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

Paleoecology and body mass distribution of horses in northern Eurasia during the Pleistocene

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The "grazing horses" (Equinae) were successful large herbivores that arrived from North America to Eurasia at the Plio–Pleistocene boundary. The adaptiveness of high-crowned (hypsodont) *Equus* spp. allowed them to conquer environments from open to forested, resulting in different body sizes. Few large-scale studies on horse body mass in northern Eurasia exist. Despite controversial systematics of Equidae, their ecomorphological features are quantifiable. The Pleistocene habitat and *Equus* spp. body mass changes were studied across northern Eurasia. Mean non-equid ungulate hypsodonty demonstrated progressive opening of landscapes throughout the Pleistocene, returning towards more humid and closed environments (taiga) below 70°N by the Holocene. Landscape heterogeneity across northern Eurasia indicated different zoogeographic provinces. Mean *Equus* spp. body mass decreased during the Middle Pleistocene to resemble the Holocene estimates. The Holocene domestication might have prevented small-sized and grazing-adapted horse lineages from extinction when taiga forests spread across northern Eurasia.

Introduction

The arrival of the so-called "grazing horses" or Equinae, from North America to Eurasia at the Plio–Pleistocene boundary gave rise to a successful evolutionary radiation of the members of the genus *Equus* across the continents into several lineages and numerous species, adapting to a variety of climates and habitats (Gromova 1949, Kurtén 1968, Azzaroli 1991, Janis & Bernor 2019, Cirilli *et al*. 2021, 2022). The subfamily Equinae includes monodactyl Equini and tridactyl Hipparionini, all of which are hypsodont, i.e., possess high molar crowns, which is an adaptation to cope with increased tooth wear rates caused by feeding on abrasive food sources (silica-rich and fibrous plants such as grasses), and ingestion of soil and grit in open environments (Fortelius *et al.* 2002, Damuth & Janis 2011).

Within the family Equidae, the genus *Equus* is the only one with extant representatives. *Equus* spp. are in general large-bodied with modern horses ranging between 200–400 kg, and some extinct species estimated to have weighed on average around 600 kg (Janis & Bernor 2019, Saarinen *et al.* 2021, Cirilli *et al*. 2022, 2023, 2024).

Despite the absence of critical periods of mass extinctions during the Pleistocene, and a remarkable capacity of *Equus* to adapt, a

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dramatic decline in both the number of horse species and horse numbers occurred in Eurasia and North America by the end of the Pleistocene (Guthrie 1984, Vereshchagin & Baryshnikov 1984, Azzaroli 1991, Kuzmina 1997, Guthrie 2003, Vershinina *et al*. 2021), which could indicate prehistoric overkill (Azzaroli 1991). Human involvement is debatable in the case of horses though (Guthrie 1984, Vereshchagin & Baryshnikov 1984, Kuzmina 1997, Guthrie 2003, Vershinina *et al*. 2021).

The studies that have recently analysed horse (*Equus* spp.) origin and distribution in Americas and Europe have to some extent touched northern Eurasia (Vershinina *et al.* 2021, Libraldo *et al.* 2021, Saarinen *et al.* 2021, Uzunidis 2021, Cirilli *et al.* 2021, 2022, 2024). However, comprehensive and large-scale studies on equid body mass are almost absent in the context of the Eastern European Plain and Siberia.

Body size variations depend on resource availability, climatic conditions and physiological and biomechanical factors that have positive or negative effects on populations or species (Damuth & MacFadden 1990, Blackburn & Gaston 1994, 1998, Saarinen *et al.* 2021, Uzunidis 2021). For example, body size decline in equids can indicate deteriorating climatic conditions, changes in vegetation composition and cover and low-quality food resources (Guthrie 2003, Saarinen 2014, Uzunidis 2021).

Although equid systematics and taxonomic relationships are still debated, and the number of the Pleistocene horse species on the Eastern European Plain and in Siberia is uncertain, obvious size differences in horse specimens allow equids at any locality to be sorted into discrete taxonomic groups, whatever the actual species may have been, and provide the basis for understanding evolutionary trends in distribution and adaptations of ancient horses.

Here I demonstrate equid habitat and body mass changes from the Late Pliocene, throughout the Pleistocene, to the Holocene across northern Eurasia on a large scale, based on currently collected data in the NOW Database of fossil mammals (https://doi.org/10.5281/zenodo.4268068, Žliobaite *et al*. 2023) and literature sources. The main emphasis is on the Pleistocene *Equus* spp. from the former USSR territories.

Material and methods

Occurrence data

The data were obtained from the NOW Database of fossil mammals (https://doi.org/10.5281/zenodo.4268068, Žliobaite *et al*. 2023), and from Russian studies (Sher 1971, Gromov 1972, Vangengeim & Sher 1972, Vangengeim 1977, Alexeeva 1980, Gerbova & Krasnov 1982, Vangengeim & Zhegallo 1982, Kahlke 1986, Azzaroli *et al.* 1988, Stuart 1991, Kahlke 1999, Vangengeim *et al.* 2001, Khromov *et al.* 2001, Vasil'ev *et al.* 2002, Sher *et al.* 2005).

The study data set included the Pliocene, Pleistocene and Holocene sites from the former USSR territories, and one Mongolian site due to the availability of extensive data and similarity in temporal and taxonomic approaches. Overall, 575 Equinae occurrences with body mass data on 488 specimens from 444 localities were used for the equid data (Table 1). For the mean ordinated hypsodonty analysis, data from 849 localities were used.

Periods

Species occurrences originated from the Pliocene, early Early Pleistocene, late Early Pleistocene, early Middle Pleistocene, late Middle Pleistocene, early Late Pleistocene (Eemian and Early Weichselian), late Late Pleistocene (Middle and Late Weichselian) and Holocene periods (Table 1 and Appendix 1).

Species

Large terrestrial herbivores of the orders Perissodactyla, Artiodactyla, Proboscidea and Primates were included in the mean ordinated hypsodonty analysis, following the conventional use of hypsodonty as an ecometric (Fortelius *et al*. 2002, Liu *et al*. 2012). A few unidentified species were used at the generic level if their hypsodonty was determinable (e.g. *Bison* or *Bos* indet., *Capra* or *Ovis* indet.; *see* Appendix 2).

Although the main emphasis of the study was on *Equus* spp., there were also Hipparionini species in the Pliocene (*Hipparion hippidiodus*, *H. crusafonti*, *Baryhipparion tchicoicum*, *Plesiohipparion houfenense* and *Plesiohipparion/Proboscidipparion crassum*) along with *Equus stenonis*. Here, the species names are given as in the literature or NOW (https://doi.org/10.5281/zenodo.4268068) (Table 2 and Appendix 2). For example, *E. caballus* in the Middle and Late Pleistocene may well be the caballoid *E. ferus* or some other species. The caballoid horses (named after the domestic horse) are more evolutionary advanced and characterized by a U-shaped ento- or linguaflexid in the double knot, whereas more primitive stenonid horses are characterized by a V-shaped ento- or linguaflexid (Gromova 1949, Forstén 1988).

The following *Equus* species were included in the study:

Early Early Pleistocene:
E. stenonis, *E. major*, *E. livenzovensis*, *E. sanmeniensis*, *E. verae* (Vera Gromova horse) and *E. pamirensis.*

Late Early Pleistocene:
E. verae, *E. suessenbornensis*, *E. hippari-oinoides*, *E. stenonis*, *E. altidens*, *E. namadicus*, *E. asinus* (African wild ass), *E. mosbachensis*, *E. sanmeniensis*, *E. hemionus* (Asiatic wild ass) and *E. nalaikhensis.*

Early Middle Pleistocene:
E. altidens, *E. suessenbornensis*, *E. sanmeniensis*, *E. caballus*, *E. hydruntinus* (European wild ass), *E. chosaricus*, *E. mosbachensis*, *E. namadicus*, *E. nordostensis*, *E. coliemensis* and *E. verae.*

Late Middle Pleistocene:
E. hydruntinus, *E. ferus*, *E. asinus*, *E. latipes* (broad-hooved horse), *E. caballus latipes*, *E. caballus*, *E. beijingensis*, *E. chosaricus*, *E. caballus nordostensis*, *E. caballus orientalis*, *E. hemionus*, *E. taubachensis*, *E. mosbachensis germanicus*, *E. mosbachensis*, *E. steinheimensis* and *E. namadicus*.

