Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years

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ABSTRACT

Fossil teeth of terrestrial plant-eating mammals offer a new, quasi-quantitative proxy for environmental aridity that resolves previously unseen regional features across the Eurasian continent from 24 to 2 million years ago. The pattern seen prior to 11 million years ago are quite different from today's. Thereafter, a progressively modern rainfall distribution developed at about 7 to 5 million years ago when East Asia remained unexpectedly humid while Europe experienced a transient phase of strong aridity. Mean hypsodonty is a geographically extensive and stratigraphically well-resolved palaeoprecipitation proxy that can be used to constrain the regional details of vegetation and climate models.

Keywords: Eurasian continent, fossil mammal tooth, mid-latitude aridity, Neogene, palaeoprecipitation proxy.

INTRODUCTION

The understanding of Neogene (*c.* 24 to 2.5 million years ago) climatic history and verification of continental-scale predictions from climate models are hampered by the lack of temporally and geographically continuous geological evidence of past climates (Ruddiman *et al.*, 1997). A newly compiled, continent-wide data set of fossil mammal localities and species offers such evidence with both geographic and temporal resolution. This detailed proxy record of continental-scale change can be used both to sketch a broad scenario for 20 million years of Eurasian climatic history and to identify regional and temporal features of relevance to modelling efforts.

The link between fossil mammals and environmental conditions that we exploit is the relationship between food properties and dental wear observed in living mammals. Increased tooth height or hypsodonty is fundamentally an adaptive response to increasing demands for wear tolerance and functional durability brought about by the development of more fibrous or abrasive plants in a progressively more open and arid-adapted vegetation (Van Valen, 1960; Fortelius, 1985; Janis and Fortelius, 1988; Solounias *et al.*, 1994; Fortelius and Solounias, 2000). Recent advances in the handling and analysis of fossil mammal data (Damuth, 1993; Fortelius *et al.*, 1996) suggest that details reflecting regional ecology are recorded in the dental morphology (Fortelius and Hokkanen, 2001; Jernvall and Fortelius, 2002). The factors favouring hypsodonty 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 nutritive value) (Fortelius, 1985; Janis, 1988; Janis and Fortelius, 1988). Hypsodonty thus implies a condition of the vegetation that might be termed 'generalized water stress', either in overall conditions, or perhaps more commonly, as a regularly occurring extreme period, such as a dry season. Preliminary analysis suggests that there is, indeed, a strong relationship between local mean hypsodonty and local mean annual precipitation in modern mammal communities (Damuth and Fortelius, 2001). In a global sample of 254 recent mammal communities, the correlation coefficient for mean hypsodonty and local mean annual precipitation was -0.67 (unpublished data from the NCEAS working group on Habitat and Climate Inference from the Structure of Mammal Communities; John Damuth, convener). Here we use locality-specific mean large mammal herbivore hypsodonty as a proxy for palaeoprecipitation patterns for the Eurasian continent in five time slices covering the last 20 million years of the pre-Quaternary.

DATA AND METHODS

Data

We used a data set derived from the NOW database of Neogene fossil mammal localities and species of Eurasia (NOW: http://www.helsinki.fi/science/now/) and from ongoing compilation projects for the Former Soviet Union (FSU) and China. The combined data set is available from the authors. The FSU and Chinese data have not been systematically revised and we consider them somewhat less reliable than the public NOW data, but the uncertainties are mostly taxonomic in nature and should not affect hypsodonty scores significantly. The age information for these data sets has been reviewed by A.T. and Z.Z. respectively. We included all large mammal taxa classified as plant eaters or plant-dominated omnivores. Thus, all pigs were included but no carnivoran omnivores.

