

# On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology

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## ABSTRACT

High-crowned (hypsodont) teeth are widely found among both extant and extinct mammalian herbivores. Extant grazing ungulates (hoofed mammals) have hypsodont teeth (a derived condition), and so extinct hypsodont forms have usually been presumed to have been grazers. Thus, hypsodonty among ungulates has, over the past 150 years, formed the basis of widespread palaeoecological interpretations, and has figured prominently in the evolutionary study of the spread of grasslands in the mid Cenozoic. However, perceived inconsistencies between levels of hypsodonty and dental wear patterns in both extant and extinct ungulates have caused some workers to reject hypsodonty as a useful predictive tool in palaeobiology, a view that we consider both misguided and premature.

Despite the acknowledged association between grazing and hypsodonty, the quantitative relationship of hypsodonty to the known ecology of living ungulate species, critical in making interpretations of the fossil record, was little studied until the past two decades. Also, much of the literature on ungulate ecology relevant to understanding hypsodonty has yet to be fully incorporated into the perspectives of palaeontologists. Here we review the history and current state of our knowledge of the relationship between hypsodonty and ungulate ecology, and reassert the value of hypsodonty for our understanding of ungulate feeding behaviour. We also show how soil consumption, rather than the consumption of grass plants *per se*, may be the missing piece of the puzzle in understanding the observed correlation between diets, habitats, and hypsodonty in ungulates. Additionally, we show how hypsodonty may impact life-history strategies, and resolve some controversies regarding the relevance of hypsodonty to the prediction of the diets of extinct species. This in turn strengthens the utility of hypsodonty in the determination of past environmental conditions, and we provide a revised view of a traditional example of evolutionary trends in palaeobiology, that of the evolution of hypsodonty in horses and its correlation with the Miocene spread of grasslands in North America.

*Key words:* hypsodonty, ungulates, grazing, palaeoecology, dental wear, soil consumption, Cenozoic, palaeoenvironments, grasslands, diet prediction.

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## I. INTRODUCTION

This paper reviews the history of ideas about hypsodonty (high-crowned teeth) and what we currently know about its relationship to diet and ecology among ungulates (hoofed mammals). We also discuss some perceived conflicts that have arisen in the past decade with regards to the evolutionary and functional significance of hypsodonty, and to the interpretation of hypsodonty in the ungulate fossil record. We are concerned by a current trend among some researchers to dismiss hypsodonty as a tool for understanding dietary shifts over evolutionary time, and as a valuable component of methods for the interpretation of diets in extinct animals. Part of the problem that we perceive is an apparent lack of appreciation of both the extent and content of the published knowledge on living species concerning the functional implications of a hypsodont dentition, the factors that lead to increased tooth wear in ungulate feeding, and the reasons for the statistical association between hypsodonty and diet.

### (1) Definition and usage

Hypsodont teeth (usually referring to molars and, to a lesser extent, premolars) are those teeth that are high crowned: that is, the tooth crown has been vertically elongated over the primitive mammalian condition of brachydonty. In a brachydont tooth the entire crown of the tooth is above the level of the jawbone on initial eruption (as in humans), while in a hypsodont tooth some of the crown is retained within the jaw, and will erupt later in life as the exposed portion of the crown wears down (somewhat like the emergence of new lead in a mechanical pencil) (Janis, 1988).

Hypsodonty has evolved numerous times among mammals (in multituberculates, and multiple times within marsupials and placentals). Hypsodont dentitions are often termed “durable” (e.g. Janis & Fortelius, 1988), but this is not because the teeth are actually more resistant to wear; rather, it is because they wear for a longer time (in the sense that a longer candle might be more “durable” in terms of hours of light provided). A hypsodont tooth takes longer to be worn away, by virtue of the fact that there is more tooth material to be ground down. This increased durability, in turn, is universally recognized as an adaptation to resist high rates of tooth wear during the mastication of food (Janis & Fortelius, 1988). Because mammals that include a large amount of grass in their diets are usually hypsodont, the notion that grazing and hypsodonty are inexorably linked has become a truism in the literature.

Hypsodonty, as conventionally defined above, is a continuous, metric variable and not a terminal, qualitative state. That is, non-brachydont teeth can be somewhat hypsodont, more hypsodont, even more hypsodont, extremely hypsodont, and so on. For convenience, researchers have often applied various names to different degrees of hypsodonty along the hypsodonty continuum (e.g. “mesodont” for species showing relatively intermediate degrees of hypsodonty—see also the discussion in Section III). Many such schemes reserve the unqualified term “hypsodont” for the end (or near-end) state of the series, and, unfortunately, this has led to frequent confusion. It is not always clear what a researcher means by describing a species as being, simply, “hypsodont”, and in this case a reader might be led to conclude that only extremely hypsodont species exhibit “hypsodonty”. By contrast, other researchers call teeth of only moderate

hypsodonty “hypsodont” (see discussion of the extinct equid genus *Merychippus* in Section VIII).

Hypsodonty is seen in mammal species of all sizes, rodents as well as ungulates, so a continuous hypsodonty index that standardizes crown height for overall body mass has been found to be useful when comparing degrees of hypsodonty among species (Janis, 1988; Van Valen, 1960). For example, the traditional hypsodonty index—the ratio of the unworn height of the tooth crown to its length or width—can be considered to be independent of body mass because all dental dimensions, including crown height, have been found to scale approximately isometrically (Fortelius, 1985; Janis, 1988). In this review, as in most current literature, when we refer to a particular degree of hypsodonty in a certain species, we base this on such a standardized index.

Once hypsodonty has evolved it appears to be ordinarily retained in a lineage. However, many lineages have remained persistently brachydont throughout their evolutionary history. In any particular species, hypsodonty reflects the evolutionary history of selection imposed by the effects of high rates of dental abrasion in its lineage. At the same time, because individuals of different species may experience different levels of dental abrasion during their lifetimes (depending upon their species-specific dietary and habitat preferences), the resistance to wear conferred by different degrees of hypsodonty may impose constraints on the contemporary ecology of individuals. For example, low-crowned species cannot sustain themselves for long on extremely abrasive diets that would wear out their teeth at an early age, and are not likely to compete successfully with more hypsodont species for such resources. Hypsodonty is an adaptation to endure wear, and, as in the case of any phenotypic trait subject to a history of selection, it contributes to adaptation when the ecological circumstances of an individual match those of its ancestors. Thus it is reasonable to assume—and published analyses confirm—that an index of hypsodonty will have some predictive power for the ecology of both past and present species, although, as with other palaeoecological proxies, such predictive ability will likely not be perfect.

## (2) Distribution of hypsodonty among mammals and its evolutionary record

Hypsodonty has evolved among ungulates, living and extinct, a minimum of 17 times among the orders Artiodactyla and Perissodactyla alone, not counting individually different times within families (e.g. multiple times within the Bovidae; Janis & Fortelius, 1988).

Hypsodonty has been widely interpreted as being associated with diet, especially in ungulates, which are the focus of this review: grazers [those taking almost entirely (>90%) grasses in the diet] in general are highly hypsodont, but browsers [those taking almost entirely (>90%) leaves of dicotyledonous plants] are in general brachydont, while mixed feeders (taking both browse and grass in mixed proportions over the seasons) are often hypsodont or, depending on the diet and/or habitat preference of the

species, may remain brachydont or have an intermediate condition (“mesodonty”). It is generally assumed that grass is a more abrasive food than browse. However, hypsodonty is also associated with feeding at ground level in open habitats in general, irrespective of the proportion of grass in the diet, so a more important agent of abrasion is likely to be soil particles (grit) adhered to the food surface (as will be discussed in Sections III and IV). Finally, the actual amount of food eaten per day may contribute to the level of hypsodonty: for example, equids eat more food per day than ruminant artiodactyls of a similar size, due to their system of hindgut fermentation, and are correspondingly more hypsodont than ruminants of similar diet (see discussion in Janis, 1988).

The earliest appearance of hypsodonty in mammals was among the small gondwanatherian mammals (likely the sister taxon of multituberculates: Gurovich & Beck, 2009) of the Late Cretaceous and early Palaeocene of South America. Their hypsodonty is likely related to subterranean foraging of roots and tubers containing sediment (Koenigswald, Goin & Pascual, 1999). The stylinodontid taeniodonts, pig-sized animals of the Palaeocene and early Eocene of North America, were also hypsodont, and one taxon (*Stylinodon*) was hypselodont (i.e. it had ever-growing teeth). Stylinodontid taeniodonts had postcranial skeletons suggestive of digging adaptations, and their hypsodonty is also likely related to eating roots and tubers (rhizophagy) and thus ingesting large amounts of soil (Lucas, Schoch & Williamson, 1998).

The appearance of hypsodonty in many species of ungulates (and also in rodents and lagomorphs) in the mid Miocene is broadly coincident with the spread of grassland habitats, as will be discussed in some detail in Section VIII. However, an important point to note is that there are additional rare instances of hypsodonty in ungulates during the Palaeogene, when extensive grasslands were certainly absent. The extremely hypsodont camelid *Stenomylus* is common in the Oligocene of North America, before the purported spread of grasslands, and its very narrow muzzle suggests highly selective feeding (albeit evidently on an abrasive diet) rather than grazing (see Clauss, Kaiser & Hummel, 2008, for a review of craniodental adaptations associated with diet in ungulates).

Hypsodonty has also evolved among marsupials, although to a lesser extent than among placentals. Kangaroos comprise the major (extant) radiation of herbivorous marsupials: a certain degree of hypsodonty is seen among the mixed-feeding and grazing forms, although they never attain the degree of hypsodonty seen in ungulates (see Janis, 1990, for discussion and a possible explanation). Hypsodonty was also seen in some diprotodontids (rhino-sized wombat-related forms), and hypselodonty (ever-growing cheek teeth) is seen in wombats. Wombats are predominantly grazers, but they are also burrowers and their extreme degree of dental durability is likely related in part to a rhizophagous habit, as with the forms discussed above. The transition to hypsodonty in certain lineages of Northern Hemisphere placentals was in the mid Cenozoic, but the limited hypsodonty of marsupials is not seen until the Plio-Pleistocene, which may be related

to the later spread of grasslands in Australia (Archer, Hand & Godthelp, 1994). The exception to this is wombats, where a hypsodont form is known as early as the late Oligocene or early Miocene (Brewer, Archer & Hand, 2008), but in this taxon hypsodonty likely reflects rhizophagy rather than adaptation to grasslands. Finally, there is the issue of so-called “precocious hypsodonty” in many South American mammals, most notably in the endemic notoungulates, and this has often been cited as evidence for early (late Eocene) spread of grasses and grazing on this continent. However, other explanations can be offered for the timing of the appearance of hypsodonty in South America (Billet, Blondel & Muizon, 2009; Kay *et al.*, 1999; Strömberg *et al.*, 2010).

### (3) Alternative ways of resisting wear, and the potential costs of hypsodonty

Fortelius (1985) notes that hypsodonty reflects the total amount of dental wear encountered by an animal in its lifetime. This may relate to phytoliths in grasses, grit present on the food, high occlusal stress, or mastication of large amounts of food; i.e. many possible processes besides a simple diet of grasses. Hypsodonty, as opposed to alternative ways of altering tooth morphology to resist wear, is an effective adaptation for ungulates for a number of reasons. Increased occlusal area has been proposed as a mechanism to increase the durability of the dentition, but in fact it is ineffective at resisting the rate of wear (Fortelius, 1985).

In bunodont forms, famously including hominoid primates, enamel thickness can be the main trait affecting dental durability (e.g. Martin, 1985). However, this solution is likely to be counterproductive in an herbivore with lophed teeth where the functional occlusal surface is reliant on the initial wearing away of sections of the enamel crown to expose the dentine, thereby creating multiple enamel/dentine ridges that cut the food (Janis & Fortelius, 1988). This is not to say that differential hardness or thickness of dental tissues have no effect on dental durability in mammals, only that they appear subordinate to changes in crown height, especially in lophodont and selenodont forms.

Janis & Fortelius (1988) also note that, *contra* Mones (1982), the hypsodonty seen in ungulates cannot be considered to be an intermediate stage on the evolutionary pathway to hypselodonty (ever-growing cheek teeth) as seen in many rodents. This is because, due to the way that teeth develop, the complex crown pattern of enamel ridges upon which ungulate dentitions depend for their function, and which are formed in part as enamel-encased pockets (infundibula), cannot be renewed after the crown that was initially laid down prior to eruption has been worn away. Hypselodont teeth can renew only the enamel rim because enamel is an ectodermally derived tissue. A few cases of hypselodonty are nevertheless known among extinct ungulates (e.g. the rhinoceros *Elasmotherium*), usually with compensatory infolding of the external rim of enamel to recreate the original occlusal pattern (see Janis & Fortelius, 1988).

Although the multiple times that hypsodonty has evolved lead us to conclude that it is a fairly easy feature to develop, nevertheless the lack of hypsodonty in many forms also leads us to speculate that there may be some cost to its acquisition in terms of performance and/or overall craniodental function. Obviously, if an animal is eating an abrasive diet then the benefits of hypsodonty will outweigh any disadvantages. Certainly, anything more than a moderate degree of hypsodonty necessitates various changes in skull shape to accommodate the higher-crowned cheek teeth (see Janis, 1995), and this, too, may have some sort of evolutionary cost. The type of hypsodont tooth typical of specialized grazers, with a flat occlusal surface, may not be a good morphology for browsing (i.e. cutting leafy material). This type of flat, multiridged surface (elephants representing an extreme example of this), where an infilling of cementum is laid down prior to eruption protecting the lophs that extend through the entire height of the tooth (see Janis & Fortelius, 1988), may be a good morphology for processing flat blades of grass but is likely not optimal for cutting material of different physical properties such as dicotyledonous leaves or twigs.

