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The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome

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Abstract

We have documented elsewhere, and briefly reviewed here, the anomalously high species richness of browsing ungulates (hoofed mammals) in the mid Miocene (~ 18–12 Ma) woodland savanna habitats of North America. In the mid Miocene these habitats supported substantially more brachydont (browsing) species than do any present-day savanna habitats. We present some preliminary data to show that such species-rich browser communities are not observed after the mid Miocene. The data also suggest that these mid Miocene browser communities and their subsequent disappearance may have been a global phenomenon. We then focus on possible explanations for these observations. We discuss the possibility that the high species numbers are a preservational artifact, and conclude that taphonomic factors are unlikely to be responsible for the level of species richness observed. We then consider various possible explanations for high species richness, including the unique aspects of climatic change (cooling, drying, increased seasonality), unique biotic interactions (the effects of competition, keystone herbivores, changes in predator pressure), and consider that none of these are fully consistent with the available data. The most likely explanation for the observed species-rich browser palaeocommunities is an elevated level of primary productivity, relative to the present day, within (at least some) mid Miocene grassland habitats. Such an increase in productivity could possibly have been the result of higher-than-present levels of atmospheric carbon dioxide in the mid Miocene, but this conflicts with current interpretations of geochemical evidence, and a satisfactory mechanism for the inferred increased primary productivity is an unresolved issue.

Keywords: Grasslands; Herbivorous taxa; Mammalia; Miocene; Productivity; Communities

1. Introduction

The story of the evolution of the North American grassland habitats in the late Cenozoic is a familiar one, often told in association with the story of the evolution of horses or other grazing mammals (e.g., Matthew, 1912; Stirton, 1947; Shotwell, 1961; Webb, 1977, 1983; Stebbins, 1981; MacFadden and Cerling, 1994; Webb et al., 1995). There is a well-documented change during the later half of the Miocene (~ 15–5 Ma), as illustrated by both the flora and the

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fauna, from an ecosystem dominated by woodlands and apparently browsing mammals to one dominated by savanna grasslands (i.e., treed grasslands/bushlands) and apparently grazing mammals. Note that similar ecosystem shifts occurred in all continents during the Cenozoic, but at different times on different continents (see Fig. 1).

Based on the environmental correlates of present-day vegetation types, the principle cause for this evolutionary change wherever and whenever it occurred has been presumed to be related to increased cooling and, especially, drying. For higher latitudes in the Miocene, the cooling is documented from palaeotemperature curves obtained from deep sea foraminifera (e.g., Miller et al., 1987). In contrast, for North America the drying is largely inferred from the apparent floral and faunal changes themselves (Leopold and Denton, 1987; Webb and Opdyke, 1995; Retallack, 2001a; also see Fox and Koch, 2004).

The end of the Miocene (8–6 Ma) in North America is also associated with a change of the isotopic composition of the palaeosols and of the dental enamel of grazing mammals. This is interpreted as reflecting a switch in grass photosynthesis from the C_3 photosynthetic pathway to the C_4 pathway, or an increase in the frequency of C_4 grasses (MacFadden and Cerling, 1994; Cerling et al., 1998; Fox and Koch, 2004; Smith and White, 2004). This isotopic shift is coincident with the initial appearance of the tall sod grassland in North America (Retallack, 1997, 2001a), and it has been thought that the floral changes at this time heralded the first appearance of extensive, open grasslands in North America (e.g., Axelrod, 1985). However, the presence of apparent grazing herbivores in older faunas provides evidence for the existence of a savanna grassland type of ecosystem since at least 10 Ma (i.e., the "Clarendonian chronofauna" of Webb, 1983; see also MacFadden, 2000). At least short sod grassland appears to have been in existence in North America by the late early Miocene, around 18 Ma (Retallack, 1997, 2001a) and Strömberg (this volume) proposes that grassland habitats were evident in North America even earlier in the Miocene (~ 19.2 Ma).

Thus, there is ample evidence for a habitat shift during the Miocene that explains why browsing

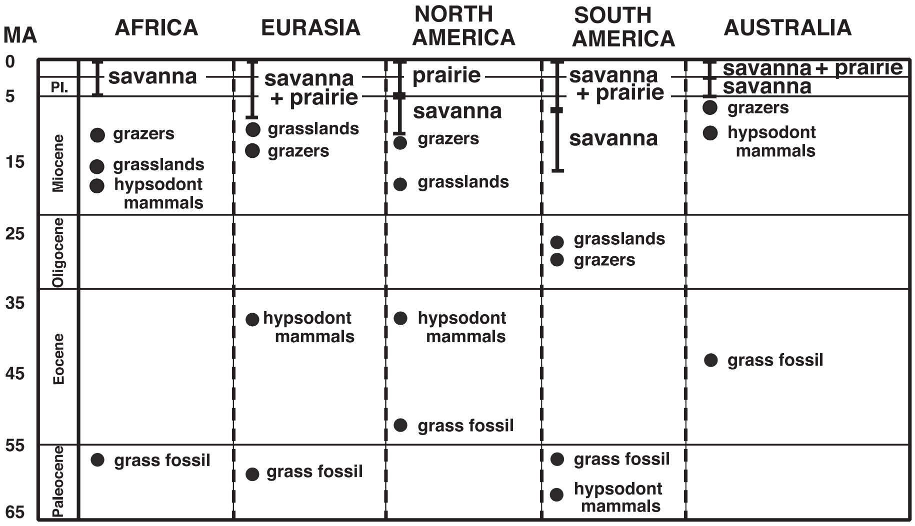

Fig. 1. Timing of grassland evolution. Bars indicate times of widespread grasslands: prairie (also equivalent to steppe) = treeless grasslands; "savanna" = treed grasslands (inc. woodland savanna and bushland). "GH" = grassy habitats (= habitats containing some grass, most likely woodland savanna of some sort, but not widespread in local extent). "Grazers" indicate mammals with craniodental adaptations indicative of a diet of at least 90% grass, equivalent to such extant ungulates as zebras or bison. Adapted from data in Jacobs et al. (1999) with addition from Strömberg (2004).

species declined during the latter part of the epoch. Starting at around 17 Ma, and continuing over at least 13 My, grass-containing habitats in the Great Plains changed from types that today produce relatively abundant resources for browsers (woodland savannas) to ones that produce relatively few (open grasslands), and the numbers of browser species have declined accordingly. However, until recently this decline in browsing species has not been examined in detail. There seems to have been the tacit assumption that, as the numbers of browsers declined with changing habitats, the numbers of grazers rose to fill the "vacated niches" (which were now suitable for grazers rather than for browsers). Fig. 2A shows this assumption in a schematic form, where the average total species richness within communities remains constant. However, our previous work (Janis et al., 2000, 2002) shows a different pattern: that is, that there is an initial increase of grazers (or at least of species taking a significant proportion of grass in the diet) at a time when the numbers of browsing species in communities were also high—in fact, higher than the number of browsing ungulates found today even in lowland tropical rainforests. Subsequent decline in total species richness in communities of the Great Plains mainly reflects a decrease in the numbers of the browsing species (with a decline in the number of grazers occurring only towards the end of the Miocene). This is shown in schematic form in Fig. 2B, and the original data are shown in Figs. 3 and 4. Note that Fig. 4 shows this pattern at the level of the species composition of individual Great Plains ecological communities, but a similar pattern can also be seen in continent-wide numbers of genera (Janis et al., 2000).

Our particular interest is in the faunas of the mid Miocene, which we define for the purposes of this paper as the period from 18 Ma (late early Miocene) to 12 Ma (late middle Miocene). This time period more-or-less encompasses the North American land-mammal ages of late Hemingfordian, early Barstovian and early late Barstovian. We have shown elsewhere (Janis et al., 2000, 2002) that the mid Miocene habitats of the Great Plains, at a time when food resources for browsers were presumably at a high level, supported numbers of browsing ungulates (hoofed mammal) species far in excess of those supported in *any* present-day habitat, no matter how productive of browse (see Fig. 4 and Appendix A). Also, overall species numbers are sometimes unusually high in these mid Miocene faunas because of the additional presence of non-browsing herbivores.

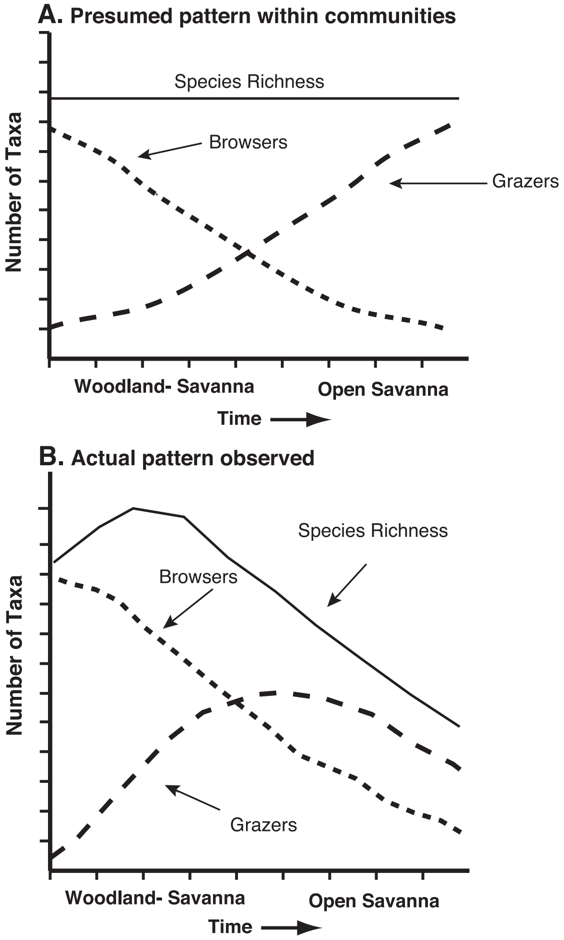

Fig. 2. A schematic representation of changes in species richness of ungulate species of different feeding types during the Miocene of North America. (A) Presumed species richness pattern. Ungulate species richness is comparable to that observed in present-day habitats and remains more or less constant within communities as grazers gradually replace browsers. (B) Actual species richness pattern. Browsing species are initially superabundant in communities, with nonbrowsing species rare or absent. Grazing species appear and begin to diversify in communities while those communities still maintain a superabundance of browsing species. Browser species numbers then drop sharply and steadily towards modern levels, while grazer species numbers peak in the late Miocene and then decline as well. Compare with Fig. 4.

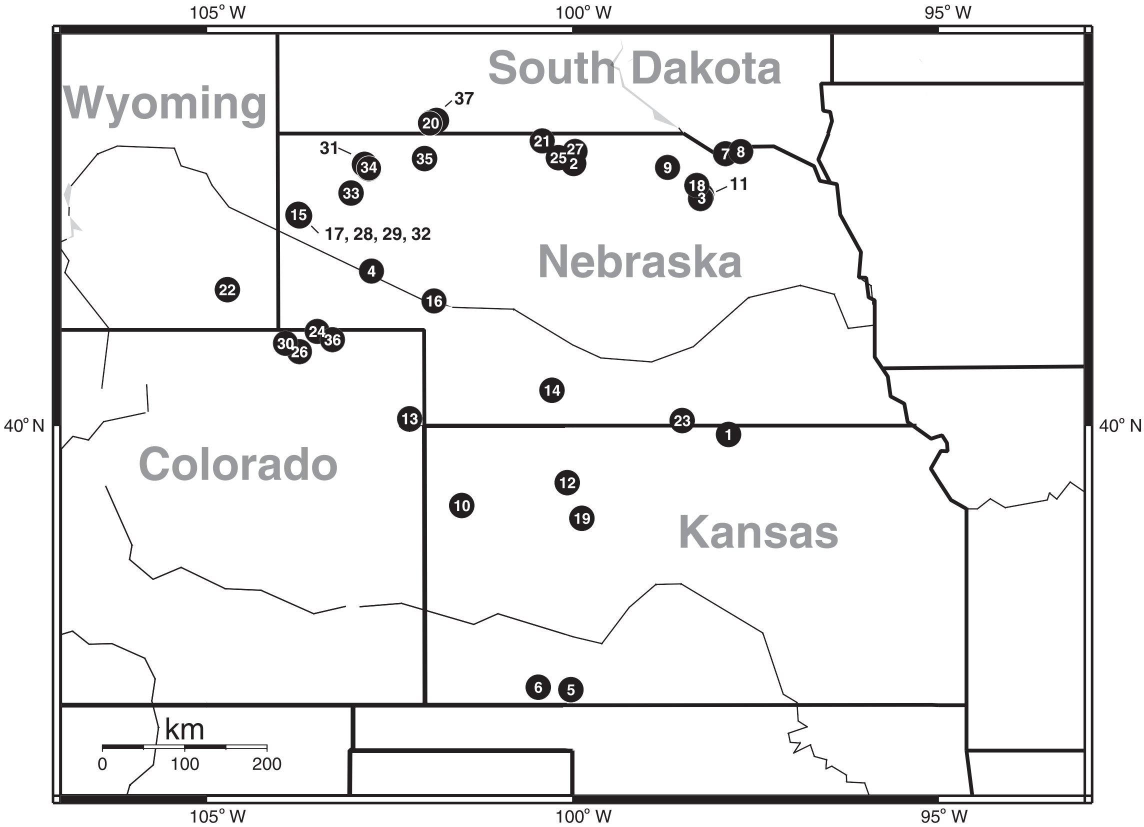

Fig. 3. Geographic distribution of the 37 Great Plains palaeofaunas used in this study. Numbers refer to the faunas as listed in Appendix A.

