



Grit not grass: Concordant patterns of early origin of hypsodonty in Great Plains ungulates and Glires

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ABSTRACT

A major step in mammalian evolution was the shift amongst many herbivorous clades from a browsing diet of leaves to a grazing diet of grasses. This was associated with (1) major cooling and increasing continentality and the enormous spread of grasslands in most continents, replacing closed and open forests, and (2) hypsodonty, the possession of high-crowned teeth. Hypsodonty is traditionally linked with eating grass because of the contained phytoliths, silica-rich granules, which are presumed to wear away mammalian dental tissues. However, we present evidence from the Great Plains of North America that the origins of hypsodonty in different clades of ungulates (hoofed mammals) and Glires (rodents and lagomorphs) were substantially out of synchrony with the great spread of grasslands, 26–22 Myr ago (latest Oligocene/earliest Miocene). Moderate hypsodonty was acquired by some Oligocene artiodactyls and several rodent families (mainly burrowers) at least 7 Myr earlier. Highly hypsodont ungulates and hypselodont (= ever-growing cheek teeth) rodents post-date the spread of grasslands by 4 to 9 Myr. Lagomorphs follow a different trend, with hypselodont forms present from near the Eocene–Oligocene boundary. These results indicate that hypsodonty was not a simple adaptation for eating grasses, and may have originated in some clades to counteract the ingestion of grit and soil.

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1. Introduction

The evolution of hypsodont (high-crowned) molars in grassland herbivores is a classic palaeontological narrative (Stirton, 1947; White, 1959; Webb, 1977, 1978; Stebbins, 1981; MacFadden, 1997; Janis et al., 2000). Climatic cooling and drying in the late Palaeogene and Neogene led to forest fragmentation and the spread of open grassland environments (Retallack, 1997; Jacobs et al., 1999; Strömberg, 2002; Retallack, 2004; Strömberg, 2004, 2005). Grass is considered to be more abrasive to chew than leaves, because of higher concentrations of phytoliths, microscopic silica bodies that occur in plant cells and tissues (Strömberg, 2002, 2011; Prasad et al., 2005; Massey and Hartley, 2006). The long-held view is that a dietary shift in the herbivorous fauna, from browsing on leaves to grazing on grass, triggered an adaptive evolutionary response in tooth morphology to hypsodonty as a result of this increased wear (Stebbins, 1981). The presence of hypsodont dentitions has been used to infer the development of grasslands in the absence of diagnostic palaeobotanical data (White, 1959; Jacobs et al., 1999; Flynn et al., 2003).

There are two challenges to this seemingly simple story, however. First, the amount of soil or grit ingested during feeding may be a more important abrasive agent than grass phytoliths (Stirton, 1947; Janis, 1988; Williams and Kay, 2001; Janis et al., 2002a; Damuth and Janis, 2011). Herbivores can inadvertently consume large quantities of soil or grit, either because it has been deposited on the vegetation by wind or rain splash, or through wholesale uprooting of plants during feeding (Mayland et al., 1975; Damuth and Janis, 2011). Disentangling the relative importance of grit-driven versus grass-driven hypsodonty is complicated because the same processes that favoured the ecological expansion of silica-rich grasses – climatic cooling and drying and the fragmentation of forest cover – would also have led to an increase in the amount of grit being ingested by herbivores during feeding (Fortelius et al., 2002, 2006; Eronen et al., 2010b, 2010c; Damuth and Janis, 2011). The abundance of lower stature vegetation (herbs, shrubs or grass) co-varies with the openness of the environment, and the amount of soil and airborne grit adhering to vegetation increases with decreasing feeding height (Damuth and Janis, 2011). Smaller plants are also more likely to be ripped up and consumed whole, with soil-covered roots still attached. Herbivores feeding closer to ground level are therefore expected to ingest more abrasives than those browsing at higher levels, regardless of what plant matter they are feeding on.

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Second, the timing of hypsodonty acquisition amongst herbivores does not match the emergence of grassland environments as closely as was once thought. Recent work on the phytolith fossil record, which provides a much more complete and taxonomically refined palaeobotanical record of grass than either leaf fossils or pollen (Strömberg, 2011), has shown that open, grass dominated areas, and thus grass as a food resource, were present in the North American Great Plains region by ~22 Ma (Strömberg, 2004, 2005), and possibly as early as ~26 Ma (Strömberg, 2011). Although a slight increase in the tooth height of Great Plains horses occurred at ~23 Ma with the first appearance of *Parahippus*, the first truly hypsodont horses did not appear until ~17 Ma, within the genus *Merychippus*, the earliest member of the subfamily Equinae (MacFadden and Hulbert, 1988; Strömberg, 2006; Damuth and Janis, 2011; Muhlbachler et al., 2011). Subsequent diversification occurred across both high and low-crowned horse lineages, and highly hypsodont equines appeared at ~14 Ma (Damuth and Janis, 2011). Other Miocene ungulate clades that evolved hypsodont forms, antilocaprids (pronghorns) (Semperebon and Rivals, 2007) and camelids (Semperebon and Rivals, 2010), show a later rise in hypsodonty, in the late Middle Miocene, echoing the transition in the horses. Amongst the more derived rhinos that first appear in the late Early Miocene, *Teleoceras* is fairly hypsodont from the beginning, but the originally more brachydont *Aphelops* also becomes hypsodont in the late Miocene (Janis, unpublished data from the Nebraska State Museum).

Our understanding of hypsodonty acquisition has been limited by focussing on specific taxa, typically horses (Stirton, 1947; White, 1959; MacFadden and Cerling, 1994; Strömberg, 2006; Muhlbachler et al., 2011), or the entire large herbivore guild (and especially the hoofed mammals, or ungulates) (Janis et al., 2000, 2002a, 2004; Jernvall and Fortelius, 2002; Eronen et al., 2010c; Damuth and Janis, 2011). Hypsodont and hypselodont (= ever-growing) molars evolved in a number of lineages of Glires (rodents and lagomorphs) (Schmidt-Kittler, 2002; Bair, 2007; Lazzari et al., 2008), but these trends have not been as thoroughly studied as, or compared directly with, those in the larger herbivore fauna (although see Williams and Kay, 2001). Glires are of interest because they are ecologically different from larger mammals, and as a group incorporates broader diets and more varied modes of life, including burrowing (fossorial) forms (French et al., 1976; Schmidt-Kittler, 2002; Hopkins, 2005; van Dam, 2006; Evans et al., 2007; Caledo et al., 2011).

