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Ungulate cheek teeth: developmental, functional, and evolutionary interrelations

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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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Contents

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 misunderstadings 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 (preformed 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

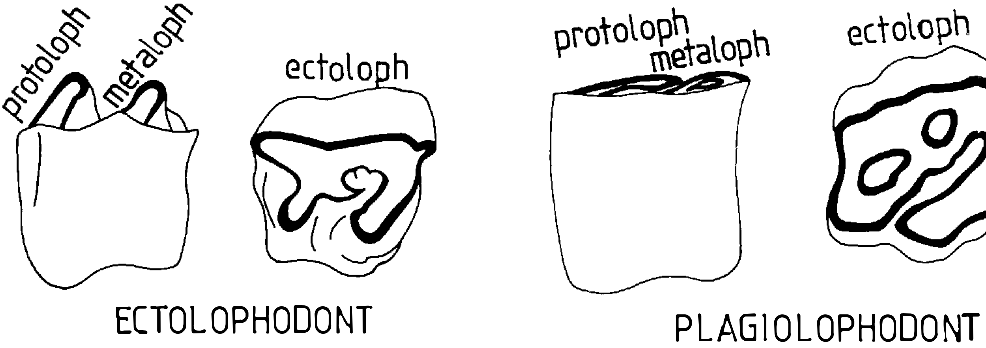

Fig. 1. Ectolophodont (*Diceros bicornis*) and plagiolophodont (*Ceratotherium simum*) upper molars. Adapted from Fortelius 1981.

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 direect 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 seleno-lophodont. 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).

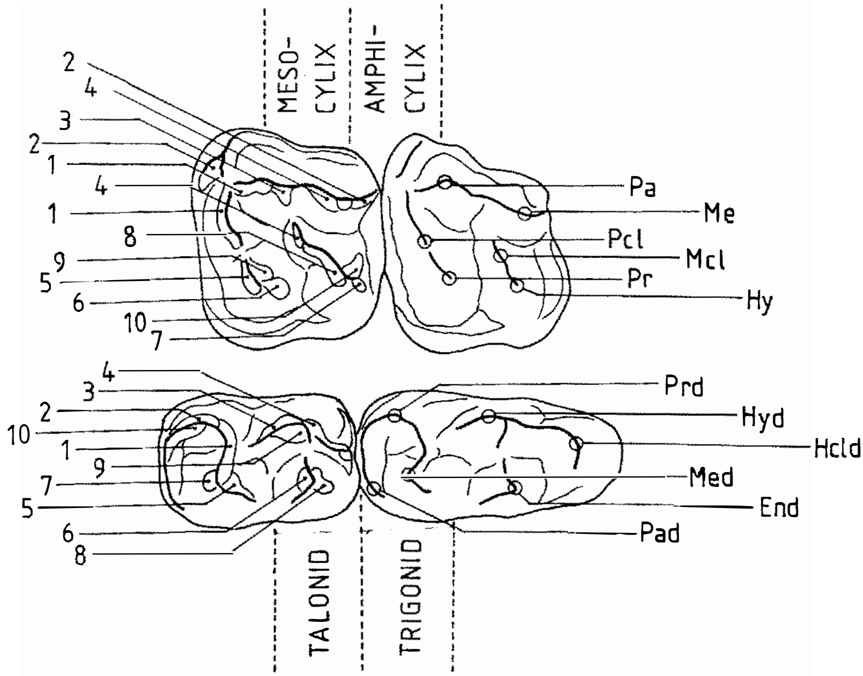

Fig. 2. Second and third upper (above) and lower (below) molars of *Hyracotherium*, to show cusp and facet nomenclature as used in this text. Redrawn and modified from Radinsky (1969). Based also on Butler (1952a) and Kay & Hiiemäe (1974). – Abbreviations: End = entoconid, Hy = hypocone, Hyd = hypoconid, Hcld = 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 & Hiiemäe 1974).

Larger structural and functional units may be referred to by two sets of terms: trigonid and talonid for the lower teeth and amphicylix and mesocylix (Butler 1952a) for the upper ones. I prefer the latter terms to trigon and talon because they describe functional units. The mesocylix is, of course, synonymous with the 'trigon basin', but the amphicylix 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 redefine '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.

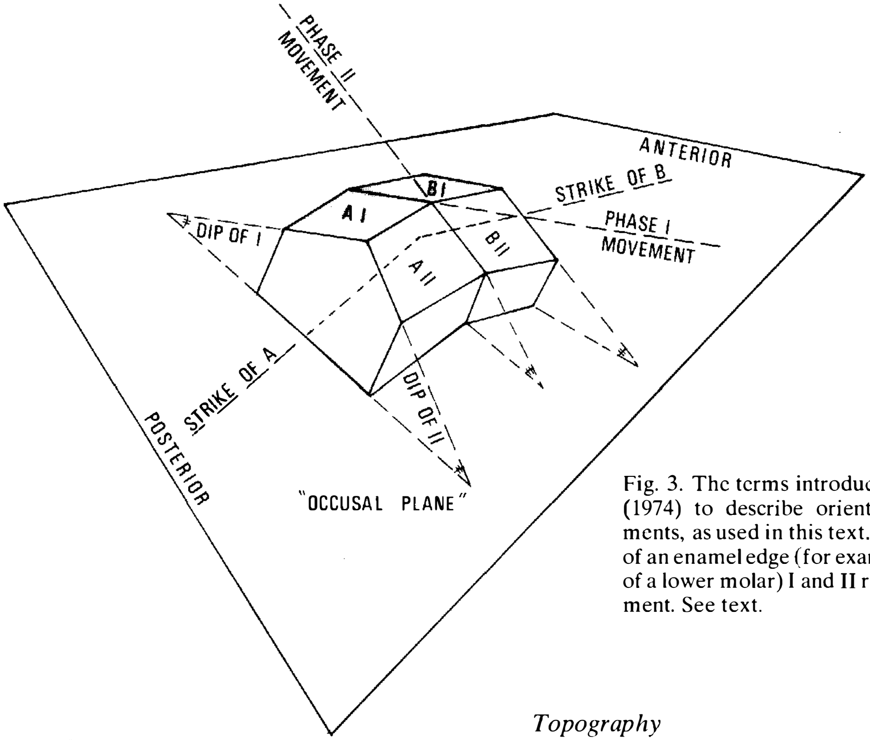

Fig. 3. The terms introduced by Kay & Hiiemäe (1974) to describe orientation of occlusal elements, as used in this text. A and B are segments of an enamel edge (for example, at the protoconid of a lower molar) I and II refer to phases of movement. See text.

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 perissodactyls 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).

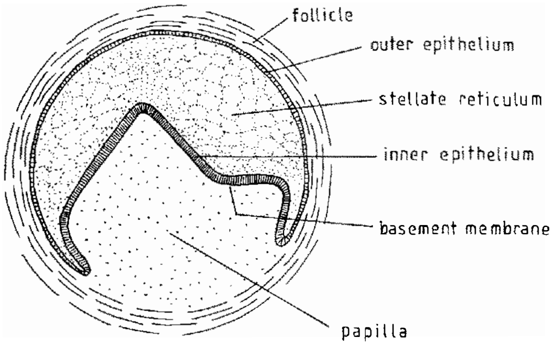

Fig. 4. Vertically sectioned tooth germ. The basement membrane of the inner epithelium (the epithelio-mesenchymal interface) becomes the enamel-dentine junction of the tooth, and its topography determines the main features of coronal morphology. After Butler (1956).

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

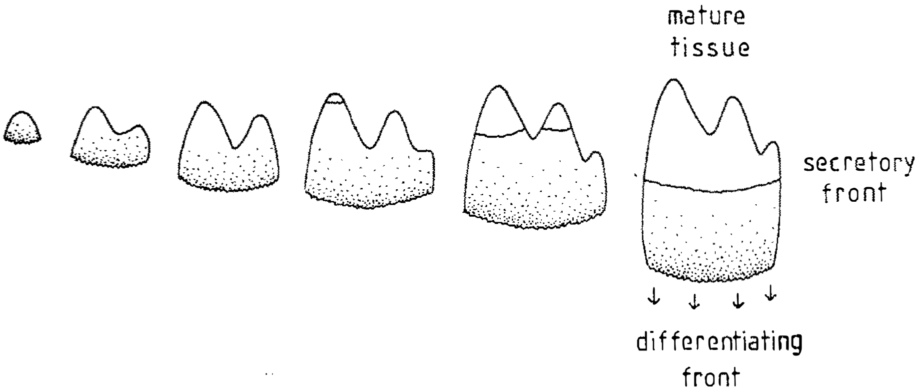

Fig. 5. Schematic representation of sequential stages in the development of a tooth. The surface shown is the epithelio-mesenchymal interface (after secretion the enamel-dentine junction). Differentiation and secretion start at cusp tips and proceed as successive zones towards the cervical margin. The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

cusp 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 hypsodont 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 selenodont 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 notoungulate *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).

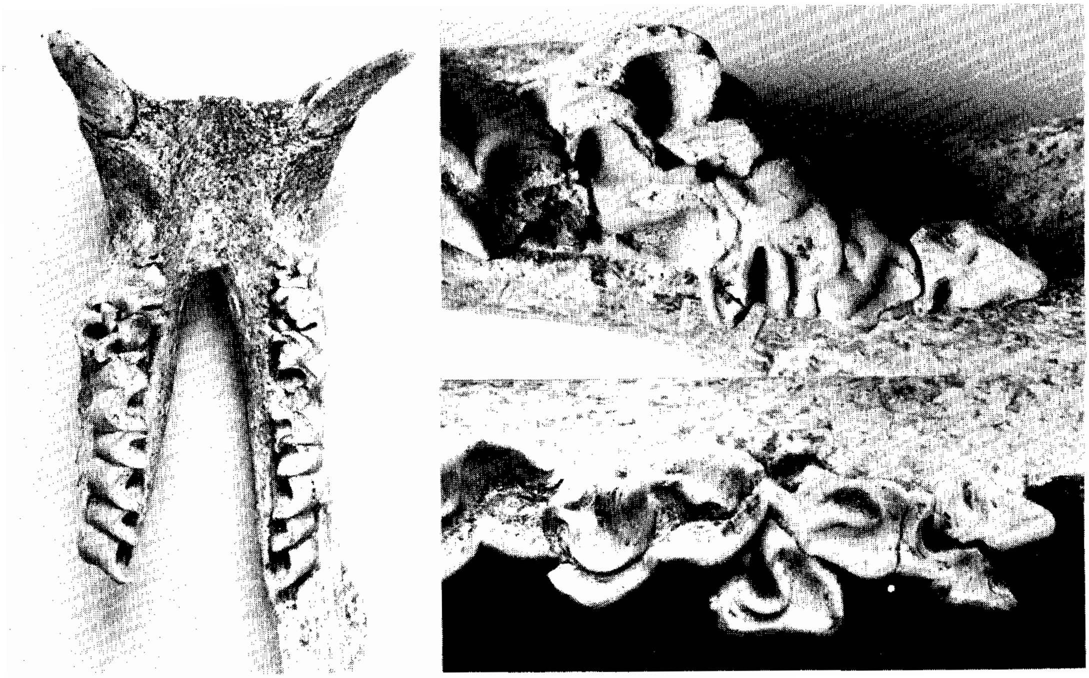

Fig. 6. *Chilotherium habereri* (UP M 487), Upper Miocene, China. P_2 dext. and P_4 sin. are double, and all premolars (but particularly P_3) are deformed, presumably as a result of mechanical disturbance during development.