Note that bilophodont cheek teeth (such as are found among tapirs and kangaroos, among extant mammals) are never made highly hypsodont, as they are composed entirely of slicing blades that would be rendered functionless by an infilling of cementum. Grazing kangaroos (all bilophodont) are somewhat more hypsodont than browsers, but the amount that they can increase their crown height is limited, and they adopt a complex type of molar progression to effect a more durable dentition (Sanson, 1978). The Eocene African megaherbivore *Arsinoitherium* may be unique in having evolved a significantly increased tooth crown while still retaining the bilophodont occlusal shape (Court, 1992). Another exception is the ever-growing (hypselodont) bilophodont teeth of extinct ground sloths; but sloth teeth maintained a continually replacing cutting edge by having two layers of dentine (of differing hardness) rather than dentine and enamel (as dentine is a mesodermally derived tissue this does not entail the developmental constraints on continual tooth growth that are encountered with enamel; see further discussion in Janis & Fortelius, 1988).

Thus the optimal morphology for hypsodont cheek teeth may be in conflict with the morphology best suited to cut browse rather than to process grass. If the diet leads to severe dental abrasion then of course having a dentition that lasts a lifetime is a more pressing issue than cutting efficiency. But this is different from the notion that adding hypsodonty might simply enable an herbivore to broaden its diet (e.g. Feranec, 2007; Rivals, Semperebon & Solounias, 2010) and explains why many taxa remain persistently brachydont despite this apparently appealing option.



## II. HISTORY OF IDEAS ABOUT HYPSONDONTY

### (1) Introduction

One of the stranger aspects of the scientific discussion of hypsodonty is that it has been almost entirely limited to the palaeontological literature. Furthermore, although the story of the Neogene spread of grasslands and the evolution of high tooth crowns in ungulates entered general texts in the late Nineteenth Century, there was never a scientific, evidence-based consensus on exactly what it was about the diet of hypsodont forms that was causing the increased abrasion that was presumably acting as the selective force on tooth crown height. Over a century passed before systematic and quantitative studies of living ungulates were undertaken to determine how hypsodonty is today functionally and statistically related to diet and ecology (Janis, 1988). Although we now understand a great deal more about the subject, the long history of informal speculation in the literature has led to a persistent, widespread misconception about what we know, how long we've known it, and what the empirical evidence shows. Specifically, one gets the impression from literature published since the 1960s that it has been established that hard silica bodies (phytoliths) secreted by plants, which are abundant in grass (and less commonly so in browse plants; Piperno, 2006), are the primary (or even sole) agents of high tooth abrasion in ungulates. It is difficult to trace the origin and spread of this idea, since without a body of empirical observations to frame the discussion, most authors have expressed their ideas about the specific causes of tooth abrasion in ungulates somewhat noncommittally and in the briefest possible way.

### (2) The first century

Vladimir Kovalevsky (1874) first recognized what we now regard as the adaptive significance of ungulate hypsodonty, noting that it was an independent evolutionary trend within different lineages of ungulates that had progressively adapted to the open, grassy habitats spreading in the later Cenozoic, where (among other things) the ungulates presumably included increasing amounts of grass in their diet. After describing how, in his view, the increased lateral component of chewing necessary to comminute grass would increase tooth wear, he went on to say (p. 211): "Moreover, graminivorous animals take up a considerable amount of sand and dirt along with grass, which causes even more rapid wear on the molars." [*Ausserdem aber greifen graminivore Thiere zusammen mit Gras auch viel Sand und Erde auf, was eine noch raschere Usur der molaren bedingt.*] Kovalevsky did not elaborate further or suggest any other causes of increased wear.

Subsequent authors universally recognized the association of the evolution of hypsodonty and the spread of grasslands, and tersely expressed many variations on putative causes of wear. Many researchers remained noncommittal, however, and often the topic was treated in a sentence or less. Huxley (1886) focused on the fact that grazers needed effective and "long-lasting" grinding teeth, but avoided identifying an

abrading agent. Likewise, Osborn (1910) and Lull (1917), rather ambiguously, referred only to the fact that grass is "hard" or "harsh", and this caution was echoed by many later authors (e.g. Carroll, 1988; Webb, 1977, 1978). Matthew (1913, 1926) explained that it is the increased chewing necessary to extract nutrients from "tough" grass that is the selective force behind hypsodonty. On the other hand, Scott (1913) stated, without further elaboration, that it is the phytoliths in the grass that cause tooth abrasion, as if this were already an established fact. Stirton (1947, 1959) believed that the primary abrasive agent was grit adhering to open-country vegetation, and not phytoliths. Simpson (1944) clearly implied that grass itself was "abrasive" without mentioning silica, but later (Simpson, 1953) was careful to include three factors—diets high in fibre, silica, or grit—in part to explain hypsodonty also observed in non-ungulates. Stock & Howard (1963) explained that horses needed grinding molars to chew "harsh" grasses effectively, but attributed hypsodonty and high tooth abrasion to "sand grains taken into the mouth while grazing." Romer (1966) repeated the phytolith hypothesis but was sceptical of it, preferring an explanation involving increased food requirements of larger species.

Possibly the only writer to propose a non-adaptive reason for the evolution of hypsodonty was White (1959), whose neo-Lamarckian perspective considered tooth crown height to be primarily the result of the mineral content of the food and the activity of the endocrine glands rather than the result of selective forces resulting from the diet or rate of tooth wear.

As these examples show, at the end of the first century of discussion of hypsodonty there were many statements in the English-language literature implying that there was "something" about grass—or feeding on grass—that led to tooth abrasion, but there was no evident consensus about what it was.

### (3) Recent trends

In recent decades there seems to have been a comparatively rapid coalescence about the view that grass phytoliths are the primary (or even sole) cause of high tooth wear in large ungulates. This is surprising in that there seems to be no new evidence cited in direct support of such a hypothesis. The result has been that the habitat, or external grit, component of the previous array of explanations has become secondary or has disappeared; grass alone is now frequently portrayed in secondary and general biology texts as the sole factor causing rapid abrasion in ungulates (though phytoliths are not always mentioned, and the ungulates are usually simplified to horses alone) (e.g. Brooker *et al.*, 2008; Futuyama, 1986).

Coincident with this increased focus on phytoliths has been a trend to identify the evolution of horses and grasses as a significant example of coevolution (a term coined by Ehrlich & Raven, 1964; e.g. Herrera, 1985; MacFadden & Cerling, 1994; McNaughton & Tarrants, 1983; McNaughton *et al.*, 1985; Stebbins, 1981). Coevolving species drive each other's evolution by imposing reciprocal selection pressures—the

horse-tooth *versus* grass-phytolith system has proven to be an appealing postulated example. However, by definition inorganic grit cannot play a part in any coevolutionary scenarios.

Whether influenced by this novel focus, or simply reflecting conceptual “drift” in the absence of a well-cited body of research upon which to draw, current discussions are framed almost entirely by tacit acceptance of the primacy of phytoliths in causing ungulate tooth wear. Nonspecialists (e.g. Judson, 2010) can perhaps be forgiven for believing that there is a long-standing consensus for the phytolith story based on a substantial body of evidence, but the story’s relatively uncritical acceptance by so many active researchers in the field is not easy to justify.

### III. HYPHODONTY, DIET AND ECOLOGY IN EXTANT UNGULATES

The first, and so far only, comprehensive collation of measures of hypsodonty indices for extant ungulates (including X-rays of the jaws of hypsodont forms) was by Janis (1988). In this paper Janis examined the correlation of hypsodonty index, third molar height, third molar volume,

Table 1. Dietary categories of Janis (1988), taken from Hofmann & Stewart (1972)

Grazer (GG): taking >90% of grass in the diet (lumps together “roughage grazers” and “dry region grazers” of Hofmann & Stewart, 1972).
Fresh grass grazer (FG): grazer feeding in edaphic, or near-water, habitats.
Mixed feeder in open habitats (MFO): taking <90% and >10% grass in the diet, found in prairie (= treeless grasslands) or savanna (= treed grasslands) habitats [broadly, but not entirely, equivalent to the Hofmann & Stewart (1972) category of “intermediate feeder preferring grasses”].
Mixed feeder in closed habitats (MFC): taking <90% and >10% grass in the diet, found in bushland, woodland or forest habitats [broadly, but not entirely, equivalent to the Hofmann & Stewart (1972) category of “intermediate feeder preferring forbs, shrubs, and tree foliage”].
Browser (BB): taking <10% of grass in the diet, subsisting on dicotyledonous herbage (= “tree and shrub foliage eater” of Hofmann & Stewart, 1972).
Selective browser (SB): a “selective” browser taking a considerable portion of fruit, buds and berries in its diet, and preferring young leaves to mature ones (= “fruit and dicot foliage selectors” of Hofmann & Stewart, 1972). (Note: the reference to such animals as “succulent feeders” has on occasion been mistakenly interpreted as feeding on cacti, which was not the original intention of this category.)
High level browser (HB): a browser habitually feeding at levels considerably above the ground, such as giraffe, gerenuk, or moose (category not considered by Hofmann & Stewart, 1972).
Omnivore (O): taking a considerable amount of animal material as well as herbage (suoids only) (category not considered by Hofmann & Stewart, 1972).

and total postcanine tooth volume, with diet and habitat, using the dietary classification of Hofmann & Stewart (1972) (see Table 1 for a definition of their dietary classes). These data are frequently cited, but the conclusions of Janis (1988) are often, unfortunately, either ignored or misconstrued. For this reason, we review here some of the major conclusions of that paper (and summarize the statistical results in Table 2).

- (1) Hypsodonty should be defined, not by any relative dental measurement, but by the condition where the base of the crown of the newly erupted tooth lies within the bone of the jaw, rather than the junction between crown and root occurring at the level of the jaw bone (= the gum line in life), as is the condition in most mammals. Mones (1982) defined hypsodonty as the condition when the crown height of the tooth exceeds the antero-posterior length, and while this may provide a practical assessment, it does not address what has actually happened in terms of achieving this derived dental condition: i.e. a shift in timing in tooth development. Obviously there may then be “degrees of hypsodonty”, but it is this first step that represents the deviation from the generalized, primitive brachydont condition. Hypsodonty is, moreover, distinct from simply exhibiting taller cusps, a derived condition that

Table 2. Results of statistical analyses of Janis (1988)

#### Hypsodonty index:

GG > all other taxa [also true when equids (more hypsodont than ruminants) are excluded] MFO > MFC, BB, SB, HB, O (but not distinguishable from FG).

FG > MFC, BB, HB, O (>SB if small bovids excluded).

MFC, BB, SB, HB, and O cannot be distinguished from each other.

#### M<sub>3</sub> height:

GG > all taxa except MFO

MFO > all remaining taxa except O

No other taxa can be distinguished from each other.

#### M<sub>3</sub> volume:

GG > all taxa except MFO

MFO > all remaining taxa

FG > MFC, BB, SB, HB, O

MFC > HB, O

BB > HB

SB > HB

No other taxa can be distinguished from each other.

#### Total postcanine tooth volume (excluding equids):

GG > all taxa except MFO, O

MFO > all remaining taxa except O

MFC > HB

BB > HB

No other taxa can be distinguished from each other.

Dietary categories and abbreviations as in Table 1. With the exception of the hypsodonty index, all values are from residuals calculated from a log/log least-squares regression line of the value plotted against body mass. [Certain caveats applied for the species included in the construction of the regression line, see Janis (1988) for details].

may be seen in some herbivorous species, including brachydont forms. High cusps may contribute to the measured height of the tooth crown, but are not the result of a developmental delay in root formation, and are more likely to relate to tooth function rather than tooth durability.

- (2) Janis (1988) defined a hypsodonty index as the unworn M<sub>3</sub> crown height divided by the occlusal width of the same tooth, and proposed the following definitions of “degrees of hypsodonty” based on the hypsodonty index (HI): brachydont HI < 1.5; mesodont HI > 1.5 < 3.0; hypsodont HI > 3.0 < 4.5; highly hypsodont HI > 4.5.
- (3) Janis (1988) concluded that grit and dust on the food were likely to be more important as abrasive elements than silica, for the following reasons:
  - (i) Third lower molar crown height (i.e. the level of hypsodonty) could not distinguish between grazers and mixed feeders in open habitats.
  - (ii) Mixed feeders in open habitats had significantly higher-crowned teeth than mixed feeders in closed habitats. Note that this was not simply related to the amount of grass in the diet: some open-habitat mixed feeders, such as the pronghorn *Antilocapra americana*, consume relatively small amounts of grass yet are highly hypsodont.
  - (iii) Fresh grass grazers (species eating grass in floodplains, etc., where water might wash grit and other substances off the plant) had molar crown heights significantly lower than either regular grazers or mixed feeders in open habitats (but were significantly more hypsodont than other feeding types).
  - (iv) High-level browsers (species habitually browsing well above ground height) were significantly less hypsodont than low-level feeding browsers in the same habitat [for example, giraffe (*Giraffa camelopardalis*) versus kudu (*Tragelaphus strepsiceros*)].
- (4) Janis (1988) thus concluded that hypsodonty alone could not be taken as evidence for grazing behaviour in extinct ungulates, although other aspects of the morphology (e.g. muzzle width or dental microwear) might certainly help in distinguishing grazers from similarly hypsodont mixed feeders in open habitats. Although it may be true that most highly hypsodont taxa today are grazers, some grazers have a lesser degree of hypsodonty (i.e. HI of <4.5). Note that Janis (1988) did not assert (*contra*, e.g. implications in MacFadden & Cerling, 1994: p. 485) that grit was the only causal factor in the evolution of hypsodonty.

Janis used these data subsequently to demonstrate the correlation between hypsodonty and the percentage of grass

in the diet in living ungulates (Janis, 1995). The correlation, while significant, had a low  $r^2$  value (0.39) and the scatter of the points around the regression line further made it clear that hypsodonty was related to other factors in addition to grass *per se*.

