Late Miocene and Pliocene large land mammals and climatic changes in Eurasia

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Abstract

The fossil teeth of land mammals offer a powerful tool to map the regional details of past climate change in the terrestrial realm. We use mean plant-eater hypsodonty (molar crown height) of late Neogene mammal localities to map late Miocene and Pliocene palaeoprecipitation on the Eurasian continent and, with higher temporal resolution, in Europe. The results show that the mid-latitude drying in Eurasia affected the central parts of the continent first and that the drying of western Europe after about 7–8 Ma seems to have coincided roughly in time with a return to more humid conditions in eastern Asia, with a return to a drier east and more humid west in the Pliocene. Within Europe, the hypsodonty-based palaeoprecipitation maps suggest that the sequence from MN 9 to MN 12 (ca. 11.1–6.8 Ma) was dominated by an east–west (continental-marine) humidity gradient, which gradually intensified and with a shift of dryer conditions eastwards in MN 12 (ca. 7.5 Ma). This was partly overlain from MN 13 onwards by a north–south oriented gradient, which persisted at least to the end of the Pliocene. The maps for both the earliest late Miocene (MN 9, ca. 11.1–9.7 Ma) and the earliest Pliocene (MN 14, ca. 4.9–4.2 Ma) show very low regional differentiation, possibly suggesting perturbed phases in the evolution of the mammal communities. Analysis of hypsodonty and dietary structure of the mammalian plant-eater community in Europe during the entire interval shows that the Miocene–Pliocene boundary was marked by a strong decrease in mesodont species and mixed feeders, and an increase in brachydont species and omnivores. In this view, the shift in the latest Miocene from east–west to partly north–south-polarised hypsodonty patterns corresponds mainly to an increase in hypsodont species and grazers. It seems probable that the east–west gradient was primarily driven by precipitation, while the north–south gradient would also have been strongly influenced by temperature-related effects of humidity.

1. Introduction

Paradoxically, one of the main difficulties affecting the empirical study of past environments and ecosystem changes is the wealth of information available. The difficulty lies not in the amount itself (which is, after all,

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modest compared with many other scientific disciplines), but in the disparate nature and uneven distribution of the information. This would not be a problem if most of the information would be convertible to some common currency like temperature, rainfall or primary productivity, but such is not yet the case, as the contributions to the present volume eloquently testify. There seems little doubt that such conversions will become increasingly feasible and common, but while we wait for this it seems useful to search for internally consistent, quantifiable environmental indicators with sufficient geographical coverage and sampling density and sufficient stratigraphic resolution to allow mapping of comparable time slices on the continental or global scale. We believe that much progress would result if such maps, based on independent, quantified evidence, could be directly compared and analysed in combination. This paper presents an example, using the recently developed parameter of mean hypsodonty (molar crown height) of large plant-eating mammals as a proxy for rainfall (Fortelius et al., 2002; Jernvall and Fortelius, 2002; Fortelius et al., 2003).

The functional link between hypsodonty and rainfall that we exploit is the relationship between food properties and dental wear observed in living mammals (for a summary of the evidence, see Fortelius et al., 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 as a regularly occurring extreme period, such as a dry season. Except in high latitudes, this condition should depend closely on rainfall. A 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).

The evolutionary and ecological nature of mean hypsodonty is not entirely clear. The increase in mean hypsodonty recorded during the Miocene is known to be driven almost entirely by species and morphological classes that are "common", i.e., that occur at many localities (Jernvall and Fortelius, 2002). This suggests that in each interval a substantial proportion of the species that were most able to increase their share of available resources were found in the hypsodont category, implying that increased hypsodonty was often highly adaptive. However, instances of secondarily reduced hypsodonty are virtually unknown

and some hypsodont species are known to subsist today on food that does not require hypsodont teeth (Fortelius, 1985). It is therefore possible that short intervals of increased humidity within an overall drying trend might not be reflected in mean hypsodonty. However, the main proximate mechanism determining mean hypsodonty is not evolutionary change but geographic sorting of species and a lowering of mean hypsodonty is easily accomplished by immigration of species with low-crowned teeth, even in the unlikely case of all hypsodont species remaining unaffected by the change. We suggest that mean hypsodonty provides a reasonably faithful record of relative rainfall within and between intervals, a view supported by the actualistic results referred to above.

The mammalian fossil record of the late Miocene and early Pliocene of Eurasia is relatively well known (Lindsay et al., 1989; Bernor et al., 1996; Rössner and Heissig, 1999). The main difficulties for the present purpose concern the age and correlations of localities, both of which still depend mainly on biochronology (e.g., the MN system; Mein, 1989; De Bruijn et al., 1992) and extrapolation between tiepoints dated by independent means (Steininger et al., 1996; Krijgsman et al., 1996; Alroy et al., 1998; Agustí et al., 2001). The difficulties are greatest for intervals of little taxonomic change. Curiously, as far as large mammals are concerned, the Miocene–Pliocene transition in Europe is such an interval of very minor taxonomic turnover and it is often difficult to decide whether localities belong in the latest Miocene or earliest Pliocene (e.g., Schmidt-Kittler et al., 1995). It is therefore necessary to emphasise that our analysis does not depend on high precision of dating or correlations. We have accepted that continent-wide correlations are insecure and have used a very crude stratigraphic subdivision for the continental-scale maps. Both for this and for the finer MN-unit resolution employed for Europe we contend that biases introduced by false locality age assignments are expected to be mainly in the conservative direction, decreasing the apparent differences between adjacent intervals. Needless to say, our focus is on the broad patterns rather than on the local details.

