

serpentinized peridotite (Fig. 2c). Assuming a lower-crustal velocity of  $3.6 \text{ km s}^{-1}$ , the estimated maximum S-velocity perturbation of 10% near the wedge corner could represent a level of serpentinization as high as 50–60%. However, steadily diminishing levels are implied away from the corner as the velocity perturbation decreases through zero to normal polarity. Permeability within altered peridotite is likely to be fracture controlled, and the presence of free fluids may also serve to lower velocities. The degree of hydration diminishes eastwards, producing, in succession, reduced velocity contrast, disappearance of the aberrant Moho and, finally, restoration to a normal polarity crust–mantle boundary 40 km west of the arc.

In addition to a thermal model of Cascadia, we have produced thermal models for more typical cold continental (for example, northeast Japan) and oceanic (for example, Izu-Bonin) subduction zones. In cold subduction zones, the forearc temperatures are still lower, and in oceanic subduction zones with thin crust, the forearc mantle region is often larger. Thus although dimensions and geometry vary, all models predict the presence of a hydrated (and, hence, serpentinized) mantle wedge, suggesting that such structures are a generic feature of convergent margins. This inference is supported by recent studies in central Japan<sup>17</sup> and northern Chile<sup>18</sup> that employed travel times from local earthquakes to identify material with high Poisson's ratio above the subducting plate with serpentinized peridotite. Documentation of active serpentine mud volcanoes in the Mariana forearc<sup>19</sup> provides further supporting evidence.

The ubiquitous presence of a serpentinized mantle forearc in subduction zones has at least two important implications. It has been noted previously that the down-dip rupture limit of great subduction zone earthquakes in cold subduction zones usually coincides in depth with the continental Moho<sup>20</sup>. This observation can be explained through the presence of an altered mantle wedge<sup>21</sup>. Serpentine<sup>22–24</sup>, and its companion alteration products brucite and talc<sup>8</sup>, are believed to exhibit stable sliding behaviour at plate velocities, thus impeding rupture into the forearc mantle. A second consequence is that large-scale flow in the mantle wedge will be modified by the presence of serpentinized forearc mantle. In particular, the positive buoyancy and weak rheology of serpentine should serve to isolate most of the hydrated forearc wedge from the mantle-wedge corner flow system, while basal portions could be dragged down by the subducting plate. □

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# Common mammals drive the evolutionary increase of hypsodonty in the Neogene

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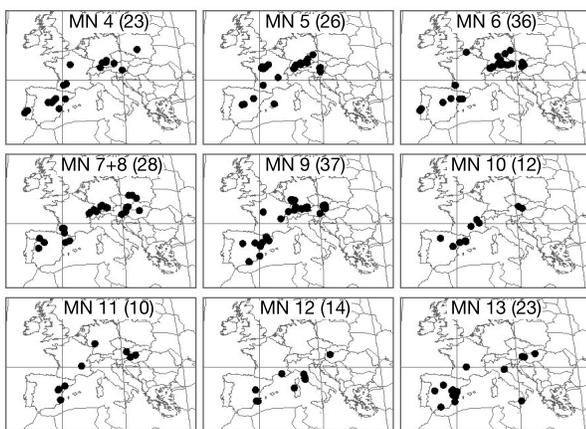
During the past 20 million years, herbivorous mammals of numerous lineages have evolved hypsodont, or high-crowned, cheek teeth. Hypsodonty is informative ecologically because it is well developed in mammals eating fibrous and abrasive foods that are most abundant in open and generally or seasonally dry environments<sup>1–5</sup>. Here we report that in the Neogene of Europe mammals with the greatest locality coverages showed an increase in hypsodonty. We used a data set of 209 localities to measure whether large mammals occurring in many fossil localities show a similar increase in hypsodonty to mammals occurring in single or few localities. Taxonomic and morphological groupings show a low average hypsodonty in the early Miocene epoch. From the middle Miocene onwards, only the hypsodonty of commonly found mammals shows a marked increase. Therefore, in the drying Europe of the late Miocene, only increasingly hypsodont mammals may have been able to expand their share of habitats and food resources. These results suggest that the relatively small number of species known from multiple localities are palaeoecologically informative by themselves, irrespective of the rest of the known species.