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 cuspule (see e.g., Mayhall et al. 1982). Butler (1979) further supported Jørgensen's (1956) conclusion that the so-called 'delta variation' of dm_1 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 M^3:s. Ringström (1924, Plate IX:7) figured a supernumerary, peglike molar behind the left M^3 in the Chinese Miocene rhinocerotid "*Diceratherium*" *palaeosinense*. The right M^3 is normal, with reduced metaloph, but the left is more like an M^2, 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 deformed by mechanical obstruction. Fig. 6 shows an example from another Chinese Miocene rhinoceros, *Chilotherium habereri*, in which the right P_2 and the left P_4 are double and all the premolars, particularly the P_3: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 carnivores, 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 *Trichecus*). 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 coincidence 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, $Ca_5(PO_4)_3OH$, 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).

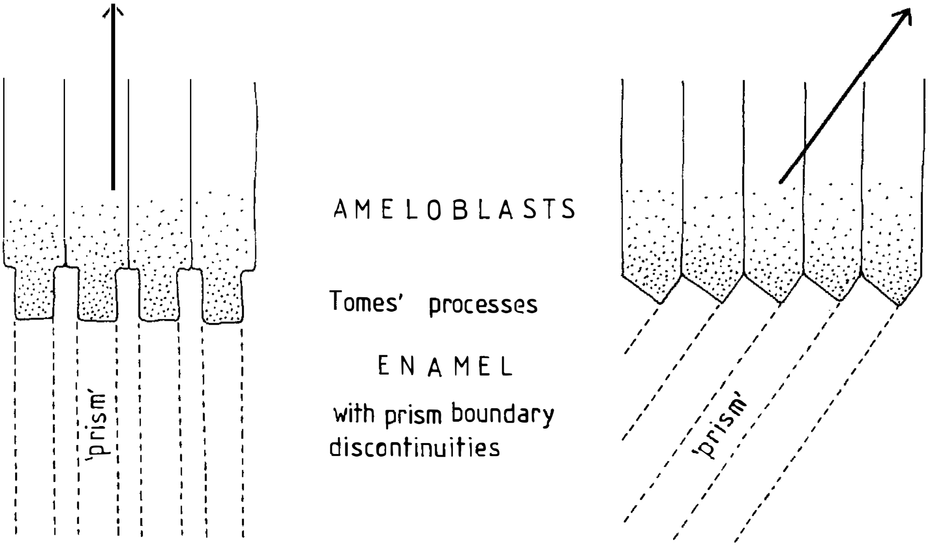

Fig. 7. The relationship between ameloblasts, Tomes' processes and enamel 'prisms'. The arrows denote the direction of ameloblast movement, which determines the orientation of the prism boundary discontinuities. To the left the ameloblasts do not translate across their substrate, and Pattern 1 enamel 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, although 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-

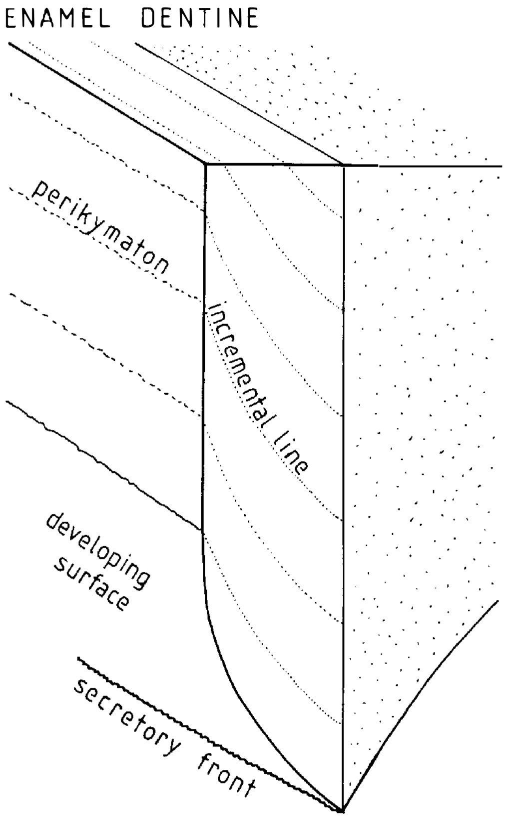

Fig. 8. Schematic representation of the incremental structure of enamel. The developing surface is covered with secretory ameloblasts, the 'youngest' next to the secretory margin and the 'oldest' at its occlusal margin, where secretion ends. Incremental lines are sectioned incremental planes, corresponding 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 μm2) 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 μm/day) and Pattern 3 with fast (5–7 μm/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).

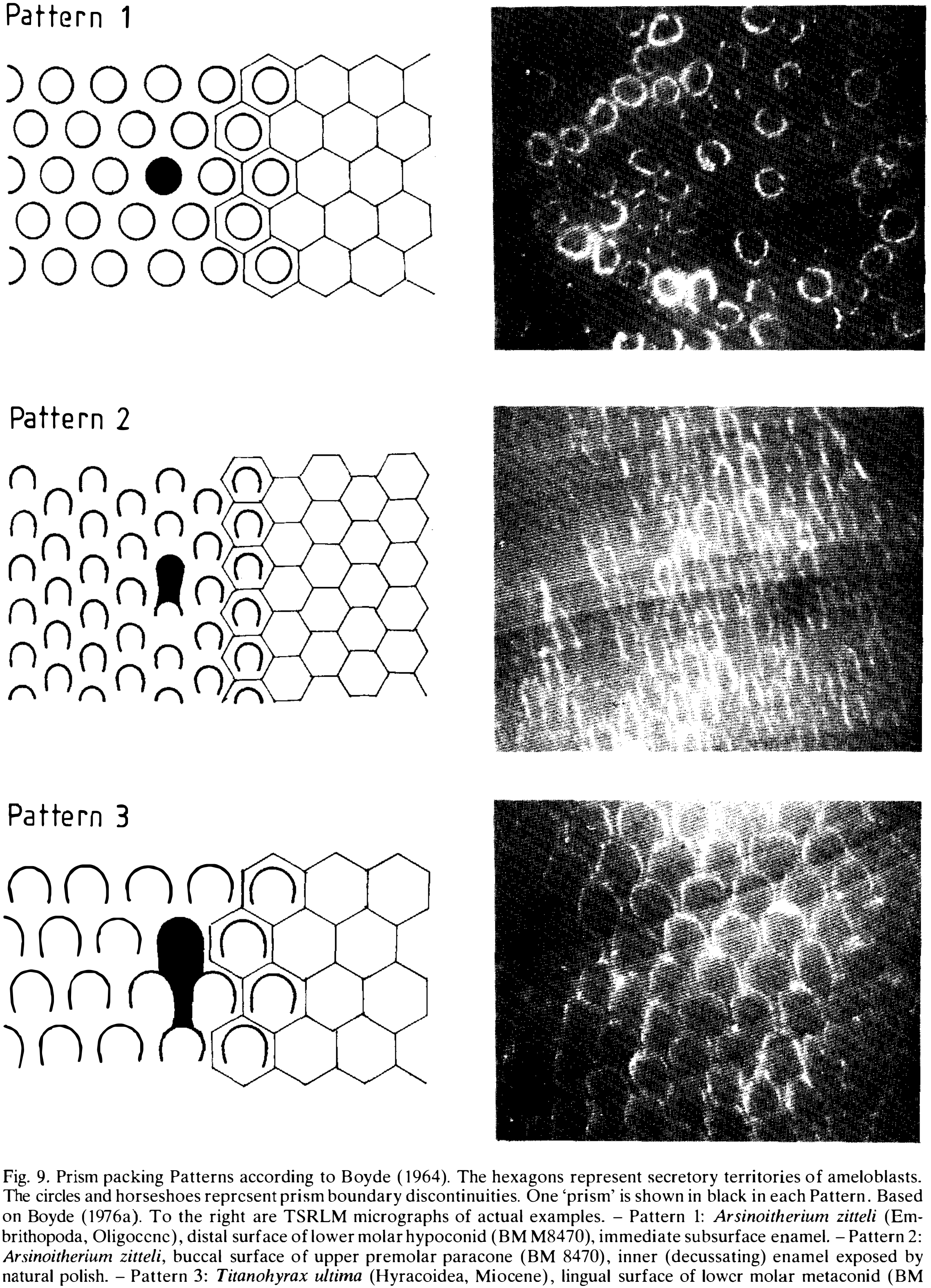

Fig. 9. Prism packing Patterns according to Boyde (1964). The hexagons represent secretory territories of ameloblasts. The circles and horseshoes represent prism boundary discontinuities. One 'prism' is shown in black in each Pattern. Based on Boyde (1976a). To the right are TSRLM micrographs of actual 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 μm, 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.

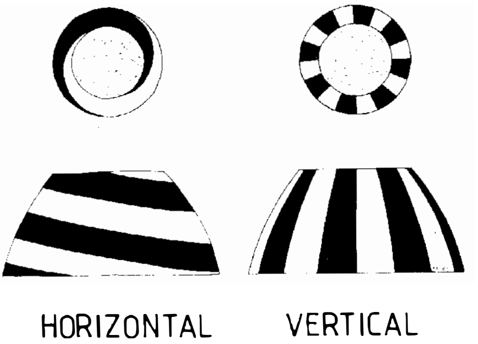

Fig. 10. Schematic representations of tooth cusps to show horizontal (left) and vertical decussation (right). Note the concentric and radial patterns in the sections on top (black and white bands are HSB's, stippled area is dentine). From Fortelius 1984.

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 decussation 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

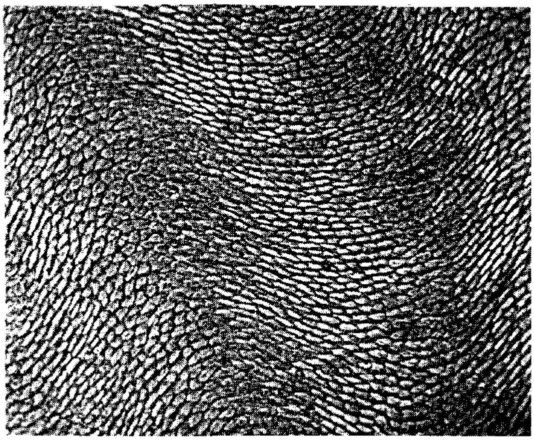

Fig. 11. Pattern 2 enamel with gradual shift in prism orientation between two extremes, horizontal decussation. *Anchitherium aurelianense* (Equidae, Miocene), polished and acid etched vertical transverse section through buccal enamel of upper molar metacone (occusal towards top, enamel-dentine junction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

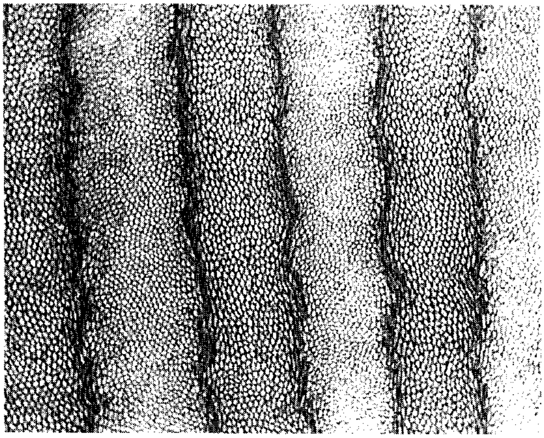

Fig. 12. Vertical decussation with sharp zone boundaries (the Pattern is 3, although that can not be seen in this preparation). *Astrapotherium* sp. (Astrapotheria, Miocene), horizontal section through ectoloph of upper molar (enamel-dentine junction towards bottom). HP unregd. fragment. SEM (BSE+SE) 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 loose 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+δX 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+δX 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 (Rens berger 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 marsupials. 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 Hiiemäe (1978).

Crompton & Hiiemäe (1970) introduced the useful concepts of puncture-crushing and shearing; the latter was later called chewing (sensu stricto) by Hiiemäe (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 (Hiiemäe 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 (Hiiemäe 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 (Krause 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 powerstroke 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 anteriad 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).

