

ON THE MEANS WHEREBY MAMMALS ACHIEVE INCREASED FUNCTIONAL DURABILITY OF THEIR DENTITIONS, WITH SPECIAL REFERENCE TO LIMITING FACTORS

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I. INTRODUCTION

The class Mammalia is unique among living vertebrates in the number of species that have adopted a herbivorous diet. Out of the 34 orders of living and fossil mammals (as listed by Simpson, 1945), approximately two-thirds (24) contain herbivorous species (including frugivores), and thirteen orders comprise entirely herbivores (see Table 1). No living bird or reptile orders are exclusively herbivorous, and no herbivores are known among living amphibians. The degree of convergent evolution of herbivory within mammals is probably rivalled only by the past diversity of herbivorous dinosaurs.

Plant foods induce more wear of the dentition than animal foods, for several reasons reviewed below. Thus herbivorous mammals have been driven to morphological adaptations that increase the functional durability of their dentitions. We recognize several different types of solution to the problem of intense dental wear. These types of solution can be related to different historical, developmental and functional constraints in different mammalian groups. In this review we discuss these different

Table 1. *Herbivorous orders within the class Mammalia*

Order	Herbivorous species	Herbivores only
Subclass PROTOTHERIA		
Infraclass ORNITHODELPHIA		
Monotremata	—	—
Infraclass EOTHERIA		
Triconodonta	—	—
Docodonta	x ?	x ?
Subclass ALLOTHERIA		
Multituberculata	x	—
Subclass THERIA		
Infraclass TRITUBERCULATA		
Symmetrodonta	—	—
Pontodonta	—	—
Infraclass METATHERIA		
Marsupialia	x	—
Infraclass EUTHERIA		
Proteutheria	—	—
Insectivora	—	—
Dermoptera	—	x
Chiroptera	x	—
Primates	x	—
Condylarthra	x	—
Tillodontia	—	x
Taeniodonta	—	x
Notoungulata	—	x
Litopterna	—	x
Dinocerata	—	x
Pantodonta	—	x
Cetacea	—	—
Artiodactyla	x	—
Perissodactyla	—	x
Xenarthra	x	—
Pholidota	—	—
Tubulidentata	—	—
Lagomorpha	—	x
Rodentia	x	—
Carnivora	x	—
Creodonta	—	—
Hyracoidea	—	x
Embrithopoda	—	x
Proboscidea	—	x
Sirenia	—	x
Desmostylia	x ?	x ?

types of solutions, emphasizing the constraints which can help to explain why a particular solution was first 'chosen' by a particular lineage and persisted in its later evolution.

Both the earliest mammals of the late Triassic, and the early therians of the early Cretaceous, were probably insectivorous, as can be judged both from the morphology of their cheek teeth and their small body size (see Kay & Covert, 1984). The original type of therian cheek tooth is tritubercular, with high, pointed cusps. The type of cheek

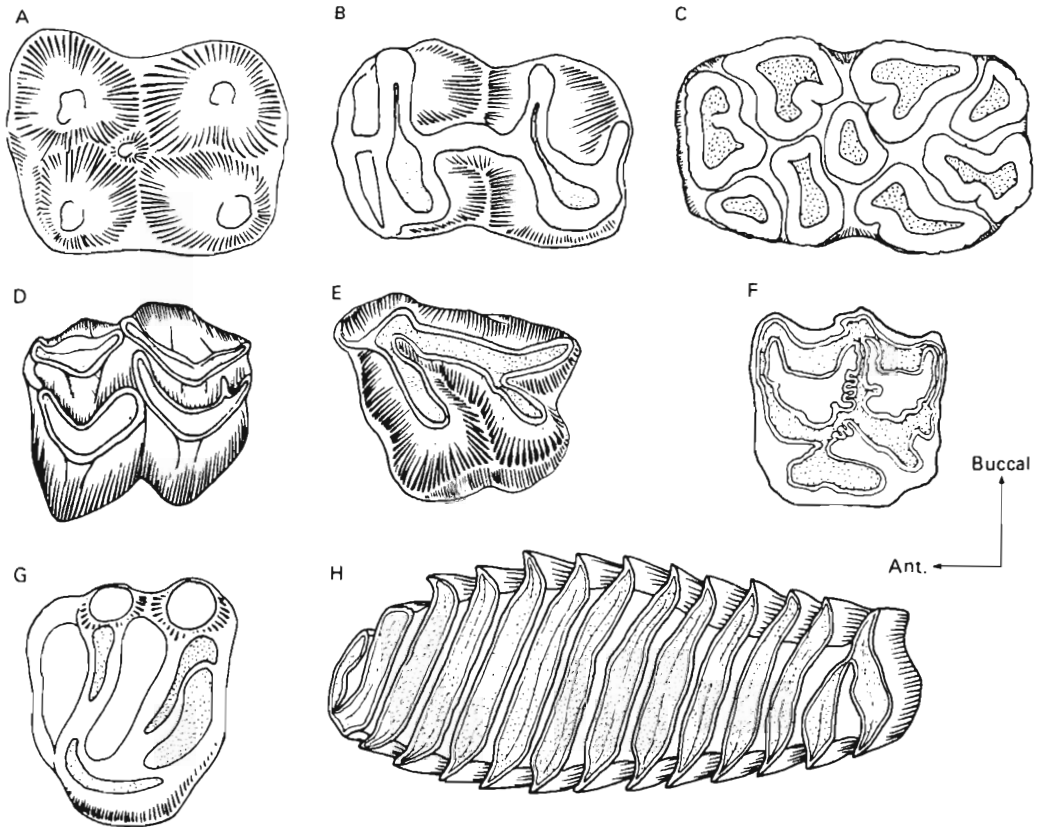


Fig. 1. Types of molar morphologies in herbivorous mammals. (A) Bunodont: peccary (*Tayassu* sp.); Brown University E 18. (B) Bilophodont: kangaroo (*Macropus* sp.); Brown University unnumbered specimen. (C) Columnar: warthog (*Phacochoerus aethiopicus*); Museum of Comparative Zoology 23031. (D) Selenodont: Deer (*Odocoileus virginianus*); Brown University E 1011. (E) Trilophodont (Ectolophodont). Rhinoceros (*Subhyracodon* sp. From cast of fossil specimen, Oligocene, North America); Brown University unnumbered specimen. (F) Plagiolophodont: horse (*Equus caballus*); Brown University unnumbered specimen. (G) Lophodont/Bunolophodont: rodent (woodchuck, *Marmota* sp.); Brown University 619. (H) Lamellar: rodent (capybara, *Hydrochaeris hydrochaeris*); Museum of Comparative Zoology 31778. All figured specimens are of left M², except for H. which is of left M³. ■, Exposed dentine.

tooth that is seen in more omnivorous/herbivorous mammals, the simple 'bunodont' type of tooth that is quadritubercular and possesses low, rounded cusps and wear striations indicating a more horizontal movement of the lower teeth across the uppers, was not apparent in therian mammals until the advent of taxa of larger body size, such as the early ungulate *Protungulatum*, in the late Cretaceous. (Non-therian multituberculates did evolve teeth evidently specialized for herbivory at an earlier date but, with the exception of a single Palaeocene genus which will be discussed later, they do not appear to show adaptations for increased dental durability, and thus are not considered as a group in this paper.) The possession of 'lophed' teeth, derived from these simpler bunodont teeth, in which the individual cusps were combined together in various fashions to form low-relief cutting ridges, was common in therian mammal taxa

Table 2. Solutions to the problems of dental durability seen in herbivorous mammals

(x) signifies that this feature occurs in certain species only within the broader taxon (or, in the case of hypsodonty, may signify low levels of hypsodonty). (x) in 'hypsodonty' column signifies 'incipient hypsodonty' i.e. root formation suppressed, but not indefinitely as in true hypsodonty).

	Occlusal morphology	More durable enamel	Hypsodonty	Hypsodonty	Enlarged individual teeth	Delayed eruption	Supernumerary teeth
Subclass ALLOTHERIA*							
<i>Lambdopsalis</i>	Lamellar	x (siderose?)	—	—	—	—	—
Subclass METATHERIA							
MARSUPICARNIVORA							
Arytolagidae*	Lamellar	—	—	x (crown)	—	—	—
Patagonidae*	Lamellar	—	—	x (crown)	—	—	—
DIPROTODONTA							
Macropodidae	Bilophodont	—	(x)	—	—	(x)	—
<i>Peradorcas</i>	Bilophodont	—	—	—	—	x	x
Vombatidae	Lamellar	—	—	x (crown)	—	—	—
<i>Rhizophascolomus</i> *	Lamellar	—	x	—	—	—	—
Subclass EUTHERIA							
XENARTHRA							
PILOSA							
Bradyrodidae	Peg-like	—	—	x (root)	—	—	—
Choloepidae	Peg-like	—	—	x (root)	—	—	—
Megalonychidae*	Peg-like	—	—	x (root)	—	—	—
Megatheriidae*	Peg-like/ Bilophodont	—	—	x (root)	—	—	—
Mylodontidae*	Peg-like	—	—	x (root)	—	—	—
DASYPOIDEA							
Dasypodidae	Peg-like	—	—	x (root)	—	—	x (small)
Glyptodontidae*	Peg-like	—	—	x (root)	—	—	x (small)
'INSECTIVORA'							
Dimylidae*	Quadrutubercular	x	—	—	(x)	—	—
Pantolestidae*	Tritubercular	x	—	—	—	—	—
Soricidae (certain genera)	Quadrutubercular	x (siderose)	—	—	—	—	—
CARNIVORA							
Mustelidae							
<i>Enhydra lutris</i>	Bunodont	x	—	—	—	—	—
Canidae							
<i>Otocyon megalotis</i>	Tritubercular	—	—	—	—	—	x

Table 2. (cont.)

