Mikael Fortelius[1], Jussi Eronen[1], Liping Liu[1,2], Diana Pushkina[1], Alexey Tesakov[3], Inesa Vislobokova[4] & Zhaoqun Zhang[2]

[1] Department of Geology, University of Helsinki

[2] Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing

[3] Geological Institute, Russian Academy of Sciences, Moscow

[4] Paleontological Institute, Russian Academy of Sciences, Moscow

Continental-scale hypsodonty patterns, climatic paleobiogeography and dispersal of Eurasian Neogene large mammal herbivores

The dispersal of land mammals depends not only on the availability of physical connections but also on the presence of habitats that can support viable populations. Here we use mean molar hypsodonty of large mammal plant-eaters to map environmental conditions in Eurasia during the Neogene in order to establish a framework for discussing the distribution and dispersal of Neogene land mammals. The first Early Miocene centres of hypsodont faunas are seen in Iberia and central Asia. In the Middle Miocene Iberian values are low and a strong East-West contrast is seen within Europe, with another centre of hypsodonty developing in eastern Asia. From the Late Miocene onwards we show a pattern of high values in the central part and low values in the humid areas of western Europe and southern China (no suitable data are now available for southernmost Asia). This pattern has remained relatively stable since the Late Miocene, with only regional changes and a general increase in the overall level of hypsodonty. These results suggest that the hypsodonty pattern is primarily controlled by climatic effects of Himalayan-Tibetan uplift, specifically to the drying and increased seasonality of humidity predicted by climate models, rather than to the cooling that would have been most noticeable in the northern half of the continent. The strong and persistent relationship between position on the continent and relative degree of hypsodonty suggests that adaptation to local conditions by natural selection has been the main determinant of ungulate hypsodonty in the Neogene. A logical consequence of this would be that regional climatic conditions have been a major determinant of the geographic ranges of individual species throughout the Neogene, except perhaps at times of major faunal turnover. For example, an initial dispersal of hipparionine horses across the arid Central Asia appears highly improbable compared with dispersal along a more humid northern route, and the apparently early arrival of hipparions in Spain may well reflect this circumstance.

Correspondence: Mikael Fortelius (to whom correspondence should be addressed), Jussi Eronen and Diana Pushkina, Department of Geology, P O Box 64, FIN-00014 University of Helsinki, Finland (e-mail: mikael.fortelius@helsinki.fi; jussi.t.eronen@helsinki.fi; diana.pushkina@helsinki.fi); Liu Liping and Zhang Zhaoqun, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, P.O. Box 643, Beijing 100044, China (e-mail: cnowliu@mx.cei.gov.cn; zqzhang@mx.cei.gov.cn); Alexey Tesakov, Geological Institute, Russian Academy of Sciences, Pyzhevsky 7, 109017 Moscow, Russia (e-mail: tesakov@yahoo.com); Inesa Vislobokova, Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya, 123, 117868 Moscow, Russia (e-mail: ivisl@paleo.ru)

INTRODUCTION

It has been customary to discuss the dispersal of fossil land vertebrates in terms of physical barriers and connections. While there can be no doubt that these factors are ultimately decisive, it must also be acknowledged that land mammals appear to be very good at crossing seemingly insurmountable barriers (Solounias *et al.* 1999), and that the low temporal resolution of the mammal record usually makes it difficult to propose a direct relationship between dispersal events and specific geophysical changes with confidence. Moreover, the successful crossing of a bridge or a barrier remains invisible to the fossil record unless it results in successful colonisation of the new area, and this depends not on the details of topography or land-sea configuration but (apart from luck) on the nature of the invaded habitat. Indeed, the distribution patterns themselves - quite apart from dispersal dynamics - must ultimately depend to a major degree on environmental conditions.