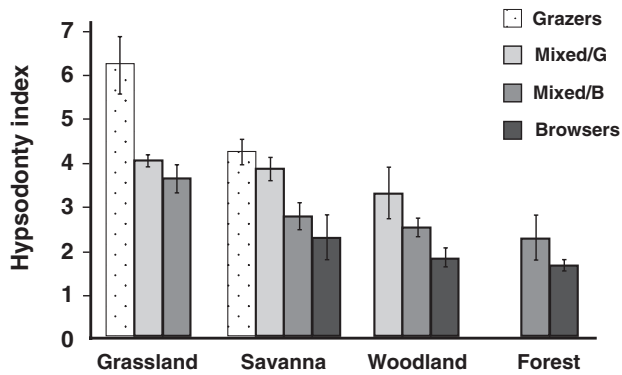
Numerous subsequent analyses, based largely on the Janis (1988) dataset and using a variety of different statistical and comparative techniques, have uncovered additional details but agree with Janis’ major conclusions from 1988 (e.g. Codron *et al.*, 2008; Clauss *et al.*, 2008; Mendoza, Janis & Palmqvist, 2002; Mendoza & Palmqvist, 2008; Pérez-Barberia & Gordon, 2001; Williams & Kay, 2001). All—including analyses based on phylogenetic contrasts (Williams & Kay, 2001)—confirm the strong correlation of hypsodonty with diet, and also confirm patterns in the data that can best be explained by postulating a predominant role for grit in influencing hypsodonty.

Fig. 1 is based on the data of Janis (1988) and summarizes graphically the major relationships between the degree of hypsodonty on the one hand, and diet and habitat on the other. The figure shows the mean hypsodonty index observed in the extant ungulates, grouped by feeding type and habitat type. This pattern indicates the very clear, statistically independent relationships of hypsodonty with both diet and habitat in living species. Species eating greater proportions of grass in any given habitat have, on average, a higher hypsodonty index; at the same time, species living in more open habitats have higher hypsodonty than those in closed habitats, irrespective of diet.

Fig. 1 shows that there is a component of hypsodonty, and, by inference, of wear, associated with habitat that is independent of diet. However the fact that we can statistically distinguish a dietary and a habitat component to HI variation in Fig. 1 does not mean that we have distinguished two distinct causes of tooth wear, one involving the food material itself and one the habitat. For example, if grit is more abundant in open habitats, and, simultaneously, if eating grass in any habitat simply leads an individual to consume even more grit, then the statistical pattern in the figure could be causally explained without any contribution of plant tissues to tooth abrasion. Likewise, if grass has more phytoliths than browse (and is thus supposedly more abrasive), and plants for some reason all make more phytoliths in more open habitats, the pattern would be explicable without any involvement of grit. Understanding the actual causes underlying the observed relationships requires more detailed, critical comparisons of the kind undertaken by Janis (1988) and subsequent researchers working with that dataset, and analysis of the empirical evidence for what causes tooth wear in extant ungulates.

#### IV. CAUSES OF TOOTH WEAR IN EXTANT UNGULATES

Ideas about the causes of tooth wear influence not only our understanding of the broad patterns of ungulate evolution in



**Fig. 1.** Relationship of mean hypsodonty index (HI) to diet and habitat type based upon 133 species of living ungulates of known dietary and habitat preference. Grazer =  $\geq 90\%$  grass in the diet; Mixed/Grazer (Mixed/G) = 50–89% grass in the diet; Mixed/Browser (Mixed/B) = 11–49% grass in the diet; Browser =  $\leq 10\%$  grass in the diet. Forest = closed forest, with few or no clearings; Woodland = more open forest where canopy is still mostly continuous but ground cover may include grass; Savanna = open habitat with grass and scattered trees and bushes; Grassland = grassland steppe with no significant woody plant cover. Height of bars indicates mean HI, and error bars show  $\pm 1$  standard error. Statistical analysis was by analysis of variance (ANOVA), under the following considerations: an interaction plot and preliminary analysis supported the assumption that there was no significant interaction effect, so we tested the main effects (diet and habitat) in an ANOVA using “Type V” sums of squares for unbalanced data (Hill & Lewicki, 2007). The ANOVA revealed significant independent effects of both diet ( $P < 0.0001$ ) and habitat ( $P < 0.0001$ ) on hypsodonty index (*Statistica*, Version 9, StatSoft, Tulsa Oklahoma; *JMP*, Version 7, SAS Institute Inc., Cary, NC, 1989–2007). This figure is based on one published in Janis *et al.* (2002), using data from Janis (1988, 1995), with an updated analysis and dataset. Primary literature references on dietary composition are available from C.M. Janis on request.

relation to their environments, but also our reconstruction of the of the probable diets of extinct species, in which hypsodonty and patterns of tooth wear play a major part. Although the general patterns of hypsodonty described above are suggestive, we can go further in attempting to resolve the dominant causal influences of presumed causes of abrasive wear using the available evidence from extant species.

The higher tooth wear rates experienced by hypsodont ungulates have generally been ascribed to three classes of causal abrasive agents: the nutritional, physical and biomechanical properties of plant tissues; the presence of hard silica bodies (phytoliths) secreted by the plants and contained in their tissues; and the action of soil or grit ingested with the food. We consider the current evidence for the contribution of each in turn to increased dental abrasion associated with hypsodonty. In particular, we review in detail the substantial empirical literature on soil ingestion in ungulates, which has not been widely appreciated in the literature on hypsodonty, but appears to have considerable explanatory power.

### (1) “Fibrousness” and “toughness”

Throughout the long literature discussion of ungulate hypsodonty, authors have frequently made reference to physical properties of plant foods in the context of explaining the association of some diets (especially, grass) with high rates of tooth wear. As we have seen, grass is variously described as “fibrous”, “tough”, “hard”, “harsh”, “abrasive”, “difficult to chew”, and as being of “poor [nutritional] quality”. These partly overlapping terms refer to a variety of different kinds of properties thought to affect tooth wear—mostly indirectly—and have not always been used consistently.

As used by most researchers on extant species, the term “fibrousness” is a property of plant tissues that refers to the volumetric ratio of cell contents to the fibrous cell wall containing cellulose and lignin. The soluble cell contents are easily digested, but cellulose requires bacterial fermentation to release nutrients that the ungulate can use, and lignin is almost entirely indigestible by ungulates. Therefore the crude fibre ratio has been considered a rough measure of nutritional quality and digestibility, with more fibrous foods (such as grass) considered to be of “low quality” compared to “high quality” browse. The inference drawn by many is that a more fibrous diet leads to higher tooth wear simply because a greater volume of food must be eaten if it is of poor quality, necessitating more chewing.

However, crude fibre content oversimplifies and does not accurately represent differences in diet quality among browsers and grazers. Natural browse and graze diets may not differ in crude fibre content as much as has been thought (Clauss & Dierenfeld, 2008). Further, digestibility of forage depends upon details of the composition of the fibre component—browse can actually be a lower quality diet than one of grass due to the greater amount of contained lignin (Clauss, Hume & Hummel, 2010; Codron *et al.*, 2007). Since as a result both brachydont browsers and hypsodont grazers may be eating diets of a similar range of digestibilities (albeit of different structure), it seems unlikely that much variation in tooth wear rates is due indirectly to variation in nutritional quality of the diet *per se*. Also, fibre itself is not sufficiently hard to abrade tooth enamel, so high crude fibre content *per se* is also unlikely to contribute directly to increased tooth abrasion.

Fibre also contributes to another property of plant tissue, its “toughness”. Toughness is the resistance of a substance to cutting, and much of the toughness of plant material is related to cell wall thickness and the presence and orientation of fibres. Grass is a particularly tough food because of its parallel venation and high degree of lignification in mature stages (Sanson, 2006). Toughness and related biomechanical properties of different plant foods are difficult to model and have not been well studied experimentally (Lucas, 2004). However, it is thought that the properties described for grass lead to the evolutionary changes in occlusal morphology (multiple small blades, horizontal chewing strokes) and high occlusal forces that characterize specialized ungulate grazers (Fortelius, 1985). With respect to abrasion, it seems likely that higher occlusal forces needed to process tough foods like



grass may increase the effect of abrasive particles (phytoliths, grit, etc.) in the food, but the fibrous tissue itself is not likely to be a significant abrasive agent. The magnitude of such a presumed enhancement of abrasion by occlusal forces alone has not been measured, and is difficult to distinguish from the effects of tooth-on-tooth attrition.

In conclusion, “fibrousness” and “toughness” represent different potential agents with regards to chewing biomechanics, and it might well be the case that neither is directly related to increased hypsodonty (i.e. increased abrasion). Rather, increased hypsodonty might be related to abrasion-causing factors that often accompany fibrousness and toughness (such as phytoliths in grasses or soil and grit on low-lying foods). Thus, strictly, a “fibrous diet” may or may not be tough or abrasive; an “abrasive” diet may or may not include foods that are particularly fibrous or tough. Note that this interpretation undermines the common, informal assumption of a simple grass/browse dichotomy in thinking about causes of hypsodonty: that is, that grass itself is somehow the causal agent of dental abrasion. This might indeed be true, whether or not phytoliths are also themselves significant agents of abrasion, but we note that there is no evidence to actually demonstrate this. Below we present data that suggest that hypsodonty is likely associated with a grazing diet for other reasons than the physical properties of the grass plant itself.

## (2) Phytoliths

Phytoliths (also known as opaline silica and plant silica) are hard, non-crystalline siliceous bodies that some higher plants deposit in their tissues (Piperno, 2006). The abundance of phytoliths in plant tissue varies widely among species, and, although grasses usually exhibit relatively high volumes, some browse plants also secrete high densities of phytoliths (Hodson *et al.*, 2005). Phytoliths are thought to serve a number of adaptive functions in plants, from physical support to defence against herbivores and fungal infections (Piperno, 2006). Phytoliths physically deter some invertebrate pests, and for mammals they decrease the digestibility of plant tissues (Van Soest & Jones, 1968). Excessive consumption of silica can potentially cause serious disease in ungulates (Bailey, 1981; Mayland & Shewmaker, 2001). Phytoliths appear to be an inducible defence in response to herbivory (Massey, Ennos & Hartley, 2007; McNaughton & Tarrants, 1983). However, there is no direct evidence establishing that the adaptive value to the plant of phytoliths comes specifically from an increase in tooth wear of large mammals. Small mammal herbivores (such as voles) seem strongly to prefer plants with low phytolith densities, and suffer nutritional stress when feeding on highly siliceous feed (Gali-Muhtasib, Smith & Higgins, 1992; Massey & Hartley, 2006). However, large-grazer dietary preference is overwhelmingly dominated by general responses to palatability and nutritive value, which are not simply correlated with phytolith content (Blank, Allen & Young, 1994; Launchbaugh, Provenza & Pfister, 2001; Massey *et al.*, 2009; Minson, 1971; Shewmaker *et al.*, 1989). Very high phytolith content may act as an irritant (Laca,

Shiple & Reid, 2001; Massey *et al.*, 2009), but phytoliths do not in general deter feeding by ungulates. Grass phytoliths may indeed be an example of plant-herbivore coevolution, but if so the herbivores involved seem more likely to have been small mammals and insects, rather than mid-Cenozoic ungulates. Significant Cenozoic coevolution with ungulates is even less likely given the recent discovery from dinosaur coprolites that an extensive radiation of grass phytoliths had already occurred by the Late Cretaceous (Prasad *et al.*, 2005).

Literature on mammalian tooth wear usually cites Baker, Jones & Wardrop (1959) as the source of our knowledge of the potential for phytoliths to abrade mammalian teeth. Baker *et al.* (1959) analyzed phytoliths in oats and found that they were harder than tooth enamel, and thus would easily abrade teeth. Recently, Sanson, Kerr & Gross (2007) analyzed phytoliths from four species of pasture grass and found that they were softer than tooth enamel, suggesting that the role of phytoliths in tooth wear may have been overestimated. At present, we have no additional information on the variation in hardness of grass phytoliths that would permit resolution of this issue.

## (3) Soil ingestion and the dominance of grit

### (a) Introduction

As we have seen, the ingestion of abrasive particles that are not part of plant tissue, such as soil, dust, sand, wind-blown grit, etc., was among the first explanations for the high tooth abrasion experienced by ungulate species adapting to the open habitats of the mid and later Cenozoic (Kovalevsky, 1874). Although never completely disappearing from the literature, grit has in recent years been discounted in favour of grass phytoliths (and, perhaps, other characteristics of grass tissue such as “fibrousness”), probably in part because of the obvious (but imperfect) association between high tooth wear and a diet containing a large proportion of grass (Fig. 1; Janis, 1995). This interpretation is in spite of the detailed patterns of statistical relationships among hypsodonty, feeding height, habitat and diet in living species that suggest a more important role for grit (Janis, 1988). Consideration of empirical, quantitative knowledge of soil ingestion among ungulates may suggest a resolution of this conflict, and further suggests a comprehensive explanation of (1) the apparent dominance of grit levels in determining levels of ungulate tooth wear, (2) the habitat associations of hypsodonty and tooth wear, and (3) the association between high tooth wear, hypsodonty and grazing. We also suggest why the general dominance of grit is expected regardless of the degree to which phytoliths themselves abrade tooth enamel.