Early Late Pleistocene:
E. lenensis (Chersky or Lena horse), *E. caballus lenensis*, *E. nordostensis*, *E. orientalis*, *E. caballus orientalis*, *E. coliemensis*, *E. ferus*, *E. caballus*, *E. hemionus*, *E. hydruntinus*, *E. hemionus binagadensis*, *E. ovodovi*, *E. asinus*, *E. latipes*, *E. caballus latipes*, *E. chosaricus*, *E. taubachensis*, *E. uralensis*, *E. mosbachensis* and *E. przewalskii*.

Late Late Pleistocene:
E. ferus, *E. caballus*, *E. hemionus*, *E. lenensis*, *E. caballus lenensis*, *E. latipes*, *E. caballus latipes*, *E. uralensis*, *E. hydruntinus*, *E. chosaricus*, *E. dalianensis* (Ussurian horse) and *E. przewalskii.*

Holocene:
E. caballus, *E. asinus*, *E. hemionus*, *E. latipes* and *E. gmelini* (tarpan). Some of the Holocene *E. caballus* here could be domesticated. *Equus caballus* marked in the sources as large or small were not used in the study.

Hypsodonty

Hypsodonty describes molar crown height in herbivorous mammals: a tooth is hypsodont when its

Table 1. Numbers of Equinae localities, as well as *Equus* spp. occurrences and body mass estimates per period.

Period	Age (Ma)	Equinae localities	*Equus* spp. occurrences	*Equus* spp. body mass estimates
Holocene	< 0.017	39	53	50
Late Late Pleistocene	0.057–0.017	174	215	204
Early Late Pleistocene	0.130–0.057	104	136	107
Late Middle Pleistocene	0.430–0.130	44	65	47
Early Middle Pleistocene	0.790–0.430	22	29	25
Late Early Pleistocene	1.80–0.790	17	24	17
Early Early Pleistocene	2.6–1.80	23	26	21
Pliocene	> 2.6	21	8 (19*)	6 (11*)
Total		444	556 (575**)	477 (488**)

* Hipparionini, ** including Hipparionini.

height (dorso-ventral) notably exceeds its length (antero-posterior). The extent of the molar crown height development indicates an adaptation to higher rates of tooth wear experienced in open and dry habitats (Flerov 1962, Fortelius 1985, Janis & Fortelius 1988, Damuth & Janis 2011).

Table 2. Equinae body masses used in the study. Only the species with recorded body mass values were used in the analyses; * = new estimates calculated from M2 length.

Genus	Species/subspecies	Locality	Body mass estimate (kg)
Equus	*altidens*		373.7
Equus	*asinus*		250
Equus	*beijingensis*		large, similar to *E. sanmeniensis*
Equus	*caballus*		400
Equus	*caballus latipes*		507.1
Equus	*caballus lenensis*		363.4
Equus	*caballus nordostensis*		large
Equus	*caballus orientalis*		large
Equus	*caballus*	Botai	268.2
Equus	*chosaricus*		large, similar to *E. ferus/E. latipes*
Equus	*coliemensis*		590.5, similar to *E. verae*
Equus	*dalianensis*		513.8 kg*
Equus	*ferus*		459.8
Equus	*gmelini*		255.7*
Equus	*hemionus*		198.9
Equus	*hemionus binagadensis*		198.9
Equus	*hydruntinus*		241.7
Equus	*hydruntinus*	Emine Bair Khosar	153.8*
Equus	*hydruntinus*	Prolom 2	139.2*
Equus	*hipparioinoides*	Akhalkalaki	283.6*
Equus	*latipes*		507.1
Equus	*lenensis*		363.4
Equus	*lenensis*	Aldan River	326.3*
Equus	*lenensis*	Kotelnyj island	304.7*
Equus	*livenzovensis*		503.1
Equus	*major*		653.3
Equus	*mosbachensis*		568.7
Equus	*mosbachensis*	*germanicus*	568.7
Equus	*nalaikhensis*		398.9
Equus	*namadicus*		large
Equus	*nordostensis*		large
Equus	*orientalis*		large
Equus	*ovodovi*	Proskurjakov cave	196.5*
Equus	*pamirensis*		large
Equus	*przewalskii*		255.7
Equus	*sanmeniensis*		424.9*
Equus	*sanmeniensis*	Tologoj	336.9*
Equus	*steinheimensis*		large, similar to *E. ferus*
Equus	*stenonis*	Adyrgan	333.2*
Equus	*stenonis*	Dmanisi	473.8
Equus	*stenonis*		448.4
Equus	*suessenbornensis*		590
Equus	*suessenbornensis*	Akhalkalaki	631.1
Equus	*taubachensis*	Prolom 2	301.2*
Equus	*uralensis*		412.5
Equus	*verae*		590.5
Baryhipparion	*tchicoicum*		151
Hipparion	*hippidiodus*		195.4
Plesiohipparion	*houfenense*		249

Hypsodonty values are assigned to each species according to the ratio of height to length or the ratio of the unworn molar height to width(Janis & Fortelius 1988). These values were obtained from the NOW database (https://doi.org/10.5281/zenodo.4268068, *see* also Appendix 2). I followed the classification of Fortelius *et al.* (2003), in which teeth are considered brachydont or low-crowned when the ratio of height to length (or dorsal-ventral to anterior-posterior ratio) is smaller than 0.8 (ordinated hypsodonty value = 1), mesodont or medium-crowned with the ratio from 0.8 to 1.2 (ordinated hypsodonty value = 2), and hypsodont or high-crowned, or continuously growing or hypselodont (only the genus *Elasmotherium*), with the ratio greater than 1.2 (ordinated hypsodonty value = 3). Measured individual hypsodonty values were not recorded.

To demonstrate habitat openness, I plotted mean ordinated hypsodonty on maps, using large ungulates from the same localities where the horse body mass data came from, excluding hypsodont Equidae. The mean ordinated hypsodonty was mapped for each locality per time period.

Body mass

Body mass estimates used in this work were obtained from the NOW Database of fossil mammals (https://doi.org/10.5281/zenodo.4268068) and the mean species body mass data from Cirilli *et al.* (2022) (Table 2).

New estimates of the mean body mass for *E. sanmeniensis* (Kuzmina 1997, Wei *et al.* 2023), *E. gmelini*, *E. hipparioinoides* and *E. stenonis* (Kuzmina 1997), *E. lenensis* from the Aldan River and Kotelnyj Island and *E. caballus* from Botai (Vereshchahin & Lazarev 1977), *E. hydruntinus* and *E. taubachensis* (Eisenmann & Baryshnikov 1995), *E. hydruntinus* and *E. ovodovi* (Plasteeva *et al.* 2015) and *E. dalianensis* (Spasskaya *et al*. 2021) (Table 2) were calculated based on the length (in the direction of the tooth row) of the second upper molar tooth (M2) with the following equation (MacFadden & Hulbert 1990, Saarinen *et al.* 2021):

$$\log(M) = a + b \times \log X,$$

where M = body mass, X = skeletal measurement (in this case M2 length), a = intercept of the regression line, b = slope of the regression line. The body mass was calculated as follows:

$$M = 10^{a + b \times \log X}$$

The slopes and intercepts for calculating body mass from M2 length of the Equidae skulls were $a = 0.94$ and $b = 3.15$. (MacFadden & Hulbert 1990).

Data analysis

The data were tested for normality with an Anderson-Darling test which is applicable to data series with many identical values. It indicated that the body mass data were not normally distributed ($A^2 = 35.6$, $p < 0.0001$), thus, I chose a Kruskal-Wallis test to verify whether there were differences in the means of body mass among periods (data for Hipparionini were excluded) followed by a post-hoc χ^2-test.

Results

Hypsodonty

Mean ordinated hypsodonty maps demonstrated paleoclimatic conditions from most humid (coded as dark blue in Fig. 1) to most arid (coded as red in Fig. 1) from the Pliocene to the Holocene, indicating progressive opening of landscapes throughout the Pleistocene and returning towards more humid and closed environments at the very end of the Pleistocene and during the Holocene. The mean ordinated hypsodonty for the Pliocene sites was 1.99 and almost evenly distributed geographically (Fig. 1A).