The first serious attempts to understand the continental-scale evolution of Eurasian environments and biota seem to have been made by Soviet workers of the 1940's to 60's (e.g. Borissiak & Beljaeva 1948; Orlov 1962; Dorofeyev 1966), probably the only professionals at the time with access to fossil material of sufficient geographical range to contemplate such a task. Although hampered by major stratigraphical problems these syntheses did in fact establish a coherent view, based on both the nature of the fossil assemblages and multidisciplinary study on stratigraphy, tectonics, paleoclimatology and paleogeography. It was thus clearly recognised that the general trend towards increasingly open environments observed over the entire area did not proceed at a uniform pace over the entire continent, but took place much earlier and proceeded further in the continental interior than in the climatically more moderated margins, especially Europe with its complicated system of large seaways. The influence of environmental and climatic changes on the history of some dominant groups of mammals

were analysed in the series of the fundamental works of next generations of Russian scientists (e.g., Zhegallo 1978; Vislobokova 1990). But it was only with the seminal work of Bernor (1983; 1984) that the concept of diachronous biotic and environmental change rather belatedly became incorporated in western work on Eurasian Cenozoic mammal evolution.

It may seem surprising that fossil mammals should have been so central to developing our ideas about environmental change during the Cenozoic, but there are in fact good reasons for this. Fundamentally, plants enjoy a more direct relationship with climate than do animals, of course, but neither macroscopic plant remains nor fossil pollen floras have the stratigraphic and geographic coverage offered by fossil mammals, nor do they permit particularly detailed or reliable reconstructions of regional vegetation types. Fossil mammals are therefore simply one of the best sources available for reconstructing past vegetation patterns and thus of climate. Not only have fossil mammals been a main focus of research for a long time and are therefore relatively well understood, but the environmental signal reflected in mammalian morphology and community structure is also one of the strongest and best resolved. Damuth (1982) showed that the original community structure is robustly preserved in mammalian fossil assemblages, and Janis (1984) argued explicitly for the use of fossil mammal communities to reconstruct past vegetation patterns. Fortelius *et al.* (1996) used fossil mammals to chart large-scale patterns of environmental change on a gradient from closed to open vegetation in the Miocene of western Eurasia. More recently, we (Fortelius 2003; Fortelius & Hokkanen 2001) showed persistence during 20 Ma of a difference in mean molar capability of ungulates from different regions of Eurasia, over an interval during which the same measure increased about threefold in all areas compared. Finally, work in progress by a group coordinated by John Damuth (http://www.nceas.ucsb. edu/

fmt/doc?/nceas-web/results/projects/
98DAMUT1) has shown that community
structure and ecomorphology of living mam-
mals can be used to successfully predict
modern vegetation patterns worldwide.

The relationship between herbivore hypso-
donty and a wear-inducing diet is now almost
universally recognised (Janis & Fortelius
1988; Romer 1970; Van Valen 1960;
MacFadden 2000). It is well documented
empirically and easily understandable theore-
tically in terms of functional demands and
adaptive evolution. The factors potentially
involved are many, but virtually all increase
in effect with increasing aridity and openness
of the landscape (increased fibrousness,
increased abrasiveness due to intracellular
silica or extraneous dust, and decreased nutri-
tive value) (Fortelius 1985; Janis 1988).
Hypsodonty should thus record a condition of
the vegetation that might be termed generali-
sed water stress, either in overall conditions,
or (perhaps more commonly) as a regularly
occurring extreme period, such as a dry seas-
on. We therefore propose here to use the
simple property of mean hypsodonty of mam-
malian large herbivores to map the develop-
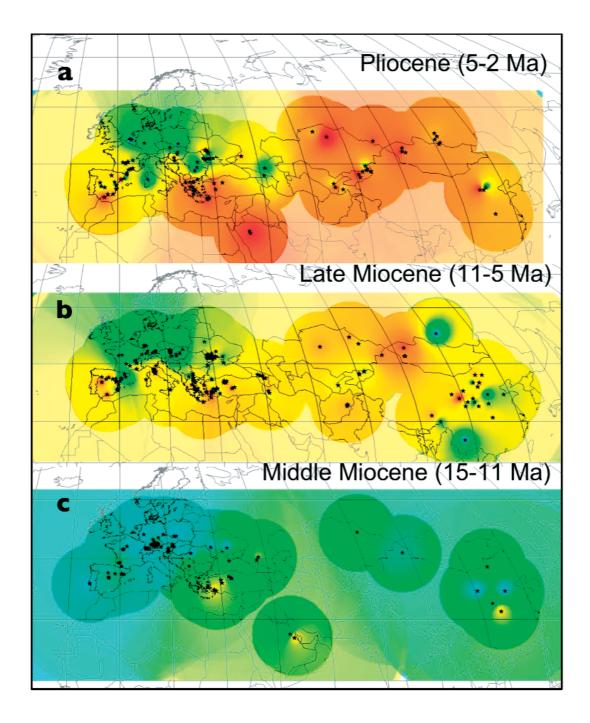ment of this 'generalised aridity' during
Neogene time.