Palaeoecological inference relies on information derived from individual fossil localities. Increased sampling and methods that correct for uneven sampling<sup>6,7</sup> or are insensitive to sampling<sup>8,9</sup> allow a more accurate, less biased description of evolutionary patterns. Large data sets including numerous localities now allow us to evaluate new aspects of community evolution, such as whether species found in many localities show similar palaeoecological

changes to those of species found in a limited number of localities. This information is lost when conventional tabulations of regional faunal lists are used for analysis, because every species is tabulated only once. Such analyses tend to over-emphasize rare taxa, whose specializations may not reflect overall trends in the biota.

We used the NOW database of Eurasian Neogene fossil mammals (<http://www.helsinki.fi/science/now/>), from which we included European localities up to 20° E longitude. This area corresponds roughly to 'West' of previous analyses of western Eurasian Neogene mammals, an area found to represent a biogeographically and biochronologically relatively uniform region<sup>9</sup>; thus providing a good geographic scale for exploring the effects of environmental change on biota<sup>10</sup>. The localities from 18 to 5 million years (Myr) ago were divided into nine intervals corresponding to the MN (Mammal Neogene) units 4 to 13 of European mammal chronology<sup>11–13</sup>. The number of localities in each interval ranged from 10 to 37 with a relatively constant geographic coverage (Fig. 1). We present here the results after grouping localities that are within one degree of geographic separation from each other in each time interval. This grouping makes the analysis more conservative as multiple-locality complexes (such as Oberdorf, Austria) may bias the results, although equivalent results were obtained using the ungrouped set of localities. We included all large, non-carnivorous mammals in the analysis. Three classes of tooth crown height recorded in the database were assigned the values 1, 2 and 3, respectively: low (brachydont), medium high (mesodont) and high (hypsodont). This is a relatively conservative tabulation as the difference in crown height between a hypsodont and a brachydont species is usually more than 3:1. We tabulated hypsodonty values for species, genera and cheek tooth crown types. We placed more emphasis on the genus and crown-type level tabulations because even after correcting for known synonyms (see the NOW database above), species level inferences may be biased by the high number of species found at very few localities (36 to 57 per cent of species have one locality occurrence in each MN unit). The ecomorphological crown type tabulation is based on tooth morphology alone and cuts across taxonomic groups<sup>14,15</sup>.

First we examined changes in hypsodonty in taxa that are common (defined as present in more than 25 per cent of localities within an MN interval) as opposed to taxa which are rare (represented in less than 25 per cent of localities). The results show that

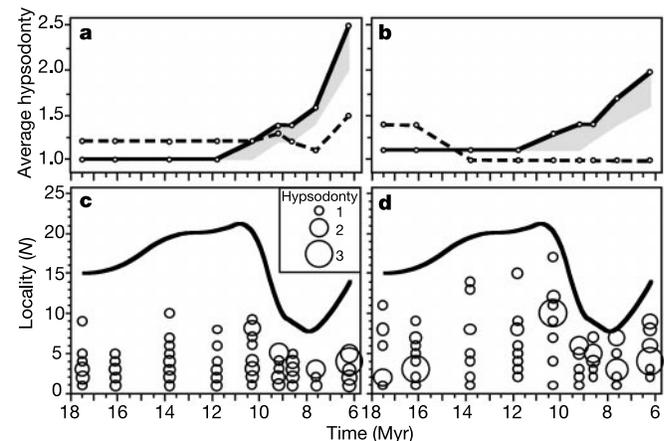


**Figure 1** The nine locality intervals and number of localities (in parenthesis) analysed. The corresponding number of localities for each MN unit after grouping localities situated within one degree of geographic separation from each other are: 15, 15, 20, 20, 22, 10, 9, 7 and 14. Grouping the short-duration MN units 10 and 11 does not change the results. The average centroids along the longitude and the latitude of the taxa or crown types found in many localities (Fig. 2) did not differ from those found in fewer localities ( $P = 0.57$  to  $0.76$ , Mann–Whitney  $U$ -test).

the average hypsodonty increased markedly in the late Miocene in common genera (Fig. 2a). In contrast, rare genera show less change in their hypsodonty. Moreover, in the early Miocene rare genera show slightly higher hypsodonty averages than common genera (Fig. 2a). We next examined species grouped only by molar crown type. Individual crown types are sampled from more localities than genera because several taxa can share the same crown type but the pattern of results nevertheless appears similar between genera and crown types. Average hypsodonty again shows a marked increase only among common crown types in the late Miocene (Fig. 2b). This increase partly coincides with a decrease in overall sampling intensity as reflected in the number of localities known (Fig. 2c, d). Because we define frequency of occurrence in relative terms within each time interval, our analysis should be insensitive to differences in level of sampling.