The early Early Pleistocene mean ordinated hypsodonty was 2.12 (Fig. 1B) divided between the sites with more mesodont species in Europe and central Asia, represented mostly by cervids, early rhinos and low-crowned antelopes, and hypsodont species in eastern Siberia, represented by high crowned Antilopini and early mammoths. Regional high hypsodonty centres were associated with elevated regions (the Caucasus,

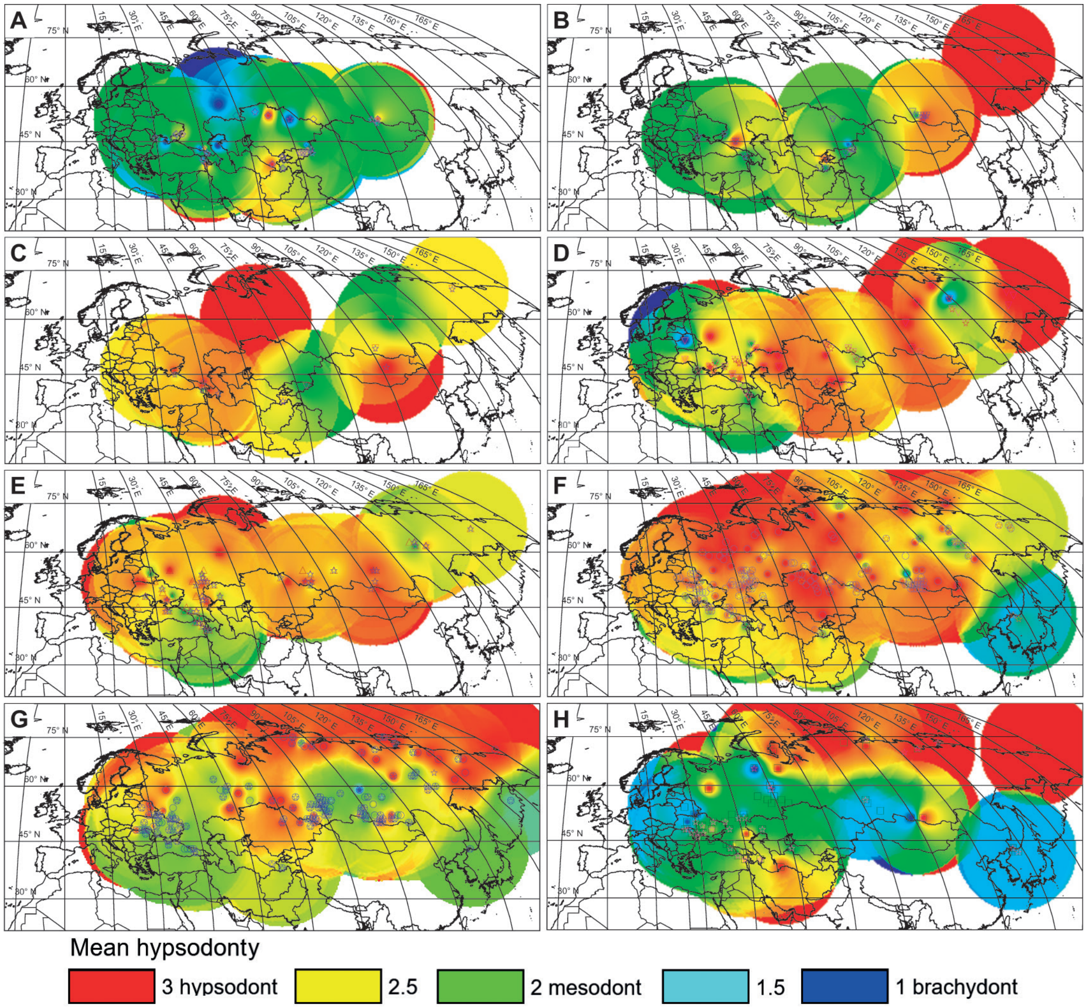

Fig. 1. Mean hypsodonty without Equidae (stars indicate localities with horses, triangles, circles or squares are localities without horses). — **A**: Pliocene. — **B**: Early Early Pleistocene. — **C**: Late Early Pleistocene. — **D**: Early Middle Pleistocene. — **E**: Late Middle Pleistocene. — **F**: Early Late Pleistocene. — **G**: Late Late Pleistocene. — **H**: Holocene.

northern Tian Shan, Altai Mountains). Interestingly, the subdivision across 75°–90°E corresponded to the difference in elevation between the Western Siberian Plain with elevations ≤ 300 m a.s.l. and the Central Siberian Plateau with elevations 306–610 m a.s.l. (Fig. 1B).

Increase in mean ordinated hypsodonty was seen during the late Early Pleistocene (2.46; Fig. 1C), the early Middle Pleistocene (2.5; Fig. 1D), the late Middle Pleistocene (2.42; Fig. 1E), and the early Late Pleistocene (2.56; Fig. 1F). During the late Early Pleistocene Europe became relatively drier than central Asia and north-eastern Eurasia, whereas the south-east of central Asia (based on one locality) appeared dry (Fig. 1C). During the early Middle Pleistocene, Europe appeared more humid, with regionally drier sites, while more humid Western Siberian Plain and north-eastern Eurasia alternated with arid central Asian steppes, Central Siberian Plateau and Russian Far East (Fig. 1D).

During the late Middle Pleistocene drier conditions appeared to have expanded (Fig. 1E), having been more humid in southern Europe (the Caucasus) and north-eastern Eurasia. The maximum extent of dry and open landscapes, characterised largely by the Mammoth steppe, was present during the early Late Pleistocene (Fig. 1F), the stage which was represented by the majority of the Late Pleistocene sites in this study. The Russian Far East (south and north) appeared more humid than the rest of the relatively dry northern Eurasia, where north-eastern and south-western regions appeared similarly moderately dry.

A slight decrease in mean ordinated hypsodonty was seen already during the late Late Pleistocene with the mean value 2.39, when a somewhat higher proportion of lower-crowned species was present below 60°–70°N across Eurasia (Fig. 1G), indicating the spread of relatively more humid and perhaps locally wooded habitats during the Late Glacial Interstadial. The Holocene presence of more humid and closed habitats was clearly seen under 60°N with the mean hypsodonty 2.01 with regional centres of high mean hypsodonty in the north and south, associated with deserted, elevated or human occupied areas (Fig. 1H).

Body mass

During the Pliocene, smaller Hipparionini with the mean mass of 203.7 kg were present in the north-east, whereas larger *E. stenonis* (448.4 kg) appeared to the south-west (Fig. 2A).

During the Early Pleistocene and the early Middle Pleistocene, *Equus* spp. body masses were comparatively large, ranging from 241.7 kg (*E. hydruntinus*) to 653.3 kg (*E. major*), with the mean body masses in the early Early Pleistocene, the late Early Pleistocene and the early Middle Pleistocene being 464 kg (Fig. 2B), 462 kg (Fig. 2C) and 452 kg (Fig. 2D), respectively. In general, during the Early Pleistocene and the early Middle Pleistocene, very large *Equus* spp. of around 600 kg were present in Europe and Russian Far East, as well as during the early Middle Pleistocene in the Caucasus and central Asia. The Early Pleistocene large and medium-sized horses (300–400 kg) in the south of the Western Siberian Plain (Fig. 2B) and Baikal area (Fig. 2C) were represented by *E. stenonis* and *E. sanmeniensis*, which had smaller estimated body masses in those regions than considered average for those species (Table 2).

Starting from the late Middle Pleistocene, the mean *Equus* body mass decreased by almost 100 kg. During the late Middle Pleistocene, early Late Pleistocene and the late Late Pleistocene, mean *Equus* spp. body masses were 377 kg (Fig. 2E), 356 kg (Fig. 2F) and 358 kg (Fig. 2G), respectively, ranging during those periods from 198.9 kg (*E. hemionus*) to 590.5 kg (*E. coliemensis*). During the late Middle Pleistocene very large horses (*E. mosbachensis* > 500 kg) appeared in the south of the Western Siberian Plain and small horses (*E. hemionus*, 200 kg) in the Baikal area, while medium-sized horses appeared in Europe and slightly larger horses in the Far East (Fig. 2E).

During the Late Pleistocene, body mass of horses in Europe increased, and during the Holocene decreased. Very large horses (*E. mosbachensis*) were present in the north-eastern Siberia during the early Late Pleistocene, and in south-eastern Siberia during the late Late Pleistocene (*E. dalianensis*) (Fig. 2F–H). The dry central Asia and southern Siberia were represented by small horses (*E. hemionus*, *E. hydruntinus*).

The mean *Equus* mass during the Holocene was 343 kg, ranging from 198.9 kg to 507 kg (*E. latipes*) (Fig. 2H). Horses in Siberia appear to have been larger that those in Europe. A reference estimate for an early domesticated *E. caballus* from Botai (Kazakhstan) was 268.2 kg only.

Equus spp. body masses differed among the periods (Kruskal-Wallis $H = 75.5$, df = 7, $p < 0.0001$), decreasing from the early Middle to the late Middle Pleistocene (Fig. 3). A post-hoc median test indicated significant differences ($p < 0.0001$) in *Equus* spp. body mass between the periods.