### (b) Incidental soil ingestion while feeding

Observations among extant ungulate grazers reveal that some species inadvertently consume a surprisingly large amount of soil while feeding. This represents soil that is unintentionally consumed because it is mixed with or adhering to the grass as it is eaten. Incidental soil ingestion

by domestic cattle can range from 1% to 18% of their daily dry matter intake (DMI), depending upon the season (Green & Dodd, 1988; Kirby & Stuth, 1980; Mayland *et al.*, 1975; Mayland, Shewmaker & Bull, 1977; Sneva, Mayland & Vavra, 1983; Thornton & Abrahams, 1983); annual or grazing season averages are about 4–6%. Sheep, which crop the grass closer to the ground, can show peak soil intakes of as much as 33% of DMI in New Zealand (Healy & Ludwig, 1965*a, b*), though average values tend to be in the range of 5–9% (Abrahams & Steigmajer, 2003; Healy & Ludwig, 1965*b*; Hedley, Loganathan & Grace, 2007; Rhind *et al.*, 2002; Vaithyanathan & Singh, 1994). These values are comparable to those observed for feral horses (5%; Sneva *et al.*, 1983), bison (*Bison bison*) (6.8%; Beyer, Connor & Gerould, 1994), and the mixed-feeding pronghorn (*Antilocapra americana*) (4.1–5.4%; Arthur & Gates, 1988; Sneva *et al.*, 1983). By contrast, in the mixed-feeding wapiti (*Cervus canadensis*), and in primarily browsing species such as moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*), soil intake has been measured as <2% DMI, which is usually below the level of further resolution of the techniques (Arthur & Alldredge, 1979; Beyer *et al.*, 1994; Sneva *et al.*, 1983).

Although not all soil particles are likely to be harder than tooth enamel, major soil constituents such as quartz certainly are (Mayland & Shewmaker, 2001; Mayland *et al.*, 1977; Sanson, 2006). Thus ingested soil should be highly effective at abrading teeth, and there are numerous anecdotal reports to that effect (e.g. Rue, 1997: p.130; Mayland & Shewmaker, 2001; Mayland *et al.*, 1977; Robinette *et al.*, 1957). Healy and colleagues demonstrated that incisor wear rates in sheep are directly proportional to the amount of soil ingested on different farms and in experimental situations (Healy & Ludwig, 1965*b*; Ludwig, Healey & Cutress, 1968).

The dominant influence of variation in soil consumption on variation in ungulate tooth wear rates, and, by inference, hypsodonty indices, may be understood by comparing the percentage of phytoliths in plant foods with the above values for soil ingestion. Median phytolith mass, as a percentage of the dry matter of plant tissue in grass leaves and shoots, was 2.68% in a compilation of 130 non-crop species of Poaceae (Hodson *et al.*, 2005). Individual grass species seldom exhibit values exceeding 4%, though values above this range for some species (up to 8%) have been reported in some heavily grazed tropical savannas (McNaughton & Tarrants, 1983; Melzer *et al.*, 2010; Piperno, 2006). In Healy & Ludwig's (1965*b*) study of tooth wear and soil ingestion in sheep, measured phytolith abundances were between 0.6% and 1.9% of dry plant matter (and showed no consistent relationship with tooth wear rates). Values for total faecal silica (which does not distinguish between silica derived from phytoliths and that from soil) are reported by Hummel *et al.* (2010) for 15 African savanna large herbivores. Under reasonable assumptions of forage digestibility and phytolith content, the soil ingestion levels that these values imply are consistent with those observed for other ungulates, as described above. Thus, if the available soil ingestion values

for ungulates are typical, it appears that an ungulate will on average consume at least as great—and often many times greater—mass of soil particles than of phytoliths, even when feeding on a diet entirely of grass. Therefore we should not be surprised that variation in soil consumption appears to be so significant in statistically explaining patterns of hypsodonty.

Comparison of browsing (mule deer), mixed-feeding (pronghorn) and grazing species (cattle, feral horses) in the same semi-arid shrub-steppe locality in Oregon forms an illustrative example (Sneva *et al.*, 1983). Here the pronghorn, a species showing comparable hypsodonty to grazing cattle and horses (Janis, 1988), and which in similar habitats in Montana shows molar tooth wear rates comparable to those of specialized grazers (Lubinski, 2001; Solounias, Fortelius & Freeman, 1994), also consumes annually approximately the same proportion of soil in its diet as do the two grazers. However, since it feeds on grass only in the early spring and December, and browses the rest of the time, it must annually consume a considerably lower volume of phytoliths than do the grazers. Moreover, there is a period in the spring when all four species, including the mule deer, are feeding on grass, and at this time they all show similar levels of soil consumption. Yet, when the mule deer, a brachyodont species characterized in open range habitats by low annual rates of tooth wear (Robinette *et al.*, 1957), later switches to browsing, its soil ingestion rate drops dramatically, while at the same time the pronghorn—even though browsing on many of the same plant species as the mule deer—maintains very high levels of soil ingestion, presumably because it usually feeds closer to the ground than does the mule deer. This is during a time of year when both species are consuming no grass and thus very low proportions of phytoliths. Thus, in this example, hypsodonty and wear rates (measured in similar habitats elsewhere) vary with levels of soil ingestion, but not with presumed phytolith consumption, nor, entirely, with proportion of grass in the diet.

Nevertheless there is globally a positive correlation between a grazing diet and hypsodonty index (Janis, 1988, 1995), and a similar relationship can be seen above between a grazing diet and quantity of soil ingested when comparing typical values for grazers and browsers. We may understand how these associations come about by considering the physical relationship between soil and vegetation in ungulate habitats, and the way that different forages require ungulates to feed.

The major processes responsible for resuspension of soil and its deposition on the surface of plants are wind, rain splash, and disturbance by animals (either the grazers themselves or other species) (Healy & Ludwig, 1965*a*; Pinder *et al.*, 1991). Mass loadings of soil on standing vegetation have been measured in a variety of circumstances and the general patterns conform to common intuition. Soil loading varies from approximately 1–250 mg g<sup>-1</sup> of dry plant mass, varies with plant morphology (e.g. leaf shape and size), and is strongly related to height above the ground (Beresford & Howard, 1991; Green & Dodd, 1988; Sheppard, 1995; Smith & Jones, 2000). In a study in European sheep pastures,

above 10 cm from the ground the mass of soil adhering to the grass dropped more than threefold (Hinton, Stoll & Tobler, 1995). Above 40 cm the amount of soil can be more than an order of magnitude less than at ground level, in a variety of habitats (Dreicer *et al.*, 1984; Pinder *et al.*, 1991; Sheppard, 1995). Similarly, the soil adhering to leaves of trees and bushes is reported to be more than an order of magnitude below values measured on grass near ground level (Cary & Kobota, 1990; Sheppard, 1995; Smith & Jones, 2000).

Open and dry habitats clearly have more potential for wind to resuspend soil and deposit it on leaves. However, rain splash also can transmit substantial amounts of soil to plants below 40 cm in height, and this effect depends partly on the energy of the rain (Dreicer *et al.*, 1984). Volumes of adhering soil caused by rain splash can equal or exceed the volumes attributable to wind (Li, Gerzabek & Mück, 1994). Rain splash is particularly effective in arid environments with patches of bare soil; in wetter environments with substantial vegetation cover rain is more likely to remove soil from plant surfaces. However, damp or muddy ground may lead to increased soil loading by enhancing the effect of disturbance and trampling by animals (Hinton *et al.*, 1995). The behaviour of the herbivores thus interacts with the effects of physical factors such as wind and rain, as well as the lushness of the vegetation, to result in variation in soil loading on plant surfaces.

Palaeontologists have generally assumed that wind-blown particles adhering to plant leaves are the major source of grit in the diets of species feeding in open habitats [hence Stirton's (1947) emphasis on grass morphologies that could catch and hold such grit]. Thus, they have often concluded that grit cannot be a major source of wear in closed habitats such as forests. Surprisingly, suspended dust particles sufficiently large to cause potential tooth wear are found even in the canopies of tropical dry forests and rainforests (Ungar *et al.*, 1995). However, soil adhering to leaf surfaces is not the only, nor necessarily the most important source of dietary grit for ungulates in various habitats.

In some situations grazing ungulates consume a large amount of soil by uprooting grass plants while feeding, and in such cases the total soil intake can be many times greater than could be accounted for by soil loading on grass leaves and stems alone (Mayland *et al.*, 1975). In those seasons where browsers such as mule deer are briefly feeding on grass, and experiencing high rates of soil ingestion as a result, they have been observed to uproot the grass as they feed (Arthur & Alldredge, 1979). The stomach contents of small rainforest frugivore/browsers (species that ordinarily encounter little soil) show visible amounts of soil when the individuals have been uprooting entire seedlings while browsing (Dubost, 1984).

Finally, there is a widespread pattern noted by many researchers that rates of soil ingestion increase with food scarcity and intensity of grazing, and with correlates of these such as herbivore density (Green & Dodd, 1988; Healy & Ludwig, 1965a; Hinton *et al.*, 1995; Ludwig *et al.*, 1968). The reason appears to be primarily the effect of grazing

on lowering sward height and forcing the animals to feed closer to the ground, where they encounter greater concentrations of soil (Beresford & Howard, 1991; Hinton *et al.*, 1995). Tooth wear rates in sheep vary proportionally to the soil ingestion rates that in turn reflect different intensities of grazing (Healy & Ludwig, 1965b; Ludwig *et al.*, 1968). Japanese sika deer (*Cervus nippon*) also show higher molar wear rates as food resources become scarce, although soil ingestion rates in these populations have not been reported (Takahashi, Kaji & Koizumi, 1999). Thus, the height-related distribution of soil on the plants in different habitats, the requirement for animals in more open habitats to feed closer to the ground (because of the vegetation structure), and the requirement for grazers often to feed especially close to the ground (because of plant stature), is completely consistent with the relationships of habitat and feeding height observed for hypsodonty, and with the inference that grazing species on average experience greater rates of tooth wear because they consume more grit in their diet.

#### (c) Geophagy

In addition to incidental soil ingestion, many ungulates are known to ingest soil intentionally (geophagy). Often the soil is consumed at certain natural locations, misleadingly known as "licks". Geophagy has usually been considered as a way for ungulates to supplement a mineral-deficient diet, but it has also been suggested as a way to help counteract the toxic effects of plant secondary compounds in forage (Houston, Gilardi & Hal, 2001; Kreulen, 1985; Launchbaugh *et al.*, 2001). As such, it would appear to be of greatest value to animals that include mostly browse in their diet and do not consume very much soil otherwise, but there is wide variation in the occurrence and intensity of geophagy (Ayotte *et al.*, 2006; Kreulen, 1985; Skipworth, 1974). Although geophagy is not common among small rainforest frugivores, larger species feeding in tropical and temperate forests are known to frequent licks (Dubost, 1984; Klaus, Klaus-Hügi & Schmid, 1998; Tobler, Carillo-Percastegui & Powell, 2009; Turkalo & Fay, 2001). Open-habitat species are less likely to do so but have also been observed intentionally eating soil (Langman, 1978; Salter & Pluth, 1980).

Geophagy is relevant to the present discussion because a variety of species are known to chew the soil when ingesting it (Calef & Lortie, 1975; Clayton & MacDonald, 1999; Kennedy *et al.*, 1995; Langman, 1978; Rea, 2007; Weeks, 1978). Such species will suffer tooth wear as a result, but the amount is difficult to estimate or predict, and may differ among populations of the same species. Geophagous species thus could exhibit the wear features caused by soil ingestion and usually associated with eating grass, even if they eat no grass and live in a habitat where grass does not occur.

#### (4) Implications of the empirical data

This review of the published data confirms the importance of soil consumption in explaining patterns of variation in hypsodonty, and suggests that variation in soil consumption



will be generally dominant to other potential contributors to mammalian tooth abrasion such as phytoliths. We are not arguing that grass phytoliths contribute nothing at all to aggregate tooth wear. Phytoliths might vary in hardness across grass species, with some being as hard or harder than tooth enamel, and some softer; at present, we have conflicting information and an inadequate basis for generalization (Baker *et al.*, 1959; Sanson *et al.*, 2007). Furthermore, softer materials, subject to forces such as those that occur during chewing, can physically erode harder materials with which they come into contact (Boyde, 1984; Lucas & Teaford, 1995; Teaford, 1988). In simulated chewing experiments, phytoliths alone can produce microwear features, implying the ability to wear enamel (Gügel, Grupe & Kunzelmann, 2001). Finally, even if phytoliths do not significantly abrade enamel they may abrade softer dental tissues such as dentine and cementum.

However, regardless of how effective grass phytoliths are as abrading agents, ingested soil (“grit”) is likely to be more abundant in ungulate diets than phytoliths and have a greater role in causing variation in tooth wear. Such an interpretation is consistent with detailed relationships among hypsodonty, feeding height, diet and habitat in extant ungulates, and with what we know about the distribution of soil on plant surfaces and among habitats.

The association between greater ungulate hypsodonty and a grazing diet comes about because grazers are feeding on a particular resource (grass) in a particular habitat (open), in a particular way (near to the ground). Whether or not grass phytoliths or other characteristics of plant tissues are significant in causing tooth wear, this combination of factors maximizes the amount of soil that the animal is likely to encounter and unavoidably ingest. Specialized grazers tend to show the highest levels of soil ingestion, the highest rates of tooth wear, and the highest values of hypsodonty among extant species.

Even if an ungulate species is feeding in an environment that in general might seem to have little grit and dust available, such as a forest, it may be feeding in such a way that it ingests considerable soil—for example, by pulling plants out of the ground and consuming the roots, or feeding close to the ground in areas of disturbance by animal activity. Some populations of grazing or mixed-feeding species are reported as living in rainforest regions (e.g. the tamaraw or Phillipines dwarf buffalo, *Bubalus mindorensis*, or the African buffalo, *Syncerus caffer*), but such species do not graze in the primary forest itself, where grass is essentially absent. Rather, such species depend upon edges of watercourses and open areas (sometimes of anthropogenic origin) where grass is abundant, and thus when feeding they are exposed to soil in the same way that grazers are in any open habitat (Bekhuis, de Jong & Prins, 2008; Custodio, Lepiten & Heaney, 1996). Ordinarily, though, lower volumes of soil are ingested in closed habitats, largely because in most places there is little for ungulates to eat in the forest that obliges them to feed very close to the ground or to uproot the plants. High-level browsers in open habitats are likely to encounter only slightly

more grit in their diets than do those browsing in closed habitats, compared with the large amount of soil ingested in open habitats by grazers and mixed feeders that feed primarily at ground level.