MATERIALS AND METHODS

The data used were downloaded from the
NOW database on March 8, 2001 and inclu-
ded non-public datasets for the Former Soviet
Union (FSU) and China. The Chinese dataset
was further supplemented from an ongoing
compilation project. A subset limited to
Eurasia and large land mammals was selec-
ted. All analyses reported here were limited
to species characterized as plant-eaters or
plant-dominated omnivores. Hypsodonty was
ranked according to the following scheme:
brachydont=1, mesodont=2, hypsodont or
hypselodont=3 and means were calculated for
individual localities or other subsets
(SPLOC-analysis; see Fortelius & Hokkanen
2001). The possible range of mean hypsodon-

ty is thereby constrained to the range 1-3,
beyond which this metric cannot resolve
(paleo)precipitation. Values based on single
species were excluded from all analyses.

The data were grouped into 1 Ma time sli-
ces on the mean value of minimum and maxi-
mum age estimates as reported in the databa-
se. Except for some Chinese localities, locali-
ties with a difference between minimum and
maximum estimates of more than 3 Ma were
excluded. The correlation table of the NOW
database follows Steininger *et al.* (1996),
with ad hoc additions by AL and ZZ for the
FSU and Chinese data. For investigation of
geographic gradients, the data were grouped
into sectors of 10 degrees longitude and
zones of 5 degrees latitude.

For the GIS maps, the time slices were
combined into four larger temporal groupings
(see Figs. 1 a-d for details). All GIS maps
were made in MapInfo Professional 6.0 using
the inverse distance weighted (IDW) algo-
rithm and the following settings: cell size 30
km, search radius 3000 km, grid border 1100
km, number of inflections 9, values rounded
to 1 decimal. The inflection values were
manually set to the range 0.7-3 for all maps,
and a mask was manually superimposed to
fade out areas more than 1000 km from the
nearest data point (opacity 50%). We delibe-
rately use modern maps as a background for
these patterns partly because of the lack of
palinspastic paleogeographic maps (on which
the localities could be automatically plotted
in their correct positions) and partly because
our time slices span more time than any pale-
ogeographic configuration. We also use
modern geographic names (such as 'China' or
'Iberia') as neutral landmarks. It is devoutly
to be wished that palinspastic paleogeograp-
hic maps of the Eurasian continent will beco-
me available, since discussing dispersal in
relation to a modern basemap is difficult at
best and can easily be misleading.

The dataset used is available from the aut-
hors, and the latest public NOW dataset can
be downloaded from http://www.helsinki.fi/

Pliocene (5-2 Ma)

a

Late Miocene (11-5 Ma)

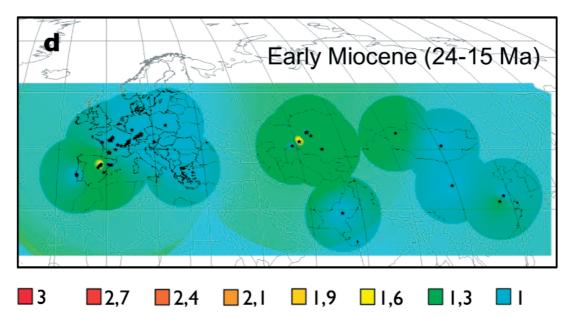**b**

Middle Miocene (15-11 Ma)

c

Figure 1   Colour-interpolation map of mean hypsodonty in Eurasia during five intervals. **a** Pliocene (5-2 Ma); **b** late Miocene (11-5 Ma); **c** middle Miocene (15-11 Ma); **d** Early Miocene (24-15 Ma). See Methods for technical details.

science/now/, where further details regarding the data may also be obtained.