The Pliocene data contained the body mass estimate for *E. stenonis* only. From the early Early Pleistocene, body mass data for 5 species, from 21 occurrences were available (Table 1 and Fig. 3). More body mass data were available from the later periods starting with the late Early Pleistocene. The body mass means and from the Holocene, the late Late Pleistocene, the early Late Pleistocene and the late Middle Pleistocene were smaller than those from the early Middle Pleistocene, the late Early Pleistocene, the early Early Pleistocene, and the Pliocene.

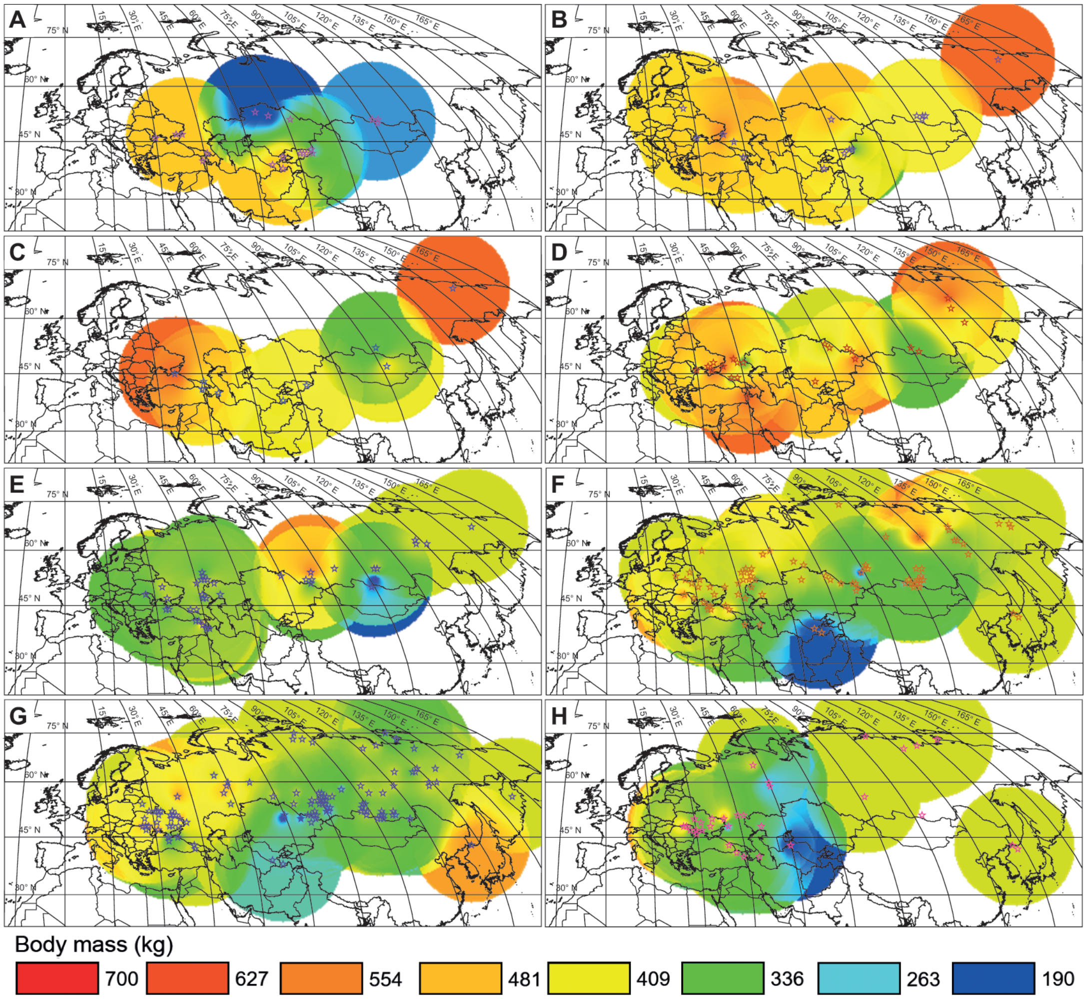

Fig. 2. Equinae body mass (stars indicate localities with Equinae). — **A**: Pliocene. — **B**: Early Early Pleistocene. — **C**: Late Early Pleistocene. — **D**: Early Middle Pleistocene. — **E**: Late Middle Pleistocene. — **F**: Early Late Pleistocene. — **G**: Late Late Pleistocene. — **H**: Holocene.

Discussion

Hypsodonty

Since the Middle Miocene (~15–11 Ma), central Asia had been the focal point of the transformation in northern Eurasia towards more arid and open environments with drying at times extending into western Europe (Dorofeev 1966, Fortelius *et al.* 1996, 2002, 2003, 2006, Hurka *et al.* 2019). Aridification, cooling and opening of landscapes continued into the Pleistocene with more rapid and extensive climatic oscillations and environmental changes, followed by the transition towards more humid and closed habitats during the latest Late Pleistocene (Late Glacial warming interval) and the Holocene.

The mean ordinated hypsodonty revealed remarkable trends of climatic and environmental changes, which are supported by the Late Pleistocene precipitation and vegetation zone data, that demonstrate a more detailed chronologic and geographic subdivision in northern Eurasia (Grichuk 1984, Velichko 1984, Frenzel *et al.* 1992, Hurka *et al.* 2019), and indicate the existence of different zoogeographic provinces. Despite the crude chronological division and

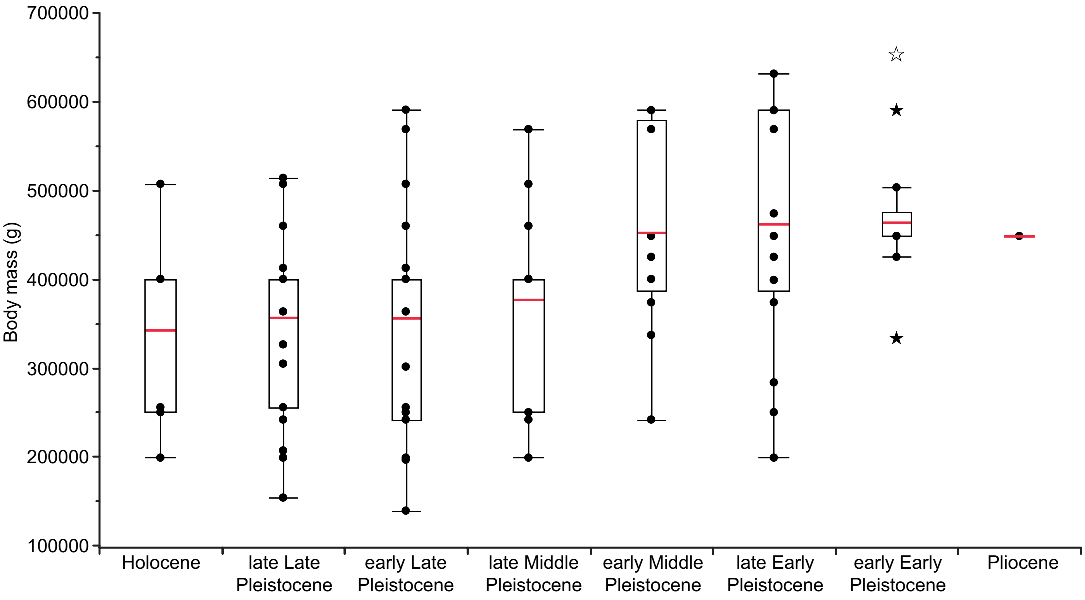

Fig. 3. *Equus* spp. body masses in different periods. The boxes indicate the first and third quartiles, the red lines inside the boxes indicate means, the whiskers indicate 1.5 × interquartile ranges. The dots are mass estimates and stars are outliers.

relative scarcity of data for some periods, the expansion of the steppe-tundra, known as the Mammoth steppe, appears to have started from the Russian Far East and western Siberia already during the Early Pleistocene. Since then, the Mammoth steppe paleobiome persisted in northern Eurasia until the beginning of the Holocene (Sher 1971, Hurka *et al*. 2019). The cold-adapted *Mammuthus–Coelodonta* faunal complex was evolving in constantly changing environments for about 1 million years (Sher 1971, Ukraintseva 1985, Sher 1992, 1997, Lister & Sher 2001, Lister 2004, Lister *et al*. 2005).