As the crown type tabulation suggests, the increase in hypsodonty among common taxa is not limited to any single taxonomic group. Of special interest are the hipparionine horses, which contribute heavily to the classic increase in hypsodonty among ungulates<sup>1</sup>. However, the increase in hypsodonty in common genera or crown types is not eliminated by removing the family Equidae or corresponding crown types from the common groups (Fig. 2a, b). Rather, hipparionine horses, many of which are found in many localities, appear as the first wave of the increase in hypsodonty followed by other ungulates later in the Neogene (Fig. 2a, b). This is evidently a result of their having evolved hypsodonty in North America before their dispersal to the Old World at the beginning of the late Miocene<sup>1,16</sup>.

A significant aspect of the results is the increase in hypsodonty among the common groups beginning around 11 Myr ago. This was a time of major climatic changes, including the first development of Eurasian mid-latitude aridity<sup>17</sup>, widely believed to have been ultimately driven by the Himalayan–Tibetan uplift<sup>18,19</sup>. Up to that



**Figure 2** Increase in hypsodonty is limited to common groups (present in over 25 per cent of localities within MN interval). **a**, Average hypsodonty increases sharply in common genera (solid line) while rare taxa show very little change in hypsodonty (present in less than 25 per cent of localities, dotted line). **b**, Ecomorphological groupings of teeth based on crown types shows increase in hypsodonty among common crown types (solid line). We note how in the early Miocene, the common groups are less hypsodont than the rare groups. The increase in hypsodonty persists when hipparionine horses are removed from the common groups (in grey in **a** and **b**). **c**, The distribution of genera is well below the number ( $M$ ) of localities (solid line) whereas the distribution of crown types (**d**) approaches the locality curve, representing the broader cross-taxonomic range of ecomorphological groupings. We note how the average hypsodonty of genera and crown types found in many localities increase in the late Miocene (large bubbles). We show genera in **a** and **c** because genus level can be considered a more robust measure of diversity. Species level tabulations gave equivalent results to the tabulation based on genera. See Methods for details.

point, hypsodont mammals are confined to fewer than five localities (Fig. 2c, d). Comparing further the pre- and post-11-Myr-times, average locality coverage of hypsodont species (tabulations 2 and 3) increases from 11 to 18 per cent ( $P = 0.017$ , MN-randomization test on medians) and for brachydont species (tabulation 1) from 13 to 16 per cent ( $P = 0.054$ ). The locality coverage of hypsodont genera increases from 12 to 25 per cent ( $P = 0.022$ ) and for brachydont genera from 16 to 18 per cent ( $P = 0.148$ ). Similarly, locality coverage of hypsodont crown types increases from 8 to 52 per cent ( $P = 0.028$ ) and for brachydont crown types from 30 to 33 per cent ( $P = 0.570$ ). These changes are consistent with the documented decrease in overall provinciality<sup>9</sup>, here shown to be most conspicuous in hypsodont mammals. We propose that in the drying Europe of the late Miocene mostly mammalian lineages possessing advanced (such as the hipparionine horses) or incipient (such as many rhinoceroses and bovids) hypsodonty were able to increase their relative share of habitats and food resources. At the population level this increasing presence of hypsodont taxa may have been related to, and consistent with, life-history differences observed between modern hypsodont and brachydont ungulates, such as large group sizes found in hypsodont taxa<sup>20–22</sup>. We note that while common taxa (as defined above) appear to be also abundant in relative numbers of individuals within a locality (for example, the hipparionine horses), this will require further study when locality-specific taxon abundance data become available.