To understand better the relative importance of grass-driven versus grit-driven hypsodonty acquisition, we carried out a regional-scale study of tooth height changes across the entire herbivore species pool of the US Great Plains region. We focus on the following questions: 1) When did hypsodonty evolve in Glires and large mammals (ungulates and xenarthrans), and how does this relate to the spread of grasslands? 2) How many families acquired hypsodont dentitions in the two groups (i.e., how widely distributed is hypsodonty as a morphological trait amongst taxa)? 3) How did the pattern and timing of hypsodonty evolution differ between fossorial (burrowing and/or underground-dwelling) and non-fossorial rodents?

2. Materials and methods

We have compiled incidence (= presence/absence) data from Janis et al. (2008, 1998) for ungulates and xenarthrans, and Janis et al. (2008) for Glires, from the US Great Plains region. The data were analyzed at this broad spatial scale, rather than by localized samples or collections (e.g. Alroy, 1998; Janis et al., 2000), to minimize the effect of different sampling strategies for small and large mammals. Our dataset extends from 39.6 Ma to 1.9 Ma, and thus covers 37.7 Myr from the late Middle Eocene (Bartonian) to the early Pleistocene (Gelasian) (Fig. 1). The data are binned into 23 divisions of the North American Land Mammal Ages (NALMAs) (Fig. 1, Supplementary Table 1). The dataset is provided in the Supplementary material

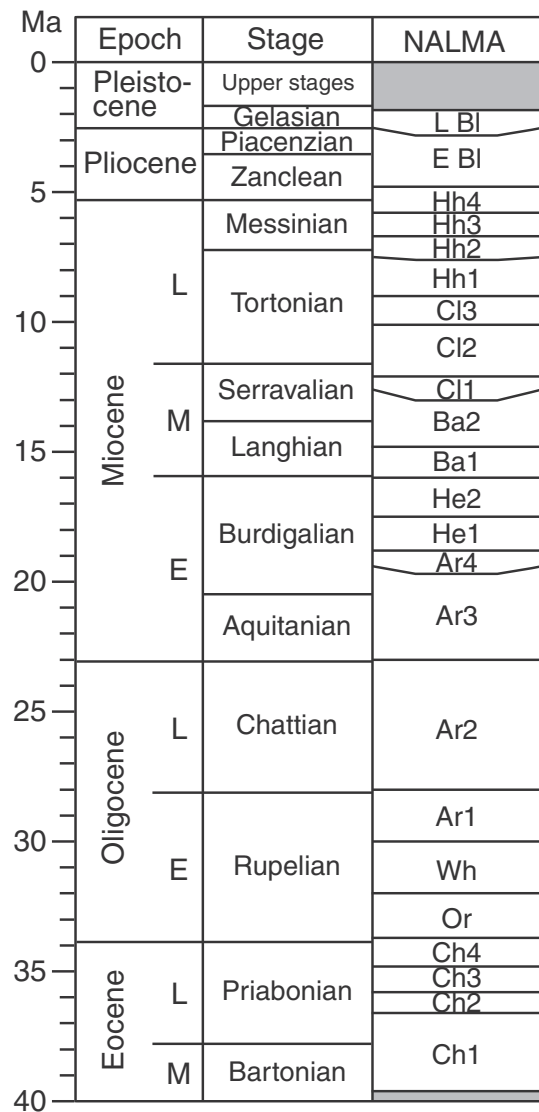


Fig. 1. Timescale for this study, which covers the interval 39.6 to 1.9 Ma. Timescale based on Gradstein et al. (2004), with updated information from the Geologic Timescale Foundation website (<https://engineering.purdue.edu/Stratigraphy>). NALMA = North American Land Mammal Age; see Supplementary Table 1 for NALMA start, end and midpoint ages. Ch = Chadronian, Or = Orellan, Wh = Whitneyan, Ar = Arikarean, He = Hemingfordian, Ba = Barstovian, Cl = Clarendonian, Hh = Hemphillian, E BI = Early Blancan, L BI = Late Blancan.

(Supplementary Table 2). Only taxa with a dominantly herbivorous mode of life were included in the dataset. Armadillos (Dasypodidae) were therefore not included in the xenarthrans, and the small mammal group was restricted to Glires, and does not incorporate any members of Eulipotyphla (these taxa being dominantly insectivorous).

Each taxon was categorized by tooth height. For ungulates we used the hypsodonty index (HI), which is calculated by dividing the crown height of the unworn third molar by its occlusal width (Janis, 1988; Damuth and Janis, 2011). HI values are based on measurements, made by one author (Janis), of specimens held in the American Museum of Natural History and the University of Nebraska State Museum. For Glires, proboscideans and xenarthrans, we determined tooth height qualitatively using descriptions and measurements in Janis et al. (2008, 1998). All taxa were then classified as brachydont (HI < 1.7), submesodont (HI = 1.7–2.5), mesodont (HI = 2.5–3.5), hypsodont (HI = 3.5–5.0), or highly hypsodont (HI > 5.0)/hypselodont (rhinos were assigned slightly lower values, to reflect the correlation of

hypsodonty with diet amongst modern rhinos that has reduced HI values compared to that in horses and artiodactyls [Janis, 1988]). Similar categorizations have been employed by previous authors (e.g. Janis et al., 2000; Fortelius et al., 2002; Jernvall and Fortelius, 2002; Eronen et al., 2010b, 2010c, 2012) to analyze hypsodonty trends, and allow us to compare consistently the various groups of mammals. Glires typically have reduced HI values due to curvature of the cheek teeth (Bair, 2007); using tooth height categories therefore avoids biases that would be imposed by comparing raw continuous measurements. Finally, the numbers of taxa in each tooth height category were tabulated for each time bin. Tabulations were carried out with a range through assumption; that is, taxa were assumed to be present in the study area from their first to last occurrence in the dataset.

