgrimi*	NHMW no number	1			1	
Gazella aff. *pilgrimi*	NHMW 1965	1		1		
Gazella aff. *pilgrimi*	NHMW 1965	1			1	
Gazella aff. *pilgrimi*	NHMW 1965	1			1	
Gazella aff. *pilgrimi*	NHMW 1958.1/3	1		1		
Gazella aff. *pilgrimi*	NHMW 1956.1/5	1		1		
Gazella aff. *pilgrimi*	NHMW 1956.1/5	1		1		
Gazella aff. *pilgrimi*	NHMW 1956.1/6	1			1	
Gazella aff. *pilgrimi*	NHMW 1956.1/6	1		1		
Hippotherium indet.	NHMW No. 002246 (1972)	1			1	
Hippotherium indet.	NHMW No. 1973	1		1		
Hippotherium indet.	NHMW 14 (1981)	1		1		
Hippotherium indet.	NHMW 2 (1960)	1			1	
Hippotherium indet.	NHMW 3 (1961)	1		1		
Micromeryx indet.	NHMW 86 (1967,74,91)	1		1		
Micromeryx indet.	NHMW 86 (1967,74,91)	1		1		
Micromeryx indet.	NHMW 94	1		1		
Micromeryx indet.	NHMW 76 (AM 8)	1		1		
Micromeryx indet.	NHMW 98	1		1		
Miotragocerus indet.	NHMW 1982i	1		1		
Miotragocerus indet.	NHMW 1974/1686/39	1			1	
Orygotherium heinzi	NHMW 2004z0051/0003	1		1		
Orygotherium heinzi	NHMW Ko 14 (1963)	1		1		
Palaeoryx sp.	NHMW no number	1		1		
Palaeoryx sp.	NHMW 172 (1981)	1		1		
Palaeoryx sp.	NHMW 173	1		1		
Palaeoryx sp.	NHMW 173	1			1	
Palaeoryx sp.	NHMW 1980	1		1		
Palaeoryx sp.	NHMW 1980	1		1		
Procapreolus aff. *lockzyi*	NHMW 2005z0025/0002-Anz:1	1		1		
Procapreolus aff. *lockzyi*	NHMW 105	1			1	
Procapreolus aff. *lockzyi*	NHMW 103	1		1		
Procapreolus aff. *lockzyi*	NHMW no number	1		1		
Procapreolus aff. *lockzyi*	NHMW no number	1		1		
Procapreolus aff. *lockzyi*	NHMW no number	1		1		
Procapreolus aff. *lockzyi*	NHMW no number	1		1		
Protoryx sp.	NHMW 182	1			1	
Protoryx sp.	NHMW 182	1		1		
Protoryx sp.	NHMW 182	1		1		
Protoryx sp.	NHMW 1957	1		1		
Protoryx sp.	NHMW 1957	1			1	

continued

Appendix 2. Continued.

