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Ungulate cheek teeth: developmental, functional,
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Ungulate cheek teeth: developmental, functional, and evolutionary interrelations

Mikael Fortelius

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Developmental and functional factors interact in complex ways reflected in evolutionary patterns. The paper addresses problems of coronal morphogenesis, amelogenesis, food comminution and digestion, mastication, tooth eruption and wear, in order to identify functional interrelations and developmental constraints in the evolution of cheek tooth morphology. A general mechanism explaining differential (levelling) wear of teeth in a row is proposed. The paradox of predicted positive allometry but observed isometry of tooth size to body size is resolved by inclusion of the time dimension in the equation. The reasons for the commonness of isometric scaling in animals are discussed. Relative width of antagonists is found to discriminate between functional categories in terms of the dynamics of the power stroke in mastication, and can be used to interpret the functional meaning of major patterns of dental morphological radiation. Enamel structure at the level of arrangement of Hunter-Schreger bands is interpreted in terms of different mechanical requirements (resistance to crack propagation) in major morphological and functional categories. It is concluded that many aptive features probably or certainly did not arise for their current functions, but are one-time constraints which have become incorporated into functional systems (exaptations rather than adaptations).

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I won't say the pieces were beginning to fall into place, but at least they were getting to look like parts of the same puzzle. Which is all I ever get or ask.

Raymond Chandler: The Little Sister

1. Introduction

For three reasons mammalian teeth are uncommonly suitable objects of study for anyone interested in the interrelationships of growth, function and evolution. First, the structure of the enamel is also a record of its growth, which means that not only the structure but the cell movement patterns responsible for it can be studied, and the changes in such patterns followed through phylogeny. Few other tissues show with equal clarity that morphological evolution is the evolution of ontogenetic processes. Second, tooth shape strongly reflects function. There is no reasonable doubt that major morphological categories have corresponded to major dietary groupings in the past as they do today, and that the widespread occurrence of parallel evolution at least partly reflects dietary histories. This is different from, for example, the shape of gastropod shells, where the functional demands are less clear (and perhaps less varied) (cf. Gould 1984). The secondary wear-induced shape of teeth also bears direct witness to the nature of the food actually eaten. And third, mammalian phylogeny is documented mainly by fossil teeth, so no better part of the skeleton could be chosen on grounds of availability. Indeed, teeth are ideal in every way, except one; they are part of complex functional and developmental contexts that are not well understood (although this, too, might be considered an advantage by some).

It may seem paradoxical that dental functional morphology has been part of vertebrate paleontology so long (e.g. Cuvier 1815), and yet still so little is known about tooth function in the ultimate sense; i.e., of how foods actually break between teeth. However, this was not seen as a problem by the old (pre-evolutionary) paleontologists, and it is rarely perceived as a problem today. Most 'functional' analyses of teeth bypass the problem of food comminution by assuming optimal design and/or using analogy with kitchen technology. Although the terms employed apparently refer to processes ('slicing', 'grinding', 'crushing'), they are in fact purely morphological and descriptive. To Cuvier, optimal design was an axiom: animals are wholes of perfectly integrated parts, and change can only be deleterious

(see also Rudwick 1972). Darwin and most theorists since seem to have assumed a less than optimal design, approaching or tracking an optimal condition (defined by the environment) under the influence of natural selection. Such optimizing change or adaptation lies at the heart of the 'synthetic' evolutionary theory, and applied in its most vulgar and simplistic form the idea becomes what Gould & Lewontin (1979) labelled 'adaptationism': everything is assumed to be adaptive, and 'explained' on this assumption.

It is not easy to see how one could determine just how 'good' or 'bad' animal design is, on average or in single cases, absolutely or even relatively. Physiologists (e.g. Schmidt-Nielsen 1984), and probably most ecologists, tend to assume that design is good ('optimal'), and that this is why so many size-dependent relationships are found. 'Optimal' is clearly a relative concept here, related to some set of limiting prerequisites or 'constraints'; however, apart from conflicting functional demands, these are rarely considered beyond recognition in the abstract that such exist (see below). It is evident that the design of all extant organisms is at least adequate for the present conditions, and that their ancestors were also adequately designed for their living conditions. This may be more relevant than the degree of optimality, although it is unclear to what extent the functional performance of coexisting forms is, through competition, part of the environmental conditions.

For example, Webb (1983) has shown that the North American late Miocene (Clarendonian) ungulate fauna, although composed of species belonging to quite different groups and lineages, was remarkably similar in inferred ecological composition to the modern African ungulate fauna. Webb argues that the Clarendonian fauna evolved and became extinct as a whole, and that this can only be understood in terms of coevolution and coextinction of interdependent species. Among the more striking examples of morphological (and presumably ecological) convergence with present day African forms are the camelid *Aepycamelus giraffinus*, convergent on *Giraffa*, and the rhinocerotid *Teleoceras fossiger*,

convergent on *Hippopotamus*. For the present study it is particularly interesting that these pairs do *not* display convergence in details of dental morphology, despite being equivalent in terms of molar volume relative to estimated body weight, interpreted by Webb (1983) as evidence of ecologically equivalent dietary adaptation.

In a recent review, Butler (1983) found considerable evidence that tooth shape is under the control of natural selection: tooth shape is highly heritable and there are many examples of morphological change related to dietary specialization. However, he also suggested that minor differences between related forms may often be random, due to genetic drift. Butler further stressed the role of teeth as an integrated part of a functional whole; a point of view which I have tried to emphasize in this paper. It seems reasonable to speculate that functionally equivalent systems with differently shaped teeth exist, and that forms with different histories (different genes) may respond to the same functional demands in equally adaptive but morphologically different ways. A random element (with respect to function) might occur on (at least) two levels: chance differences between dentitions and chance differences between food processing systems.

It does not seem profitable to speculate here on the role of competition (at whatever level) in evolution, nor on the relative importance of gradual and sudden evolutionary change (whatever these terms may signify in absolute time). It is relevant, however, to ask what factors influence the shape of teeth, and how they interact to cause evolutionary change. Gould &

Lewontin (1979; Gould 1980a, 1980b, 1984) have emphasized the importance of 'constraints'; i.e., the factors that limit and channel the realization of form: instead of inventing plausible stories about function we should investigate how form comes about; why some shapes are much more common than others, and why some do not occur at all.

From a purely theoretical point of view it may be meaningless to speak of 'constraints', insofar as any factor that influences something is constrained in its effect by all the other factors that also influence that same something and in turn constrains them. Any one factor may be arbitrarily chosen as a reference; the others are then constraints. In the sense of Gould & Lewontin (1979), constraints are everything except functional demands (which may themselves be conflicting); i.e., all factors that limit the effect of optimizing natural selection. Such constraints may be intrinsic to the organism, like inherited ontogenetic processes or behaviours, or extrinsic like the mechanical properties of the building materials, or even the physico-chemical properties of elements or the general nature of the universe; it is difficult to exclude anything with confidence. The main issue, however, is not whether something is a constraint or not, but that several conflicting and limiting factors interact (see Sect. 5). To identify such factors and study their interaction must be a main concern of morphology; to recognize their existence in the abstract is only marginally helpful. It is for these reasons that this paper addresses such a variety of problems in what may seem to some readers a haphazard fashion.

2. Terminology

It is unlikely that any other organ system in any other group has been described by as many names as have mammalian molars. Terms describing whole teeth are plentiful, but the terminology that deals with their parts is inflated beyond all reason (see Hershkovitz 1971). It is not my purpose here to review the literature or to establish a new standard, but some clarification is necessary to avoid misunderstandings of my usage. This section deals with general terminology, while special terms that apply only to a particular problem will be discussed in their context.

2.1. Functional crown shape: primary and secondary

The functional shape of teeth may be either primary or secondary (performed or acquired, in the terminology of Lumsden & Osborn 1977). Primary

shape means that the tooth is functional in the shape it has on eruption, when it is entirely covered by enamel. Slight wear may be required to perfect occlusion, but in principle the functional shape gradually deteriorates as the tooth is worn down. In contrast, secondary shape is brought about and maintained by wear. For a discussion of this process see Section 3.4.

2.2. Dental morphological categories

It is a curious and rather amusing anomaly that practically all dental morphological terms are of the form [descriptive noun] + [-dont]. A low-crowned tooth is thus usually called brachydont or 'short-toothed', which is absurd. Obviously terms of this form originally referred to something more inclusive, such as dentitions or animals (as indeed they still do

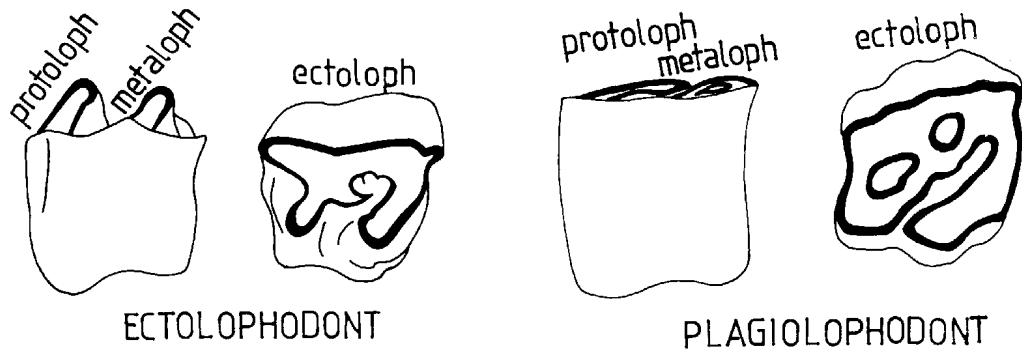


Fig. 1. Ectolophodont (*Diceros bicornis*) and plagiolophodont (*Ceratotherium simum*) upper molars. Adapted from Fortelius 1981.

as well). The current misuse is universal and of long standing (see e.g. Osborn 1907). Since few people seem to find it disturbing and since the risk of confusion is remote, it is probably best to accept this terminological oddity.

Osborn (1907) introduced most of the morphological terminology that is still in use, including the terms bunodont, lophodont and selenodont, one or another of which may be applied to most ungulate teeth. His own use of these terms was somewhat ambiguous, and characterized by a rather excessive use of combinations (he described the molars of the hyrax *Sagatherium* and the chalicothere *Schizotherium* as "buno-lopho-selenodont", for example). Osborn's original ambiguity is still seen in the blurred distinction between selenodont and lophodont. Romer (1970) made the distinction that selenodont teeth have cusps that are individually flattened into crescents, whereas the cusps of lophodont teeth have coalesced to form continuous lophs. This is probably close to Osborn's original idea, and contains the same ambiguity: at what stage do two flattened cusps become a loph? In discussions with colleagues I have come across two other criteria which seem to be relatively common among paleontologists. The first is that lophodont teeth have either transverse or combined transverse and longitudinal crests, while selenodont teeth have only longitudinal ones. The second is that selenodont teeth are confined to the order Artiodactyla. I agree with the first of these criteria, but not with the second, which is in direct opposition to Osborn's (1907) intention. It is clear that the terms were purely descriptive to Osborn, and that he considered changes in any direction possible.

There is no particular reason why molar morphology should conform to clear-cut categories, and Osborn's slightly vague use of his own terms perhaps reflects his acceptance of this fact. I use his terminology

in a similar way, according to the criteria listed below, and with noted additions.

Bunodont. (Gr. 'bounos'; hill, mound, knob; Brown 1956). Teeth with more or less blunt, separate cusps and mainly primary functional morphology.

Lophodont. (Gr. 'lophos'; mane, crest, comb, tuft; Brown 1956). Teeth with cusps united to form lophs. Functional morphology may be primary but is more often secondary. To Osborn (1907) the full expression of the lophodont type involved the π -shaped arrangement of lophs in the upper molar, with ectoloph, protoloph and metaloph (Fig. 1). This I will refer to as *trilophodont*. The situation where the ectoloph (and the corresponding buccal portions of the lower tooth) is absent I will refer to as *bilophodont*. When the transverse lophs lose their individuality in early stages of wear and the ectoloph is the dominant cutting edge I will use the term *ectolophodont*. There is a tendency for teeth to go from trilophodont to ectolophodont with phylogenetic increase of hypsodonty. In some forms a condition analogous to selenodonty evolves, as in hypsodont horses, where the originally transverse lophs turn longitudinal. An appropriate term for such teeth might be *selenolophodont*. When the occlusal surface is flat the term *plagiolophodont* is sometimes used, and I will employ it here for teeth such as those of *Equus*. Fig. 1 shows examples of ectolophodont (*Diceros bicornis*) and plagiolophodont (*Ceratotherium simum*) upper teeth.

Selenodont. (Gr. 'selene'; moon; Brown 1956). Teeth with more or less crescentic (hence the name), longitudinally flattened cusps and usually secondary occlusal morphology. No transverse joining of cusps. Purely selenodont teeth are perhaps only found among artiodactyls, but this is not part of the definition.

The chief category of ungulate cheek teeth not covered by the preceding terms is the various high-crowned modifications of bunodont teeth with secondary, flat occlusal surfaces. These are a rather heterogeneous group, however, and special terms would be superfluous in this context. Examples include the teeth of elephants and hypsodont suids, particularly *Phacochoerus*. For the latter, the name 'columnar' is available (Osborn 1907).

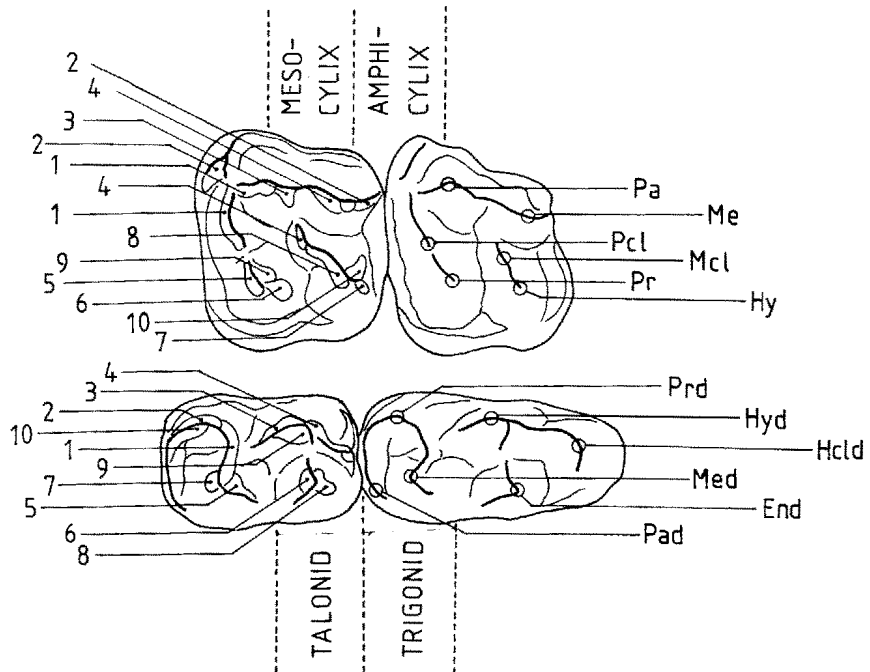


Fig. 2. Second and third upper (above) and lower (below) molars of *Hyracotherium*, to show cusp and facet nomenclature as used in this text. Redrawn and modified from Radinsky (1969). Based also on Butler (1952a) and Kay & Hiimäe (1974). - Abbreviations: End = entoconid, Hy = hypocone, Hyd = hypoconid, Hclld = hypoconulid, Mcl = metaconule, Me = metacone, Med = metaconid. Pa = paracone, Pad = paraconid, Pr = protocone, Prd = protoconid.

2.3. Cusps

Although the theoretical foundations of the Cope-Osborn cusp nomenclature (Osborn 1907) are no longer accepted, there is no objection to its continued use (Fig. 2). In fact, it is the only nomenclature familiar to most people and thus helps rather than hinders communication, as pointed out by Butler (1978a). For a general context such as this it is clearly the most appropriate, but I will discuss the possibility that only a limited number of ontogenetic events may be hidden under the inflated terminology and that a simpler system could be based on such events once they are recognized (Section 3.1.1). I use the nomenclature in the pragmatic spirit of Butler (1978a:452): "Cusp names refer to species of cusp as defined by topographical and functional relations, and do not necessarily imply strict homology". For more detailed description the nomenclature developed by Van Valen (1966) and modified by Crompton (1971) is available (Kay & Hiimäe 1974).

Larger structural and functional units may be referred to by two sets of terms: trigonid and talonid for the lower teeth and amphi-cylx and meso-cylx (Butler 1952a) for the upper ones. I prefer the latter terms to trigon and talon because they describe functional units. The meso-cylx is, of course, synonym-

ous with the 'trigon basin', but the amphi-cylx is made up of the talon of one tooth and the anterior part of the trigon of the next (Fig. 2).

2.4. Crown height

The terms brachydont and hypsodont refer to crown height and are purely morphological in principle. A generally accepted criterion is that a tooth is hypsodont when its height (i.e., root-crown dimension) exceeds its antero-posterior length, but the terms are more frequently used in a relative sense; this tooth is more hypsodont than that one. A special case of hypsodonty is hypselodonty, or rootlessness; the tooth crown goes on forming throughout the life of the individual, and eruption is continuous. There is fairly general agreement that hypsodonty (and hypselodonty) is mainly an evolutionary response to increased wear, and attempts have been made to re-define 'hypsodonty' in a functional sense (e.g. Van Valen 1960, see also Fortelius 1982). I now believe that brachydonty and hypsodonty should be used in their traditional morphological sense, and that if special functional terms are needed, they must be constructed separately. The functional aspects of hypsodonty are discussed in Section 3.4.3.

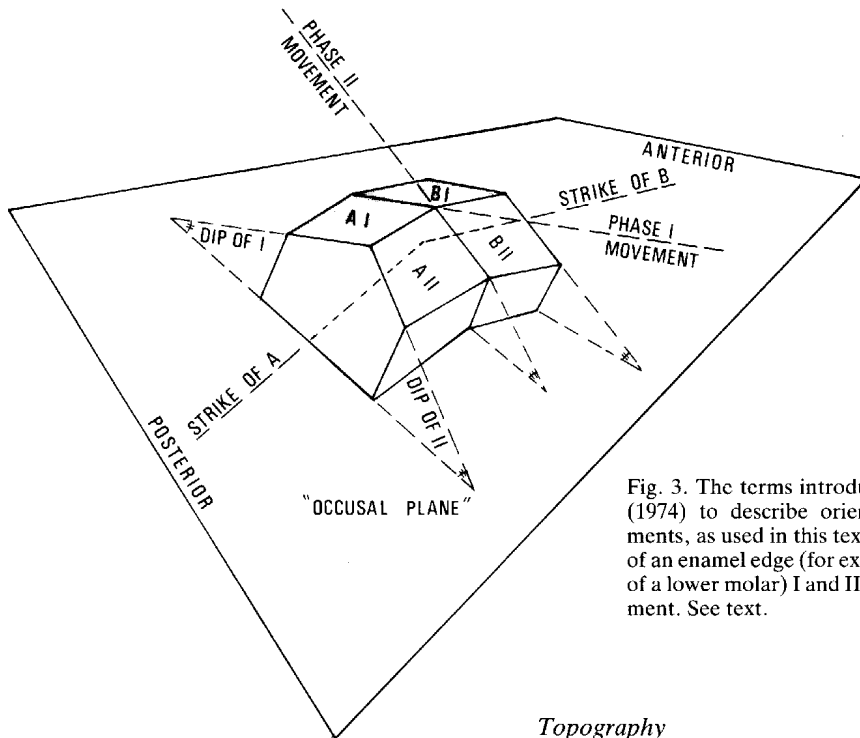


Fig. 3. The terms introduced by Kay & Hiiemäe (1974) to describe orientation of occlusal elements, as used in this text. A and B are segments of an enamel edge (for example, at the protoconid of a lower molar) I and II refer to phases of movement. See text.