Stratigraphy

The localities were grouped into five time intervals according to the age estimates given in the database. Each NOW locality has a maximum and a minimum age estimate, in most cases based on the boundaries of a stratigraphic unit. For this paper, we used the mean of these estimates, excluding localities where the difference between maximum and minimum estimates exceeded 3 million years, except for some Chinese localities where we accepted greater uncertainty. The use of Steininger *et al.* (1996) as the main correlation scheme of the

NOW database means that the early to middle Miocene boundary is placed at 15 million years ago. This is merely a technical matter and it should obviously be equated with the corresponding boundary in other correlations, not with a time 15 million years ago as such. For the late Miocene and Pliocene, the discrepancies between recent mammal zonations are relatively minor, except for the question of the *Hispanotherium* fauna addressed below. The division between our 'earlier' and 'later' late Miocene is dictated by the Chinese stratigraphy and divides the European late Miocene within the Turolian faunal unit. The relatively humid pattern seen in the earlier late Miocene of Europe is, however, strongly dominated by the many Vallesian localities included. The age of the Anatolian localities Inönü I, Paşalar and Candir is treated here as the middle Miocene, following Steininger *et al.* (1996) and the NOW database. It is, however, also possible to interpret these localities as early Miocene (Şen, 1990), and this is in fact done in the latest, as yet unpublished, rodent zonation for Anatolia (E. Ünay, personal communication). 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, but an increase in hypsodonty would still be confined to the interval later than 18 million years ago.

Hypsodonty

Three classes of hyposodonty are recorded in the NOW database: brachydont, mesodont and hypsodont. The criteria for assigning species to these classes are ultimately up to the taxonomic coordinators of the NOW advisory board, but the rule of thumb is based on the ratio of height to length of the second molar (upper or lower). Brachydont teeth have a ratio of less than 0.8, mesodont teeth a ratio of 0.8–1.2 and hypsodont teeth a ratio > 1.2. For this study, the hypsodonty classes were assigned values of 1, 2 and 3, respectively, a relatively conservative procedure as the difference in crown height between a hypsodont and a brachydont species is usually more than 3:1 (Fig. 1). The mean hypsodonty value was calculated for each locality by averaging these ordinated scores, and the mean values (excluding cases based on a single species) were plotted on maps using interpolated colours to indicate regional differences (Figs 2 and 3). It should be noted that grass eating and the Neogene spread of grasslands is only a subordinate theme in the evolution of hypsodonty. Hypsodonty is not restricted to grass eaters today, and not all modern grazers are hypsodont (Fortelius and Solounias, 2000). There is a growing consensus that many species of Neogene hypsodont equids were mixed feeders and even browsers (Hayek *et al.*, 1991; Quade *et al.*, 1994; MacFadden *et al.*, 1999; Kaiser *et al.*, 2000), and the same is evidently true of the hypsodont ruminants (Fortelius and Solounias, 2000).
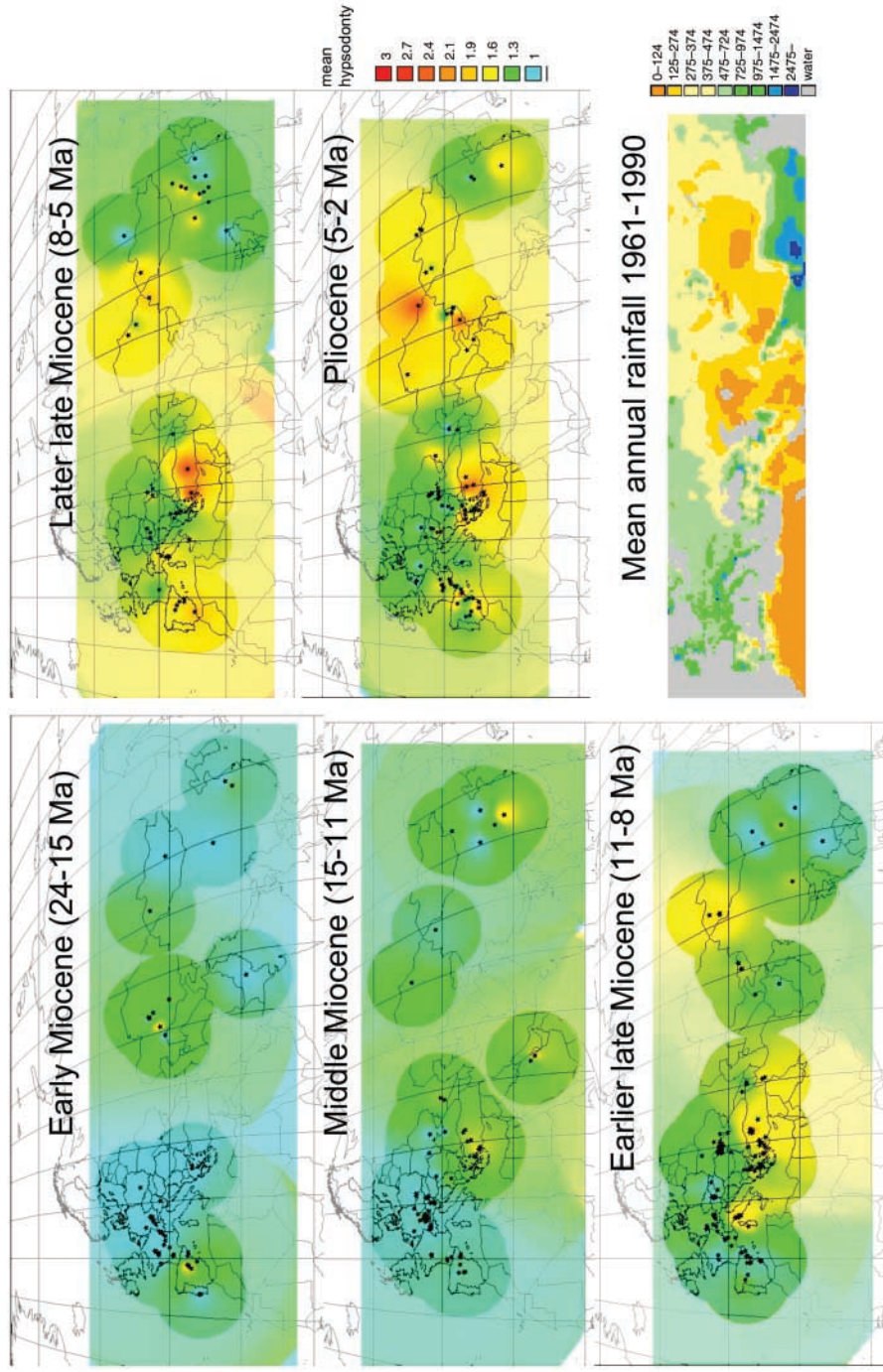
Maps