The more pronounced increase in hypsodonty among common taxa is an indication that large-scale data sets provide unique insights into evolution. The most immediate implication is that common taxa could be used to retrieve and map evolutionary changes that might otherwise be swamped by noise from rare groups. Moreover, to the extent that the occurrence of fossil species in a locality may reflect past abundance<sup>23</sup>, the use of regional or global taxon presence lists may underestimate past ecological changes at the community level. We thus predict that analysis of other large-scale data sets with primary locality–occurrence information will reveal that common taxa show generally stronger evolutionary trends than do all taxa. □

## Methods

We analysed hypsodonty in species, genera and crown types of orders Artiodactyla, Perissodactyla, Primates and Proboscidea. Analyses were insensitive to details of handling genera or crown types that contained species with different hypsodonty values, and here we used averaged hypsodonty for each locality. The MN-wide hypsodonty was the average of all the localities. Four genera (*Alicornops*, *Brachypotherium*, *Plesiaceratherium* and *Tragoportax*) out of 98 genera and three crown types (L2212 (ectolophodont), L2220 (selenodont) and R2200 (bunodont)) out of 12 crown types had species with different hypsodonty values within MN units. These were also the only groups that had species with different hypsodonty values across MN units, predominantly showing an increase in hypsodonty during their temporal ranges. We assigned uncertain species (20) and genera (4) to be certain, although alternative handling did not change the pattern of results.

We analysed only large mammals, which by itself should minimize taphonomic or collecting biases. All reconstructed body masses exceed 5 kg and 79 per cent of species are at least 20 kg. There are no temporal trends excluding an increase in body mass of brachydont suoids<sup>23</sup>, which, if it causes a bias, might dampen the hypsodonty trends. On the other hand, hypsodont species are 2.8 times the average mass of brachydont species (544 kg versus 197 kg), which, if it causes a bias, might exaggerate the hypsodonty trends. We note that such a bias should not affect the trends calculated separately for brachydont and hypsodont groups. In horses hypsodonty results in a more compact dental design but their exclusion did not eliminate the patterns. Exclusion of Primates and Proboscidea, which could have distinct taphonomic or collecting biases, did not alter the pattern of results.

Although the MN units are distributed in time, the general problem with the application of time-series methods to fossil data is that sampling intervals and efforts vary and samples do not represent single points. Therefore, because we needed a robust measure of the overall trends in the increase of hypsodonty during the Neogene, we examined whether the medians of observed cumulative hypsodonty curves were significantly shifted to younger MN units. Such a shift would indicate a disproportional presence of high hypsodonty values in the younger MN units. We used a randomization test<sup>24</sup> to obtain significance values for each median separately by randomly reshuffling the temporal order of MN units 1,000 times and calculating a median for each randomization (medians expected to be clustered around MN 7 + 8 and 9). These null distributions of medians provide a robust measure of trends because only overall increases or decreases depart significantly from the randomizations. For example, common groups had medians

between MN 9.6 and 9.9, indicating an increase in hypsodonty, and we calculated how many times these high, or higher, values were obtained from the random distribution of medians. Because the larger number of relatively brief MN units in the late Miocene may bias the medians, we performed the analyses also after combining MN units 10 and 11, and these  $P$  values are given below in parentheses. Our primary interest was not to estimate the absolute increases but to portray trends among common and rare groups, which should be relatively insensitive to differences in MN duration.

The resulting probability values for common (present at  $\geq 25$  per cent of localities) species, genera and crown types are  $P = 0.010, 0.008, 0.008$  (0.017, 0.024, 0.007), and the corresponding values for rare groups are  $P = 0.054, 0.371, 1.000$  (0.071, 0.480, 1.000). The crown types have slight decrease in hypsodonty,  $P = 0.157$  (0.107), Fig. 2b. The values for common groups excluding hipparionine horses are  $P = 0.536, 0.012, 0.048$  (0.598, 0.024, 0.100). The non-significant value for species results from the fact that the cut-off point defining common groups leaves only one common hipparionine species in MN 13. When common and rare groups are combined the increase in hypsodonty is intermediate. The values for species, genera and crown types are  $P = 0.025, 0.079, 0.032$  (0.005, 0.299, 0.076).

To test how the relative locality coverage increased in brachydont and hypsodont groups, we examined the shifts in medians of cumulative locality coverage curves. In the few cases where a genus or a crown type had species with a different degree of hypsodonty (see above), we considered these groups hypsodont when their locality averages of hypsodonty were at least 1.5. The probability values obtained from reshuffling MN units for hypsodont species, genera and crown types are  $P = 0.017, 0.022, 0.028$  (0.079, 0.065, 0.013), and the corresponding values for brachydont groups are  $P = 0.054, 0.148, 0.570$  (0.461, 0.597, 0.553).

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