RESULTS

Hypsodonty maps

The Early Miocene hypsodonty pattern (Fig. 1d) suggests two centres of early increase in crown height: Central Asia and the Iberian Peninsula. In both cases the increase is seen only in localities from the end of the interval, later than c. 18 Ma. Data for eastern Europe and Asia are scarce and there is little detail, but the western and central European coverage is satisfactory and the lack of hypsodont species outside Iberia is well established. The high-crowned species involved in this early phase are primarily mesodont and hypsodont rhinoceroses of the '*Hispanotherium* fauna', known in the Early Miocene only from Central Asia and Spain and later also from south-western Asia (Heissig 1976; Köhler 1987). The age of the Anatolian localities Inönü I, Pasalar and Çandir is treated here as middle Miocene, following the NOW databa-

se, Bernor & Tobien (1990), and Steininger *et al.* (1996). It is, however, also possible to interpret these localities as early Miocene (Sen 1990), and this is in fact done in the latest rodent zonation for Anatolia (Ünay *et al.* this volume). If an Early Miocene age is accepted for any of these localities the Early Miocene development of hypsodont ungulate communities would be circum-Mediterranean and the difference between the Early and Middle Miocene patterns smaller than it now appears.

The Middle Miocene pattern (Fig. 1c) is strongly dominated by the contrast between western and eastern Europe, the 'West' and 'East' previously recognised from taxonomic and biogeographic as well as ecomorphological comparisons of mammal data (Fortelius *et al.* 1996; Werdelin & Fortelius 1997; Fortelius & Hokkanen 2001). The data points for Asia are few but there is an indication of hypsodont faunas beginning to evolve in northern China. These assemblages, typified by the famous Tunggur fauna (Qiu 1989), are characterised by mesodont and hypsodont

bovids and rhinoceroses occurring in a context still dominated by brachydont ruminants and suoids. The few data points in Central Asia show little sign of increasing hypsodonty at this time.

The Late Miocene pattern (Fig. 1b) shows the emergence of more hypsodont faunas dominated by bovids and horses in the Mediterranean region and central Asia, especially the areas north of the Tibetan Plateau. This pattern is quite unlike the modern distribution of mean annual temperature (Fig. 2a) and strikingly similar to the modern mean annual rainfall distribution (Fig. 2b), especially in the areas of persistently low hypsodonty in the humid western Europe and southern China. A temporal breakdown of the Late Miocene localities shows that the later part of the interval appears relatively drier in the western part of the continent, while the reverse is true for the eastern part. (In this preliminary survey we have chosen not to delve too deeply into the effects of time-averaging, which obviously influence all our maps to a greater or lesser extent.)

The Pliocene pattern (Fig. 1a) generally resembles the latest Miocene one but is even more similar to the modern rainfall pattern. Overall hypsodonty is higher, the main centre of hypsodonty has shifted from the eastern Mediterranean to Central Asia, and China is now included in the realm of high hypsodonty. The low hypsodonty values seen in the Caucasus may reflect local climatic conditions the explaining presence there in the Pliocene and Early Pleistocene of African elements, including early humans (Gabunia *et al.* 2000).

Geographic hypsodonty gradients
The history of increasing hypsodonty illustrated by the maps shows considerable regularity with respect to geography. A coarser view with hypsodonty values reduced to latitudinal and longitudinal group means shows that this regularity developed gradually over time (Fig. 3 a,b). The appearance of the modern latitudinal gradient with higher values in the

south took place in the Middle Miocene and remained in place while the overall level almost doubled during the Neogene (Fig. 3a). The relationship between hypsodonty and longitude is less regular but shows the successive development of a pattern with higher values in the interior of the continent and lower values near the coasts (Fig. 3b). The shift of the highest values from the west towards the east in the course of the Neogene is also seen.