We deliberately use modern maps as a background for these patterns partly because of the lack of palinspastic palaeogeographic maps (on which the localities could be automatically plotted in their correct positions) and partly because our time slices span more time than any one palaeogeographic configuration. We also use modern geographic names, such as 'China' and 'Iberia', as neutral landmarks. All GIS maps were made in MapInfo Professional 6.0 using the inverse distance weighted (IDW) algorithm and the following settings: cell size 30 km, search radius 3000 km, grid border 1100 km, number of inflections
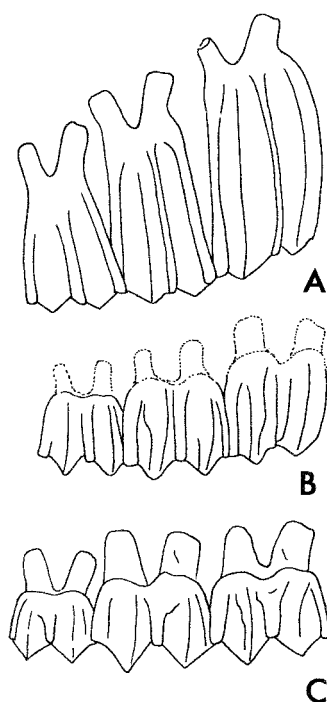
Fig. 1. Representative hypsodont (A), mesodont (B) and brachydont (C) teeth of ruminant ungulates, the largest group included in this study. Modified from Fortelius and Hokkanen (2001), courtesy of the American Museum of Natural History.