Here we will focus on two main issues in our discussion of these palaeofaunas. The first issue relates to the validity of the palaeocommunities. That is, did these apparently anomalous mid Miocene ungulate communities in North America in fact contain the elevated species richness that we observe—and if so, is this evidence of something unusual in the mid Miocene? The second issue relates to the possible explanation for the existence of such palaeocommunities.

With respect to the first issue, it could be the case that, rather than representing actual species richness, of the Miocene palaeocommunities, the species numbers observed in these faunas merely represent a taphonomic or interpretational artifact. A secondary consideration concerns the apparently unique nature of the communities. If these palaeofaunas actually do capture real past ecological species richness, these conditions might actually be the norm for tropical woodland savannas in the Cenozoic, and it might only be present-day communities that are unusually depauperate (perhaps due to recent extinction events).

With respect to the second issue: if these browser-rich communities are both real and characteristic of the mid Miocene only, what could explain their occurrence at that time, and the reason for their absence from any later forest, woodland or grassland ecosystem?

2. Background: mid Miocene browsing ungulate communities

In this paper, we consider the community structure of only the large ungulates. Although significant and, to some extent, different kinds of ecological information may be reflected in data from the smaller mam-

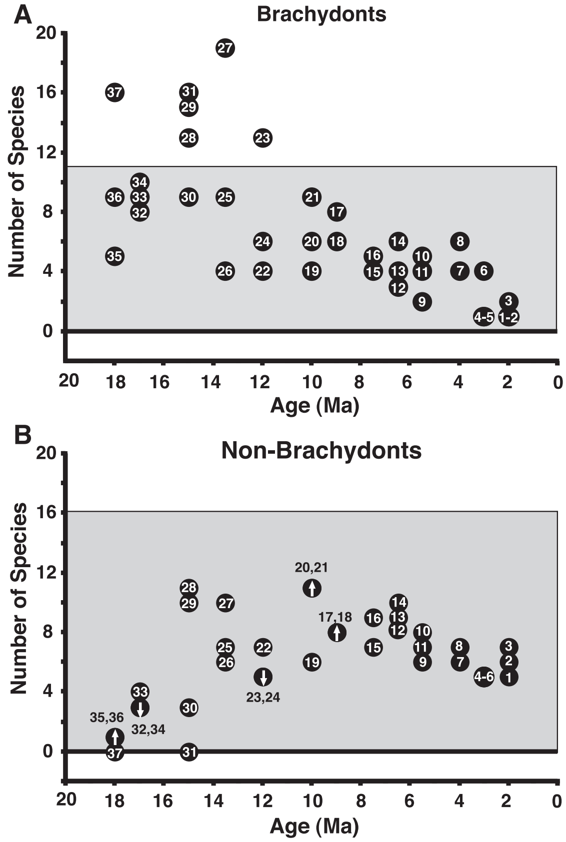

Fig. 4. Species richness of ungulates in Great Plains palaeofaunas, according tooth crown height. Numbers refer to the faunas as listed in Appendix A and as depicted in Fig. 3. Grey rectangle in each graph encompasses the range of values observed over all habitats in the present day (see Fig. 7). (A) Brachydont species (hypsodonty index < 2.5). (B) Non-brachydont (i.e., mesodont and hypsodont) species (hypsodonty index ≥ 2.5).

mals (e.g., Badgley et al., 2001), these taxa are beyond the scope of our current investigations. However, large mammalian herbivores can be expected to reveal much about past environmental conditions (e.g., Andrews and O'Brien, 2000). Climate and other environmental factors affect both the type of vegetation and its level of productivity, and the characteristics of the plants then affect the composition of the community of mammals feeding on them.

2.1. Dietary interpretations

The single osteological feature of fossil mammals that has been used most commonly to interpret dietary habits is the height of the crown of the cheek teeth (i.e., molars and premolars), also known as the level of hypsodonty (Stirton, 1947; Van Valen, 1960; Janis, 1988). Mammals with high-crowned cheek teeth are termed *hypsodont*, and those with low-crowned cheek teeth (the plesiomorphic condition) are termed *brachydont*. Greater hypsodonty is an evolutionary adaptation that serves to increase the functional lifetime of a tooth in the face of high rates of dental wear (Janis and Fortelius, 1988). Thus, differences in hypsodonty should reflect dietary differences to the extent that these entail processing of plant material with different physical characteristics.

Large mammalian herbivores employ one of three major dietary strategies—*browsing*, *grazing*, or a combination of browsing and grazing usually called *mixed feeding* (Hofmann and Stewart, 1972). Browsers have a diet 90% or more of which consists of leaves of dicotyledonous plants (shrubs, tree leaves, etc.). Note that while some browsers do include some grass in their diet, this is usually a seasonal dietary component of young spring growth that is not highly fibrous, and so does not result in abrasive tooth wear. Grazers have a diet 90% or more of which consists of grass. Mixed feeders exhibit intermediate combinations of dicot leaves and grass.

Among extant ungulates, tooth crown height depends both upon diet (with mixed feeders and grazers always being, on average, more hypsodont than browsers) and upon the openness of the habitat (with hypsodonty of all dietary groups being greater in more open, less forested habitats; Janis, 1988; Janis et al., 2002). Almost all brachydont ungulates are browsers, since species with low tooth crowns are not able to endure the high wear rates associated with feeding on large amounts of mature grass, and do not live in the most open grasslands. (In particular, brachydont species cannot be the kind of specialized grazer such as those that appeared in the late Miocene.) Thus we can be fairly certain that virtually all brachydont fossil species, here defined as species whose *hypsodonty index* (Janis, 1988) ≤ 2.5, were browsers or, perhaps, in the Miocene and later, mixed feeders whose diet was nevertheless predominantly browse. Note that it is essential to calculate the hypsodonty index from unworn teeth.

This index is derived from crown height divided by the tooth width at the occlusal surface: in more worn teeth, not only is the crown height reduced, but the occlusal width is now greater, and so the hypsodonty index will be lowered by both factors. (Compare the hypsodonty indices for extant camelids *Camelus dromedarius* [2.53], *Lama guanacoe* [3.46], and *Vicugna vicugna* [4.33] reported by Janis, 1988, based on unworn third molars, with those obtained by Feranec [2003] for the same species [1.48, 1.30, and 1.60, respectively].)

Here we refer to all of these brachydont species as "browsers" (in contrast to all of the more hypsodont ungulates which include almost entirely mixed feeders and grazers) to emphasize their very probable ecological roles rather than simply their tooth morphology. However, the patterns of faunal change and comparisons with extant faunas that we describe do not depend upon dietary reconstructions of any particular fossil species, since the patterns are just as striking when looking at crown height directly (compare Figs. 6 and 7).

When hypsodonty is combined with other morphological variables or observations of tooth wear, highly reliable reconstructions of ungulate diets are possible (Janis, 1995; Fortelius and Solounias, 2000; Solounias and Semprebon, 2002). However, adequate data for such analyses are available for only some fossil species, and a detailed dietary reconstruction for each species analyzed is in any case beyond the scope of this paper.

2.2. Modern ungulate communities and environmental conditions

Fig. 5 shows how the distribution of present-day major vegetational types relates to both annual temperature and rainfall (adapted from Holdridge, 1947, 1967). It is worth noting that grassland biomes, in the broadest sense, actually occupy a fairly narrow range of temperature and rainfall parameters. Grasslands (including both treeless grasslands, or prairie, and treed grasslands, or savanna) occur today in areas where the availability of soil water is too low to maintain forest, but is sufficient to maintain grassland (versus desert in areas of even lower rainfall) (Milchunas et al., 1988). Grassland areas have a mean annual precipitation (MAP) of between 250 and 1000 mm, and can be divided into subarid grasslands (MAP < 500 mm) and subhumid grasslands (MAP>500 mm), which have somewhat different characteristics and respond differently to ungulate grazing pressure (Milchunas et al., 1988).

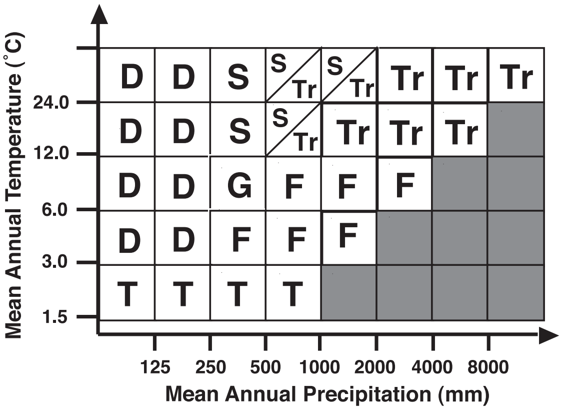

Fig. 5. Schematic relationship of present-day major vegetational types in relation to temperature and precipitation (modified from Holdridge, 1947, 1967). Although recently more sophisticated vegetation models and classifications have been developed, the broad patterns are sufficiently well represented for the purposes of this paper by practical and widely known schemes such as that of Holdridge (Prentice, 1990; Yates et al., 2000). Key: D = desert (including arid scrub); F = temperate forest; G = temperate treeless grassland (steppe, prairie); S = tropical savanna; T = tundra; Tr = tropical forest. Grey rectangles indicate combinations that currently do not exist on earth.

There is a strong correlation between MAP and annual primary productivity in arid and grassland biomes, up to approximately 700–800 mm MAP (Rosenzweig, 1968; Coe et al., 1976). MAP in turn correlates well with ungulate biomass over the same range (Coe et al., 1976; Fritz and Duncan, 1994) and with mammalian species richness (Greenacre and Vrba, 1984; Andrews and O'Brien, 2000; Badgley and Fox, 2000; see also Badgley et al., 2001; van Dam et al., 2001). However, beyond a MAP of around 1000–1500 mm conditions will be too wet for the maintenance of grassland, and the ecosystem will revert to forest. This will result in a reduced ungulate biomass, as grazers cannot survive in the absence of grasses, and a forest environment does not support the densities of ungulates seen in grassland habitats (e.g., Cumming, 1982).

Figs. 6 and 7 show the numbers of ungulate species for present-day African habitats plotted against MAP.

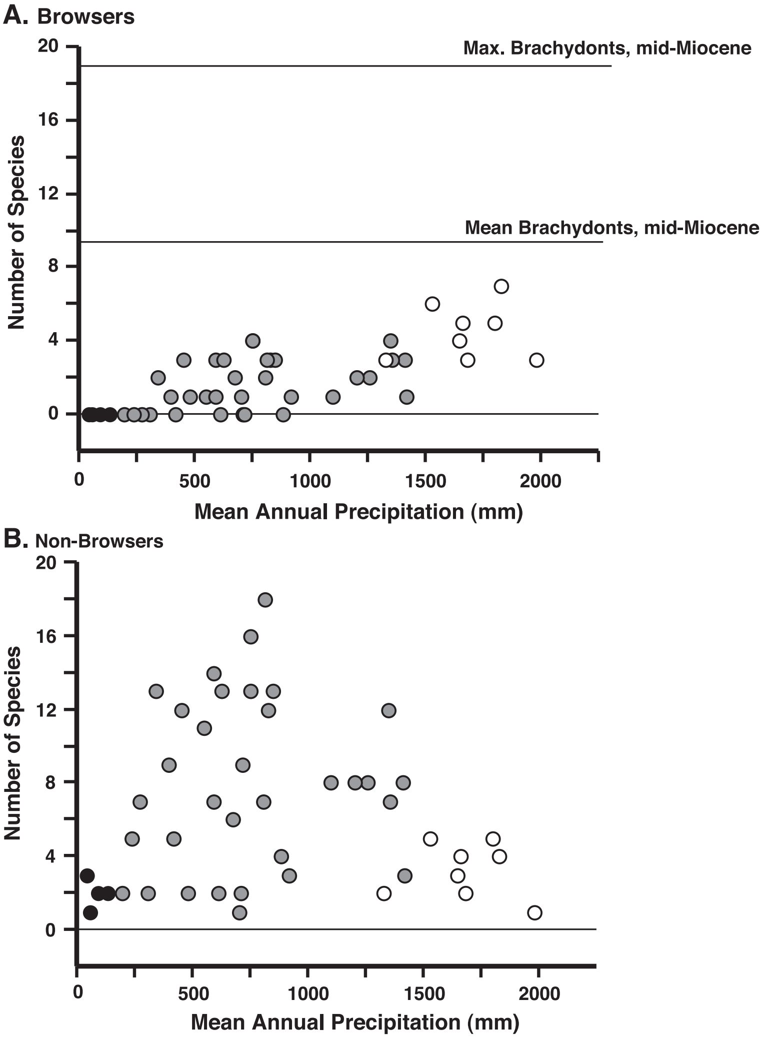

Fig. 6. Numbers of browsing and nonbrowsing ungulate species in 45 extant African localities. Each circle represents a single locality. (A) Browsing species. (B) Grazer/mixed-feeding species. Black circles = desert habitats; grey circles = savanna habitats; white circles = tropical forest habitats. Data come from the data set compiled by the National Center for Ecological Analysis and Synthesis (NCEAS) workshop on Mammalian Communities, which was organized by John Damuth, and in which the other authors were participants (see Dam et al., 2001; Damuth et al., 2002).