To compare the overall pattern of tooth height changes between Glires and large mammals statistically, we used Mantel correlation tests (Legendre and Legendre, 1998) of Q mode (time bin × time bin) distance matrices derived from the tooth height counts (both as raw count data and as proportions of the within-bin total). The Euclidean distance metric was used to construct the distance matrices, and the non-parametric Spearman rank-order correlation coefficient was used to assess the strength of the correlation between them, with 9999 permutations of the data to derive *p* values. We also used chi-squared tests to compare the distributions of Glires and large mammal taxa across the tooth height categories within each time bin, so as to identify any departures from the overall pattern determined by the Mantel test. Taxon counts within individual categories were frequently less than five, violating the assumptions of a traditional chi-squared test (Hammer and Harper, 2006). Monte Carlo simulation with 9999 permutations was therefore used to produce a null distribution of the chi-squared test statistic, and from this to derive *p* values. Data analysis was carried out using R version 2.14.1 (R Development Core Team, 2011), with the package Vegan 2.0-3 (Oksanen et al., 2012).

The large mammal dataset comprises 416 taxa and 813 occurrences, and the Glires dataset comprises 489 taxa and 726 occurrences. A total of 201 (48%) of the large mammals, and 329 (67%) of the Glires, have durations of one time bin (= singleton taxa). Tabulations, Mantel tests and chi-squared tests were carried out both with and without singletons, to investigate the robustness of the observed trends to the effects of sampling and short duration taxa. The observed timings and overall patterns of hypsodonty acquisition were highly similar when singletons were included or excluded. We therefore present the results from the full dataset below; results for the dataset with singletons removed are provided in the Supplementary material (Supplementary Figs. 1 to 5 and Supplementary Table 3).

3. Results

The timings of the first appearances of hypsodont and highly hypsodont/hypselodont taxa in each major mammal group are shown in Table 1. The Glires show a gradual transition from a low-crowned to high-crowned dominated species pool (Fig. 2A). The first

hypsodont taxa occur in the late Eocene (NALMA Ch2; see Fig. 1, and Supplementary Table 1 for full NALMA names), and there is a high proportion of hypsodont taxa from ~30 Ma onwards. The first hypselodont Glires occur in the earliest Oligocene (Or), and always represent a low proportion of species richness.

Rodents represent 89% of Glires species richness in this dataset. Non-fossorial rodents (Fig. 2B) show a similar pattern of hypsodonty acquisition to Glires as a whole, but with a lower proportion of hypsodont taxa in the middle of the time series. The first hypsodont taxa occur in the early Oligocene (Wh), and the first hypselodont taxon appears in the late Middle Miocene (Ba2: the geomyoid genus *Phelosaccomys*).

Fossorial rodents (Fig. 2C) are dominated by mesodont and hypsodont taxa throughout most of the time series. Hypselodont fossorial taxa are only present from ~6 Ma onwards, and there is only one brachyodont taxon, and no submesodont fossorial taxa. There is a large increase in the number and proportion of fossorial rodents from ~32 to 22 Ma, which is followed by a sharp decline. The early fossorial rodents are members of the family Cylindrodontidae (Fig. 2D), but the increase in numbers of fossorial taxa is driven by castorids (subfamily Palaeocastorinae), mylagaulids and geomyids (subfamily Entoptychinae). Fossorial castorids and entoptychine geomyids decline by ~18 Ma, after which time mylagaulids comprise the entire burrowing rodent fauna. There is a change at ~6 Ma with the loss of the burrowing mylagaulids, and the appearance of hypselodont geomyine geomyids and mesodont burrowing sciurids.

Lagomorphs (Fig. 2E) follow a different trend as compared to both burrowing and non-burrowing rodents. Hypselodont leporid lagomorphs first appear at or near the Eocene–Oligocene boundary, and with the decline of mesodont taxa through the Oligocene, are the predominant forms in the Neogene. Ochodontine lagomorphs first appear (as immigrants) at the very end of the Oligocene. They originally comprised mainly hypsodont forms, but by the middle Late Miocene (Cl3) only the modern hypselodont genus, *Ochotona*, remained.

When rodents are tabulated by family (Fig. 3), it can be seen that several early brachyodont to mesodont taxa (e.g. the families Ischyromyidae, Helioscomyidae, and Florentiamyidae; Figs. 3N, L and I, respectively) declined and became extinct in the Great Plains between 30 and 20 Ma; Dipodidae (Fig. 3F) and Eomyidae (Fig. 3G) are the only low-crowned taxa that range through the whole time series. Amongst the hypsodont taxa, apodontids (Fig. 3A), arvicolids (Fig. 3B), castorids (Fig. 3C), cricetids (Fig. 3D), heteromyids (Fig. 3M), and sciurids (Fig. 3P) show a trend from low to high-crowned molars; mylagaulids (Fig. 3O) and taxa that are *incertae sedis* within Geomyoidea (Fig. 3K) are exclusively high crowned (\geq mesodont). Hypselodonty in non-fossorial taxa is seen only in the middle Miocene to Pliocene geomyoid *Phelosaccomys* (Fig. 3K), and the late Pliocene heteromyid *Dipodomys* (kangaroo rat; Fig. 3M). The lagomorphs are dominated by the single family Leporidae, which contains 41 of the 52 lagomorph taxa, and so lagomorph families were not tabulated separately.

Large mammals (ungulates and xenarthrans; Fig. 4A) also show a gradual decline in the proportion of brachyodont taxa over time, and an increase in the proportion of hypsodont and highly hypsodont (or hypselodont in the case of Xenarthra) taxa. The first hypsodont taxa occur in the late Early Oligocene (Ar1), and the first highly hypsodont taxa first appear in the early Miocene (He1) (Table 1).

The majority of large mammals in the current dataset belong to the orders Artiodactyla (Fig. 4B) and Perissodactyla (Fig. 4C), which means that these groups drive the pattern for large mammals as a whole. Artiodactyls comprise 62% of the large mammal fauna, and perissodactyls 33%. Both groups show the same gradual transition from brachyodont to highly hypsodont taxa, although highly hypsodont taxa make up a higher proportion of perissodactyls than artiodactyls. Proboscideans (Fig. 4D) only account for 4% of large mammals, and range in age on the Great Plains from the late Middle Miocene (Ba2) to the end of the time series. They are mostly brachyodont, with one hypsodont taxon

Table 1
First appearance times of hypsodont and highly hypsodont taxa for each faunal group. Numbers in parentheses give NALMA midpoint.