Locality/species	Specimen	High	Low	Sharp	Rounded	Blunt
Kohfidisch						
Tragoportax gaudryi	NHMW 142	1		1		
Tragoportax gaudryi	NHMW 155	1			1	
Tragoportax gaudryi	NHMW 153	1		1		
Tragoportax gaudryi	NHMW 143	1		1		
Tragoportax gaudryi	NHMW 143	1		1		
Tragoportax gaudryi	NHMW 143	1		1		
Maragheh						
Ancylotherium pentelici	MMTT37/2300	1		1		
Bohlinia attica	NHMUK-PV-M3867	1		1		
Bohlinia attica	CM458	1		1		
Chilotherium persiae	NHMW 2020/0014/0031	1		1		
Chilotherium persiae	NHMW 2020/0014/0003	1			1	
Chilotherium persiae	NHMW 2020/0014/0005	1		1		
Chilotherium persiae	NHMW 2020/0014/0091	1		1		
Chilotherium persiae	A4819	1		1		
Chilotherium persiae	A4822	1			1	
Chilotherium persiae	A4792	1		1		
Chilotherium persiae	A4805	1			1	
Cremohipparion aff. *moldavicum*	NHMW 2022/106/0004	1			1	
Cremohipparion aff. *moldavicum*	NHMW 2022/106/0002		1	1		
Cremohipparion aff. *moldavicum*	NHMUK-PV-M3924		1	1		
Cremohipparion matthewi	GIUP100-1958		1		1	
Cremohipparion moldavicum	MNHNMar_RLB7914	1		1		
Cremohipparion moldavicum	MNHNMar62	1			1	
Cremohipparion moldavicum	MNHNMar466	1			1	
Cremohipparion moldavicum	MNHNMar1476	1			1	
Cremohipparion moldavicum	MNHNMar469	1		1		
Cremohipparion moldavicum	MNHN.F.MAR3428		1	1		
Cremohipparion moldavicum	MNHN.F.MAR1477		1		1	
Cremohipparion aff. *moldavicum*	NHMW Mar-1808	1			1	
Cremohipparion aff. *moldavicum*	NHMW A 4848		1	1		
Cremohipparion aff. *moldavicum*	NHMW Mar-1809		1		1	
Criotherium argaloides	NHMUK-PV-M7412	1		1		
Gazella anycerus	MMTT13/MCW80	1		1		
Gazella indet.	NHMW Mar-3202	1			1	
Gazella indet.	NHMW Mar-3190		1		1	
Gazella indet.	NHMW Mar-3200	1			1	
Gazella indet.	NHMW Mar-3208	1			1	
Gazella indet.	NHMW Mar-2525		1	1		
Gazella indet.	NHMW Mar-2655	1			1	
Gazella indet.	NHMW Mar-2770	1			1	
Gazella indet.	NHMW Mar-2783		1		1	
Helladotherium duvernoyi	MMTT7/602	1			1	
Helladotherium duvernoyi	BSP 1973 XXI 60	1			1	
Palaeotragus coelophryes	BSP 1973 XXI 59	1		1		
Hipparion campbelli	MMTT 13/1342		1		1	
Hipparion campbelli	MMTT13/1342	1			1	
Hipparion campbelli	MMTT13/1291	1			1	
Hippotherium brachypus	NHMW 2022/105/0002		1		1	
Hippotherium brachypus	NHMW 2022/105/0001		1		1	
Hippotherium brachypus	MNHNMar1474	1			1	
Hippotherium brachypus	MNHNMar1475	1			1	
Hippotherium? *brachypus*?	NHMW Mar-1760	1			1	
Honanotherium bernori	MMTT7/2164	1			1	

continued

Appendix 2. Continued.