Variation in precipitation, more than temperature, is suggested to have controlled the extent of both floral and faunal exchange and allowed more diversity in mammalian faunas (Kvasov, 1977, Tormidiaro 1977, Kowalski 1980, Vereshchagin & Baryshnikov 1985, Kowalski 1989, von Koenigswald 2002). Drying of the central part of Eurasia probably hampered the spread of temperate or mesophilic species between western and eastern sides of the continent, and created conditions for origination of the cold- and arid-adapted grazing fauna in north-eastern Eurasia (Sher 1971, Vereshchagin & Kuzmina 1984, Sher 1992, 1997). However, humid and forested corridors existed between 45°N and 60°N and along the river valleys on the Eastern European Plain and in eastern Siberia (Vereshchagin 1959, Vereshchagin & Baryshnikov 1980, Baryshnikov 1987).

The spread of taiga appears to have taken place during the late Late Pleistocene (Grichuk 1984, Velichko 1984, Frenzel *et al.* 1992, Hurka *et al*. 2019), and was seen in this study in the Ural and Altai Mountains and on the Central Siberian Plateau, where mesophilic or temperate species were found in refugia during the Late Pleistocene glaciations, during the time when the mammoth steppe-tundra was still extensive throughout northern Eurasia. These sites are also associated with the occurrences of *Homo* spp. (Vasil'ev *et al.* 2002), which started appearing during the late Middle Pleistocene, and become more prevalent during the Late Pleistocene and the Holocene. Forest or taiga was present across northern Eurasia during the Holocene (Grichuk 1984, Velichko 1984, Frenzel *et al.* 1992, Hurka *et al*. 2019) as demonstrated here south of 60°N and more northwards in the Urals and the Lena River valley (south of 70°N) (*see* Fig. 1).

Body mass

Despite the crudeness of the data biased towards large mammals in localities containing equids, a decrease in *Equus* spp. body mass from the Pleistocene to the Holocene is seen, accompanied by temporal and geographical variations. A more noticeable change appears to have occurred from the early Middle Pleistocene to the late Middle Pleistocene to resemble the body mass distribution in the Holocene. These variations, however, require a more thorough study taking into account *Equus* species' response to climate change and intra- and interspecific competition. However, mean body mass change in Equidae during the early Middle and late Middle Pleistocene corresponds to the accelerated rates of the global environmental changes during the Middle Pleistocene and the mammalian faunal transformation (Galerian–Aurelian faunal exchange) (Sardella & Strani 2023) towards the Late Pleistocene (Lister 2004). During that transformation, the modern faunal composition started to form, with many species adapting to increasingly dry and cold environments by decreasing in size.

Heterogeneity of landscapes across northern Eurasia is reflected in the body mass distribution of horses. During the Pliocene, both hipparionini and a more open-adapted *E. stenonis* occurred in rather humid and closed habitats (intermediate mean ordinated hypsodonty). The appearance of *E. stenonis* in open habitats is seen in central Asia, at several sites in the Caucasus and on the Eastern European Plain. The stenonids are the earliest monodactyl horses that dispersed from North America into northern Eurasia and quickly spread throughout Eurasia (Forstén 1988), to be later replaced by more advanced caballoid horses at the beginning of the Middle Pleistocene (Forstén 1988, Azzaroli 1991).

During the early Early Pleistocene, associated with the Khaprov and early Psekups faunal complexes on the Eastern European Plain (Markova *et al.* 1995, Khromov *et al.* 2001), very large horses (≥ 500 kg, *E. major*, *E. livenzovensis*) were found in humid habitats in Europe and parts of central Asia, and in open and drier habitats in eastern Siberia and the Far East (*E. verae*). The Vera Gromova horse (*E. verae*) was quite slender and slim-legged despite the size, which is an adaptation to moving in dry landscapes on hard substrates (Sher 1971, Kuzmina 1997). This species finds are associated with temperate cold vegetation (Sher 1971). Large and medium-sized horses (*E. stenonis*, *E. sanmeniensis)* (300–400 kg) are found associated with various types of habitats.

During the late Early Pleistocene, which is roughly associated with Psekups/Odessa and Taman complexes on the Eastern European Plain (Markova *et al.* 1995, Khromov *et al.* 2001), very large horses (around and over 600 kg) appeared in moderately open habitats in Europe (*E. mosbachensis*, *E. suessenbornensis*) and the Russian Far East (*E. verae*), whereas large and medium-sized horses (*E. stenonis*, *E. altidens*, *E. sanmeniensis*) are found in varyingly arid habitats (mean ordinated hypsodonty 1.75–2.5), and the small *E. nalaikhensis* and *E. hemionus* in arid habitats. Central Europe, which was comparatively more humid, is not discussed here.

During the early Middle Pleistocene, associated with the Tiraspolian faunal complex on Eastern European Plain and in the northern Caucasus, with mammals adapted to steppes and forest–steppes (Gromov 1972, Sher 1972, Markova *et al.* 1995, Khromov *et al.* 2001), very large horses (around and over 600 kg) are found in association with relatively humid and closed habitats on the Eastern European Plain, in the south of western Siberia (*E. mosbachensis E. suessenbornensis*) and in the Far East (*E. verae*, *E. coliemensis*), although some of them are found associated with drier and more open habitats (mean ordinated hypsodonty = 1.8–2.8). The medium-sized horses — *E. sanmeniensis* and *E. caballus* that may be *E. ferus* or some other species — are found in localities where hypsodonty indicates drier and more open habitats in central Asia and the Baikal region during this period.

During the late Middle Pleistocene, associated with the Khazarian faunal complex with mammals adapted to cold and open landscapes (Markova *et al.* 1995, Khromov *et al.* 2001), very large horses are almost uniformly replaced by medium-sized and small horses (in terms of lesser occurrences of the large horses) in very dry open habitats on the Eastern European Plain. Similarly, the remaining large horses in southern

Siberia are replaced by medium-sized and small ones, whereas in the Far East, larger medium-sized horses (400 kg) appear to have been present in less arid and open habitats. Smaller medium-sized horses (300 kg) were present in the Caucasus where the hypsodonty proxy indicates more humid conditions compared to the above-mentioned regions.

The opposite is seen here between Europe and Siberia, where during the Late Pleistocene the body mass of horses appears to have increased on the Eastern European Plain, while it appears to have decreased in Siberia, due to alteration in the presence of the large (*E. latipes*, *E. uralensis*) and medium to small species (*E. lenensis*, *E. hemionus*, *E. hydruntinus*). On the Eastern European Plain this could be associated with the change from very dry and open environments towards more humid and, perhaps, more wooded during the late Late Pleistocene (which includes the Late Glacial warming). For example, *E. latipes* was large and stocky with broad hooves, an adaptation to moving on soft and moist substrates in increasingly humid and rather warm habitats (Gromova 1949, Vereshchagin & Lazarev 1977, Kuzmina 1997). The diet of *E. latipes*, however, was predominantly graze-dominated based on my yet unpublished mesowear data. On the other hand, *E. uralensis*, was lightly built, found in more arid habitats along the Ural Mountains northward of *E. latipes*, and adapted to a more continental climate and harder substrates based on its narrow hooves, although there were regional variations across the Urals (Kuzmina 1997).

Equus lenensis was small and stockily built, found mostly in Northern Siberia above 60°N, and adapted to cold and relatively humid habitats with graze-dominated diet (Vereshchagin & Lazarev 1977, Kuzmina 1997). The small *E. hemionus* was adapted to dry continental climate and harder substrates. Similarly, the small-sized *E. hydruntinus* is suggested to have been adapted to dry and warm conditions (Kuzmina 1997).

Very large horses appear to have occupied humid habitats in north-eastern Siberia during the early Late Pleistocene (*E. mosbachensis*), and in south-eastern Siberia during the late Late Pleistocene (*E. dalianensis*). In Siberia, medium-sized and small horses (*E. lenensis* and *E. hemionus* having grazing diet) appear to have persisted in arid habitats during the Late Pleistocene. Medium-sized and small horses in southern Siberia and central Asia (the western Siberian Plain) appear to have existed in more arid habitats during the early Late Pleistocene, and somewhat more humid habitats during the late Late Pleistocene. The Pleistocene variation in body mass in the Altai (90°E) and Baikal (105°E) regions suggests presence of refugia habitats for both more mesophilic and more arid adapted species.

The Holocene division across the Ural Mountains (60°E) is seen between small horses (mean body mass 200 kg), present on the Eastern European Plain in relatively humid and closed habitats, and larger *E. caballus* (400 kg, possibly *E. ferus*) in Siberia, occupying more open habitats in the north-east or elevated regions. A few specimens of large *E. latipes* are also dated to the Holocene. *Equus lenensis* is not found in the Holocene (Vereshchagin & Lazarev 1977). *Equus* spp. mean body mass decreased from the late Late Pleistocene towards the Holocene on the Eastern European Plain and appear to have increased in Siberia. The extreme south-east appears humid and forested with quite large horses (mean 350 kg) probably due to maritime effect.