Fig. 6 divides these species by dietary type (browser versus nonbrowser), while Fig. 7 divides them by tooth crown height (brachydont versus non-brachydont). Although we have argued that these two categories are broadly equivalent, and indeed the two figures are very similar to each other, slight differences exist. Other areas of the world are currently low in numbers of ungulate species in comparison to their pre-Holocene values, so Africa gives the best picture of the range of values and the maxima observed. For simplicity, we have distinguished desert (all deserts and desert scrub), savanna (all tropical woodland, bushland, grassland habitats), and tropical forest. Several interesting patterns emerge from this analysis.

Firstly, the greatest species richness of ungulates is to be found in semi-humid savannas, with a precipitation of between 500 and 1000 mm/year. In

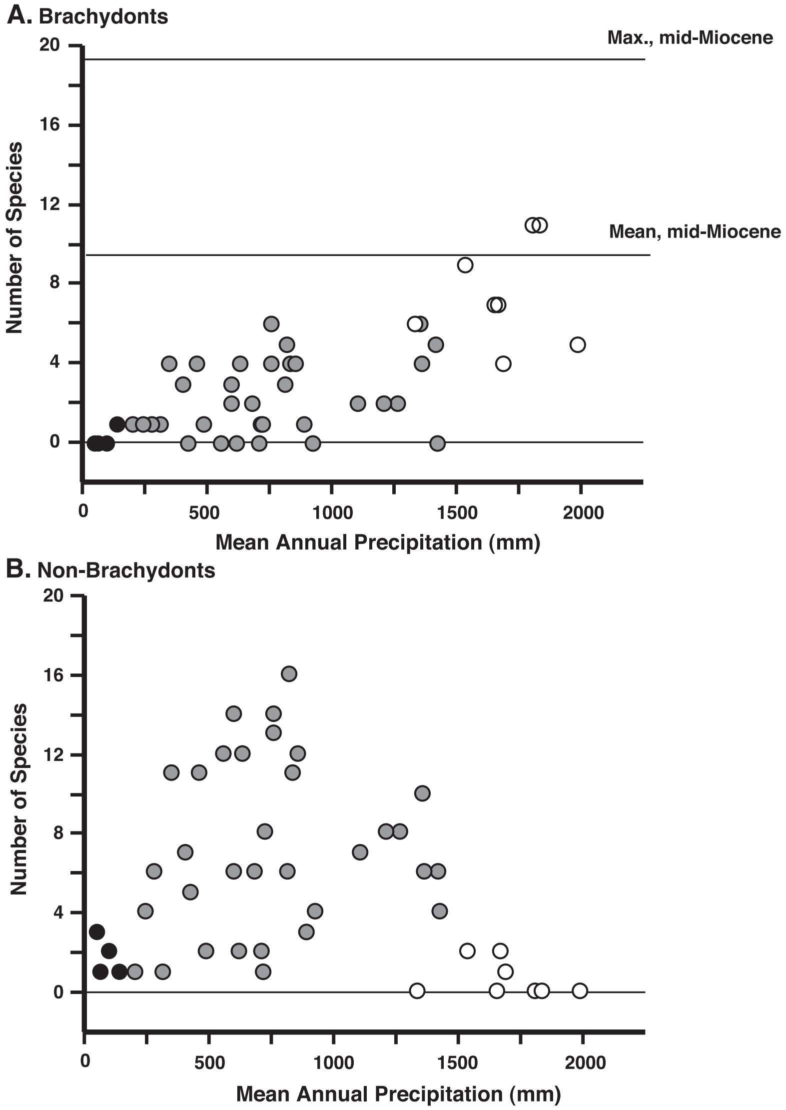

Fig. 7. Numbers of species of brachydont and non-brachydont species in 45 African localities. (A) Brachydont species (hypsodonty index of <2.5). The mean and maximum numbers of brachydonts observed in the mid Miocene localities reported in Janis et al. (2000) are indicated by horizontal lines. (B) Non-brachydont species. Data source, localities, and symbols are the same as for Fig. 6.

these environments, the number of grazer/mixed feeders range between 1 and 18 species, and the number of browsers range between 0 and 4 species. Patterns contrasting non-brachydonts and brachydonts are similar (maxima of 16 and 6 species, respectively). Note that there are few or no browsers/brachydonts in desert habitats and semiarid savannas (MAP < 500 mm), and the numbers of grazer/mixed feeders are lower in arid regions than in the subhumid grasslands.

In environments that receive between 1000 and 1500 mm of rainfall per year, the vegetation may be either savanna or tropical forest, depending on other factors including seasonality of temperature and rainfall and soil characteristics. In savanna habitats in this moisture range the numbers of grazer/mixed-feeders (and of non-brachydonts) in localities are generally lower than in the moisture range of 500–1000 mm/year, whereas the numbers of browsers (and of brachydonts) remain similar, and browsers (or brachydonts) are always present. In the tropical forests in this moisture range, the numbers of browsers (or brachydonts) equal or outnumber the grazer/mixed-feeders (or non-brachydonts). In environments where mean annual temperatures are high and the rainfall is greater than 1500 mm/year the type of vegetation is tropical forest, and there are always more browsing (or brachydont) species present (three to six) than grazer/mixed-feeders (or non-brachydont) species (one to five). Note that in these wet forest environments the species richness of browsers (or brachydonts) does not seem to continue to increase with increasing levels of rainfall. This might reflect the fact that as tropical forests experience progressively higher levels of MAP there is a tendency towards increase in canopy height, with a corresponding decrease in understorey vegetation and, in general, a decrease in resources available to terrestrial browsing mammals. Thus even browser species numbers might be expected to decline as rainfall increases beyond levels where closed forest has become the typical vegetation type.

The average number of brachydont (i.e., presumed browsers) species (9.5) in mid Miocene localities of the Great Plains (Janis et al., 2000, 2002) exceeds the number of browser/brachydont species found in any present-day African savanna habitat. This number is exceeded today only by the number of browser/brachydonts in African tropical rainforests (11). The maximum number of brachydonts (19) in the mid Miocene localities far exceeded numbers known anywhere today.

These results suggest that these brachydont/browser-dominated faunas were living in habitats of higher primary productivity than the ones that support diverse browsing ungulate faunas today. Even if factors other than high productivity contributed to the increased species richness, the habitats still must have been highly productive of browse, as even the rarest species must have a large enough population to survive.

These observations cannot be used to propose that the Great Plains were covered by a vegetation type more productive than savanna (such as rainforest); we know from palaeobotanical data that this was not the vegetation type present (see below). Moreover, most of the mid Miocene faunas themselves contain some non-brachydont species whose diet likely included a component of grass. Furthermore, these species are often among the most abundant in their fauna. For example, taking relative abundances at face value, in the two Olcott Formation localities (15 Ma; Appendix A) energy flow through the ungulate community is dominated by two to four species, as one finds in African ungulate communities today (Cumming, 1982). One of these dominant species in each locality is the non-brachydont *Merychippus isonesus*, most probably a mixed feeder (Solounias and Semprebon, 2002). Thus, even in these mid Miocene browser-rich communities a significant proportion of the plant resources consumed by the ungulate fauna overall was probably grass. Thus the faunal composition suggests strongly that these were indeed woodland savannas, and the high species richness suggests that these savannas were more productive than any comparable woodland savannas of the present (Janis et al., 2000, 2002).

It is important to note that these fossil faunas are anomalous in comparison with modern ones on two accounts. Firstly, as stressed above, the numbers and proportions of brachydont taxa (presumed browsers) substantially exceed those in modern habitat analogs. Secondly, these additional brachydonts often occur in faunas that support an equal or greater total number of ungulate species (including species of all tooth crown heights) than seen in modern habitat analogs (compare Figs. 4 and 7). These observations are independent of what one considers to have been the diets of fossil brachydonts. Thus the reliability of the hypsodonty index to determine the diet of any particular species is irrelevant to our argument that these faunas suggest unusually high levels of primary productivity, and that this productivity supported unusually high numbers of brachydont species (contra the views presented in Feranec, 2003, p. 238).

2.3. Environmental context of the Great Plains faunas

There has long been general agreement that the mid Miocene (18–12 Ma) localities of the Great Plains represent some sort of woodland savanna habitats, on both faunal (MacFadden, 2000) and floral (Axelrod, 1985; Leopold and Denton, 1987; Jacobs et al., 1999) grounds. Based on phytolith data, Strömberg (2002, 2004) suggested woodland savanna habitats were present since at least the early Miocene (~ 19.2 Ma). Based upon soil and floral evidence average MAP in mid Miocene localities of the Great Plains was somewhere in the range of 500–1000 mm (Axelrod, 1985; Leopold and Denton, 1987; Retallack, 1997). Mean annual temperatures would have been as much as 10° warmer in these latitudes in the mid Miocene than today (Miller et al., 1987). These conditions would correspond to a climate that today would support tropical woodland savanna vegetation, but would be too dry for tropical forest.

2.4. Patterns of occurrence and faunal change in the Great Plains

The faunal changes during the Miocene, from a fauna dominated by brachydont ungulates (here interpreted as browsers) to one dominated by hypsodont ones (interpreted as mixed feeders or grazers), has usually been considered as a simple replacement, with the hypsodont taxa being better-adapted for the grassland habitats (e.g., Shotwell, 1961). However, we have shown (Janis et al., 2000, 2002) that at both the continental-wide generic level, and the locality-specific species level, the decline of the brachydont ungulates was not tightly coupled with the rise of the hypsodont ones. Rather, a diversity of hypsodont ungulates appears rather early (by 15 Ma), with hypsodont species initially coexisting with brachydont ones rather than replacing them. This addition without replacement resulted in faunas that appear to be "over-rich" in the numbers of taxa at both regional and local levels (see Figs. 2 and 4). Subsequent extinctions among the brachydont ungulates, most notably at 11, 8.5, and 4.5 Ma, are not correlated with origination events among the more hypsodont taxa, although the hypsodont ungulates also show major extinctions at 4.5 Ma. The pattern of mid–late Miocene ungulate faunal taxonomic diversity is of overall decreasing numbers of genera from a high point at around 16 Ma, resulting almost entirely from extinctions among the brachydont taxa.

More importantly, some mid Miocene faunas of North America exhibit large numbers of brachydonts, with as many as 19 (and a mean of 9.5) coexisting species (Janis et al., 2000, 2002). These numbers of brachydonts are in excess of the numbers of browsers or brachydonts seen in comparable present-day habitats (see the previous section). However, by late Miocene times (approximately 10 Ma), the number of browser species had decreased to numbers similar to those seen in today's savanna habitats. Non-brachydont ungulates, in contrast, gradually increase in numbers throughout the Miocene and, though they dominate the ungulate faunas of most late Miocene and later woodland and more open habitats, they never exceed the numbers of species seen in comparable habitats today, anywhere in the world.

2.5. Anomalous combinations of hypsodonty, species richness and rainfall

Work in progress has developed a metric of "per-species mean hypsodonty" (PMH) to investigate rainfall in palaeocommunities (Damuth et al., 2002). The PMH of a community is obtained by dividing the average hypsodonty of the ungulate fauna by the numbers of all mammalian species present (over 1 kg in body mass). Logarithmic regression of rainfall on PMH can account for over 60% of the variance in precipitation in present-day communities ($p < 0.0001$). This relatively tight correlation allows the amount of rainfall to be predicted from fossil mammal communities, provided that combinations of hypsodonty values and species richness in the fossil communities are within the range of variation seen in present-day communities (Damuth et al., 2002).