	Occlusal morphology	More durable enamel	Hypsodonty	Hypselodnty	Enlarged individual teeth	Delayed eruption	Supernumerary teeth
SIRENIA							
Dugongidae	Peg-like	—	—	x (root)	—	—	—
<i>Dugong</i>	Bilophodont	(x)	—	—	—	x	(x)
Trichechidae							
DESMOSTYLIA*							
Desmostylidae	Columnar	x	x	—	x	x	—
EMBRITHOPODA*							
Arsinoitheriidae	Bilophodont	V†	(x)	—	(x)	(x)	—
HYRACOIDEA							
Pliohyracidae*	Trilophodont	—	(x)	—	—	—	—
Procavidae	Trilophodont	—	(x)	—	—	—	—
PROBOSCIDEA							
Elephantidae	Lamellar	—	x	—	x	x	—
Gomphotheriidae*	Bunodont	x	—	—	x	x	—
Mammutidae*	Bunodont/lamellar	x	(x)	—	x	x	—
Stegolophodontidae*	Lamellar	—	(x)	—	x	x	—
ASTRAPHOTHERIA*							
Astraphotheriidae	Trilophodont	V	x	—	—	—	—
PYROTHERIA*							
Pyrotheriidae	Bilophodont	V	—	—	—	—	—
LITOPTERNA*							
Macrauchenidae	Trilophodont	—	(x)	—	—	—	—
NOTOUNGULATA*							
Archaeohyrcidae	Trilophodont	—	x	—	—	—	—
Archaeopithecidae	Trilophodont	—	x	—	—	—	—
Hegetotheriidae	Trilophodont	—	x or	x (crown)	—	—	—
Interatheriidae	Trilophodont	—	x	—	—	—	—
Mesotheriidae	Trilophodont	—	x or	x (crown)	—	—	—
Notohippidae	Trilophodont	—	x	—	—	—	—
Toxodontidae	Trilophodont	—	x or	x (crown)	—	—	—
PANTODONTA*							
Coryphodontidae	Bilophodont	V	—	—	—	—	—
DINOCERATA*							
Uintatheriidae	Bilophodont	V	—	—	—	—	—

PERISSODACTYLA									
CERATOMORPHA									
Amyodontidae*	V	Trilophodont	—	—	—	—	—	—	—
Deperetellidae*	V	Bilophodont	—	—	—	—	—	—	—
Hyracodontidae*	V	Trilophodont	(x)	—	—	—	—	—	—
Rhinocerotidae	V	Trilophodont	(x)	—	—	—	—	—	—
<i>Ceratolherium</i>	V	Plagiolophodont	x	—	—	—	—	—	—
<i>Elasmotherium</i> *	V	Plagiolophodont	—	x (crown)	—	—	—	—	—
HIPPIOMORPHA									
Equidae (later species)	—	Plagiolophodont	x	—	—	—	—	—	—
<i>Pseudhipparion simpsoni</i> *	—	Plagiolophodont	—	(x)	—	—	—	—	—
Palaeotheriidae*	—	Trilophodont	(x)	—	—	—	—	—	—
ARTIODACTYLA									
SUINA									
Hippopotamidae									
<i>Hippopotamus</i>	—	Bunodont/ Bilophodont	(x)	—	x	—	—	—	—
Suidae	x	Bunodont	—	—	x	—	—	—	—
<i>Phacochoerus</i>	—	Columnar	x	—	x	—	—	—	—
TYLOPODA									
Protoceratidae*	—	Selenodont	(x)	—	—	—	—	—	—
Camelidae (later species)	—	Selenodont	x	—	—	—	—	—	—
Stenomylinae*	—	Selenodont	x	—	x	—	—	—	—
Merycoidodontidae*	—	Selenodont	(x)	—	—	—	—	—	—
RUMINANTIA									
Antilocapridae									
<i>Antilocapra americana</i>	—	Selenodont	x	—	—	—	—	—	—
Bovidae (most later species)	—	Selenodont	—	(x)	—	—	—	—	—
<i>Ovis spp.</i>	—	Selenodont	x	—	—	—	—	—	—
Cervidae	—	Selenodont	(x)	—	—	—	—	—	—
Climacoceridae*	—	Selenodont	(x)	—	—	—	—	—	—
Giraffidae	—	Selenodont	(x)	—	—	—	—	—	—
Sivatherinae*	—	Selenodont	(x)	—	—	—	—	—	—
Moschidae	—	Selenodont	(x)	—	—	—	—	—	—
Palaeomerycidae* †	—	Selenodont	(x)	—	—	—	—	—	—

* Signifies extinct taxon.

† V in 'More durable enamel' column signifies vertical Hunter-Schreger bands.

‡ *sensu* Janis & Scott, 1987.

by the late Palaeocene or early Eocene. Lophed teeth were derived independently in the different herbivorous orders, and thus differ in their detailed morphology and descriptive terminology (although the terms are, indeed, only simple descriptive ones, and do not imply homology between different lineages). Varieties of lophed teeth can be termed bunoselenodont, selenodont, bunolophodont, lophodont, bilophodont, trilophodont [subdivided into ectolophodont and plagiolophodont (Fortelius, 1985)] and we have added the terms columnar and lamellar to this list (see later discussion). It should also be noted that the type of 'bunodont' tooth seen in primates, suines and early proboscideans is considerably modified from the simple type of bunodont tooth seen in early ungulates, and possesses lower, more rounded cusps. Fig. 1 depicts these various types of morphologies, and a comprehensive listing of occlusal morphologies in those mammalian taxa which have adaptations for increased dental durability is provided in Table 2.

'Hypsodont', or high-crowned, cheek teeth are common in herbivorous mammals, and although hypsodonty was not prevalent in Northern hemisphere taxa until the Miocene, many South American taxa had achieved a considerable degree of hypsodonty by the early Eocene. The first incidence of hypsodonty in South American mammals was seen as early as the middle Cretaceous (Bonaparte, 1986), and a xenarthran with possibly hypselodont (evergrowing) cheek teeth, *Sudamerica ameghinoi*, was known from the Palaeocene of Argentina (Scillato-Yane & Pascual, 1985). It is thus clear that even early mammals were capable of developing hypsodont teeth, despite the relatively late evolutionary appearance of hypsodonty among most living mammalian herbivorous lineages. Hypsodonty is clearly related to simple functional requirements, and is not necessarily an 'advanced' mammalian feature, as is sometimes assumed.

II. CONSTRAINTS ON THE DESIGN OF MAMMALIAN DENTITIONS

(1) *Historical constraints: origins of dentitions typical of herbivorous mammals*

One of the characteristic features of mammals is the reduction of the continual tooth replacement series primitive for toothed vertebrates to a mere double set: the 'diphyodont' condition of possessing 'milk' and 'permanent' dentitions. The whole issue of therian tooth replacement and homology is still unsettled (see Novacek, 1986, for a recent review), but from the viewpoint of dental durability these problems are of little relevance. Diphyodonty first evolved in early Mesozoic mammals (Parrington, 1971), perhaps in functional association with lactation (Pond, 1977). The consequences of diphyodonty for these early mammals were considerable. With the earliest deciduous or 'milk' teeth being replaced early in life by the permanent dentition (which included the specialized molar teeth), the jaws now contained a dentition that would not be periodically disrupted by loss and addition of individual teeth in the row. In effect, the tooth row was now a permanently integrated unit, and this made possible the development of the uniquely mammalian attribute of precise occlusion with complex interlocking cheek teeth.

It is evident that the primitive function of vertebrate teeth was to subdue and prehend the food prior to swallowing. This was probably true of the mammal-like reptiles to a certain extent, although some of them (notably most cynodont taxa) had a differentiated dentition with complex postcanine teeth, and may well have chewed their food to some extent. It seems, however, that diphyodonty and precise dental occlusion

are uniquely mammalian attributes, seen in the earliest Mesozoic mammals (see Crompton & Sun, 1985). The high-cusped cheek teeth with sharp, shearing facets, characteristic of early mammals, are in fact only possible with precise occlusion. Such occlusion is thus a prerequisite for the development of a mammalian type of efficient comminution of non-brittle foods by reciprocal pairs of blades (see Crompton & Sitalumsden, 1970) and, since gut passage-time is proportional to particle size of the ingesta, for rapid digestion. Efficient comminution, rapid digestion, and high metabolic rate are evidently part of a single functional complex in mammalian evolution. An indication of this might be the stereotyped triangular masticatory orbit, seen in all living mammals studied (Hiimäe, 1976, 1978). Presumably this reflects a very old physiological pattern, inherited from the earliest mammals.

(2) *Functional demands, with a note on dental wear*

The unique mammalian feature of diphyodonty, which was essential for the precise occlusion of the early insectivorous mammals, proved to be a mixed blessing for those later mammals which secondarily adopted a more plant dominated diet. A diet of insects and other invertebrates represents a concentrated source of protein. The intake demands of such a diet are small relative to those of a plant diet, and the food itself is not particularly abrasive. Although the tough chitinous exoskeleton of insects must be fractured and crushed by the cheek teeth, little masticatory work must be performed in order to release the soft inner contents. Moreover, chitinases are found in the digestive tract of insectivorous mammals (Jeuniaux, 1961).

The structural materials of both insect and plant material (chitin and cellulose respectively) are polysaccharides of similar physical and chemical properties (Wainwright *et al.*, 1976), and it is ironic that plants and insects should pose such different problems to mammals in terms of the design of the masticatory apparatus. (Plant cell wall constituents other than cellulose include hemicelluloses, which are also polysaccharides, and lignin, which is neither a polysaccharide nor apparently digestible at all. For simplicity we refer to all these cell wall polysaccharides as 'cellulose'). The problems of herbivory lie both in the structure of plant material and in the digestive physiology of mammals. Cellulose (and lignin) is not deposited on the outside of plant structures, as is chitin around the body of an insect, but instead is incorporated into each cell wall. Thus in order to release the nutritious cell contents, the cellulose envelope around each cell must be fractured. (The percentage of cellulose present in any part of a plant is correlated with the structural requirements of that part, and also with its age. For example, leaves have more cellulose in their cell walls than do reproductive or storage structures such as fruits or roots, and stems have more cellulose than leaves. Also, old leaves contain a greater proportion of cellulose than young leaves.) Compounding the problem resulting from this feature of plant structure is the fact that no multi-cellular animal has been able to evolve a cellulase enzyme (the reasons for this are still not clearly understood). Even in the presence of symbiotic microorganisms which can chemically digest the cellulose, the dentition of a herbivorous mammal must function to disrupt the cell walls mechanically in order to release the cell contents before the food reaches the site of digestion (see Janis, 1976).