	Hypsodont	Highly hypsodont/hypselodont
Glires	Ch2 (36.2)	Or (32.85)
Non-fossorial rodents	Wh (31)	Ba2 (13.7)
Fossorial rodents	Ch2 (36.2)	Hh3 (6.25)
Lagomorphs	Ar3 (21.2)	Or (32.85)
Large mammals	Ar1 (29)	He1 (18.15)
Artiodactyla	Ar1 (29)	He1 (18.15)
Perissodactyla	He1 (18.15)	Ba2 (13.7)
Proboscidea	E.B1 (3.65)	–
Xenarthra	–	Hh1 (8.25)

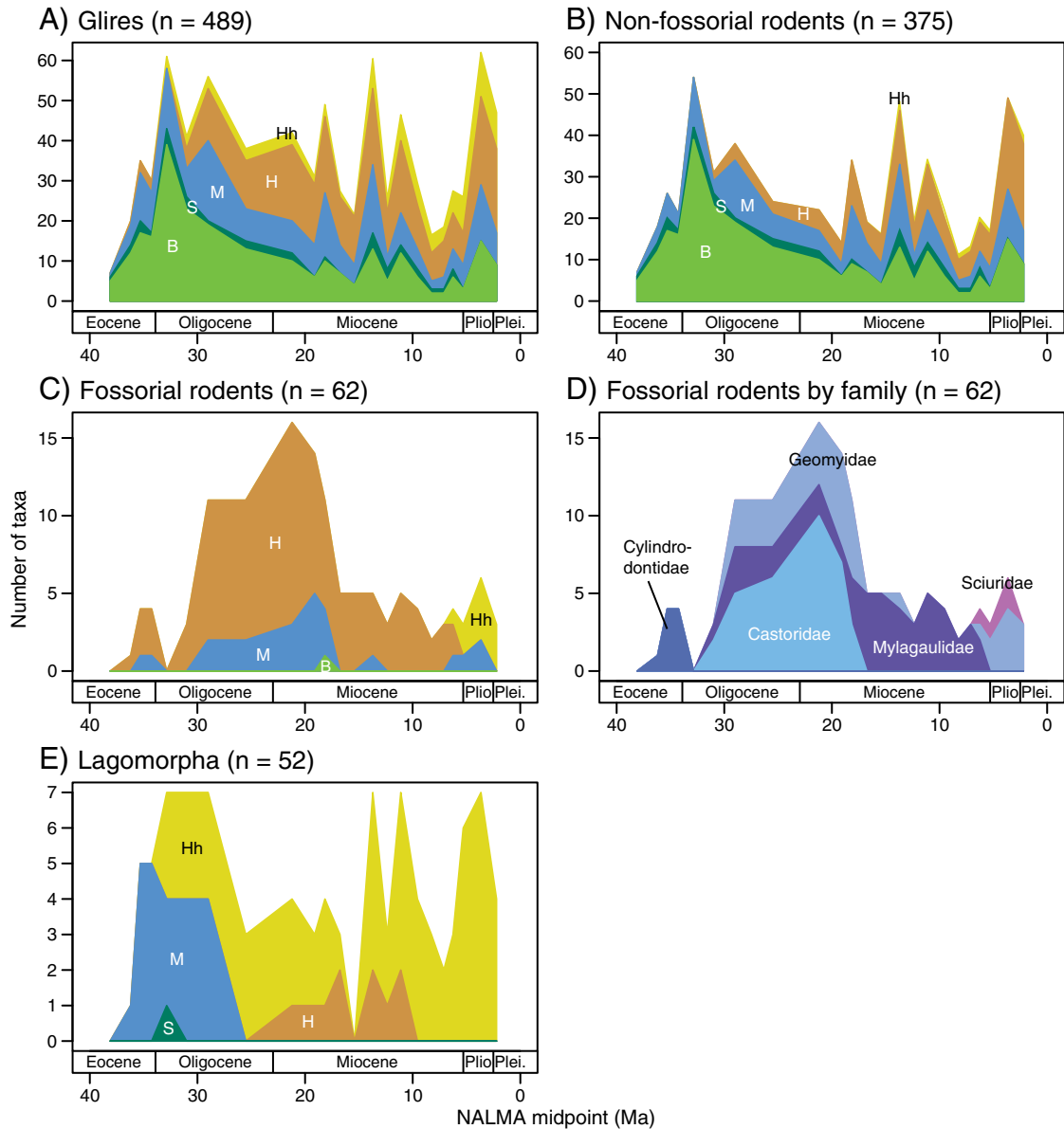


Fig. 2. Cumulative standing richness plots for Great Plains Glires, showing contributions of tooth height categories (B = brachydont, S = submesodont, M = mesodont, H = hypsodont, Hh = highly hypsodont or hypselodont).

(the genus *Stegomastodon*) in the Blancan; this taxon may be an immigrant from Asia (Webb, 1992), as were the hypsodont mammoths that first appeared in the Pleistocene. Xenarthrans (Fig. 4E), immigrants from South America in the Late Miocene, comprise just 1% of large mammals, and range from the late Late Miocene (Hh1) to the end of the time series. These taxa are all hypselodont ground sloths.

Many artiodactyl and perissodactyl families (Fig. 5) are exclusively low crowned (\leq mesodont); only Antilocapridae (Fig. 5B), Camelidae (Fig. 5C) and the oreodont family Merycoidodontidae (included with Agriocheridae in Fig. 5H) amongst the artiodactyls, and Equidae (Fig. 5N) and Rhinocerotidae (Fig. 5O) amongst the perissodactyls, attained hypsodont or highly hypsodont dentitions. With the exception of Antilocapridae (pronghorns) (Fig. 5B), which appeared as immigrants in the early Miocene (mesodont at the time of immigration), these high-crowned families range through the majority of the time series, and show a trend from brachydont to hypsodont or highly hypsodont molars. The early higher-crowned taxa occurred as a “first wave” in clades unrelated to Neogene taxa: these represent

leptauchenine oreodonts (Fig. 5H) and stenomyline camelids (Fig. 5C) (and a degree of hypsodonty is also seen amongst the hypertraguline traguloids [Fig. 5L]). The first highly hypsodont ungulate that appears in the early Miocene (He1) is the last surviving stenomyline camelid (Fig. 5C). A “second wave” of hypsodonty is seen in horses (Fig. 5N), rhinos (Fig. 5O), and pronghorns (Fig. 5B) in the early Miocene (He1), with highly hypsodont taxa (and the first of the hypsodont later camelids [Fig. 5C]) first appearing in the late Middle Miocene (the Barstovian).