Fig. 8 contrasts the predicted rainfall in the late Cenozoic of the Great Plains as estimated from the PMH values of the mammal faunas with rainfall estimates derived from soils (Retallack, 1997) and palaeofloras (Leopold and Denton, 1987) from the same region. As discussed above, the soil and floral data indicate MAPs consistent with some sort of savanna environment throughout the Miocene, suggesting values between 250 and 750 mm/year over most of the period, with plant macrofossils suggesting as much as 1000 mm before 15 Ma (see Fig. 5).

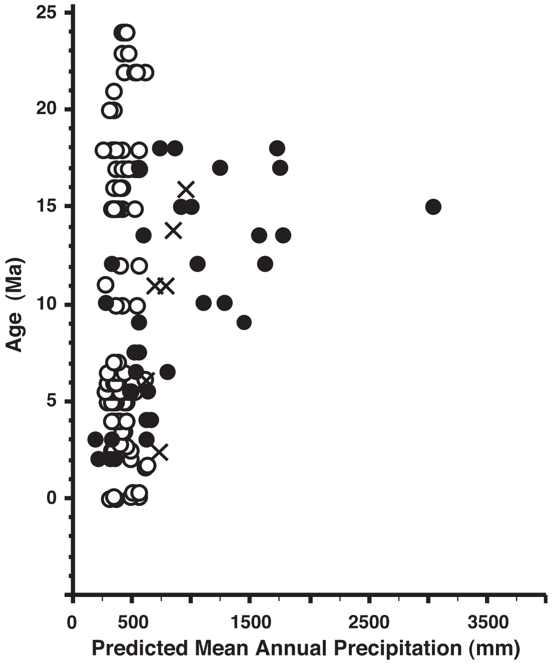

Fig. 8. Estimates of the mean annual precipitation of the Great Plains of North America throughout the late Cenozoic by three different methods: open circles = soils (from Retallack, 1997); crosses = palaeofloras (from Leopold and Denton, 1987); filled circles = ungulate faunas (from PMH values, see text).

Rainfall estimates based on faunal PMH are in agreement with those for other methods for localities younger than approximately 9 Ma. In contrast, the results from the faunas give highly anomalous results in localities older than 9 Ma. Many MAP predictions based on mammal faunas in this time period exceed 1500 mm, which today is always associated with a tropical forest environment—in some cases, the mid Miocene predicted values suggest wet rainforest. Obviously, in the light of all other existing evidence, the amount of rainfall during the mid Miocene could not have been as high as these PMH values predict. The reason for this anomalous result is that nowhere in the present-day are such low levels of hypsodonty associated with such high species numbers as are found in the mid Miocene faunas. The exceptionally high number of brachydont species (and overall ungulate species richness) is off-scale and causes the PMH regression—which is based solely on patterns among extant species—to predict unrealistically high values for the mid Miocene.

3. Are high mid Miocene browser numbers truly real and/or unusual?

We next consider whether there are factors that might lead us to misinterpret mid Miocene brachydont species richness itself or its ecological significance.

3.1. Are these mid Miocene communities a taphonomic artifact?

Because fossil assemblages form over time, it is possible that they record in a single locality species that were never contemporaneous inhabitants of that location. Such time-averaging could potentially inflate the numbers of browsing species, although it is unlikely that degrees of time averaging would be uniquely high in mid Miocene localities. In any case, the length of fossil accumulation time that our North American localities could have averaged is no more than approximately 1.3 my (based on the average time between faunas in our sample; Janis et al., 2000); however, typical values of time-averaging thought to characterize fluvial systems are orders of magnitude less (Behrensmeyer, 1982, 1992; Behrensmeyer and Chapman, 1993). We believe that it would be difficult for time-averaging alone to have artificially increased the representation of browsing species from numbers similar to those of present day to the levels that we observe in our fossil samples. Although we cannot test this directly, some insight to the likely magnitude of severe time averaging can be gained by considering a series of tightly time-controlled samples from the Pliocene Shungura Formation of Ethiopia described by Bobe and Eck (2001).

Members B-H of the Shungura Formation sample a diverse fauna of browsing and nonbrowsing Bovidae over a time span of approximately one million years (Bobe and Eck, 2001; Fig. 9). Most species are found in more than one member of the formation. As expected for a Pliocene fauna, the number of specialist browsing species is no greater than in any present-day habitat, with a maximum of seven observed (Figs. 6 and 7). Sample size appar-

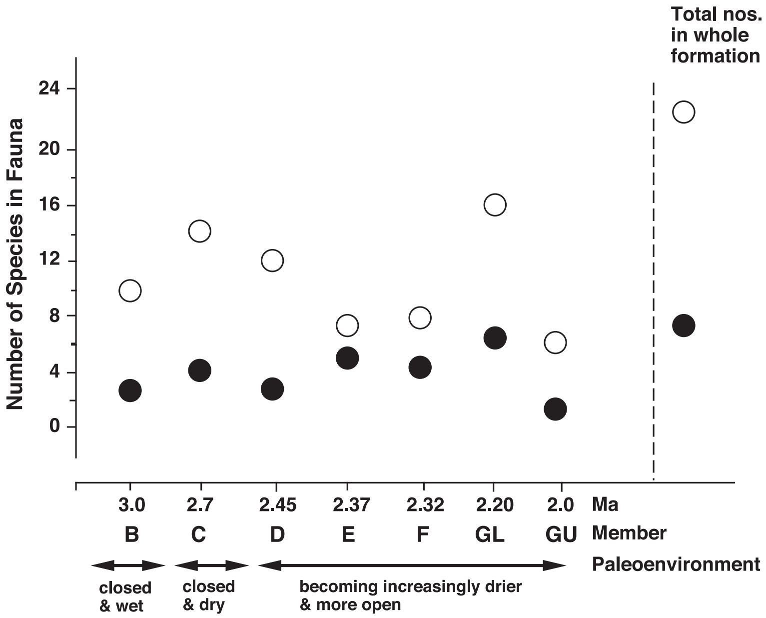

Fig. 9. Numbers of ungulate taxa in the various levels Shungura formation, Kenya (Pliocene). Filled circles = browsers; open circles = grazer/mixed-feeders. Modified from Bobe and Eck (2001).

ently affects the poor representation of species in many localities (Bobe and Eck, 2001). Considerable habitat change (from closed woodland at 3 Ma to open, dry savanna by 2 Ma) is inferred from the observed faunal changes, which include variation in both species composition and relative abundances. These ecological changes, involving browser faunas of "modern" species richness, are at least as great as ones that we infer occurred in the Miocene of North America over similar time spans.

Yet, if we were to artificially "time-average" the Shungura sequence by combining the faunas of all members, creating a single "locality" whose fauna spans a million years of time, we do not increase the number of browser species (8) significantly above the value seen in the most species-rich and well-sampled member (GL)—nor does this value approach the numbers of browsers seen in the mid Miocene. On the other hand, among the grazers and mixed feeders artificial time-averaging results in a slight increase in species richness (although not by a great amount, 22 versus a maximum at any given locality of 16). Again, this value is barely greater than observed in the most species-rich extant faunas (Figs. 6 and 7) and is comparable to values seen in many late Miocene and Pliocene faunas (Table 1).

3.2. Are such high browser/brachydont numbers restricted to mid Miocene?

Although the mid Miocene North American ungulate communities were overly rich in the numbers of brachydont taxa, by the late Miocene the numbers of species were similar to those seen in present-day African savannas; that is, approximately five to eight browser/brachydonts and around twice that number of grazer/mixed-feeding (non-brachydont) taxa. We concluded (Janis et al., 2002) that these community similarities reflected the fact that environmental conditions in the later Miocene of North America had come to resemble the conditions of today's world. This resemblance to modern faunas presumably was the result of some environmental change that occurred prior to approximately 9 Ma.

However, comparison with even the most species-rich modern ungulate faunas of Africa could be misleading if current faunas are not representative of late Cenozoic faunas.

Table 1
Numbers of browsing versus grazer/mixed-feeding ungulates in East African localities

Locality	Age	No. of browsers[a]	No. of grazer/ mixed feeders[a]	Reference
Lainyamok	Pleistocene (0.037 Ma)	5	20	Potts and Deino (1995)
Shungura	Pliocene (2.20 Ma)	7	16	Bobe and Eck (2001)
Koobi For a	Pliocene (~ 3.5 Ma)	8	19	Bernor and Pavlakis (1987)
Kanapoi 1	Pliocene (~ 4 Ma)	5	11	Bernor and Pavlakis (1987)
Logatham 1	Pliocene (~ 5 Ma)	6	16	Bernor and Pavlakis (1987)
Chemeron	L. Miocene (~ 5.5 Ma)	4	11	Hill et. al. (1986)
Luikeno A	L. Miocene (~ 7 Ma)	4	8	Bernor and Pavlakis (1987)
Ngorora	L. Miocene (~ 10 Ma)	12	11	Bernor and Pavlakis (1987)
Fort Ternan	M. Miocene (~ 14 Ma)	11	7	Shipman et al. (1981)

[a] Dietary interpretations are based on literature interpretations from craniodental features, including hypsodonty.

3.2.1. Were pre-Holocene African woodland savannas unusually high in browsers?

Perhaps pre-Holocene African savanna faunas were as species-rich as those of the North American mid Miocene, and the current values the result of Quaternary extinctions or other disturbance. In this case, the reduction in species richness in the later Miocene of North America would most likely reflect merely the trend of progressive drying and cooling in the higher latitudes. It is certainly true that the end of the Pleistocene was coincident with the extinction of a number of very large browsers in the Old World faunas, such as chalicotheres (Perissodactyla) and deinotheres (Proboscidea).

Although we have not made an extensive investigation of African faunas, a preliminary survey of the available literature has failed to reveal any late Cenozoic African fauna (younger than approximately 10 Ma) with numbers of presumed browsers that exceed those of present-day faunas (i.e., no more than eight brachydont taxa; see Table 1). Additionally, the numbers of presumed grazer/mixed-feeder (non-brachydont) species are also similar to those of present-day African faunas (see Fig. 6). Thus, it does not appear that the overall late Cenozoic species richness of ungulates in tropical savannas was significantly different from that of today.

3.2.2. Were high mid Miocene browser numbers a global phenomenon?

There could be special circumstances that led the Great Plains faunas to be unique in mammalian history. Do contemporaneous faunas unrelated to those in North America also show similar patterns? Note that some African Miocene faunas older that 9 Ma do contain a greater number of browser/brachydonts than seen in present-day faunas, resembling the numbers seen in the mid Miocene North American localities (Table 1). Kay and Madden (1997) noted a similar kind of community anomaly at the South American middle Miocene (13.5–11.8 Ma) mammal locality of La Venta, Colombia. Kay and Madden used 18 faunal proxies to estimate MAP at this site, most of which yielded predictions of between 1200 and 2100 mm/year (mean of 1818 mm). However, similar to our results for the Great Plains during the same time period (Fig. 8), the prediction obtained from the number of browsing species (all terrestrial) was highly anomalous, yielding a prediction of 5440 mm/year. Kay and Madden attribute this anomalous prediction to the fact that there are far more browsers in the La Venta fauna than in present-day Neotropical forest faunas (15 as opposed to a maximum of 5 today, a disparity comparable with our mid Miocene faunas).

These unusually browser-rich ungulate faunas from outside of North America, contemporary with the browser-rich faunas we observe in the Great Plains, suggest that habitats of exceptionally high primary productivity supporting diverse browsing faunas may have been a global phenomenon in the mid Miocene.

4. Explanations for high numbers of browsers in mid Miocene faunas

From the data and arguments presented in the previous section, it seems likely that we are observing a real phenomenon in the Great Plains. Furthermore, it is possible that the same changes we see there are echoed globally. Now we turn our attention to possible explanations for the high numbers of browsers in mid Miocene faunas.

4.1. Effects of unique climatic conditions or of climatic change

The progressive changes in both plant and herbivore communities observed throughout the later Tertiary are associated with widely accepted general trends in climate change, towards progressively cooler, drier conditions, and possibly increased seasonality (e.g., Webb and Opdyke, 1995). These climatic trends as well as the inferred vegetation types are based partly on palaeobotanical evidence, which relies on the relationships between plant formations and climatic factors observed in the present (Fig. 5). For example, Miocene woodland savannas can be assumed to have existed wherever environmental conditions were within the range that permits woodland savannas today, and to have contained similar suites of species—consisting primarily of close relatives of extant taxa. The existence of such savannas at high latitudes in the Miocene, where only temperate woodland and prairie exist today, is testament to the higher temperatures at high latitudes during the past. Direct palaeobotanical evidence for widespread later Miocene grasslands is actually rather limited, with both whole fossil and pollen evidence being mainly of woodland environments, but this may reflect preferential taphonomic sampling of wetland plants (see review and discussion in Wing, 1998).