It is certainly possible to be a herbivorous vertebrate without complex teeth and mastication, even without a complex fermentation site in the gut to house symbiotic

cellulase-producing microorganisms. The cell contents will certainly find eventual release from the cellulose envelopes if left to stew in the digestive system for long enough (R. Hansen, pers. comm.). For example, many present-day herbivorous lizards lack any notable morphological adaptations to herbivory except for the possession of flattened teeth to grasp the food, although some herbivorous reptiles possess a fermentation chamber in the hind gut (see Farlow, 1987, for review). However, mammals are endothermic, and hence require a higher rate of intake and turnover of the digesta. They would be unable to tolerate the very long passage time typical of herbivorous ectotherms. Herbivorous birds obviously lack complex cheek teeth, and show little in the way of physiological digestive adaptations (Morse, 1975), but use the uniquely archosaurian feature of a gizzard in the digestive tract to grind up the food. They have, however, a lower digestive efficiency than mammals (see Morse, 1975). Complex cheek teeth and mastication of the food were developed convergently with mammals in certain herbivorous dinosaur lineages, most notably among the hadrosaurs where the dentitions are highly comparable to those of living ungulates, although the masticatory mechanisms involved were quite different from those of mammals (Norman & Weishampel, 1985).

The chemical breakdown of cellulose (which takes place in the digestive tract) happens after mechanical comminution in the mouth, but both are part of one process, and are functionally coadapted. The caecum is a primitive mammalian feature, probably allowing the capacity for a limited degree of cellulose fermentation in association with gut symbiotes in most mammals, quite apart from the later parallel evolution of diverse complex fermentation chambers housing symbiotic cellulase-producing microorganisms in more specialized herbivores (Hume & Warner, 1981). It seems probable that the initial function of a fermentation chamber within the mammalian digestive tract was to provide a chemical means for the disruption of the plant cell wall, so that the cell contents could be released for digestion, notwithstanding the fact that cellulose itself may serve as a nutritional source. Among present-day herbivores, it is apparently only the ruminant artiodactyls that obtain a large proportion of their nutritional requirements from the plant cell wall (Van Soest, 1982). Other herbivores are more dependent on the nutritional value of the plant cell contents. They rely on a large daily intake and a rapid passage time to achieve the required bulk of cell contents, and although cellulose may be used as a nutritional source, it is not the focus of their nutritional requirements. It is even possible to be a herbivorous mammal with little, if any, specialization for cellulose fermentation, provided that the diet is not too fibrous, and the body size of the animal is large enough to make a relatively large daily intake a physiological possibility. This type of herbivorous strategy is seen among many primates and pigs.

Thus the key to understanding why plant foods must be so thoroughly masticated is the nature of cellulose. Whether or not the animal is able to use cellulose as food, it must break down the cell walls mechanically in order to obtain nutrients at a rate sufficient to satisfy its metabolic needs. This necessity imposes a heavy burden on such animals, which have inherited a diphyodont dentition from their insectivorous ancestors. Their diet is much more taxing on the teeth, and it is a problem to make the teeth sufficiently durable to sustain a lifetime of mastication.

Thus the teeth of herbivores need to be more durable for a variety of reasons. Volume

for volume, vegetable matter is less nutritious than animal matter, in part at least because of the large amount of cellulose incorporated into the plant tissue. Protein, in particular, may be a limiting factor dictating a large daily intake of herbage (see, for example, Owen-Smith & Novellie, 1982), as may be the availability of certain elements such as calcium and magnesium (Owen-Smith, 1982). Thus a greater volume of vegetable food must be consumed per day than would be necessary if the diet comprised animal tissues. Also, the dentition must function to disrupt mechanically the cellulose-containing plant cell walls to ensure an adequate level of absorption of the plant cell contents with the typically rapid mammalian passage of ingesta. So, a given volume of plant material must be masticated more thoroughly than the equivalent volume of animal material. Finally, as considered per individual chewing cycle, vegetable matter is tougher and more abrasive than animal matter, and contributes more to the abrasion of the surface structure of the teeth. In particular, the opaline phytoliths contained in grasses produce deep scratching and pitting on the occlusal enamel surface (see Walker *et al.*, 1978), and must contribute significantly to dental abrasion. However, analysis of the diet and the crown height of the cheek teeth in living ungulates suggests that dust and grit accumulated on plant material may be more important than the abrasive nature of the plant material itself in determining the rate of wear (Janis, 1988). (Naturally, the accumulation of grit on the surface structures is a more typical feature of plant food items than of animals!)

We still know little about what happens to the teeth during chewing, and how the tissue loss we know as 'wear' actually comes about. This is clearly shown by the problems encountered in interpretations of 'microwear' features (see reviews by Teaford & Walker, 1984; Teaford, in press). More experimental work and more observations are clearly needed, but meanwhile it may be helpful to approach the problem of wear from a purely theoretical point of view. Such a view is offered by a consideration of isometric scaling of mammalian cheek teeth to body size.

Generally speaking, mammals masticate food at a rate correlated with the metabolic rate. The amount of food comminuted during one chew is proportional to the volume enclosed between the opposing teeth, and, for isometrically scaled teeth, to the body mass. Chewing rate scales as body mass to the power 0.25, which results in food comminution rate scaling with metabolic rate, as body mass to the power 1 minus 0.25 = 0.75 (Fortelius, 1985). This isometric scaling applies not only to horizontal dimensions, but also to tooth height (Janis, 1988). In other words, hypsodonty is independent of body size; large animals have neither relatively higher nor lower-crowned teeth, although both claims have been made on the grounds of 'metabolic' scaling. Now, life-span in mammals scales approximately as body mass to the 0.25 (studies compiled by Peters, 1983), which means that the total number of chews during an animal's lifetime will, statistically, be a constant independent of body size, just as the number of heartbeats and breaths. This has the important implication that the thickness of dental tissue lost during one chew scales isometrically with body size. This fact is far from self-evident.

Consider the problem. If teeth and chewing muscles both scale (at least very nearly) isometrically with body size, as appears to be the case (Cachel, 1984; Fortelius, 1985), then occlusal stress, being a direct function of tooth area, will also be more or less independent of body size. One might imagine that, for any one food type, the thickness

of tissue lost per chew would be a direct function of occlusal stress, but this is evidently far from true. Were that the case, absolute (rather than relative) tooth height would have to be independent of body size, which it is not (Janis, 1988). The conclusion must be that food *volume* somehow determines wear. Wear always takes place at the surface of the tooth, so food volume as such cannot have any influence (since only the area presented by the tooth can be worn, no matter how high the pillar of food above it). The only way out of this dilemma seems to be to postulate some element or 'particle' present in the food and evenly distributed in it, that is responsible for wear at the occlusal surface. (These hypothetical 'particles' might be small hard elements such as plant phytoliths, or wind-blown dust particles.) Larger animals have absolutely larger mouths, and thus have an absolutely taller pillar of food between the occlusal surfaces at the start of each sequence of mastication. The higher the pillar of food above any one unit area of the tooth, the higher the probability will be that such a 'particle' contacts the surface when the teeth are brought together.

Thus if both occlusal area and the height of the pillar of food between the teeth scale isometrically with body size, large and small animals will wear their teeth at the same relative rate (Fortelius, 1987). If correct, this model may have far-reaching implications for microwear studies, especially in the case of foods which are abrasive only because they contain such extraneous 'particles', and do not in themselves cause wear to any great extent. For the present we are content to note that our model explains the observed isometric scaling of relative crown height (hypsodonty) with body size, and that, if it is falsified, the need for an alternative explanation is urgent. (However, wear may still be relatively slightly more rapid in smaller animals, for reasons which will be discussed later.)

Although all truly herbivorous mammals show specialization of the occlusal morphology, they do not all exhibit specializations to increase the durability of the dentition. No major specializations of this nature are seen in the herbivorous orders Condylarthra, Dermoptera, Dinocerata and Pantodonta, and among the diversity of herbivorous marsupials specializations are seen only in the living families Macropodidae and Vombatidae, and the extinct families Argyrolagidae and Patagonidae (see Pascual & Carlini, 1987). It is certainly possible to subsist on a herbivorous diet of relatively low fibre content without increasing the durability of the dentition. This is demonstrated in the many living ungulates with low-crowned teeth. These members of the orders Artiodactyla and Perissodactyla ingest mainly dicotyledonous plant material in forest or woodland habitats (see Janis, 1988). However many herbivores, especially those that take a more fibrous diet, with a large proportion of monocotyledonous species, do show marked specializations for increasing dental durability.

(3) *Developmental constraints*

In our usage, developmental constraints are limits imposed upon the possibility for modification of a structure in an animal by the processes inherent in the ontogeny of that structure. Developmental constraints are distinct from functional constraints, which may be imposed by the nature of the structural material, the laws of the physical universe, or a conflict between the optimal design of a particular structure and the design of the animal as a whole. However, developmental and functional constraints may sometimes interact, if the original functional design of a structure may later act in opposition to further evolutionary change of that structure. A pertinent example is the

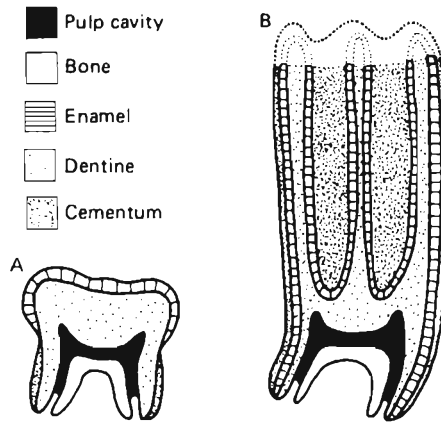


Fig. 2. Longitudinal sections of cheek teeth. (A) Low crowned (brachydont) tooth (human molar). (B) High-crowned (hypsodont) tooth (horse molar). Modified from Steel & Harvey (1977).

case of diphodonty in mammalian dentitions. Exact occlusion demands the non-replacement of teeth, but, once established, this condition becomes a constraint on the possibility of increased durability of the dentition as a whole. This particular developmental constraint is apparently not absolute, as examples show that it has been overcome at least twice in mammalian history (see below). Some other developmental constraints do appear to be absolute, although this assumption must remain based on negative evidence.

A definite developmental constraint lies in the manner in which teeth are formed (von Koenigswald, 1982; Fortelius, 1985). Teeth, and related dermal structures such as dermal denticles and placoid scales, arise in ontogeny through an interaction between ectodermally derived epithelium and mesodermally derived mesenchyme tissue. In the dental papilla, the epithelium (forming the outer enamel) envelops the mesenchyme (forming the dentine, cementum and roots). Enamel is secreted towards the basement membrane of the epithelium, i.e. towards the mesenchyme. Dentine is secreted in the opposite direction, towards the epithelium, so that the hard tissues grow in opposite directions from each other, and away from their junction at what was originally the basement membrane of the epithelium (see discussion and references in Fortelius, 1985). Thus the enamel layer of the crown of the tooth, whether in the form of a simple cap, or as a covering of a complex series of infoldings of the epithelio-mesenchymal interface, must be laid down before the tooth erupts through the secretory epithelium, and cannot be renewed after eruption.