All correlations between distance matrices were highly significant (Table 2), confirming the similar temporal trends between Glires and ungulates shown in the graphs (Figs. 2 and 4). Correlation coefficients were generally higher for the data without singletons, when terrestrial rodents were used in the correlations rather than all Glires, and when proportion data were used to calculate the distance matrices, rather than raw counts of tooth height frequencies. Chi-squared tests for all time bins were not statistically significant whether singletons were included (Fig. 6) or not (Supplementary Fig. 5). Similarity of taxon count

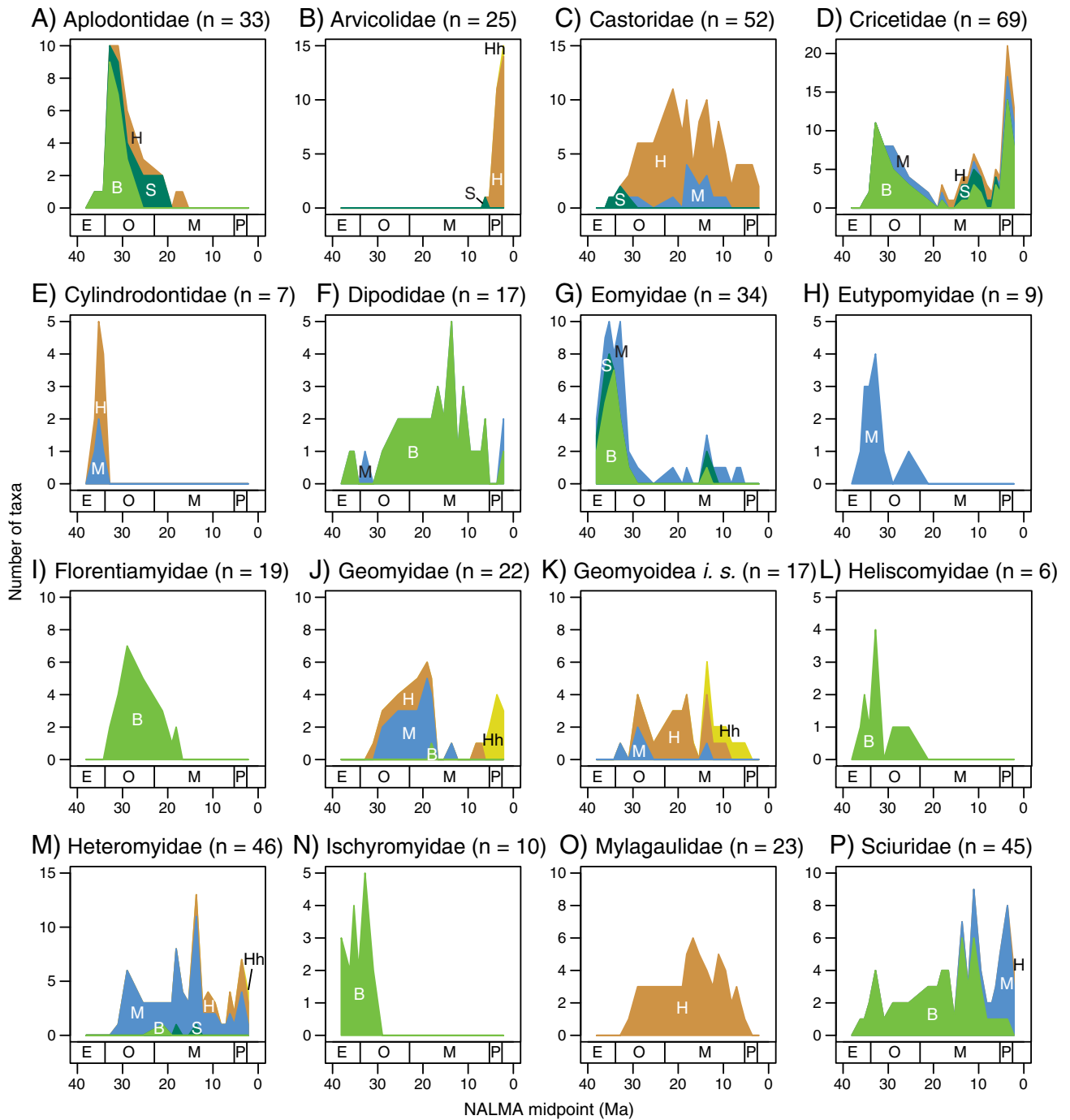


Fig. 3. Cumulative standing richness plots for Great Plains rodent families containing >1 taxon, showing contributions of tooth height categories (details as for Fig. 1).

distributions across tooth height categories between Glires/non-fossorial rodents and large mammals is therefore not rejected.

4. Discussion and conclusions

Our results show that the pattern and timing of hypsodonty acquisition amongst small and large herbivores on the Great Plains were highly similar. Both groups show a gradual transition to higher crowned taxa through the Oligocene and Miocene. The first occurrence of hypsodont dentitions pre-dated the appearance of grasslands at ~22 Ma (Strömberg, 2004) by over 7 Myr in both ungulates and Glires. With the exception of precociously high-crowned lagomorphs, highly hypsodont or hypselodont taxa appeared at least 4 Myr after

the spread of grasslands had begun. Excluding singletons (see Supplementary material) made very little difference to the timing or pattern of hypsodonty acquisition in either ungulates or Glires, which demonstrates that these results are robust and not just a product of sampling biases. Mantel correlations between Glires and large mammals were generally weaker with singletons included (although the opposite is true for the correlation between ungulates and non-fossorial rodents using proportion data). Visual inspection of the graphs, especially amongst the non-fossorial rodents, reveals the large amount of noise that is added to the standing richness and tooth height trends by including singletons, and suggests that the Great Plains Glires fossil record is hampered more by sampling biases than the ungulate record.