Locality/species	Specimen	High	Low	Sharp	Rounded	Blunt
Maragheh						
Honanotherium bernori	MNHN MAR670	1		1		
Iranotherium morgani	NHMW 2020/0013/0002		1			1
Iranotherium morgani	NHMW 2014/0425/0001	1			1	
Iranotherium morgani	MNHN.F.MAR 1647 (skull)		1		1	
Miodiceros neumayri	NHMW 2014/0424/0001	1			1	
Miodiceros neumayri	NHMW 2014/0424/001a, holotype	1			1	
Miotragocerus indet.	NHMUK-PV-M3838	1		1		
Oioceros atropatenes	MNHN.F.MAR3146	1		1		
Oioceros atropatenes	MMTT13/1206	1			1	
Oioceros atropatenes	MMTT13/1205	1		1		
Oioceros atropatenes	MMTT13/1357	1		1		
Oioceros atropatenes	MMTT13/1361	1		1		
Ovibovini? indet.?	NHMW Mar-2620	1		1		
Ovibovini? indet.?	NHMW Mar-2619	1		1		
Ovibovini? indet.?	NHMW Mar-2864	1			1	
Palaeoreas lindermayeri	MMTT7/2159		1		1	
Palaeoreas indet.	MMTT7/2159		1		1	
Palaeoreas indet.	NHMW no number	1			1	
Palaeoreas indet.	NHMW Mar-3209		1		1	
Palaeoreas indet.	NHMW Mar-3219	1			1	
Palaeoreas indet.	NHMW Mar-3220	1			1	
Palaeoreas indet.	NHMW Mar-3221	1			1	
Palaeoreas indet.	NHMW Mar-3237	1		1		
Protoryx carolinae	MNHN.F.MAR3206	1			1	
Protragelaphus skouzesi	MNHN.F.MAR1307		1		1	
Protragelaphus skouzesi	MNHN.F.MAR1397	1			1	
Protragelaphus skouzesi	MMTT7/2294	1			1	
Samoceros minotaurus	MNHN.F.MAR3209	1			1	
Samotherium neumayri	NHMW Mar-3375	1			1	
Samotherium neumayri	NHMW Mar-3384	1			1	
Samotherium neumayri	NHMW Mar-3386	1			1	
Samotherium neumayri	NHMW Mar-3385	1			1	
Samotherium neumayri	NHMW Mar-3372	1		1		
Tragoportax amaltheus	NHMW Mar-2584	1		1		
Tragoportax amaltheus	NHMW Mar-2579	1			1	
Tragoportax amaltheus	NHMW Mar-2585	1			1	
Tragoportax amaltheus	NHMW Mar-2582	1			1	
Tragoportax amaltheus	NHMW Mar-2583	1			1	
Tragoportax amaltheus	NHMW Mar-2522	1			1	
Tragoportax amaltheus	NHMW Mar-2661	1			1	
Tragoportax amaltheus	NHMW Mar-2769	1			1	
Tragoportax amaltheus	MMTT13/1346	1			1	
Tragoportax amaltheus	NHMW Mar-2906	1			1	
Tragoportax amaltheus	NHMW Mar-2907	1			1	
Urmiatherium polaki	NHMW A 4916		1		1	
Urmiatherium polaki	NHMW Mar-2886	1			1	
Urmiatherium polaki	NHMW Mar-2885	1		1		
Urmiatherium polaki	DOE M356		1		1	
Mt. Luberon						
Gazella deperdita	MNHN.F.Lub-557	1			1	
Gazella deperdita	MNHN.F.Lub-515	1		1		
Gazella deperdita	MNHN.F.Lub-555	1			1	

continued

Appendix 2. Continued.

Locality/species	Specimen	High	Low	Sharp	Rounded	Blunt
Mt. Luberon						
Gazella deperdita	MNHN.F.Lub-550	1		1		
Gazella deperdita	MNHN.F.Lub-681	1		1		
Hipparion prostylum	MNHN.F.Lub-45		1		1	
Hipparion prostylum	MNHN.F.Lub-206		1		1	
Hipparion prostylum	MNHN.F.Lub-451		1	1		
Hipparion prostylum	MNHN.F.Lub-230		1		1	
Hipparion prostylum	MNHN.F.Lub-91		1	1		
Hipparion prostylum	MNHN.F.Lub-455		1		1	
Hipparion prostylum	MNHN.F.Lub-44		1		1	
Hipparion prostylum	MNHN.F.Lub-454	1		1		
Hipparion prostylum	MNHN.F.Lub-97		1			1
Hipparion prostylum	MNHN.F.Lub-857		1		1	
Hipparion prostylum	MNHN.F.Lub-854		1		1	
Pliocervus matheronis	MNHN.F.Lub-798	1			1	
Pliocervus matheronis	MNHN.F.Lub-812	1		1		
Tragoportax amaltheus	MNHN.F.Lub-719	1			1	
Tragoportax amaltheus	MNHN.F.Lub-728	1			1	
Tragoportax amaltheus	MNHN.F.Lub-727	1		1		
Pikermi						
Ancylotherium pentelicum	Univ. Wien 1754	1		1		
Ancylotherium pentelicum	NHMUK-PV-M4064	1		1		
Acerorhinus neleus	AMPG: K4/119.37	1		1		
Bohlinia attica	MNHN.Pik-1661	1		1		
Bohlinia attica	MNHN.Pik-1610	1		1		
Bohlinia attica	BSP AS II 640	1		1		
Cremohipparion mediterraneum	NHMUK-PV-M16395		1		1	
Cremohipparion mediterraneum	NHMUK-PV-M11189	1		1		
Cremohipparion mediterraneum	NHMUK-PV-M100237		1	1		
Cremohipparion mediterraneum	NHMUK-PV-M16392	1		1		
Cremohipparion mediterraneum	NHMUK-PV-M11178		1		1	
Cremohipparion mediterraneum	NHMUK-PV-M16396		1	1		
Cremohipparion mediterraneum	NHMUK-PV-M16393	1		1		
Cremohipparion mediterraneum	NHMW 1854/0003/0028		1	1		
Cremohipparion mediterraneum	NHMW 2017/0038/0019		1	1		
Cremohipparion mediterraneum	NHMW 1863/0001/0102a		1	1		
Dihoplus pikermiensis	NHMW 1863/0001/00019	1		1		
Dihoplus pikermiensis	NHMUK-PV-M10143	1		1		
Dihoplus pikermiensis	NHMUK-PV-M10144	1		1		
Dihoplus pikermiensis	NHMUK-PV-M10142	1		1		
Dihoplus pikermiensis	NHMW-GEO-2009/z/0085/0001	1			1	
Dihoplus pikermiensis	NHMW A 4672	1		1		
Dihoplus pikermiensis	NHMW 1863/0001/0019	1		1		
Gazella capricornis	NHMUK-PV-M11440	1		1		
Gazella capricornis	NHMUK-PV-M11441	1			1	
Gazella capricornis	NHMW 1863.I.47	1		1		
Gazella capricornis	NHMW 1860 XXXII 21	1		1		
Gazella capricornis	NHMW 1854 III. 33	1			1	
Helladotherium duvernoyi	Gaudry 1861 skull	1		1		
Helladotherium duvernoyi	MNHN exhibition mandible	1		1		
Hippotherium brachypus	NHMUK-PV-M11188	1			1	
Hippotherium brachypus	NHMUK-PV-M11170	1			1	
Hippotherium brachypus	NHMUK-PV-M11183	1		1		
Hippotherium brachypus	NHMUK-PV-M11191		1		1	
Hippotherium brachypus	NHMUK-PV-M11185	1		1		