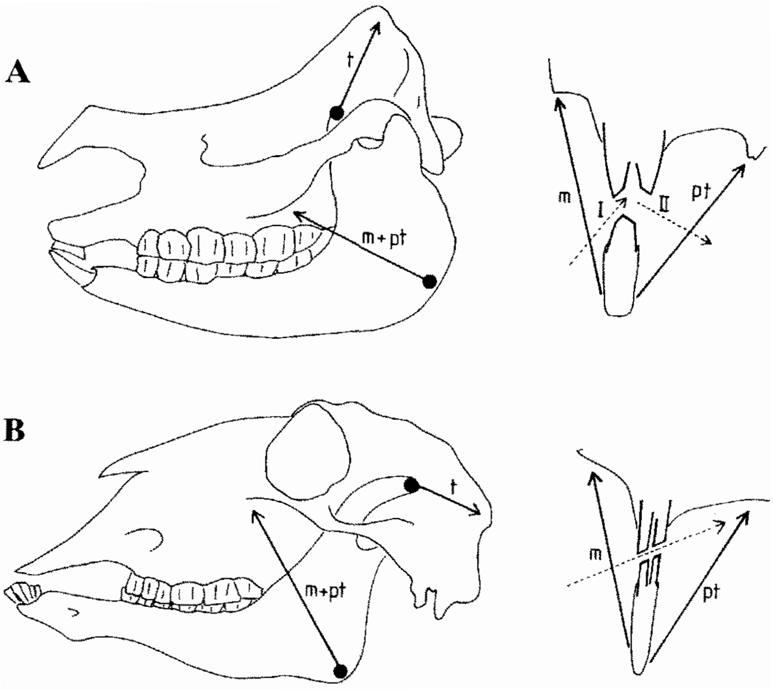

Fig. 13. Highly schematic representations of the main masticatory muscle vectors. – *Rhinoceros unicornis* (A), with two-phase occlusal morphology. – *Ovis aries* (B), with one-phase occlusal morphology. To the right are (imaginary) vertical transverse sections. The single-phase arrangement allows greater 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 & Hiiemäe (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 & Hiiemäe: "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 muscle 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 & Hiiemäe 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 & Hiiemäe (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 & Hiiemäe (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 & Hiiemäe (1974), is movement into unilateral centric occlusion (Crompton & Hiiemäe 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 horizonal in derived primates (Hiiemäe 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. Hiiemäe 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 (dorsomediad) 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 & Hiiemäe 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 Hiiemäe (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

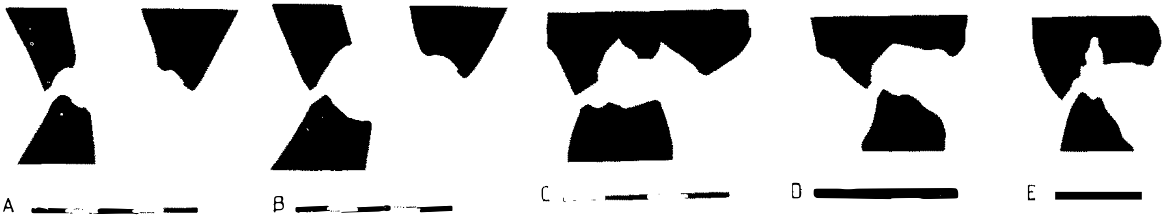

Fig. 14. Transverse profiles of occluding upper and lower molars of trilophodont forms with distinct two-phase occlusal morphology. See App. 4. for method. One segment of scale bar = 5 mm. Abbreviations refer to collections as detailed in App. 2—3. – A. *Dicerorhinus sumatrensis* M^1, M_1 (KO 617). – B. *Diceros bicornis* M^1, M_1 (TE R.G. 7974). – C. *Anchitherium aurelianense* (isolated first or second molars) (MU 1959 II 520 & 614). – D. *Dendrohyrax* sp. M^2, M_2 (ST 4415 (102)). – E. *Procavia habessinica* M^2, M_2 (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* M^3, M_3 (KO CN 1694). – B. *Ceratotherium simum* M^2, M_2 (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 dicussion 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 anteromediad 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

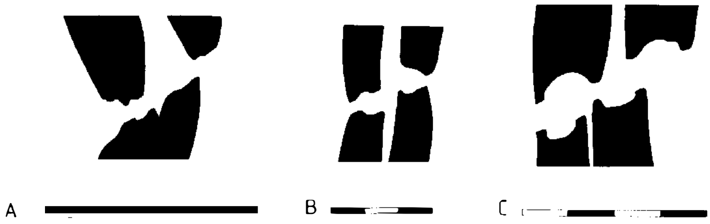

Fig. 16. Transverse profiles of occluding upper and lower molars of selenodont forms. See caption of Fig. 14. – A. *Moschus moschiferus* M^3, M$_3$ (KO 635). – B. *Taurotragus oryx* M^3, M$_3$, different individuals (GB 4617 & 4618). – C. *Oryx beisa* M^2, M$_2$ (KO CN 1655).

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 Weijs & 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 brachydont, 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 & Hiiemäe (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 paleoanthropologists. 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

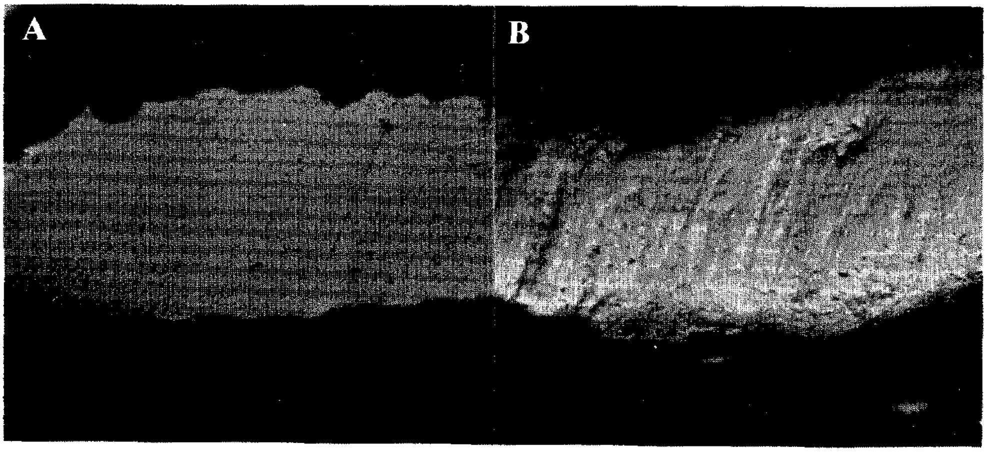

Fig. 17. Difference between wear morphology of lingual facets of browsing (A) and grazing (B) ruminants. A is *Alces alces* M^2 facet 6, MF private coll. B is *Oryx gazella* M^2 facet 5, GB 7541. Light micrographs of transparent epoxy replicas illuminated obliquely from below (App. 7.1). Field width 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-

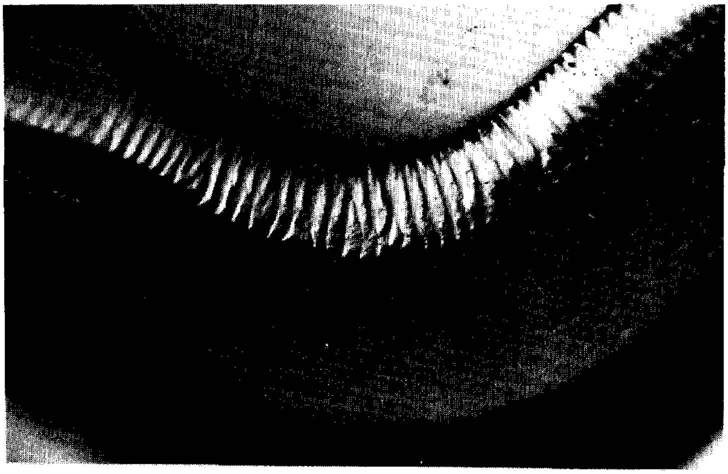

Fig. 18. Difference in wear properties between outer (non-decussating) and inner (decussating) enamel on buccal edge (hypoconid, facets 3 and 4) of *Rhinoceros sondaicus* second lower molar (KO 29). Alternate zones (HSB's) in the inner enamel are less resistant than their neighbours and the outer enamel, 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-

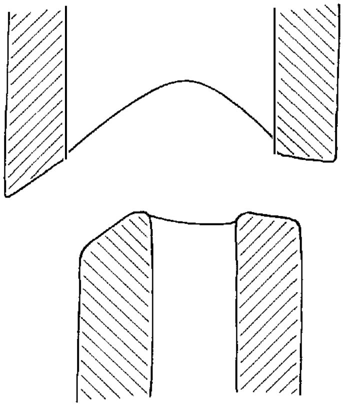

Fig. 19. Sketch showing different angle of interception of occlusally inclined enamel prisms in upper and lower teeth. The transversely intercepted prisms of the lower teeth may make these relatively more wear resistant, as discussed in text.

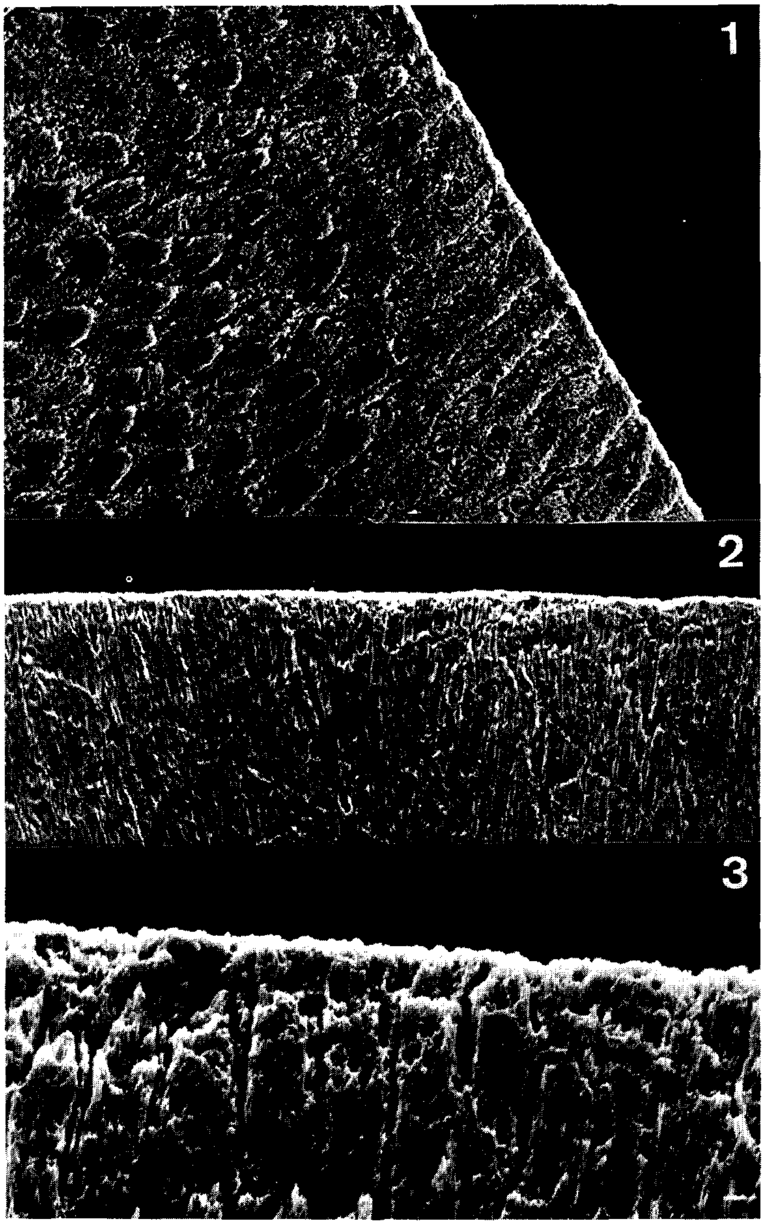

Fig. 20. Transversely sectioned natural wear facets (facets extend away from plane of page), showing prisms reaching all the way out to facet surface. Polished and H_3PO_4 etched. SEM (SE) images. – 1: *Anchitherium aurelianense* (Equidae, Miocene) upper molar buccal phase I facet (specimen gift from 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 brachydont 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 *Hippopotamus*. 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 dm_2 to M_1 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.