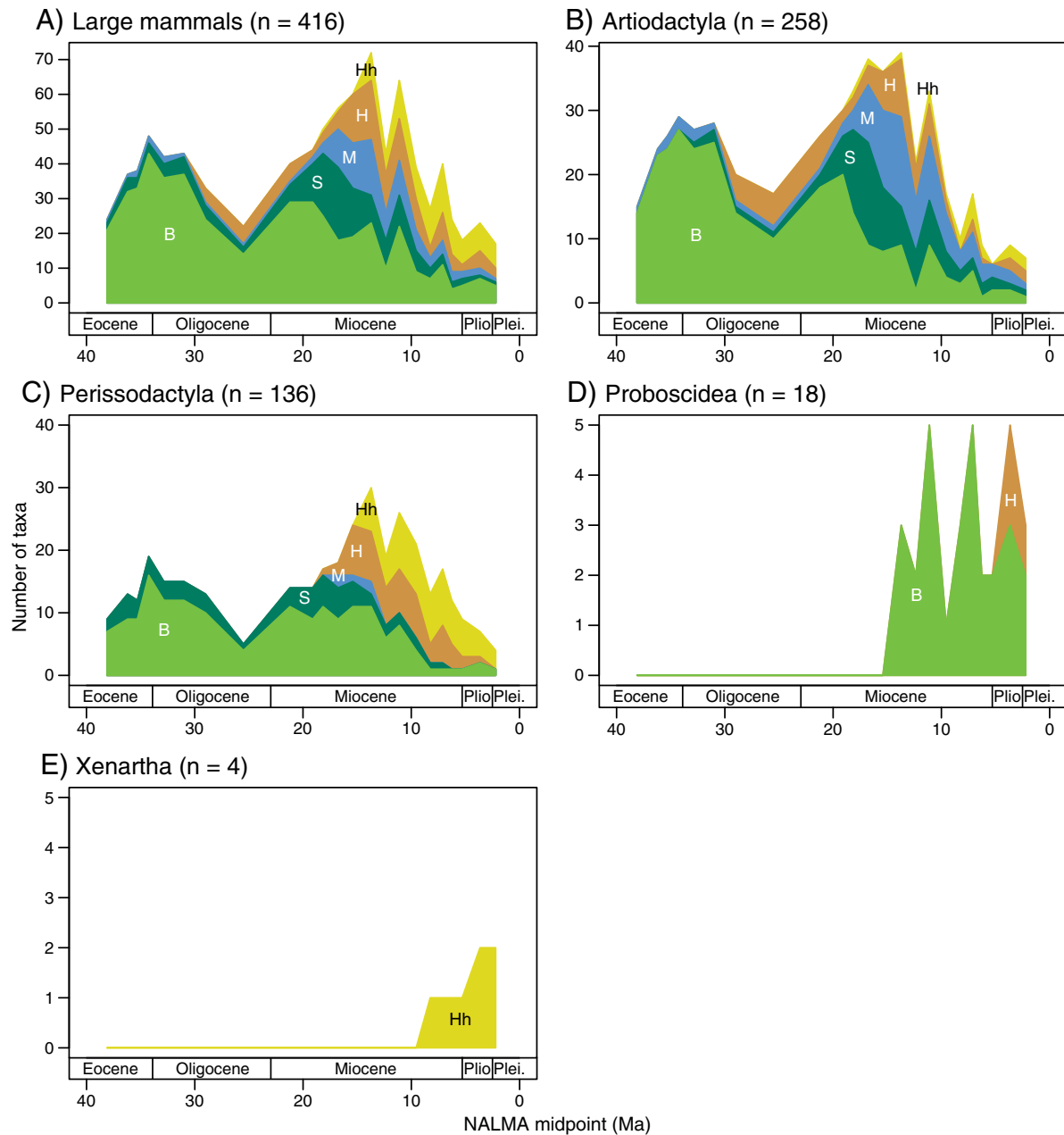


Fig. 4. Cumulative standing richness plots for Great Plains large mammals (ungulates and xenarthrans), showing contributions of tooth height categories (details as for Fig. 1).

The majority of lineages that acquired hypsodont dentitions, including the earliest appearances of high-crowned taxa in both Glires (Leporidae [included in Fig. 2E], Aplodontidae [Fig. 3A] and Geomyoidea [Fig. 3] and K) and ungulates (Camelidae [Fig. 5C]), did so *via in situ* evolution rather than immigration (see Janis et al., 1998, 2008, and relevant chapters therein). Rhino (Fig. 5O) diversity was sustained by a number of immigration events during the Miocene, and in the late Miocene the ground sloths (Fig. 4E) and arvicolid rodents (Fig. 3B) migrated into North America. Aside from these groups, however, the acquisition of hypsodonty in the Great Plains lineages was very much an endemic process, and so can be interpreted in the context of North American environmental change, rather than some other place of evolution and dispersal.

The observed pattern of hypsodonty acquisition is not consistent with a shift to a diet of grass as the main adaptive driver for dental morphological change in the Great Plains herbivores. A more likely

source of abrasive material is therefore grit and soil that are ingested during feeding (Janis, 1988; Damuth and Janis, 2011). Studies of Great Plains palaeosols indicate more open environments during the Oligocene (Retallack, 1997, 2004), and the evolution of camelid foot morphologies associated with a pacing gait, and therefore increased ranging locomotion, also occurred by the late Oligocene (Janis et al., 2002b). This evidence for Oligocene forest fragmentation implies a shift to feeding on lower level vegetation in increasingly open environments, and thus provides a plausible increase in the ingestion of soil and grit prior to the development of substantial grasslands in the early Miocene. The hypsodont ungulates of the Oligocene show no cranial adaptations associated with predominantly grazing behaviour, such as broader muzzles.