Both humidity and temperature are suggested to affect the size of horses. Generally, the most favourable condition for large sizes is high humidity and moderate temperatures, whereas the favoured conditions for smaller sizes are high aridity and high or low temperatures (Gromova 1949). My results, indicating the presence of the large horses in humid forested habitats and the small horses in arid open habitats, are also consistent with the latest studies (Saarinen *et al.* 2021, Uzunidis 2021, Cirilli *et al.* 2022, 2023, 2024). I have also found the opposite patterns in some regions, which could have resulted from partial overlap of long time periods but also from mosaics of habitats and horses' ecological niche sharing. In most of these exceptional cases, large horses were associated with high-hypsodonty (open) environments occurring in the highest-latitude localities (e.g., north-eastern Siberia), where the climate would have been colder than at the lower latitudes. Thus, low temperature rather than aridity may have been responsible for the harshness of the environment in these cases. It is possible that resource availability and quality were seasonally high and competition low at the high latitudes of the north, and large body size could also have helped keeping warm and survive in harsh conditions according to Bergmann's rule (Saarinen 2014). On the other hand, it is also possible that low population densities and thus less competition in the Arctic region could have enabled larger body size (Saarinen *et al.* 2021).

In general, there were three co-occurring types of *Equus* spp. during the Pleistocene across the territory of the former USSR: small *Equus*, large *Equus* and the wild ass (Vereshchagin & Lazarev 1977, Vangengeim & Zhegallo 1982, Kuzmina 1997) that depending on the zoogeographic province could have had individualistic habitat and diet strategies. Especially, this is the case in the Holocene, when domestic horses appear in the fossil record.

Although geographic and temporal origins of modern domestic horses have remained unknown (Libraldo *et al.* 2021), the centres of horse domestication might have been south of 50°–60°N. This is the boundary of the modern vegetation zones between steppes and forests, where during the Holocene the habitats became more humid, human populations expanded and the mean body size of horses was rather small. Kuzmina (1997) noted that domestication occurred somewhere between 48°N and 53°N between the Carpathians and northern Kazakhstan. Apart from western Eurasian and Kazakhstanian steppes that are currently understood to have been the centres of horse domestication (e.g., Botai horses) (Libraldo *et al.* 2021), a rather small stocky Lena or Chersky horse (*E. lenensis*) from Siberia might have been domesticated as well (Vereshchagin & Lazarev 1977). The Lena horse was similar in size to *E. caballus* from the suggested place of origins of the domestication at Botai. Practically, it must have been easier to tame a modest-sized wild animal than a larger one, unless the animal was taken care of since a young age. This suggests that small-sized and grazing-adapted horses were favoured as the subjects of domestication in the Holocene, which might also have prevented them from extinction, which other horse lineages experienced.

Conclusions

Paleoclimatic changes in horse habitats and body mass differences are demonstrated from the Pliocene, throughout the Pleistocene to the Holocene across northern Eurasia. The mean ordinated hypsodonty of non-equid ungulates reveals remarkable trends of association with the physical environment and shows the existence of heterogenic zoogeographic provinces, demonstrating progressive opening of landscapes during the Pleistocene, and the opposite trend towards more humid and closed environments south of 70°N at the very end of the Pleistocene and during the Holocene, corresponding to the modern boreal forest (taiga) zonation.

The body mass of horses varied temporally and geographically, and decreased from the Pleistocene to the Holocene. A noticeable decrease appears to have been between the early Middle and late Middle Pleistocene, corresponding to global climatic and environmental changes (Galerian–Aurelian or Tiraspol–Khazar faunal exchange). Although large horses are usually associated with more closed habitats and have more mixed-diets, whereas small horses are usually associated with open habitats and are grazers, some cases are found with a contrasting pattern across northern Eurasia. Such cases mostly occur in the highest latitudes, where temperature or cold climate rather than precipitation or aridity could have driven the "harshness" and openness of these environments.

The Holocene domestication might have prevented some horse lineages from extinction, e.g., small-sized and grazing-adapted, when taiga forests spread across northern Eurasia. More detailed information on horse systematics and comprehensive analyses of their body masses will provide a better understanding of horse paleoecology. Revision of the old material, containing *Equus* spp. measurements of the Pleistocene and early Holocene horses can shed a brighter light on the horse species adaptation and survival.

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Appendix 1. Localities with Equidae occurrences used in the study.

Pliocene
Ajdyrlja
Ajgyrzhal
Akterek
Beldersaj
Berdjansk
Beregovaya 1
Bessarabia
Beteke
Chonbulak
Dzhylgyndykoo
Esekartkan
Fort Aleksandrovskij
Groznyj (Solenyj)
Gulizindon
Ichketasma
Kojbyn river
Koktyurlyuk
Kopala 1
Kvabebi
Lebyazhje 1
Ljapino
Lok-Batan
Malgobek
Nakhichevan
Nikolaevka
Nurnus
Obigarm1
Odessa 3
Ostraja Sopka
Rostov (na Donu)–Taganrog
Selim-Dzhevar
Shakhrizyabz
Simbugino
Tologoj 1
Udunga
Zhabyrtau
Zhdanov

Early Early Pleistocene
Adyrgan
Bolshaja Kamyshevakha 1
Charyn lower
Charyn upper
Dodogol 1
Karamajdan
Khapry
Klochnevo 1
Kopala 2
Krestovka
Kudun
Kuruksaj
Liventsovka (Rostov-on-Don)
Podpusk-Lebyazhje
Podpusk-Lebyazhje 2
Saty upper
Smorgon’ lower
Tsalka
Tutak
Ust-Obor
Vinodelnoe (Kutsaj)
Yakkabed
Zhevakhova Gora lower

Late Early Pleistocene
Akhalkalaki
Binagady old (Baku)
Bolshaja Chukochja #21
Bolshaja Chukochja #25
Bolshaja Chukochja #27
Bolshaja Chukochja #36
Dmanisi
Lakhuti 1
Lakhuti 2
Nalajkha
Obigarm
Sennaja: Tsimbala
Sinjaja Balka/Bogatyri
Tash-Kala
Tepke 1

continued

Appendix 1. Continued.

Late Early Pleistocene
Zasukhino 3
Zasukhino 4

Early Middle Pleistocene
Amga (Chichimakh)
Azov (Kagalutskij)
Azykh: layer 6
Chernojarka
Denisova Cave l. 12–14
Kolkotova Balka (Tiraspol)
Krasnojarka
Mamontova Gora
Marganets
Moiseevka
Nizhnee Zajmishche
Rajgorod
Shashkin khutor
Tikhonovka 1
Tologoi 2.5
Tologoj 2
Treugolnaja cave l. 6–7
Ulakhan Sullar middle
Vjatkino
Zelenokumsk
Zyrjanovsk lower

Late Middle Pleistocene
Aldan river: terrace 50 m
Azykh
Azykh: layer 5
Belovo
Bijsk
Bolshoj Irgiz
Buzduzhany 1 grotto
Chujskoe
Denisova Cave l. 22
Kalaus: Stavropol fauna
Khoroshevskij island
Khvorostjanka
Klochnevo 1 mid Pleisto
Klopikha
Kosh Koba
Krasnojarsk (Enisej r.)
Kundoj mid Pleisto
Kuznetskaja kotlovina l. IV-V
Kuznetskaja kotlovina l.III-IV
Leninakan (Kazachij Post)
Lipovka
Lubni
Mikhajlovka (Astrakhan) l.7
Molotkovskij kamen #47:48:49
Nikolskoe: Volga
Novonikolskoe
Peschanyj Umjet
Pionerlager #2124
Pologoe Zajmishche (Kolobovka)
Rokhmanovka
Sakazhija
Severobajkalsk 1 (7)
Shaitan Koba
Sholokhovo
Tandinskoe alluvial
Tatarka
Treugolnaja cave l. 5
Trostjan ovrag
Tsopi
Tunguz peninsula
Ural river Khazar
Uralsk
Utkinskij kamen #46
Voronij island