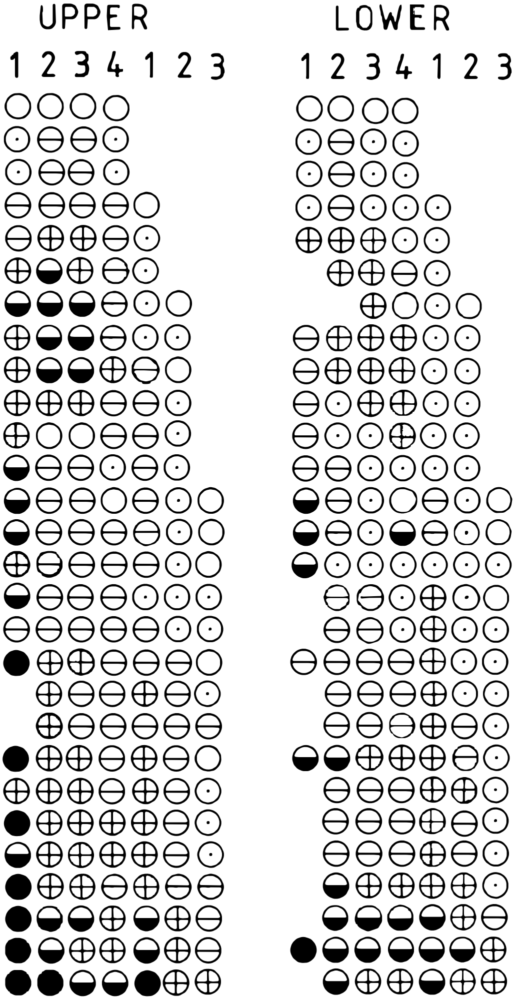

Fig. 21. *Diceros bicornis*, wear of upper and lower toothrows. Wear stages are arbitrary and determined by easily recognizable changes in occlusal morphology. Neither the stages of different teeth in the row nor those of upper and lower teeth correspond exactly.

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.

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

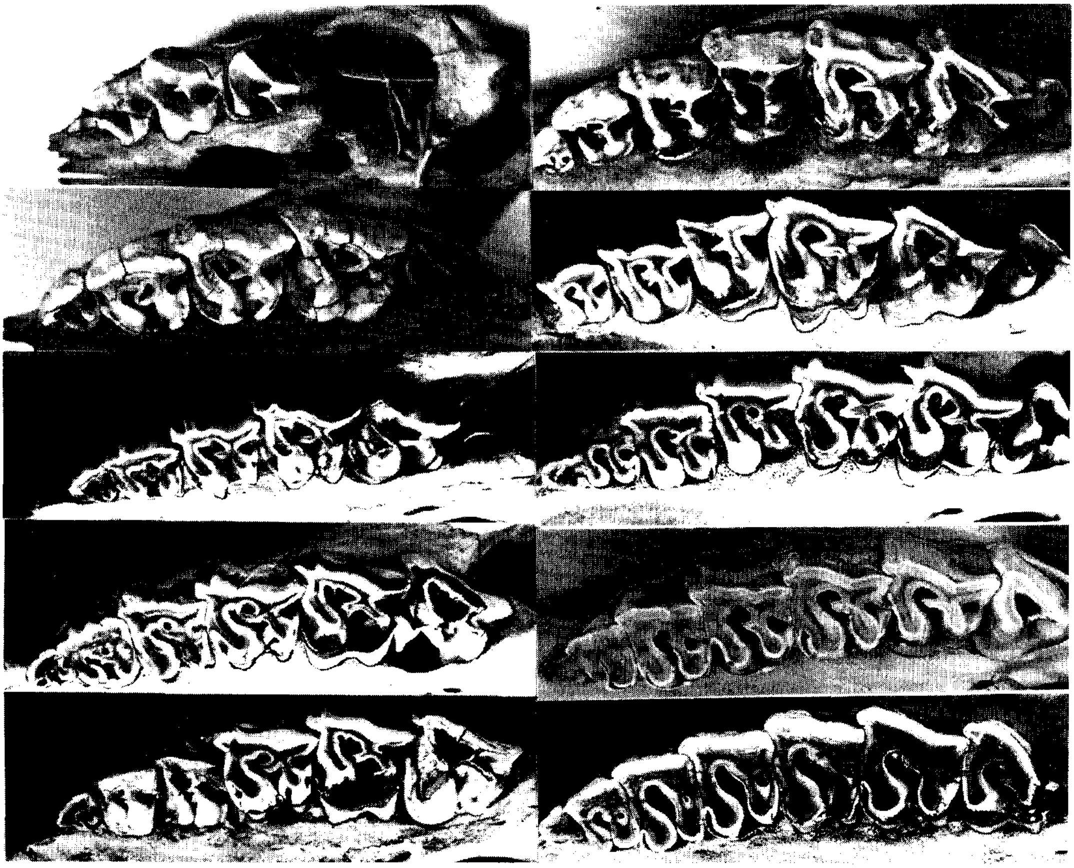

Fig. 22. *Diceros bicornis*, upper toothrow in different stages of eruption and wear. Note nearly simultaneous eruption of deciduous molars, their replacement and the gradual eruption of molars. Teeth in different stages of wear are present almost throughout. See also Fig. 21 and discussion in text. 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.

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
Merychippus primus	M^1	23	2.3	11	1
M. cf. *perditus*	M^1	c.40	3.3	13	1
Pseudhipparion retrursum	M^1	45	4.1	12	1
Neohipparion cf. *leptode*	M^1	50	4.2	13	1
Hipparion spp.	M^1, M^2	53	5.1	11	2
Equus burchelli ♂♂	M^1	73	3.3	24	1
E. caballus (domestic)	?	?	2.6	?	3
Urmiatherium intermedium	M^2	38	5.1	9	4
Plesiaddax depereti	M^2	35	4.6	9	4
Pachytragus solignaci	M_2	20	1.9	11	5
Rangifer tarandus	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).

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 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 toothrow 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

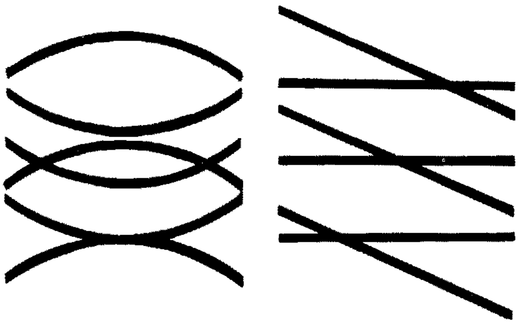

Fig. 23. Reciprocally curved blades (A) and straight, inclined blades (B). See text.

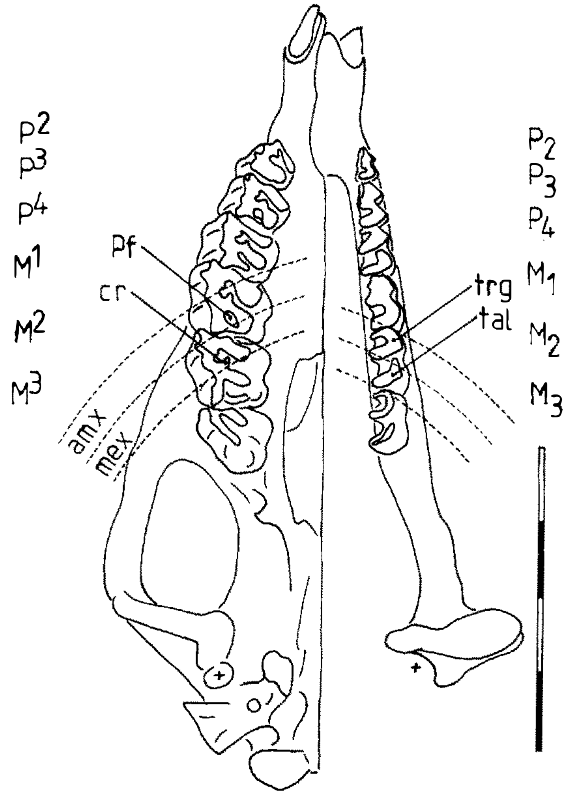

Fig. 24. Occlusal relationships in a skull of *Dicerorhinus sumatrensis* (CA H. 6383), as discussed in text. The apparent non-correspondence is an artefact of perspective. Drawn from photographs, one segment on scale bar = 5 cm. – Abbreviations: amx = amphicylix, cr = crochet, mex = mesocylix, pf = postfossette,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

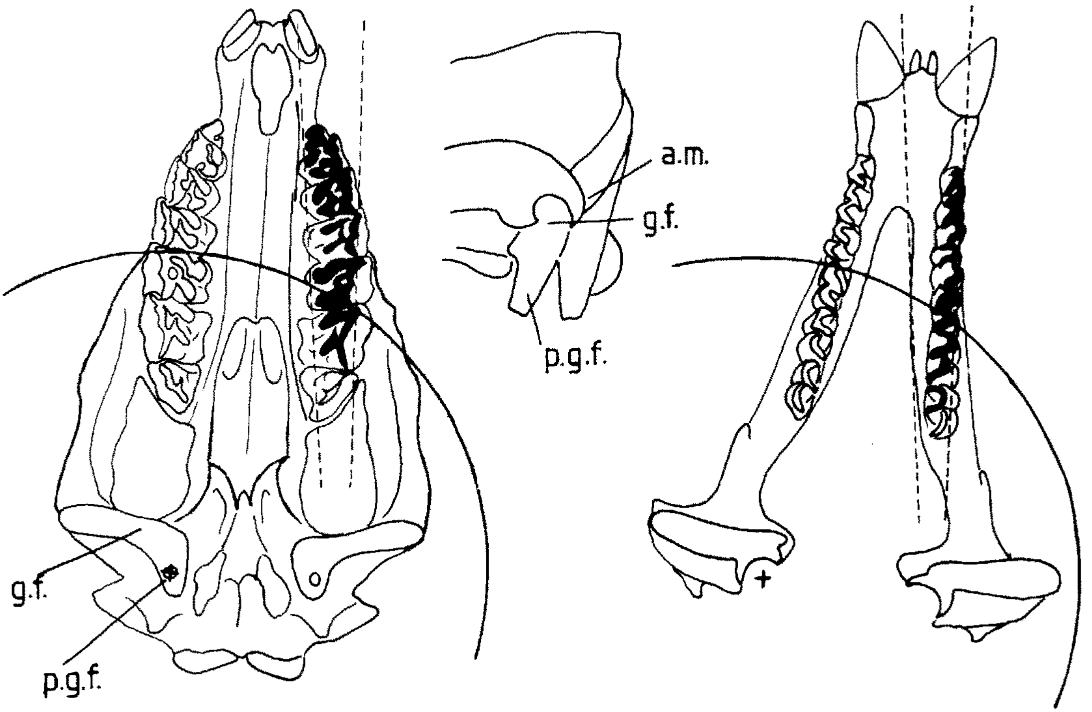

Fig. 25. Rotation of the mandible about the contralateral postglenoid process in a skull of *Rhinoceros unicornis* (UZ unnumbered). Occlusal surfaces on working side are shown in black, and the 'occlusal sector' of the upper toothrow is marked by broken lines. Sectors of circles with centres at the fulcrum 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 organs. 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

South American hystricomorph rodents (see Table 2). Many investigators since have found that postcanine occlusal area is nearly isometric to body size in most mammals (see below and Table 2).