The critical issue for explaining the North American mid Miocene faunal communities is overall plant productivity (which would thus be able to support a greater number of browsing species) rather than plant diversity or floristic change per se. For a purely climatic explanation, what is required is a climatic model whereby changes temperature or precipitation (or the seasonal distribution of either; Fox and Koch, this volume) might increase productivity of dicotyledonous vegetation, *without* changing the plant structure to that of a different vegetation type (such as a shift from woodland savanna to more open savanna or to forest).

Thus, for example, the general cooling trend in the late Neogene (from around 14 Ma onwards; Miller et al., 1987) would be expected to force many tropical (in today's terms) savanna habitats to change to habitats dominated by other types of vegetation (e.g., to cool-temperate grassland steppe). These regional vegetational changes would alter the global geographical locations in which tropical-type savannas are found. However, this cooling would not in itself affect the productivity or vegetation characteristics of tropical savanna where conditions of temperature and moisture remained appropriate for the maintenance of this vegetation type.

Likewise, unusually high levels of plant productivity, especially of woody, dicotyledonous plants (as eaten by browsers), cannot be achieved simply by postulating amounts of mid Miocene rainfall at levels in excess of that seen in present-day savannas, as this would have transformed the mid Miocene environments into tropical forest. As we have seen, this would be unlikely to increase the number of brachydont species beyond those seen today in the most humid rainforests, and it would fly in the face of extensive evidence that these habitats did not support tropical forests of any nature.

Some recent isotopic evidence from δ^{18}O enrichment of dental enamel provides information on patterns of climatic drying in the late Cenozoic of the Great Plains. In summary, animals that are more reliant on water have lower δ^{18}O values than those who are more drought tolerant (Koch et al., 1991; Bryant and Froelich, 1995), and it is postulated that tracking average community isotopic values over time provides a picture of the degree of environmental aridity. Passey et al. (2002) pursued this approach in an examination of Great Plains equids, looking both at oxygen isotopes and also aspects of carbon isotopes that might be expected to be indicative of water stress. Both values showed a change to patterns indicative of increased aridity, but not until within the late Miocene (between Clarendonian and Hemphillian land mammal ages, around 8 Ma). The patterns they observed were complex, and will not be discussed further here. However, the interesting point is that this proposed aridity, while occurring at an appropriate time to explain the demise of the "Clarendonian chronofauna" (Webb, 1983), is much too late to contribute to an explanation for the demise of the numbers of browsers.

It is also difficult to see how patterns of seasonality (in temperature or moisture) would produce savanna habitats of exceptional productivity for browsers during the mid Miocene, but would not do so today. The factors that led to the progressive development of grassland ecosystems in the Tertiary involved increasing seasonality at higher latitudes, and this may have contributed to the gradual transformation of forest to grass-dominated habitats. However, such changes in seasonal patterns (e.g., Fox and Koch, 2004) can explain the decreases in ungulate species richness throughout the Miocene, but not why browsing species are superabundant in mid Miocene communities. Moreover, low seasonality is observed today in many low-latitude regions, associated with high temperatures (such as those inferred globally for the mid Miocene) and various levels of rainfall. Thus it is unlikely that mid Miocene savannas were found outside of the climatic limits that today constrain the occurrence of tropical savannas and largely determine their potential productivity.

Thus, although numerous lines of evidence document climatic changes that were broadly coincident with the timing of faunal changes, this still does not explain the anomalous numbers of species in communities before these climatic changes took place.

4.2. Effects of unique biotic interactions

Other possible explanations for the high mid Miocene species richness of browsing ungulates involve the possible occurrence of different types of biotic interactions. Many of these ideas have been proposed to us by other researchers, and we take the opportunity here to discuss the implications of a number of them.

4.2.1. Competition, niche subdivision, and species packing

One proposal is that there could have been some difference in niche division or species packing in these mid Miocene environments, perhaps resulting from some novel processes of species competition among the mammalian herbivores. Such an explanation suffers from two difficulties. First, no ecological or evolutionary process is known that would lead the species of entire faunas to change spontaneously (and apparently permanently) their maximum levels of species packing or their tolerances to competition, in the absence of any environmental change. Second, such an explanation begs the question, since it is little more than a restatement of the fact that there is an unusually high number of browsing species present. A high number of browsers may well indicate a greater degree of subdivision of resources, and narrowing of niches (although it would not necessarily mean this). But the question raised by the data is, what environmental (or other) change permitted unusually large numbers of browsers to coexist, with whatever implications that has for levels of resource overlap or intensity of competition?

Note that the mid Miocene ungulates were not that dissimilar to those of the present day. The North American ungulates were almost all closely related to extant ungulates of similar dietary type (e.g., deer, antelope, horses, rhinos, etc.). The only ungulates to which this might not apply are oreodonts (extinct pig or sheep-like artiodactyls), that made up only a very small percentage of the species in mid Miocene localities. Additionally, there is no pronounced turnover in the types of species present at the end of this mid Miocene period. Thus there is no evidence from the faunas to suggest that the behavior of herbivores or their tolerance of competition would suddenly have changed at this time, and continued in this changed state to the present day.

4.2.2. Unique effects of keystone species

Another idea is that the presence of some (as yet unidentified) ‘‘keystone herbivore’’ (Owen-Smith, 1987; Mills et al., 1993) may have kept mid Miocene savanna woodland in a state that was unusually favorable to the support of large numbers of browsing species. Subsequent extinction of this species would then have rendered all later comparable habitats less capable of supporting browsers. However, it is not easy to imagine a way in which mammalian herbivores could have exerted the required effect. Herbivores regarded as keystone species usually affect community composition through habitat modification (Mills et al., 1993). Among African ungulates today only the megaherbivores (>1 ton) are observed to have any significant effect on vegetation structure (Cumming, 1982). Grazing by white rhino and hippopotamus is known to alter habitats such that, under the right conditions, woody plants can invade (Owen-Smith, 1987). Reversion of grassland to bushland is also a frequent outcome of overgrazing in semiarid savannas (Walker et al., 1981).

Thus in a habitat with such low rainfall that it ordinarily would support an open savanna or prairie, herbivore-mediated suppression of grass might lead to an increase in woody vegetation or even reforestation, and thus increased resources for browsing species (Walker et al., 1981). But, such a habitat would be at best a relatively unproductive representative of its vegetation type—a type that ordinarily would occur only under conditions of higher rainfall and thus yield higher levels of primary productivity. So these hypothetical altered habitats, maintained by a grassland-suppressing keystone species, would be unlikely to support greater numbers of browsing species than do any of the more productive habitats where browsers today are seen to thrive. Furthermore, specialized grazers that would be required to achieve such habitat effects on a large scale did not appear until the late Miocene (Janis et al., 1998a).

Alternatively, the immigration of a new keystone herbivore might have caused habitat alteration at the end of the mid Miocene, and contributed to the severe and rapid decline of browsing species. Modern elephants are known to cause extensive transformation of their local environments, and to change woodland savanna into more open types of grasslands (Cumming, 1982; Owen-Smith, 1987, 1988). It is true that proboscideans made their first appearance in North America at around the start of the mid Miocene, and had more extensive radiations in the later Miocene. Could the immigration of proboscideans to North America have resulted in such habitat destruction that the types of community structure typical of earlier Miocene times were irrevocably altered?

The first proboscideans known in North America are the genera *Zygolophodon* (Mammutidae) and *Gomphotherium* (Gomphotheriidae), which made a first appearance at around 17 and 16 Ma, respectively (Lambert and Shoshani, 1998). These taxa are initially known from only a very few localities, and proboscideans did not become more common in the North American fossil record until the late middle Miocene, around 12 Ma, with the appearance of other genera such as *Megabelodon*, *Eubelodon* and *Serbelodon* (all gomphotheres).

However, these animals would not have been the ecological equivalent of present-day elephants; they all had low-crowned, bunodont cheek teeth, and are likely to have been browsers of some sort; they were also smaller than modern proboscidians (Lambert and Shoshani, 1998). Proboscideans with elephantid-like teeth (the gomphotheriid genera *Stegomastodon* and *Cuvieronius*), indicative of at least some degree of grazing, do not appear in North America until the latest Miocene or Pliocene, by which time the diversity of other proboscideans was greatly reduced.

Thus it is questionable whether the appearance of proboscideans in North America led to habitat transformations disfavoring browsers. Moreover, if these proboscideans had been transforming the habitat to be less productive for browsers, since they appear to have been browsers themselves this would mean that they were causing the demise of their own habitat in the face of their subsequent radiation, which seems unlikely at best. And, finally, any opening of habitats that these proboscideans might have wrought would explain only the timing and severity of the decrease in browser species. Proboscidean-induced habitat change would not explain why earlier Miocene localities could support numbers of browsers in excess of any habitats of the world today (which include elephant-free habitats).

4.2.3. Changes in predator pressure

A final suggestion about biotic change concerns predator pressure. Could some sort of change in predator taxonomic composition or mode of predation have influenced ungulate species numbers? This idea incorporates elements of both spontaneous changes in species packing and the effects of keystone species, but translated to a higher trophic level. That is, predators would presumably increase herbivore species richness in one of two ways. Members of a diverse predator fauna might specialize on different ungulate species, and by depressing their populations make more resources available for exploitation by additional species that are (at least initially) less subject to predation. Alternatively, predators might keep one or more super-competing herbivores in check that otherwise would outcompete other ungulates and thus decrease diversity or herbivore species richness.

Both of these scenarios suggest that the causal reason for a decrease in species richness from the mid Miocene to more recent faunas would involve a net decrease in predation pressure. This implies that mid Miocene predators were replaced by species that were less effective predators, and the new species and their descendants never regained the abilities of the mid Miocene carnivores. Both of these implications seem unlikely.

Alternatively, it could be that predator pressure, as represented by numbers or diversity of predator species, was unusually high in the mid Miocene and has been low ever since. However, patterns of carnivore faunal change do not support this idea. There was a notable turnover in taxonomic composition of predator species in the late early Miocene, at around 17.5 Ma, with the immigration of felids to North America, and their replacement of existing hypercarnivorous carnivores such as hesperocyonine canids and hemicyonine ursids (Van Valkenburgh, 1999). However, this turnover event entails the replacement of taxa within an existing carnivorous guild, not the introduction of a new type of predator. There were no other dramatic events affecting predator diversity during the Miocene, with the exception of a turnover replacement of apparently more forest-dwelling taxa such as amphicyonids with more open-habitat taxa such as borophagine canids in the late Miocene (Janis et al., 1998b; Van Valkenburgh, 1999). This latter event seems to reflect general habitat change rather than a change in the basic types of predators present, and it seems that pursuit (rather than ambush) predators were not known in North America until the Pliocene (Janis and Wilhelm, 1993). Thus the decline of the number of browsing taxa in the late middle Miocene cannot be correlated with any marked change in predator abundance or ecomorphological diversity.

4.3. Changes in geography, topography or landscape heterogeneity

One might reason that if a fossil locality sampled a region that was highly diverse ecologically, with many different habitat types represented in close proximity, each with its own characteristic suite of narrowly adapted ungulate species, the resulting fauna would appear to be over-rich in species relative to a locality that sampled only a single habitat type. Likewise, if a fossil locality was located in an ecotone, or transition zone, between two distinct habitat types, might it not over time incorporate most of the elements of both faunas? Could this be the key difference between mid Miocene and later localities in the Great Plains?

This issue is related to the taphonomic issues discussed above, but includes also a question about changing external controls on local species richness on the scale of local landscapes. However, there is no evidence of which we are aware that the Great Plains experienced any significant changes in local topographic diversity throughout the Miocene and Pliocene that would be sufficient to account for the observed temporal patterns of species richness. Moreover, woodland savanna ecosystems are themselves often somewhat heterogeneous habitats, and what we usually consider to be a woodland or grassland ungulate fauna already usually represents the species that range over a variety of local subhabitats (see discussion in Wing, 1998). There is no evidence among our localities for taphonomic changes in the size of the geographic area that they sample (Appendix A), and in any case it would be difficult to explain why mid Miocene localities uniquely stood out in this (or any other taphonomic) regard.

Likewise, if one postulates that the mid Miocene species-rich localities happen all to be geographically ecotonal, then one must account for the fact that such ecotonal localities occur frequently in the mid Miocene of the Great Plains over a wide geographic area (Fig. 3), as well as in South America and Africa at the same time, but seldom, if ever, appear anywhere in younger sediments.