Early Late Pleistocene
Aldan river: terrace 30 m
Aldan river: terrace 50 m: all
Aldan river: terrace 50 m loess
Alekseevka
Aman Kutan
Babyk Burluk
Bar
Barakaevskaya stoyanka
Binagady
Bliznetsov grotto
Bolshaja Oreshnaja cave
Bolshie Tarkhany
Botsy
Chokurcha I cave
Denisova Cave l. 19–21
Denisova Cave l. 8–10
Desna river
Devichji Gorki
Djuktajsakaja cave VIIa–IX
Dushelan
Engorboj
Erevanskaja cave
Gajsin
Geographical Society cave l. 4–5
Gorkhon
Ikhnenskoe openning
Iljinka
Inargida
Irkutsk
Irtysh lower course
Jurish 1
Kamenka
Kaminnaja BVGD
Kara-Bom M1–M2
Kherson Pleisto
Khudji
Kiik-Koba
Kopanovka
Krasnaja Glinka
Krasnoe Ozero
Krasnyj Kljuch
Krestovka l. 7
Kujtun
Kumora
Kundoj late Pleisto
Kuntsevo
Kyra Sullar
Mamat-Koba
Minsk
Mokraja Bugurna
Mysovaja
Mysy-Mansurovo
Naedino
Nikolskoe: Bajkal
Nizhnie Karmalki
Okhnenskoe
Omolono-Anjujsjkaja edoma
Pestravka
Porovskoe
Prolom 2
Proskurjakov cave
Rumlovka
Russkaja Talovka #502
Rzhishchev
Samara
Selenga river
Selishche
Sengilej (Uljanovsk)
Severobajkal’sk 2 (5)
Shajtanskij grot: l. 3 lower
Shapki Kirsinskie
Shkurlat
Spjashchaja Krasavitsa
Stanchikovskij Yar
Staraja Kurba
Staroselje
Starye Algashi
Stolbovoi Grotto
Studenyj Ovrag
Sukhaja Mechetka l.4
Tajmyr p-la LtPl
Taltsy
Teterev r. (Zhitomir)
Tobolsk: Irtysh: Yvat
Torgashinskaja cave
Trinka I l. 3–4
Troitskosavsk (Kjakhta)
Tsarev Kurgan
Ukyr-Gulon
Ulakhan Sullar
Uljanovsk 2
Ural river later
Ust-Izhul
Ust-Kanskaja cave
Ust-Karakol l. 18a
Ust-Kharlun
Vilyuj river
Volsie Kholmy
Volsk Kommunar

continued

Appendix 1. Continued.

Zaktyj (Belyj Jar)
Zaskal’naya IX lower
Zhana-Aul
Zhelezinka
Zyrjanovsk

Late Late Pleistocene
Achinskaja
Afontova Gora I
Afontova Gora II
Afontova Gora III
Afontova Gora V
Aldan river: terrace 30 m loess
Aleshkina zaimka
Anabar-Olenek: Olenekskaja r.
Anetovka II
Anui I: l. 3
Arta II 1–3
Avdeevskaja
Balyshevo III
Batpak river: 7
Bazhintaj
Bedarevo II
Berdyzhskaja stojanka
Berelekh
Berelekh kitchen
Berezovyj Ruchej I
Birjuza I B:C: 1–4
Bolshaja Slizneva 4–9
Bolshoj Glukhoj grot l. V–IX
Bolshoj Jakor I 3v-12
Bolshoj Lyakhovskij isl: 1 TC
Bolshoj Lyakhovskij: shore-cape
Brazhnoe
Bukhtarma cave
Buret
Buret II
Bykovskij p-la: MKh main/shore
Cheremushnik I
Cheremushnik II: 1–2
Chernoozerje II
Chindant
Chulatov (Chulatovo I)
Don settlements
Dovginichi
Druzhinikha
Dvuglazka 5
Dvuglazka 6–7
Dvuglazka cave l. 4
Eliseevichi
Emine Bair Khosar
Engelgardt L: Tajmyr
Ezhantsy
Fedjaevo
Gmelinskaja Kostenki 21 lower
Golubaja I: 1:3
Holocene shore: Bykovskij p: L
Igetejskij Log I
Ikhine I 1–3
Ikhine II 1–2 g
Ilskaja 1&2
Irtysh left bank
Jamburg
Kaiskaja Gora
Kajstrova Balka
Kamenka I A:C
Kaminnaja 11–14
Kaminnaja A1: A3: 10
Kandabaevo
Kanev
Kara-Bom 3–6
Kara-Tenesh
Karaulnyj Byk l. 3–9
Kashtanka I: l. 1–2
Kharkov
Khatanga: Talalakh L: Popugaj
Kokorevo I: 1–6
Kokorevo II
Kokorevo III
Kokorevo IV A:B
Kokorevo VI
Korman IV
Korovij Log II
Kosoutsy Cosauti I: l. I–VIII Molodova V
Kostenki I: l. 1
Kotelnyj island: Novosibirskie
Krasnyj Jar I: l. 2–4
Kulakovo I
Kunalej
Kupchiktach L: Tajmyr
Kurtak IV main
Kurtak V
Kuznetskaja kotlovina l. VI
Lena delta late:Bykovskij:main
Lena delta: Bykovskij: MKh main
Lena delta: MKh: shore & bar
Lena lower course: Sangary r.
Listvenka 1–19
Logata r: Tajmyr
Lugovskoe
Maininskaja l. 4–9
Maininskaja l. A1–3: B
Makarovo II 3–4
Makarovo III
Malaja Syja l. 1–2
Malaja Syja l. 3
Maloialomanskaja l. 2
Malta main 8
Malyj Yankul: Kalaus
Medvezhja cave
Mezherich
Mezinskaja
Mgvimevi
Minusinskaja kotlovina
Mogochino I: exc. 1–3
Mokhnevskaja cave
Mokhovo II
Molodova I l. 1–3 LtPal
Molodova I: l. 4
Nepa
Novgorod-Severskij
Novopokrovka
Novoselovo XII
Novoselovo XIII 1–2
Novyj Leten I
Ogzi-Kichik
Okladnikov cave
Osokorivka balka
Oznachennoe I
Pereselencheskij Punkt
Pogorilivka
Priiskovaja
Pushkari
Samarkand
Sannyj Mys 3-5
Selerikan
Shajtanskij grot: l. 2 upper
Shamotnyj Zavod 1–2
Shestakovo
Shlenka
Smorgon late Pleist
Sokhatino II
Sosnovyj Bor l. 3–4
Sosnovyj Bor l. 5
Srostki
Starye Duruitory l. 2 upper
Staryj Kodak
Strashnaja cave 3a–b
Strizhova Gora l. 4: 8–16: 17
Suchan river
Sukhotino 4
Sungir
Tarachikha loc. 1
Tashtyk I l. 1–3: exc. 2
Tashtyk II 1-2
Tolbaga
Trinka I l. 2
Tytkesken III l. 7
Ui I: 2–2/3
Ui II: 2–7: exc. 1
Ushki I
Ushlep VI: l. 2
Ushlep VI: l. 3
Ust-Karakol l. 13–17
Ust’-Katavskaja cave
Ust-Kjakhta IV (1–2)
Ust-Kjakhta XVII (3:5)
Ust-Kova lower
Ust-Kova middle
Ust-Kova upper
Ust-Menza II
Ust-Mil II A–C
Varvarina Gora

continued

Appendix 1. Continued.

Verkhne-Troitskaja
Verkholenskaja Gora 1 l. 3
Voennyj Gospital
Volchij Grot
Volchja Griva
Voroshilovgrad
Yudinovo
Yurevichi
Zaskalnaya V-VI

Holocene
Akhshtyrskaja cave Hol
Andreevka Hol
Baku
Bolshoj Lyakhovskij island Hol
Bykovskij p.: Lena delta Hol
Cherkasskaya
Geographical Society cave Hol
Jurish 2 Hol
Karachevka
Karmir Blur (Tejshebaini) cast
Khalep (Tripilja) Hol
Khitryj Kljuch grot
Khoresm: Uchashchi st.
Kichkas
Kiev zemljanki
Kisilivka mountain
Laksejskaja cave
Lobvinskaja cave
Lovushka cave (Belaja)
Molodova I
Mukhor-Tala
Olenek r: Anabar-Olenek
Parutino
Pechora: Unja caves
Rud'
Sabatinovka
Sagvardzhile
Sarajbulakhskij: Urtskij khreb
Sarkel castle (Belaja Vezha)
Sevan lake
Shajtanskij grot: layer 1
Skok
Suchan caves
Tajmyr Hol
Trinka I l. 1
Ural river Holocene
Usatove
Varfolomeevka
Vishgorod

Appendix 2. Hypsodonty values used for the mean ordinated locality calculations.