In hypsodont (high crowned) cheek teeth, the gaps between the tall pillars of enamel-wrapped dentine are often filled with (coronal) cementum, also laid down before eruption. Like bone and dentine, cementum is of mesodermal origin. It is softer than dentine, of a similar mineral content to bone (68% rather than 80%; Fawcett, 1986). In certain hypsodont mammals, the whole crown is covered with cementum prior to eruption. As the tooth is worn, a complex occlusal pattern of enamel ridges alternating with basins of dentine and cementum is revealed (see Fig. 2). Presumably the crown is strengthened by the presence of such fill-in support between the high and slender cusps.

It follows from this mode of dental ontogeny that, if cheek teeth are to grow

continuously throughout life, as frequently occurs in small mammals and occasionally in large ones, severe developmental constraints apply, as the enamel covering cannot be renewed at the surface of the crown after the initial eruption of the tooth. There are two main types of continuously growing or 'hypselodont' cheek teeth, which we will refer to as 'crown' or 'root' hypselodont (modifying terms introduced by White, 1959). We acknowledge that these terms are broad ones, and may disguise important differences between types of teeth included in the same category, but we take these terms as useful descriptive ones for the time being, pending further study.

Crown hypselodont teeth are formed by the indefinite suppression of root formation, and the crown continues to grow after eruption. Obviously, any enamel pits (closed fossae of enamel on the occlusal surface of the tooth) must be formed before eruption, and will eventually be worn away. The enamel of the persistent part of the hypselodont tooth is formed by a ring-shaped enamel-organ surrounding the base of the crown, and the occlusal enamel pattern can thus only consist of shapes that can be produced by infolding of the outer enamel ring. Not all parts of the ring need be secretory, and non-secretory portions will result in corresponding 'dentine tracts' (or vertical strips of tooth lacking the enamel covering). Since the complex occlusal morphology of hypselodont ungulates usually includes closed enamel fossae as an integral part of its pattern ('cusp' hypselodonty, *sensu* White, 1959), it is clear that the transition from hypselodonty to hypselodonty cannot be easy for such animals, and in fact very few examples are known. Teeth which lack closed fossae in their occlusal morphology, and which in the worn state consist essentially of a folded enamel sheet surrounding an enamel core (crown base hypselodonty, *sensu* White, 1959) are not affected by this constraint, and this may be the reason why so many rodent lineages have made this transition without apparent difficulty. We shall return to this problem and its various solutions in a later section.

Root hypselodont teeth are formed when the true crown is lost through wear at an early stage, and the root continues to grow and erupt as a dentine peg without enamel covering. Often (as in sloths) the dentine is not homogenous, but includes hypermineralized layers which form ridges and thus allow some control of occlusal shape. Root hypselodont teeth are usually covered with an outer layer of cementum. A vestigial enamel crown is frequently present initially, but is rapidly worn off (as in the dugong; Marsh, 1980). All hypselodont teeth lack completed roots, and are often called 'rootless'. This term is obviously misleading if the whole functional tooth happens to consist of root-derived tissue.

III. MEANS OF INCREASING THE DURABILITY OF THE DENTITION

(1) *Types of solutions available*

There are two ways to increase the functional life of the dentition, which need not be mutually exclusive: increasing the wear resistance of the dental tissues, and increasing the amount of dental tissue available for wear. The amount of dental tissue available can be increased in three different, non-exclusive ways. Individual teeth may be increased in size without any change in shape, the number of teeth may be increased, or the height of the individual teeth may be increased.

(2) *Increased wear resistance of dental tissues*

Wear resistance is naturally a matter of hardness to some extent, but also of resistance to cracking. Glass teeth, although very hard, would certainly be almost useless because of their great brittleness. Enamel is much softer than glass, and indeed somewhat softer than its main component hydroxyapatite, but it more than compensates for this by its resistance to crack propagation. This highly desirable property is achieved in several ways, and at several levels of structural organization. First and most importantly, the long apatite crystals are glued together by a very thin film of protein, which greatly increases the elasticity of the enamel. Secondly, the apatite crystals are organized into bundles, commonly (and somewhat misleadingly) referred to as 'prisms'. The course of a prism through the tissue reflects the movements of the ameloblasts that contributed material to it, which means that the relative movements of ameloblasts during secretion of the enamel will determine the spatial organization of the enamel prisms. Such movement usually occurs in highly organized ways, and gives rise to the phenomenon of regular prism decussation and its optical manifestation, the Hunter-Schreger bands (Boyde, 1964, 1976). The relationship between prism decussation and crack propagation has been the subject of considerable interest (e.g. Von Koenigswald, 1980, 1988; Rensberger & von Koenigswald, 1980; Boyde & Fortelius, 1986; von Koenigswald *et al.*, 1987; Pfretzschner, 1988). Essentially cracks are deflected, and often stopped, at the boundaries between zones of differently oriented (decussating) prisms. This means that large blocks of enamel will not easily cleave off under occlusal stress, which of course adds considerably to the wear resistance of the tooth.

On the other hand, the presence of prisms, and particularly prism decussation, decreases the density of the enamel, and thus its hardness. Interestingly enough, structurally very complicated enamels are found in the hypselodont molars of voles and lemmings, where dental wear is extremely rapid (von Koenigswald, 1980; von Koenigswald & Golenishev, 1970). Presumably the complicated structure increases the internal cohesion of the extremely thin enamel found in these teeth. Thin enamel edges make for high local occlusal stress, but in hypselodont teeth rapid (but even) wear is of little consequence, as the eroded material is continually replaced. The hardest known enamel is apparently that possessed by humans. The normal mammalian condition is teeth with an inner enamel layer with pronounced prism decussation, and an outer layer with limited or no decussation, so that the outer enamel is harder, and also more brittle, than the inner enamel (see Fortelius, 1985, for further discussion). In humans the outer layer is exceptionally thick and covered by a thin layer of prismless surface enamel (see Karlström, 1931, for hardness data).

Thus there is a limit to how much the wear resistance of enamel (and, of course, other dental tissues) can be increased. The wear resistance of a tooth can obviously be increased by increasing the amount of enamel (i.e. its thickness), rather than its hardness or density. (We refer to 'thick' enamel only in an approximate sense in this paper, but see Martin (1983) for a precise definition.) However, various constraints may also affect the thickness of the enamel. Firstly, since enamel has to be secreted onto a predentine mould (Boyde, 1976), there must be at least a core of dentine present. Since secretory ameloblasts do not divide, the surface area of this core cannot be very much

smaller than the surface area of the finished enamel covering. This presumably limits the ratio of enamel to dentine thickness in a tooth.

A potential means of increasing the durability of the enamel would be to substitute some harder mineral for the hydroxyapatite. Many rodent species incorporate iron pigments into the incisor enamel, which can be readily observed as an orange colour of the tooth, but no rodent extends this incorporation of iron in the enamel into the enamel of the cheek teeth. However, certain shrews (family Soricidae) are able to secrete iron hydroxide ($\text{FeO}(\text{OH})$) in the form of goethite on top of the normal enamel, and their teeth have the orange colour typical of many rodent incisors (Akersten *et al.*, 1984, and MS). Apparently the goethite layer is produced because the ameloblasts secrete an iron binding protein prior to secretion of the surface enamel. The goethite thus comes to rest underneath the thin apatite layer of non-prismatic surface enamel. This raises the possibility that other iron-rich enamels, which Akersten *et al.* propose to call 'siderose' enamels, also include iron in the same or some similar form. The important point is that this layer of goethite is harder than enamel, and Akersten *et al.* consider that in shrews it aids in resisting dental wear resulting from sand and silt adhering to the surface of their soft-bodied invertebrate prey, or contained within the gut of the prey.

Siderose enamel in the cheek teeth is known in the living shrew genera *Blarina* and *Notiosorex*, and pigmented shrew cheek teeth are known from as long ago as the Oligocene (Repenning, 1967). No other therian mammal is known to have had pigmented cheek teeth, but such teeth have been found in a Chinese Palaeocene multituberculate, *Lambdopsalis bulla* (Minchen Chow & Qi Tao, 1978). This species has red-coloured enamel on the upper and lower second molars, and on the lower first and upper second and third incisors. 'Gigantoprismatic' enamel is seen in most taeniolabid multituberculates (Fosse *et al.*, 1985; Krause & Carlson, 1986), and two layers of enamel are seen in some multituberculate species (Moss, 1969), but the function of these features is not known.

From a functional point of view, increasing the wear resistance of the enamel is mainly advantageous as long as wear can be prevented from penetrating the enamel covering, thus destroying the performed (Lumsden & Osborn, 1977) occlusal morphology. Once this happens, and the preformed occlusal morphology is replaced by an acquired one, differential wear becomes an important agent of control of the subsequent occlusal morphology. Hard, thick enamel is only useful when chewing requires little or no exact occlusion, essentially in animals which either crack hard food items or crush soft ones without cutting them. Thick enamel edges do not wear to produce sharp blades. In animals which require the teeth to cut (or 'shred') the food, thin cutting enamel blades are produced by differential tooth wear, so that thin blades of enamel (which may also be of unequal thickness in different parts of the crown) appear on the occlusal surface interspersed with softer areas of dentine (and also of cementum in many hypsodont teeth). (In the formation of these types of teeth, the enamel is not only laid down as an external cap, but thin sheets of enamel are laid down over pillars of dentine in the body of the tooth, as shown previously in Fig. 2.) Thus as the teeth experience initial wear, the enamel blades are exposed. This 'acquired' occlusal morphology is the functionally optimal topography for teeth of this type (it would obviously be developmentally impossible to deposit the crown enamel so that the

teeth erupted with this pattern preformed). Continued wear sustains this acquired topography during most of the life of the tooth, although as the teeth are progressively worn, the ratio of the surface enamel blades to the exposed dentine is reduced.

In other words, increased wear resistance of the teeth can be achieved to some degree by increasing the durability of the enamel, but it is only advantageous up to a certain point, and is of advantage only to those animals which employ predominantly orthal motions of the jaw to crack or crush food items. (Those animals that rely on an acquired occlusal morphology to cut or shred their food usually employ a predominantly lateral mode of jaw movement.) Once the rate of wear of the teeth is fast enough to destroy the preformed occlusal morphology at an early stage in the life of the animal, the *amount* of dental tissue, rather than its wear resistance, must be increased in order to produce teeth of sufficient functional durability. The wear resistance of the tissues themselves is probably frequently reduced in this process.