2.5. Occlusal shape

Wear facets

A facet is a wear surface, the orientation of which is dictated by interactive wear against one or several other facets (see Sect. 3.4.1.). Just as it is possible to homologize cusps of different species it is possible to homologize the wear facets that develop in a very conservative relationship to the cusps (Butler 1952a, 1952b, 1982; Kay 1977). If the criterion of homology is continuity of information (Van Valen 1982), there is no conceptual problem even when facets change their original relationship to cusps; in principle it should be possible to trace all facets back to their origin. Cusps and facets form independent systems of homologies. Strictly speaking it is not possible to invoke position on a cusp as a criterion of homology of facets, although this is commonly done. At the present stage of knowledge it may be best to be pragmatic about the homologies of both cusps and facets. Recognition of homologies between groups is further hindered by the confused state of the facet nomenclature (see review in Kay 1977). It was tempting here to use the numbering originally introduced for perisodactyls by Butler (1952a, 1952b), but for the sake of communication I thought it wiser to use a version of the system introduced by Crompton (1971), which seems to be gaining increasing acceptance. Application here is as in Kay (1977) for primates (Fig. 2), with homologies (incorrectly) based on position relative to cusps.

Topography

Some set of terms is needed to describe the geometry of the occlusal topography. Kay & Hiiemäe (1974) applied the terms 'dip' and 'strike' to planar facets (Fig. 3). As originally used in geology, dip is the angle that a bed is inclined below an imaginary horizontal plane, and strike is the compass direction of any line made by the intersection of the inclined bed with an imaginary horizontal plane (Putnam & Bassett 1971). Dip is always measured at right angles to strike. Kay & Hiiemäe substituted 'occlusal plane' for the horizontal and the anteroposterior axis of the tooth for the North (0°) of the compass.

The line of occlusal movement can be calculated from the dip and strike of intersecting facets corresponding to the same phase of movement, or determined by sighting along such facets. Since dip and strike refer to and define planes, Kay & Hiiemäe suggested the corresponding terms 'plunge' and 'orientation' for the line describing occlusal movement. Plunge is "the angle between the line and its projection in the occlusal plane", orientation is "the angle between the anteroposterior axis and the projection of the line into the occlusal plane" (Kay & Hiiemäe 1974:242). A weakness of this system is that neither the 'occlusal plane' nor the anteroposterior axis of the tooth have been defined or are likely to be exactly comparable between groups, but the problem may be more apparent than real. For general comparative and descriptive purposes the terminology is excellent, and I will employ it here.

2.6. Position

That the study of teeth lies at the intersection of many disciplines becomes particularly obvious in the terminology describing position and directions. To a dentist looking into the mouth of a patient from 'mesial', 'distal' is obviously what lies behind a tooth. This progression is much less clear to the zoologist who lacks a natural direction of reference, and so tends to use the general anatomical terms 'anterior' and 'posterior'. However, the corresponding terms 'lateral' and 'medial' are almost never used about teeth, probably because 'buccal' and 'lingual' are more specific and a tactile reference is constantly available. I use this historically anomalous quartet of anterior-posterior and buccal-lingual in this text, including combinations such as 'antero-buccal'. To designate the position of something relative to the root-

crown axis of a tooth I use 'occlusal' (towards the occlusal surface) and 'cervical' (towards the root apex).

2.7. Chewing direction

I recognize three ideal modes of chewing in terms of direction of the power stroke. 'Orthal' chewing involves no horizontal, translatory movement of occlusal surfaces past each other during the power stroke; the teeth just meet and move apart. 'Lateral' chewing involves oriented movement from buccal to lingual during occlusal contact, and 'palinal' chewing movement is from posterior to anterior. I argue below that these terms, although they do not describe absolutely distinct categories, nevertheless correspond to major groupings in the design of the masticatory apparatus as a whole.

3. Problems

3.1. Tooth growth

3.1.1. Coronal morphogenesis

Tooth crowns attain their shape through ontogenetic processes of growth and remodelling (in a general, descriptive sense). Hence the evolution of dental shape ultimately depends on the availability of ontogenetic processes capable of generating certain morphological effects. Although the older literature does contain some accurate descriptions of the formation of tooth germs (reviewed by Butler 1956), little is known about the causal relationships involved (Kollar & Lumsden 1979, Lumsden 1979, Butler 1982). Yet it is necessary to discuss the problem here, if only to trace its outlines. Any theory of dental evolution must include an ontogenetic model with which it is consistent.

It is well known that teeth are the product of an epithelio-mesenchymal interaction, a complex, multiphase sequence of events. According to Kollar & Lumsden (1979) the processes involved are of three major kinds: initiating events, morphogenetic events and cytodifferentiative events.

The tissue masses from which teeth develop are derived from branchial arch mesenchyme, primitive ectoderm, and mesenchyme cells migrating from the neural crest. These neural crest cells are associated with the development of dental papillas, but how and when morphogenesis is initiated is unknown. Once established, the competence for odontogenesis of both mesenchyme and epithelium is long-lived and stable (Kollar & Lumsden 1979).

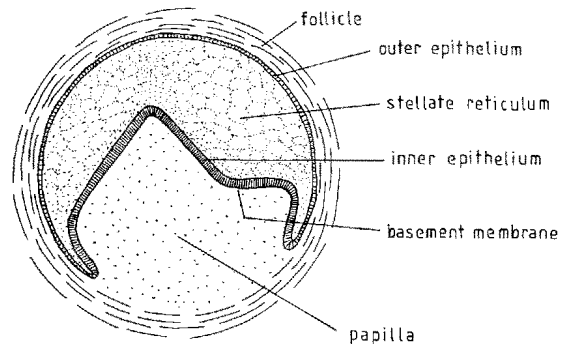


Fig. 4. Vertically sectioned tooth germ. The basement membrane of the inner epithelium (the epithelio-mesenchymal interface) becomes the enamel-dentine junction of the tooth, and its topography determines the main features of coronal morphology. After Butler (1956).

Morphogenesis is the growth of the dental papilla and the folding of its epithelio-mesenchymal interface, the basement membrane that later becomes the enamel-dentine junction of the tooth (Fig. 4). The topography of the epithelium is dictated by the underlying mesenchyme (Kollar & Lumsden 1979), which establishes the morphology of the crown prior to the cytodifferentiative events that bring the tooth itself into being. However, morphogenetic and cytodifferentiative events may occur simultaneously on the same tooth, in sequential zones proceeding from

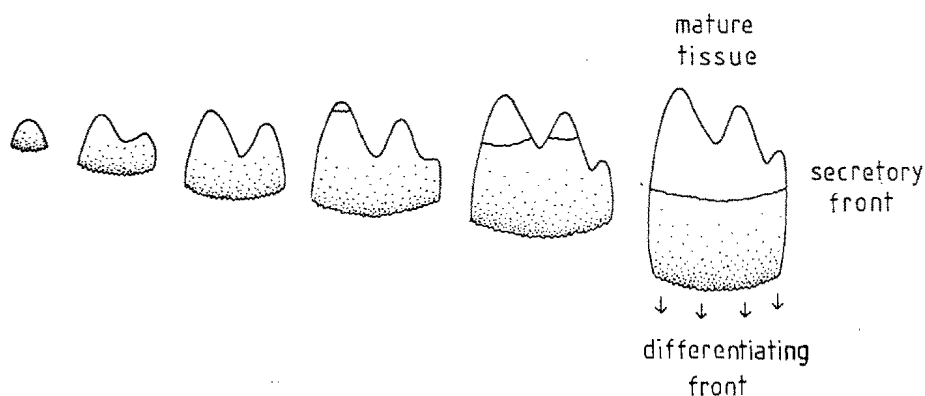


Fig. 5. Schematic representation of sequential stages in the development of a tooth. The surface shown is the epithelio-mesenchymal interface (after secretion the enamel-dentine junction). Differentiation and secretion start at cusp tips and proceed as successive zones towards the cervical margin. The topography of the interface is determined by combinations of cytodifferentiative and morphogenetic events, including (differential) mitosis and mechanical interaction with adjacent tissues.

cusps tips towards the cervix (Fig. 5), so it is conceivable that form actually results from an interaction of 'morphogenetic' and 'cytodifferentiative' processes (Butler 1956, Kollar & Lumsden 1979).

The sequence of events involved in cytodifferentiation itself proceeds from occlusal towards cervical in a similar manner. In hypselodont forms the crown base may still be forming when the tooth erupts, and hypselodont (ever-growing) teeth continue to form and erupt indefinitely. It would seem that increased crown height is a relatively simple matter of delayed termination of morphogenesis/cytodifferentiation, and that hypselodonty is simply the extreme outcome of such delay (cf. von Koenigswald 1982). There would thus be no more ontogenetic discontinuity between rooted and evergrowing teeth than there is between high- and low-crowned ones (and, indeed, Van Valen (1966) described almost rooted incisors which had ceased to grow in an abnormal rat). There is one constraint, however; enamel pits (closed fossae) and similar structures which must be formed "from the top"; i.e., by an intact enamel organ which envelops the forming crown, can not be formed after eruption. This is why closed fossae are not found in evergrowing teeth (von Koenigswald 1982). For example, the only perissodactyl ever known to have developed hypselodonty, the Pleistocene rhinoceros *Elasmotherium*, differed from all other rhinoceroses in this respect. When the fossae form an essential part of the occlusal morphology, as in horses and scelodont artiodactyls, it may be that the evolutionary path towards hypselodonty is blocked. Why hypselodonty is so rare in ungulates (the only known cases seem to be *Elasmotherium* and the toxodontid notungulate *Toxodon*), when it is so common in rodents, is an unsolved problem of considerable interest.

It is worth noting that an increase in crown height involves less ontogenetic change than an increase in overall tooth size, which presupposes either more or larger secretory cells. Possibly for this reason, occlusal area tends to be isometric to body size (see Sect. 4.1), while increased wear is compensated for either by increased crown height or by serial replacement of teeth (see below).

What actually causes the basement membrane of the dental papilla to become folded in a particular way remains unknown, but in principle it may be a relatively simple combination of growth and shape change due to mitosis and cell movement. The main morphological features of the developing and the finished crown are cusps, characterized by the presence of a tip, and folds, which may be anticlinal 'ridges' or synclinal 'sulci'. Initially, cusps are relatively smooth and rounded projections on the developing surface; later they frequently become angular due to folding (Butler 1956). Cusp tips also represent the origin of hard tissue formation, as noted above. Butler (1956) suggested that some folds on developing teeth might represent lines of tension set up in the epithelium by its unequal growth, or by growth of some areas after others have already become mineralized. The distinction between cusps and ridges is not always clear in the finished tooth, and cusps are often identified as junctions of folds in different planes, particularly in many lophodont forms. Even in a bunodont form such as man the cusps are less rounded at the enamel-dentine junction than at the true enamel surface, which is modified by unequal deposition of enamel (Butler 1956, Korenhof 1982). Sakai (1982) emphasized the role of a fine, sharp ridge, the 'spiniform projection', in the early evolution of new cusps from ridges on pre-existing cusps or from basal folds (cingula).

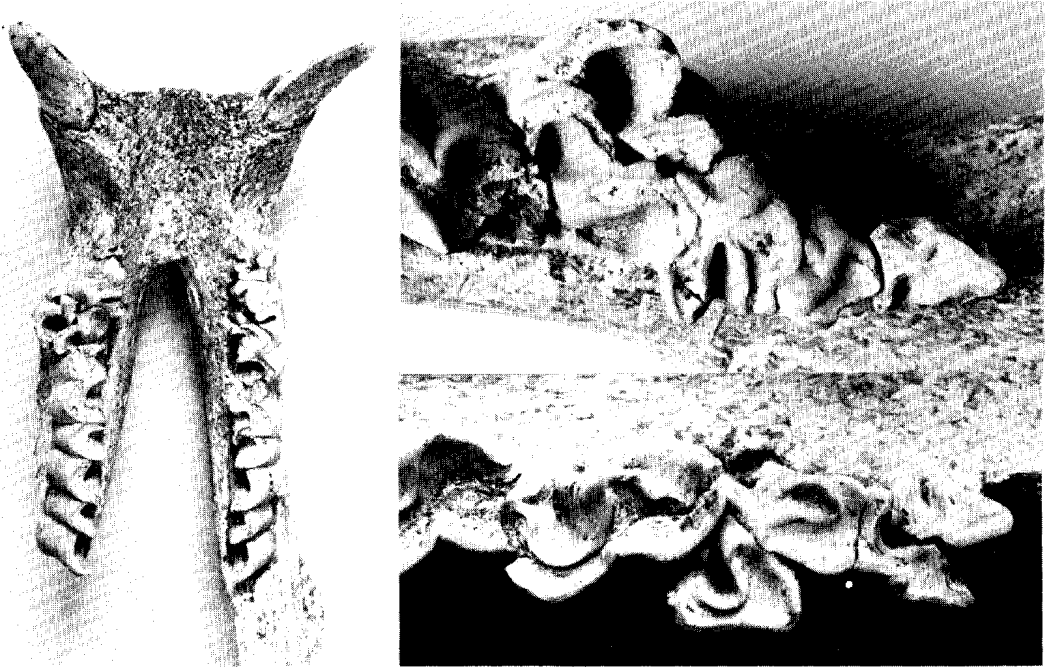


Fig. 6. *Chilotherium habereri* (UP M 487), Upper Miocene, China. P₂ dext. and P₄ sin. are double, and all premolars (but particularly P₃) are deformed, presumably as a result of mechanical disturbance during development.

Butler's (1979) study of unerupted human deciduous molars revealed several morphs distinguishable mainly by their folding patterns. It also showed very clearly that homologous structures may take on different shapes in different morphs. Another example of this is the so-called 'Carabelli's cusp' on human maxillary molars, which may appear as an indentation, a cingulum or a cusplule (see e.g., Mayhall et al. 1982). Butler (1979) further supported Jørgensen's (1956) conclusion that the so-called 'delta variation' of dm₁ in man results from external pressure due to lack of space during development, and suggested that environmental factors such as pressure might also play a significant part in normal dental development. A similar idea was expressed by Taylor (1982), on the basis of aberrant shapes in human M³'s. Ringström (1924, Plate IX:7) figured a supernumerary, peglike molar behind the left M³ in the Chinese Miocene rhinocerotid "*Diceratherium palaeosinense*". The right M³ is normal, with reduced metaloph, but the left is more like an M², with a distinct metaloph, perhaps because of 'squashing' during growth. Pathologically deformed teeth are not unusual in fossil collections, and although they may not in themselves contribute much to our understanding of normal tooth growth, they are at least tangible proof that teeth are capable of being de-

formed by mechanical obstruction. Fig. 6 shows an example from another Chinese Miocene rhinoceros, *Chilotherium habereri*, in which the right P₂ and the left P₄ are double and all the premolars, particularly the P₃'s, are deformed.

If one could identify ontogenetic events, each perhaps with a limited number of possible outcomes in terms of, for example, folding patterns, a considerably improved understanding of dental evolution might emerge. It is easily conceivable that morphological evolution is channeled by the availability of such ontogenetic events, and the very widespread and remarkable occurrence of parallel evolution of dental morphology might partly reflect such constraints. Many authors have at times expressed doubts as to whether such patterns can be adequately explained as a result of natural selection for similar function alone.

A central issue in crown morphogenesis is the question of how the shapes of occluding upper and lower teeth are controlled. Whether the teeth in a row develop under intrinsic or extrinsic influence (see below), it is difficult to understand how growth in separate jaws is coordinated to the extent that it appears to be. Kurtén (1953) showed that occluding teeth are the most tightly correlated in their dimensions of all possible pairs in several species of carni-

vores, ungulates and primates, and this finding has been repeated for several more species (see review in Butler 1983). Marshall & Butler (1966) investigated crown development in the molars of the bat *Hipposideros beatus*, which has crowns with a high relief and interlocking occlusion, and therefore must have very accurately controlled development to avoid malocclusion. They found that the molar tooth germs in each jaw develop in serial order from M1 to M3, with each lower molar slightly in advance of its upper serial homologue. Since the lower molar occludes with the posterior half of the upper molar preceding it and with the anterior part of its serial homologue (see below Sect. 3.4.4.), it follows that each molar is at an intermediate stage of development between its two antagonists throughout its growth. A similar anteroposterior gradient is seen within each tooth, so that metacones lag behind paracones and talonids behind trigonids. This means that the parts which are going to occlude are at all times at corresponding developmental stages. Corresponding shapes are also maintained by upper and lower teeth throughout ontogeny, so that truncated (and, presumably, extended) development would, in principle, result in functional occluding molars. Stronger or weaker expression of morphological features in related species, and evolutionary changes in such expression, can perhaps be understood in terms of such conceptually simple truncation or extension of the development of a basic pattern (cf. Alberch et al. 1979).

The fundamental question of how genetic information gives rise to tooth shape, or indeed organic form in general, is largely unsolved, although new techniques may well considerably increase our understanding in the near future (Slavkin et al. 1984). Lumsden (1979) distinguished two main types of models which he termed 'gradient' and 'cell lineage' theories. In the former, exemplified by the 'morphogenetic field' model (Butler 1939 et seq., e.g. 1982) and the 'prepattern gradient' model (Van Valen 1970), some extrinsic factor(s) determine morphology, while in the latter, such as in the 'clone' model (Osborn 1973, 1978), and the 'progress zone' model (Lumsden 1979), control is intrinsic to the developing tissue. It would be futile here to enter into this very complex field, but it may be noted that strong arguments against the clone model have been raised by Butler (1978b), and against gradient models in general by Lumsden (1979). Westergaard (1980, 1983), however, opted for a gradient model. It is clear that any satisfactory model of tooth development, and thus of tooth evolution, must ultimately include the crucial link between genes and form, but it is equally clear that we must manage without one at the moment.

Despite differences of interpretation, there is general agreement that each tooth class behaves as a unit in which one or a few morphological patterns are expressed with varying intensity in the individual teeth,

as originally emphasized by Butler (1939). Usually the pattern is most strongly expressed at one tooth and decreases away from it. In ungulates the molar and premolar classes often tend to merge ('molarization' of the premolars), in which case the tooth in which the pattern is most strongly expressed may be any molar (or sometimes, although not in ungulates, the last premolar). By taking the number of teeth as given and postulating one prepattern, 2 or 3 gradients and 3 dichotomous signals, Van Valen (1970) was able to account for postcanine dental morphology in the Cretaceous insectivore *Procerberus formicarum*. Whether the causal background is the one postulated or not, this illustrates the morphological unity which is indeed the rule for mammalian cheek teeth: change is gradual and orderly.

Since heterodonty (morphological differentiation of the toothrow) is originally derived from homodonty (absence of differentiation), and since tooth classes may merge secondarily, the presence of such gradients of form clearly does not impose absolute limits on the evolution of individual teeth. Examples of teeth that have 'escaped' from their gradient and attained highly individual shapes are the sectorial premolars of some macropod marsupials, and particularly those of ptilodontid multituberculates. The carnassials of carnivorous forms are another example; it is interesting to compare the highly differentiated, individual carnassials of derived forms with the more uniform cheek teeth of their primitive relatives, both among placentals and marsupials (Butler 1946).