DISCUSSION
It is helpful to discuss the present results in relation to present-day climatic patterns, especially the basic variables temperature and precipitation (Fig. 2). It is immediately obvious from a comparison of the hypsodonty maps with these that the pattern seen from the Late Miocene onwards is quite similar to the distribution of rainfall and quite different from the regular zonation of temperature. This suggests that the basic assumption of our approach is valid, and that hypsodonty can indeed be used as a proxy for variables that correlate with rainfall, such as the 'generalised aridity' proposed in the Introduction. The development of the modern climatic pattern of the Eurasian continent is clearly a Late Miocene phenomenon, and the earlier Neogene development of less humid regions apparently took place under a different climatic regime. One does not need to search far for a plausible mechanism for dividing the climatic history of Eurasia near the Middle/Late Miocene boundary. Indeed, the literature on the later Neogene climate history of Eurasia has recently focused on the issue of the effects of uplift of the Tibetan Plateau on winds and precipitation patterns (apart from high-latitude cooling). The distinct change from the Middle to the Late Miocene seen here can be taken to coincide with a major phase of uplift in the Higher Himalayas (Amano & Taira 1992) and the Tibetan Plateau at about 10 Ma (An *et al.* 2001) and with evidence of major contemporaneous environmental change (Tanaka
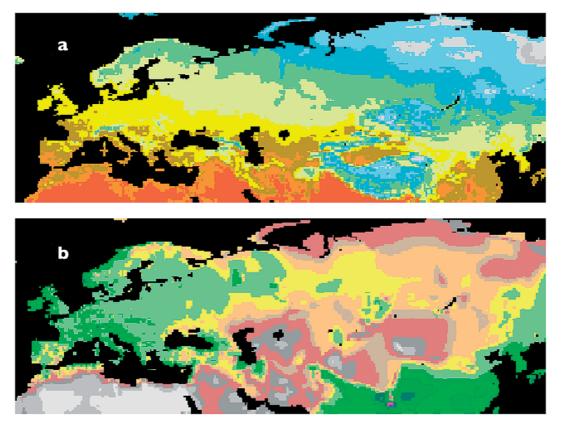
Figure 2 Maps of present-day mean annual temperature (**a**) and mean annual precipitation (**b**) in Eurasia. Created from public data provided by the Food and Agriculture Organization of the United Nations, Environment and Natural Resources Service (Leemans & Cramer 1991) using the public WinDisp application. For temperature, reds indicate the highest values, blues and whites the lowest. For precipitation, greens indicate the highest values, browns and greys the lowest. Data and software were downloaded from http://www.fao.org/WAICENT/FAOINFO/SUSTDEV/eidirect/CLIMATE/EIsp0002.htm.

1997). The 'Mid-Vallesian Crisis' (Agustí & Moya-Sola 1990) of western Europe is perhaps the best-documented (Fortelius *et al.* 1996) example of a major Eurasian mammal event at about 10 Ma, and recent reviews of the evidence suggests a continent-wide event this time (Agustí *et al.* 1999; Fortelius & Hokkanen 2001).

Specific predictions from general circulation models concerning the climatic effects of late Miocene Tibetan uplift include decreasing mean annual precipitation to the north and west of the plateau and increasing precipitation to the south and east (Kutzbach *et al.* 1993). The hypsodonty pattern shows just such an effect, although with considerably

more detail. It is particularly striking that the rise of hypsodonty values is much lower in China than elsewhere on the continent, and that the main single difference between the Middle and the Late Miocene pattern is in the aridification of Asia to the north of the Tibetan Plateau. The development of persistent geographic gradients (Fortelius 2003; Fortelius & Hokkanen 2001) is reflected here in the relatively stable latitudinal and longitudinal hypsodonty profiles, where the increase in overall hypsodonty proceeds without major changes of the relative proportions (Fig. 3). This seems to suggest that these patterns fundamentally reflect overall climatic relationships of a continent, such as the difference
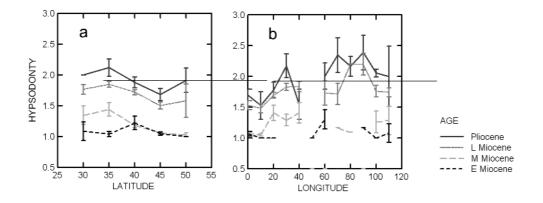
Figure 3 Development of Eurasian latitudinal and longitudinal hypsodonty gradients over Neogene time. **a** Latitudinal gradient, **b** longitudinal gradient. Bars show standard error.

between the oceanically moderated rim and the 'continental' interior, and that this deep pattern is modified but not fundamentally altered by tectonic changes.