2. Data and methods

2.1. Data

We used a dataset derived from the NOW database of Eurasian Neogene fossil mammals and from ongoing compilation projects for the Former Soviet Union (FSU) and China. The latest public version of the NOW data can be downloaded from http://www.helsinki.fi/science/now and our combined dataset is available from the authors. It

should be noted that many localities in the NOW database have incomplete faunal lists, a fact arising from the history of the database, which was originally built for the revision of taxonomic groups (Fortelius et al., 1996). For the large plant-eater species on which our analyses are based the coverage is quite good, however. 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 and should not affect hypsodonty scores significantly. The age information for these datasets has been reviewed by AT and ZZ, respectively. We included all large mammal taxa classified as plant-eaters or plant-dominated omnivores. Thus, all pigs were included but no carnivoran omnivores.

2.2. 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 Ma, except for some Chinese localities where we accepted greater uncertainty. For the late Miocene and Pliocene the discrepancies between recent mammal zonations are relatively minor. 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. For the European comparisons of single MN-units, we accepted only localities assigned to a single MN-unit in the NOW database. The MN calibration of the NOW database is still Steininger et al. (1996), but for this paper we used the calibration of Agustí et al. (2001).

2.3. Hypsodonty

Three classes of hypsodonty 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 have a ratio in the range 0.8–1.2 and hypsodont over 1.2. For this study, the hypsodonty classes were assigned the values 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. The mean hypsodonty value was calculated for each locality by averaging these ordinated scores and the mean values (ex-

cluding cases based on a single species) were plotted on maps using interpolated colors to indicate regional differences (Figs. 1 and 2). It should be said here 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, nor are all modern grazers hypsodont (Fortelius and Solounias, 2000). There is growing consensus that many species of Neogene hypsodont equids were mixed feeders and even browsers (Hayek et al., 1991; Quade et al., 1994; Mac-Fadden et al., 1999; Kaiser et al., 2000), and the same is evidently true of the hypsodont ruminants (Fortelius and Solounias, 2000). Finally, we stress that mean hypsodonty measures aridity in a very generalized sense and cannot (as far as known) distinguish between total and seasonal rainfall, for example. This lack of specificity must be applied throughout to the interpretation of our results.

2.4. Diet

The comparison of dietary categories (Fig. 3) uses a subset of the "diet_3" assignments as given in the NOW data: plant-dominated omnivory (plant_dom), browsing (browse), mixed feeding (br/gr) and grazing (graze). These values are not assigned primarily from hypsodonty, but emphasise dental wear patterns (Janis, 1990; Fortelius and Solounias, 2000) and cranial proportions (Solounias and Moelleken, 1993; Janis, 1995).

2.5. Maps

We deliberately 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 one paleogeographic configuration. We also use modern geographic names (such as "China" or "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 9, values rounded to 1 decimal. The inflection values were manually set to the range 0.7–3 for all maps. For the maps of all Eurasia (Fig. 1), where large areas are far from the nearest data point, a mask was manually superimposed to fade out areas more than 1000 km from the nearest data point (opacity 50%). Map 1d was 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
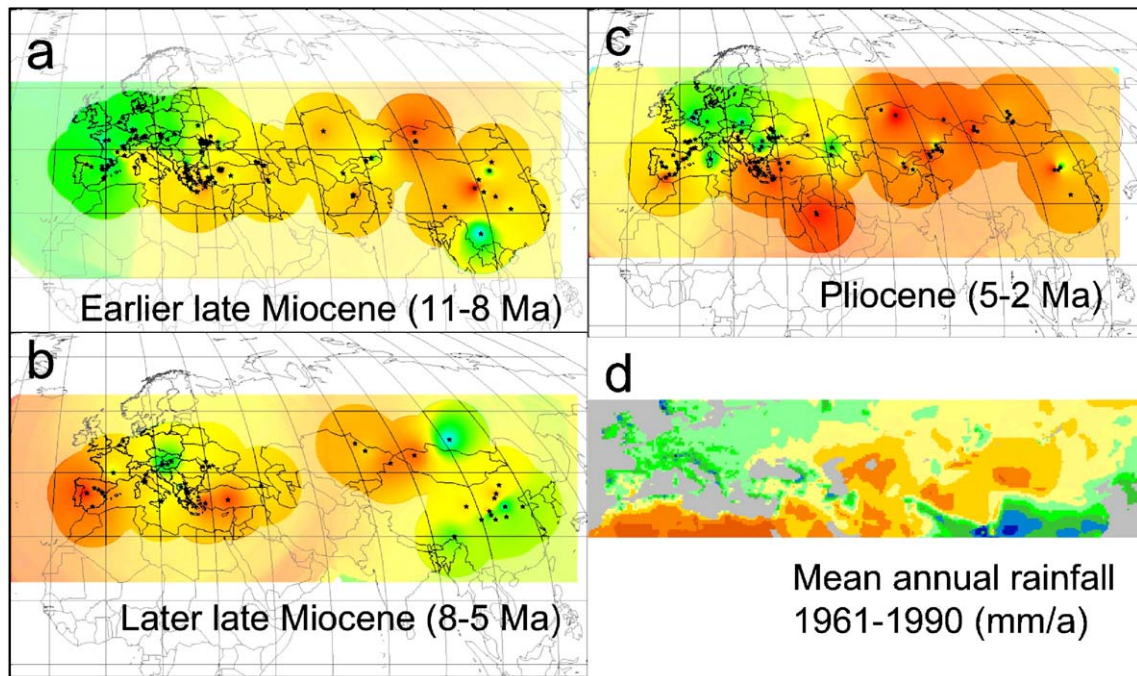
Fig. 1. Colour-interpolated maps (a–c) of Eurasian large mammal plant-eater mean hypsodonty by locality during the late Miocene and Pliocene (see Data and methods). Greens, yellows and reds show the successive increase in crown height interpreted here as increasing aridity. The colours are faded beyond 1000 km from the nearest data point. Map of modern (present interglacial) mean annual precipitation in Eurasia (d). Oranges represent less than 124 mm/year, yellows 125–474 mm/year, greens 475–1474 mm/year and blues over 1475 mm/year. Note that maps a–e lack data for Africa and Southeast Asia, and that no precise correspondence is intended in the colour schemes between hypsodonty and precipitation. Data for map d are based on Leemans and Cramer (1991).