An interesting aspect of form gradients is the production of supernumerary teeth. The classical example is the South American canid *Otocyon* (e.g. Van Valen 1964), which has a variable number of supernumerary molars. More important in this context are perhaps the species in which an apparently unlimited number of supernumerary molars continue to form and erupt throughout life. Among living mammals, such a condition is known in one species of macropodid marsupials (the Nabarlek, *Peradorcas concinna*) and in the manatees (genus *Trichechus*). In both cases there is continuous drift of molars from posterior to anterior, with shedding of worn molars at the anterior end of the row, and in both cases there are strong reasons to regard the arrangement as an adaptation to unusually abrasive food materials (Domning 1982, Sanson 1983). It is in a sense a functional alternative to hypselodonty, and it is interesting that the only surviving dugongid (*Dugong dugon*) has evolved continuously erupting teeth (without enamel covering, somewhat as in sloths) (Domning 1982). The main functional difference between hypselodonty and continuous replacement is that the former presupposes secondary occlusal surfaces, whereas the latter allows largely primary surfaces to be part of the dentition throughout life. A bilophodont occlusal morphology apparently cannot be maintained secondarily, and it is probably no coinci-

dence that it is among bilophodonts that continuous replacement has evolved, while trilophodonts have evolved hypselodonty.

The ontogenetic change from normal sequential eruption to unlimited mesial drift need not necessarily involve any developmental discontinuity. The same mechanism that keeps the toothrow closed despite interstitial wear (a kind of eruption?, see Sect. 3.4) is conceivably responsible for such limited mesial drift as is observed in elephants, for example (Hooijer 1981), and also for more dramatic mesial drift as in macropodid marsupials, including the nabarlek. The unlimited development of supernumerary teeth is particularly easy to fit into the 'progress zone' model of Lumsden (1979), but is also compatible with gradient models which do not postulate fixed tooth positions.

In summary, all evidence suggests that the same genetic information is used in part for all the teeth in the dentition, and shared more or less by classes as well as by antagonists. The important consequence is that changes will primarily affect not just single teeth but substantial portions of the dentition. In ungulates the most independent unit in this system is probably the pair of upper and lower tooth classes, with premolars and molars often more or less merged into two single series. Changes that modify whole genetic 'programmes' (e.g., relative durations of ontogenetic stages; cf. von Koenigswald 1982) will affect whole classes (although not necessarily all teeth equally but as gradients). Suppression of gene expression results in evolutionarily reversible loss of teeth or dental characters (Kurtén 1953, 1963), while supernumerary teeth in principle arise by repetition of an entire pre-existing 'programme', or perhaps suppression of its suppression. Since change tends to affect the whole system and antagonists in corresponding ways, evolutionary change is partly channeled along paths which maintain occlusal relationships, not by natural selection but by the ontogenetic setup of the dentition (see also Sect. 5).

3.1.2. Amelogenesis and enamel structure

In all ungulate cheek teeth and in most mammalian teeth in general, enamel covers the primary occlusal surface, and contributes to the most important functional structures of the secondary surface. The ultrastructure of the enamel affects its mechanical properties and the morphology of the worn surface (von Koenigswald 1977, 1980; Rensberger 1978, 1983; Rensberger & von Koenigswald 1980; Fortelius 1984; Boyde & Fortelius in press). Thus the ultrastructure of the enamel is an important aspect of the morphology. The relationships between structure and wear properties will be the subject of Sections 3.4 and 4.3., while this section deals with the development of the enamel structure. I do not wish to

imply that enamel is the only important tissue in teeth, but little comparative work on dentine and cementum exists. Enamel is also of a very special relevance in an evolutionary context since it directly preserves the history of its ontogeny in its structure, even after fossilization. It is probably the only vertebrate tissue which directly connects phylogeny with ontogeny.

Mature mammalian enamel is very highly mineralized, and contains only a few percent water and protein. The mineral component which makes up the rest is chiefly calcium phosphate in the form of variously impure hydroxyapatite, $\text{Ca}_5(\text{PO}_4)_3\text{OH}$, in which Mg and Sr may substitute for the Ca, CO_3 for the PO_4 and F for the OH (Boyde 1976a). The apatite crystals are extremely elongated 'whiskers', of some 50 nm diameter, which means that their fracture stress is very high (Gordon 1968). Because of this and because of the thin film of protein which 'glues' the crystals together, enamel is a very strong material and in certain respects comparable to glass fibre compounds.

Basic structural elements and their development

Enamel develops extracellularly in a protein matrix secreted by the epithelial ameloblasts of the enamel organ. The matrix is laid down on a predentine (mineralizing collagen) mould produced by the mesenchymal odontoblasts, which was in turn secreted onto the inner surface of the epithelium (Boyde 1976a). This is how the epithelio-mesenchymal interface comes to determine the shape of the enamel-dentine junction, as discussed above.

The ameloblasts are columnar exocrine secretory cells with reversed polarity; i.e., they secrete towards (rather than away from) the basement membrane. In mammals, the secretory end of each ameloblast has a projection known as Tomes' process, and the surface of the forming enamel has corresponding pits formed and occupied by these (Fig. 7). Usually the pits have a relatively planar floor and a circular wall, which correspond to the end and sides of the Tomes' process, respectively. Similarly the area between the pits corresponds to the cell surface between Tomes' processes. The shape of the pits reflects both the shape and the dynamics of the secretory surfaces, which means that the developing enamel surface can be used to reconstruct ameloblast movements during secretion (Boyde 1964, 1967). As the structure of the enamel is to a large extent determined by these ameloblast movements, the developing surface is a source of crucial information for understanding the mature tissue. Successive positions of the developing surface are marked in the tissue by incremental lines, the brown striae of Retzius of traditional light microscopy (Retzius 1836) (Fig. 8).

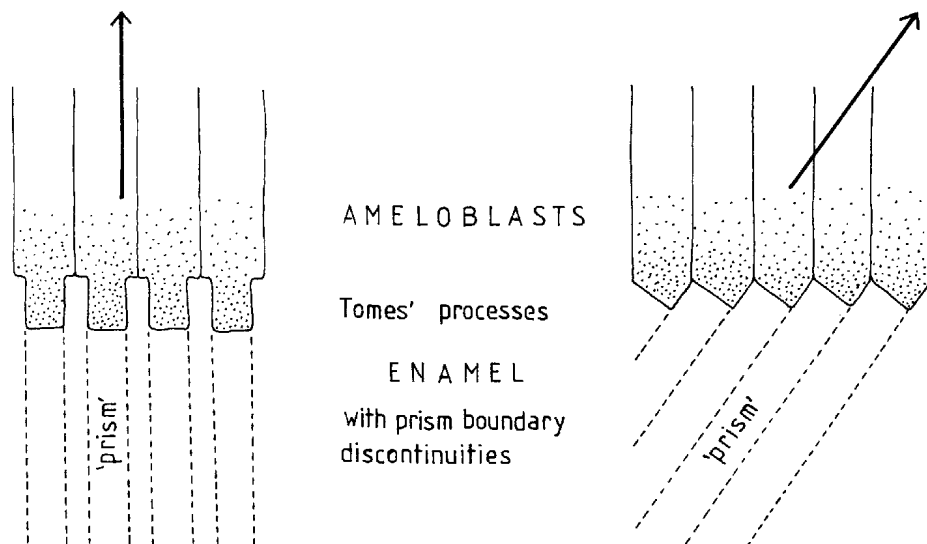


Fig. 7. The relationship between ameloblasts, Tomes' processes and enamel 'prisms'. The arrows denote the direction of ameloblast movement, which determines the orientation of the prism boundary discontinuities. To the left the ameloblasts do not translate across their substrate, and Pattern 1 enamel is formed, with complete prism boundary discontinuities corresponding to the cylindrical Tomes' processes. To the right the ameloblasts do translate across their substrate, the Tomes' processes are inclined, and Pattern 2 or in this case Pattern 3 enamel is formed. The prism boundary discontinuities are incomplete, with a break where the Tomes' process joins the next ameloblast. See Fig. 9 and text. After Boyde 1964, 1976a, much simplified.

The protein matrix is the medium in which the apatite crystals grow to full size, and it somehow must be responsible for the highly controlled growth displayed. In the maturing enamel the proteins are apparently degraded and the protein content drops as the crystals grow from less than 10 nm to 40–60 nm in diameter (Boyde 1976a).

It appears that the apatite crystals tend to be oriented perpendicular to the secretory surface below which they develop. Thus there will be discontinuities in crystal orientation between portions secreted by different parts of the surface of the Tomes' processes. These discontinuities show up in the mature structure, and are responsible for the appearance of so-called enamel prisms or rods (Figs. 7 & 9). When the Tomes' process pit has a complete cylindrical wall, the corresponding prism is completely bounded by a discontinuity, and in principle one may speak of a 'prismatic' and an 'interprismatic' phase in the enamel. When the ameloblast translates across its secretory product, the Tomes' process and its pit become inclined relative to the forming surface and consequently the prism boundary discontinuity becomes incomplete and the prismatic phase continuous with the interprismatic phase. In other words, al-

though prisms are a useful concept in the description of enamel structure, they have no reality apart from their boundary discontinuity. This discontinuity is less dense (contains more water and protein) than the rest of the enamel, which is one reason why it is made visible by various etching processes.

The break in the boundary discontinuity is situated on the side of the Tomes' process that is not 'buried' in the matrix; i.e., on the side facing away from the direction of movement (Figs. 7 & 9). The incomplete boundary is thus an 'arrow' pointing in the direction in which the ameloblast moved.

Boyde (1964) recognized three main types of prisms (Patterns 1, 2 and 3), based on a combination of cross sectional shape and packing pattern (Fig. 9). These patterns can be related to the movement of ameloblasts across their substrate (Boyde 1964, 1967), to the size of their secretory territories (Boyde 1969), and perhaps to the rate of secretion (L.B. Martin 1983).

Boyde's Patterns are simple in principle. Pattern 1 is unambiguously defined by the presence of complete prism boundary discontinuities while Patterns 2 and 3 have incomplete boundaries. All are hexagon-

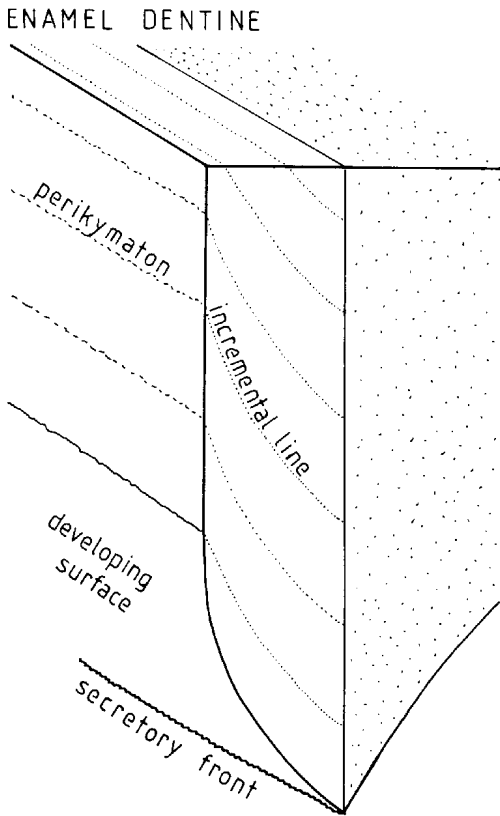


Fig. 8. Schematic representation of the incremental structure of enamel. The developing surface is covered with secretory ameloblasts, the 'youngest' next to the secretory margin and the 'oldest' at its occlusal margin, where secretion ends. Incremental lines are sectioned incremental planes, corresponding to former positions of the developing surface (i.e. to some event affecting secretion at a given moment). In reality there are incremental features with longer and shorter repeat intervals, down to the cross striations of prisms, which probably reflect a circadian rhythm (Boyde 1976a). The lines indicated in this figure are meant to correspond to the 'brown striae' of Retzius.

ally packed, but in Pattern 2 the open end of the discontinuity faces a side of its imaginary hexagon, whereas in Pattern 3 it faces a corner between two sides; i.e., in Pattern 2 ameloblast movement was along rows, whereas in Pattern 3 it was across rows. This has the consequence that in Pattern 2 prominent 'inter-row sheets' tend to develop between the rows of prisms, whereas no 'interprismatic' material can be distinguished in Pattern 3. It should be noted that there is no logical gap between Patterns 2 and 3, and indeed one occasionally finds indeterminate patches within areas of mainly one Pattern. Similarly, although Pattern 1 is by definition distinct from the

others, in practise it sometimes intergrades almost indistinguishably with them, particularly with Pattern 3. In the vast majority of cases, however, the pattern is clearly one or the other.

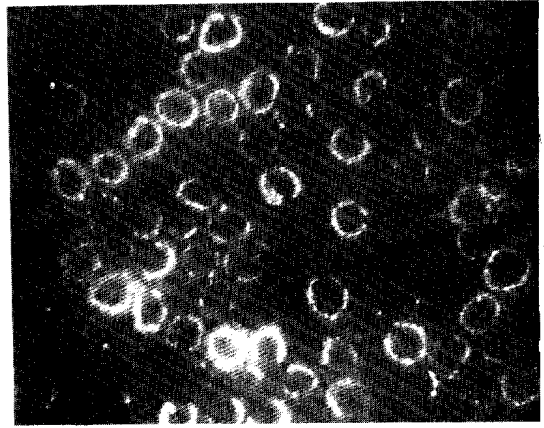
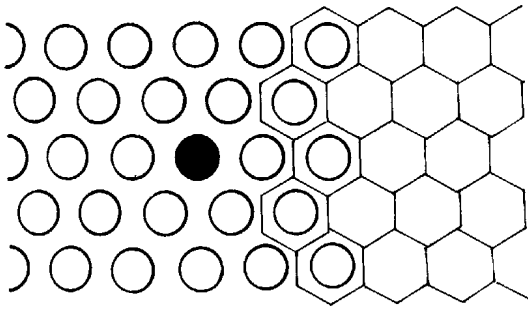
Pattern 1 prisms are produced by one ameloblast each. However, two ameloblasts contribute to each Pattern 2 prism and four to each Pattern 3 prism. Correspondingly, each ameloblast contributes to two Pattern 2 and four Pattern 3 prisms, so that the numbers of ameloblasts and prisms are always equal (Boyde 1976a) (Fig. 9). This is clearly only because the 'prism' is an arbitrary concept, created by joining separate boundary discontinuities. Each discontinuity is made by a single ameloblast, and thus represents the 'trail' of that ameloblast through the tissue. This gives the prism a natural polarity which is useful for descriptive purposes. The 'direction' of the prism is from the enamel-dentine junction to the surface, and it is thus possible to speak of prisms which turn right, left, occlusal, cervical, or toward some other specified direction.

Pattern 2 prisms tend to be smaller (about 0.7–1.2 μm^2) and Pattern 3 prisms larger (about 1.6–2.0 μm^2) than Pattern 1 prisms (about 1.2–1.6 μm^2) (Boyde 1969). The relationship cuts across taxonomic groups and is very consistent. Boyde suggested that they may reflect some relatively simple mechanical constraints, but if such exist they remain unknown. In primates, Pattern 1 prisms are associated with slow (less than 2 $\mu\text{m}/\text{day}$) and Pattern 3 with fast (5–7 $\mu\text{m}/\text{day}$) secretion (L.B. Martin 1983, 1985). Prism packing patterns also appear to reflect taxonomic relationships to some extent, but not as simply as has sometimes been thought (see below).

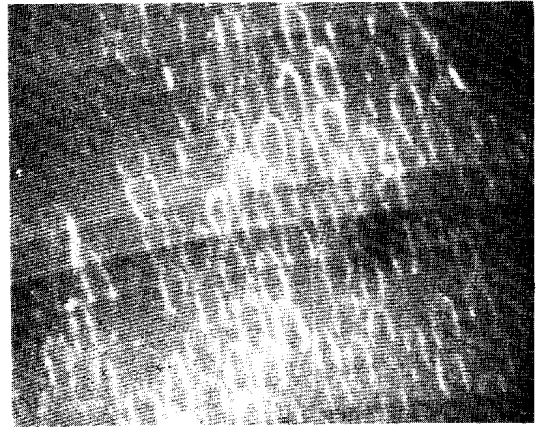
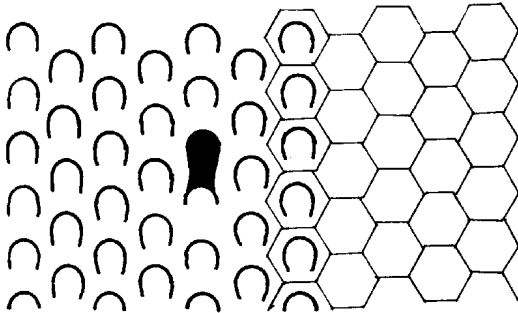
Pattern 1 prisms are found throughout the enamel in some forms (many sirenians, whales, insectivores and bats; Boyde 1964, 1969), but it occurs in most mammals near the enamel-dentine junction and near the tooth surface. This reflects the fact that ameloblasts do not translate across the forming enamel surface at the beginning and end of their secretory life. In some forms, such as in man, there is a true surface layer of enamel in which no prisms are seen. Such enamel is formed by ameloblasts which have lost their Tomes' processes (Boyde 1964, 1967). It tends to be denser and more resistant to wear than prismatic enamel (Karlström 1931), probably because of the absence of prism boundary discontinuities.

There are thus systematic differences in prism packing patterns at different depths into the enamel. There are also differences among areas on teeth, although these differences are less commonly recognized. A preliminary survey of the molars of selected species of fossil equids showed that Pattern 3 dominated cingula and styles, whereas the interstylar and supracingular areas had predominantly Pattern 2 (Alan Boyde & Mikael Fortelius, unpublished data).

Pattern 1



Pattern 2



Pattern 3

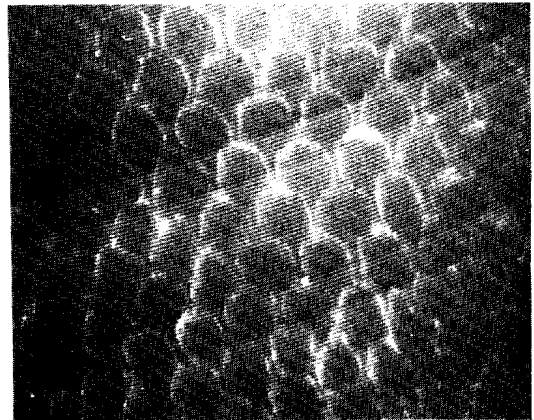
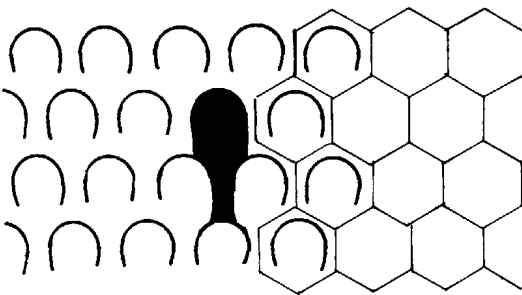


Fig. 9. Prism packing Patterns according to Boyde (1964). The hexagons represent secretory territories of ameloblasts. The circles and horseshoes represent prism boundary discontinuities. One 'prism' is shown in black in each Pattern. Based on Boyde (1976a). To the right are TSRLM micrographs of actual examples. – Pattern 1: *Arsinoitherium zitteli* (Embrithopoda, Oligocene), distal surface of lower molar hypoconid (BM M8470), immediate subsurface enamel. – Pattern 2: *Arsinoitherium zitteli*, buccal surface of upper premolar paracone (BM 8470), inner (decussating) enamel exposed by natural polish. – Pattern 3: *Titanohyrax ultima* (Hyracoidea, Miocene), lingual surface of lower molar metaconid (BM M12058), decussating enamel revealed by natural polish. Field width of all images 43 μ m, lines are due to imperfections in the Nipkow disk of the microscope (see App. 7.3).

Equivalent differences can be observed in other species, and suggest that packing patterns are influenced by the mechanical or geometrical factors involved. There are, however, no obvious correlations between packing pattern and tooth size, shape, enamel thickness or taxonomic relationships that would apply to more than restricted groups. Much more basic work of simple recording of data is needed in this area; most investigations published so far are marred by the fact that they only apply to such scraps of tissue as have been available to the investigator, and do not consider variation in any of the senses mentioned above, nor variation between individuals.