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%). The maps reproduced as Figs 2f and 3f were created for approximate reference from public data provided by the Food and Agriculture Organization of the United Nations, Environment and Natural Resources Service using the public WinDisp application. Data and software were downloaded from http://www.fao.org/WAICENT/FAOINFO/SUSTDEV/eidirect/CLIMATE/EIsp0002.htm.

The precipitation values shown in Figs 2f and 3f were restricted to the interval resolved by hypsodonty in modern mammal communities (approximately 100–2500 mm·year^{-1}), but there is no precise relationship between the colour schemes of this map and those based on hypsodonty. The entry of hypsodont hipparionine horses from North America at the middle to late Miocene boundary had an abrupt and strong impact on the mean hypsodonty values; therefore, we plotted the data both with and without horses. Excluding the horses weakens the abruptness of the middle to late Miocene transition and suppresses overall hypsodonty levels since the late Miocene, but this has little effect on the general pattern (Figs 2 and 3). Needless to say, values interpolated from a few widely scattered localities are unreliable and we have emphasized well-sampled areas in our interpretations here. The colours in Figs 2 and 3 show the same relationship to mean hypsodonty but obviously not to precipitation, which is only treated in a relative sense in this discussion, for comparison between or within maps.

Fig. 2. Colour-interpolated maps (a–e) of Eurasian large mammal plant-eater mean hypsodonty by locality during five intervals of Neogene time (see 'Data and methods'). Blue values indicate lack of increased crown height; greens, yellows and reds show the successive increase in crown height interpreted here as increasing aridity. Scale shows colours at inflection values; intermediate colours are interpolated between these. (f) Map of modern (present interglacial) mean annual precipitation in Eurasia. Oranges represent less than 124 mm · year^{−1}, yellows 125–474 mm · year^{−1}, greens 475–1474 mm · year^{−1} and blues over 1475 mm · year^{−1}. Note that maps (a–e) lack data for Africa, and that no precise correspondence is intended in the colour schemes between hypsodonty and precipitation. Data for map (f) based on Leemans and Cramer (1991).
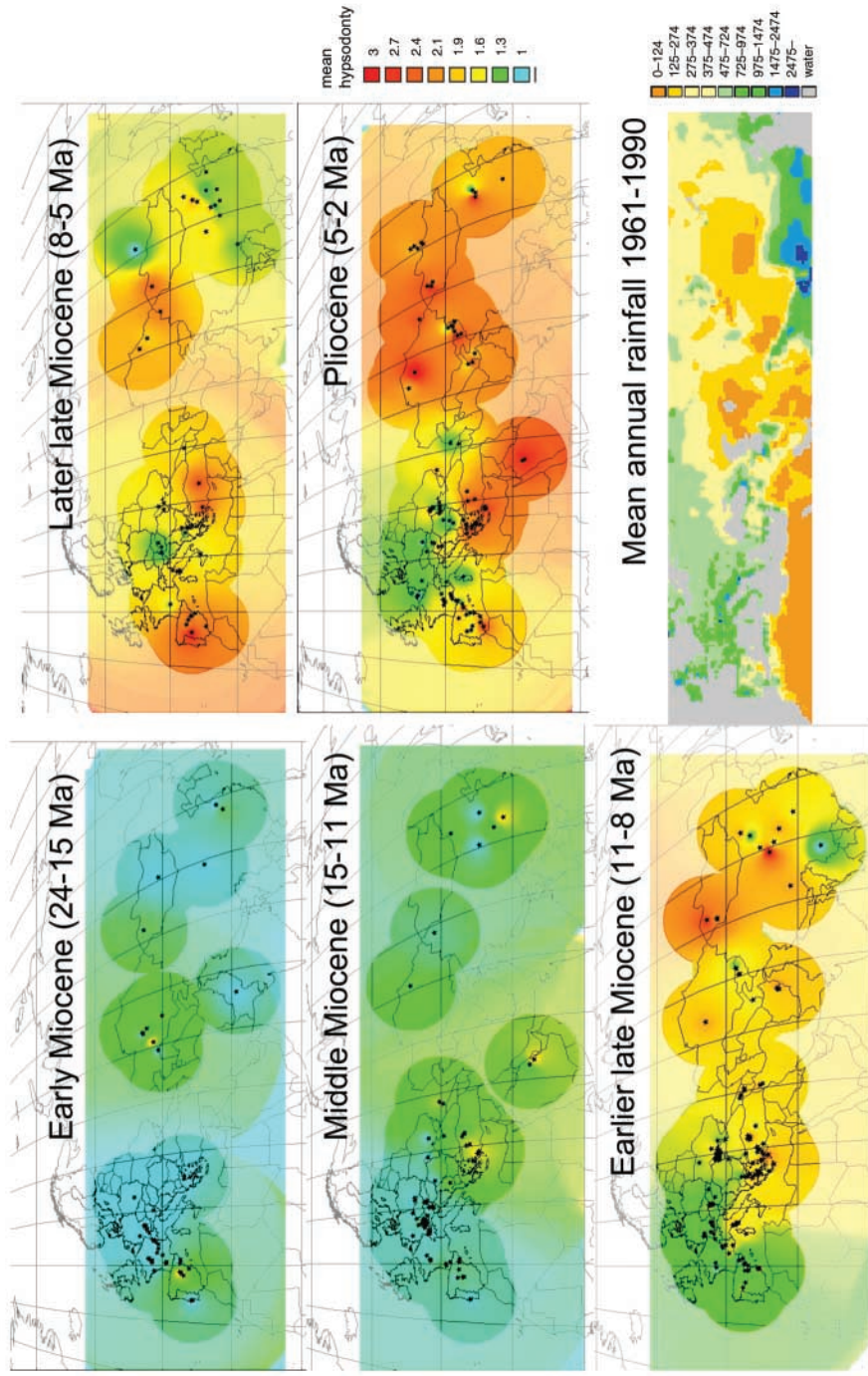
Fig. 3. Same as Fig. 2 but with horses included. See legend to Fig. 2.