4.4. Effects of changes in atmospheric carbon dioxide

We have suggested elsewhere (Janis et al., 2000, 2002) that elevated levels of atmospheric CO_2 in the mid Miocene could have permitted higher levels of primary productivity which, in turn, could potentially have allowed woodland savanna habitats to support a greater number of species of browsing ungulates. Numerous studies have shown that C_3 plants grown under conditions of elevated CO_2 show increased photosynthetic rates and growth (e.g., Bazzaz, 1990; Bazzaz et al., 1997; Bucher et al., 2000; Koerner, 2001; Lilley et al., 2001). Even a relatively modest increase in atmospheric CO_2 to double the current values might be expected to increase primary productivity in C_3 dominated ecosystems by approximately 17% (Campbell and Smith, 2000).

This explanation is consistent with our hypothesis that primary productivity was higher in vegetation types that otherwise appear similar to modern woodland savannas. No unusual environmental conditions or novel vegetation types need be postulated. Furthermore, this explanation is the only one of which we are aware that can account for global, simultaneous changes in ecosystem capacities to support diverse browsing faunas. Finally, a mid-to-late Miocene drop in CO_2 to nearly current levels would explain the widespread and long-lasting nature of the change from over-rich to modern-level browser/brachydont faunas since approximately 9 Ma.

Unfortunately, the history of late Cenozoic atmospheric CO_2 concentrations is highly controversial, and at this time there is no convincing evidence that CO_2 concentrations were above current levels at any time in the last 20 My. However, evidence from different sources conflicts (Kürschner, 1997; Schwarz, 1997; Pagani et al., 1999a,b; Pearson and Palmer, 2000; Retallack, 2001b; Royer et al., 2001) and we consider that the issue is not settled.

4.5. Historically unique ecosystems

Yet another explanation for unusually productive savanna vegetation in the mid Miocene might simply be a historical one. Perhaps the highly productive mid Miocene woodland savannas do not indicate unusual environmental conditions, but rather represent a unique stage in the evolution of plant communities. That is, species making up these savanna communities were fundamentally different than those that make up similar vegetation formations today. The evolutionary transition in higher latitudes from the tropical-like woodlands during the Palaeogene to more open types of grassland habitats in the Neogene (Jacobs et al., 1999) may thus have included a form of woodland savanna more productive (at least from the point of view of browsing ungulates) than any seen today. It might have been the case that after this type of habitat was lost in the late Tertiary in the transition from woodland to grassland, it was impossible to reassemble—through migration or evolution—woodland savannas of this degree of productivity.

Such an explanation has its difficulties. Palaeobotanists working on the Miocene floras of the Great Plains and other areas in North America find plant taxa and associations that are similar to those of the present day, but which today are found in other geographical regions (e.g., Axelrod, 1985, 1995; Leopold and Denton, 1987). For example, Strömberg (2002, this volume) reports the presence of palm in the Great Plains in the early Miocene. The unique-history explanation requires that there is no habitat in existence today where the mid Miocene vegetation types, or the species that made them up, have been preserved even though the global climatic zones would presumably have provided suitable conditions, somewhere, throughout the later Cenozoic. The high-latitude savannas of the Miocene cannot exist under today's global temperature regime. However, low latitudes should preserve remnants of such ecosystems. For example we know that a similar woodland-to-grassland transition to the one that occurred in the later Miocene of North America also occurred in tropical Africa in the Plio-Pleistocene, but present-day Africa retains some woodland savanna habitats. If these habitats were relicts of the original woodland savannas, according to the unique-history explanation one would expect them to retain the similarly high numbers of browsing taxa seen in the mid Miocene (Table 1), but this is not the case. Thus this unique-history explanation would lead to the implication that all of the present day savanna woodland in Africa was at some time turned into more open habitat, and that the savanna woodlands seen today represent a secondary condition. Evidence for such a scenario is lacking.

5. Conclusions

The mid Miocene ungulate faunas of North America exhibit numbers of coexisting inferred browser (brachydont) species that, under present-day climatic conditions, would occur only in a wet tropical forest. However, we know from palaeobotanical evidence, as well as from the presence of some ungulates with dental adaptations for feeding on abrasive foods, that the vegetation of the Great Plains was at this time most likely some sort of woodland savanna, with a substantial grass component. How do we explain the apparent ability of these mid Miocene woodland savannas to support numbers of browsers substantially in excess of those supported by similar habitats today—habitats that exhibit the same vegetation structure as inferred for the palaeocommunities and whose vegetation is composed of plants with presumably similar environmental tolerances?

Taphonomic time-averaging is unlikely to be responsible for the differences we see between mid Miocene browser numbers and those in later Neogene, Quaternary, and present-day localities. The anomalously high numbers are also not the result of comparing fossil assemblages with Recent faunas that had suffered Pleistocene megafaunal extinctions; low, "modern" levels of browser species numbers seem characteristic of Cenozoic faunas younger than approximately 9 Ma. Preliminary surveys suggest that anomalously high browser numbers in localities before that date are a widespread, if not global, phenomenon.

Changes in community structure or species-packing as a result of various purely biotic, evolutionary, or historical changes do not seem consistent with the observed patterns, or have no plausible mechanisms that would explain their occurrence at a particular time in the Miocene. The most likely direct implication of the observed species-rich browser palaeocommunities is an elevated level of primary productivity, relative to the present day, within the mid Miocene woodland and grassland habitats (and perhaps other palaeohabitats as well). This leads to the question of what permitted anomalously high levels of primary productivity at this time.

Although we cannot rule out the possibility that some combination of environmental variables not seen in any habitat today might have accounted for increased primary productivity in the past, the absence of any type of modern precedent makes a purely environmental explanation unlikely. The simplest explanation for increased levels of primary productivity in the mid Miocene may be elevated levels of atmospheric carbon dioxide. This hypothesis is a controversial one, as it contradicts the current consensus from geochemistry (e.g., Pagani et al., 1999a,b; Pearson and Palmer, 2000), but it is possibly supported by some palaeobotanical evidence (Kürschner, 1997; Retallack, 2001b). However, whether or not current or future evidence provides support for the idea of higher mid Miocene levels of CO_2, the anomalous faunas provide evidence of environmental conditions for which we cannot account in terms of the climatic and biotic parameters of today's world, and demand an explanation.

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Appendix A

Data used for locality analyses. "Cf. taxa" were included in the count unless there was another species of that genus present at that locality. B = brachydont; SM = submesodont (counted with brachydont taxa); M = mesodont; H = hypsodont.

Late Blancan (late Pliocene)

(1) White Rock Local Fauna, Belville Formation, Kansas:

Refs: Eshelman (1975).

Brachydont (1): *Platygonus* sp. (B) (Tayassuidae).

Non-Brachydont (5): *Gigantocamelus* sp. (M), *Hemiauchenia blancoensis* (M) (Camelidae); *Capromeryx* sp. (H) (Antilocapridae); *Equus simplicidens* (H) (Equidae); *Stegomastodon mirificus* (H) (Proboscidea).

(2) Sand Draw Local Fauna, Kiem Formation, Nebraska:

Refs: Hager (1974), Voorhies and Corner (1986), Morgan and Morgan (1995).

Brachydont (1): *Platygonus* sp. (B) (Tayassuidae).

Non-Brachydont (7): *Camelops* sp. (M), *Gigantocamelus spatula* (M) (Camelidae); cf. *Capromeryx tauntonensis* (H) (Antilocapridae); *Equus simplicidens* (H), *Nannippus minor* (H) (Equidae); *Stegomastodon primitivus* (H) (Proboscidea).

(3) Big Springs Local Fauna, Long Pine Formation, Nebraska:

Refs: Voorhies (1987).

Brachydont (2): *Tapirus* sp. (B) (Tapiriidae); *Mammut* sp. (B) (Proboscidea).

Non-Brachydont (7): *Camelops* sp. (M), *Gigantocamelus spatula* (M), *Hemiauchenia* sp. (M), *Titanotylopus nebraskensis* (M) (Camelidae); *Capromeryx* sp. (H) (Antilocapridae); *Equus* sp. (H) (Equidae); *Stegomastodon* sp. (H) (Proboscidea).

Early Blancan (early Pliocene)

(4) Broadwater Local Fauna, Broadwater Formation, Nebraska:

Refs: Hager (1974).

Brachydont (1): *Platygonus* sp. (B) (Tayassuidae).

Non-Brachydont (5): *Camelops* sp. (M), *Gigantocamelus spatula* (M) (Camelidae); *Capromeryx arizonensis* (H) (Antilocapridae); *Equus simplicidens* (H) (Equidae); *Stegomastodon mirificus* (H) (Proboscidea).

(5) Deer Park Local Fauna, Deer Park Formation, Kansas:

Refs: Hibbard (1950), Skinner and Hibbard (1972).

Brachydont (1): *Platygonus* sp. (B) (Tayassuidae).

Non-Brachydont (5): *Camelops* sp. (M) (Camelidae); *Equus simplicidens* (H), *Nannippus peninsulatus* (H) (Equidae); *Rhyncotherium* sp. (H), *Stegomastodon mirificus* (H) (Proboscidea).

(6) Rexroad Local Fauna, Rexroad Formation, Kansas:

Refs: Hibbard (1950), Dalquest (1978).

Brachydont (4): *Platygonus* sp. (B) (Tayassuidae); *Odocoileus brachyodontus* (B), *Odocoileus* sp. (B) (Cervidae); *Mammut* sp. (B) (Proboscidea).

Non-Brachydont (5): *Hemiauchenia blancoensis* (M) (Camelidae); Antilocaprid indet. (H); *Equus simplicidens* (H), *Nannippus peninsulatus* (H) (Equidae); *Stegomastodon primitivus* (H) (Proboscidea).

Latest Hemphillilan (early Pliocene)

(7) Ash Hollow Formation, Santee Local Fauna, Nebraska:

Refs: Voorhies (1990).

Brachydont (4): *Platygonus* sp. (B) (Tayassuidae); *Pediomeryx* sp. (SM) (Dromomerycidae); *Aphelops mutilis* (B) (Rhinocerotidae); Gomphothere indet. (SM) (Proboscidea).

Non-Brachydont (6): *Hemiauchenia vera* (M), *Megacamelus merriami* (M) (Camelidae); *Dinohippus* sp. (H), *Nannippus ingenuus* (H), *Neohipparion eurystyle* (H) (Equidae); *Teleoceras* sp. (H) (Rhinocerotidae).

(8) Ash Hollow Formation, Devil's Nest Airstrip Local Fauna, Nebraska:

Refs: Voorhies (1990).

Brachydont (6): *Platygonus* sp. (B) (Tayassuidae); *Pediomeryx* sp. (SM) (Dromomerycidae); Cervid indet. (B); *Tapirus* sp. (B) (Tapiriidae); *Aphelops mutilis* (B) (Rhinocerotidae); Gomphothere indet. (SM) (Proboscidea).

Non-Brachydont (7): *Hemiauchenia vera* (M), *Megacamelus merriami* (M) (Camelidae); Antilocaprid indet. (H); *Dinohippus* sp. (H), *Nannippus ingenuus* (H), *Neohipparion eurystyle* (H) (Equidae); *Teleoceras* sp. (H) (Rhinocerotidae).

Late Hemphillian (late late Miocene)

(9) Ash Hollow Formation, Honey Creek Fauna, Nebraska:

Refs: Voorhies (1990).

Brachydont (2): Tayassuid indet. (B); Gomphothere indet. (SM) (Proboscidea).

Non-Brachydont (6): *Hemiauchenia vera* (M), *Megatylopus gigas* (M) (Camelidae); *Dinohippus leidyanus* (H), *Nannippus* sp. (H), *Neohipparion leptode* (H) (Equidae); *Teleoceras fossiger* (H) (Rhinocerotidae).

(10) Ogallala Formation, Edson Quarry Fauna, Kansas:

Refs: Harrison (1983).

Brachydont (5): *Platygonus* Edson sp. (B), Tayassuid indet. (B) (Tayassuidae); *Pediomeryx hemphilliensis* (SM) (Dromomerycidae); *Aphelops mutilis* (B) (Rhinocerotidae); *Amebelodon britti* (SM) (Proboscidea).

Non-Brachydont (8): *Alforjas taylori* (M), *Hemiauchenia vera* (M), *Megatylopus gigas* (M) (Camelidae); cf. *Texoceros guymonensis* (H) (Antilocapridae); *Dinohippus interpolatus* (H), *Nannippus* sp. (H), *Neohipparion eurystyle* (H) (Equidae); *Teleoceras* new sp. (H) (Rhinocerotidae).