In both ungulates and Glires only certain taxa developed hypsodont or highly hypsodont molars; other taxa either remained brachydont throughout (e.g. mammutid proboscideans [Fig. 4D], tapiroids [Fig. 5P],

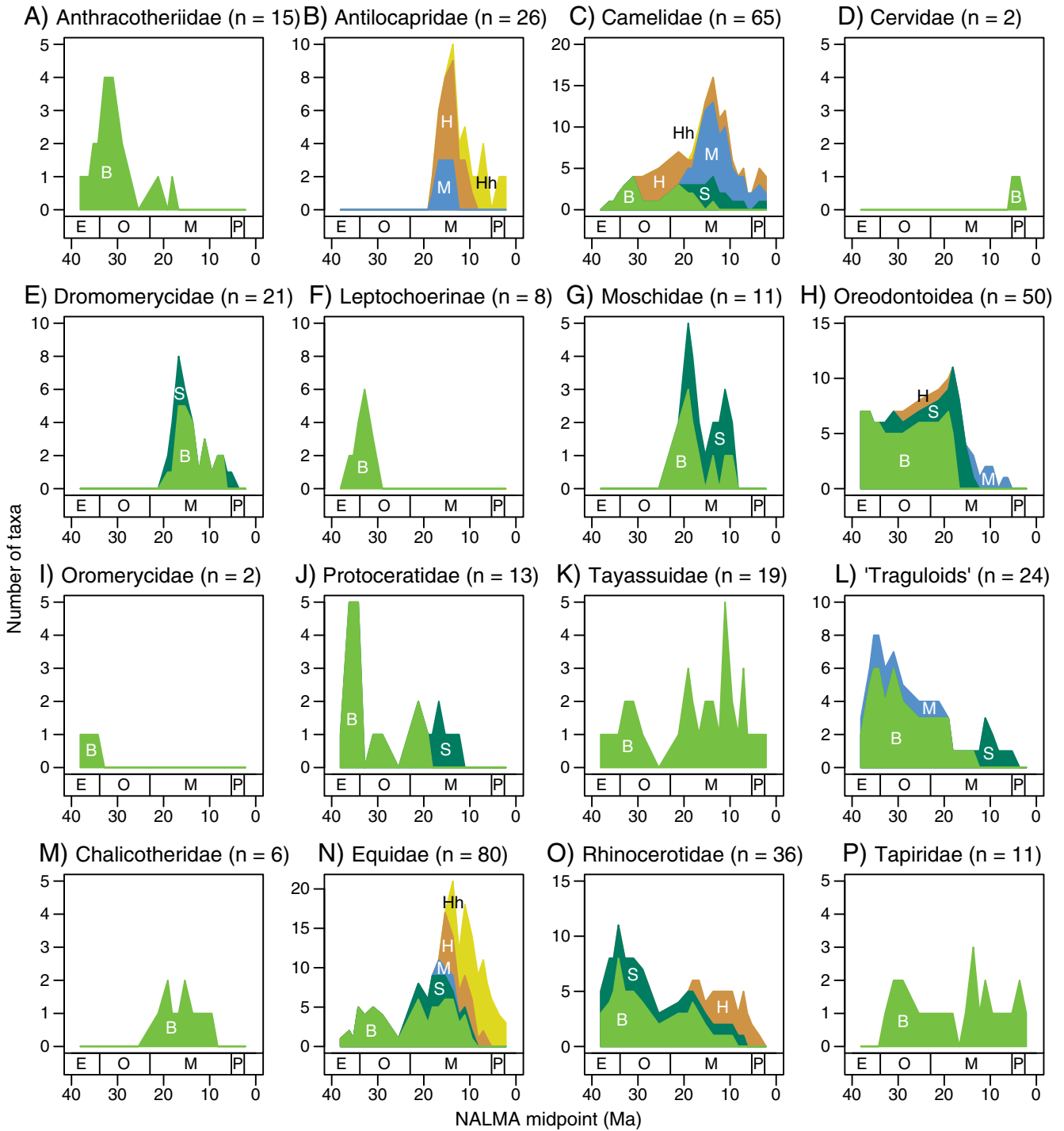


Fig. 5. Cumulative standing richness plots for Great Plains artiodactyl (upper three rows; graphs A–L) and perissodactyl (lower row; graphs M–P) families containing >2 taxa, showing contributions of tooth height categories (details as for Fig. 1). The superfamily Oreodontoidea (graph H) comprises the families Agriochoeridae and Merycoidodontidae; the informal grouping ‘Traguloids’ (graph L) incorporates the families Gelocidae (the genus *Pseudoceras*), Hypertragulidae and Leptomerycidae.

florentiamyid rodents [Fig. 3I]) or showed a transition from brachyodonty to mesodonty (e.g. traguloid ruminants [Fig. 5L], dromomerycids [Fig. 5E], merychyine oreodonts [Fig. 5H], eomyid rodents [Fig. 3G]). No obvious changes in tooth height distributions within families relate to grassland development, which suggests that the ‘delayed’ pattern observed in horses (see, e.g. Strömberg, 2006) is just part of a varied response of the small and large herbivore biota to environmental change, with different lineages (within and amongst families) evolving high-crowned teeth at different rates, and other taxa conserving their

low-crowned dentitions. Camels diversified at the same time as horses (Fig. 5C and N), but the cause(s) of these radiations between 15 and 10 Ma are not currently clear (Damuth and Janis, 2011).

If increased levels of ingested soil/grit preceded the wide distribution of grass as a food resource, and thus drove pre-grassland hypsodonty in some taxa (e.g. Camelidae [Fig. 5C], geomyoid rodents [Fig. 3K]), these may have been sufficiently high-crowned to take some grass without compromising their dentitions. Recent phytolith data has shown that despite a gradual increase in the area of open,

Table 2

Spearman's rank order correlation coefficients (r) for Mantel tests, using tooth height count data (upper panel) and proportion data (lower panel). Numbers in parentheses are p values, based on 9999 permutations of the distance matrices.

Count data	With singletons	Without singletons
Ungulates versus Glires	0.25 (0.0013)	0.48 (0.0001)
Ungulates versus non-fossorial rodents	0.28 (0.0006)	0.47 (0.0001)
Proportion data	With singletons	Without singletons
Ungulates versus Glires	0.61 (0.0001)	0.62 (0.0001)
Ungulates versus non-fossorial rodents	0.80 (0.0001)	0.72 (0.0001)

grass covered, habitats during the early and middle Miocene, the landscape remained spatially and temporally heterogeneous with considerable forest cover until the late Miocene, when fully open savannas developed (Strömberg, 2005; Strömberg and McInerney, 2011). It is therefore likely that even taxa taking some grass as part of their diet were at most mixed feeders during this interval (see also Muhlbachler et al., 2011). Grass silica may have played a role as a supplementary abrasive agent for these taxa (e.g. pronghorns [Fig. 5B] and horses [Fig. 5N]), in addition to the grit and soil that they would have consumed by feeding close to ground level. Note, however, that the extant pronghorn, *Antilocapra americana*, is highly hypsodont yet takes only around 12% of grass in its diet (see Damuth and Janis, 2011).