Sampling

The problematic issue of sampling that plagues all studies of fossil biodiversity (see Alroy *et al.*, 2001, for a recent review) is not critical here, since mean hypsodonty is a relative measure describing community structure and should be comparatively robust with respect to sampling (Damuth, 1982). Mean hypsodonty calculated for individual localities also emphasizes the most commonly occurring species (Fortelius and Hokkanen, 2001; Jernvall and Fortelius, 2002) and is, therefore, relatively insensitive to the presence or absence of rarely sampled species. Because of their relatively low temporal resolution, mostly due to uncertain stratigraphic correlations, mammal data are not suitable for showing continental-scale short-term responses to rapid environmental fluctuations. Similarly, the fact that large land mammals tend to have wide geographic ranges precludes their use when high geographic resolution is required. However, the continuous and dense occurrence of fossil land mammals makes them eminently useful for resolving regional details within and trends across time units. For this purpose, moderate temporal and spatial averaging is actually an advantage, as it serves to suppress noise from local conditions and short-term fluctuations. A related issue concerns the influence from biogeography and evolutionary history: if the spread of hypsodont species is delayed, areas will appear less arid than they really are. Conversely, a highly successful hypsodont species may invade humid areas and cause them to appear too arid. On the relatively homogeneous Eurasian continent, where barriers to dispersal will have been mostly ecological rather than physical, the problem is not expected to be a major one, however. The main exception is the dispersal of the highly exapted hipparionine horses from North America at the beginning of the late Miocene, a case that we have taken into account by making the maps with and without horses (see above).