WinDisp application. Data and software were downloaded from http://www.fao.org/WAICENT/FAOINFO/SUSTDEV/eidirect/CLIMATE/EIsp0002.htm. The precipitation values shown on map 1d were restricted to the interval resolved by hypsodonty in modern mammal communities (approximately 100–2500 mm/year), but there is no precise relationship between the color schemes of this map and those based on hypsodonty.

2.6. Sampling

The problematic issue of sampling that plagues all studies of fossil biodiversity (for a recent review, see Alroy et al., 2001) 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). The analyses of crown height and dietary structure uses the SPLOC method (Fortelius and Hokkanen, 2001), whereby each species is counted each time it occurs, and the result is therefore weighted in proportion to the commonness and presumed ecological impact of the species. Mean hypsodonty calculated for individual localities also emphasizes the most commonly occurring species (Jernvall and Fortelius, 2002) and is therefore

relatively insensitive to the presence or absence of rarely sampled species.

3. Mio-Pliocene palaeoprecipitation patterns based on mean hypsodonty

3.1. The Eurasian continent

The suit of maps shown in Fig. 1 summarises continental-scale results discussed in more detail elsewhere (Fortelius et al., 2002; Fortelius et al., 2003). According to mean hypsodonty, the earlier part of the late Miocene (ca. 11–8 Ma) was characterised by moderately dry conditions except in the western part of Europe and southern China (the Lufeng locality), with a clustering of the driest localities in east–central Asia (Fig. 1a). The bipartition of Europe into a more humid (oceanic) western part and a drier (continental) eastern part is very well established (Fortelius and Hokkanen, 2001; Fortelius et al., 1996) and will be shown in more detail in the next section. In the later part of the late Miocene (ca. 8–5 Ma) western Europe appears mostly "dry", with very high hypsodonty values in Iberia (Fig. 2b). More humid conditions are indicated only in central Europe and eastern Asia in this interval,