## V. TOOTH WEAR, SELECTION AND LIFE HISTORY

The major factors influencing rates of tooth abrasion operate widely and constantly, which raises the question of whether we can detect ongoing or recent selection for increasing or maintaining hypsodonty among populations of living species. Is excessive tooth wear deleterious to fitness of extant individuals or populations, and has variation in hypsodonty been the response to such selection? Both of these relationships may be difficult to detect in studies of extant animals. Consider the case of a population of ungulates living in a habitat to which the members are currently well adapted: excessively worn teeth will be found only in older, senescent individuals, which may be in poor condition for many reasons unrelated to decreased chewing effectiveness. Interannual variation in food availability, or in factors affecting grit in particular habitats, may obscure the conditions that led to even fairly recent episodes of selection. Finally, within a species wear rates may not differ very much among populations, because individuals may differ little in dietary and habitat preferences. Thus it may take large sample sizes to detect the relatively small average differences in hypsodonty that result from small differences in wear rates. We may underestimate the degree of ongoing selection on hypsodonty simply because the situations where the relevant effects are strong enough to be easily measured are unusual and rarely encountered by researchers. These difficulties notwithstanding, there is clear evidence for ongoing selection on tooth crown height in the current literature.

### (1) Rate of tooth wear in relation to diet

In a pioneering paper, Solounias *et al.* (1994) estimated the rates of the wear of the first or second molar of nine ruminant species in known-age individuals. The results clearly showed that wear rates varied with diet: the single browser had wear rates of 0.33 mm year<sup>-1</sup>, the mean rate of the four mixed feeders was 1.2 mm year<sup>-1</sup>, and the mean rate of the four grazers was 2.93 mm year<sup>-1</sup>, all categories being significantly different from each other at the 95% level.

Note that rates of wear are independent of body mass. Although Solounias *et al.* (1994) showed a positive correlation, they speculated that this was an artefact of the fact that the single browser was the smallest animal in the sample, while the largest ones were all grazers. This speculation was supported by the study of Veiberg *et al.* (2007), who showed that mixed-feeding red deer (*Cervus elaphus*) had wear rates twice that of the larger, browsing moose (*Alces alces*). Ozaki *et al.* (2010) also show that body size



has no influence on the rate of tooth wear in Japanese sika deer (*Cervus nippon*).

## (2) Effect of dental wear on life history: body condition, life expectancy and reproductive output

If more abrasive diets result in more rapid dental wear, then ungulates eating diets more abrasive than their usual ones should show consequences of increased molar wear in terms of reduced ability to process food, resulting in a loss of body condition and/or a shorter life span. Van Valen (1960) was exceedingly prescient in recognizing that hypsodonty was ultimately related to issues of lifespan and reproductive fitness (“Its functional significance is to permit a longer maximum life span for an animal of given size, or to allow coarser and more abrasive food to be eaten without decreasing the life span,” p. 531), and that hypsodonty needs to be considered in the context of relative reproductive fitness of populations.

The only paper to examine directly the relationships between diet, molar wear and life expectancy is that of Ozaki *et al.* (2010), who showed that molar wear rates differed among different populations of wild Japanese sika deer. Molar wear rates showed a positive correlation with the amount of grass in the diet, and a negative correlation with precipitation. The durability of the third molars (i.e. their unworn crown height) was also positively associated with lifespan in these populations. Ozaki *et al.* (2010) consider the likelihood that individual deer are eating more dirt and grit in the more arid habitats, but they did not explicitly measure soil consumption. [See also Jordana & Köhler (2011), who document the positively correlated evolution of lifespan and hypsodonty in the fossil bovid *Myotragus balearicus*.]

Given that the rate of dental wear is related to diet, with more abrasive diets wearing the teeth down more rapidly, the possibility arises that an animal taking such an abrasive diet could wear its teeth down completely before the end of its natural reproductive lifespan. Are there indeed documented life-history consequences for animals that wear their teeth down too fast? That is, are there negative fitness consequences for animals with low-crowned cheek teeth subsisting on diets more abrasive than those they would usually encounter, and/or can reduced reproductive capacity at later ages be related to problems of food comminution with worn dentitions?

Skogland (1988) looked at the effect of rapid tooth wear in reindeer (*Rangifer tarandus*), which are relatively brachydont ruminants [HI of 1.52 (all hypsodonty indices here from Janis, 1988)]. Populations of female deer living in poor winter conditions had molar wear rates that were twice as rapid as those living in good conditions, apparently because they were forced to incorporate more abrasive material such as rock lichen in their diets. Despite the fact that all populations had access to good summer resources, the ones with increased tooth wear suffered from depleted body reserves, and lowered reproductive success. Their reproductive output started to decline after six years of age, where in the other populations reproductive output did not decline until the thirteenth year.

Skogland (1988) surmised that the more highly worn teeth were less efficient for mastication, with the result that these deer were less able to convert the rich summer food into the fat deposits important to sustain the young through their pregnancies. Thus this study clearly suggests that worn teeth have a direct deleterious effect on reproductive output, and one might expect the winter-stressed populations to be under selective pressure to increase tooth crown height.

Kojola *et al.* (1998) showed that lichen limitation in reindeer, forcing them to eat more abrasive shrubs, resulted in a substantial increase in dental wear rate. This in turn led to older females having reduced body mass, apparently as the result of less efficient food processing because of the heavily worn teeth. Additionally, a number of studies show that male ruminants have a greater rate of tooth wear than females (see Loe *et al.*, 2003, for red deer): this difference is apparently related to the fact that males select a more abrasive diet, and this may explain, at least in part, why they have a shorter life expectancy than the females.

Nussey *et al.* (2007) showed that female red deer in areas of greater population density and/or lower quality food had faster rates of tooth wear, suggesting an effect of resource quality and availability on dental wear. In this study, an apparent lack of correlation between rate of tooth wear, longevity, and later-life reproductive success led them to conclude that high rates of wear did not have an effect on masticatory efficiency. However, red deer are more hypsodont than reindeer (HI of 2.11), and these measurements of dental wear (as is customary in these studies) were made on the first molar. In more hypsodont ruminants, the second and third molars are higher-crowned than the first one, and so retain high functionality after the first molar has been heavily worn (Solounias *et al.*, 1994). (Indeed, in museum collections it is common to see ruminant jaws where the third molar has only just fully erupted, and yet the first one has been severely worn.) Thus, in these red deer with severely worn first molars, it is likely that the second and third molars retained good functionality, precisely because these deer have dentitions more adapted to abrasive diets (i.e. more hypsodont) than reindeer. Ozaki *et al.* (2010) also make this point about the greater durability of third molars compared with first molars in Japanese sika deer.

Finally, there are examples of the effect of tooth wear on life histories in non-ungulate mammals. Sanson (2006) reviews a number of studies on marsupial herbivores (including possums and koalas) showing the deleterious effects of profound tooth wear on food digestibility and life-history parameters. A rare longitudinal study of tooth wear and reproductive success in the lemur *Propithecus edwardsi* (King *et al.*, 2005) demonstrated a clear link between dental wear and infant survival through the effect of masticatory performance on lactation, a classic scenario for Darwinian selection for increased tooth crown height.

## (3) Evidence for selection for increased hypsodonty

Ozaki *et al.* (2007) examined different levels of hypsodonty within a species in relation to diet and environment, or

environmental history, showing evidence that the effects of selection may have led to altered morphology (i.e. increased hypsodonty). They compared various populations of Japanese sika deer with different diets (*Cervus nippon* is hypsodont for a cervid, HI of 2.79). These deer populations could be grouped into northern and southern lineages, which molecular evidence showed had been isolated for 300,000–500,000 years. The northern deer were significantly more hypsodont than those in the southern lineage (and also took more grass in the diet in general), but among populations of each lineage there was no obvious difference in hypsodonty indices related to diet (i.e. populations that were primarily grazers *versus* those that were mixed feeders), although in both lineages the grazers had more rapid molar wear rates than the mixed feeders. One isolated northern island (Kinkazan) population, encountering particularly harsh environmental conditions, showed a measurable (although nonsignificant) increase in hypsodonty, and extremely rapid rates of molar wear, even though the deer here did not take a greater percentage of grass in their diet than those in other northern populations. The conclusions were that the founding members of the northern lineage, which likely migrated into the Japan archipelago from China during the last glacial period, had acquired their greater degree of hypsodonty during harsher environmental conditions than those encountered by the founders of the southern lineage. Thus while current differences in diet seem insufficient to produce selection for different degrees of hypsodonty in the Japanese sika deer (except perhaps for the Kinkazan island population), past environmental conditions during the glacial period may have led to differences between northern and southern populations.

## VI. HYPSONDONTY AND DIET IN UNGULATES: CURRENT CONTROVERSIES AND CONFUSIONS

Below we discuss a number of topics concerning hypsodonty about which there has been some confusion or controversy in the recent literature, and include some new perspectives about the value of hypsodonty in reflecting environmental conditions.

### (1) Confusion about the definition of a hypsodonty index

Some confusion has arisen about hypsodonty indices due to different workers using somewhat different metrics. The hypsodonty index was defined by Janis (1988) as the unworn  $M_3$  crown height divided by the occlusal width of the same tooth, but other authors have used tooth length as the denominator (e.g. MacFadden, 2000, for extinct horses).

Janis (1988) used lower teeth for the determination of the hypsodonty index because mandibles are more likely to be found in the fossil record, and it was easier to obtain X-ray data for the lower jaws of the extant animals surveyed. The third molar was chosen because in many ungulates (most

notably ruminant artiodactyls) this is the most hypsodont of the cheek teeth, and the aim was to obtain an index of maximum hypsodonty for comparison across different ungulate groups. Additionally, in the case of ruminants, third molars are easily recognizable, while first and second molars usually are more difficult to distinguish from each other, even though the second molar may be considerably more high-crowned than the first one. (By contrast, the molars of perissodactyls are more similar to one another in both morphology and crown height.) A width measure was chosen instead of a length one, as the length of the third molar varies greatly among taxa [from relatively short in rhinos, to elongated in camelids and many ruminants, to encompassing virtually the entire dentition in warthogs and (extinct) stenomyline camelids], whereas the relative width remains fairly constant across all ungulates (at least modern forms, but see Damuth, 1990). Thus, a hypsodonty index using tooth width as the denominator allows for direct comparison between perissodactyls and artiodactyls, and for calculating the index from a single tooth, while that using tooth length does not.

### (2) Persistence of brachydont forms

Brachydonty is not merely the primitive condition for ungulates and mammals in general, but the brachydont teeth of ungulates may also represent optimal morphologies for an ungulate consuming a non-abrasive (or an only moderately abrasive) diet (Fortelius, 1985). Such relatively non-abrasive food resources abound in present-day tropical and temperate forests, as well as being represented in lesser abundance in virtually all other terrestrial habitats.

An underlying assumption, common in the literature, is that hypsodonty is in general superior to brachydonty in today's world (e.g. Feranec, 2007; Rivals *et al.*, 2010), and therefore brachydont forms might not be expected to be prevalent in modern faunas. In our opinion, one of the reasons that people are surprised that brachydont forms persist is because of the classic Simpsonian (e.g. Simpson, 1951) evolutionary story, in many biology textbooks, of the "Great Transformation" from browsing to grazing during the Miocene in North America (e.g. MacFadden, 1997). Simpson himself was well aware of the complex evolutionary history of ungulate dental adaptations, including the persistence and diversification of brachydont lineages alongside lineages in which hypsodonty was increasing. However, when he introduced his novel concept of an adaptive zone (Simpson, 1944, 1953) he used a highly simplified (almost cartoon-like) example of browsing horses transforming over time into grazers to illustrate the idea of a transition between adaptive zones. Likewise, Simpson's (1944, 1953) discussion of evolutionary rates used, for concreteness, rates of increase in tooth crown height throughout a lineage of horses. The conceptual significance of both of these topics for evolutionary theory has led people to focus on these sections of Simpson's text, and the simplified examples, interpreted as the whole story, seem to have conveyed to

many the erroneous impression that horses (and other ungulates) made steady, continuous evolutionary progress *en masse* towards an ideal, optimal hypsodont condition, finally manifested in modern *Equus*. Such mistaken interpretations of the fossil record continue to cause occasional confusion (see Janis, 2007). Although many ungulate taxa did evolve increased hypsodonty at this time, a large proportion of the ungulate fauna did not, and this “transformation” was not an issue of hypsodont taxa replacing brachydont ones on a one to one basis (see Janis, Damuth & Theodor, 2000, 2002, 2004).

Brachydont browsers remain a common element of the ungulate fauna today, even in habitats dominated by grazers and mixed feeders—for example in the East African savannas. In the present day, brachydont browsers are most diverse in temperate woodlands and tropical forests, but may also be found in tropical savannas. The present-day East African savannas contain not only the high-level browsing giraffe [*Giraffa camelopardalis*, hypsodonty index (HI) = 1.20], but a diversity of lower-level feeding brachydont to mesodont browsers including the black rhinoceros (*Diceros bicornis*, HI = 2.24), the kudu (*Tragelaphus strepsiceros*, HI = 2.29), the bushbuck (*Tragelaphus scriptus*, HI = 2.54), and the common duiker (*Silvicapra grimmia*, HI = 2.97). These savanna browsers, being technically “open habitat” animals, are, unsurprisingly, more hypsodont than their browsing relatives living in tropical forest habitats: e.g. the Sumatran rhino (*Dicerorhinus sumatrensis*, HI = 1.67), the bongo (*Tragelaphus euryceros*, HI = 1.92), or the blue duiker (*Cephalophus monticolor*, HI = 1.90) (all data from Janis, 1988).