RESULTS AND DISCUSSION

The early Miocene (24 to 15 million years ago; Ma) hypsodonty pattern (Fig. 2a) shows faunas dominated by brachydont localities except for two areas of early increase in crown height: central Asia and the Iberian Peninsula. 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 precociously mesodont and hypsodont rhinoceroses of the '*Hispanotherium* fauna', known in the early Miocene only from central Asia and Spain. This fauna is also known from contemporaneous or somewhat later localities from south-western Asia (see subsection on 'Stratigraphy'). Overall, the early Miocene remains very 'green', with only the slightest evidence of incipient aridity, and the localities showing increased hypsodonty are all from the late part of the interval (later than 18 million years ago).

The middle Miocene (15 to 11 million years ago) pattern (Fig. 2b) shows only slightly more evidence of increasing aridity. It is strongly dominated by the contrast between western and eastern Europe, the 'West' and 'East' previously recognized from ecomorphologically based analyses of mammal data (Fortelius *et al.*, 1996; Werdelin and Fortelius, 1997; Fortelius and Hokkanen, 2001) and, in principle, from earlier analyses of taxonomic and biogeographic patterns (Bernor *et al.*, 1979; Bernor, 1983, 1984). 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 character-

ized by mesodont and hypsodont bovids and <mark>rhinoceroses</mark> occurring in a context still dominated by brachydont ruminants and suoids of middle Miocene aspect. The few data points in central Asia show little sign of increasing hypsodonty at this time. The patterns before 11 million years ago thus reflect the development of regionally diversified climate systems different from the present one.

The earlier late Miocene (11 to 8 million years ago) pattern (Fig. 2c) shows a major strengthening of the hypsodonty in the present-day Mediterranean region and the emergence of new hypsodont faunas dominated by bovids (and horses) in east-central Asia. This pattern is similar in its large-scale features to the modern rainfall distribution (Fig. 2f), especially in the areas of low hypsodonty in the humid western Europe and southern China, and the central mass of high values in between, but the centre of high hypsodonty is much further west than the main centre of aridity today. An intriguing feature is the bipartition of the main central mass of high values by an area of lower values in an area around Afghanistan and Uzbekistan, just west of the rising Tibetan Plateau. This is due to the localities Molayan and Sor, with mean hypsodonty values (without horses) based on eight and four species, respectively (brachydont and mesodont bovids and giraffids, brachydont proboscideans, a chalicothere and a primate). If horses are included, the transition from the middle Miocene is more abrupt and has a much stronger expression in central and eastern Asia, but otherwise the same general pattern, including local maxima, are seen in both versions (Fig. 3c).

In Europe, there is an apparent change from the middle Miocene in that the area of high values now stretches westwards into northern Italy and southern France, but this may be due to lack of data for this area in the middle Miocene. We have shown elsewhere (Jernvall and Fortelius, 2002) that western Europe shows little regional differentiation within itself when a finer time resolution is used, so part of this pattern is evidently an artifact of plotting localities of different ages on the same map. Iberia still remains an area of predominantly low hypsodonty in the middle Miocene, and in the Ukraine hypsodonty values are distinctly lower than in the eastern Mediterranean.

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 and Taira, 1992) and the Tibetan Plateau about 10 million years ago (An *et al.*, 2001) and with evidence of major contemporaneous environmental change (Tanaka, 1997). The 'Mid-Vallesian Crisis' (Agusti and 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 million years ago, but recent reviews of the evidence suggest a continent-wide event this time (Agustí *et al.*, 1999; Fortelius and Hokkanen, 2001).

In the later late Miocene (8 to 5 million years ago), the pattern changes in ways that appear to reflect regional changes ultimately due to tectonic processes (Fig. 2d). In Europe, Iberia is now included in the area of high hypsodonty, and only eastern Europe remains clearly dominated by brachydont forms (only central Europe if horses are included; Fig. 3d). In eastern Asia, hypsodonty levels remain moderate, and decrease substantially relative to the preceding interval if horses are included in the data (Fig. 3d). Compared with the impoverished bovid- and horse-dominated faunas of the preceding interval (Zhang *et al.*, in press), the Red Clay faunas show a greater spread of hypsodonty values. In particular, they contain a distinctive selection of brachydont species, including deer, a small pig and even brachydont anchitherine horses, apparently otherwise extinct since about 3 million years previously. This temporary reversal of the global trend is unexpected and