Decussation of prisms

That enamel prisms of successive layers may cross each other at an angle has long been recognized, and the term 'decussation' (from the Latin numeral X, decussis) was first used to describe this phenomenon by Owen (1845) (see Boyde 1969 for a review of the early literature). From the preceding discussion it is clear that the development of decussation requires that ameloblasts move relative to each other on the forming surface. This movement is active, rather than induced by asymmetric secretion; the ameloblast 'leads' the prism (Boyde 1969). It is also clear that Pattern 1 enamel cannot be associated with decussation, which consequently always involves either Pattern 2 or Pattern 3 prisms.

Decussation may be of single layers of prisms, as in the inner enamel of murine and sciurine rodent incisors (uniserial enamel sensu Korvenkontio 1934). More commonly, however, decussation involves layers of several prisms, with a transition that may be abrupt or gradual (pluriserial enamel sensu Korvenkontio 1934). These layers or lamellae of prisms are known as decussating zones or Hunter-Schreger bands, although they were known long before the days of Hunter and Schreger, indeed, the first to describe them may have been Havers (1689) (Boyde 1969). It is these zones that are responsible for the alternating light and dark bands that can often be seen in enamel, particularly under unidirectional light (for a lucid explanation of this phenomenon see Rensberger & von Koenigswald 1980).

The most commonly observed mode of prism decussation is in the horizontal sense, with prisms in different zones inclining alternately towards right and left with respect to the root-crown axis of the tooth (Fig. 10). This decussation usually develops parallel to the developing front of the enamel, and consequently, parallel to the incremental lines (and their surface manifestations, the perikymata). Perhaps for this reason Hunter-Schreger bands are sometimes thought to be incremental features, but this is clearly incorrect. The zones in horizontal de-

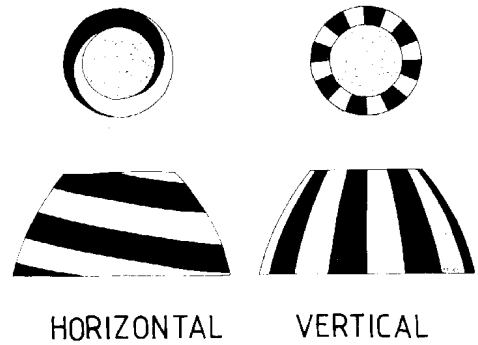


Fig. 10. Schematic representations of tooth cusps to show horizontal (left) and vertical decussation (right). Note the concentric and radial patterns in the sections on top (black and white bands are HSB's, stippled area is dentine). From Fortelius 1984.

cussation are concentrically arranged around the cusp tips, in what often appears to be a spiral pattern (e.g. Kawai 1955; see also Fortelius 1984). A second mode of decussation is in the vertical sense (Korvenkontio 1934, Rensberger & von Koenigswald 1980, Rensberger 1983, Fortelius 1984). Here prisms decussate up and down relative to the root-crown axis, and the zones are arranged radially about the cusp tip (Fig. 10). The zones develop transversely to the developing margin, and are thus transverse to the perikymata. For further discussion see Section 4.3.4.

In uniserial enamel, decussation is necessarily always clear-cut, but in pluriserial enamel it may be anything from a continuous change in direction between two extremes to an abrupt change without any intermediate prisms. The former is commonly found in association with Pattern 2 enamel, and indeed it is clear upon reflection that abrupt changes in orientation are impossible if the Pattern 2 arrangement with inter-row sheets is to be maintained (Fig. 11). Decussation of Pattern 3 enamel is usually more abrupt but commonly features some number of prisms of intermediate orientation at the zone boundaries (Fig. 12).

Decussation in which the 'zones' are very irregular also occurs, for example, in proboscideans (Boyde 1969). Whether such an arrangement is primitive or derived is unclear, as is the whole problem of the origin of decussation. This and the functional aspects of decussation will be discussed in Sections 3.4.1. and 4.3.

At this point it is convenient at this point to summarize the 'generalized' mammalian enamel structure in terms of the ameloblast epithelium and its development during secretion. A more detailed discussion of development in rhinoceroses is given in Boyde & Fortelius (in press). Enamel secretion starts at one

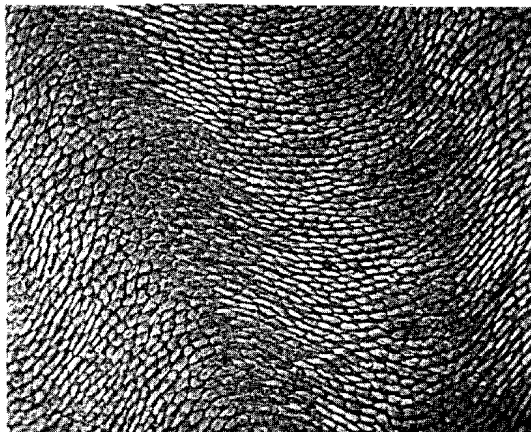


Fig. 11. Pattern 2 enamel with gradual shift in prism orientation between two extremes, horizontal decussation. *Anchitherium aurelianense* (Equidae, Miocene), polished and acid etched vertical transverse section through buccal enamel of upper molar metacone (occusal towards top, enamel-dentine junction towards left). Specimen gift from Dr. Susanne Abusch-Siewert. SEM (BSE) image, field width 230 μm .

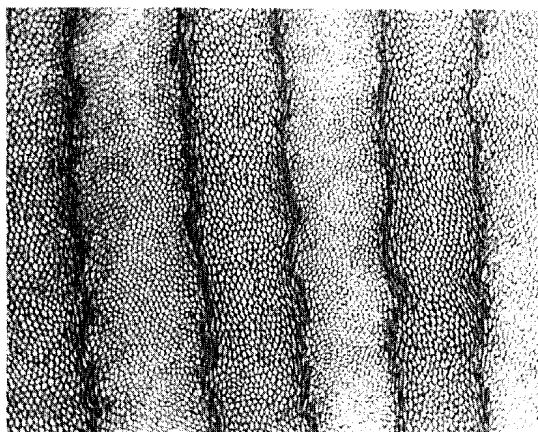


Fig. 12. Vertical decussation with sharp zone boundaries (the Pattern is 3, although that can not be seen in this preparation). *Astrapotherium* sp. (Astrapotheria, Miocene), horizontal section through ectoloph of upper molar (enamel-dentine junction towards bottom). HP unregd. fragment. SEM (BSE+SE) image, field width 400 μm .

or several centers of origin, usually at cusp tips, and spreads from these as ameloblasts in successive, more or less concentric zones turn secretory. Thus the developing tooth is covered by ameloblasts in different stages of development, the 'youngest' at the forming margin and the 'oldest' at the center(s) of origin. All ameloblasts go through the same developmental stages, so that the resulting tissue shows a regular layering parallel to the enamel-dentine junction and the finished surface. The two main layers most commonly found are the inner, decussating enamel and the outer, more or less non-decussating enamel. Korvenkontio (1934) referred to these layers as *portio interna* and *portio externa*, respectively. The incremental features, which mark successive positions of the developing surface, cut across this layering at an angle which is a function of the relative rate of coverage. The more rapidly the tooth is covered (relative to the rate of secretion) by secretory ameloblasts, the more parallel are the incremental lines to the enamel-dentine junction.

During early secretion the ameloblasts do not translate across their substrate, and consequently Pattern 1 enamel is formed close to the enamel-dentine junction. Soon, however, bands of ameloblasts begin to move relative to each other, and decussating enamel with Pattern 2 or 3 prisms is formed. The degree of interference of these groups with each other determines how abrupt the zone boundaries become.

When the groups move with great independence, the decussation is abrupt with few prisms of intermediate direction, while much interference leads to decussation where zone boundaries are indistinct and a gradual transition of prism orientation occurs. One ameloblast can change from one group to another, even several times, which means that individual prisms may pass through several different zones on their way from the enamel-dentine junction to the surface. The degree of regularity in the arrangement of decussating zones depends on how controlled the behaviour of ameloblasts groups are during development, or more specifically on how well oriented the ameloblasts are relative to the tooth axes.

During later stages of development the tendency of ameloblasts to move relative to each other is reduced, and less decussating or non-decussating enamel is formed. In the final stages the ameloblasts may lose their Tomes' processes, in which case a true surface layer of non-prismatic enamel is formed. In other cases no such layer is found, and the finished surface displays Tomes' process pits. In ungulates this situation is not unusual, and may often serve to increase the area of attachment of coronal cementum. In horses, however, cementum is attached after parts of the enamel have been resorbed by osteoclasts, which leave large irregular pits (Jones & Boyde 1974). The cementum is formed by cementoblasts of mesenchymatic origin, and deposition occurs after the ameloblasts have died and disappeared.

3.2. Comminution and digestion of food

In terms of making nutrients available to the organism it is meaningless to separate comminution from digestion. However, since we are concerned mainly with cheek teeth, the primary function of which is to serve as the vehicles of food comminution, such a distinction is defensible. This should not obscure the fact that comminution and digestion are parts of one whole, and that strong interrelationships exist, as will be shown below.

3.2.1. Comminution

Food particles must be small enough to pass through the oesophagus for swallowing to be possible. This trivial fact marks the upper limit of acceptable particle size at the end of a chewing bout. That a corresponding lower limit may exist is less obvious, but one occurs at least in ruminants, where retention of food in the rumen and reticulum depends on particle size (Janis 1976). The general function of mastication, expressed in physiological terms, is to increase the surface/volume ratio of the food and thus speed up chemical degradation, but the properties of individual kinds of foods affect the issue. In particular, leaves are flat and comminution does not increase the exposed surface area very much. On the other hand, the cellulose walls of plant cells are highly resistant to chemical action and can only be degraded by specific enzymes produced by symbiotic microorganisms. If the cell walls and other protective structures such as wax layers are broken mechanically, digestion of the cytoplasm can proceed independently of the breaking down of the wall. The mechanical requirements of such 'pulping' are not necessarily the same as those of reduction of particle size (cf. Rensberger 1973).

The theoretical aspects of food comminution have been analyzed by Lucas (1979, 1980). In principle, foods may be considered along a gradient from brittle to ductile, where the main difference in comminution is that for a given equipment design, temperature and loading rate, crack propagation and consequently the tendency to shatter decreases towards the ductile end. When cracks are not propagated, a solid can only be comminuted by structures that push all the way through it. The brittle-ductile gradient is really only applicable to isotropic solids, which are very rare among plant foods. However, in the matter of crack propagation many plant tissues probably resemble ductile solids, in that cracking does not occur to any appreciable extent. The comminution of such foods requires equipment capable of dictating fracture, in other words, blades (cutting edges). In contrast, foods that shatter may be comminuted by stressing them between essentially flat surfaces.

Data on the mechanical properties of plant foods are scant (see Lucas 1980 for a review), and data on tough, fibrous foods seem to be lacking entirely (an exception is Vincent 1982, who analyzed the behaviour of grass leaves in tension experiments). Equally little is known about the actual comminution of food in the mouth; among the very few published reports are Sheine & Kay (1977) and Lucas & Luke (1983a). The latter article is of particular interest here.

As a starting point, Lucas & Luke (1983a) chose the work of Epstein (1947), who studied the industrial comminution of coal and rock ores. According to Epstein (as related by Lucas & Luke), comminution may be described in terms of selection (positioning of material within the comminution apparatus) and breakage (the degree of fragmentation of a particle). As defined by Gardner & Austin (1962, cited by Lucas & Luke 1983a:813), the selection function $S(x)$ is "the proportion of ($0 \leq S \leq 1$) of particles, by volume or weight, of a small but finite size range X to $X + \delta X$ that break per unit cycle of action of the equipment". Similarly, the breakage function $B(y, x)$ is "that proportion of ($0 \leq B \leq 1$) of selected particles, by volume or weight, of size range X to $X + \delta X$ that break to below a size Y per unit cycle (where $Y \leq X$)".

It is very clear that selection will depend on the dental morphology and the action of the mouth as a whole (e.g. food circulation). For a given set of conditions, for example man chewing carrot, as analyzed by Lucas & Luke, selection appears to be principally dependent on particle size (large particles are more likely to be selected than small ones). In contrast, breakage proved to be essentially independent of absolute particle size, and the authors suggest that each selected particle is broken only once per chew and that the number of fragments produced is small. Computer simulation based on these assumptions produced results similar to those obtained empirically (Lucas & Luke 1983b).

Just how far these results can be generalized is unclear. They probably apply to non-brittle solids comminuted by blades, since the probability of breakage of a particle caught between two blades is likely to be close to 1 (see below), and the probability of being caught is likely to be a function of particle size. If so, then there will exist for each combination of animal and food an optimum number of chews corresponding to a minimum particle size beyond which additional chewing will be essentially a waste of energy. For the man and carrot, the results of Lucas & Luke (1983a) suggest that this number may be as low as about ten chews.

It is interesting that absolute size may have relatively little effect on comminution, other than in terms of 'grain', i.e. the size of the animal relative to the size of the elements of its environment (more generally, extension in all dimensions; cf. Levins

1968). Thus the stress between occluding teeth is likely to be nearly independent of absolute size, since it is a direct function of load; i.e., muscular (physiological) cross-sectional area, and an inverse function of the area of contact. If ingested particle size is isometric to mouth size (i.e. if there is no effect of 'grain'), then there is no reason to suppose that selection and breakage would be different at different sizes, and consequently for a given food and comminuting morphology the optimum number of chews would be independent of absolute size. That is to say, the ratio of particle size to tooth size should be constant for corresponding stages of the process, such as at swallowing.

Rapid ingestion is probably at a premium in most mammals, and particularly herbivores spend a substantial portion of their existence feeding. It is thus likely that comminution achieved by a fairly low number of chews is a necessary requirement which may account for the commonness of multiple-bladed systems in mammalian dental morphology (see also Lucas & Luke 1984). Many blades would serve to increase selection, which must be a function of the number of 'comminuting locations'; e.g., blade pairs, available. Specialized grazers (among non-ruminants, see below) tend to have a greater number of enamel crests transverse to the direction of chewing motion than their non-grazing relatives, and it is possible to study the shift in some lineages (see Rensberger et al. 1984 for horses, Fortelius 1981, 1982 for rhinoceroses and Maglio 1972 for proboscideans). This probably reflects the need to chew a greater volume of food for a constant amount of energy and nutrients.

The initial size and shape of the food ingested is another important variable in comminution. Voluminous, non-brittle particles may only be divided by blades long and deep enough to push all the way through. Meat-eaters such as felids typically possess slender, single-bladed dentitions. Among herbivores, systems dominated by one major blade pair are found among rhinoceroses and several extinct ungulate groups (see Sect. 4.2.), where it appears to be a correlate of feeding on bulky browse such as twigs and tubers (cf. Kingdon 1979). The comminution of tough sheets and thin rods, effectively grass, presents other problems mainly associated with loading. Pairs of blades sliding past each other in the manner of mammalian teeth would theoretically seem to load the food in shear. When tough sheets are loaded in this manner they show a tendency to buckle and slide (Atkins & May 1979), which is probably the difficulty encountered by a cat chewing grass. This may be, and often is, overcome by applying a compressive load perpendicular to the direction of relative movement, which is why Lucas (1980) rather convincingly argued that no practical distinction between compressive and shearing load exists in mastication. Serial blades in one plane allow more

stable loading, but the depth of the blades is reduced dramatically (see, e.g., Figs. 14 and 15). As I pointed out earlier (Fortelius 1981), these conflicting requirements of different types of foods appear to explain the rather clear-cut differences in occlusal morphology between browsing and grazing perissodactyls better than the conventional invocation of the abrasiveness of grass.

Ultimately, comminution of food is a matter of stress (or 'pressure'), i.e. of load per unit area (Rensberger 1973). Ignoring for the moment the food strained between opposing teeth, occlusal stress increases with the load normal to the plane of contact and with decreasing contact area. The load is the vector sum of all the muscular forces acting in the system at a given moment, or the masticatory force vector (Rensberger 1973). The critical stress ('pressure') introduced by Rensberger (1973) is equal to the strength ('failure threshold') of the food material. Lower stress will waste energy straining the food without breaking it, while higher stress will waste energy through friction and cause excessive wear without increase of breakage, since at critical stress all particles loaded break and the teeth come into direct contact.

Thus both the number of cycles per chewing bout and the degree of muscular contraction during each cycle have theoretical optima for each combination of animal and food. The two are independent in principle, although a connection via loading rate may exist. The latter becomes important when it is sufficiently high to cause shatter, but its influence is probably otherwise negligible.

Insofar as stress is inversely proportional to contact area, increased stress may in principle be achieved by a reduction of the area of contact as well as by an increase in load. However, a decreased contact area decreases selection, so that a greater number of chews is required for equal comminution. Conversely, the number of chews necessary may be reduced by increasing contact area and selection, but this requires increased load; i.e., larger muscles. Data are lacking, but the suggestion by Weijs & Dantuma (1981) that rodents with their shortened toothrow have maximized for stress while ungulates with molarized premolars have maximized for selection (they did not use these terms) is eminently plausible. Although little more than speculation exists at the moment, it is clear that recognition of specific and conflicting functional requirements (such as those discussed above) will help to generate testable predictions regarding functional relationships of dental morphology. This is in some contrast to the conventional descriptive treatment, based on analogy with man-made comminuting equipment, in which a plethora of undefined terms are used to describe vaguely inferred properties or processes (such

as grinding, milling, shearing, shredding etc.; see discussion by Lucas 1980).

3.2.2. Digestion

How the food should optimally be prepared in the mouth depends to a large extent on how it is to be digested in the alimentary canal. In herbivorous mammals it is above all the digestion of cell wall constituents that has to be considered, since this requires enzymes provided by symbiotic microbes. The site of cellulose fermentation varies, but apparently it is always situated either before the true stomach or after the large intestine. Thus one may speak of two groups: foregut and hindgut fermenters. Janis (1976) has considered the theoretical and evolutionary aspects of these two 'digestive strategies'.

Foregut fermentation has traditionally been regarded as the more 'advanced' system. Schmidt-Nielsen (1979) considers that foregut fermentation has three advantages over hindgut fermentation. First, fermentation occurs at the beginning and all the products of digestion can pass through the small intestine. Second, regurgitation and cud chewing is possible. Third, urea that would otherwise be lost can be recycled and fed via the saliva to the microbes in the fermentation chamber. This last arrangement allows foregut fermenters to exist on food with very low nitrogen content. They are also effectively independent of the amino acid proportions in the diet, since everything is broken down and resynthesized by the microbes.

Janis (1976) pointed out, however, that the fermentation of soluble carbohydrates and protein along with the cellulose can equally be regarded as a disadvantage of foregut fermentation. In particular, almost all available glucose is lost and the major part of the animal's glucose must come from deaminated protein. Adult ruminants have extremely low blood sugar levels which show poor tolerance to fasting (McCandless & Dye 1950, cited by Janis 1976). Also, coprophagy offers a path whereby hindgut fermenters can achieve an effect similar to foregut fermentation in some respects (Janis 1976, Schmidt-Nielsen 1979).

As for the difference between ruminating artiodactyls and hindgut fermenting ungulates, especially equids, Janis (1976) has emphasized the role of passage time regulation. In ruminants this is achieved by means of the reticulo-omasal orifice, which acts as a passive sieve through which only particles below a certain size may pass. Thus the food is chewed, fermented and re-chewed, and the process is repeated until a sufficiently low particle size is reached. The food enters the rumen or the reticulum depending on the mode of swallowing (for example, calves can pass the milk into the reticulum and

omasum without prior fermentation in the rumen), but the passage from the reticulum onwards depends on particle size. With decreasing digestibility of the food, a ruminant will eventually reach a point where it cannot process the food fast enough to meet its energy demands. No comparable restriction applies to hindgut fermenters; a horse can pass large, undigested particles through its alimentary canal and utilize only what can be digested relatively rapidly. Janis (1976) has generalized this to the principle that ruminants are primarily limited by food quality and hindgut fermenters by food quantity. A cow can get by on a quantity of forage insufficient to support a 'wasteful' horse of equal size, but the horse is able to maintain itself on hay of a quality too low to keep the 'choosy' cow going. It should be noted that 'quality' here refers specifically to digestibility in terms of the rate of particle size reduction. In terms of available nutrients the case is probably the reverse (Schmidt-Nielsen 1979).