At the time of the mid Miocene rise of hypsodont ungulates, various brachydont forms such as anchitheriine equids and palaeomerycid ruminants were a significant component of the faunas of both North America and Europe. They not only persisted throughout the transformation from woodlands to more grass-dominated habitats, but both groups actually later radiated and diversified (e.g. evolved forms of larger body size) during the middle and early late Miocene (over a time span of 7–8 million years). (The North American anchitheriine equids are discussed further in Section VIII.) These brachydont ungulates may have been largely ignored by palaeontologists because of their eventual extinction, perhaps being perceived as “evolutionary failures” in comparison with their hypsodont cousins. However, it does appear to be the case that both anchitheres (Eronen *et al.*, 2010a) and palaeomerycids (Semperebon, Janis & Solounias, 2004) were capable of increasing their level of hypsodonty to a certain extent in some situations, and so were not doomed by their brachydonty. Many of these taxa were extraordinarily successful in terms of geographic and temporal range, a reminder, should one be needed, that not all species in a community strive to exploit the same resource.

We emphasize this persistence of brachydont taxa because it appears that, although the story of increasing hypsodonty among some horse lineages through time is well known among palaeontologists and members of the wider public, many people apparently overlook the fact that even

today there is a large diversity of apparently successful brachydont ungulate species. Explanations for the evolution of hypsodonty that propose that its primary adaptive value is the broadening of the feeding niche (e.g. Feranec, 2003, 2007; Rivals *et al.*, 2010) seem to make sense only if one expects hypsodonty to be generally increasing over time, rather than with the actuality that at those points in evolutionary history where a “transition to hypsodonty” can be observed, only some species in a fauna become hypsodont. Moreover, it is well known that some extant ungulates (e.g. many cervids) incorporate a considerable amount of grass in the diet (especially less fibrous young-growth grass in the spring), and thus have an exceedingly broad year-round diet, without becoming hypsodont. Note that in the late Pleistocene of South Africa, when the climate changes from more arid to more mesic, previously common hypsodont ungulates (equids and alcelaphine bovids) now become rare, while more brachydont forms (tragelaphine and cephalophine bovids) become more common (Klein, 1976). This type of faunal shift would not be expected if the primary ecological role of hypsodonty were to allow the hypsodont animal to thrive while eating any kind of available vegetation.

### (3) Non-grazing hypsodont forms

In principle, a hypsodont animal can eat food of low abrasive properties without dire dental consequences, while a brachydont animal cannot sustain itself on highly abrasive foods (as discussed further in Section VI.4). Modern equids (all highly hypsodont) can, and do, consume considerable quantities of browse in some habitats (see, e.g. Kaiser & Franz-Odenaal, 2004). Browsing in equids can be seen today among feral horses in Costa Rica (e.g. Janzen, 1981); in feral horses in the Great Basin of North America, which may consume significant quantities of sagebrush (Berger, 1986); and in the Asiatic wild horse (*Equus przewalskii*), where shrubs are often the only available food in the saline *Salsola* high steppes (Mohr, 1971). The suggested case of browsing in the extinct equid *Dinohippus* (MacFadden, Solounias & Cerling, 1999) may be an example of this sort of opportunistic behaviour, while the Eurasian hipparionine radiation of the late Miocene evidently shows a rich diversity of mixed feeders and even a few browsers (e.g. Hayek *et al.*, 1992; Bernor *et al.*, 2003; Kaiser, 2003; Kaiser & Bernor, 2006).

However, there are also extant, moderately to highly hypsodont, species whose natural diet does not include a large amount of grass. Unlike the extant equids just discussed, these are not grazing specialists feeding outside of their usual dietary range, but browsers or mixed feeders whose hypsodonty suggests selection to endure the high levels of abrasive wear usually encountered by grazers. The prime example is the pronghorn antelope, *Antilocapra americana*, which is often mentioned in the literature as an “exception” that requires an “*ad hoc*” explanation (Mihlbachler & Solounias, 2006) to reconcile it with the received view of hypsodonty. Similarly, Semperebon & Rivals (2007) interpret



the hypsodonty index of this sole extant antilocaprid taxon as a type of phylogenetic holdover from ancestors with a more grazing type of diet. However, empirical documentation of the pronghorn's feeding and tooth wear, combined with the fuller understanding of the sources of abrasion in ungulate diets argued herein, largely do away with these perceptions.

Recall that, as argued above, the primary abrasive agent affecting specialized grazers is most likely the large volume of soil that they ingest while feeding close to the ground in open habitats, rather than the composition of grass itself. As we have seen in Section IV, the pronghorn has a year-round diet low in grass (averaging 12% over a range of studies; Janis, 1995). It is highly hypsodont (HI = 4.61; Janis, 1988) and, consistent with this, exhibits a molar wear rate (4.19 mm year<sup>-1</sup>; Lubinski, 2001) that is equivalent to wear rates seen in specialized grazers such as *Bison bison* (3.65 mm year<sup>-1</sup>; Solounias *et al.*, 1994) or the zebra *Equus burchelli* (3.1 mm year<sup>-1</sup>; Spinage, 1972). We also know that the pronghorn's yearly intake of soil (4.1% of dry matter intake, Sneva *et al.*, 1983; 5.4%, Arthur & Gates, 1988) is equivalent to the amount consumed by the grazing cattle and horses in the same or similar habitat (5.0% and 5.8%, respectively, Sneva *et al.*, 1983). Thus, the pronghorn experiences high tooth wear as a result of high abrasion rates, just like the grazers, which in turn results from the similarly large amount of soil all of these species consume. The percentage of grass in the diet, in this case, at least, has no noticeable relationship to wear rates or hypsodonty. Rather than being an inexplicable paradox, the pronghorn's hypsodonty exemplifies exactly the same underlying cause of high abrasion that makes the hypsodonty of grazers adaptive—level of soil ingestion. The lesson to take from this example is not that hypsodonty tells us little about the feeding ecology of extinct species (e.g. Muhlbachler & Solounias, 2006), but rather that hypsodonty in fossil species is telling us about wear rates and soil consumption, not about grass consumption *per se*. There is nothing implausible about browsers or mixed feeders consuming high amounts of soil, especially in open habitats, and showing adaptations to resist the concomitant higher levels of abrasion they suffer.

#### (4) Supposed brachydont grazers

No examples of brachydont ungulates that eat predominantly grass can be found today. However, various workers have proposed that certain extinct brachydont ungulates were in fact grazers.

For example, Rivals & Solounias (2007) examined the dental wear on a diversity of fossil reindeer populations and, noting a population from Alaska with extremely worn teeth, concluded that “the diet of a brachydont taxon can vary across most of the dietary morphospace of ungulates” (p. 190). However, as noted in Section V, reindeer with extremely worn teeth (from eating abrasive vegetation and/or grit but not grass) are known from extant populations, and these animals are severely compromised in their lifetime reproductive success (Skogland, 1988). While it is impossible to know the eventual fate of the

lineage of these fossil Alaskan reindeer, it seems likely that the population would have rapidly gone extinct had such severe environmental conditions persisted. Other celebrated cases of non-hypsodont taxa from the fossil record with microwear interpreted as some level of grazing [e.g. the mesodont giraffid *Samotherium* (Solounias & Dawson-Saunders, 1988)] may merely reflect the levels of seasonal grazing seen in extant brachydont or mesodont taxa, such as many cervids (described in Section VI.2).

#### (5) Consequences of eating an adaptively inappropriate diet

It is obvious that a browser cannot readily eat grass in natural habitats without adverse consequences due to high dental abrasion. However, the structural modifications that a specialized diet of grass entails (that is, hypsodonty in combination with a relatively flat occlusal surface) can also impose functional limitations on processing other herbage. By this we mean that a dentition adapted for a specialized diet of grass may not be advantageous for processing a diet of browse. For an extreme example, domestic horses fed primarily an artificial diet of non-abrasive commercial foods need their cheek teeth filed annually otherwise they develop sharp points rather than wearing flat; these sharp points result in malocclusion and can damage the horses' oral tissues (Jeffrey & Allen, 2003; also, the equine dentistry bills of C.M. Janis). Similar malocclusion features have likewise been observed in the mesodont mixed feeder *Gazella dorcas* fed an artificial pellet-based diet in captivity, in contrast to individuals allowed to browse and graze on a more natural diet (Molnar *et al.*, 2006). Kaiser *et al.* (2009) provide a review of studies of abnormal dental wear and its biological consequences, including other mammals besides ungulates.

Other studies suggest that if captive browsers are fed a diet more suitable for grazers, their life expectancy is reduced. It is possible, although not explicitly shown by these studies, that they are wearing their teeth down at an abnormal rate, resulting in loss of dental function in mid life. Jurado *et al.* (2008) showed that, in necropsy reports of captive wild ruminants, irregular tooth wear (affecting between 18% and 48% of the 12 species studied) was associated with atrophy of coronary and kidney fat, suggesting that disrupted dental wear led to a loss of condition. Müller *et al.* (2010), in a study of 31 cervid species in various zoos, showed that relative life expectancy correlated positively with the percentage of grass in the natural diet, with species that are browsers in the wild having shorter lives than grazers. They suggested that a possible reason for this is that zoo animals are usually fed on hay (i.e. grass), irrespective of their natural food habits, and that the dentition of browsers is ill equipped to handle such a diet.

#### (6) Can hypsodonty be used as an environmental signal?

It has long been appreciated that the composition of communities of large herbivorous mammals reflects their



local habitat: obviously grazers are more prominent in grasslands and browsers in forests, but the mixture of animals of different dietary preferences can reveal subtleties about the habitat structure. This being the case, it would be expected that levels of hypsodonty in a faunal community would also reveal aspects of the habitat structure.

A significant relationship between hypsodonty and environmental variables can be inferred from inspection of Fig. 1. On the horizontal axis habitats have been arranged (from left to right) in order of decreasing openness, from treeless steppe to closed forests. The primary climatic determinant of the amount of tree cover is annual precipitation, with grassland steppes being relatively dry habitats and precipitation progressively increasing in habitats as trees become more dominant (Holdridge, 1947; Janis *et al.*, 2004). Thus, the horizontal axis of Fig. 1 largely represents a rainfall axis. The mean value of hypsodonty (the average height of the bars) in each habitat type increases consistently without respect to diet across habitats of decreasing precipitation. Thus, it is clear from the figure that mean hypsodonty index has the potential to predict statistically the amount of precipitation.

Studies over the past decade have confirmed this view, showing that the mean hypsodonty levels of mammalian communities are indeed strong predictors of the levels of precipitation of their habitat (see Damuth *et al.*, 2002; Janis *et al.*, 2004; Eronen *et al.*, 2010*b*). Eronen *et al.* (2010*b*) show that, with present-day communities, the correlation between precipitation and levels of hypsodonty ( $r^2 = 0.658$ ) is only slightly inferior to the correlation between precipitation and diet ( $r^2 = 0.665$ ) (and with the combination of diet and hypsodonty levels the correlation increases to 0.742). The hypsodonty levels of Eurasian fossil communities of large herbivores track levels of increasing aridity over the Neogene that agree well with proxies from palaeovegetation (Eronen *et al.*, 2010*c*).

Note that the origins and maintenance of these kinds of habitat associations with species of different feeding types do not require that species or faunas evolve in place in the face of climate or vegetation change. Rather, species composition of particular communities may more often reflect the ecological sorting of species among habitat types on the basis of their current adaptations. Thus, changes in fossil communities may track local or regional environmental changes geologically instantaneously and far more effectively than if significant evolutionary changes were required among multiple lineages.

The correlation here is not with hypsodonty and diet directly, but results from the fact that vegetational habitats are highly sensitive to levels of precipitation. More arid habitats tend to be dominated by grasses, but as noted previously, in such habitats herbivores experience greater rates of tooth wear because of soil ingestion and levels of grit on the food, regardless of the actual plants ingested. As shown in Fig. 1, hypsodonty today correlates with both diet and habitat, but it is not necessarily the consumption of grass that is driving this pattern.

These papers show that hypsodonty levels in mammalian communities do indeed carry a strong signal about aspects of the environment, in both today's world and in the past. This is in contrast to the expressed doubts of some palaeontologists (e.g. Mihlbachler & Solounias, 2006; Strömberg, 2006) that hypsodonty is not a reliable indicator of palaeodiet, and so hypsodonty levels of extinct mammals may not carry a signal of their habitat.

## VII. HYPSONDONTY VERSUS MESOWEAR, MICROWEAR AND ISOTOPES

Resolution of the major influences on ungulate tooth wear has significant implications for how we think about and interpret diets of fossil species, since dental evidence is at the basis of the most widely applicable techniques. Because of the obvious statistical association of hypsodonty and diet in extant species, hypsodonty has long been used as an indicator of the diet of fossil ungulates. If one believes that phytolith ingestion is paramount in determining wear rates, and takes this line of reasoning to its conclusion, ungulate hypsodonty (unlike that of rhizophagous burrowing forms) would be seen as a specific result of specializing on a diet of grass; if an ungulate species is not eating grass there would be no reason to expect it to be hypsodont. On the other hand, regarding soil ingestion as paramount in determining wear rates means that a grass diet is not strictly necessary for there to be selection for hypsodonty; species eating something other than grass may experience high rates of tooth wear if they are feeding close to the ground in an open habitat.

A number of other significant inferential techniques have been developed that complement hypsodonty and in part make up for some of its limitations. Microwear, the study of microscopic scratches and pits on the enamel surface of the teeth, was initially pioneered by anthropologists and primatologists, and the technique was later adopted for ungulates by Solounias (e.g. Solounias, Teaford & Walker, 1988; Solounias & Semprebon, 2002). Mesowear, the study of the mode of wear of the individual tooth cusps, was devised by Fortelius & Solounias (2000) (see Kaiser *et al.*, 2009, for review). Microwear and some components of mesowear are different measures of the wear accumulated on the dentition during different periods of the life of the animal, and both have been shown to be good predictors of the diet. As noted by Fortelius & Solounias (2000, p. 2; see also Solounias & Semprebon, 2002, pp. 39–40), microwear, mesowear and hypsodonty measure different aspects of dental wear, and to some extent operate on different time scales. The isotopic content of ungulate tooth enamel, in research pioneered by MacFadden & Cerling (1994), reflects the carbon isotopes laid down in the tooth during formation (so actually represents the diet of the mother, rather than of the animal itself). This can distinguish between a diet of C4 plants (usually taken to represent grasses), and C3 plants (usually taken to represent browse). Obviously this technique

is of little use before the late Miocene transition to C4 grasses in many parts of the world.