(11) Ash Hollow Formation, Mailbox Fauna, Nebraska:

Refs: Voorhies (1990).

Brachydont (4): Tayassuid indet. (B); cf. *Pediomeryx* sp. (SM) (Dromomerycidae); *Tapirus* sp. (B) (Tapiriidae); Gomphothere indet. (SM) (Proboscidea).

Non-Brachydont (7): *Hemiauchenia vera* (M), *Megatylopus gigas* (M) (Camelidae); Antilocaprid indet. (H); *Dinohippus leidyanus* (H), *Nannippus* sp.

(H), *Neohipparion leptode* (H) (Equidae); *Teleoceras fossiger* (H) (Rhinocerotidae).

Late early Hemphillian (late late Miocene)

(12) Ash Hollow Formation, Minium Quarry, Kansas:

Refs: Thomasson et al. (1990).

Brachydont (3): Tayassuid indet. (B); *Aphelops* sp. (B) (Rhinocerotidae); *Torynobelodon loomisi* (SM) (Proboscidea).

Non-Brachydont (8): *Hemiauchenia vera* (M), *Megatylopus* sp. (M), *Procamelus* sp. (M) (Camelidae); *Calippus* sp. (H), *Cormohipparion occidentale* (H), cf. *Neohipparion trampasense* (H), *Protohippus* sp. (H) (Equidae); *Teleoceras fossiger* (H) (Rhinocerotidae).

(13) Wray Fauna, Ogallala Group, Colorado:

Refs: Cook (1922), Tedford et al. (1987).

Brachydont (4): cf. *Prosthennops serus* (B) (Tayassuidae); *Yumaceras figginsi* (B) (Dromomerycidae); *Aphelops* sp. (B) (Rhinocerotidae); *Amebelodon floridanus* (SM) (Proboscidea).

Non-Brachydont (9): *Megatylopus gigas* (M) (Camelidae); *Texoceros vaughani* (H) (Antilocapridae); ?*Neotragocerus* sp. (M) (Bovidae); *Cormohipparion occidentale* (H), cf. *Dinohippus interpolatus* (H), *Neohipparion* sp. (H), *Pliohippus mirabile* (H), *Protohippus gidleyi* (H) (Equidae); *Teleoceras hicksi* (H) (Rhinocerotidae).

(14) Ash Hollow Formation, Cambridge Ft.- 40 Fauna, Nebraska:

Refs: Voorhies (1990).

Brachydont (6): *Prosthennops serus* (B) (Tayassuidae); *Pseudoceras* sp. (SM) (Gelocidae); *Yumaceras figginsi* (B) (Dromomerycidae); *Tapirus simpsoni* (B) (Tapiriidae); *Aphelops mutilis* (B) (Rhinocerotidae); *Amebelodon britti* (SM) (Proboscidea).

Non-Brachydont (10): *Alforjas* sp. (M), *Hemiauchenia vera* (M), *Megatylopus* sp. (M) (Camelidae); cf. *Texoceros guymonensis* (H) (Antilocapridae), *Calippus* sp. (H), *Dinohippus leidyanus* (H), *Hipparion forcei* (H), *Nannippus ingenuus* (H), *Neohipparion leptode* (H) (Equidae); *Teleoceras fossiger* (H) (Rhinocerotidae).

Early early Hemphillian (late late Miocene)

(15) Snake Creek Formation (Johnson Member), Aphelops Draw Fauna, Nebraska:

Refs: Skinner et al. (1977).

Brachydont (4): *Merychyus* sp. (SM) (Merycoidodontidae); *Aphelops mutilis* (B) (Rhinocerotidae); *Gomphotherium* sp. (SM), *Mammut matthewi* (B) (Proboscidea).

Non-Brachydont (7): *Megatylopus* sp. (M), *Procamelus* sp. (M) (Camelidae); *Texoceros altidens* (H) (Antilocapridae); *Neotragocerus improvisus* (M) (Bovidae); *Dinohippus leidyanus* (H), *Nannippus ingenuus* (H), *Neohipparion eurystyle* (H) (Equidae).

(16) Ash Hollow Formation, Feltz Ranch Fauna, Lemoyne Quarry, Nebraska:

Refs: Voorhies (1990).

Brachydont (5): *Prosthennops serus* (B) (Tayassuidae); *Pseudoceras* sp. (SM) (Gelocidae); *Yumaceras* sp. (B) (Dromomerycidae); *Aphelops malacorhinus* (B) (Rhinocerotidae); *Amebelodon* sp. (SM) (Proboscidea).

Non-Brachydont (9): ?*Alforjas* sp. (M), ?*Hemiauchenia* sp. (M), ?*Megatylopus gigas* (M) (Camelidae); cf. *Plioceros* sp. (M) (Antilocapridae); *Calippus* sp. (H), *Nannippus* sp. (H), *Neohipparion eurystyle* (H), *Pliohippus nobilis* (H) (Equidae); *Teleoceras fossiger* (H) (Rhinocerotidae).

Late Clarendonian (early late Miocene)

(17) Snake Creek Formation, Laucomber Member, Nebraska:

Refs: Skinner and Johnson (1984), contributors to Janis et al. (1998).

Brachydont (8): Tayassuid indet. (B); *Merychyus major* (SM), *M. novomexicanus* (SM) (Merycoidodontidae); *Longirostromeryx wellsi* (SM) (Moschidae); *Cranioceras unicornis* (B) (Dromomerycidae); *Hypohippus* sp. (B) (Equidae); Chalicothere indet. (B); *Gomphotherium* sp. (SM) (Proboscidea).

Non-Brachydont (8): *Megatylopus* sp. (M) (Camelidae); *Cosoryx* sp. (M) (Antilocapridae); *Cormohipparion occidentale* (H), *Hipparion forcei* (H), *Nannippus* sp. (H), *Neohipparion affine* (H), *Protohippus supremus* (H), *Pseudhipparion gratum* (H) (Equidae).

(18) Ash Hollow Formation, Merrit Dam Member, Blue Jay Quarry, Nebraska:

Refs: Voorhies (1990).

Brachydont (6): *Merychyus major* (SM) (Merycoidodontidae); *Miolabis* sp. (B) (Camelidae); *Cranioceras unicornis* (B) (Dromomerycidae); *Hypohippus* sp. (B), *Parahippus* sp. (SM) (Equidae); *Serbelodon barbouri* (SM) (Proboscidea).

Non-Brachydont (8): *Megatylopus primaevus* (M), *Pliauchenia magnifontis* (M), *Procamelus grandis*

(M) (Camelidae); *Calippus* sp. (H), *Cormohipparion occidentale* (H), *Protohippus supremus* (H), *Pseudhipparion gratum* (H) (Equidae); *Teleoceras* sp. (H) (Rhinocerotidae).

Early Clarendonian (early late Miocene)

(19) Ogallala Formation, Wakeeney Fauna, Kansas:

Refs: contributors to Janis et al. (1998).

Brachydont (4): Prosthennops serus (B) (Tayassuidae); *Merychyus medius* (SM) (Merycoidodontidae); *Hypohippus* sp. (B) (Equidae); *Torynobelodon campester* (SM) (Proboscidea).

Non-Brachydont (6): *Procamelus* sp. (M) (Camelidae); *Ramoceros kansanus* (M) (Antilocapridae); *Calippus martini* (H), *Cormohipparion occidentale* (H), *Nannippus* sp. (H), *Neohipparion affine* (H) (Equidae).

(20) Ash Hollow Formation, Big Spring Canyon, South Dakota:

Refs: Gregory (1942).

Brachydont (6): *Prosthennops* sp. (B) (Tayassuidae); *Merychyus novomexicanus* (SM) (Merycoidodontidae); *Longirostromeryx wellsi* (SM) (Moschidae); *Cranioceras* sp. (B) (Dromomerycidae); *Hypohippus affinus* (B) (Equidae); Gomphothere indet. (B) (Proboscidea).

Non-Brachydont (11): *Megatylopus* sp. (M), *Pliauchenia magnifontis* (M), *Procamelus grandis* (M) (Camelidae); *Cosoryx furcatus* (M) (Antilocapridae); *Calippus martini* (H), *Cormohipparion occidentale* (H), *Nannippus* sp. (H), cf. *Pliohippus pernix* (H), *Pliohippus* sp. (H), *Pseudhipparion gratum* (H) (Equidae); *Teleoceras major* (H) (Rhinocerotidae).

(21) Ash Hollow Formation, Cap Rock Member, Little Beaver B Quarry, Nebraska:

Refs: Voorhies (1990).

Brachydont (9): "*Prosthennops*" *niobrarensis* (B) (Tayassuidae); *Merychyus novomexicanus* (SM) (Merycoidodontidae); *Longirostromeryx wellsi* (SM) (Moschidae); *Cranioceras unicornis* (B) (Dromomerycidae); *Hypohippus affinus* (B), *Megahippus matthewi* (B) (Equidae); *Aphelops* sp. (B) (Rhinocerotidae); *Eubelodon morrili* (SM), *Gomphotherium* sp. (SM) (Proboscidea).

Non-Brachydont (11): *Megatylopus* sp. (M), *Procamelus grandis* (M), *Protolabis heterodontus* (M) (Camelidae); *Cosoryx furcatus* (M), *Proantilocapra platycornea* (M) (Antilocapridae); *Calippus placidus* (H), *Cormohipparion occidentale* (H), cf. *Merychippus insignis* (M), *Pliohippus pernix* (H), *Pseudhipparion gratum* (H) (Equidae); *Teleoceras major* (H) (Rhinocerotidae).

Late late Barstovian (middle Miocene)

(22) Ash Hollow Formation, Trail Creek Quarry Local Fauna, Wyoming:

Refs: Forstén (1970).

Brachydont (4): *Merychyus medius* (SM) (Merycoidodontidae); *Aepycamelus* sp. (SM) (Camelidae); *Hypohippus affinus* (B) (Equidae); *Zygolophodon proavus* (B) (Proboscidea).

Non-Brachydont (7): *Procamelus leptocolon* (M) (Camelidae); cf. *Cosoryx furcatus* (M), *Ramoceros* sp. (M) (Antilocapridae); *Merychippus coloradense* (M), *Merychippus* sp. (M), *Pseudhipparion retrusum* (M) (Equidae); cf. *Teleoceras* sp. (H) (Rhinocerotidae).

(23) Valentine Formation, Crookston Bridge Member, Myers Farm, Nebraska:

Refs: Voorhies (1990).

Brachydont (13): "*Prosthennops*" *xiphodonticus* (B) (Tayassuidae); *Merychyus medius* (SM) (Merycoidodontidae); *Lambdoceras* sp. (B) (Protoceratidae); *Pseudoparablastomeryx francescita* (B) (Leptomerycidae); *Longirostromeryx blicki* (SM) (Moschidae); *Procranioceras skinneri* (B) (Dromomerycidae); *Hypohippus osborni* (B), *Kalobatippus* sp. (B), *Parahippus cognatus* (SM) (Equidae); *Tapiravus polkensis* (B) (Tapiriidae); *Peraceras superciliosum* (B) (Rhinocerotidae); *Gomphotherium* sp., (SM), *Zygolophodon* sp. (B) (Proboscidea).

Non-Brachydont (5): *Procamelus occidentalis* (M) (Camelidae); *Ramoceras kansanus* (M) (Antilocapridae); *Calippus placidus* (H), *Merychippus republicanus* (M) (Equidae); *Teleoceras medicornutum* (H) (Rhinocerotidae).

(24) Ogallala Formation, Kennesaw Fauna, Colorado:

Refs: Galbreath (1953).

Brachydont (6): *Merychyus medius* (SM) (Merycoidodontidae); *Miolabis longiceps* (B) (Camelidae); *Dromomeryx pawniensis* (B) (Dromomerycidae); *Hypohippus osborni* (B) (Equidae); *Aphelops* sp. (B) (Rhinocerotidae); *Gomphotherium* sp. (SM) (Proboscidea).

Non-Brachydont (5): *Procamelus leptocolon* (M) (Camelidae); *Cosoryx* sp. (M), *Meryceros warreni* (M) (Antilocapridae); *Calippus* sp. (H), *Cormohipparion sphenodus* (H) (Equidae).

Early late Barstovian (middle Miocene)

(25) Valentine Formation, Cornell Dam Member, Carrot Top Quarry, Nebraska:

Refs: Voorhies (1990).

Brachydont (9): Tayassuid indet. (B); *Aepycamelus* sp. (SM), *Miolabis* sp. (B) (Camelidae); *Blastomeryx gemmifer* (B) (Moschidae); *Hypohippus osborni* (B), *Parahippus cognatus* (SM) (Equidae); *Aphelops megalodus* (B), *Peraceras superciliosum* (B) (Rhinocerotidae); *Gomphotherium* sp. (SM) (Proboscidea).