From the point of view of comminution the central issue is whether or not the food is regurgitated for repeated chewing. In hindgut fermenters the food is typically chewed only once, and no mechanical comminution occurs after that. The food is chewed in the form that it is ingested, with its original structural and mechanical properties. This is in marked contrast to the situation in ruminants, which chew their food only cursorily the first time around. What is properly chewed in ruminants is the 'cud'; i.e., the partly fermented, regurgitated material. This is of a much more uniform nature structurally and mechanically than the untreated food.

From the above, a number of general predictions can be derived. First, specialists on really fibrous, slowly disintegrating foods will be found among hindgut fermenters (Janis 1976). Second, hindgut fermenters will have a dental morphology that reflects their dietary adaptations more than is the case in ruminating forms. Third, hindgut fermenters should have a relatively greater masticatory performance capacity, with, for example, relatively larger occlusal area (selection) and/or larger masticatory muscles (breakage) than ruminants with the same diet. In addition there are predictions related to body size discussed by Janis (1976), which say that foregut fermenters will not be found among very small and very large forms.

I do not propose to test these predictions here, but I will refer to them again in later sections. Qualitatively they all appear plausible. Molar morphology has certainly been more diverse among the non-ruminant artiodactyls and the perissodactyls than among the ruminating (selenodont) artiodactyls, in which differences are mainly of crown height but not of occlusal design. Another group with a singularly uniform dental design, despite varied dietary specializations (Strahan 1983), is the macropod marsu-

pials. These are also foregut fermenters, and at least some of them (e.g. *Macropus rufus*) do ruminate (Schultz (1976). Rodents are hindgut fermenters and have varied and highly specialized teeth which reflect diet (Vorontsov 1967). The wombat, a hindgut fermenting marsupial, has complex, rodent-like teeth. In respect to occlusal area and selection, molarization of the premolars is more complete in the hindgut fermenting perissodactyls and hyracoids than in the foregut fermenting artiodactyls. And finally, although a European bison is a considerably larger grazer than a horse, the masticatory muscles of the horse weigh about three times as much as those of the bison (2304 g against 734 g; Becht 1953).

In summary, whether one regards rumination as 'progressive' or not, it certainly results in relaxed demands on the masticatory apparatus as far as comminution performance is concerned. Teeth that reflect the properties of foods are more likely to be found in non-ruminants, and this applies both to morphology and to macro- and microscopic wear.

3.3. Mastication

Mastication is the breaking of food in compressive loading due to contraction of the elevator muscles of the mandible. A vast literature on jaw mechanics and the dynamics of chewing exists, but will not be reviewed here. An excellent general review is Hiimäe (1978).

Crompton & Hiimäe (1970) introduced the useful concepts of puncture-crushing and shearing; the latter was later called chewing (*sensu stricto*) by Hiimäe (1978). In the following, 'chewing' refers to chewing (*sensu stricto*) unless otherwise stated. As originally defined, puncture-crushing is mastication with only tooth-food-tooth contact, whereas chewing ('shearing') is mastication involving tooth-tooth contact, and this distinction is adopted here. Puncture-crushing and chewing are thus not necessarily distinct modes of mastication, but rather parts of a continuum of particle size reduction occurring through successive chewing cycles and terminated by swallowing. The path traversed by the mandible as well as the pattern and amount of muscular contraction depend on the mechanical properties and size of the food particles at least in the rabbit (Weijs & Dantuma 1981), and probably generally. Both transverse movement and firing levels in the rabbit decrease from hay to laboratory pellet to carrot; i.e., from small and tough to large and brittle. This is in good agreement with the theoretical predictions derivable from the discussion of comminution (Sect. 3.2.1).

When premolars are not molarized they are probably mainly organs of puncture-crushing, while the molars are organs of chewing. This polarity is largely confirmed by wear patterns; true facets in the sense

of Rensberger (1978) (wear surfaces produced by near or direct occlusal contact) occur mainly on molars. Since comminution of non-brittle solids requires that the blades meet, facets are a sign of true chewing. However, wear patterns are complex and are treated in more detail in Section 3.4.

According to established usage (Hiimäe 1978), a chewing cycle extends from one maximum gape position to the next. It consists of three parts: the closing stroke, the power stroke and the opening stroke. The power stroke is the portion of loaded movement; i.e., of direct or food-mediated occlusal contact.

Although a great variety of paths traversed by the mandible during the chewing cycle have been recorded (Hiimäe 1978, Weijs & Dantuma 1981), there seems to be some unity among therian mammals in that the orientation is either towards lingual, towards anterior, or (most commonly) something in between, and at least initially plunges towards dorsal. (In fascinating contrast, the non-therian multituberculates, or at least *Ptilodus*, seem to have chewed by retraction of the mandible (Kraus 1982)!) Contrary to common misconception, no back-and-forth movements are known to occur during mastication. Indeed, from the point of view of food circulation and selection, there would appear to be little point in such movements.

3.3.1. Muscles

The muscles that load the jaws during the power-stroke and control movement during the chewing cycle are numerous and interact in intricate ways (e.g. Weijs & Dantuma 1981). For the present purpose it is sufficient to regard only the muscles responsible for compressive loading; i.e., the elevator muscles of the mandible. It is customary to distinguish three muscle masses: masseter, pterygoid and temporalis (Fig. 13; for details see e.g. Turnbull 1970). Very generally speaking, the masseters arise on the zygoma and insert on the external (lateral) surfaces of the angle of the mandible. Usually a deep masseter with more or less vertical fibre orientation may be distinguished from a more oblique superficial masseter with a marked anterior force component. The corresponding pterygoid muscles arise on the skull base (pterygoid process, adjacent areas of the pterygoid, sphenoid and palatal bones) and insert on the internal (medial) surface of the mandible. A larger medial pterygoid with a more vertical orientation is usually distinct from a more horizontal and anterior lateral pterygoid. The temporalis muscles, finally, arise on the temporal and parietal bones of the skull and insert on the coronoid process of the mandible. More details are given by, for example Turnbull (1970), Janis (1983).

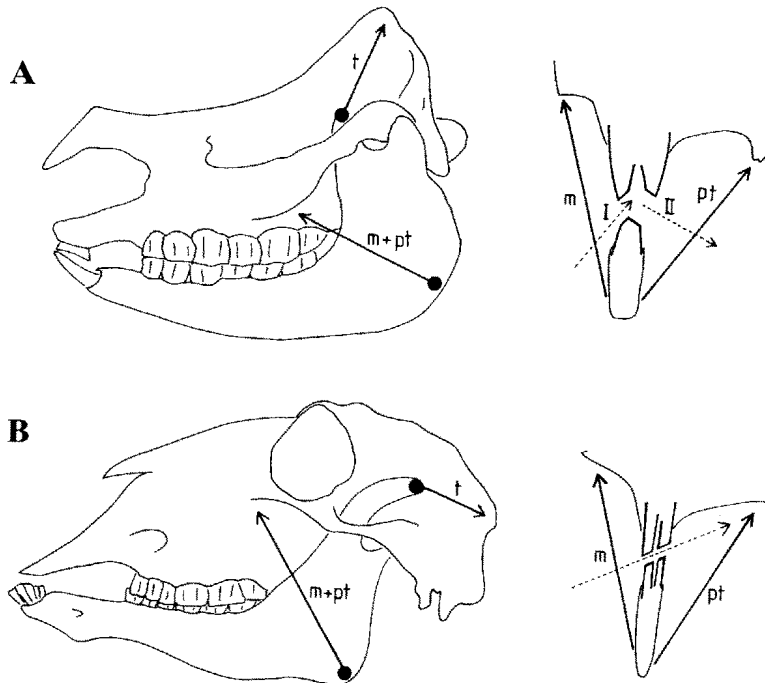


Fig. 13. Highly schematic representations of the main masticatory muscle vectors. – *Rhinoceros unicornis* (A), with two-phase occlusal morphology. – *Ovis aries* (B), with one-phase occlusal morphology. To the right are (imaginary) vertical transverse sections. The single-phase arrangement allows greater overlap in muscular activity during the power stroke. The dotted arrows denote directions of lower molar movement during the power stroke, but are not meant to indicate the true path of mandible movement. I and II refer to the phases of the power stroke. m = (superficial) masseter, pt = (medial) pterygoid, t = temporalis.

A further useful simplification suggested by Crompton & Hiimäe (1969b) is to consider this complex in terms of two blocks of pairs of lateral and medial muscles, one with an essentially vertical muscle resultant, the other with a resultant inclined forwards. The first block consists of the deep masseter and the temporalis, the second of the superficial masseter and the (medial) pterygoid. In the words of Crompton & Hiimäe: "A reasonable generalization is that the temporalis and deep masseter are primarily responsible for the upward movement of the jaw, whereas the superficial masseter and the pterygoid produce and control a combination of upwards, forwards and sideways movement". Consequently, "...in herbivores, where sideways movements are important, the second block consisting of the pterygoid and superficial masseter muscles will be the larger of the two muscle blocks" (Crompton & Hiimäe 1969b:30). Much of the dental morphology of ungulates is understandable in terms of two muscle masses which are partly antagonistic, one contributing a component towards lateral and the other one towards medial (see below).

3.3.2. Transverse chewing

The transverse power stroke found in most ungulates is sometimes almost linear but often the direction changes while occlusal or near-occlusal contact is maintained. Butler (1952a) distinguished three 'stages' (1,2,3) of deduced mandibular movement from wear facets on the mandibles of the Eocene horse *Hyracotherium*. Mills (1955, see also 1978) distinguished two 'phases' (buccal, lingual) of similarly deduced movement in primates, while Kay & Hiimäe (1974) described two 'phases' (I,II) of inferred and observed movement in primates. The latter have been widely adopted and are used in this text; however, Butler's (1952a) original notion of three stages often fits the observed wear patterns better, and indeed Kay & Hiimäe (1974) and Kay (1977) distinguish between 'a' and 'b' versions of phase I facets, which clearly correspond to Butler's stages 1 and 2.

Phase I, according to Kay & Hiimäe (1974), is movement into unilateral centric occlusion (Crompton & Hiimäe 1970), and always appears to

plunge towards dorsal (Fig. 13A). Phase II is movement out of centric occlusion that primitively plunges towards ventral but has become progressively more horizontal in derived primates (Hiimäe 1978). While the notion of 'centric occlusion' may be useful in primates, it is often of ambiguous significance in ungulates. Weijs & Dantuma (1981) emphasize that jaw movement in the rabbit is smooth and the muscles contract in an overlapping sequence so that sudden changes in load do not occur (at least not through muscular action). Data on large ungulates are lacking, but the inertia of their massive mandibles would seem to preclude sudden changes in direction or brief cessation of movement in midstroke (the 'isometric phase', cf. Hiimäe 1978). The results on pygmy goats obtained by De Vree & Gans (1976) also suggest a relatively smooth and linear path during the power stroke.

Becht (1953) suggested that the buccal dip of the occlusal surfaces of bovids enables them to use the superficial masseters and medial pterygoids bilaterally during chewing, as the total muscle resultant will always have a component parallel to and in the direction of (dorsomedial) occlusal movement (Fig. 13B). Greaves (1980) elaborated the suggestion and found that the principle only applies if the glenoid joints lie above the (continuations of) the occlusal planes and when the fulcrum is at the balancing side joint or situated between the working and balancing side joints. The raised position of the glenoid joint seems to be the rule in ungulates as pointed out by many (e.g. Maynard-Smith & Savage 1959, Crompton & Hiimäe 1969b). Weijs & Dantuma (1981) tested Greaves' hypothesis (originally proposed from a different theoretical line of reasoning by Greaves (1978)) with data from the rabbit and found that "The proportion between working and balancing side muscle firing levels appears to be such that the balancing side joint becomes the fulcrum. In other words, at a given level of working side muscle activity the balancing side muscles fire as strongly as possible (to increase the bite force as much as possible) without inducing tensile, dislocative stresses at the working side joint" (p. 139). They found that this corresponds to a ratio of 0.69 between contractive forces on the balancing and working sides.

Both Hiimäe (1978) and Weijs (1980) stressed the futility of static analysis of the masticatory muscular system. However, very little dynamic analysis seems to have been carried out. A golden spike in this general vagueness is the analysis of rabbit chewing by Weijs & Dantuma (1981), extensively cited above. Of particular interest for the present discussion is their demonstration that during the power stroke the total bilateral resultant force vector resolved into the transverse plane gradually shifts from a slightly lateral to a distinctly medial inclination from the dorsal. The angular data are not given, but measurement from their fig. 11.B. indicates a total shift

of about 10 degrees. This shift corresponds to a two-group muscular activity sequence. The balancing side superficial masseter and medial pterygoid contract first, together with the working side temporalis, while the working side masseters and medial pterygoid follow with the balancing side temporalis. It appears that the medial component is mainly due to the contraction of the working side medial pterygoid.

Although rabbits are not ungulates in any acceptable sense of the word, their masticatory apparatus is not altogether different. The direction of the power stroke is mediad, and like ungulates, rabbits possess the large medial pterygoids that make transverse chewing possible (Weijs 1980). Therefore, a tentative application of the rabbit data to ungulates seems justified. This brings us back to the matter of phases of the power stroke.

Recall that for breakage to occur, critical stress must be achieved. For a given area of contact, stress is proportional to the load normal to the plane of contact. When the angle of plunge between phase I and phase II movement is large, as for example in rhinoceroses where it is about 90 degrees (Figs. 13A & 14A,B), considerable change in the direction of the total resultant force vector is required if surfaces in both phase I and phase II planes are to be loaded sufficiently. The existence of true facets in both planes is evidence that near or direct occlusal contact is achieved during both phases, and unless it is postulated that no food normally occurs between phase II surfaces (a most improbable explanation), this means that critical stress is indeed reached during both phases. By sectioning casts of upper and lower teeth in planes parallel to the orientation of movement during the power stroke, it is possible to measure the angles of plunge during different phases (App. 4). Quantitative analysis could be undertaken, but here I use the method only to illustrate the differences in a qualitative way (Figs. 14-16).

It is unfortunate that ungulates with well-developed phase II facets have not been investigated for muscular activity during chewing. The closest approximation is perhaps Janis (1979), who studied mandibular movement in the hyrax *Procavia*, but although she was able to demonstrate phase II movement, she regarded it as being of little functional significance. According to her, the phase II facets are much more prominent in browsing hyraxes (*Dendrohyrax*, *Heterohyrax*) than in the grazing *Procavia*, a statement supported by the present study (Figs. 14 E&D). According to Janis (1983), the muscular anatomy does not differ 'obviously' between *Procavia* and *Heterohyrax*, but clearly real data on muscular activity are needed.

Still the fact remains that if ungulate dentitions are to be discussed the matter of phases of occlusion can hardly be ignored, and some functional interpretation is necessary. I speculated previously (Fortelius

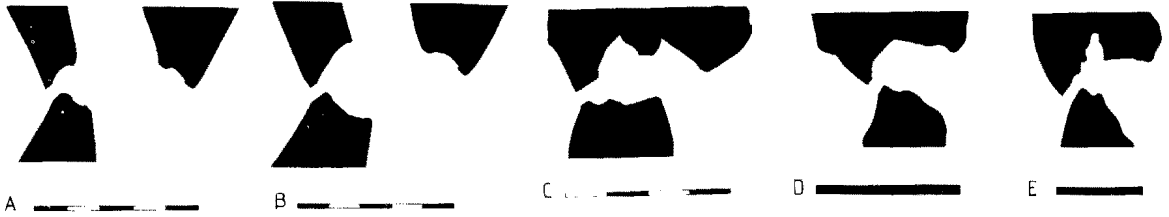


Fig. 14. Transverse profiles of occluding upper and lower molars of trilophodont forms with distinct two-phase occlusal morphology. See App. 4. for method. One segment of scale bar = 5 mm. Abbreviations refer to collections as detailed in App. 2–3. – A. *Dicerorhinus sumatrensis* M¹, M₁ (KO 617). – B. *Diceros bicornis* M¹, M₁ (TE R.G. 7974). – C. *Anchitherium aurelianense* (isolated first or second molars) (MU 1959 II 520 & 614). – D. *Dendrohyrax* sp. M², M₂ (ST 4415 (102)). – E. *Procavia habessinica* M², M₂ (ST “6”).



Fig. 15. Transverse profiles of occluding upper and lower molars of trilophodont forms with one-phase occlusal morphology (plagiolophodont forms). See caption of Fig. 14. – A. *Equus grevyi* M¹, M₁ (KO CN 1694). – B. *Ceratotherium simum* M², M₂ (TE R.G. 5925).

1981) that the partial antagonism between working side superficial masseter and medial pterygoid might be sufficient to explain the essentials of the two-phase wear morphology and jaw movement. The large masseter is responsible for high stress at the phase I surfaces, while the phase II surfaces must be loaded by the smaller medial pterygoid, since downwards movement of the mandible is clearly incompatible with full (ipsilateral) masseter contraction. Consequently the load must be considerably smaller during phase II, and sufficiently high stress for facet formation is a result of the relatively small total area represented by phase II surfaces. Consideration of the balancing side musculature may alter this conclusion to some extent, but not its main point; that masseters and pterygoids of one side can not load surfaces in both phase I and phase II planes on the same side, so the degree of potential overlap of muscular contraction is limited. No such restrictions need apply to essentially single-phase surfaces dipping gently towards buccal (Figs. 15 & 16), such as those of the bovids and horse discussed by Becht (1953) and Greaves (1978, 1980), or to those of rabbits.

Horizontal movement during the power stroke is clearly a convergently derived feature of mammalian

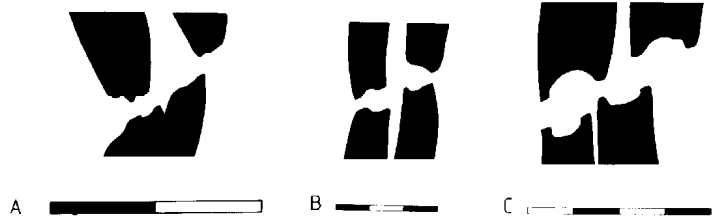
herbivores, and near-horizontal single-phase surfaces are derived from two-phase ones in at least rodents, perissodactyls and artiodactyls (see e.g. Romer 1945, Thenius 1969, Butler 1972, 1980). The discussion above suggests that the development of single-phase surfaces allows greater overlap of muscular contraction and higher load and stress for a given muscle mass and contact area. In reference to the discussion of comminution, such surfaces allow serial blades and increased selection, but reduce the depth of the blades and thus the size of particles that can be comminuted.

3.3.3. Orthal and palinal chewing

Truly orthal chewing, if it exists at all among therians, is probably restricted to puncture-crushing. True chewing apparently always contains a horizontal component, which may, however, be slight (see e.g. Butler 1972). Judging from the morphology of basal ungulate ('condylarth') molars, the primitive condition was a distinctly two-phased power stroke involving little more in the way of translation than a simple anteromedial movement of the lower molars into and out of centric occlusion with the uppers. Among living ungulates, peccaries, some suids, tapirs and macropod marsupials are forms with relatively little translatory motion in mastication, judging from dental morphology (and cursory inspection of captive animals). In the fossil record, similar forms are common (see Sect. 4.2.).