Microwear represents the direct effect of the food on the tooth, but as rates of tooth wear are sufficiently high for new microwear to replace the old on the enamel surface every few days, it only reflects what the animal was eating for the last few days before it died (Solounias *et al.*, 1994), and this “Last Supper” phenomenon may not reflect the animal’s usual diet. Another problem with microwear is that not all patterns observed in extinct taxa are yet known in extant taxa, rendering interpretation of diet difficult [e.g. an apparently unique form of fine scratches seen in the late Eocene equid *Mesohippus* (Solounias & Semprebon, 2002, p. 40), an animal whose level of hypsodonty would otherwise indicate an ordinary browsing diet, and whose teeth show little evidence of pronounced wear during life].

The large amount of soil ingested by many ungulates, both incidentally and intentionally (geophagy), also has implications for microwear studies. The microwear scratches found on the teeth of fossil ungulates, and currently believed by many researchers to have been caused by phytoliths, cannot necessarily be taken as direct evidence of a diet of grass, as is often assumed (Solounias & Semprebon, 2002; Solounias *et al.*, 1988). Such scratches cannot easily be distinguished from scratches left by abrasive soil particles (Covert & Kay, 1981; Kay & Covert, 1983), and given the large amount of soil eaten by grazing ungulates such microwear features may reflect mostly soil consumption. In comparative studies of microwear in sheep, the failure of phytolith ingestion to produce the expected microwear features, and instead the observed association of these features with high levels of soil ingestion (Mainland, 2003), supports this view.

Mesowear is cumulative over months or years, and so potentially represents the “habitual” diet of a species, although care must be taken to not take information from an animal that has teeth that are too worn down, or only minimally worn. The mesowear technique is based on the distribution of wear scores in a sample of individuals (Fortelius & Solounias, 2000, suggest at least 10).

Hypsodonty represents the history of adaptation of the species, probably also carrying with it phylogenetic effects, as there is little evidence that hypsodonty is reversed in a lineage once attained (although a possible exception may be in the case of the high-level browsing gerenuk, *Litocranius walleri*, which is considerably less hypsodont than other gazelles, or most other bovids in general). Hypsodonty may also vary to a degree within a species, but this has rarely been documented (but see Carranza *et al.*, 2004, *versus* Loe *et al.*, 2003, for *Cervus elaphus*; Veiberg *et al.*, 2007, for *Cervus elaphus* and *Alces alces*; Takahashi *et al.*, 1999, and Ozaki *et al.*, 2007, for *Cervus nippon*, as discussed in Section V.3).

Thus these three proxies for dental abrasion, and hence for diet, differ from each other not only in time scale, but also in evolutionary terms, as hypsodonty is the only trait that is entirely subject to selection. All three measure somewhat

different aspects of the interaction of the dentition with the food in a mechanical sense.

It should be noted that mesowear considered alone has similar predictive ability for the dietary classes (browser, grazer, and mixed feeder) as does the hypsodonty index, although discriminant analyses in Fortelius & Solounias (2000, pp. 16–17) showed that mesowear combined with hypsodonty provided slightly better predictions than either measure considered alone. Mesowear alone provided at best a 72% correct classification (CC) of the diets of species included in the sample. Hypsodonty considered alone provided a similar 65% CC. Hypsodonty in combination with mesowear provided 76% CC. Use of logistic regression (which makes fewer statistical assumptions than the discriminant analysis used by Fortelius & Solounias, 2000) confirms this picture for the variable types taken alone, but shows that a model combining hypsodonty and mesowear can exhibit substantially greater predictive power (J. Damuth & C.M. Janis, in preparation).

It is clear that the mesowear technique captures some aspects of dental wear that are independent of those represented by hypsodonty, especially with respect to what the members of a population in a particular habitat were eating during their lifetime [as opposed to their final meals (microwear), or the long-term adaptations of their species (hypsodonty)]. However, given the fact that the predictive power of a model that contains both mesowear and hypsodonty is markedly superior to one that contains either one alone, we find it perplexing that certain workers consider, as previously discussed, that only one technique can provide the true answer, and, where there is conflicting evidence, mesowear must be accorded priority.

Mihlbachler & Solounias (2006) have criticized the studies demonstrating correlations between diet and hypsodonty in living animals as suffering from the problem of being “geologically instantaneous” (p. 30), and continue that “Growing evidence from paleontology suggests that dental morphology” [i.e. hypsodonty] “is often misleading with respect to diet...” (p. 30). But how can palaeontological studies provide evidence for the correlation of morphological features with diet? Palaeontological studies can show only the values of hypsodonty, mesowear and microwear, and how they vary among species; but all three of these measures are proxies for diet that provide a similar, imperfect predictive ability (~70%) for modern forms, despite claims that some techniques generally yield superior results. We will never have certain knowledge of diet in fossil animals, so diet itself cannot be compared with morphology in extinct forms. Mesowear may be compared with hypsodonty, to determine whether they give compatible signals, but this is not precisely the same thing. All osteological (inherent or acquired) and isotopic methodologies are merely proxies, whose correlations with diet have been determined by studies of living animals.

Direct evidence of palaeodiets might possibly be provided by preserved stomach contents (e.g. the equoid *Palaeotherium*: Schmitz-Münker & Franzen, 1988) or food retained on

the teeth (the rhinoceros *Teleoceras*; Voorhies & Thomasson, 1979), but even then this might indicate a genuine “last supper” and might not be representative of the usual diet in life (one would not correctly surmise that Socrates had a habitual diet of hemlock from his post-mortem stomach contents).

Although both mesowear and microwear may provide some direct evidence of the way a particular animal used its teeth during its lifetime, whereas hypsodonty reflects longer adaptive trends and functional capacities, these correlations of wear with diet have been determined from data on extant animals of known diets, so must perforce suffer from the same problems of being “geologically instantaneous” information as are ascribed to hypsodonty. Indeed, if dental wear measures were superior to hypsodonty at capturing diets at the geological instant of the present day, then one would expect the correlation between wear measures and diet to be far superior to that between hypsodonty and diet, which has not been demonstrated.

What do conflicts among dietary proxies mean for understanding palaeodiets? The answer is not yet clear, but declaring one proxy to be superior is hardly the solution. Problems also arise when isotopic evidence conflicts with morphological evidence, as will be discussed further below. However, a point to make here is that there is a clear relationship between the biomechanical properties of dental materials, the fact that food will abrade the teeth, and the population dynamics of large, slow-breeding mammals. That is, if the teeth become worn out before the end of the natural reproductive lifespan of the animal, then the reproductive rate will fall, the population will decline and the species will not survive. It is not merely a case of whether or not a brachydont animal eats grass or some other food: if a brachydont animal eats food that is highly abrasive (whatever the reason for its abrasive nature) then it will likely wear its teeth out before it can produce enough viable offspring to ensure the propagation of its genetic material.

In addition to possible conflicts between palaeodiet signals from dental wear and hypsodonty, there may also be a conflict with isotopic evidence. For example, MacFadden & Shockey (1997) report the instance of brachydont camelids in the Pleistocene of Bolivia with an isotopic signal of a C4 (thus likely grazing) diet. However, this potential problem cannot be resolved by stating (p. 91) “Recent work has also shown that grazing ruminant artiodactyls ‘cheat’ by having more highly durable teeth (Solounias *et al.*, 1994) that are less prone to rapid wear by feeding on abrasive foodstuffs.” This seems to be a misunderstanding of what was actually presented in the Solounias *et al.* (1994) paper. Here it was indeed stated that among grazers, the third molars were more “durable” than the first and second ones, but this was because the third molars were larger and more hypsodont than the others, and so took longer to wear down, not because they were mysteriously somehow more resistant to wear. The conflict between isotopic and dental proxies in these Pleistocene camelids is puzzling, but any resolution

must take into account the issue of the effect of rate of tooth wear with abrasive diets.

In terms of mismatches between isotopic and dental proxies of diet, as previously discussed a hypsodont animal possessing a signal of a browsing diet is not necessarily a problem. However, a brachydont animal appearing to have a grazing diet does present a greater problem: in this situation, additional information, such as the apparent rate of dental wear, would be informative. Were such animals caught at a moment of time, like Skogland’s reindeer (Section V.2), when they were struggling to maintain themselves in the face of an inappropriate diet? If so, their teeth should show signs of extreme wear. If not, they must have been eating grass (or other C4 material) that, for some reason, was not highly abrasive, perhaps because it was being foraged underwater and so free of grit (recall the lower degree of hypsodonty in extant “fresh grass grazers”, Section III.3.iii). Whatever the reality, at any instance of geological time, past or present, it would be impossible for a brachydont species to have a sustained highly abrasive diet without having rapid tooth wear and then suffering the consequences: dental material cannot somehow be made significantly more wear resistant.

Moreover, dietary adaptations of ungulates involve more than just craniodental features; the morphology and physiology of the digestive system differs between browsers and grazers (see Clauss *et al.*, 2010), emphasizing that ungulates cannot just simply select any diet at whim. Ungulate lineages are conservative enough in their diets that among extant species there is a strong statistical correlation between current diet composition and hypsodonty. If, instead, hypsodonty were related solely to idiosyncratic evolutionary history it would be a highly unreliable predictor of extant species’ diet, which is demonstrably not the case. To suggest that such correlations as we see today generally did not characterize mammalian faunas of the past implies that the correlations we see now somehow emerged only in the Recent, from a background of randomness. However, as discussed here, the correlations today are caused primarily by physical processes that are not dependent on evolutionary history. There is no reason to assume that what is true among mammals today would not also be true for animals in similar situations in the past.

## VIII. THE EVOLUTION OF HYPSONDONTY IN EQUIDS AND THE ISSUE OF “ADAPTIVE LAG”

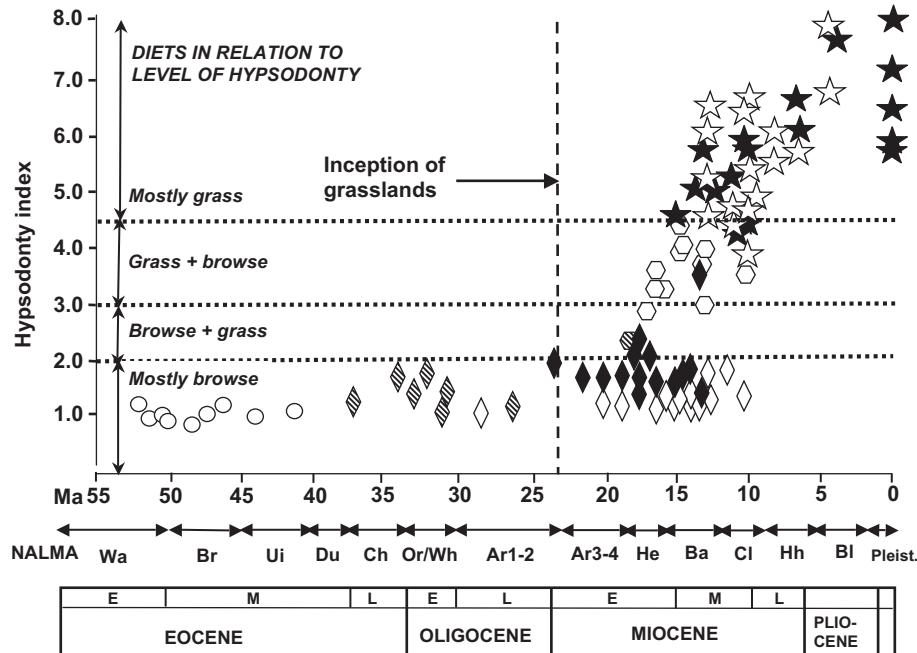
A final topic concerning the evolutionary significance of hypsodonty relates to new work on the origin of grasslands, habitats that were unknown prior to the Miocene (although they might have existed somewhat earlier in South America: see Jacobs, Kingston & Jacobs, 1999; but also see Billet *et al.*, 2009; Strömberg *et al.*, 2010). In the traditional evolutionary story (e.g. Matthew, 1926), grasslands were assumed to become prevalent in North America with the initial radiation of the genus *Merychippus* (a more hypsodont horse than its predecessors, and the earliest member of the generally

highly hypsodont subfamily Equinae) at around 17.5 Ma (late early Miocene). Strömberg (2006) provides palaeobotanical evidence from plant phytoliths for the presence of extensive grasslands in North America considerably earlier in the Miocene, at around 22 Ma. This discovery resulted in a perceived problem related to the evolution of hypsodony, inasmuch there was an apparent “adaptive lag” in the equid lineage between the origin of the grasslands and the rapid cladogenesis at the base of the Equinae (see also Muhlbachler & Solounias, 2006).

Strömberg (2006) noted (p. 237): “In the light of this [i.e. the earlier appearance of the grasslands] the validity of assumptions regarding the adaptive nature of hypsodony must be re-examined.” Indeed, these new palaeobotanical data certainly change the traditional story of equid evolution: they show that some time elapsed after the appearance of grasslands before extreme hypsodony became widespread among equids (and also among other ungulates). Strömberg (2006) does carefully discuss the implications of the adaptive nature of hypsodony, and does not assert that these equids must have been eating grass in the absence of the appropriate dental equipment. However, we show below that the pattern of acquisition of hypsodony in equids actually does reveal an interesting evolutionary pattern, albeit somewhat different from the traditional story (Fig. 2).