Increased wear resistance of dental tissues and/or increased thickness of the enamel, apart from the example already discussed of the goethite layer in the cheek teeth of certain shrews and multituberculates, is seen in the following groups of mammals: in primates, in the living genera *Cebus*, *Cercocebus*, *Pongo* and *Homo*, in the extinct hominoids of the *Sivapithecus* group and in the australopithecines (Kay, 1981); in certain species of the Suidae (e.g. *Potamochoerus porcus* and *Phacochoerus aethiopicus*) (Cooke & Wilkinson, 1978; Hatley & Kappleman, 1980); in the extinct 'insectivoran' (proteutherian) family Pantolestidae (Savage & Long, 1986); in the extinct insectivoran (lipotyphlan) family Dimylidae (Schmidt-Kittler, 1973); and in early proboscideans such as members of the Gomphotheriidae and Mammutidae. Thick enamel was also seen in the teeth of early manatees (Domning, 1982), and in desmostylians, especially in the later, hypsodont forms (Vanderhoff, 1937). The highest ratio known of enamel to dentine in a mammalian tooth was probably that seen in the molars of the Miocene marine mammal *Desmostylus* (Vanderhof, 1937). Most authors have regarded the Desmostylia as herbivorous, but the exact nature of their diet is unknown. They appear to have used a predominantly transverse occlusal stroke in chewing (D. P. Domning, pers. comm.). The extinct giant sthenurine kangaroos (subfamily Sthenurinae) also had enamel that was somewhat thicker than seen in the living kangaroos (subfamily Macropodinae). Mollusc-eating vertebrates have at all times tended to develop blunt teeth with a thick covering of hard tissue; a recent mammalian example is the sea otter, *Enhydra lutris* (Ewer, 1973), and mollusc-eating has been suggested as the reason for the thick enamel in the dimylids and the pantolestids (see Savage & Long, 1986).

It should be mentioned in this context that, in forms with an acquired occlusal morphology, the enamel is often modified in various ways which appear to be related to wear resistance, especially crack propagation. Such modification typically involves the mode of prism decussation and the three-dimensional arrangement of Hunter-Schreger bands. For example, lophodont ungulates in a number of orders have evolved vertically oriented Hunter-Schreger bands (Fortelius, 1985). This has been interpreted as an adaptation to resist cracking when the enamel edges are loaded in a direction away from the supporting dentine (Boyde & Fortelius, 1986). Vertical Hunter-Schreger bands were first discovered in rhinocerotid enamel (Rensberger & von Koenigswald, 1980), and have since been discovered in the pantodont *Coryphodon*, in members of the order Dinocerata, in the embrithopod *Arsinoitherium*, in members of the South

American orders Astrapotheria and Pyrotheria, in the rhinocerotoid families Hyracodontidae and Amynodontidae and in the tapiroid family Deperetellidae (see Fortelius, 1985 for review). However, both the histological details and the functional significance of modified decussation patterns are still incompletely understood.

(3) *Increased tooth size*

Although an increase in the size of the individual teeth may appear to be the simplest solution to the problem of increased dental wear, this solution involves developmental and functional complications that probably account for its rarity. To make larger teeth, the tooth germs must contain more or larger secretory cells. In contrast, teeth with higher crowns can be made without increasing the number of cells if the cells simply remain secretory for a longer time. Functionally, larger teeth mean a larger area of occlusal contact and thus lower occlusal stress, unless the masticatory muscles are increased in proportion, which will in turn have effects on cranial morphology. Furthermore, if wear per chew is proportional to the volume enclosed between the opposing teeth, as suggested above, and if this volume is a function of tooth size (White, 1959; Fortelius, 1985), larger teeth will also mean more rapid wear.

The reason for this is as follows: The wear per chewing stroke will increase in proportion to the height of the food between the teeth, which is proportional to the size of the tooth. However, the volume comminuted per chewing stroke will increase with tooth volume, so the teeth will still be able to comminute a larger volume before becoming worn out. Theoretically, two extreme possibilities are available, or any stage in between the two. In the first instance, the height of the food between the teeth remains unchanged, in which case wear per chewing stroke does not increase, and the volume comminuted per chewing stroke increases only in proportion to dental area. In this case, dental durability increases in proportion to the lowered chewing rate, which is proportional to the increase in comminuted volume, or to the dental area. In the second, the volume between the teeth increases in proportion to the volume of the teeth, in which case the volume comminuted per chewing stroke will increase in proportion to the increase in dental volume. But since wear per chewing stroke now increases in proportion to food and tooth height, durability will be proportional to reduced chewing rate divided by increased wear rate, or again, to the equivalent of dental area. When only tooth height is increased, durability of course increases directly in proportion to tooth height.

Larger teeth also means wider spacing of the functional elements on the occlusal surface, which will be disadvantageous if the precise spacing was optimal for the animal's original diet (see later discussion). An increase in the size of individual cheek teeth has occurred in certain members of the orders Proboscidea (families Elephantidae, Gomphotheriidae, Mammutidae and Stegodontidae), Embrithopoda (family Arsinoitheriidae), Desmostylia (family Desmostylidae), Rodentia (family Hydrochaeridae) and Artiodactyla (families Camelidae, Hippopotamidae and Suidae). Increase in individual tooth size (which in many cases only affects the posterior molars) is usually accompanied by a delay in sequential tooth eruption, and in cases where the diet is additionally abrasive may be further accompanied by hypsodonty (see further discussion in later section). However, in the hydrochaerid rodents (capybaras), certain cheek teeth are greatly enlarged (most notably M^3 , see Fig. 1, but also M_3 to a certain

extent), and the teeth are additionally hypselodont, but no sequential eruption is observed. The enlarged third molars erupt fully into place with the rest of the dentition, and their increase in size appears to be at the expense of the relative reduction of the more anterior teeth. The reason for these enlarged teeth is not clear; they are probably not functionally analogous with the type of enlarged teeth that are combined with sequential eruption in the other mammalian herbivores cited here.

A caveat is in order at this point. It is important to keep in mind that teeth do not exist primarily in order to resist or tolerate wear, but to act as the vehicles of food comminution. It may be quite misleading to interpret dental morphology primarily from the point of view of wear resistance. Thus a large occlusal area might theoretically mean a low chewing rate and low rate of wear, but usually appears to reflect a high food intake (large volume per chewing stroke at normal chewing rate). This is illustrated by a comparison of equids (hindgut fermenters) and ruminant artiodactyls (foregut fermenters). Hindgut fermenters require a greater daily food intake than do foregut fermenters of similar diet and body size (Janis, 1976). Equids have a larger occlusal surface area (relative to body size) than ruminants, due to the possession of large, molarized premolars (Janis, 1988). This presumably reflects the greater daily intake needs of horses. In fact, hypselodont ruminants even tend to *decrease* the length and volume of the premolar row in comparison with more brachydont (lower crowned) ruminants, while the converse is observed in horses and other hindgut fermenters (other perissodactyls and hyraxes) (Janis, in press). Additionally, horses also have much more hypselodont cheek teeth (particularly premolars) in comparison with ruminants. Even in the most hypselodont ruminants, the premolars are considerably more low crowned than the molars, which results in a much lower total cheek-tooth volume than that seen in an equid of similar body size and dietary type (Janis, 1988).

The greater occlusal area of horses necessarily means that they must process a greater volume of food per chewing stroke than a ruminant of similar body size. In addition, the greater dental volume implies that the wear per unit dental surface is greater, and/or that horses undergo more chewing strokes per lifetime than ruminants, either or both factors being necessary to compensate for the greater total intake of food during the lifetime. [In accordance with this, horses also have relatively larger masticatory muscles than ruminants (Becht, 1953; Turnbull, 1970)].

(4) *Additional teeth, and a discussion of bilophodonty*

Production of supernumerary teeth would also appear to be a simple solution to the production of increased dental tissue to combat wear of the dentition, and could possibly be initiated by the simple repetition of an existing genetic programme. It should be noted that supernumerary teeth will not result in increased wear resistance of the dentition unless the teeth remain at their original size. More, but smaller, teeth within the existing length of jaw would not increase the amount of dental tissue available for wear. A longer jaw to accumulate more teeth simultaneously would theoretically increase durability, but would be subject to the same problems and constraints as described for the acquisition of larger teeth, and would also require considerable modification to the skull morphology. This might be disadvantageous to the existing design of the masticatory apparatus (for example, it would have an effect on the moment arms of the masticatory muscles). The most reasonable solution is thus

one where the whole tooth row shows a delay in eruption, so that additional teeth are erupted from the back of the jaw to replace the anterior teeth as they become worn down.

Addition of supernumerary teeth of *small size* is seen in certain omnivorous mammals (for example in aardvarks and armadillos), and in some carnivores (for example in aquatic carnivores and also in the bat-eared fox, *Otocyon*), but this is not observed in any herbivore apart from manatees, and the presumably herbivorous, extinct, armadillo-related glyptodonts. We conclude that the addition of small, supernumerary teeth (which in all these examples except for the bat-eared fox and the manatees is also associated with a simplified, homodont form of the dentition) must be for other reasons besides increasing the durability of the dentition, possibly to increase the number of enamel cutting edges in teeth with a simple occlusal pattern. [(This has been suggested as an explanation for the condition in manatees (Domning, 1982).)]

There may well be developmental reasons for the invariable addition of supernumerary teeth at the back of the jaw (see, for example, Lumsden, 1979), but a simple functional explanation may suffice. Continuous replacement by addition of teeth within the dental row would severely disrupt precise occlusion (as discussed in Section II), and even additional elements at the back of the tooth row gradually travelling towards the anterior of the jaw would probably preclude most kinds of precise occlusion. Indeed, it seems that continuous replacement of teeth has evolved mainly in forms with a bilophodont molar morphology (see discussion below): in the Trichechidae (manatees, Order Sirenia) (Domning, 1982; Domning & Hayek, 1984), although the earliest manatees were bunodont rather than bilophodont (Domning, 1982); and in one species of the Macropodidae (kangaroos and wallabies), the rock wallaby or nabarlek *Peradorcas concinna* (Thomas, 1904; Sanson, 1983). Many macropodids (species in the genera *Macropus*, *Onychogalea*, *Lagorchestes* and *Petrogale*) have delayed sequential eruption without supernumerary teeth (Bartholomai, 1973, 1975; Sanson, 1980), and earlier manatees have only a limited number of supernumerary teeth (Domning, 1982; Domning & Hayek, 1984), although the genera *Ribodon* and *Trichechus* have an unlimited number.