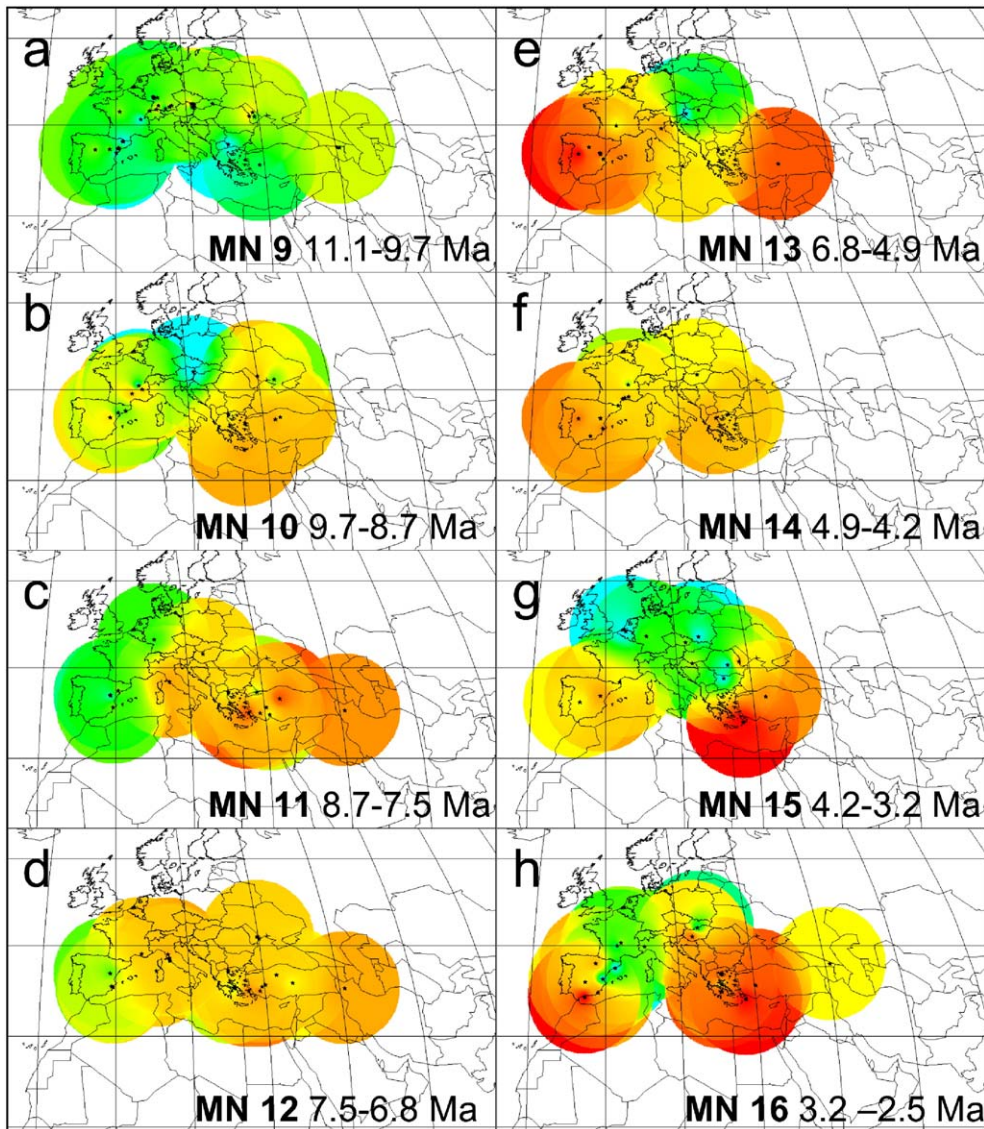
Fig. 2. Colour-interpolated maps of European large mammal plant-eater mean hypsodonty by locality during the MN units of the late Miocene and Pliocene (see Data and methods). Greens, yellows and reds show the successive increase in crown height interpreted here as increasing aridity. The colours are restricted to a radius of 1000 km from the nearest data point. The age assignments of the MN units follow Agustí et al. (2001).

with north China appearing distinctly less dry than in the preceding interval. In the Pliocene (ca. 5–2 Ma), western Europe again appears less dry, while the eastern Mediterranean and central to eastern Asia now appear quite arid (Fig. 1c). The apparent expansion of the relatively humid region in central Europe may be partly an artefact of less data for this region than in the preceding interval, but the "greening" of Ukraine and the Caucasus appears real. In broad outline the Pliocene pattern is quite similar to the modern rainfall distribution (Fig. 1d), bearing in mind that neither northern Africa nor southeastern Asia are sampled for the Pliocene.

3.2. Europe

A finer stratigraphic subdivision reveals a striking, two-part history for the interval combined late Miocene and Pliocene (ca. 11.1–2.5 Ma). The MN-unit age assignations in the following are given according to Agustí et al. (2001). During the Vallesian (MN 9–10, ca. 11.1–8.7 Ma) the east–west contrast arises as part of a trend of generally increasing aridity (Fig. 2a,b). This contrast is most pronounced in the early Turolian (MN 11, ca. 8.7–7.5) and is followed in the middle Turolian (MN 12, 7.5–6.8 Ma) by a "transgression" of the open
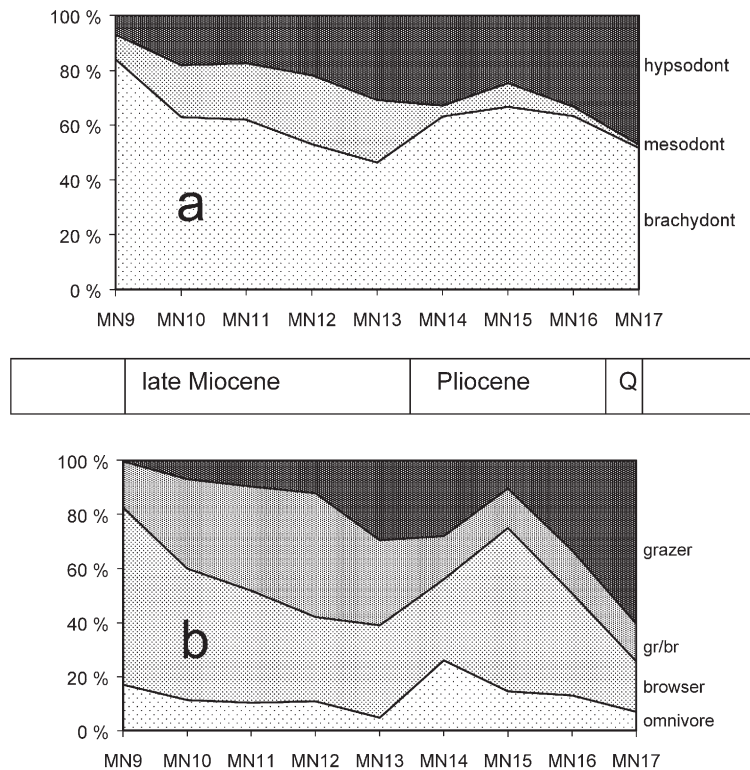
Fig. 3. Relative frequencies of molar crown height classes (a) and dietary categories (b) in the large mammal plant eater communities of the late Miocene, Pliocene and early Pleistocene of Europe (see Data and methods).