Non-Brachydont (7): *Procamelus* sp. (M) (Camelidae); *Merycodus nectatus* (M) (Antilocapridae); *Calippus proplacidus* (H), *Merychippus insignis* (M), *M. republicanus* (M), *Protohippus* sp. (H) (Equidae); *Teleoceras medicornutum* (H) (Rhinocerotidae).

(26) Pawnee Creek Formation, Horse and Mastodon Quarry, Colorado:

Refs: Tedford et al. (1987).

Brachydont (4): *Merychyus medius* (SM) (Merycoidodontidae); *Dromomeryx pawniensis* (B) (Dromomerycidae); *Gomphotherium* sp. (SM), *Zygolophodon* sp. (B) (Proboscidea).

Non-Brachydont (6): *Merycodus nectatus* (M), *M. warreni* (M), *Paracosoryx* sp. (M), (Antilocapridae); *Merychippus sejunctus* (M), *Pliohippus mirabilis* (H) (Equidae); *Teleoceras medicornutum* (H) (Rhinocerotidae).

(27) Valentine Formation, Cornell Dam Member, Norden Bridge Quarry, Nebraska:

Refs: Voorhies (1990).

Brachydont (19): “*Prosthennops*” *xiphodonticus* (B) (Tayassuidae); *Merychyus medius* (SM), *Ticholeptus* sp. (SM) (Merycoidodontidae); *Aepycamelus robustus* (SM), *Miolabis* sp. (B) (Camelidae); *Pseudoparablastomeryx* sp. (B) (Leptomerycidae); *Blastomeryx gemmifer* (B) (Moschidae); cf. *Bouromeryx americanus* (B), *Dromomeryx borealis* (B) (Dromomerycidae); *Archaeohippus* sp. (B), *Hypohippus osborni* (B), *Megahippus mckennai* (B), *Parahippus cognatus* (SM) (Equidae); Tapirid indet. (B); *Aphelops megalodus* (B), *Peraceras superciliosum* (B) (Rhinocerotidae); Chalicotheriid indet. (B); *Gomphotherium* sp. (SM), *Zygolophodon* sp. (B) (Proboscidea).

Non-Brachydont (10): *Procamelus occidentalis* (M), *Protolabis* sp. (M) (Camelidae); *Merycodus nectatus* (M), cf. *Ramoceros kansanus* (M), *Submeryceros minor* (M) (Antilocapridae); *Calippus proplacidus* (H), *Merychippus insignis* (M), *M. republicanus* (M), *Protohippus perditus* (H) (Equidae); *Teleoceras medicornutum* (H) (Rhinocerotidae).

Early Barstovian (middle Miocene)

(28) Olcott Formation, Humbug Quarry, Nebraska:

Refs: Skinner et al. (1977), AMNH collections.

Brachydont (12): *Hesperhys* sp. (B) (Tayassuidae); *Brachycrus vaughni* (SM), *Ticholeptus zygomaticus* (SM) (Merycoidodontidae); *Aepycamelus procerus* (SM), *Miolabis princetonianus* (SM) (Camelidae); *Pseudoparablastomeryx scotti* (B) (Leptomerycidae), *Blastomeryx elegans* (B) (Moschidae); *Bouromeryx americanus* (B), *Dromomeryx whitfordi* (B), *Rakomeryx* sp. (B) (Dromomerycidae); *Hypohippus wardi* (B) (Equidae); *Aphelops megalodus* (B) (Rhinocerotidae).

Non-Brachydont (11): “*Homocamelus*” sp. (M), *Paramiolabis singularis* (M), *Procamelus* sp. (M), *Protolabis* sp. (M), (Camelidae); *Merriamoceros coronatus* (M), *Merycodus sabuloris* (M), *Ramoceros* sp. (M) (Antilocapridae); *Merychippus insignis* (M), *M. intermontanus* (M), *M. isonesus* (M) (Equidae); *Teloceras medicornutum* (M) (Rhinocerotidae).

(29) Olcott Formation, Echo Quarry, Nebraska:

Refs: Skinner et al. (1977), AMNH collections.

Brachydont (15): “*Prosthennops*“ *xiphodonticus* (Tayassuidae); *Brachycrus vaughni* (SM), *Ticholeptus zygomaticus* (SM) (Merycoidodontidae); *Lambdoceras siouxensis* (Protoceratidae); *Aepycamelus procerus* (SM), *Miolabis princetonianus* (SM) (Camelidae); *Blastomeryx elegans* (Moschidae); *Bouromeryx americanus*, *Dromomeryx whitfordi*, *Rakomeryx* sp. (Dromomerycidae); *Desmatippus integer* (SM), *Hypohippus equinus*, *Kalobatippus* sp. (Equidae); *Aphelops megalodus* (Rhinocerotidae); *Moropus merriami* (Chalicotheriidae).

Non-Brachydont (10): “*Homocamelus*” sp. (M), *Paramiolabis singularis* (M), *Procamelus* sp. (M), *Protolabis* sp. (M), (Camelidae); *Merycodus sabuloris* (M), *P. minor serpentinus* (M) (Antilocapridae); *Merychippus insignis* (M), *M. intermontanus* (M), *M. isonesus* (M) (Equidae); *Teloceras medicornutum* (M) (Rhinocerotidae).

(30) Pawnee Creek Formation, Eubanks Fauna, Colorado:

Refs: Galbreath (1953), University of California, Berkeley collections.

Brachydont (9): “*Prosthennops*” *xiphidonticus* (B) (Tayassuidae); *Brachycrus siouense* (SM) (Merycoidodontidae); *Bouromeryx pawniensis* (B) (Dromomerycidae); *Hypohippus osborni* (B), *Megahippus* sp. (B), *Parahippus paniensis* (SM) (Equidae); *Aphelops megalodus* (B) (Rhinocerotidae); ?*Moropus matthewi* (B) (Chalicotheriidae); Proboscidean indet. (B)

Non-Brachydont (3): *Protolabis heterodontus* (M) (Camelidae); *Merychippus coloradense* (M), *M. sejunctus* (M) (Equidae).

(31) Sand Canyon Beds, Observation Quarry, Nebraska:

Refs: Tedford et al. (1987).

Brachydont (16): "*Prosthennops*" *xiphodonticus* (B) (Tayassuidae); *Brachycrus siouense* (SM), *Merychyus relictus* (SM), *Ticholeptus zygomaticus* (SM) (Merycoidodontidae); *Lambdoceras siouxensis* (B) (Protoceratidae); *Pseudoparablastomeryx scotti* (B) (Leptomerycidae); *Blastomeryx elegans* (B) (Moschidae); *Bouromeryx supernebraskensis* (B), *B. pseudonebraskensis* (B), *Dromomeryx borealis* (B), *D. whitfordi* (B), *Drepanomeryx matthewi* (B), *Rakomeryx* sp. (B) (Dromomerycidae); *Hypohippus* sp. (B), *Kalobatippus* sp. (B) (Equidae); *Moropus merriami* (B) (Chalicotheriidae).

Non-Brachydont (0).

Late Hemingfordian (Late early Miocene)

(32) Sheep Creek Formation, Thomson Quarry, Nebraska:

Refs: Skinner et al. (1977), AMNH collections.

Brachydont (14): cf. *Hesperhys* sp. (B) (Tayassuidae); *Merychyus relictus* (SM), *Brachycrus laticeps* (SM) (Merycoidodontidae); *Lambdoceras* sp. (B) (Protoceratidae); *Aepycamelus priscus* (SM) (Camelidae), *Blastomeryx medius* (B) (Moschidae), *Bouromeryx milleri* (B), *Sinclairomeryx riparius* (B), *Subdromomeryx scotti* (H) (Dromomerycidae); *Archaeohippus penultimatus* (B), *Kalobatippus* sp. (B), *Parahippus* sp. (SM) (Equidae); *Aphelops megalodus* (B) (Rhinocerotidae); *Tylocephalonyx skinneri* (B) (Chalicotheriidae).

Non-Brachydont (12): "*Homocamelus*" sp. (M), *Paramiolabis tenuis* (M), *Protolabis* sp. (M), *Michenia* sp. (M), (Camelidae); *Merycodus sabuloris* (M), *Paracosoryx alticornis* (M), *P. minor serpentinus* (M), *P. wilsoni* (M) (Antilocapridae); *Merychippus primus* (M), *M. tertius* (M), *M.* sp. (M) (Equidae); *Brachypotherium americanum* (M) (Rhinocerotidae).

(33) Box Butte Formation, Foley Quarry, Nebraska:

Refs: Galusha (1975).

Brachydont (9): *Oxydactylus longirostris* (B) (Camelidae); *Merychyus smithi* (SM) (Merycoidodontidae); *Barbourmeryx* sp. (B), cf. *Bouromeryx submilleri* (B), cf. *Sinclairomeryx tedi* (B) (Dromomerycidae); *Archaeohippus* sp. (B), *Hypohippus* sp. (B), *Kalobatippus* sp. (B) (Equidae); new acerathine genus (B) (Rhinocerotidae);

Non-Brachydont (4): *Michenia* sp. (M) Camelidae; *Paracosoryx dawesensis* (M) (Antilocapridae); cf. *Merychippus primus* (M), *M. tertius* (M) (Equidae).

(34) Sheep Creek Formation Equivalent, Ginn Quarry, Nebraska:

Refs: Galusha (1975), contributors to Janis et al. (1998), AMNH collections.

Brachydont (10): *Merychyus relictus* (SM), *Brachycrus sweetwaterensis* (SM) (Merycoidodontidae); *Blastomeryx* sp. (B), *Problastomeryx* sp. (B) (Moschidae); *Dromomeryx* sp. (B), *Rakomeryx* sp. (B), *Sinclairomeryx tedi* (B), *Sinclairomeryx* sp. (B) (Dromomerycidae); *Kalobatippus* sp. (B) (Equidae); *Tylocephalonyx skinneri* (B) (Chalicotheriidae).

Non-Brachydont (3): *Aletomeryx* sp. (M) Dromomerycidae; *Paracosoryx dawesensis* (M), *Submeryceros minor* (M) (Antilocapridae).

Early Hemingfordian (late early Miocene)

(35) Running Water Formation, Aletomeryx Quarry, Nebraska:

Refs: Hunt (1981), Skinner and Johnson (1984).

Brachydont (8): *Hesperhys* sp. (B) (Tayassuidae); *Merychyus elegans* (B), *M. arenanrum* (B) (Merycoidodontidae); *Oxydactylus longirostris* (B) (Camelidae); *Blastomeryx marshi* (B) (Moschidae); *Archaeohippus* sp. (B), *Parahippus* sp. (SM) (Equidae); *Menoceras barbouri* (B) (Rhinocerotidae).

Non-Brachydont (1): *Aletomeryx gracilis* (M) (Dromomerycidae).

(36) Martin Canyon Beds, University of Kansas Quarry A, Colorado:

Refs: Galbreath (1953).

Brachydont (9): ?*Hesperhys* sp. (B) (Tayassuidae); *Merycochoerus magnus* (B), *Merychyus minimus* (SM) (Merycoidodontidae); *Oxydactylus* sp. (B) (Camelidae); cf. *Blastomeryx elegans* (B), cf. *B. medius* (B) (Moschidae); *Parahippus pawniensis* (SM) (Equidae); *Peraceras profectum* (B) (Rhinocerotidae); *Moropus* sp. (B) (Chalicotheriidae).

Non-Brachydont (1): *Merychippus* sp. (M) (Equidae).

(37) Batesland Formation, Flint Hill Local Fauna, South Dakota:

Refs: Harksen and Macdonald (1967), Macdonald (1970).

Brachydont (16): *Dinohyus hollandi* (B) (Entelodontidae); *Arretotherium fricki* (B) (Anthracotheriidae); cf. *Stibarus* sp. (B) (Leptochoeridae); *Hesperhys pinensis* (B) (Tayassuidae); *Merychyus elegans* (SM) (Merycoidodontidae); *Lambdoceras hessei* (B) (Protoceratidae); ?*Oxydactylus* sp. (B) (Camelidae); *Pseudoparablastomeryx galushi* (B) (Leptomerycidae); cf. *Parablastomeryx advena* (B), *Problastomeryx* sp. (B) (Moschidae); ?*Barbouromeryx* sp. (B) (Dromomerycidae); cf. *Archaeohippus blackbergi* (B), cf. *Kalobatippus agatensis* (B), cf. *Parahippus cognatus* (SM) (Equidae); *Menoceras barbouri* (B) (Rhinocerotidae); *Moropus* sp. (B) (Chalicotheriidae).

Non-Brachydont (0):

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