Kangaroos in the subfamily Macropodinae may be constrained to a bilophodont molar morphology by their mode of incision. The lower diprotodont incisors fit *inside* the upper incisor arcade. This fit of the incisors, which initially evolved in early, presumably browsing forms, would preclude the later development of the more transverse movement of the lower jaw during occlusion that is essential to the functioning of the trilophodont or selenodont teeth of ungulates. Later, grazing, kangaroo species would thus be unable to parallel ungulate grazers in the adoption of these types of molar morphology. As bilophodont teeth cannot be easily made hypsodont, molar progression would be the only possible mode of increasing dental durability, although grazing kangaroos are *somewhat* more hypsodont than browsers (see Janis in press). The greatest degree of molar progression (with the exception of the example of supernumerary molars in *Peradorcas concinna*) is seen in the large grazing kangaroos, *Macropus fuliginosus*, *Macropus giganteus* and *Macropus rufus*. While Sanson (1978) has suggested that the genus *Procoptodon* (subfamily Sthenurinae) may have been a grazer, this animal displays neither molar progression nor hypsodonty [which would be less difficult to develop in sthenurines, as they lack the derived macropodine type of incision (Flannery, 1983)].

Bilophodont teeth consist of a simple pattern of two high-ridged transverse crests on each molar (the last lower molars often have three crests); they are common in relatively large mammalian herbivores, but are rare in small ones. (Such teeth are usually possessed, at least in living forms, by animals that browse on vegetation of moderate fibre content.) The chewing mechanisms are probably similar for bunodont and bilophodont teeth, and jaw movement is predominantly orthal. As these teeth consist of two long cutting blades, there may be an optimum absolute size for this type of morphology to function effectively to slice up vegetation. This would explain the size distribution of bilophodont mammals, but this explanation is admittedly speculative.

In addition to the previously discussed examples of the macropodids and the manatees (which both apparently developed the bilophodont condition from the bunodont one), numerous other kinds of mammals have independently evolved bilophodonty without the addition of supernumerary teeth, although a limited amount of delayed eruption of the dentition may also be apparent in these forms. The Miocene suid *Listriodon* and its relatives show various morphological stages between bunodonty and full bilophodonty, and the same applies to hippopotamids. The pygmy hippo (*Choeropsis liberiensis*) has bilophodont teeth, whereas the teeth of the common hippo (*Hippopotamus amphibius*) are more bunodont (and also more hypsodont), and rapidly wear to a flattened clover-leaf pattern, although the teeth of Pleistocene dwarfed species of *Hippopotamus* were often more bilophodont. Tapirs of the families Tapiridae and Deperetellidae also have bilophodont teeth, though these were originally derived from a trilophodont pattern. Bilophodont teeth are further found in some primates, in the primitive artiodactyl family Dacrytheriidae (e.g. in the genus *Tapirus*), in the proboscidean family Deinotheriidae, in certain sloths (e.g. the genus *Megatherium*), and in several 'archaic' Palaeocene ungulate lineages, such as pantodonts, uintatheres and arsinotheres.

It is worth noting that a bilophodont occlusal morphology apparently cannot usually be maintained by differential wear. Exceptions include certain large extinct sloths, such as *Megatherium*, and the African Oligocene rhino-like ungulate *Arsinoitherium*. *Megatherium* maintained a bilophodont morphology with root hypselodont teeth through having dentine layers of unequal hardness, a solution that would not be possible merely from the differential hardness of enamel and dentine because of developmental constraints within a continually growing tooth. The molars of *Arsinoitherium* were fairly hypsodont, and in lateral view the lophs curved over towards the mesial side, so that a more or less bilophodont occlusal pattern persisted despite wear. However, hypsodonty is not a generally available response to the pressure of increased dental wear in bilophodont forms. With the exceptions noted above, the dentition of bilophodont animals does not show much evidence of increased wear tolerance, but commonly shows some degree of delayed sequential replacement of teeth. The occurrence of supernumerary teeth presumably represents an additional factor in lineages that have already adopted the strategy of delaying tooth eruption.

In contrast, bunodont forms commonly show increased crown size (and frequently increased relative crown height), often in conjunction with a limited pattern of sequential replacement of teeth, but rarely show the acquisition of supernumerary teeth. (Early manatees are the only example that we know of, and later manatees become bilophodont.) Enlarging the individual teeth would not be a viable strategy for a bilophodont animal, as it seems probable that the effectiveness of the bilophodont

dentition depends on the total number of cross crests in the dentition, not the total amount of occlusal surface. Some manatees actually decrease the size of the individual cheek teeth, and increase the complexity of the enamel infolding, to increase functionally the number of shearing cross crests (D. Domning, pers. comm.). Manatees and kangaroos also have a fairly low basal metabolic rate in comparison with most placental mammals (Gallivan & Best, 1980; McNab, 1980), and this fact may have some relevance to their convergent evolutionary solutions to the problem of dental durability.

(5) *Increased tooth height*

By far the most common solution to the problem of increasing the durability of the dentition is increased tooth crown height, frequently accompanied by a modification of the occlusal morphology. There is a certain amount of terminological confusion over this issue, which requires clarification. Conventionally, a tooth is said to be hypsodont when its antero-posterior length is exceeded by its dorso-ventral height (Van Valen, 1960; Mones, 1982), and 'somewhat hypsodont' teeth which do not actually meet this criterion may be called 'mesodont' (Wood & Patterson, 1959). Attempts have been made to define hypsodontology in functional terms (Van Valen, 1960), or in terms of both crown height and occlusal morphology (Fortelius, 1982), but it is probably best to retain the term as a simple morphological concept in the conventional sense. Mones (1982) has suggested that the terms 'protohypsodont' and 'euhypsodont' should replace the current terms hypsodont and hypselodont respectively, to avoid the confusion between these terms that exists in the current literature. We sympathize with the attempt to avoid confusion, but disagree about the means. In our experience, 'hypsodont' is a widely and reasonably well understood term (at least outside of the rodent literature considered by Mones), and its abolishment is unlikely to clarify matters. Furthermore, we disagree with the implication that 'protohypsodonty' is an intermediate evolutionary stage on the path towards 'euhypsodonty'. For developmental reasons discussed above, and functional ones reviewed below, high crowned but rooted (hypsodont) cheek teeth are the final evolutionary stage in most larger mammals.

At any rate, increased crown height of the cheek teeth is extremely common among herbivorous mammals, and the most important means of increasing the durability of the dentition. Hypsodonty and hypselodonty have evolved in parallel many times in many mammalian orders, as documented in Table 2, and as further discussed in this section. In a highly hypsodont mammal, such as a horse or zebra (genus *Equus*), the enormously high crowned cheek teeth must be practically fully formed before eruption in order to ensure the continuity, throughout wear, of the elements of the occlusal surface (which are made up from isolated enamel fossae). The volume of unerupted cheek teeth that must be contained in the skull and jaw has resulted in considerable modification of skull design in equid evolution (Radinsky, 1984). Horses are considerably more hypsodont than other living ungulates (Janis, 1988), and even delay root formation until some time after tooth eruption (Kovacs, 1971), presumably to allow for a greater length of crown to be accommodated within the skull and lower jaw during odontogenesis. As discussed previously, the transition from hypsodonty to hypselodonty is very difficult for an animal like a horse that relies on enclosed enamel fossae in its occlusal morphology.

However, a case of an incipiently hypselodont equid (that is, where root formation was suppressed for considerably longer than in other equids, but not infinitely suppressed as in true crown hypselodonty) was seen in the late Miocene North American species *Pseudhipparion simpsoni* (Webb & Hulbert, 1986). The present degree of hypselodonty in equids [which has not shown an increase since the late Miocene (Janis, 1984)] may be the maximum attainable without a major restructuring of the masticatory apparatus. However, Webb & Hulbert (1986) point out that some recent ruminant artiodactyls, such as sheep species (*Ovis*) and the pronghorn (*Antilocapra americana*) approach the condition seen in *Pseudhipparion simpsoni*, with the suppression of root formation and the loss of the closed enamel fossettes in the lower part of the crown. They consider that this type of tooth morphology is only possible in relatively small ungulates (*P. simpsoni* was a small equid of similar size to the pronghorn), due to the mechanical limitations of a tooth supported only by an external shell of enamel. However, we note that notoungulates (some of which were as large as present day rhinos) followed this pathway to full hypselodonty (compare, for example, *Nesodon* with *Toxodon*). At any rate, no living ungulate is hypselodont, and even among extinct ungulates true hypselodonty is only known in two cases: species of the South American order Notoungulata, where the condition evolved in parallel numerous times (Simpson, 1980) and in the upper Miocene to Pleistocene rhinocerotid genus *Elasmotherium* (Brandt, 1878; Heissig, 1976). (The incidence of hypselodonty in ungulates will be discussed further in this section.)

High-crowned cheek teeth can be more easily accommodated inside the skull (and perhaps also in the mandible) if they are curved rather than straight, and in fact many hypselodont and hypselodont forms have such curved teeth. This was a common feature in many South American notoungulates, where the upper teeth were usually curved towards the lingual side, and the lower ones were either straight or curved, usually towards the buccal side (but at least in the genus *Toxodon* were also curved towards the lingual side). The root hypselodont glyptodonts (giant armoured xenarthrans related to the armadillos) had teeth that were weakly curved in the opposite directions (uppers towards the buccal side and lower towards the lingual), with the additional feature of a helical twist to the teeth. Beavers (order Rodentia, genus *Castor*) also have teeth that curve in this fashion, and this is developed to an even greater extent in the marsupial wombats (genera *Lasiorhinus* and *Vombatus*). It is intriguing that the Pleistocene South American equid genus *Hippidion* 'mimicked' the notoungulates in the evolution of upper cheek teeth strongly curved towards the lingual side (Sefve, 1912). Whether or not this actually indicates that the South American vegetational environment somehow favoured such teeth remains uncertain. Certainly the cheek teeth of *Hippidion* were not outstandingly hypselodont for a Pleistocene equid.