habitats (or at least the open-adapted Pikermian mammals) westwards (Fig. 2c,d), as originally noted by Bernor et al. (1979) and later described quantitatively by Fortelius et al. (1996) and Fortelius and Hokkanen (2001). This westward expansion of the Pikermian Biome (Solounias et al., 1999) is seen here to represent the culmination of the late Miocene climatic trend of decreasing humidity in a framework of a predominantly continental-oceanic (east–west) dynamic. It is followed in the late Turolian (MN 13, ca. 6.8–4.9 Ma) by what we interpret as a pattern polarised on a north–south gradient, with relatively dry conditions dominating in the Mediterranean (especially Iberia and Anatolia, the southernmost parts sampled), and predominantly humid conditions north of the Alps (Fig. 2e). Although the hypsodonty proxy does not directly measure temperature, we expect cooling at higher latitudes to come across as increasing humidity resulting from decreased evaporation, as is seen today. We therefore interpret the north–south gradient as reflecting temperature in part. Thus, according to the hypsodonty signal, the main break in climatic conditions is not between the Miocene and the Pliocene, but between the middle and late Turolian, corresponding approximately to the Tortonian/Messinian boundary in the marine

chronology (Steininger et al., 1996). The early Pliocene (MN 14, ca. 4.9–4.2 Ma) appears here as a curiously featureless interval (Fig. 2f), followed by a return to the north–south pattern in the middle and late Pliocene (MN 15–16, ca. 4.2–2.5 Ma) (Fig. 2g,h). This pattern is difficult to interpret and we prefer not to press the evidence here. It is perhaps best regarded as a less strongly developed version of the north–south-polarised pattern seen in the preceding and subsequent intervals. An interesting observation is that, throughout these changes, the least affected area appears to be the northwestern Mediterranean (southern France and northern Italy).

4. Plant-eater community structure: hypsodonty and diet

The European map series may be compared with a breakdown by crown height and dietary category for the corresponding intervals (Fig. 3). For crown height, the Vallesian Crisis (Agustí et al., 1984) stands out clearly as an increase of mesodont and hypsodont species in MN 10 (Fig. 3a), and corresponds to an increase in the proportion of mixed feeders and grazers (Fig. 3b). Both for crown height and diet, the interval MN 10–12 is remarkably uniform. The arrival of the north–south-

polarised world in MN 13 is reflected in the hypsodonty structure by only a moderate increase in the proportion of hypsodont species, but by a major increase in the proportion of grazers. Unlike the maps, the geographically unresolved crown height and diet structure both record substantial change at the Miocene–Pliocene boundary, consisting of a marked increase of brachydont species at the expense of mesodont ones and a corresponding marked increase in the proportion of omnivores. This pattern remains relatively stable throughout the Pliocene but changes at the beginning of the Pleistocene, when hypsodont species and grazers again increase markedly.

5. Discussion

5.1. Mean hypsodonty and palaeoclimate reconstructions

We have previously argued (Fortelius et al., 2002, 2003) that the climatic changes suggested by the hypsodonty maps are in agreement with general predictions from palaeoclimate models and palaeoclimatic proxy data from both the marine and the continental realm (e.g., Prell and Kutzbach, 1992; Kutzbach et al., 1993; Broccoli and Manabe, 1997; Ruddiman, 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. Of particular interest in the continental-scale sequence is the return to more humid conditions in northern China in the latest Miocene, coinciding in time with evidence of strengthened monsoon circulation at about 8 Ma (Molnar et al., 1993; Rea et al., 1998; Griffin, 1999). While we do not necessarily wish to claim a causal connection here between the increased humidity in eastern Asian and the contemporaneous humidity decrease of western Europe, we do wish to point out that general circulation models as well as partial models like the desert/monsoon system described by (Griffin, 2002) do require that the same change in circulation pattern will have different and often opposite effects in different regions. Thus, the climatic effects observed in north-eastern Africa and attributed by Griffin (2002) to the development of the monsoon system seem to coincide in time with the presumably monsoon-driven changes seen in northern China, with a more humid phase beginning at about 8 Ma, followed by more arid conditions from 4 Ma onwards (Ding and Yang, 2000; Zhang et al., 2002—compare Fig. 1c). The rhythm of climatic change in the Sub-Himalayan Zone was similar, but the direction of change was more like that of western Eurasia, with

evidence of drying at 8 Ma and cooling at about 6.5 Ma (Hoorn et al., 2000).