It is undeniable that the energy which drives the animal's metabolism comes (at the very least mainly) from its food, which is comminuted between the postcanine teeth. (Exceptions such as toothless forms are irrelevant to the discussion of the scaling of tooth size.) Relationships must exist between tooth size, comminution performance, body size and metabolism, so the discrepancy between theory (positive allometry) and empirical data (isometry) is therefore unsatisfactory. In this section I will attempt to resolve this apparent paradox, which may be due to a simple misconception.

Simpson (1953) already considered allometry a concept familiar to all biologists, and there is no need to discuss its general significance here, although it must be noted that the issue is still far from unproblematic. In this text I treat allometric relations as empirical generalizations, not as the expressions of laws, but it cannot be denied that the high incidence of exponents close to 1/4 and 3/4 relating physiological variables to body mass is suggestive of some general underlying law(s) (see e.g. Peters 1983 for examples and a discussion). There are several methodological problems, some of which are particularly relevant in the present context (for more general discussions see e.g. Reeve & Huxley 1945, White & Gould 1965, Gould 1966, 1971, Harvey 1982, Harvey & Mace 1982, R.D. Martin 1983, Peters 1983 and Schmidt-Nielsen 1984).

First, although an allometric function of the form $Y = aW^b$ (where a and b are empirical constants) can be fitted to practically any two size or size-dependent variables W and Y, the underlying biological relationship is not always the same. Thus allometric ontogenetic growth (heterauxesis) is not the same biological phenomenon as 'static' allometry (allomorphosis) between adults of different size or between taxa (of which several kinds may be distinguished), and neither is the same as allometric change in an evolving lineage (Simpson 1953). The last case is particularly problematic, since it includes components of morphological change as such, and also change related to trends of increasing or decreasing size (Gould 1966, R. D. Martin 1983). Much confusion has arisen from this in the past, but the difficulties are now generally recognized.

Second, dimensionality creates problems of several kinds. Relevant here are two: (a) that the relationship proposed by Pilbeam & Gould (1974) relates an area to a mass, and (b) that either or both often have to be estimated from linear dimensions. Let V be a volume (substituted for mass), A an area and L a linear dimension: for geometrically similar objects $V \propto A^{3/2} \propto L^3$. In this text I will use the term 'isometry' of relationships described by these exponents, regardless of the dimensionality of the variables actually compared (i.e., regardless of how body size and tooth size have been estimated in a particular case).

Allometry between the size of two organs may theoretically occur even when both organs are geometrically similar at all sizes, if their rates of size change are unequal (e.g. the toothrow might increase in size relative to the skull but both might retain their proportions). In such a case simple arithmetical manipulation gives the expected allometric exponent at any combination of dimensions. For example, the relation $A_y \propto V_w^{3/4}$ can be transformed into

$$A_y \propto L_w^{3 \times 3/4} = L_w^{9/4},\ L_y \propto L_w^{1/2 \times 9/4} = L_w^{9/8},$$

and so on. It is clear that this ideal situation is rarely if ever encountered in reality, and that allometry usually involves changes in shape that make it impossible to exactly estimate one dimension from another (cf. Hills & Wood 1984). Nevertheless, these transformed relations give estimates of the exponents expected from direct metabolic scaling of postcanine occlusal area as proposed by Pilbeam & Gould. They can not be regarded as exact 'null hypotheses', but they are given in the tables as a guideline.

Third, several curves may be fitted to the data to give the constants a and b. The problem of which one should be used has been subject to some discussion recently. I follow Gould (1975) and Harvey & Mace (1982) in using logarithmically transformed variables and the ('unreduced') major axis. This gives a linear relationship $\log Y = b \log W + \log a$, in which the variance in both variables is treated equally (Model II regression; Sokal & Rohlf 1981). Recent criticism of the empirically justified use of log-transformed variables appears to have been adequately met by Harvey (1982). Major axis regression analysis is really bivariate principal components analysis, and it might be argued that multivariate analysis should be used instead. However, the problem of how tooth size scales to body size is essentially bivariate, and multivariate analysis also presents unsolved problems of interpretation which are undesirable in this context (Harvey & Mace 1982). For these reasons bivariate analysis appears to be more appropriate here. All calculations were executed according to the procedure suggested by Sokal & Rohlf (1981) (see also App. 8).

Fourth, the relationship between two variables is not the same at all taxonomic levels. The species of a genus, the genera of a family or the families of an order often give different lines, and it is not always obvious which one is the most relevant to the problem at hand. Plots including several hierarchic levels (e.g. the species of an order) often show several linear clusters (e.g. families), usually with nearly identical slopes but different intercepts (Fig. 26). As recognized at least by Kurtén (1954), Meunier (1959) and Gould (1971), this offsets the effect of lower-

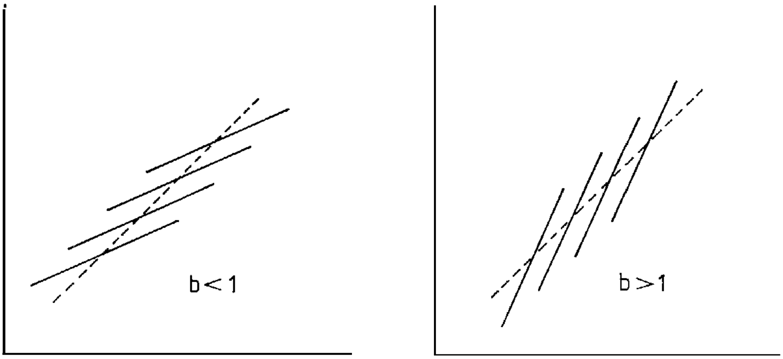

Fig. 26. How transposition may result in overall isometry, based on Gould (1971).

level allometry at higher levels. Meunier, who considered intra- versus interspecific relations, introduced the term Transposition for this phenomenon: "Die kompensierende Transposition ... hebt die im Zuge der innerartlichen Allometrie eingetretene Gestaltverzerrung wieder auf.“ (1959:347). Gould (1971) noted that this is true for both positive and negative allometry (see Fig. 26), and gave examples.

For all these and other reasons (see Harvey & Mace 1982) it is difficult to choose the appropriate taxonomic level for analysis, although it is obvious that it should be one pertaining to the problem under study. Many orders contain few families, many families few genera and many genera few species, so the choice is often a compromise between statistical (sample size) and biological considerations. In this investigation I have used species means as data points at all levels except the intraspecific. This is a relatively minor problem as the higher level relationships are all nearly isometric (see below).

4.1.2. Tooth size and body size: data

This section deals with the published data on tooth size body size relationships, and with original data collected for this study (App. 1 & 2). Most of the data suffer from two faults; they are based on few individuals and the body mass data are from different individuals than are the cranial and dental measurements. Use of some cranial or skeletal dimension as an estimate of body mass eliminates the second problem but introduces the complication that this dimension may itself be allometric to body mass. However, better data are simply not available, and the overall pattern is sufficiently uniform to suggest that these problems may not be too serious at the level of general comparison. For clarity this section is divided into five parts: (i) interspecific allometry at the family level and higher (most ungulate genera include only one or two species), (ii) intraspecific allometry between adults, (iii) ontogenetic dentition allometry, (iv) dwarfing, and (v) sex.

Higher level relationships

The first person to challenge the hypothesis of direct metabolic scaling of occlusal area as proposed by Pilbeam & Gould (1974) was probably Kay (1975). He presented data to show that the area of crushing surfaces on second lower molars of various primates scales at exponents significantly lower than 0.75 to body weight, and that postcanine tooth area also scales at such exponents in non-cercopithecoid primates and in bovids (Table 2). Kay (1978) presented further evidence that among the Cercopithecidae, five different dimensions on M_2 (crown length, hypoconid height, metaconid height, area of crushing surfaces, and cristid oblique length) scale isometrically with body weight in both sexes, separately as well as pooled. In the male and pooled samples the width of M^2 scaled at significantly negative allometry and entocristid length with significant positive allometry. Kay concluded that the hypothesis of ‘metabolic scaling’ was in disagreement with his data. Lucas (1980) presented data on postcanine tooth area for anthropoids and bovids (Table 2), and reached a similar conclusion. Creighton (1980) presented data for M_1 area and head-and-body length for a large sample of ‘all mammals’, and for selected orders and families. He found isometry except in Mammalia, Insectivora, Rodentia and Felidae, in which significant negative allometry was found (Table 2). Prothero & Sereno (1982) likewise found isometry of postcanine tooth area to body weight in suine artiodactyls and ceratomorph perissodactyls. Gingerich et al. (1982) showed that the central teeth (P4, M1) scale at lower than isometric and the terminal teeth at higher than isometric exponents in primates. This result gives some support to the argument of Pilbeam & Gould (1974, 1975) and Gould (1975), that the entire postcanine area must be used, not just single teeth. However, Gingerich et al. (1982) found that total postcanine area scaled approximately isometrically with body weight in the primate sample (Table 2).

Table 2. Tooth size (Y) – body size (W) relationships at and above the family level. Selected data from the literature. Slope estimates are generally closer to the isometric than the "metabolic" value. Abbreviations see p. 75.

Taxon	W	Y	*N*	*r*	Slope used	Slope value	Isom. slope	'Metab' slope	Source
Mammalia	HBL	M_1A	288	0.952	r.m.a.	1.82	2.00	2.25	4
Insectivora	HBL	M_1A	20	0.897	r.m.a.	1.59	2.00	2.25	4
Erinaceidae	MAL	MRUL	30	–	l.sq.	0.87	1.00	1.12	9
Primates	HBL	M_1A	14	0.909	r.m.a.	1.75	2.00	2.25	4
Primates	AWT	TRUA	78	0.949	m.a.	0.62	0.67	0.75	7
Primates	AWT	TRLA	77	0.964	m.a.	0.69	0.67	0.75	7
Lemuroidea, males	BL	TRUA	11	0.945	m.a.	2.18	2.00	2.25	1
Ceboidea, males	BL	TRUA	14	0.975	m.a.	2.18	2.00	2.25	1
Cercopithecoidea, males	BL	TRUA	14	0.953	m.a.	1.95	2.00	2.25	1
Cercopithecoidea, males	AWT	TRUA	10	0.971	m.a.	0.80	0.67	0.75	1
Cercopithecoidea, females	BL	TRUA	11	0.931	m.a.	2.19	2.00	2.25	1
Cercopithecoidea	MAL	MRUL	59	0.990	l.sq.	0.75	1.00	1.12	9
Cercopithecidae, males	AWT	M_2A	49	0.926	l.sq.	0.70	0.67	0.75	3
Cercopithecidae, females	AWT	M_2A	49	0.900	l.sq.	0.65	0.67	0.75	3
Cercopithecidae	AWT	M_2A	49	0.889	l.sq.	0.62	0.67	0.75	3
Rodentia	HBL	M_1A	136	0.927	r.m.a.	1.73	2.00	2.25	4
Hystricomorpha	MAL	MRUL	50	0.974	l.sq.	1.05	1.00	1.12	9
S.Amer. Hystricomorpha	BL	TRUA	34	0.967	m.a.	2.49	2.00	2.25	1
S.Amer. Hystricomorpha	AWT	TRUA	14	0.971	m.a.	0.72	0.67	0.75	1
S.Amer. Hystricomorpha	HBL	M_1A	17	0.921	r.m.a.	2.01	2.00	2.25	4
Sciuridae	HBL	M_1A	47	0.905	r.m.a.	1.88	2.00	2.25	4
Muridae	HBL	M_1A	13	0.884	r.m.a.	1.75	2.00	2.25	4
Cricetidae	HBL	M_1A	40	0.845	r.m.a.	1.96	2.00	2.25	4
Carnivora	HBL	M_1A	74	0.859	r.m.a.	1.99	2.00	2.25	4
Mustelidae	HBL	M_1A	17	0.883	r.m.a.	2.25	2.00	2.25	4
Canidae	HBL	M_1A	18	0.707	r.m.a.	2.45	2.00	2.25	4
Felidae	HBL	M_1A	15	0.960	r.m.a.	1.59	2.00	2.25	4
Viverridae	HBL	M_1A	18	0.910	r.m.a.	1.79	2.00	2.25	4
Ceratomorpha	TRUA	AWT	7	0.969	l.sq.	1.59	1.50	1.69	6
Ceratomorpha	CPL	TRUA	7	0.976	l.sq.	1.99	2.00	2.25	6
Equidae (fossil hyps.)	BRCL	TRUL	13	0.977	r.m.a.	1.26	1.00	1.12	8
Equidae (fossil brach.)	BRCL	TRUL	12	0.972	r.m.a.	1.01	1.00	1.12	8
Artiodactyla	HBL	M_1A	12	0.852	r.m.a.	2.01	2.00	2.25	4
Suina	BL	TRUA	9	0.953	m.a.	2.31	2.00	2.25	1
Suina	CPL	TRUA	9	0.926	l.sq.	2.24	2.00	2.25	6
Suina	TRUA	AWT	8	0.926	l.sq.	1.52	1.50	1.69	6
Cervidae	FEL	TRUA	17	0.962	m.a.	2.17	2.00	2.25	1
Bovidae	AWT	TRUA	10	–	l.sq.	0.52	0.67	0.75	2
Bovidae males	AWT	TRUA	7	0.992	l.sq.	0.59	0.67	0.75	5
Bovidae females	AWT	TRUA	7	0.991	l.sq.	0.63	0.67	0.75	5