Characteristic of teeth involved in mainly orthal chewing is that their morphology is to a large extent preformed rather than mainly acquired by wear, as tends to be the case with teeth involved in horizontal translation. Upon wear, they gradually lose their original form, and as the enamel is worn through, the cusps and lophs originally present are replaced by dentine basins surrounded by raised enamel edges. The general topography becomes progressively flatter, and one may concur with Maglio (1972) that the plunge of occlusal movement decreases during the

Fig. 16. Transverse profiles of occluding upper and lower molars of selenodont forms. See caption of Fig. 14. – A. *Moschus moschiferus* M³, M₃ (KO 635). – B. *Taurotragus oryx* M¹, M₃, different individuals (GB 4617 & 4618). – C. *Oryx beisa* M², M₂ (KO CN 1655).



life of the individual. To some extent this parallels phyletic change, particularly among the elephantids and some suid lineages. Primary morphology is lost and replaced by a secondary one, which is essentially in one occlusal plane. This plane may be flat or curved, depending on the mechanics of chewing (essentially the construction of the glenoid joint). Similar changes are common among rodent lineages (e.g. Butler 1980, Thenius 1969).

The difference between orthal and palinal chewing is one of degree. Recalling Butler's (1952a) notion of three stages of occlusion, one might say that it consists in the insertion of an intermediate stage between phase I and phase II. This is a corollary of acquired molar morphology: it is difficult to see how teeth could be constructed that would maintain a clear-cut two-phase morphology through wear, particularly if loading is stable and/or changes gradually during the power stroke. On the other hand, the relationship between orthal and palinal chewing resembles that between two-phase and one-phase transverse chewing, and is clearly functionally analogous. An important difference is that the combination of hypsodonty and secondary two-phase morphology which is possible in transverse chewing (e.g. rhinoceroses) is impossible in orthal/palinal chewing (e.g. tapirs, elephants, pigs).

Among ungulates, truly palinal chewing is confined to the Proboscidea. Maglio (1972) discussed the modification of the masticatory apparatus during the evolution of the Elephantidae. By what appears to have been a relatively gradual process, the glenoid was lifted forwards to lie above the centre of gravity. The jaw is thus suspended in balance in modern elephants, and the occlusal plane is curved along the periphery of a circle with its centre somewhere above the joint. Load is chiefly provided by the temporalis, which accounts for 70 % of the total masticatory muscle mass, while the masseter (20 %) is primarily responsible for forwards movement during the power stroke (relative weights from Stocker 1957, as cited by Maglio 1972). A problem with palinal chewing discussed by Weijjs & Dantuma (1981) is that translation requires corresponding displacement of the joints. Elephants have overcome part of the problem by curving the occlusal plane, but more

movement of the joint is still needed per unit translated tooth surface than in transverse chewing.

3.4. Eruption and wear

Because humans are brachyodont, we do not intuitively sense the strong relationship that exists between dental wear and compensatory eruptive movements which is so characteristic of hypsodont mammals and culminates in the continuous eruption of rootless teeth. Such movements are actually known to occur in man also (Bhaskar 1980), and seem to be a general phenomenon of mammals with functional cheek teeth. How the calibration of eruption rate to wear rate is brought about is unknown, but it is clearly a fundamental prerequisite to maintain a mammalian-type accurate occlusion despite constant wear.

The mechanism or mechanisms that bring about eruptive and other tooth movements are not well understood, but it seems that the main factor involved is traction provided by the periodontal ligament. The collagen fibres of the ligament (which attach the tooth to the alveolar bone) are constantly being degraded and re-synthesized by fibroblasts, and it is probable that the fibroblasts themselves provide the contractile force, even though so-called myofibroblasts have not actually been demonstrated from the periodontal ligament (Bhaskar 1980). Bone remodelling and cementum infilling are associated with eruption but are not its cause (Bhaskar 1980).

As soon as a tooth emerges through the gingiva it becomes subject to abrasive wear in the mouth, but significant wear begins only when it reaches contact with its antagonist. Since wear is cumulative, it may be used as a criterion of individual age, and a substantial part of wear studies have had this objective (e.g. Lundholm 1947, Miller 1974). A particularly fruitful application has been the analysis of the population dynamics of extinct mammals by this method, pioneered by Kurtén (1953). Another important area of research concerns the interpretation of wear facets in terms of occlusal movement and homologies (Butler 1952a,b, Mills 1955, and a prolific literature since, last reviewed by Kay & Hiemäc (1974) and Kay (1977)). A third topic in wear studies, which has emerged only recently, is the study of 'microwear' to

establish correlations between wear and diet (e.g. Walker et al. 1978, Rensberger 1978, Walker 1980, Gordon 1982, Teaford & Walker 1984). The potential of this method for paleoecological and evolutionary studies is yet to be realized, and it seems particularly important to take into account the (so far rather neglected) relationships between enamel structure and wear morphology in these studies. Finally, wear has been much discussed (but less studied) as a factor limiting potential longevity (Flower 1931, Huxley 1953, Kurtén 1953), and most discussions of hypsodonty contain this idea in implicit or explicit form (Van Valen 1960, Rensberger 1973). Nevertheless, the process of wear itself has received relatively little attention.

3.4.1. Wear processes

Kinds of wear

Under natural conditions the most wear-resistant tissue in the tooth is enamel. On a secondary occlusal surface enamel areas stand proud of dentin and cement, and form the main structural and functional features. Practically all studies of tooth wear have concentrated on the wear of enamel, and the present study is no exception. It should be made clear, however, that a proper understanding of how teeth wear must come from analysis of wear of the whole tooth, or indeed the whole dentition.

It has been customary to distinguish between two theoretical kinds of wear processes: wear caused by direct contact between teeth and wear caused by contact between teeth and food or other extraneous matter in the mouth. In the vernacular of dentistry these kinds of wear have been known as 'attrition' and 'abrasion', respectively (Butler 1972). These terms have been adopted by many paleontologists and paleo-anthropologists. According to Gordon (1982) attrition surfaces have been thought always to be striated and abrasion surfaces unstriated. Because all worn surfaces, at least on chimpanzee molars, are striated when studied at sufficient magnification (Gordon 1982), she suggested that the terms attrition and abrasion should be abolished as being too ambiguous. This issue requires some clarification.

It is a well known principle in engineering that 'like wears like', direct contact between parts of identical material tends to result in high friction and wear. This problem is avoided through the use of lubricants. Whether the principle applies to teeth is unknown, but it is certainly true that teeth rarely function without the presence of a 'lubricant' of food and saliva. However, just as the lubricant of a machine may eventually become a polishing slurry through inclusion of extraneous particles, so the mixture in the

mouth may have a whole range of wear properties. Rensberger (1978) argued that all striations must be due to extraneous material, since enamel fragments would not cause striae in enamel. This may not be literally true, since it is usually possible to scratch materials with materials of equal hardness (e.g. Putnam & Bassett 1971), but it may be true in the sense that larger enamel fragments are not dislocated as a result of 'normal' enamel-enamel contact events. Teaford & Walker (1983) found that the teeth of still-born guinea-pigs had worn occlusal surfaces without striae, which must mean that tooth-tooth wear (at least in guinea-pigs) dislocates only very small enamel elements, and that striae are indeed due to extraneous particles. That striae are found on all worn surfaces of teeth is evidence that they are all contacted by food, which is hardly surprising since the whole point of chewing is that there should be food between the teeth.

Nevertheless, there is still a useful dichotomy in the appearance of wear features, which to some extent corresponds to the traditional abrasion-attrition division. This is the criterion of whether or not the orientation of the worn surface is dictated by occlusal relationships; i.e., of whether or not a surface is formed in close interaction with one or several corresponding surfaces on the antagonist tooth. Surfaces dictated by occlusal relationships were distinguished as true facets by Rensberger (1978), and the word 'facet' has usually been employed in that sense (e.g. Butler 1952 et seq., Mills 1955 et seq., Kay & Hiiemäe 1974, Kay 1977). In this text I will follow Rensberger (1978) and distinguish between facets and other kinds of wear surfaces, recognizing that food is involved in most or perhaps all natural wear. That true attrition exists is, however, proved by the unborn guinea-pigs of Teaford & Walker (1983), and direct tooth-tooth contact as a prerequisite of comminution of tough foods is predicted by comminution theory (see above, Sect. 3.2.1.). A reasonable conclusion at the present stage of understanding seems to be that most dental wear results from abrasion, which may give rise to facets if it occurs between closely occluding surfaces, or non-facet wear if it does not. There seems to be no need to abandon the terms attrition and abrasion in this original sense. (It is unclear why morphological features should be more 'true' at one magnification than at another; satellite images are as real as scanning electron micrographs. If facets can be seen and defined at one magnification, then facets do exist.)

In abrasion, crucial factors are size and size distribution of the abrading particles, and loading (Gordon 1982). Large particle size and/or high load will produce large striations, while small particle size and/or low load will result in small striations. Walker et al. (1978) found that the striations in the molars of the grazing hyrax *Procavia johnstoni* had striations

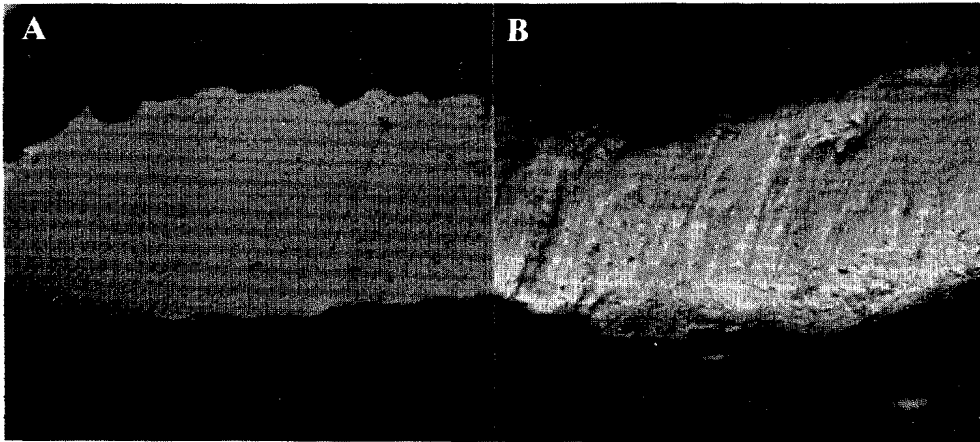


Fig. 17. Difference between wear morphology of lingual facets of browsing (A) and grazing (B) ruminants. A is *Alces alces* M² facet 6, MF private coll. B is *Oryx gazella* M² facet 5, GB 7541. Light micrographs of transparent epoxy replicas illuminated obliquely from below (App. 7.1). Field width of both images is approximately 3 mm.

considerably smaller than the cell-sized (10–20 μm) phytoliths which presumably caused them, and concluded that only parts of the phytoliths (edges or fragments) entered the surface. The very roughly striated enamel surfaces of many grazing bovids, equids, rhinocerotids and proboscideans, for example (Fig. 17B), may thus be produced by identical phytoliths under higher stress. It would be relatively simple to devise appropriate feeding experiments to test various hypotheses about the causes of striations (and wear in general), but the only one reported so far seems to be the controversial opossum experiment by Covert & Kay (1981) (see Gordon & Walker 1983, Kay & Covert 1983).

Enamel structure and wear resistance

Little attention has been paid to the wear of enamel in terms of its ultrastructure; i.e. to what is actually happening at the surface when it is 'worn'. Walker et al. (1978) showed that wear reveals the outlines of enamel prisms and dentine tubules in the browsing hyrax *Heterohyrax brucei*. In contrast, they found that wear does not bring out these structures in the grazing *Procavia johnstoni* except in the dry season when it has a diet similar to that of *H. brucei*. They interpreted the striated wear on wet season *P. johnstoni* teeth as caused by phytoliths, and suggested that cellulose and lignin are responsible for the 'polish' that brings out hard tissue structure in *H. brucei* and dry season *P. johnstoni*. Rensberger (1978) suggested that the structure of the underlying tissue was at least partly responsible for the appearance of 'furrows' on the worn enamel surfaces on the molars of the vole *Microtus*. Rensberger & von

Koenigswald (1980) showed that the transverse grooves and ridges on worn rhinoceros enamel correspond to zones of vertically decussating prisms, and a similar relationship has since been demonstrated for a number of extinct ungulate groups (Rensberger 1983, Fortelius 1984, see also this study Sect. 4.3.).

It now appears that all decussation is potentially capable of causing wear relief (Fortelius 1984), but the causal relationships are not entirely clear. Rensberger & von Koenigswald (1980) suggested that the angle between the 'abrasive vector' (the direction of force transmitted onto the tooth surface through the food) and the prism long axis is the crucial factor. According to their model, enamel resists wear most when the prisms are aligned parallel with the abrasive vector and least when they are transverse to it. However, Boyde & Fortelius (in press) found that wear resistance is strongest when prisms are intercepted transversely by the wear surface and weakest when they are parallel to it. The results are partly but not wholly contradictory (one refers to the direction of a force, the other to the orientation of a plane), and it appears that wear resistance may depend on structure at several levels.

Hardness must be an important factor in determining wear resistance, and it is a reasonable assumption that the hardness of mineralogically identical enamels is a function of density; i.e. closeness of packing of the apatite crystals. This hypothesis seems to be borne out by the relatively greater wear resistance of non-prismatic surface enamel compared with that of the prismatic enamel underneath (Karlström 1931). Sufficiently mild mechanical etching reveals the outlines of enamel prisms by remov-

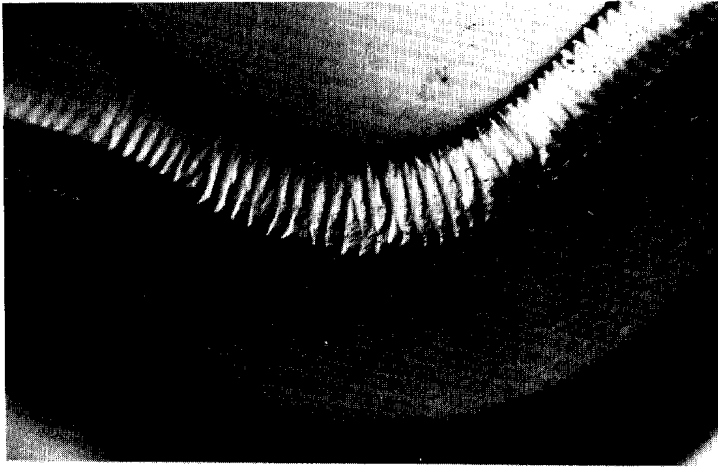


Fig. 18. Difference in wear properties between outer (non-decussating) and inner (decussating) enamel on buccal edge (hypoconid, facets 3 and 4) of *Rhinoceros sondaicus* second lower molar (KO 29). Alternate zones (HSB's) in the inner enamel are less resistant than their neighbours and the outer enamel, and consequently show up as furrows. The relief extends down onto the facets, but is best developed on top, where no direct occlusal contact occurs. Note low relief on phase II facet 10 in upper left corner. Light micrograph of transparent epoxy replica (App. 7.1). Field width approx. 11 mm.

ing material preferentially from the prism boundary discontinuity, which is less dense than the rest of the tissue (Boyde & Fortelius in press). This explains the hyrax results of Walker et al. (1978) related above.

A factor that must affect density is decussation, since prisms which cross each other at angles can not be as closely packed as prisms which are parallel. At least in rhinoceroses the outer, little-decussating enamel is indeed more wear-resistant than the inner, strongly decussating enamel (Fig. 18). On the other hand, cracks might be propagated for long distances along prism boundary planes in non-decussating enamel, resulting in the loss of major portions of enamel. The combination of decussating and non-decussating enamels may be a compromise between the requirements of hardness and resistance to crack propagation. That the outer enamel is harder also means that sharp blades develop because the inner enamel wears more rapidly, leaving an outer, projecting edge.

Given equal density, it is clear that resistance depends on prism orientation, or perhaps more accurately, crystal orientation. The exact relationship depends to some extent on the wear (or etching) regime, but low-energy mechanical processes usually result in a relief where less material is removed from transversely sectioned prisms than from longitudinally sectioned prisms (Boyde & Fortelius in press). It is likely that this reflects the simple fact that transversely intercepted crystallites are bounded on all sides by neighbours and present only a small area at the surface, whereas longitudinally intercepted crystals expose a large surface and are only shallowly 'anchored' between neighbours. Neither on experimentally polished surfaces nor on naturally worn teeth did we detect any sign of systematic removal of whole prisms or groups of prisms (see also Fig. 20). Since all wear is cumulative, worn surfaces reflect a mean

orientation property of the crystals that were removed, rather than the orientation of those that are exposed at any single moment (Boyde & Fortelius in press). This must be taken into account when surfaces are interpreted.

An interesting corollary of the above concerns the relative wear resistance of upper and lower teeth. Prisms usually have a net inclination towards occlusal, which means that on lower teeth buccally dipping buccal facets and lingually dipping lingual facets will tend to have prisms sectioned transversely, while the corresponding facets on upper teeth will tend to have longitudinally sectioned prisms (Fig. 19). In other words, when the movement during the phases of the power stroke has a dis-

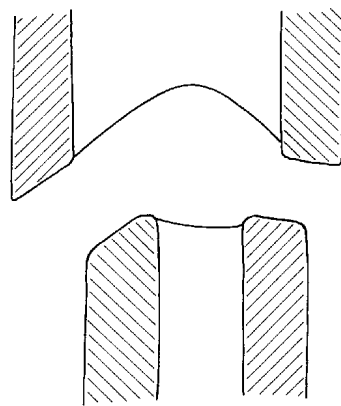


Fig. 19. Sketch showing different angle of interception of occlusally inclined enamel prisms in upper and lower teeth. The transversely intercepted prisms of the lower teeth may make these relatively more wear resistant, as discussed in text.

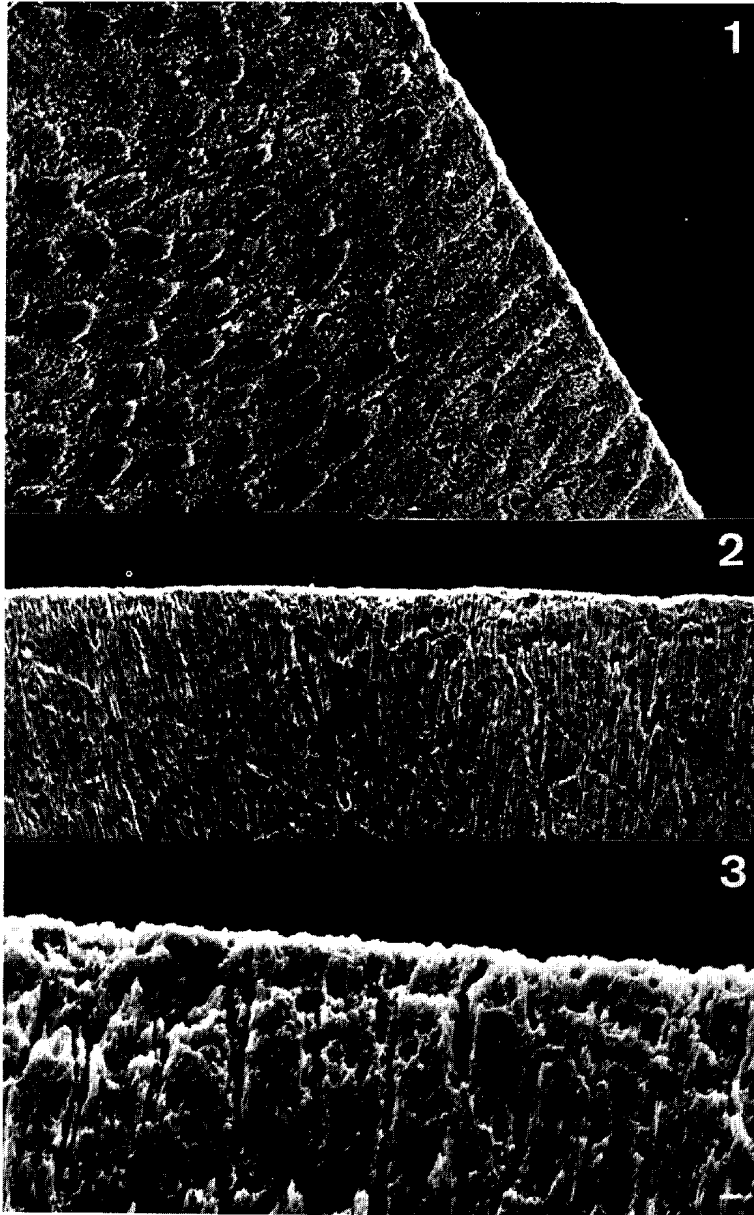


Fig. 20. Transversely sectioned natural wear facets (facets extend away from plane of page), showing prisms reaching all the way out to facet surface. Polished and H_3PO_4 etched. SEM (SE) images. – 1: *Anchitherium aurelianense* (Equidae, Miocene) upper molar buccal phase I facet (specimen gift from Dr. Susanne Abusch-Siewert), field width 40 μm . – 2 & 3: *Dicerorhinus* sp. (Rhinocerotidae, Pleistocene) lower molar buccal phase I facet 4 (tooth from Shansi, China, gift from Dr. Ann Forstén), field widths: 2 300 μm , 3 62 μm .

tinct plunge, both phase I and phase II facets will tend to be more wear resistant on lower rather than on upper teeth. This is particularly the case in trilophodonts, in which the upper teeth are considerably larger than the lower teeth, and probably explains why the lower teeth in these forms are not finished in advance of the uppers.