For Europe, or data appear largely consistent with the palaeoclimatic evidence derived from plant evidence. In particular, the major drying observed at the middle–late Miocene transition (Ivanov et al., 2002) and the relative lack of change in Europe north of the Alps (Utescher et al., 2000) as well as in the northwestern Mediterranean (Suc and Bessais, 1990; Suc et al., 1992) are entirely in agreement with the large mammal evidence. We suggest that, when data from multiple taxonomic groups have been combined and synthesised, a more detailed cross-comparison with predictions of climate models would be highly rewarding.

5.2. Mean hypsodonty and palaeogeography

There appears to be an almost complete lack of correlation between the changing land–sea configuration and the palaeoprecipitation maps derived from mean hypsodonty, in particular, the complicated history of the Paratethys (Rögl, 1998; Magyar et al., 1999) is not reflected in any simple way in the hypsodonty data. Rather than argue against the effect of water bodies on precipitation patterns in their immediate surroundings, we suggest that this result mainly reflects the typically wide geographic distribution of large mammals. Specifically, we would expect proxy data from plants and smaller animals to provide more evidence of local conditions than do large mammals. The drying (to whatever degree) and re-flooding (at whatever rate) of the Mediterranean at first sight do seem to be reflected in changes in the geographic distribution and community structure of hypsodonty and diet, but causation is difficult to prove and we cannot exclude the possibility that changes observed in the mammal data and in the hydrology of the Mediterranean are largely independent reflections of the same underlying climatic and tectonic events (Griffin, 2002).

A related aspect concerns the role of land–sea connections as barriers to mammal dispersal. In this matter, we agree with those who hold that "mammals always make it through" and that the decisive factor is not dispersal but establishing viable populations (Fortelius et al., 2003). This implies that for most large mammal species the real barriers (save for oceans and the highest mountain ranges) are ecological rather than physical. In the present context, it is useful to consider the effect on mammalian biogeography of interrelated, regionally differentiated climate changes. Could it be that times of climate change are particularly amenable to dispersal simply because the shifting of species ranges (e.g., of dominant plant species or main competitors) momentarily weakens the regional ecological differentiation affecting the mammals? It might even be speculated

that the featureless hypsodonty maps of MN 9 and MN 14 could partly reflect mammal communities "in transit", following times of external perturbation, rather than expressions of lack of regional climatic differentiation.

6. Conclusions

The large mammal data appear to fit a pattern from climatic reconstructions, suggesting major, possibly interconnected changes at two times during the late Miocene and Pliocene. The first took place at about 8 Ma and was expressed in western Eurasia as aridification, leading to a transgression of the dry-adapted Pikermian faunas westwards. In China, the Red Clay mammal faunas record an increase in humidity at about the same time, following on a dryer interval in the early late Miocene. The second change corresponds roughly to the beginning of the Messinian and was expressed in Europe as the appearance of a north–south-polarised ecological gradient, superimposed on and partly replacing the east–west-polarised system that had dominated the region since the middle Miocene. In this second event, the mammals may have responded more to cooling than to changes in humidity. These results appear generally congruent with predictions from atmospheric circulation models (Steppuhn et al., 2006-this volume), palaeovegetation models (François et al., 2006-this volume) and with evidence from other fossil groups (Bruch et al., 2006-this volume; Van Dam, 2006-this volume). There appears to be good hope that an understanding of causally interrelated regional climate changes in the Eurasian Neogene is now emerging.

Acknowledgements

References

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., Parés, J.M., 2001. A calibrated mammal scale for the Neogene of western Europe. State of the art. Earth-Science Reviews 52, 247–260.

Agustí, J., Moya-Sola, S., Gibert, J., 1984. Mammal distribution dynamics in the eastern margin of the Iberian Peninsula during the Miocene. Paléobiologie Continentale (Montpellier) 14 (2), 33–46.

Alroy, J.J., Bernor, R.L., Fortelius, M., Werdelin, L., 1998. The MN system: regional or continental? Annales Zoologici Fennici 38, 243–258.

Alroy, J., et al., 2001. Effects of sampling standardization on estimates of Phaerozoic marine diversification. Proceedings of the National Academy of Sciences of the United States of America 98 (11), 6261–6266.

An, Z., Kutzbach, J.E., Prell, W.L., Porter, S.C., 2001. Evolution of Asian monsoons and phased uplift of the Himalaya-Tibetan plateau since late Miocene times. Nature 411, 62–66.

Bernor, R.L., Andrews, P.J., Solounias, N., Van Couvering, J.A.H., 1979. The evolution of "Pontian" mammal faunas: some zoogeographic, palaeoecologic and chronostratigraphic considerations. Annales Géologiques des Pays Helléniques, Tome Hors Série (1), 81–89.

Bernor, R.L., Fahlbusch, V., Mittmann, H.-W., Rietschel, S. (Eds.), 1996. The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York.

Broccoli, A.J., Manabe, S., 1997. Mountains and midlatitude aridity. In: Ruddiman, W.F. (Ed.), Tectonic Uplift and Climate Change. Plenum Press, New York, pp. 89–121.