goes against the conventional expectation of progressively increasing aridity. We propose that it represents a regional effect of the intensification of the monsoon circulation at about 8 million years ago (Ding *et al.*, 1999; An *et al.*, 2001), which would compensate the global trend through regionally increased summer rainfall. The latest Miocene faunas in China are associated with the aeolian 'Red Clay', the deposition of which also appears to have commenced slightly before 8 million years ago (An *et al.*, 2001), and we hypothesize that the deposition of aeolian material was also a result (through improved capture of dust particles) of increased humidity and vegetation cover. The rise to dominance of C4 photosynthetic grasses in the tropics and subtropics of the latest Miocene (Cerling *et al.*, 1997) affects this pattern only marginally, since the shift appears not to have occurred until 4 million years ago in northern China (Ding and Yang, 2000) and not at all in Europe (Cerling *et al.*, 1997).

The Pliocene (5 to 2 million years ago) hypsodonty map (Fig. 2e) already strongly resembles the modern (interglacial) rainfall pattern (Fig. 2f). Compared with the latest Miocene, western Europe has reverted to lower hypsodonty and a strong centre of hypsodonty has developed in eastern Asia, perhaps reflecting the Pliocene spread of C4 grasses there (Ding and Yang, 2000). In Europe, hypsodonty levels are clearly lower than in the latest Miocene and, although part of the apparent difference may be due to a lack of data for Europe north of the Alps in the preceding interval, the change is clearly documented for Spain, northern Italy and the Ukraine. An increase in humidity after the terminal Miocene is, moreover, well documented by other non-mammalian evidence (Esu, 2000). The low hypsodonty values seen in the Caucasus may be related to the presence there in the Pliocene and early Pleistocene of African elements, including early humans (Gabunia *et al.*, 2000).

We have excluded the Pleistocene here because the rapid climatic fluctuations (Potts, 1998) of this interval make a whole-interval map virtually meaningless, but we believe that a hypsodonty-based comparison of warm and cold intervals within the Pleistocene might be rewarding.

CONCLUSIONS

The precipitation pattern inferred from mean hypsodonty is generally concordant with results from modelling and with other geological continental-scale evidence of past climate (Prell and Kutzbach, 1992; Kutzbach *et al.*, 1993; Broccoli and Manabe, 1997; Ruddiman *et al.*, 1997; An *et al.*, 2001), especially in the late Miocene aridification of Asia north and west of the Tibetan Plateau and the relative lack of change to the east and south of the plateau. This, together with the empirical support for a relationship between hypsodonty and rainfall in the modern world, suggests that hypsodonty is indeed a reasonably good proxy for palaeoprecipitation. The transfer from mean scored hypsodonty to numeric precipitation values is imprecise today and may even have been different in the past (Damuth and Fortelius, 2001), but the regional pattern seen within a time interval should still be a reasonably good representation of the relative geographic distribution of rainfall.

The maps shown here (Figs 2, 3) include some unexpected details, such as the relatively low aridity inferred for the latest Miocene of North China. Such regional details should provide useful constraints on Neogene climate and vegetation models and reconstructions. For example, one could explore whether the enigmatic peak in mean particle size around 8 million years ago observed in the marine dust record of the North Pacific, which indicates

an episode of strengthened winter monsoon at the time (Rea *et al.*, 1998), is compatible with a general strengthening of the monsoon circulation and specifically with increased precipitation over North China from a stronger summer monsoon.

The data do not permit us to distinguish the evolutionary mechanisms responsible for the regionally differentiated changes in hypsodonty, but we have shown elsewhere (Jernvall and Fortelius, 2002) that the overall increase was almost entirely due to the most common species – that is, the species sampled from many localities in an interval. These species would mainly represent the most successful competitors, with, on average, the widest ranges and highest local abundances.

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