As regards the geographic distribution of species, the close relationship with expected and observed climate patterns strongly suggests that natural selection tracking environmental change is the main mechanism responsible for the persistence of the geographic contrasts. This is further supported by the observation that the geographic contrasts may break down temporarily at times of major taxonomic turnover, but are soon re-established (Fortelius 2003). In the absence of evidence to the contrary, we propose that the case of hypsodonty is typical and that the long-term ranges of mammalian species are typically under strong and direct environmental control. This is not to say that all species are equally restricted in this regard. It is quite clear, for example, that herbivores enjoy (or perhaps more appropriately suffer from) a more direct relationship with vegetation and climate than do carnivores, a circumstance reflected in the greater geographic ranges and stratigraphic ranges of carnivores compared with herbivores (unpublished analysis of NOW data 1999). Nevertheless, there seems to be a clear relationship between overall taxonomic provinciality and the

regional hypsodonty patterns shown here, in that the breakdown of the environmental East-West contrast in Europe from the Late Miocene onwards is accompanied by a corresponding reduction in provinciality at this time (Fortelius *et al.* 1996; Werdelin & Fortelius 1997). Times of great environmental diversification are thus indeed likely to be accompanied by reduced dispersal of species, and vice versa. Koufos (this volume) provides multiple examples of open-adapted species of the eastern Mediterranean realm that failed to disperse into the closed environments of central Europe during the earlier part of the Late Miocene, while the East-West contrast was still strong.

Late Miocene hipparionine horses
We would like to end our discussion by treating briefly what is probably the most spectacular and well-known dispersal event of the Eurasian Neogene: the arrival and adaptive radiation of hipparionine horses at the beginning of the Late Miocene. The North American ancestors of the earliest Eurasian hipparions are best known from quarries in Texas and Nebraska, but the actual population from which the first Eurasian individuals would have been derived must have existed in Alaska, which would have been a relatively cool and humid place compared with the

North American interior. (Alaska is in the region where plateau uplift would induce cooling and well outside the area where model simulations predict drying; Ruddiman & Kutzbach 1991) On arrival, having perhaps crossed the Bering Strait during one convenient eustatic sealevel low, these first Eurasian hipparions would have found themselves in a place that was climatically similar to their point of departure. Although the evidence is most unfortunately lacking, such conditions must have extended westwards along the Eurasian coast all the way to western Europe, whereas vast arid regions would have been encountered to the south. Preliminary results indicate that conditions were quite dry as far south as central China in the earlier part of the Late Miocene (Zhang *et al.*, 2002).

A trajectory across central Asia, such as is traditionally shown on maps of hipparionine dispersal, therefore appears to us quite unlikely compared with the obvious choice of expanding westwards in a familiar environment. We wish to point out that although the data are woefully inadequate, such expansion would fit the raw pattern of hipparion appearances quite well, with the earliest record from the best sampled region of western Europe for that time interval (The Vallès-Penedès basin of Spain; Garcés *et al*. 1997). The initial spread would have been geologically instantaneous, whereas the subsequent colonisation of more arid regions would have proceeded at the pace of the subsequent adaptive radiation, fast but potentially detectable in long sequences with good stratigraphic control (Bernor *et al.* 2000). The process would have resulted in the secondary evolution in more arid regions of the Old World of animals eco(morpho)logically more similar to North American species known from the continental interior than to their own immediate (presumably Alaskan) New World ancestors. One could speculate that such a process might cause an evolutionary reversal of some morphological characteristics, explaining some of the perplexing systematic patterns

observed. Without going into further detail we would finally like to point out that similar dispersal scenarios might potentially apply to camels, and perhaps even to canids.

It is obvious that large herbivore hypsodonty is only one – and a crude one at that – of multiple mammal-based environmentally sensitive indicators available. In the present context we would like to end with the wish for a study of continental-scale patterns using small mammal ecomorphology.

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