continued

Appendix 2. Continued.

Locality/species	Specimen	High	Low	Sharp	Rounded	Blunt
Pikermi						
Hippotherium brachypus	NHMW 1860/0032/0002b	1			1	
Hippotherium brachypus	NHMW 1863/0001/0095	1		1		
Hippotherium brachypus	NHMW 1863/0001/0096		1		1	
Miodiceros neumayri	MNHN.Pik-3676	1			1	
Miodiceros neumayri	MNHN.Pik-936	1		1		
Miodiceros neumayri	MNHN.Pik-934	1			1	
Miodiceros neumayri	MNHN.Pik-960	1			1	
Miodiceros neumayri	MNHN.Pik-968	1		1		
Miodiceros neumayri	MNHN.F.PIK 1311	1		1		
Miodiceros neumayri	MNHN.Pik-971	1			1	
Miotragocerus valenciennesi	NHMUK-PV-M11431	1		1		
Miotragocerus valenciennesi	NHMUK-PV-M11431	1		1		
Miotragocerus valenciennesi	NHMUK-PV-M11431	1		1		
Miotragocerus valenciennesi	NHMUK-PV-M11450	1		1		
Miotragocerus valenciennesi	NHMUK-PV-M11452	1		1		
Miotragocerus valenciennesi	NHMUK-PV-M12979	1		1		
Miotragocerus valenciennesi	NHMUK-PV-M11430	1			1	
Oioceros rothii	MNHN.Pik-2240a	1		1		
Oioceros rothii	MNHN.Pik-2240b	1		1		
Oioceros rothii	MNHN.Pik-2242	1			1	
Oioceros rothii	PG 95/1502a	1		1		
Palaeoreas lindermayeri	NHMUK-PV-M110843	1		1		
Palaeoreas lindermayeri	NHMUK-PV-M11447	1			1	
Palaeoreas lindermayeri	NHMUK-PV-M11447	1		1		
Palaeoreas lindermayeri	NHMUK-PV-M11447	1		1		
Palaeoreas lindermayeri	NHMUK-PV-M11447	1		1		
Palaeoreas lindermayeri	NHMUK-PV-M13013	1		1		
Palaeoreas lindermayeri	NHMUK-PV-M13010	1		1		
Palaeoryx pallasi	NHMUK-PV-M110832	1		1		
Palaeoryx pallasi	NHMUK-PV-M110831	1			1	
Palaeoryx pallasi	NHMUK-PV-M11416	1		1		
Palaeoryx pallasi	NHMUK-PV-M13001	1		1		
Palaeotragus rouenii	MNHN.F.PIK 1670	1		1		
Palaeotragus rouenii	NHMUK-PV-M11419	1		1		
Palaeotragus rouenii	NHMUK-PV-M11419	1		1		
Pliocervus pentelici	NHMUK-PV-M11484	1		1		
Prostrepsiceros rotundicornis	BSP AS II 635	1			1	
Protoryx carolinae	NHMUK-PV-M11415	1		1		
Protoryx carolinae	NHMUK-PV-M10839	1			1	
Protragelaphus skouzesi	BSP AS II 539	1		1		
Protragelaphus skouzesi	NHMUK-PV-11439	1		1		
Sporadotragus parvidens	NHMUK-PV-M110833	1			1	
Sporadotragus parvidens	MNHN.Pik-2451	1		1		
Tragoportax amaltheus	NHMUK-PV-M11425	1		1		
Tragoportax amaltheus	NHMUK-PV-M12978	1		1		
Tragoportax amaltheus	NHMUK-PV-M11425	1		1		
Tragoportax amaltheus	NHMUK-PV-M11424	1			1	
Tragoportax amaltheus	NHMUK-PV-M11427	1			1	
Tragoportax amaltheus	NHMW 1854/0003/0034	1			1	
Tragoportax amaltheus	NHMW 1860/0032/0021	1		1		
Tragoportax amaltheus	NHMW 1863/0001/0067	1			1	
Tragoportax amaltheus	NHMW 1863/0001/0066	1			1	
Tragoportax amaltheus	NHMW 1863/0001/0065	1		1		
Tragoportax amaltheus	NHMW 1863/0001/0069	1		1		