Genus	Species	Subfamily	Unique	Hypsodonty
Alces	*alces*			1
Alces	indet.		*large*	1
Alces	indet.			1
Alces	*latifrons*		*postremus*	1
Alces	*latifrons*			1
Anancus	*alexeevae*			1
Anancus	*arvernensis*			1
Anancus	*kazachstanensis*			1
Anancus	*sinensis*			1
Antilospira	*gracilis*			2
Antilospira	indet.			2
Antilospira	*zdanskyi*			2
Arvernoceros	indet.			1
Axis	*flerovi*	Cervinae		2
Axis	*shansius*	Cervinae		2
Axis	*ubensis*	Cervinae		2
Bison	*bonasus*		*caucasicus*	3
Bison	*bonasus*			3
Bison	*georgicus*			3
Bison	indet.			3
Bison	*priscus*		*crassicornis*	3
Bison	*priscus*		*demintus*	3
Bison	*priscus*		*longicornis*	3
Bison	*priscus*		*occidentalis*	3
Bison	*priscus*		*small*	3
Bison	*priscus*			3
Bison	*schoetensacki*			3
Bison	*tamanensis*			3
Bos	indet.	Bovinae		3
Bos	*mastanzadei*	Bovinae		3
Bos	*primigenius*	Bovinae		3
Bos	*taurus*	Bovinae		3
Bos	*trochoceros*	Bovinae		3
Bubalus	*murrensis*			3

continued

Appendix 2. Continued.

Genus	Species	Subfamily	Unique	Hypsodonty
Camelus	*dromedarius*			3
Camelus	indet.			3
Camelus	*knoblochi*			3
Capra	*aegargus*			3
Capra	*caucasica*			3
Capra	*cylindricornis*			3
Capra	*hircus*			3
Capra	*ibex*			3
Capra	indet.			3
Capra	*sibirica*			3
Capreolus	*capreolus*			1
Capreolus	*constantini*			1
Capreolus	indet.			1
Capreolus	*pygargus*			1
Capreolus	*suessenbornensis*			1
Cervalces	*latifrons*			1
Cervavitus	*flerovi*			1
Cervus	*elaphus*	Cervinae	*acoronatus*	2
Cervus	*elaphus*	Cervinae	*binagadensis*	2
Cervus	*elaphus*	Cervinae	*fossilis*	2
Cervus	*elaphus*	Cervinae	*maral*	2
Cervus	*elaphus*	Cervinae	*sibiricus*	2
Cervus	*elaphus*	Cervinae		2
Cervus	*nippon*	Cervinae		2
Cervus	*philisi*	Cervinae		1
Chilotherium	*anderssoni*			3
Chilotherium	*habereri*			2
Chilotherium	*schlosseri*			3
Coelodonta	*antiquitatis*		*humilis*	3
Coelodonta	*antiquitatis*		*jacuticus*	3
Coelodonta	*antiquitatis*		*pristinus*	3
Coelodonta	*antiquitatis*			3
Coelodonta	*indet.*			3
Coelodonta	*tologoijensis*			3
Croizetoceros	indet.			1
Dama	*dama*			1
Dama	*mesopotamica*			1
Dama	*nestii*			1
Dicerorhinus	indet.			1
Dihoplus	*pikermiensis*			2
Elaphurus	*eleonorae*			2
Elaphurus	indet.			2
Elasmotherium	*caucasicum*			3
Elasmotherium	indet.			3
Elasmotherium	*sibiricum*			3
Elephas	indet.			3
Elephas	*planifrons*			3
Eucladoceros	*dicranios*			1
Eucladoceros	indet.			1
Eucladoceros	*senezensis*			1
Gazella	indet.	Antilopini		3
Gazella	*parasinensis*	Antilopini		2
Gazella	*sinensis*	Antilopini		2
Gazella	*subgutturosa*	Antilopini		2
Gazellospira	*gromovae*			3

continued

Appendix 2. Continued.

Genus	Species	Subfamily	Unique	Hypsodonty
Gazellospira	indet.			3
Gazellospira	*torticornis*			3
Gigantocamelus	*longipes*	Camelinae		3
Hemitragus	*bonali*			3
Hemitragus	indet.			3
Hippopotamus	*antiquus*			2
Hippopotamus	indet.			2
indet.	indet.	Ovibovini		3
indet.	indet.	Caprini		3
Itanzatherium	*angustirostre*			1
Leptobos	*etruscus*	Bovinae		3
Leptobos	indet.	Bovinae		3
Libralces	*gallicus*			1
Libralces	indet.			1
Macaca	indet.	Papionini		1
Macaca	*sylvanus*	Papionini		1
Mammut	*borsoni*			1
Mammuthus	*gromovi*			3
Mammuthus	indet.			3
Mammuthus	*meridionalis*		*meridionalis*	3
Mammuthus	*meridionalis*		*tamanensis*	3
Mammuthus	*meridionalis*			3
Mammuthus	*primigenius*		*advanced*	3
Mammuthus	*primigenius*		*minor*	3
Mammuthus	*primigenius*		*pavlowae*	3
Mammuthus	*primigenius*		*primigenius*	3
Mammuthus	*primigenius*			3
Mammuthus	*trogontherii*		*chosaricus*	3
Mammuthus	*trogontherii*		*trogontherii*	3
Mammuthus	*trogontherii*			3
Megaloceros	*giganteus*		*ruffi*	2
Megaloceros	*giganteus*			2
Megaloceros	*indet.*			2
Moschus	*moschiferus*			1
Naemorhedus	*caudatus*			3
Naemorhedus	*goral*			1
Orchonoceros	*gromovi*			2
Oryx	indet.	Hippotragini		3
Ovibos	indet.			3
Ovibos	*moschatus*			3
Ovibos	*pallantis*			3
Ovis	*ammon*		*antiqua*	3
Ovis	*ammon*			3
Ovis	*aries*			3
Ovis	indet.			3
Ovis	*nivicola*			3
Ovis	*orientalis*			3
Palaeoloxodon	*antiquus*			3
Palaeoloxodon	indet.			3
Palaeoloxodon	*namadicus*			3
Palaeotragus	indet.	Paleotragiinae		1
Papio	*suschkini*	Papionini		1
Parabubalis	*capricornis*			3
Paracamelus	*gigas*			3
Paracamelus	indet.			3

continued

Appendix 2. Continued.

Genus	Species	Subfamily	Unique	Hypsodonty
Paracamelus	*kujalnensis*			3
Paracamelus	*praebactrianus*			3
Parapresbytis	*eohanuman*	Colobinae		1
Parastrepsiceros	*sokolovi*			3
Poephagus	*baikalensis*			3
Poephagus	indet.			3
Poephagus	*mutus*			3
Pontoceros	*ambiguus*			1
Praemegaceros	indet.			2
Praemegaceros	*obscurus*			2
Praemegaceros	*solilhacus*			2
Praemegaceros	*verticornis*			2
Praeovibos	*beringiensis*			3
Praeovibos	indet.			3
Procapra	*gutturosa*			3
Propotamochoerus	*provincialis*	Suinae		1
Protoryx	*heinrichi*			1
Protoryx	*laticeps*			1
Protoryx	*paralaticeps*			1
Pseudalces	indet.			1
Rangifer	indet.			1
Rangifer	*tarandus*		*guettardi*	1
Rangifer	*tarandus*		*small*	1
Rangifer	*tarandus*			1
Rupicapra	*rupicapra*			3
Saiga	indet.			3
Saiga	*tatarica*		*binagadensis*	3
Saiga	*tatarica*			3
Samotherium	indet.			2
Sinomegaceros	indet.			2
Sinomegaceros	*robustus*			2
Sinomegaceros	*tadzhikistanis*			2
Sinotherium	indet.			3
Soergelia	indet.			3
Soergelia	*minor*			3
Spirocerus	indet.	Antilopinae		3
Spirocerus	*kiakhtensis*	Antilopinae		3
Spirocerus	*peii*	Antilopinae		3
Spirocerus	*wongi*	Antilopinae		3
Stephanorhinus	*beliajevi*			3
Stephanorhinus	*etruscus*			1
Stephanorhinus	*etruscus/hundsheimensis*			1
Stephanorhinus	*hemitoechus*			2
Stephanorhinus	*hundsheimensis*			1
Stephanorhinus	indet.			2
Stephanorhinus	*kirchbergensis*			2
Stephanorhinus	*megarhinus*			1
Sus	*apscheronicus*	Suinae		1
Sus	indet.	Suinae		1
Sus	*scrofa*	Suinae	*domestic*	1
Sus	*scrofa*	Suinae		1
Sus	*strozzi*	Suinae		1
Tragoportax	*indet.*	Boselaphini		2
Zygolophodon	indet.			1