A functional implication of a curved tooth is that the side of the occlusal surface that corresponds to the outer curvature must wear away more rapidly than the side corresponding to the inner curvature. If this does not happen, eruption will gradually tilt the occlusal surface more and more, disrupting the pattern of occlusion. However, given the many different combinations of curved and straight hypselodont teeth observed, we will not attempt here to follow the implications of this in terms of chewing dynamics. We merely note that in some cases curvature is clearly related to the maintenance of occlusal topography under wear (see Fortelius, 1982, for rhinoceroses,

and the discussion of *Arsinoitherium* above). It is evident that in a straight tooth the transmission of occlusal stress from tooth to bone will pass through the base of the root or, in the case of continuously growing teeth, through the area of secretion. In a curved tooth, the stress will probably pass more or less through the side of the tooth. This might be of some importance for continuously growing teeth in protecting the secretory, and newly secreted, soft tooth tissues. However, straight, continuously growing teeth are not uncommon (though they are more a feature of smaller hypselodont forms), nor are curved and rooted teeth rare. Probably several factors are involved.

Whilst most ungulates achieve durable dentitions by hypsodonty, and hypsodonty was also seen in some other large herbivores, for example among certain members of the extinct orders Tillodontia (Stucky & Krishtalka, 1983) and Taeniodonta (Schoch, 1982), the solution in smaller herbivorous species seems to have been more often that of hypselodonty. Why should this be the case? First, neither cells nor such secretory products as enamel prisms are smaller in smaller animals, or at least are not relatively smaller in proportion to body size. Therefore the dental tissues, and particularly the enamel, are relatively coarser in smaller mammals, and the fragments that may be lost at wear events will be correspondingly relatively larger (a 'grain' effect). Secondly, wear-inducing particles are larger relative to smaller teeth, and might induce a greater degree of damage (as occlusal stress is independent of absolute size, as previously discussed). Thus the teeth of small mammals might be more likely to experience damage from 'occlusal events' (Rensberger, 1978), and thus wear relatively more rapidly (although absolutely more slowly, for reasons discussed previously). A small hypselodont rodent, such as a vole, may wear down and replace an entire cheek tooth within as little as a month (von Koenigswald & Golenishev, 1979).

Furthermore, the size of herbivorous food items is, to a large extent, independent of the size of the animal eating them. (While herbivores may obviously exercise some selection in the food items they select, the difference between, for example, a large blade of grass and a small blade of grass is much less than the difference in size between a mouse and an elephant. This contrasts with food item selection by carnivores, where a lion may select an antelope, and a cat a mouse, but both prey items represent similar 'nutritional packages'). It thus seems reasonable to suppose that some optimum interval between successive dental shearing blades exists for the comminution of any one kind of food in the dentition of herbivorous mammals, and that this interval is more or less independent of the size of the owner of the teeth.

In small mammals a close spacing of enamel edges on the occlusal surface of the tooth can easily be achieved by folding the perimeter of the crown, but in large mammals this is difficult. Indeed, while rodents commonly have teeth with an occlusal pattern made up by a folded external enamel covering, in ungulates the enamel crests in the central parts of the crown are usually the sides of the enamel pits (isolated fossae) that are laid down within the body of the tooth prior to eruption. As explained previously, for developmental reasons such isolated enamel fossae cannot be produced after the eruption of the tooth, and hypselodonty in most ungulates would therefore require considerable reorganization of the occlusal morphology. (It should be noted that, at least for lophodont teeth, this observation applies primarily to the upper molars, as the occlusal pattern on the lowers is more simple. However, it would be impractical to have

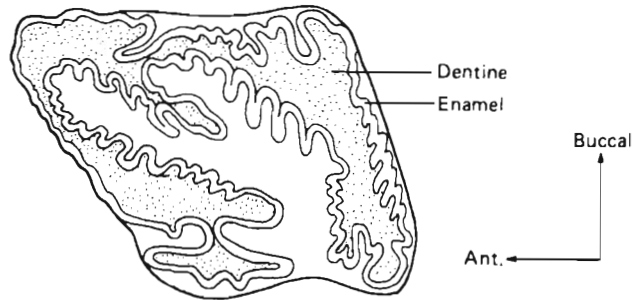


Fig. 3. Left M² of *Elasmotherium* (modified from Brandt, 1878).

hypsodont lower teeth in the absence of ever-growing uppers!) Thus, because of environmental 'graininess', teeth which ought to be mechanically equivalent independently of size in fact are not, and we suggest that this is the reason why many large herbivores are hypsodont while small ones are hypselodont.

In the few instances of large hypselodont mammals, the occlusal patterns are usually more or less modified and simplified. The loss of enamel in root hypselodont forms obviously results in cheek teeth that lack any complex pattern of enamel ridges on the occlusal surface. Examples include many xenarthrans (sloths, armadillos and glyptodonts), some sirenians, and the Tubulidentata (aardvarks) (see Table 2). However, in crown hypselodont forms considerable reorganization and simplification of the occlusal enamel pattern are also seen. The enamel covering of newly erupted teeth may be quite complex and resemble that of the ancestral rooted teeth, but sooner or later the part of the crown formed before eruption is worn away, leaving a simple enamel pattern that can be maintained by infolding of the coronal rim of enamel. This is seen in the wombats, including all extinct members of the family Vombatidae (with the exception of the earliest genus *Rhizophascolonus*) (Woodburne, 1984), in several families of the extinct order Notoungulata (Simpson, 1980), in some early south American xenarthrans, such as the Palaeocene *Sudamerica ameghinoi* (Scillanto-Yane & Pascual, 1985), and in one genus (*Stylinodon*) of the extinct order Taeniiodonta (Schoch, 1982). The only known truly hypselodont perissodactyls were species of the late Miocene to Pleistocene rhinoceros genus *Elasmotherium* (Brandt, 1878; Heissig, 1976). The evolution of hypselodontology in *Elasmotherium* presents a contrast to the simplified occlusal enamel pattern seen in other large hypselodont and incipiently hypselodont species. Although closed enamel fossae were not present after relatively early wear stages in *Elasmotherium*, the occlusal morphology remained unusually complex, due to infolding of the coronal enamel rim. In addition, the enamel became plicated, unlike the condition in other rhinoceros genera (see Fig. 3).

What might the functional effect be of a simplified occlusal enamel pattern? The evident answer is that the volume of food comminuted per stroke would probably be reduced. The animal might cope with this problem by chewing faster, or by spending more time per day chewing. However, it is interesting in this context to note that all living mammals that show loss of occlusal wear patterns with increasing growth of the tooth have a lower metabolic rate than is typical for most placental mammals (Marsh *et al.*, 1978; McNab, 1974, 1978, 1980). Sloths are known to have a very long digestive

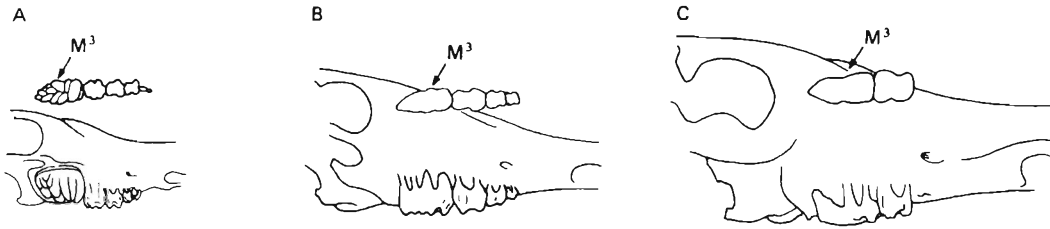


Fig. 4. Sequential eruption of molars in Suid. Age stages of giant forest hog (*Hylochoerus meinertzhageni*). (A) Juvenile; (B) subadult; (C) old adult. (Modified from Kingdon, 1979.)

passage time (Montgomery & Sunquist, 1975), and a low metabolic rate in comparison with other mammals might permit a decrease in the importance of the mechanical breakdown of the plant cell walls by the dentition. [It is also of interest that the grazing members of the Hyracoidea, in the genus *Procavia*, have a very low index of hypsodonty in comparison with other grazing ungulates (Janis, 1988), and that hyraxes also have an exceptionally low basal metabolic rate for placental mammals (Taylor & Sale, 1969).]

Of the hypselodont forms mentioned above, armadillos and armadillos are not in fact herbivorous. Armadillos are myrmecophagous and armadillos are omnivorous. However, these mammals are known to ingest a large amount of earth along with their food (Redford, 1987), which might account for the need for increased durability of their dentition. Schoch (1982) considered that taeniodonts may have been specialized below-ground feeders, which would also entail contamination of the food by earth, perhaps explaining the hypsodonty and hypselodonty seen in this extinct order.

(6) *Combinations of methods*

Various combinations of size increase, height increase, delayed sequential eruption and increased wear resistance are found in a number of forms, notably in the Proboscidea. In elephants (family Elephantidae), the premolars have been lost, and the three milk molars are followed in the eruption series by the three permanent molars. All the teeth are quite hypsodont, and are greatly enlarged in size to the extent that each tooth is now the length of the functional tooth row. There may be more than one tooth in occlusion at any one time, as one tooth is becoming worn and the one behind is coming in from the back to take its place, but the length of the functional dentition is approximately equal to the length of a single tooth (Laws, 1966; Maglio, 1972). This type of dentition was evolved to a more limited extent (with two or three teeth in the functional dentition at any one time) in the common ancestor of the Elephantidae and the extinct proboscidean families Stegolophodontidae, Gomphotheriidae and Mammuthidae (Tassy & Shoshani, 1988), although it was evidently elaborated in parallel in these different families, and only the Elephantidae possess highly hypsodont teeth.

As previously noted, a less extreme version of sequential replacement is seen in various suids. In these mammals the last molar (M_3) is greatly enlarged and erupts relatively late, by which time the first molar (M_1) has been worn to a virtual nubbin (Cooke & Wilkinson, 1978). In older animals M_3 makes up most or all of the functional dentition (see Fig. 4). A tendency in this direction is also seen in the hippopotamus

(Coryndon, 1978), but not in the more brachydont and bilophodont browsing pygmy hippo, and a similar situation was seen in desmostylians (Ijiri & Kamei, 1961), in the Oligocene genus *Arsinoitherium*, and in the extinct camelid subfamily Stenomylinae (Frick & Taylor, 1968). [In fact, a tendency to elongate the last molar with increasing fibre content of the diet is a feature of many selenodont artiodactyls (Janis, in press), although this was especially pronounced in the Stenomylinae.]