continued

Appendix 2. Continued.

Locality/species	Specimen	High	Low	Sharp	Rounded	Blunt
Lukeino						
Hipparionini indet. indet.	KNM-LU-711	1			1	
Hipparionini indet. indet.	KNM-LU-705		1	1		
Tragelaphus spekei?	KNM-LU-592	1			1	
Tragelaphus spekei?	KNM-LU-595	1		1		
Bovidae indet. indet. (large, hypsodont)	KNM-LU-11117	1		1		
Lothagam (Nawata)						
Alcelaphini indet. indet.	KNM-LT-222	1			1	
Alcelaphini indet. indet.	KNM-LT-507		1			1
Alcelaphini indet. indet.	KNM-LT-23130		1			1
Aepyceros praemelampus	KNM-LT-25985	1		1		
Madoqua indet.	KNM-LT-177	1		1		
Boselaphini indet. indet.	KNM-LT-26070	1			1	
Boselaphini indet. indet.	KNM-LT-13015	1		1		
Boselaphini indet. indet. (small)	KNM-LT-13016	1			1	
Boselaphini indet. indet. (small)	KNM-LT-26005	1		1		
Boselaphini indet. indet.	KNM-LT-28574	1			1	
Tragelaphus kyaloae?	KNM-LT-25964	1		1		
Bovini indet. indet.	KNM-LT-476A	1			1	
Bovini indet. indet.	KNM-LT-480	1			1	
Palaeotragus germaini	KNM-LT-414	1		1		
Sivalhippus turkanense	KNM-LT-136 (holotype)		1			1
Sivalhippus turkanense	KNM-LT-25464	1		1		
Sivalhippus turkanense	KNM-LT-26293	1		1		
Eurygnathohippus feibeli	KNM-LT-23687		1		1	
Eurygnathohippus feibeli	KNM-LT-25468		1		1	
Eurygnathohippus feibeli	KNM-LT-25486		1		1	
Eurygnathohippus feibeli	KNM-LT-141		1		1	
Brachypotherium lewisi	KNM-LT-94	1				1
Brachypotherium lewisi	KNM-LT-22874	1			1	
Brachypotherium lewisi	KNM-LT-88	1			1	