Sources:
1. Pilbeam & Gould 1974, 2. Kay 1975, 3. Kay 1978, 4. Creighton 1980, 5. Lucas 1980, 6. Prothero & Sereno 1982, 7. Gingerich et al. 1982, 8. Radinsky 1984, 9. Williams 1955.

An inspection of Table 2 reveals only one case of distinct positive allometry of tooth size to body size in addition to the South American hystricomorph rodents of Pilbeam & Gould (1974). This is the sample of fossil hypsodont equids investigated by Radinsky (1984). However, Radinsky used braincase length as a standard in his investigation (which was about skull proportions, not tooth size body size relationships), and it may scale with negative allometry to body mass, as does brain mass. Martin (1981) gave the slope 0.76 for brain/body mass allometry in placental mammals (*N* = 309 species). Assuming braincase length to scale isometrically with brain size, we might compensate for the negative allometry by simply multiplying Radinsky's slopes by 0.76. This would give the slope 0.96 for the hypsodont horses, but it would also lower the slope for brachydont horses to 0.77. The 'correction' is of course very crude and may be quite unwarranted, and the matter is further complicated because the material contains a factor of

Table 3. Bivariate relationships between adult body weight and cranial and dental dimensions in a sample of ungulates (App. 1–2). Note general isometry. * = value outside 95 % CL (*b*). Abbreviations see p. 75.

W-variable	Y-variable	*N*	*r*	*b*	95 % CL (*b*)	log *a*	Isom. slope	'Metab.' slope
Adult body weight	CBL	46	0.981	0.31	0.294–0.331	4.260	0.33	0.38*
	WZY	46	0.965	0.31	0.284–0.335	4.371	0.33	0.38*
	SKA	46	0.984	0.62	0.590–0.658	2.135	0.67*	0.75*
	UL	44	0.967	0.31	0.289–0.340	4.376	0.33	0.38*
	TRVA	43	0.965	0.65	0.595–0.708	2.883	0.67	0.75*
	M^{1}L	42	0.964	0.32	0.296–0.353	4.091	0.33	0.38*
	M^{1}W	46	0.952	0.34	0.308–0.374	4.610	0.33	0.38*
	M^{1}A	42	0.961	0.67	0.611–0.734	3.340	0.67	0.75*
	M^{2}L	42	0.965	0.32	0.296–0.352	4.584	0.33	0.38*
	M^{2}W	44	0.954	0.33	0.300–0.365	4.616	0.33	0.38*
	M^{2}A	42	0.965	0.66	0.606–0.721	3.301	0.67	0.75*
	M^{3}L	41	0.928	0.33	0.287–0.373	4.556	0.33	0.38*
	M^{3}W	41	0.950	0.32	0.282–0.350	4.595	0.33	0.38*
	M^{3}A	41	0.952	0.66	0.590–0.727	3.301	0.67	0.75*
	$\sum$M$^{1-3}$L	40	0.966	0.33	0.298–0.355	4.407	0.33	0.38*
	$\sum$M$^{1-3}$A	40	0.966	0.66	0.605–0.721	2.986	0.67	0.75*
	TRLL	42	0.960	0.30	0.273–0.328	4.433	0.33	0.38*
	TRLL×M^{2}W	42	0.964	0.62	0.564–0.674	3.106	0.67	0.75*
	M$_1$W	46	0.962	0.34	0.310–0.369	4.671	0.33	0.38*
	M$_2$W	42	0.953	0.31	0.278–0.341	4.691	0.33	0.38*
	M$_3$W	40	0.946	0.31	0.273–0.342	4.678	0.33	0.38*
Skull length	WZY	53	0.956	0.98	0.894–1.063	0.385	1.00	1.12*
	TRUL	50	0.907	1.08	0.941–1.233	0.319	1.00	1.12
	TRUA	49	0.949	2.09	1.898–2.311	–4.270	2.00	2.25
	M^{1}L	48	0.944	1.02	0.922–1.135	1.221	1.00	1.12
	M^{1}W	53	0.933	1.09	0.979–1.218	1.125	1.00	1.12
	M^{1}A	48	0.942	2.16	1.95[illegible]–2.412	–2.788	2.00	2.25
	M^{2}L	48	0.948	1.03	0.928–1.134	1.154	1.00	1.12
	M^{2}W	50	0.932	1.06	0.951–1.194	1.123	1.00	1.12
	M^{2}A	48	0.945	2.13	1.927–2.370	–2.915	2.00	2.25
	M^{3}L	47	0.921	1.09	0.958–1.236	1.047	1.00	1.12
	M^{3}W	47	0.928	1.00	0.889–1.133	1.219	1.00	1.12
	M^{3}A	47	0.937	2.14	1.922–2.407	–2.953	2.00	2.25
	$\sum$M$^{1-3}$L	46	0.952	1.04	0.939–1.143	0.652	1.00	1.12
	$\sum$M$^{1-3}$A	46	0.948	2.13	1.927–2.363	–3.859	2.00	2.25
	TRLL	48	0.963	0.96	0.884–1.046	0.563	1.00	1.12*
	TRLA	48	0.962	1.99	1.835–2.175	–3.661	2.00	2.25*
	M$_1$W	53	0.955	1.09	1.000–1.193	1.312	1.00	1.12
	M$_2$W	48	0.947	1.00	0.904–1.108	1.375	1.00	1.12*
	M$_3$W	46	0.942	1.00	0.895–1.113	1.387	1.00	1.12*
Skull length × skull width	TRUA	49	0.968	1.05	0.972–1.131	1.212	1.00	1.12'
	TRLA	48	0.977	1.01	0.989–1.080	1.495	1.00	1.12*
	M^{1}A	48	0.969	1.08	0.989–1.177	1.967	1.00	1.12
	M^{2}A	48	0.965	1.06	0.982–1.156	1.899	1.00	1.12
	M^{3}A	47	0.962	1.07	0.981–1.162	1.883	1.00	1.12
	$\sum$M$^{1-3}$A	46	0.970	1.06	0.987–1.150	1.411	1.00	1.12
TRUL	TRLL	48	0.987	0.97	0.926–1.021	0.050	1.00	
M^{1}A	M^{2}A	48	0.994	0.99	0.957–1.020	–0.065	1.00	
M^{1}A	M^{3}A	46	0.967	0.99	0.914–1.073	–0.088	1.00	
M^{2}A	M^{3}A	46	0.984	1.00	0.947–1.059	–0.019	1.00	

phylogenctic change. I only mention these complications here to indicate that the case can not be cited as unambiguous evidence of positive allometry of tooth size to body size. On the other hand, the number of cases of considerably lower exponents than the estimates of direct metabolic scaling is considerable (Table 2), and one might be tempted to reverse the argument of Pilbeam & Gould (1974:898) that "the pattern begins to convince by its unerring repetition".

To investigate the scaling of tooth size specifically in ungulates in more detail, I measured various dimensions on ungulate skulls and dentitions, as detailed in Appendix 2. Selected results are presented in Tables 3 and 4. Table 3 compares the relationships between different pairs of variables in the whole hyrax-to-elephant sample, while Table 5 compares selected taxa.

Table 3 may be summarized as follows:

1. No cranial or dental dimensions are significantly allometric (in the sense of deviation from isometry) to body weight except skull length times width and lower postcanine toothrow length, which are barely negatively allometric ($P < 0.05$). All the dental slopes are significantly lower than predicted by the hypothesis of direct metabolic scaling ($P < 0.05$).

2. No dental dimensions are significantly allometric to skull length, but correlations tend to be lower than for body weight and confidence limits are correspondingly wider. The best estimate in all cases but three suggests very weak positive allometry. Only four dimensions have slopes significantly lower than predicted by direct metabolic scaling (M^3L, TRLL, M_2W, M_3W).

3. No tooth areas are significantly allometric to skull length times width, but only lower postcanine area scales at a slope significantly lower than the direct metabolic. All slope estimates are very slightly above unity (isometric).

4. Dental dimensions are not significantly allometric to each other.

Thus a very extensive geometric similarity is observed, with a possible weak negative allometry of skull size to body size.

In comparing the relationships within different taxa (Table 4) sample size becomes a problem, as confidence limits expand with decreasing sample size. Despite this difficulty some taxa may be compared. (Particularly for selenodont artiodactyls many more species are potentially available, but I simply did not have access to more.) Using both upper toothrow area and M^1 area gives some extra confidence, since these parameters do not share any measurements, yet in all cases behave similarly.

1. Ceratomorpha. Prothero & Sereno (1982) used data from the five extant rhino and two extant tapir (of the four available) species to investigate dwarfism in Miocene rhinoceroses. My results largely reproduce theirs: there is a (non-significant) negative allometry of skull size to body size, and a corresponding positive allometry of tooth size to skull size, while tooth size is more nearly isometric to body size. However, this seems to be an artefact of mixing groups of different design, since excluding the tapirs changes the result (see below under "Dwarfing", p. 44).

2. Rhinocerotidae. There is no evidence of allometry. Correlations are lower than for the Ceratomorpha because the range is much smaller.

3. Suina. There is a weak (non-significant) indication of negative allometry of skull size to body size and a corresponding positive allometry of tooth size to skull size. Prothero & Sereno (1982) obtained a statistically significant result to the same effect.

4. 'Selenodont artioactyls'. Pooling bovids, cervids, tragulids, the giraffe and a camel results in this assemblage. Correlations are high, reflecting the great size range, and perhaps similarity of design. There are no significant departures from isometry, but there is a suggestion that skull size is slightly negatively allometric to body size and that tooth size is slightly negatively allometric to both.

5. Cervidae. My sample is rather heterogeneous (see App. 2), but such as it is it suggests general isometry. There is no evidence of the positive allometry of skull size to body size expected by Gould (1973, 1975), nor of the positive allometry of tooth size to body size found by Pilbeam & Gould (1974) (but their sample was larger and more homogeneous).

6. Bovidae. This sample is also heterogeneous, but correlations are all higher than 0.97, which is evidence that a similar design applies to all the species included. Slopes are not significantly different from isometry, but the pattern of negative allometry of skull to body and of teeth to both is again suggested. Kay (1975) and Lucas (1980) have presented data to show that postcanine tooth area is negatively allometric to body weight in bovids (Table 2).