The trends seen in the fossorial rodents demonstrate the role of ingested grit and soil as a driver for higher-crowned dentitions. These fossorial forms acquired hypsodont molars ~5 Myr earlier than surface-dwelling rodents, and all but one of the fossorial rodents in the dataset have mesodont or higher-crowned molars. However it is interesting that hypselodont fossorial rodents do not occur until the latest Miocene, with the first appearance of the geomyine *Pliogeomys* (Figs. 2C and 3J). This is ~7 Myr later than the first hypselodont non-fossorial rodents, and suggests that a burrowing mode of life in itself does not incorporate a sufficient selective pressure to drive tooth height increases to this extent.

It might be expected that fossorial rodent richness should track the expansion of grasslands, as increased habitat becomes available in more open areas (Hopkins, 2005). This is not observed in the Great Plains rodents, however (see also Hopkins, 2007). The peak in fossorial rodent richness (Fig. 2C and D) does coincide closely with the first appearance of grasslands at ~22 Ma (Strömberg, 2004), and the increase that begins at 30 Ma may be related to a gradual opening of the forest environment prior to the inception of extensive grassland environments (Retallack, 1997, 2004; Strömberg, 2011). Open environments continued to expand throughout the Miocene, but fossorial rodent richness declined rapidly after 20 Ma, with the loss of the castorid and entoptychine geomyid burrowing taxa (Fig. 2D, and see also Hopkins, 2007; Calede et al., 2011). The richness of mylagaulid burrowers did increase at this time, and these comprised the entire burrowing rodent fauna until the Pliocene. The transition to a geomyine geomyid-dominated burrowing rodent fauna has been linked to late Miocene/Pliocene habitat change (Calede et al., 2011), and this may have underpinned the earlier transition and overall loss of richness at ~20 Ma.

Lagomorphs do not show similar patterns of hypsodonty acquisition to rodents. All known North American lagomorphs have fairly high-crowned teeth. Although some mesodont lagomorphs (Palaeolaginae) are known in the late Eocene and Oligocene, a transition to hypselodonty is seen within the palaeolaginae in the Oligocene, and all Neogene lagomorphs are hypsodont or hypselodont. A possible explanation for this morphology is that lagomorphs have always had the behaviour that they have today: that is, close-cropping of vegetation close to ground level. Thus, whether eating grass or not, they would always have been ingesting significant amounts of soil with their food.

Fossil ungulate assemblages have recently been employed as palaeoprecipitation indicators, with community hypsodonty levels being a key character for measuring aridity (more arid environments being more open and less forested) (Fortelius et al., 2002, 2006; Eronen et al., 2010b, 2010c, 2012). The similarity between hypsodonty acquisition patterns in Great Plains ungulates and rodents suggests that small mammal assemblages can also be used as a proxy for precipitation changes. Rodents have been used as palaeoclimate indicators in terms of the proportion of invertivorous and arboreal taxa in an assemblage (van Dam, 2006), but hypsodonty levels within Glires assemblages have not yet been used in this way. The current results demonstrate that this type of analysis would have to exclude tooth height data from fossorial rodents and from lagomorphs, as these clearly respond to different selective pressures than those that co-vary with aridity. As discussed above, the proportion of burrowing rodents within a Glires or rodent assemblage is not a good proxy for the openness of the environment (Hopkins, 2007).

We have shown that the timing and overall pattern of hypsodonty evolution was similar in Great Plains rodents and ungulates. Tooth height increases in either group do not coincide with the spread of grasslands as determined by phytolith evidence, and the similarity in timing between ungulates and Glires is more consistent with ingested soil and grit than grass silica as the dominant abrasive agent for driving hypsodonty evolution. Although informative, hypsodonty measurements can only capture so much information on feeding ecology and changes in the physical environment. Phylogenetic approaches (Marivaux et al., 2004; Muhlbachler and Solounias, 2006), tooth micro- and mesowear analysis (Fortelius and Solounias, 2000; Muhlbachler and Solounias, 2006; Semprebon and Rivals, 2007, 2010; Eronen et al., 2010a; Muhlbachler et al., 2011) and the inclusion of other craniodental and postcranial characters (Janis, 1997; Janis et al., 2002b; Mendoza et al., 2002; Schmidt-Kittler, 2002; Marivaux et al., 2004; Renaud et al., 2005; Bair, 2007; Evans et al., 2007; Lazzari et al., 2008) can provide a more complete understanding of the evolutionary dynamics of grassland mammal communities than measures of tooth height alone. Future research on drivers of mammalian herbivore evolution will need

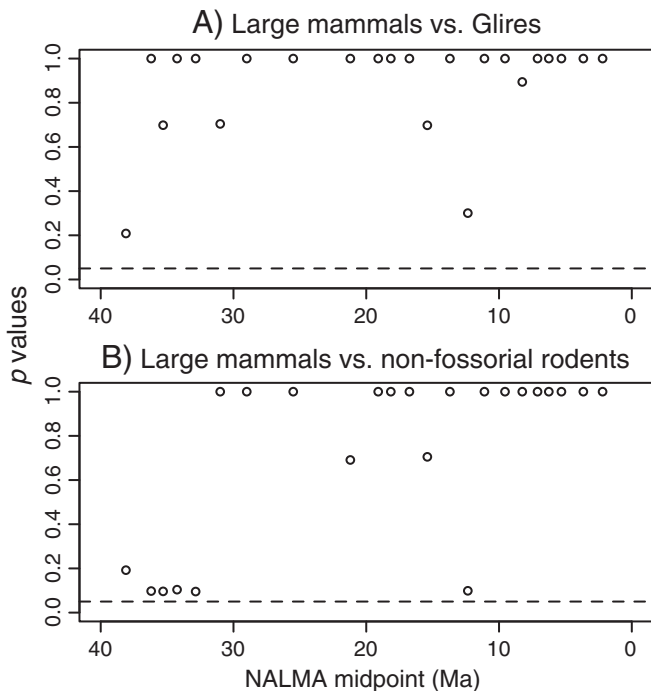


Fig. 6. p values for chi-squared tests of equality of taxon distributions across tooth height categories for each NALMA. A, large mammals versus Glires; B, large mammals versus non-fossorial rodents. The $p=0.05$ level is shown as a horizontal dashed line; none of the comparisons are significantly different.

to combine these approaches with the taxonomic and ecological breadth of the present study.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2012.09.001>.

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