Enlarged teeth that erupt in a delayed sequence have usually evolved in forms with a bunodont occlusal morphology. If the teeth are not only enlarged, but become hypsodont as well, it appears that one of two alternatives is realized for the occlusal pattern. One type of pattern is seen in the warthog (*Phacochoerus aethiopicus*) and in the extinct marine mammal *Desmostylus*. Here the cusps are retained as individual, high columns. Usually a number of additional cusps are present, so that the original cusp pattern is obscured. Following Osborn (1907) we term these teeth columnar. The other alternative is represented by the Proboscidea. Here the cusps coalesce into lamellae transverse to the tooth axis. The worn surface thus presents more or less straight enamel edges alternating with troughs of dentine and cement. By analogy with the previous term, we shall refer to such teeth as lamellar. Functionally analogous teeth are found in certain rodent families (see Table 2) and in the extinct marsupial families Argyrolagidae and Patagonidae. All lamellar dentitions in therian mammals, although derived independently by convergent evolution, are associated with proal (from back to front) jaw movement.

Both lamellar and columnar dentitions have a relatively flat occlusal morphology, that differs from the more usual high relief occlusal morphology of mammals, where the shape of the cusps guides the lower jaw into precise occlusion with the upper teeth. We consider that such low occlusal relief is important for animals where the dentition includes sequential replacement of this type, and where the direction of jaw movement is not simply an orthal one (as in the case of most simply bunodont teeth and in bilophodont teeth), as the replacement of the dentition throughout the life of the animal might otherwise disrupt the pattern of precise occlusion. The stenomyline camelids were exceptional in this respect, in combining a selenodont dentition (which usually comprises teeth of high occlusal relief in combination with a predominantly lateral movement of the jaw) with a limited degree of sequential replacement. However, the occlusal surface of the molars in the stenomylines was very flat (as is also seen in living ungulates that possess highly hypsodont teeth, such as the wildebeest, *Connochaetes taurinus*), and their occlusion would have been relatively imprecise in comparison to those selenodont forms with a high relief of the ectoloph portion of the tooth.

IV. CONCLUSION

Mammals must rely on mechanical food comminution to ensure the rapid passage of the digesta that is essential for an endotherm. Plant foods are especially demanding, for several reasons. Their energy content is often low, so that large volumes must be processed. They are often tough, requiring high occlusal stress for breakage. Many plant foods are also abrasive, either in themselves or because of contamination with extraneous grit. These factors in various combinations are responsible for the heavy dental wear found in many herbivores, and constitute a complex of major functional

demands in dental evolution. Thought of simply as 'wear', the problem to be solved would appear simple enough, and the variety of solutions actually observed might then seem bewildering. However, when the functional demands of wear resistance are related to those of food comminution, and these in turn to historical and developmental constraints, regular patterns are seen to emerge.

The functional issues involved are of two kinds, and although they obviously interact it is conceptually helpful to separate them. The first requirement is that the teeth be capable of comminuting the food eaten, and the second is that the teeth stay functionally effective for the lifetime of the individual (or at least until the animal has outlived its 'normal' reproductive lifespan). Chewing rate and lifespan scale inversely with body size so that the number of chews per lifetime is a constant independent of body size (all else being equal). Furthermore, the amount of wear per chew on a dental surface is proportional to the size of the tooth (the amount of food between the teeth), as discussed above. Body size is therefore *not* of primary importance for dental design in relation to wear resistance, and the major functional demands are consequently to be found in the properties of foods (see discussion in Fortelius, 1985, 1987).

The foods that were eaten by the most primitive ancestors of later herbivorous mammals evidently did not pose major problems of dental wear. However, in the adaptive radiation of different herbivorous mammalian lineages wear problems were encountered, and were solved in different ways. In the following discussion we describe main routes by which we believe that this differentiation happened, as documented by solutions adopted in parallel by herbivorous lineages encountering similar functional problems.

Route 1. If the food eaten is abrasive, but brittle rather than tough (so that blades are not required for its comminution), the primary response is thickened enamel resulting in a rounded occlusal morphology (bunodonty). The chewing is orthal rather than lateral, reflected in a reduced difference in the widths of upper and lower teeth (anisodonty; see Fortelius, 1985). Many primate and suid species have adopted this solution, as did many early proboscideans. Further increase in wear leads to the evolution of enlarged teeth with delayed sequential eruption, and the teeth may additionally become hypsodont with further wear demands (examples include elephantids, certain suids and desmostylians). Such enlarged teeth usually acquire a more 'lophed' type of occlusal morphology with the evolution of hypsodonty, and can be classified either as lamellar (as in elephants) or columnar (as in warthogs); the former are associated with proal jaw movement and with transverse blades analogous to the longitudinal ones found on selenodont or plagiolophodont teeth (see below). With an increase in fibrousness (toughness) enamel thickness becomes secondarily reduced to allow higher occlusal stress.

Route 2. Moderately tough and abrasive foods (such as leaves) require reciprocal blades for comminution. Orthal chewing with bilophodont teeth is a common solution, and one that imposes considerable constraints on later change. The enamel on such teeth can not be made thick without destroying the occlusal morphology of high cross crests (deep blades). Neither can they easily be made hypsodont, because the occlusal morphology cannot be maintained by differential wear (although we note that the extinct taxa *Megatherium* and *Arsinoitherium* found separate, unique solutions to this functional problem). In fact the only possibility that seems to be available for most

forms with bilophodont dentitions subject to heavy wear is that of sequential tooth replacement (as in some kangaroos), and in more extreme cases supernumerary teeth allow for continual replacement of the molar row (as in manatees and in the rock wallaby *Peradorcas*). There is a cross-connection between routes 1 and 2, in that bunodont teeth can be transformed into bilophodont ones (and vice versa) with relatively small changes of cusp shape and enamel thickness. This has undoubtedly happened, particularly among suoids. (An important factor is that both kinds of teeth are operated by a similar masticatory apparatus, with an orthal mode of occlusion; Fortelius, 1985).

Route 3. Tougher foods require higher occlusal stresses, which means that the planes of the cutting blades must be strongly inclined (nearly transverse) to the masticatory force vector. This is not the case in bilophodont teeth, where the deep blades slide past each other in a direction close to vertical. This is probably the main reason for the initial development of the trilophodont type of lophodont teeth (seen, for example, in perissodactyls) with a main buccal cutting edge (ectolophodonty; Fortelius, 1985). Trilophodont teeth are highly anisodont, which reflects lateral chewing. An alternative solution, seen in small mammals, is for a lamellar type of tooth in combination with isodonty (upper and lower teeth of equal width) and isognathy (upper and lower dentitions equally spaced), and with propalinal jaw movement. This is seen in members of the Rodentia, in the extinct marsupial families *Argyrolagidae* and *Patagonidae*, and additionally in the *Multituberculata*, where the direction of jaw movement (palinal; i.e. from front to back) was the reverse from the proal occlusion in therian mammals (Krause, 1982).

Trilophodont and lamellar teeth may become highly hypsodont (high crowned) or even hypselodont (ever growing) in response to increased wear. With a shift to structurally simple, fibrous food (e.g. grass) the occlusal morphology of trilophodont teeth tends to become flat, with serial cutting edges, as in lamellar teeth (plagiolophodonty; Fortelius, 1985), as seen in Recent horses. The evolution of trilophodont teeth is constrained by the need to keep the enamel relatively thin (as blades), and by the need to keep the corresponding longitudinal positions on upper and lower surfaces stationary (lateral chewing with exact occlusion). Thus neither thick enamel nor serial replacement are available as solutions in this case. Theoretically, lamellar teeth of this type could be made more durable by serial replacement, as seen in elephants. However, no small mammal adopts this solution, and this may be related to the relative ease with which hypselodonty (without loss of occlusal morphology) can be evolved in small mammals.

Route 4. When comminution requirements are relaxed a moderate increase in abrasiveness may lead to increased crown height unaccompanied by other changes. This seems to be the evolutionary origin of selenodont teeth. Later changes include flattening of the occlusal morphology and reorientation of cutting edges in a way reminiscent of plagiolophodont teeth, to which hypsodont selenodont teeth are in many ways functionally analogous. Selenodont teeth are strongly associated with forestomach fermentation. This digestive strategy reduces the functional load placed on the teeth, as the food is not masticated as much on initial ingestion, and even though it may later be remasticated during cud-chewing, the food has by this time been considerably softened by digestive processes in the forestomach.

Superimposed on these routes are other distinct patterns. The most obvious is the effect of 'grain', by which in this context we mean the size of the structural elements of foods and teeth in relation to the size of the teeth themselves. Thus a close spacing of cutting edges can be easily achieved in small mammals by simple patterns of infolding of the rim of the crown. For such teeth, the evolutionary path from hypsodonty to hypselodonty is developmentally simple, and hypselodont teeth are, indeed, common among small mammals. To achieve a close spacing of cutting edges large mammals must generate more complicated folding patterns, frequently including closed fossae, at least in the upper molars. Their teeth can become hypselodont, but only at the price of giving up the fossae, thereby sacrificing the central cutting edges. Examples of this are known, but they are rare in comparison to the situation in small mammals.

The size of the structural elements of the enamel (mainly the bundles of apatite crystals known as prisms) is not notably influenced by tooth (or body) size. Crack propagation and fracture in enamel is strongly dictated by the discontinuities between prisms, and thus the smallest unit of tissue that is likely to be lost is relatively larger in smaller teeth. We are not aware of relevant observational data, but the implication is that 'wear events' are relatively more damaging in smaller teeth, all else being equal. This would further increase the tendency of small forms to evolve hypselodont teeth, to compensate for disproportionate loss of dental tissue in such 'wear events'.

Another pattern relates to metabolic rate; animals with low metabolic rates can afford slow digestion and thus less thorough mastication. It appears that root hypselodont teeth, which lack enamel entirely, are found only in groups with low metabolic rate (such as sloths). There do not appear to be any small herbivorous mammals with similarly low metabolic rates (for their size), and no root hypselodont small mammals seem to be known. Absolute digestion time of plant foods may well be the ultimate regulatory factor here.

To conclude, we note that the patterns described in this paper are readily observable and largely independent of the explanatory hypotheses that we have offered. Furthermore, the hypotheses are testable, or will be when more data become available on such matters as the fracture behaviour of foods in relation to occlusal morphology. In this context, the approach taken by Lucas and coworkers seems especially promising (e.g. Lucas 1979, 1980, 1982; Lucas & Luke, 1983, 1984; Lucas *et al.*, 1986).

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