In summary, there is no compelling pattern of allometry generally or in any ungulate group, but there is some indication that isometry is less dominant at lower taxonomic levels, with deviations in both directions. This confirms Meunier's (1959) and Gould's (1971) suggestion that the transposition of lower taxa in allometric plots serves to maintain overall geometric similarity. If the conclusion that geometric similarity equals functional similarity through size-related changes in rates is accepted, it follows that departures from isometry at lower levels may not be generally related to function. Instead, they may reflect growth constraints or similar factors, as suggested by Meunier (1959). This does not preclude the possibility that allometry may be functionally adaptive in specific cases, of course. It would, for example, be interesting to know why the lower carnassial tooth scales with positive allometry to body size in mustelids and canids, but with negative allometry in felids and viverrids (Creighton 1980).

Table 4. Bivariate relationships between adult body weight and cranial and dental dimensions in selected ungulate groups (App. 1–2). Note general isometry. * = value outside 95 % CL (*b*). Abbreviations see p. 75.

Taxon	W	Y	*N*	*r*	*b*	95 % CL (*b*)	log *a*	Isom.	'Metab.'
Suina	AWT	SKA	6	0.950	0.59	0.366–0.859	2.27	0.67	0.75
	AWT	TRUA	6	0.922	0.70	0.374–1.168	2.76	0.67	0.75
	AWT	M^1A	6	0.886	0.66	0.273–1.250	3.46	0.67	0.75
	SKA	TRUA	8	0.919	1.16	0.751–1.871	0.92	1.00	1.12
	SKA	M^1A	8	0.895	1.11	0.655–1.954	2.03	1.00	1.12
	CBL	TRUA	8	0.964	2.62	2.031–3.584	–6.06	2.00*	2.25
Selenodont Artiodactyla	AWT	SKA	24	0.988	0.62	0.578–0.663	2.06	0.67*	0.75*
	AWT	TRUA	23	0.968	0.58	0.513–0.650	3.06	0.67*	0.75*
	AWT	M^1A	22	0.973	0.60	0.536–0.669	3.45	0.67	0.75*
	SKA	TRUA	25	0.974	0.95	0.862–1.053	1.55	1.00	1.12*
	SKA	M^1A	24	0.981	0.98	0.895–1.069	2.23	1.00	1.12*
	CBL	TRUA	25	0.962	1.83	1.624–2.076	–3.21	2.00	2.25*
Cervidae	AWT	SKA	7	0.974	0.65	0.489–0.843	1.84	0.67	0.75
	AWT	TRUA	6	0.932	0.59	0.317–0.951	2.96	0.67	0.75
	AWT	M^1A	6	0.911	0.56	0.256–0.970	3.51	0.67	0.75
	SKA	TRUA	7	0.969	0.96	0.710–1.298	1.54	1.00	1.12
	SKA	M^1A	7	0.955	0.90	0.614–1.289	2.45	1.00	1.12
	CBL	TRUA	7	0.965	1.76	1.309–2.506	1.48	2.00	2.25
Bovidae	AWT	SKA	13	0.988	0.63	0.566–0.678	2.07	0.67	0.75*
	AWT	TRUA	13	0.983	0.62	0.548–0.623	3.00	0.67*	0.75*
	AWT	M^1A	12	0.974	0.62	0.526–0.729	3.44	0.67	0.75*
	SKA	TRUA	14	0.985	0.99	0.889–1.112	1.45	1.00	1.12*
	SKA	M^1A	13	0.985	0.99	0.883–1.115	2.20	1.00	1.12*
	CBL	TRUA	14	0.970	1.90	1.633–2.241	–3.45	2.00	2.25*
Ceratomorpha	AWT	SKA	7	0.990	0.58	0.493–0.683	2.90	0.67	0.75*
	AWT	TRUA	7	0.980	0.72	0.563–0.905	3.03	0.67	0.75
	AWT	M^1A	7	0.974	0.97	0.736–1.270	2.76	0.67*	0.75
	SKA	TRUA	7	0.988	1.24	1.039–1.486	0.21	1.00*	1.12
	SKA	M^1A	7	0.978	1.67	1.320–2.169	–0.27	1.00*	1.12*
	CBL	TRUA	7	0.967	2.72	2.071–3.854	–8.22	2.00*	2.25
Rhinocerotidae	AWT	SKA	5	0.991	0.64	0.488–0.815	2.74	0.67	0.75
	AWT	TRUA	5	0.903	0.62	0.104–1.573	3.55	0.67	0.75
	AWT	M^1A	5	0.877	0.54	–0.004–1.535	4.26	0.67	0.75
	SKA	TRUA	5	0.898	1.01	0.232–4.457	1.10	1.00	1.12
	SKA	M^1A	5	0.852	0.88	– –	2.23	1.00	1.12
	CBL	TRUA	5	0.804	2.00	– –	5.58	2.00	2.25

Adult intraspecific allometry

There is less data on intraspecific allometry of tooth size and body size published than one would perhaps expect. Klatt (1913), working with domestic dogs, published data on tooth size and skull length, and Williams (1955), also using dogs, gave an allometric equation relating molar row length to mandible length (Table 5). Although other published data presumably do exist, I have not been able to find any except those of Radinsky (1984) giving the relationship between upper toothrow length and braincase length in the domestic horse. My own material is of limited usefulness because tooth size is difficult to measure with sufficient accuracy in most ungulates because the crown bases are exposed only late in life. In many bovids I have actually found a weak negative correlation between skull size and tooth size (unpublished data), presumably because the youngest individuals which have the least erupted and least worn teeth (with maximum length dimensions) have not yet reached maximum skull size. My sample sizes tend to be small for species unaffected by this complication. Data for three such species are given in Table 5. The bear data are from the unpublished records of Björn Kurtén.

Ignoring the horse for a moment, there is a clear distinction between the two carnivores and the three ungulates; carnivores have negatively allometric teeth and ungulates positively allometric ones. Although correlations are weak (except for the domestic forms with their artificially expanded size ranges), the 95 % confidence limits exlude isometry in all cases when they are given or can be calculated. (The slope 5.44 for *Sylvicapra grimmia* goes with the very

Table 5. Intraspecific tooth size allometry in selected cases. Note difference between carnivores and ungulates. Abbreviations see p. 75.

Species	W	Y	*N*	*r*	*b*	95 % CL (*b*)	log *a*	Isom.	Source
Canis familiaris	CBL	P^4AL	37	0.967	0.63	0.573–0.688	1.030	1.00	3
Canis familiaris	MAL	MRUL	42	0.971	0.75	– –	–0.062	1.00	4
Ursus arctos	BL	M^1L	81	0.439	0.42	0.235–0.634	1.887	1.00	2
Diceros bicornis	SKA	TRUA	24	0.648	2.19	1.368–4.329	–3.914	1.00	1
Diceros bicornis	SKA	M^2A	24	0.674	2.50	1.626–4.695	–3.532	1.00	1
Equus caballus	BRCL	TRUL	18	0.952	0.69	– –	0.463	1.00	5
Hyaemoschus aquaticus	SKA	M^2A	31	0.525	1.95	1.081–4.880	–0.010	1.00	1
Sylvicapra grimmia	CBL	M^2L	79	0.249	5.44	2.810–46.225	–3.550	1.00	1

Sources: 1. = original data, 2. = Björn Kurtén unpublished, 3. = data from Klatt (1913), 4. = Williams (1955), 5. = Radinsky (1984).

low correlation coefficient of +0.25, and is almost certainly much too high.)

Radinsky's horses display strong negative allometry (exponent 0.69 of toothrow length against braincase length). If braincase length is negatively allometric to body size, as suggested above, the allometry becomes even more pronounced. But the domestic horse sample differs from the other ungulate samples in that it includes dwarfs, and this may account for the apparent anomaly. This point will be discussed in connection with dwarfism.

In no case does the intraspecific allometry correspond to the observed interspecific isometry, but it is premature to generalize from such limited data. It would be particularly interesting to know how tooth size scales with actual body mass within species, and whether the strong patterns of allometry perhaps reflect the scaling of skull size rather than the scaling of tooth size itself. A thorough study of the intraspecific scaling of tooth size might be rewarding. At present we may note that the observed intraspecific isometry is certainly not a trivial result of isometric scaling within species, and that it therefore would seem to reflect some higher-order constraint, such as functional or ontogenetic restrictions.

Ontogenetic relationships of the dentition

Tooth growth can be studied as a conventional problem of ontogenetic allometry, but that aspect is irrelevant here. Teeth do not begin to function until they have reached their final size, and the dentition can only grow by addition of whole teeth. However, one may consider the actual size of the row of erupted teeth as a function of body size during individual growth. A sample of 11 juveniles of *Diceros bicornis* gives the slope 0.85 (95 % confidence limits 0.305 to 2.054, $r = 0.71$, $\log a = 0.734$) for erupted toothrow length against condylobasal length. This is different from the positive allometry of the adults (Table 5), but the significance is unclear.

Radinsky (1984) demonstrated a very similar ontogenetic scaling of the distance between the last erupted cheek tooth and the first upper incisor to braincase length in domestic horse (slope 0.80). In this case, however, the scaling between adults was practically identical (slope 0.86). In the fossil horse sample these dimensions scaled at exponent 1.24. Discussion of this is in the next section.

Dwarfing

Gould (1975) suggested, based on the hypothesis of positive allometry of tooth size to body size, that dwarf forms might have relatively larger teeth than their full-sized ancestors. He investigated the living and two extinct species of pygmy hippo (the living *Hippopotamus amphibius* acting as a substitute ancestor) using skull length as an estimate of body size, and found that the dwarfs indeed had relatively larger tooth area than *H. amphibius*. The exponent of postcanine tooth area against basicranial length for *H. amphibius, H. lemerlei, H. minutus* and *Choeropsis liberiensis* was 1.75. Gould also cited Maglio's (1972) observation that the dwarf *Elephas falconeri* had relatively larger molars than its ancestor *Elephas namadicus*.

Prothero & Sereno (1982) wanted to 'test' this 'prediction' on Miocene dwarf rhinos from the Gulf coast of Texas and Florida, and claimed that their results falsified it both for the rhinos and the hippos, and that Gould had been misled by negative allometry of skull size to body size. Their results do not warrant such a conclusion, however. What they demonstrated was that skull size is negatively allometric to body size in suine artiodactyls and the 'Ceratomorpha'; i.e., the five living rhinos plus two living tapirs. As discussed above, the latter conglomerate may not be very relevant biologically since tapirs are rather inadequate models of small rhinos in terms of cranial and dental design. Similarly, pigs may not be satisfatory as models of dwarf hippos. Their suggestion that dwarfs have relatively smaller skulls rather than relatively larger teeth is interesting but not demonstrated.

Table 6. Tooth size – skull size allometry in the Rhinocerotidae and 'Ceratomorpha', according to different data sets. Abbreviations see p. 75.

Taxon	W	Y	*r*	*b*	95 % CL (*b*)	log *a*	*b'*	Isom.
Ceratomorpha	CPL	AWT	0.970	3.44	2.656–4.811	–18.03	3.26	3.00
(P&S)	TRUA	AWT	0.969	1.67	1.263–2.300	–5.58	1.59	1.50
	TRUA	CPL	0.976	2.07	1.626–2.761	–6.50	1.99	2.00
Rhinocerotidae	CBL	AWT	0.864	3.54	1.551– –44.701	–19.35	2.71	3.00
(P&S)	TRUA	AWT	0.868	2.62	1.073– –44.731	–11.78	2.06	1.50
	TRUA	CPL	0.927	1.35	0.596–4.071	–3.46	1.23	2.00
Rhinocerotidae	CBL	AWT	0.974	2.80	1.920–4.796	–14.40	2.67	3.00
(From Table 4)	TRUA	AWT	0.903	1.62	0.636–9.654	–5.75	1.40	1.50
	TRUA	CBL	0.804	2.00	– –	–5.58	1.42	2.00

P&S = Prothero & Sereno (1982); *b* = major axis slope, *b'* = least squares slope

Table 6 gives the relevant relationships for the 'Ceratomorpha' and for the Rhinocerotidae, calculated from the data given by Prothero & Sereno (1982) and from data taken from Table 4. No meaningful confidence limits may be given, but the best estimate for the rhinos is that (i) tooth area is isometric to skull length, and (ii) tooth area is slightly negatively and skull length slightly positively allometric to body weight. Since Prothero and Sereno do not give the appropriate measurements for their single complete dwarf rhino skull, it is impossible to say whether or not it would plot significantly off the line for the Rhinocerotidae.