3.4.2. Wear of the dentition as a whole

Eruption gradients and wear gradients

Mammals, before reaching adult morphology must live through a period of postnatal growth during which most of what they have to chew is solid food. This is one reason why mammals have milk teeth; there is not sufficient space in the relatively minute jaws of the neonate for full-sized teeth to develop (Hunter 1839). This is reflected in the eruption pattern, which varies between groups but is similar in principle. The rhinoceroses for example usually have the sequence (dm2dm3)dm4M1M2(P2P3)P4M3, with the lower teeth erupting slightly in advance of their upper serial homologues. (This sequence is based on observation of large numbers of fossil and recent rhinoceros dentitions; parentheses signify more or less simultaneous eruption; the eruption of dm1, when present, varies.) From dm2 to M2 the erupting teeth form a series of increasing size, followed by the replacement of the brachyodont milkteeth by more hypsodont premolars (which have had space to grow in the now much deeper and wider jaws), and, finally, at adult or near-adult size, M3 erupts.

The milk molars are usually quite worn down by the time they are replaced, and a wear gradient corresponding to the eruption sequence is evident. Wear gradients are also characteristic of the permanent dentition, and are used in ageing specimens (Laws 1968, Miller 1974). It is a curious phenomenon that such gradients become less steep (i.e., the differences in amount of tooth left become less pronounced) as wear proceeds, indicating that the teeth which were initially higher are wearing at a faster rate (Lundholm 1947, Kurtén 1953, Forstén 1968, Laws 1968, Miller 1974). Forstén (1968) found a positive correlation between the initial height of the tooth and its rate of wear in *Hipparion*, but did not offer any explanation. Laws (1968) demonstrated the same for tooth weight and rate of wear in *Hipopotamus*. Kurtén (1983) suggested that wear is initially more rapid as the cusp tips are worn down, and then slows down as a larger occlusal area is exposed. While this may well apply to the bovids in question, it cannot explain the situation in *Hipparion*, the teeth of which reach their full occlusal dimensions very quickly. Another explanation, which again is not applicable to *Hipparion* but perhaps to other forms,

is that the teeth may be worn down below the 'plane of contact' as determined by the dentition as a whole, and so escape attrition. It is in fact quite common to see first molars which lie below the plane of P4 and M2, and which do not show facet wear, for example in pigs and tapirs. The only explanation which seems to account for differential wear rates of individual teeth in full occlusion, however, is differential eruption pressure. If the teeth that erupt later are pushing harder into occlusion, they will be more loaded and presumably wear faster. The correlation between initial height and wear rate observed by Forstén (1968) suggests a possible mechanism, as pointed out to me by Alan Boyde (pers. comm. 1983): the force at which the tooth is pushing out of its alveolus may be a more or less linear function of the number of fibroblasts in the periodontal ligament, which in turn may be a more or less linear function of alveolar interface area. If the above holds, eruption pressure might be a simple function of unerupted area (properly the total unerupted area of antagonists), and this 'alveolar area hypothesis' seems to account for the phenomena observed.

In an ideal case of cheek teeth shaped as identical prisms except for differences in 'height' (the zone axis dimension), the areas will scale as the heights. It is obvious upon reflection that if such teeth are worn in increments proportional to their alveolar height, they will all end up equally high when fully erupted. This is not far from the situation found by Forstén (1968, fig. 37), since the differences in horizontal dimensions between P3, P4, M1 and M2 in *Hipparion* are relatively minor.

A prediction of the alveolar area hypothesis is that if a tooth is asymmetric in such a way that one side offers a larger surface for fibroblast attachment within the alveolus, then that side should erupt faster. Such is indeed the case in, for example, rhinoceroses (Fortelius 1981) and certain late Tertiary lagomorphs (Tobien 1978). The upper teeth have much larger buccal than lingual surfaces, and they erupt turning towards lingual along the axis of the tooth row. Wear is also faster buccally, so that the orientation of the buccal facets is maintained more or less constant. To what extent the shape of the alveolus itself influences such asymmetric eruption is unknown.

That several factors are potentially involved in the determination of wear gradients was recognized by Teaford (1982), who listed dental structure, eruption timing and behaviour as relevant. He demonstrated differences in wear gradients from dm₂ to M₁ between the langur *Presbytis cristatus* and the macaque *Macaca fascicularis*, and attributed these primarily to differences in diet. Gordon (1982) found that several wear features varied along the molar row in *Pan*. Thus striation length and frequency decreased from anterior to posterior, while the diameter and frequency of pits decreased in the opposite direction,

from posterior to anterior. She proposed an explanation in terms of the amount of relative movement of occluding surfaces and the stress involved, with pits and striations of different size and shape reflecting a continuum defined by these two factors. In her model the mandible is rotated about the working side condyle, but regardless of where the fulcrum is situated (as long as it is at either joint, or between them) it will be true that the length of the arc traversed by a lower tooth will decrease towards posterior. This simple mechanical circumstance explains why striations are longer on the more anterior molars (Gordon 1982), and, if pits are considered as extremely short striations, why these increase in frequency towards posterior. To explain the increase in pit diameter towards posterior, Gordon suggested that load increases in this direction and cited evidence from human experiments as support.

It is probable that similar conditions of gradual change in wear processes are common among mammals, and furthermore it is likely that this affects relative wear rates. Thus the wear of the dentition is a complex process involving both static and dynamic factors. It is interesting, too, that Gordon (1982) found no change with position in the buccal phase I facets. Perhaps this indicates that the arc of total movement is sufficiently much wider than the extension of these facets so that the increase in arc width from posterior to anterior does not affect wear patterns. This would be even more so in ungulates with their strong lateral component to chewing.

Coordination of wear

The existence of wear gradients means that even when all the cheek teeth are very similar to each other, different occlusal morphologies must be present (Fig. 22). Quantitative data on this do not seem to exist, and are rather difficult to obtain; however, a qualitative study is also illustrative.

I noted the wear stage for a sample of complete *Diceros bicornis* skulls. The result is shown in Fig. 21. One observes how, with the exception of very late stages of wear, both much worn and little worn teeth are present at all times. This aspect of occlusal morphology is frequently overlooked through attempts to 'eliminate the effects of wear' by concentrating on single, usually early wear stages. Yet it is these teeth at various stages of wear that actually serve to comminute the food, and it is unreasonable to suppose that any one wear stage would fully express this overall morphology.

In an attempt to quantify morphological change with wear I measured a number of occlusal parameters on isolated upper molars of '*Dicerorhinus*' *etruscus* from the Galerian (Pleistocene) of Europe (Mauer, Mosbach), and plotted them against crown

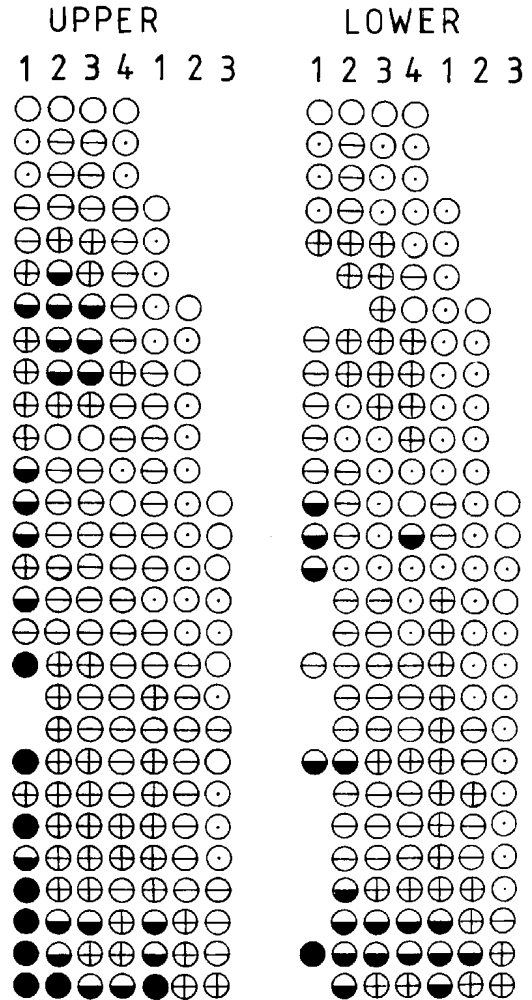


Fig. 21. *Diceros bicornis*, wear of upper and lower tooth-rows. Wear stages are arbitrary and determined by easily recognizable changes in occlusal morphology. Neither the stages of different teeth in the row nor those of upper and lower teeth correspond exactly.

Upper teeth: 1 (empty): no wear facets. - 2 (dotted): posterior aspect of metacone unworn (facet 2 absent). - 3 (split): facet 2 present, postfossette open (see Fig. 25). - 4 (crossed): postfossette closed, antero-lingual cingulum at least partly unworn. - 5 (half black): antero-lingual cingulum entirely in wear or gone, occlusal morphology regular. - 6 (black): enamel discontinuous, occlusal morphology irregular.

Lower teeth: 1 (empty): no wear facets. - 2 (dotted): trigonid and talonid form separate crescents occlusally. - 3 (split): trigonid and talonid are occlusally confluent, but a trigonid basin (Fig. 24) is present. - 4 (crossed): trigonid basin absent, talonid basin (Fig. 24) present. - 5 (half black): talonid basin absent, occlusal morphology regular. - 6 (black): enamel discontinuous, occlusal morphology irregular.

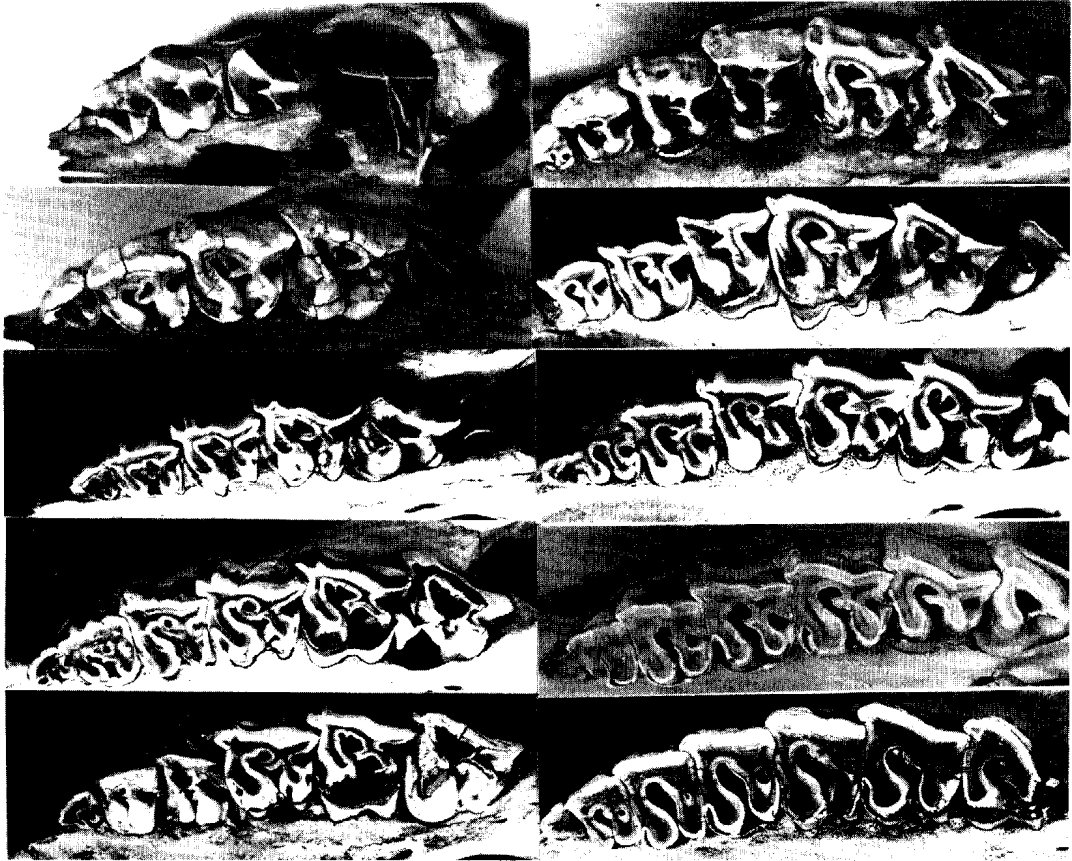


Fig. 22. *Diceros bicornis*, upper toothrow in different stages of eruption and wear. Note nearly simultaneous eruption of deciduous molars, their replacement and the gradual eruption of molars. Teeth in different stages of wear are present almost throughout. See also Fig. 21 and discussion in text. Dentitions shown are from TE and LE (App. 2).

height (Fortelius 1985). Most parameters turned out to change more or less linearly with wear; protoloph length, for example, increased throughout. A notable exception was ectoloph length, which was relatively stable for most of the wear process. The initial 'wearing in' is reflected as a rapid increase in length, while the subsequent gradual wearing down of the tooth results in a slow decrease because the tooth is shorter nearer the base. Finally, completely worn-down teeth quickly lose their enamel edges, the ectoloph among them. One may hypothesize that such stable dimensions reflect structures of major functional importance. As far as the ectoloph edge is concerned, this agrees with what is known from investigations of muscular activity and wear patterns: most of the cutting occurs at the buccal phase I facets.

If the whole molar battery is considered, the pattern becomes even more compelling since the decrease in length is compensated for by a corresponding increase in the length of M^3 , which has a different

shape, longer towards the base. Total ectoloph length of the molar row is thus constant throughout (Fortelius 1985).

Control of wear in single teeth is, at least in lophodonts like rhinoceroses, achieved to some extent through unequal wear resistance due to unequal enamel thickness in different parts of the crown (Fortelius 1982). The concave secondary shape of ectolophodont upper teeth, which allows two-phase morphology in combination with hypsodonty, is due to the very thin enamel that lines the medial portions of the crown, particularly the mediofossette. In plagiolophodont forms, like in *Ceratotherium simum*, the medial enamel is correspondingly thicker. The occlusal surfaces tend to become flatter with wear and it is also the case that the medial enamel is thicker towards the base of the crown (Fortelius 1982).

One might think that upper and lower teeth must wear at the same rate, but this is not necessarily so.

Korvenkontio (1934) noted that the lower incisors wear more rapidly than the upper incisors in rodents and lagomorphs, with wear of the uppers proceeding at some 65–70 % of the rate of the lowers. In this case the unequal wear rates are compensated for by unequal eruption rates (Korvenkontio 1934), but when teeth have a finite height the problem is more acute because upper and lower teeth should be optimally designed so that one is not finished in advance of the other. Evidence that they are so designed is that one rarely sees old individuals in which one set is much more worn than the other. This is all the more intriguing since lower teeth are usually smaller than the uppers. A suggestion as to why lower teeth should be more resistant to wear was given in Sect. 3.4.1., but more and better data are needed. Advances in the understanding of wear coordination might help to resolve problems related to wear in general and its role in dental evolution.

3.4.3. Hypsodonty and wear

Flower (1931) thought that dental durability controls potential longevity in mammals but did not provide data in support of this hypothesis except for a rather casual discussion of captive elephants based on Pocock (1917). While most zoologists would probably agree that a wild herbivore will necessarily die once its teeth are wholly worn down, few would probably now go as far as seeing dental wear as the main factor controlling actual longevity. But main determinant or not, teeth do not appear to be excessively lasting as a rule, and a hypothetical shift to a more wear-inducing (e.g. more abrasive, tougher, less nutritious) diet might easily make dental wear a major problem even in individuals of reproductive age. It is interesting that Laws (1968) found that 'mechanical senescence' is a major cause of mortality of *Hippopotamus amphibius* at ages above 30 years. The hippo is rather brachydont for a grazer, and is a relatively recent derivative of, presumably, non-grazing ancestors. The oldest known hippopotamids are of late Miocene age (Thenius 1969).

The above is the scenario underlying the now almost universal view of hypsodonty as an evolutionary response to increased dental wear (e.g. Van Valen 1960, Romer 1970; a rather lonesome dissenter was White 1959). It contrasts to some extent with the notion of continuous increase in hypsodonty through time, which is frequently found in the older literature (e.g. Boule & Piveteau 1935, see also Osborn 1918). The two versions lead to different predictions, which allows testing between them, should the need arise. If one assumes that dental wear is always a real limiting factor (and that continuous increase in hypsodonty is the rule), then more hypsodont animals should live longer than less hypsodont

Table 1. Tooth height and wear rate in various ungulates. — IH = initial (unworn) height (mm), AW = mean annual wear (mm), MPL = $IH/AW + 1$, maximum potential life span (years) (one year added for milk dentition).

Species	Tooth	IH	AW	MPL	Source
<i>Merychippus primus</i>	M ¹	23	2.3	11	1
<i>M. cf. perditus</i>	M ¹	c.40	3.3	13	1
<i>Pseudhipparion retrusum</i>	M ¹	45	4.1	12	1
<i>Neohipparion cf. leptode</i>	M ¹	50	4.2	13	1
<i>Hipparion</i> spp.	M ¹ , M ²	53	5.1	11	2
<i>Equus burchelli</i> ♂♂	M ¹	73	3.3	24	1
<i>E. caballus</i> (domestic)	?	?	2.6	?	3
<i>Urmitherium intermedium</i>	M ²	38	5.1	9	4
<i>Plesiaddax depereti</i>	M ²	35	4.6	9	4
<i>Pachytragus solignaci</i>	M ₂	20	1.9	11	5
<i>Rangifer tarandus</i>	M ₂	10	0.7	15	6

Sources:

1. Hulbert 1982, 2. Forstén 1968 (IH estimated from fig. 37, AW from table 24), 3. Lundholm 1947, 4. Kurtén 1953 (IH and AW estimated from fig. 21), 5. Kurtén 1983 (IH and AW estimated from fig. 4), 6. Miller 1974 (IH and AW estimated from fig. 13).

ones. If dental wear is not normally limiting, there should be no correlation between hypsodonty and longevity. The situation is compounded by the influences of diet and body size, but on the whole the available data suggest no correlation between hypsodonty and longevity (see Table 1). In particular, hypselodont mammals do not seem to live any longer than their relatives with finite tooth heights. Of the rodents for which maximum lifespan in captivity was given by Eisenberg (1981), the 15 species with rooted molars have a mean of 104 months (*SD* 65.2), while the 13 species with rootless molars have a mean of 99.5 months (*SD* 59.6). Note, however, that wear is slower in the domestic horse than in *Equus burchelli*, presumably because of less wear-inducing food. A similar situation was noted for *Rupicapra rupicapra* by Kurtén (1953), who interpreted it as a result of a shift from grazing to browsing on soft mountain herbage.