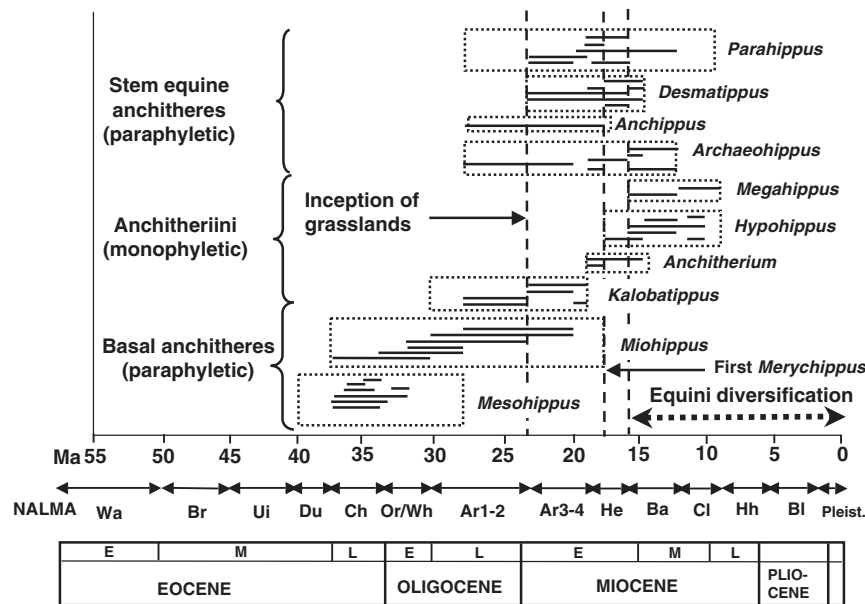
Strömberg (2006) herself notes (p. 249) that the onset of mesodony in *Parahippus*, the paraphyletic anchitheriine genus forming the stem to the more hypsodont Equinae, is in fact broadly coincident with the first appearance of grass-dominated habitats, and notes that *Parahippus leonensis* (the most derived form) had alterations in enamel microstructure that might have made the teeth more durable. In addition, various North American rodent lineages also became hypsodont at this time (Janis, Dawson & Flynn, 2008a). So, in fact, the fossil record does show a faunal response to the origin of grasslands. What is intriguing is that the equids do not undergo a rapid evolutionary radiation at this time. The earliest members of the equine (paraphyletic) genus *Merychippus* first appear at around 17.5 Ma (or possibly a little earlier), but pronounced cladogenesis of the Equinae, with the first appearance of more derived equine taxa, does not occur until the start of the Barstovian land mammal age, at around 16 Ma (Janis, Hulbert & Muhlbachler, 2008b, Fig. A6; also shown in Strömberg, 2006, Fig. 1). In the Central Great Plains region, for example, there are only two equid taxa present in the late Hemingfordian, but eight in the early Barstovian (data from Janis *et al.*, 2008b; MacFadden, 1998).

Brachydont equids of the paraphyletic family Anchitheriinae persist alongside of the mesodont equine equids in the earlier Miocene, but they also persist alongside of more



**Fig. 2.** Hypsodony indices of North American fossil equids (plus Recent Old World equids). Key to North American Land Mammal Age (NALMA) abbreviations: Wa = Wasatchian, Br = Bridgerian, Ui = Uintan, Du = Duchesnean, Ch = Chadronian, Or = Orellan, Wh = Whitneyan, Ar = Arikareean, He = Hemingfordian, Ba = Barstovian, Cl = Clarendonian, Hh = Hemphilian, Bl = Blancan, Pleist. = Pleistocene. Key to taxa: open circles = hyracotheres (*Ephippus*, *Hyracotherium*, *Orohippus*); cross-hatched diamonds = basal anchitheres (*Mesohippus*, *Miohippus*); open diamonds = anchitheriine anchitheres (*Anchitherium*, *Hypohippus*, *Kalobatippus*, *Megahippus*); filled diamonds = stem equine anchitheres (*Archaeohippus*, *Desmatippus*, *Parahippus*); hexagons = *Merychippus* equine species (cross-hatched hexagon = *Merychippus gunteri*); open stars = hipparionini equines (*Cormohipparion*, *Nannippus*, *Neohipparion*, *Pseudhipparion*); filled stars = equini equines (*Astrohippus*, *Calippus*, *Dinohippus*, *Equus*, *Pliohippus*, *Protohippus*). Diets in relation to level of hypsodony in extant ungulates from Janis (1988).





**Fig. 3.** Range of North American anchitheriine equid species. Key to NALMAs as in Fig. 2. Solid lines = ranges of named species. Dotted boxes enclose ranges of the genus if outside the range of the solid lines for individual species. Data from MacFadden (1998), with updates from Janis *et al.* (2008b).

hypsodont equines in the middle and early late Miocene (see Figs. 2, 3), so they neither add to nor detract from the story of the evolution of hypsodont forms. Note also that the original appearance of the Equinae at around 17.5 Ma is not coincident with a huge increase in hypsodonty (see Fig. 2). *Parahippus leonensis* has a HI of 2.02, slightly greater than that of the earlier *Parahippus pawniensis* (HI = 1.59): both are more hypsodont than other contemporaneous brachydont anchitheriine equids such as *Kalobatippus* and *Archaeohippus* (both with HIs of around 1.25) (all data from unpublished measurements by C. M. Janis from specimens at the American Museum of Natural History and the University of Nebraska State Museum).

However, the most primitive *Merychippus* species, *M. gunteri*, only has a HI of 2.19 (the HIs of slightly later, better known species of *Merychippus*, such as *M. insignis* and *M. primus* are in the 3.0–3.5 range). Also note that the microwear of the various species of *Merychippus* indicates that they were mixed feeders at best, not specialized grazers (Solounias & Semprebon, 2002). Equids with a hypsodonty index of greater than around 4.0 are not known until the late middle Miocene, around 14 Ma (see Fig. 2).

What Strömberg’s (2006) Fig. 1 actually shows is rapid cladogenesis of equine equids, not the diversification of the first highly hypsodont forms: moderate hypsodonty in equids is indeed coincident with the appearance of grasslands, but the acquisition of a greater degree of hypsodonty occurs considerably later than the initial radiation of the Equinae, and even postdates their explosive cladogenesis (Fig. 2). Note, also, that there appears to be a moderate degree of diversification among the brachydont anchitheriines at around 17.5 Ma, with the appearance of the genus *Hypohippus* and two more derived species of the genus *Desmatippus*. A

more profound diversification occurs at 16 Ma, with the appearance of the genus *Megahippus* and the addition of two more species of *Hypohippus* and three species of the dwarf form *Archaeohippus*, paralleling the diversification of the Equinae at this time (Fig. 3).

This parallel radiation of anchitheriines alongside of the equines persisted until around 12 Ma, when climatic changes in North America resulted in the decline of many browsing taxa, not only the equids (Janis *et al.*, 2002). Why has this radiation been largely unnoticed? Part of the issue may be that these equids are a different branch from the lineage leading to the modern horse, and thus never played an important role in classic stories of horse evolution. In addition, in contrast to most members of the Equinae, the large Miocene Anchitheriinae are individually rare as fossils (in contrast to smaller, earlier anchitheriines such as *Mesohippus*), which might have led researchers to consider them to be “unsuccessful” (especially as they became extinct). But relative rarity is to be expected given their ecological role of large browsers. In present-day Africa members of the Tragelaphini (spiral-horned browsing antelope such as kudu) are individually less numerous than members of the Alcelaphini (grazing antelope such as wildebeest): but this does not mean that tragelaphines are “unsuccessful” nor that their presence in a fauna (and/or the absence of alcelaphines) does not carry an environmental signal.

If it was not the first appearance of the grasslands that caused the rapid cladogenesis in equine equids, then what was the trigger, and were there similar events in other ungulate lineages around the same time? The parallel diversification of both anchitheres and equines might mean that some environmental or other external perturbation triggered a diversification among all equids at around 17.5–16 Ma.

Note that the late early Miocene also marked a number of immigrations into North America, most notably that of proboscideans and pecoran ruminants. These are interesting evolutionary questions raised by these new palaeobotanical data, but these new data in no way challenge the adaptive value of hypsodonty.

## IX. CONCLUSIONS

(1) The adaptive significance of hypsodonty is in extending the effective life of the tooth when an animal is feeding on abrasive materials. Historically, it has been unclear what the abrasive agents in the diet are, with little comparative and experimental data until fairly recently. Suggestions in the literature have focused on three major causal agents: the physical properties of plant tissue (“toughness”); the presence of hard silica bodies (phytoliths) secreted by the plants and contained in their tissues; and the action of soil or grit ingested with the food.

(2) The pattern of variation in hypsodonty index with diet and habitat among extant species appears to be strongly dominated by variation in the amount of soil ingested while feeding; variation in other potentially abrasive factors, such as intake of grass phytoliths, evidently plays a secondary role. This was one of the primary conclusions of the first quantitative analysis of patterns of hypsodonty and diet, undertaken by Janis in 1988, and is largely confirmed by extensive quantitative data on the amount of soil ingested by extant ungulates and the distribution of soil with respect to plant stature and habitat.

(3) High levels of tooth abrasion are likely associated with a grazing diet in ungulates because of the fact that grass is found in open habitats, and grazing animals must feed close to the ground. Nevertheless a diet other than grass, but high in soil ingestion, may also result in high rates of tooth wear. In fact, any circumstance that causes ungulates to experience a high rate of soil ingestion, in any habitat (such as the practice of pulling plants up by the roots), can result in elevated abrasion. In this regard ungulates exemplify, in their own way, the same process that explains the high degree of hypsodonty in rhizophagous and burrowing mammals.

(4) Recent studies question the degree to which plant phytoliths can be effective agents of abrasion for large mammalian herbivores, although the data on phytolith hardness are sufficiently meagre that at present the potential role of phytoliths in mammalian tooth wear remains an open question. However, regardless of the resolution of the potential role of phytoliths, the majority of the unquestionably abrasive particles (by volume) eaten by most ungulates appear to be grit and soil, and this accounts well for the patterns of covariation in the data.

(5) Hypsodonty is a robust proxy for dietary type and habitat among extant ungulates. Because the statistical association between grazing and wear rates is dominated largely by physical processes (involving abrasion from grit), the relationship between hypsodonty and diets that lead to

the ingestion of large amounts of soil is likely to have been more or less invariant throughout ungulate history. To a great extent, it does not depend upon the coevolution of herbivores and plants, nor on the specific adaptations of any ungulate clades. Instead, rates of abrasion reflected in hypsodonty are more likely to vary with soil type, vegetation structure and food plant stature (i.e. feeding height). Thus it is ungulate feeding behaviour, rather than the diet *per se*, that is the determining factor in levels of hypsodonty.

(6) Studies on living species show that there are life-history and fitness consequences to animals subsisting on diets that are “too abrasive” for their dental morphology. Thus there should be selection pressure for a brachydont species to evolve higher-crowned teeth if subjected over a period of time (i.e. generational time) to an abrasive diet. Some studies of variation in hypsodonty among different populations of extant deer lend credence to this hypothesis.

(7) Although hypsodont animals may be able to eat a relatively nonabrasive diet without serious consequences (although resultant malocclusion may be an issue), the reverse is not true: brachydont animals cannot eat an abrasive diet without negative consequences on life history (reduced reproductive output, lifespan, etc.) and thus serious consequences for fitness. Thus, in terms of perceived “mismatches” in the fossil record, “hypsodont browsers”, in the sense of hypsodont ungulates naturally consuming a nonabrasive diet (although none exist today) likely do not present a serious problem; however “brachydont grazers” (again, unknown in today’s world) do present such a problem, as they will likely wear their teeth down before sufficient reproductive success is achieved to maintain their populations. The manifest adaptive relationship between herbivore dentitions and their regular diets is evident in the extant fauna, exceptions such as browsing feral horses in abnormal habitats notwithstanding.

(8) Despite the fact that many lineages increased their levels of hypsodonty over time, many remained persistently brachydont, casting doubts on the notion that hypsodonty is invariably adaptive for all feeding types, thus enabling them to broaden their dietary niche to include grass as well as browse. Dental specializations that are optimal for eating grass may not be equally optimal for processing other types of vegetation, and hypsodonty may entail other costs, such as the necessity to transform the shape of the skull.

(9) All proxies for the diets of fossil species make statistical predictions based on variation seen among living species; we never directly observe the diets of fossil species using any of these proxies. In fact, hypsodonty used in conjunction with proxies derived from microwear or mesowear provides superior predictions in statistical analyses than does any single proxy used alone. Possible “mismatches” between the diet predicted by hypsodonty and that by other proxies in fossil mammals are cause for interest and further investigation, but not cause to dismiss hypsodonty as a relevant analytic tool.

(10) Hypsodonty is different from other frequently used proxies for diet in fossil mammals: unlike dental wear or

isotope composition it does not reflect what the animal ate during its lifetime, but rather reflects the longer term adaptive history of the lineage. This does not mean that hypsodonty has no bearing on dietary prediction for fossil mammals, as has been argued by some researchers. Tooth crown height does indeed limit the amount of abrasive material that can be consumed long term by extant brachyodont and mesodont ungulates, and the low-relief occlusal morphology of hypsodont grazing forms may also limit their effective dietary choices, such as being able to eat large quantities of browse without suffering the effects of malocclusion.

(11) The evolution of hypsodonty in North American horses has long been the poster child for the coevolution of grazers and grasslands during the early Miocene, but the fact that grasslands recently have been shown to predate the radiation of the highly hypsodont horses has caused some workers to question the use of hypsodonty as a palaeoenvironmental signal. However, the North American horses do in fact show some increase in hypsodonty with the initial spread of the grassland habitat: the slightly later (by ~5 million years) explosive radiation of more hypsodont forms appears to be related to cladogenesis rather than an adaptive shift within the subfamily Equinae, and this cladogenesis is simultaneously echoed among the persistently brachyodont horses in the subfamily Anchitheriinae. The fact that the initial cladogenesis of the more hypsodont equine equids is not precisely coincident with the palaeobotanical evidence for the first appearance of grasslands in North America does not cast doubt upon the adaptive significance of hypsodonty, nor its use in palaeoecological studies.

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