Bruch, A.A., Utescher, T., Mosbrugger, V., Gabrielyan, I., Ivanov, D. A., 2006. Late Miocene climate in the circum-Alpine realm—a quantitative analysis of terrestrial palaeofloras. Palaeogeography, Palaeoclimatology, Palaeoecology 238, 270–280. [this volume]. doi:10.1016/j.palaeo.2006.03.028.

Damuth, J., 1982. Analysis of the preservation of community structure in assemblages of fossil mammals. Paleobiology 8, 434–446.

Damuth, J., Fortelius, M., 2001. Reconstructing mean annual precipitation, based on mammalian dental morphology and local species richness. In: Agustí, J., Oms, O. (Eds.), EEDEN Plenary Workshop on Late Miocene to Early Pliocene Environments and Ecosystems. EEDEN Programme, European Science Foundation, Sabadell (Spain), pp. 23–24.

De Bruijn, H., et al., 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. Newsletters in Stratigraphy 26 (2/3), 65–118.

Ding, Z.L., Yang, S.L., 2000. C3/C4 vegetation evolution over the past 7.0 Myr in the Chinese Loess Plateau: evidence from pedogenic carbonate d13 C. Palaeogeography, Palaeoclimatology, Palaeoecology 160, 291–299.

Fortelius, M., 1985. Ungulate cheek teeth: developmental, functional and evolutionary interrelations. Acta Zoologica Fennica 180, 1–76.

Fortelius, M., Hokkanen, A., 2001. The trophic context of hominoid occurrence in the later Miocene of western Eurasia—a primate-free view. In: De Bonis, L., Koufos, G., Andrews, A. (Eds.), Phylogeny of the Neogene Hominoid Primates of Eurasia. Cambridge University Press, Cambridge, pp. 19–47.

Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. American Museum Novitates 3301, 1–36.

Fortelius, M., et al., 1996. Provinciality, diversity, turnover and paleoecology in land mammal faunas of the later Miocene of western Eurasia. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.-V. (Eds.), The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York, pp. 414–448.

Fortelius, M., et al., 2002. Fossil mammals resolve regional patterns of Eurasian climate change during 20 million years. Evolutionary Ecology Research.

Fortelius, M., Eronen, J.T., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I.A., Zhang, Z., 2003. Continental-scale hypsodonty patterns, climatic palaeobiogeography, and dispersal of Eurasian Neogene large mammal herbivores. In: Reumer, J.W.F., Wessels, W. (Eds.), Distribution and Migration of Tertiary Mammals in Eurasia. A volume in honour of Hans de Bruijn. Deinsea, 10, pp. 1–11.

François, L., Ghislain, M., Otto, D., Micheels, A., 2006. Late Miocene vegetation reconstruction with the CARAIB model. Palaeogeography, Palaeoclimatology, Palaeoecology 238, 302–320. doi:10.1016/j.palaeo.2006.03.034.

Griffin, D.L., 1999. The late Miocene climate of northeastern Africa: unravelling the signals in the sedimentary succession. Journal of the Geological Society (London) 156, 817–826.

Griffin, D.L., 2002. Aridity and humidity: two aspects of the late Miocene climate of North Africa and the Mediterranean. Palaeogeography, Palaeoclimatology, Palaeoecology 182, 65–91.

Hayek, L.-A.C., Bernor, R.L., Solounias, N., Steigerwald, P., 1991. Preliminary studies of hipparionine horse diet as measured by tooth microwear. Annales Zoologici Fennici 3–4, 187–200.

Hoorn, C., Ohja, T., Quade, J., 2000. Palynological evidence for vegetation development and climatic change in the Sub-Himalayan Zone (Neogene, central Nepal). Palaeogeography, Palaeoclimatology, Palaeoecology 163, 133–161.

Ivanov, D., Ashraf, A.R., Mosbrugger, V., Palamarev, E., 2002. Palynological evidence for Miocene climate change in the Forecarpathian Basin (Central Paratethys, NW Bulgaria). Palaeogeography, Palaeoclimatology, Palaeoecology 178, 19–37.

Janis, C.M., 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. Mémoires du Museum National d'Histoire Naturelle, Paris 53, 367–387.

Janis, C.M., 1990. The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diet of extinct species. In: Boucot, A.J. (Ed.), Evolutionary Paleobiology of Behavior and Coevolution. Elsevier, Amsterdam, pp. 241–259.

Janis, C.M., 1995. Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. In: Thomason, J.J. (Ed.), Functional morphology in vertebrate paleontology. Cambridge University Press, New York, pp. 76–98.

Janis, C.M., Fortelius, M., 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biological Reviews (Cambridge) 63, 197–230.

Jernvall, J., Fortelius, M., 2002. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. Nature 417, 538–540.

Kaiser, T.M., Solounias, N., Fortelius, M., Bernor, R., Schrenk, F., 2000. Tooth mesowear analysis on *Hippotherium primigenium* from the Vallesian Dinotheriensande (Germany) a blind test study. Carolinea 58, 103–114.

Krijgsman, W., et al., 1996. A new chronology for the middle to late Miocene continental record in Spain. Earth and Planetary Science Letters 142, 367–380.