While many instances of increase in hypsodonty through time are known, examples of decrease seem to be lacking. This suggests that teeth are not energetically 'expensive', since reduction would otherwise be expected when hypsodonty no longer adds to fitness.

Van Valen (1960) provided a brief but influential discussion of hypsodonty and designed an index for comparison of taxa. This 'functional' index considers not only crown height but also area and specific wear resistance of the exposed enamel surface and absolute body size. Thus not the height of the tooth, but

its ability (or that of the whole dentition) to tolerate wear is what is important in this functional sense. Recently Webb (1983), while curiously misquoting Van Valen (1960) as having established the traditional index of hypsodonty relating vertical to horizontal dimensions, made much the same point. According to Webb, tooth volume (specifically, the volume of the largest lower molar) should be used in comparing species in terms of their adaptations to wear-inducing foods. This has the advantage over Van Valen's index of being relatively easy to measure, but it is also less general and theoretically less satisfactory. Van Valen's index (which must be called prophetic in its inclusion of tissue-specific wear resistance) is discussed in Sect. 4.1.2.; it is sufficient here to note that he considered hypsodont dental design solely from the point of view of wear resistance.

Rensberger (1975), on the basis of computer simulation of wear, suggested that control of the occlusal morphology under heavy wear is an important factor in the functional design of hypsodont cheek teeth of geomyoid rodents. I have previously noted (Fortelius 1981) that a general increase in hypsodonty is often accompanied by a simplification of the occlusal morphology, and that the very unspecific function of general durability (wear tolerance; i.e. maintenance of occlusal shape in spite of wear and wear resistance as such) of the teeth may have quite different biological correlates. This is particularly well illustrated by the rhinoceroses. Increased hypsodonty is a common trend, but most lineages preserve the concave ectolophodont shape of the upper molars. Only in a few cases (*Ceratotherium*, *Coelodonta*, *Elasmotherium*) is a flattened (plagiolophodont) occlusal surface developed (Osborn 1903, Dietrich 1942, Fortelius 1981, 1982).

Plagiolophodont teeth are found in extant grazing hindgut fermenting ungulates (*Equus*, *Ceratotherium*), and seem designed for cutting large quantities of not very bulky food (see Sect. 3.2.1.). All hypsodont teeth are not plagiolophodont, but (with the exception of milk teeth) all plagiolophodont teeth seem to be hypsodont, and most probably represent the same grazing specialization. In contrast, selenodont teeth have much the same occlusal morphology irrespective of whether they are hypsodont or brachydont. This probably reflects the mechanical levelling effects of rumination, as discussed in Section 3.2.2. The one thing that is not affected by rumination is the abrasiveness due to inclusion of inorganic 'grit' in the food, and the gradient in crown height in ruminants probably reflects the degree of such abrasiveness of the food. Grass is known to be very abrasive because of its phytoliths, and it is these simple relationships that have led to the common misconception that hypsodonty necessarily implies grazing.

Theoretically, hypsodonty may reflect several factors, singly or in combinations. An important one is

abrasiveness, either through included phytoliths or contamination with 'earth', but foods that are in themselves unabrasive may cause much wear if their comminution requires high occlusal stress. These two factors probably cause recognizably different kinds of wear, with high stress tending to increase and high abrasiveness to decrease the distinctness of facets. Other factors may be less easily recognized, such as heavy wear due to the mastication of large quantities of low grade food. The same is true of increased food processing due to increased energy demands (for example from longer life span, or increased locomotor activity). It is perhaps sufficient here to conclude that no simple model need apply to all cases of increased crown height (or volume or wear resistance).

3.4.4. Occlusion and wear

Even when the functional morphology is largely primary it is affected by wear, and the functional interpretation of occlusal surfaces is usually based on wear facets. The evolution of primary dental morphology is also best understood in relation to occlusion and wear (Butler 1952a, 1952b).

In therian mammals the primitive condition is that the trigonid of the lower molar fits into the embrasure between two upper molars, while the talonid bites against the lingual protocone. In ungulates, primates and rodents, the system is modified by independent addition of a hypocone to bite against the trigonid. This is the origin of the regular occlusion in ungulates, where the posterior half of a lower tooth occludes with the midpart of its upper homologue, while the anterior half of a lower tooth occludes with the anterior quarter of its upper homologue and the posterior quarter of the preceding tooth (Fig. 2).

For a general description of occlusal relationships in ungulates it is very convenient to use the two couplets 'trigonid-talonid' and 'amphicylix-mesocylix' (Butler 1952a). The phase I facets dip towards buccal and line the buccal circumference of the talonid and trigonid, and the lingual circumference of the cylices. The phase II facets dip towards lingual and are on the dorsal and lingual portions of the buccal cusps of the trigonid and talonid, and on the ventral and buccal sides of the lingual cusps of the cylices (Fig. 2). Various modifications occur, but most occlusal surfaces can be understood with reference to this 'archetype' of occlusal relationships.

At least in rhinoceroses the mode of eruption appears to be designed to bring about this type of occlusion. The lower teeth which are to fit 'inside' the cylices erupt a distinct inclination towards lingual, while the upper teeth have a corresponding inclination towards buccal. The teeth are thus 'worn in' in a position that ensures correct occlusal relationships.

By the time that eruption is completed the teeth have aligned themselves with their neighbours, and occlusion is entirely between secondary surfaces.

It is important to realize that individual facets change their orientation as wear proceeds, and some are confined to a particular wear stage. If the tooth becomes very worn, often all facets disappear and only rounded, non-facet wear surfaces remain. The lingual phase I facets 5 and 6, for example, can only exist as long as the cusps on which they are situated retain their individuality. In many hypsodont forms this is not for very long, and consequently they disappear at an early stage. Similarly, the lingual part of the facet 1a that primitively extends along the posterior margin of the amphicylix (lingually from the paracone along the anterior margin of the protoloph) can exist only as long as the posterior margin of the trigonid which produces it rises above the level of the talonid. In rhinoceroses this is only during early stages of wear, and one notes how it is gradually replaced from lingual by the facet 1b, which dips much less steeply towards anterior. Similar examples could be added, but this suffices to illustrate the principle. A well-worn rhinoceros tooth retains the confluent facets 1+2 and 3+4 (without a distinct difference between a and b), but no other facets (Fig. 21). On both upper and lower teeth, the lingual parts of the teeth have only rounded, non-facet surfaces, and facets 5-10 are lost.

In principle this has nothing to do with the direction and dynamics of chewing, since the first molars reach this stage while the last molars still retain a and b facets of phase I as well as phase II facets. But phylogenetically such a change is clearly what led to the development of the flat-surfaced teeth of hypsodont lophodont forms, in which the occlusal surfaces define a single direction of movement plunging gently towards dorsal. In terms of muscular activity the question of which phase of movement these surfaces reflect thus becomes almost meaningless because they represent both, superimposed on one another. Recall that such single-phase surfaces also allow more overlap of muscular activity, and overlap of the phases in that sense. However, in terms of surface morphology one could argue that plagiolophodont and selenodont ungulates have emphasized Butler's (1952a) Stage 2 (Phase 1b of Kay & Hiiemäe 1974?); i.e., the near-horizontal surfaces that correspond to the movement with least plunge in the middle of the power stroke.

Gordon (1982) showed that microwear was systematically different between the buccal ('shearing') phase I facets and the phase II ('crushing/grinding') facets on chimpanzee molars, with striations relatively more frequent on the former and pits on the latter. She reported no systematic change with age, but remarked on the fact that facets may be composed of several subfacets at some stages. It is clear, however, that age (wear)-related differences must

exist in chimpanzees, at least in that dentine areas become exposed and increase in size, obliterating facets that existed on the original covering enamel (see also Teaford 1982). No comparable data exist for ungulates, and it is probable that these relationships vary with the type of occlusal morphology. Gordon's finding that the buccal phase I facets were the only ones which were not different along an anteroposterior gradient might suggest that surfaces dominated by translation ('shear') tend to be functionally uniform.

Breakage is a function of stress and stress is a function of the component of load normal to the plane of contact. The buccal facets 1-4 dip in pairs towards anterobuccal and posterobuccal, which results in an enlarged occlusal area in different planes not simultaneously normal to the masticatory force vector sum. The more these facets depart from such normality, the lower will be the stress for a given load and the longer the blades for a given size of tooth. One may visualize this functionally as a situation where the demands of selection (blade length) and breakage (normality of surface) are in conflict and some degree of compromise is effected. Kay & Hiiemäe (1974) suggested that forces separating one set of blades (e.g. facets 1 and 4) would force the other together (in this case 2 and 3), so that "muscular force required to maintain overall contact is ... minimized" (p. 230). It is doubtful whether such can be the case. If food is present only between one set of facets, no gain in breakage results from forcing the empty set together, and if food is present between both sets the forces simply cancel each other out.

To understand the functional implications of facets one must determine the direction of occlusal movement. For general descriptive purposes it is useful to distinguish between facet relief parallel to and facet relief perpendicular to the direction of movement. The former increases contact area at the expense of stress and determines the orientation of movement, while the latter defines plunge and allows reconstruction of phases of movement during the power stroke. Very steeply dipping facets tend to be a feature of largely primary dental morphology (e.g. in tapirs), and relief in both directions decreases with an increasing dominance of secondary morphology. When relief parallel to the direction of movement is sectioned by a near-occlusal plane, it is converted into the familiar pattern of oppositely curved cutting edges that characterizes flat-surfaced dentitions. This configuration results in a small area of momentary contact and correspondingly high stress per unit load (Rensberger 1973) and a continuous, smooth occlusal contact (von Koenigswald 1980), but it clearly did not arise through natural selection for these functions. It is a pattern inherited from ancestors with high occlusal relief parallel to the direction of the power stroke, and at least in equids it is actually replaced by more linear cutting edges in the

course of evolution (Rensberger et al. 1984). For cutting purposes, a condition where linear blades are slightly inclined to each other (as in elephants; Maglio 1972) is probably advantageous compared with that of reciprocally curved blades. The latter arrangement necessarily results in some blades meeting almost along the direction of movement (Fig. 23) and perhaps also results in uneven wear due to concentration of food in areas where they meet transversely. On the other hand, curved blades would trap food better. As in many other respects, functional demands are in conflict with each other.

The homologous facets of different teeth do not make contact simultaneously. In laterally chewing ungulates such as rhinos (and in chimpanzees; Gordon 1982), the movement of the lower tooththrow during the power stroke defines a sector that is widest anteriorly. Greaves (1980) has suggested that the fulcrum of the mandible is between the two joints in ungulates, and manipulation of dry rhinoceros skulls suggests that the mandible is rotated about the balancing side post-glenoid process during the power stroke (Fig. 25). (However, Prof. Percy M. Butler (pers. comm. 1985) informs me that in a wet skull of *Diceros bicornis* the center of rotation was clearly between the condyles, and this is probably the true situation.) The posterior teeth occlude in advance of the anterior ones, which explains the initially perplexing fact that the buccal facets dip less steeply on the anterior teeth. The reason is that the anterior teeth occlude during a later stage of the power stroke, which by then plunges less steeply. Repeated manipulation of a skull of *Dicerorhinus sumatrensis* with moderately worn teeth (Fig. 24) gave the following sequence of occlusal contacts:

Phase I. Trigonid M_3 with amphicylix M^2M^3 , trigonid M_2 with amphicylix M^1M^2 , trigonid M_1 with amphicylix P^4M^1 , talonid M_1 with mesocylix M^1 , talonid M_2 with mesocylix M^2 , talonid M_3 with mesocylix M^3 , talonid P_4 with mesocylix P^4 , trigonid P_4 with amphicylix P^3P^4 , talonid P_3 with mesocylix P^3 , trigonid P_3 with amphicylix P^2P^3 , talonid P_2 with mesocylix P^2 , trigonid P_2 with the anterior part (essentially paracone) of P^2 .

Here the teeth appear to rest in a position that one might equate with 'centric occlusion'. At this stage occlusion is as follows: P_2 protoconid with P_2 paracone, P_2 hypoconid with the mediofossette of P^2 , P^3 trigonid with P^2 postfossette, P_3 talonid with the crochet of P^3 , P_4 trigonid with P^3 postfossette, M_1 talonid with M^1 crochet and protocone, M_2 trigonid with M^1 postfossette, M_2 talonid with M^2 protocone, M_3 trigonid with M^2 hypocone, M_3 talonid with M^3 protocone.

Phase II. Everything to the anterior of protoconid M_2 and hypocone M^1 loses contact. The protoconid of M_2 glides over the postfossette of M^1 and then

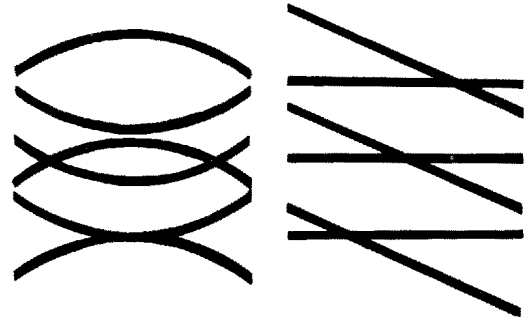


Fig. 23. Reciprocally curved blades (A) and straight, inclined blades (B). See text.

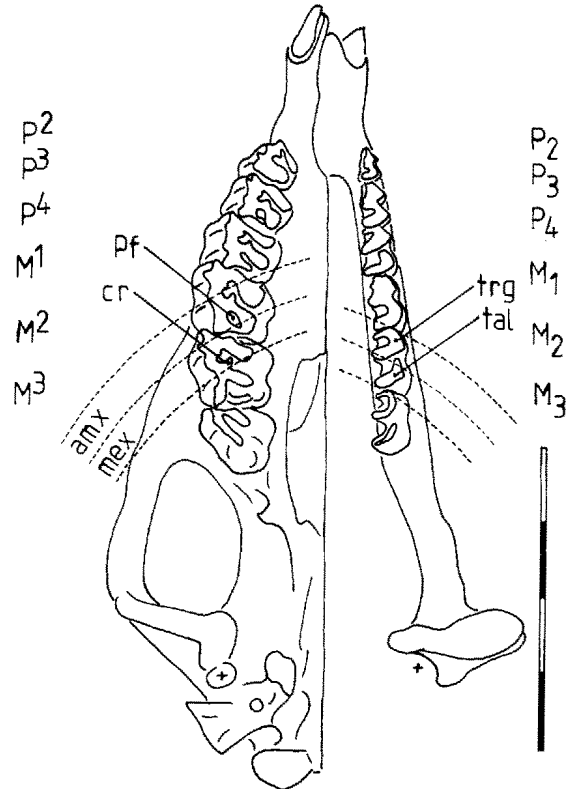


Fig. 24. Occlusal relationships in a skull of *Dicerorhinus sumatrensis* (CA H. 6383), as discussed in text. The apparent non-correspondence is an artefact of perspective. Drawn from photographs, one segment on scale bar = 5 cm. - Abbreviations: amx = amphicylix, cr = crochet, mex = mesocylix, pf = postfossette, tal = talonid, trg = trigonid. (Note lost trigonid basin on M_1 , which is thus in wear stage 4).

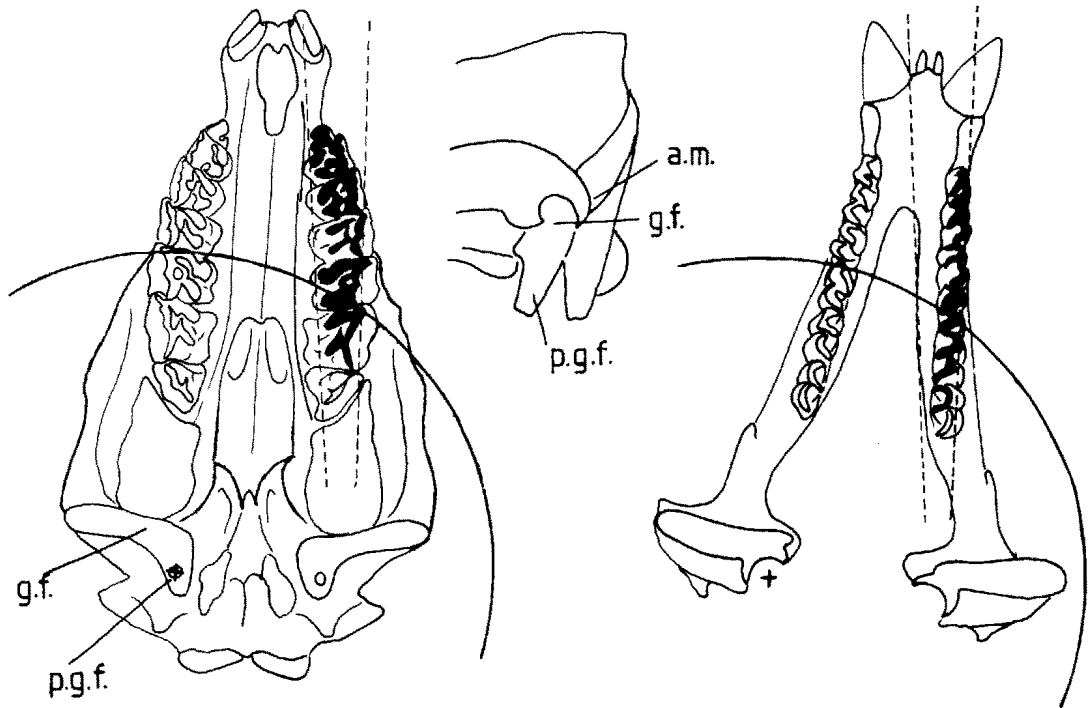


Fig. 25. Rotation of the mandible about the contralateral postglenoid process in a skull of *Rhinoceros unicornis* (UZ unnumbered). Occlusal surfaces on working side are shown in black, and the 'occlusal sector' of the upper toothrow is marked by broken lines. Sectors of circles with centres at the fulcrum indicate the path of travel and its extension in both directions. Between skull and mandible is shown a lateral view of the occipital region. - Abbreviations: a.m. = auditory meatus, g.f. = glenoid fossa, p.g.p. = postglenoid process. Drawn from photographs, mandible reversed.

loses contact. The hypoconid of M_2 reaches passing facet 10 contact with the hypocone of M^2 . The last phase II contact is facet 9 between the hypoconid of M_3 and the protocone of M^3 .

The above illustrates how the anterior teeth are the last to reach and the first to lose occlusal contact during the power stroke, which corresponds to their role as puncture-crushing rather than chewing or-

gans. It also supports the idea that in forms with partly molarized premolars a relatively smooth anteroposterior gradient from puncture-crushing to chewing exists, involving perhaps gradual transport of food from front to back during mastication. Note also how small and restricted the phase II facets are in rhinoceroses; it is difficult to believe that they have any crucial role in food comminution.

4. Patterns

4.1. Tooth size and body size

4.1.1. Introduction: allometry

Pilbeam & Gould (1974) and Gould (1975) proposed that postcanine occlusal area in mammals should scale to the metabolic requirements of the animal according to 'Kleiber's Law', i.e., as body

mass to the exponent $3/4$ (Kleiber 1947). Since for objects of the same shape and density area scales to mass at the exponent $2/3$, the 'metabolic' scaling proposed by Pilbeam & Gould represents positive allometry of tooth size to body size. However, they were only able to document significantly positive allometry of tooth size to body size in a single case: the