Kutzbach, J.E., Prell, L., Ruddiman, W.F., 1993. Sensitivity of Eurasian climate to surface uplift of the Tibetan Plateau. The Journal of Geology 101, 177–190.

Leemans, R., Cramer, W., 1991. The IIASA database for mean monthly values of temperature, precipitation and cloudiness on a global terrestrial grid. Research Report RR-91-18. International Institute of Applied Systems Analyses, Laxenburg, p. 61. November 1991.

Lindsay, E.H., Fahlbusch, V., Mein, P., 1989. European Neogene Mammal Chronology. Plenum Press, New York. 658 pp.

MacFadden, B.J., Solounias, N., Cerling, T.E., 1999. Ancients diets, ecology, and extinctions of 5-million-year-old horses from Florida. Science 283, 824–827.

Magyar, I., Geary, D.H., Müller, P., 1999. Paleogeographic evolution of the late Miocene Lake Pannon in Central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 147, 151–167.

Mein, P., 1989. Updating of MN zones. In: Lindsay, E.H., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology. Plenum Press, New York, pp. 73–90.

Molnar, P., England, P., Martinod, J., 1993. Mantle dynamics, uplift of the Tibetan Plateau and the Indian monsoon. Reviews of Geophysics 31, 357–396.

Prell, W.L., Kutzbach, J.E., 1992. Sensitivity of the Indian monsoon to forcing parameters and implications for its evolution. Nature 360, 647–652.

Quade, J., Solounias, N., Cerling, T.E., 1994. Stable isotopic evidence from paleosol carbonates and fossil teeth in Greece for forest or woodlands over the past 11 Ma. Palaeogeography, Palaeoclimatology, Palaeoecology 108, 41–53.

Rea, D.K., Snoeckx, H., Joseph, L.H., 1998. Late Cenozoic eolian deposition in the North Pacific: Asian drying, Tibetan uplift, and cooling of the northern hemisphere. Paleoceanography 13, 215–224.

Rögl, F., 1998. Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). Annalen des Naturhistorischen Museums in Wien 99, 279–310.

Rössner, G.E., Heissig, K. (Eds.), 1999. Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, München. 515 pp.

Ruddiman, W.F. (Ed.), 1997. Tectonic Uplift and Climate Change. Plenum Press, New York.

Schmidt-Kittler, N., de Bruijn, H., Doukas, C., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene): 1. General introduction. Münchner Geowissenschaftliche Abhandlungen 28, 9–18.

Solounias, N., Moelleken, S.M.C., 1993. Dietary adaptation of some extinct ruminants determined by premaxillary shape. Journal of Mammalogy 74, 1059–1071.

Solounias, N., Plavcan, J.M., Quade, J., Witmer, L., 1999. The palaeoecology of the Pikermian Biome and the savanna myth. In: Agustí, J., Rook, L., Andrews, P. (Eds.), The Evolution of Neogene Terrestrial Ecosystems in Europe. Cambridge University Press, Cambridge, pp. 436–453.

Steininger, F.F., et al., 1996. Circum-Mediterranean Neogene (Miocene–Pliocene) marine-continental chronologic correlations of European mammal units. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.-W. (Eds.), The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York, pp. 7–46.

Steppuhn, A., Micheels, A., Geiger, G., Mosbrugger, V., 2006. Reconstructing the Late Miocene climate and oceanic heat flux using the AGCM ECHAM4 coupled to a mixed-layer ocean model with adjusted flux corrections. Palaeogeography, Palaeoclimatology, Palaeoecology 238, 399–423. doi:10.1016/j.palaeo.2006.03.037.

Suc, J.-P., Bessais, E., 1990. Pérennité d'un climat thermo-xérique en Sicile avant, pendant, après la crise de salinité messinienne. Comptes Rendus de l'Académie des Sciences Paris 2 (294), 1003–1008.

Suc, J.-P., Clauzon, G., Bessedik, M., Leroy, S., Zheng, Z., Drivaliari, A., Roiron, P., Ambert, P., Martinell, J., Domenech, R., Matias, I., Julia, R., Anglada, R., 1992. Neogene and Lower Pleistocene in southern France and northeastern Spain. Mediterranean environments and climate. Cahiers de Micropaléontologie 7 (1–2), 165–186.

Utescher, T., Mosbrugger, V., Ashraf, A.R., 2000. Terrestrial climate evolution in northwest Germany over the last 25 million years. Palaios 15, 430–449.

Van Dam, J., 2006. Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe: The use of small mammals as paleoprecipitation proxies. Palaeogeography, Palaeoclimatology, Palaeoecology 238, 190–218. doi:10.1016/j.palaeo. 2006.03.025.

Zhang, Z., Gentry, A.W., Kaakinen, A., Liu, L., Lunkka, J.P., Qiu, Z., Ren, S., Scott, R.S., Werdelin, L., Zheng, S., Fortelius, M., 2002. Land mammal faunal sequence of the late Miocene of China: new evidence from Lantian, Shaanxi Province. Vertebrata PalAsiatica 40, 165–176.