Although it has not been mentioned in the recent literature, the idea that dwarfs have relatively larger teeth is of old standing. Indeed, it was "eine bekannte Tatsache" to Antonius (1922:254). Quantitative data in support of it concern tooth size relative to skull size, and isometry has usually been the implicit null hypothesis. Traditionally the problem was seen as one of domestication rather than of dwarfing, and it is conceivable that several factors are indeed involved (see below).

The first to suggest that dwarfs have relatively larger teeth may have been Leche (1904), who gave data for wild versus domestic yak and goat. Klatt (1913) gave data for domestic dog and Lundholm (1947) for domestic horse and insular versus mainland red deer. As noted above, Williams (1955) also gave data for domestic dogs and Radinsky (1984) for a domestic horse sample with a wide size range, including "a very small Shetland pony" of 36 cm skull length. In each case the smaller forms had relatively larger teeth. However, Leche (1904) also noted that domestic camels have relatively (and absolutely) larger molars than wild camels, although they are not themselves smaller. The possibility that domestication per se somehow causes relatively larger teeth (better nutrition?) cannot be ruled out, and more than one factor may well be involved. Lundholm (1947) showed that early (Bronze Age) horses had relatively the largest teeth, and that relative tooth size later decreased.

Radinsky's (1984) data suggest that in domestic horses ontogenetic and adult allometries of tooth size to skull size are identical; i.e., that adult horses of different sizes may be considered as points on an 'ontogenetic trajectory' describing changes in size and shape during individual growth (Alberch et al. 1979). However, the case is complicated by the problem mentioned above, that teeth do not grow continuously but are formed at a given size long before the skull has reached its final dimensions. In *Diceros bicornis* the relationship is apparently different from that of the domestic horse, and it would be valuable to know the situation in a wild horse population.

In view of the complexity of the problem and the almost total lack of data one should not jump to conclusions, but nevertheless two points suggest themselves: (i) domestic forms with artificially extended size ranges may not be applicable to problems of scaling in wild mammals, and (ii) positive allometry of tooth size to skull size between adults and negative allometry during ontogeny combined with large teeth in dwarfs suggest a phenomenon analogous to paedomorphism (retention of a juvenile state in the adult; see Gould 1977) as the cause of dwarfism. However, nothing requires that all dwarfism should be due to the same ontogenetic modification, and indeed such a situation appears highly unlikely. Roth (1984) found a mixture of paedomorphic and peramorphic (Gould 1977) traits in dwarf elephants.

Sexual dimorphism in tooth size and body size

In sexually dimorphic mammals cheek tooth size differs less between the sexes than body size (e.g. Gingerich 1981). Kay (1978) for primates and Lucas (1980) for various primates and bovids showed that smaller females have relatively larger teeth than larger males (see Table 7 for another example: *Kobus defassa*). Kay (1978) suggested that this might be due to higher energy requirements of females during pregnancy, but Lucas (1980) pointed out that

Table 7. Sexual dimorphism of skull size and tooth size in two bovid species. *Kobus* males are larger than females, while in *Ourebia* the reverse is true. In both cases tooth size is less dimorphic than skull size. Skulls from TE (App. 2). Abbreviations see p. 75.

	Sex	*N*	Mean	*SD*	95 % CL (mean)	% dimorphism
Kobus defassa						
CBL	♂	61	382.8	11.5	379.8–385.7	105.6
	♀	38	362.3	8.86	359.4–365.2	
M^2L	♂	61	22.34	1.27	22.02–22.67	101.6
	♀	38	21.99	1.16	21.61–22.38	
Ourebia ourebi						
CBL	♂	46	154.9	5.68	153.2–156.5	95.3
	♀	15	162.6	3.62	160.6–164.6	
M^2L	♂	46	11.8	1.18	11.50–12.20	100.8
	♀	15	11.7	0.91	11.22–12.22	
M^2W	♂	46	8.9	0.61	8.71–9.07	98.9
	♀	15	9.0	0.44	8.74–9.23	

males are known to possess higher metabolic rates for their weight than females (Benedict 1938, Morrison & Middleton 1965, Altman & Dittmer 1974 and Dale et al. 1970, all cited in Lucas 1980). Moreover, when the sexes are of equal size there is no dimorphism of tooth size, as might otherwise be expected (e.g. Gingerich & Ryan 1979). Lucas (1980) also suggested that when females are larger, the males are the ones with relatively larger teeth, and showed this for *Ateles geoffroyi*. My data for *Ourebia ourebi* (Table 7) support this suggestion.

It thus seems to be fairly well established that there is no one-to-one relationship between metabolic requirements and tooth size between the sexes, and that sexual dimorphism displays a similar intriguing negative allometry of tooth size to body size as dwarfing. Whether or not this means that processing capacity is unrelated to energy requirements at this level depends on the unknown sexual scaling of other relevant variables (see below).

4.1.3. Tooth size, body size and food comminution

Pilbeam & Gould (1974) were not the first to consider the scaling of tooth size in mammals in terms of food processing and metabolism. Simpson (1944, 1953) discussed hypsodonty in relation to body size in horse evolution and concluded that the two were independent although spuriously correlated because both increased (independently) in the same lineage. In this view, hypsodonty evolved in response to increased dental wear caused by grass eating. Huxley (1953), however, thought that the increased life span (and thus increased period of tooth use and wear) of the larger animals made higher teeth necessary, and this assumption is common in the literature.

Van Valen (1960) suggested that 'functional hypsodonty' (in principle, any adequate measure of a tooth's ability to tolerate wear while maintaining its functional efficiency) would scale with metabolic rate as $M^{3/4}$ (where M is body mass). Pilbeam & Gould (1974) and Gould (1975), who considered momentary rather than life-long metabolic requirements of food processing, suggested that post-canine occlusal area should scale similarly as $M^{3/4}$. As nothing requires that tooth shape remain constant there is no contradiction between the two statements. Since an area scales to a volume as $A = V^{2/3}$, Pilbeam's & Gould's 3/4 exponent signifies positive allometry of occlusal area to body mass. Van Valen's 'functional hypsodonty' is not fixed dimensionally, which means that no particular allometric relationship can be specified. If it were determined only by height, strong positive allometry ($M^{3/4}$ against isometry $M^{1/3}$) would be predicted. But if it is determined by volume, the predicted relationship is actually negative allometry ($M^{3/4}$ against M^1). If different mechanical properties of the dental tissues are involved, the relationship may take almost any form. It is clear, however, that Van Valen thought that hypsodonty would scale with positive allometry to body size when he wrote that ”It would be of interest to know ... whether hypsodonty ... [is] largely involved in the necessary compensation for increasing size...“ (Van Valen 1960:531). It is clear from the above that 'tooth size' may be several different things, depending on which aspect of the morphology of the tooth or biology of the animal is considered.

Gould (1975:361) described his paper as ”an unabashed plea for the entrance of more talent into an exciting and unexplored field“. A decade later one notes that the paper has been much quoted and discussed, chiefly by authors presenting data which seem to falsify the hypothesis of direct metabolic scaling of tooth area. As noted in the previous section, the accumulating empirical evidence now strongly suggests that isometry of tooth size to body size is the rule. It is, then, all the more surprising that theoretical discussion has been almost nil, and that no functional hypothesis explaining the widely observed isometry has been offered. Perhaps it has been felt that isometry requires no explanation, but one must agree with Gould that there is no compelling a priori reason to expect that particular relationship on theoretical grounds. Now that not only basal metabolic rate but a whole host of other physiological rates, including that of ingestion, are known to scale approximately as $M^{3/4}$ (Peters 1983), the need to explain the discrepancy between Van Valen's and Pilbeam & Gould's predictions on one hand and the empirical data on the other seems rather pressing.

A potential solution is offered by consideration of other biological correlates of size. To start with a simple case, Huxley's (1953) statement that the increased life span of large animals requires tooth height to scale with positive allometry to body size is, of course, testable. Peters (1983) compiled data from the literature to show that life span scales approximately as $M^{1/4}$ in mammals, which is less than the isometric relation of a linear mesasurement (height) of $M^{1/3}$. If life span alone is considered, negative allometry of tooth height to body size would thus be expected; the opposite of what Huxley thought.

The above conclusion is of obvious relevance to Van Valen's (1960) discussion of hypsodonty and life-long food requirements, since both metabolic rate and life span influence these. That is, an animal will need energy at a certain rate for a certain length of time, which defines the total amount of energy (and food) needed. This presumably in turn determines the total sum of tooth wear. If just metabolic rate and life span are considered, 'functional hypsodonty' would be expected to scale as $M^{3/4} \times M^{1/4} = M^1$; i.e., isometrically with body mass. This is consistent with Simpson's (1944, 1953) view that hypsodonty has evolved independently of body size.

As to the more complicated matter of tooth size and processing capacity, it is useful to recall the essentials of food comminution (Sect. 3.2.1.). For each food there exists a critical stress at which it breaks, and stress is independent of absolute size (since it is determined by load proportional to muscular (physiological) cross sectional area and by occlusal area, both scaling approximately as $M^{2/3}$). Breakage is thus in principle independent of absolute tooth size. Breakage also appears to be independent of particle size for the range involved in chewing (Lucas & Luke 1983a).

Selection decreases with decreasing particle size and beyond a lower size limit chewing no longer pays (Lucas & Luke 1983a). As discussed above (Sect. 3.2.1.), this may be interpreted in terms of relative rather than absolute particle size; i.e., as a limit in the ratio of particle size to the size of the occlusal surface (the comminuting equipment). If this is correct, selection, too, would be effectively independent of absolute size. Testable predictions can be derived from the above. For example, for a given dental design and food, the number of chews before swallowing should be constant and independent of absolute tooth size, and particle size at corresponding stages (for example at swallowing) should be isometric to tooth size.

Gould (1975) assumed that the volume processed per chew would scale as occlusal area, for isometric teeth as $M^{2/3}$. Since this assumption is crucial to the whole hypothesis of direct metabolic scaling of tooth size, it is worth examining in some detail. Consider a body of food trapped between upper and lower toothrows. When the teeth move into occlusion, the food is first deformed and then separated into a number of smaller portions, some of which end up between blades or at other 'comminuting locations'. If all such selected particles break, the volume comminuted will depend on selection; i.e., area. But consider the entire system in several sizes: is there any reason to suppose that the shape of the body of food between the teeth will change as the teeth become larger or smaller? I believe not, except for foods that consist of particles that must be treated as individuals (for example, nuts). For foods that can be shaped into a bolus in the mouth and manipulated as a plastic mass during chewing it is reasonable to assume that, for a given occlusal morphology, the body of food placed between the occlusal surfaces before each power stroke will be of a constant shape. If so, and if particle size at corresponding stages of comminution is isometric to tooth size as suggested above, it is difficult to see how the volume comminuted per stroke could be proportional to area. A more reasonable assumption is that it is proportional to the volume placed between the teeth, which for isometric teeth will scale as M^1.

If the volume comminuted per chew scales as M^1, larger animals will need relatively fewer chews per unit time to satisfy their metabolic requirements scaling as $M^{3/4}$. They might spend less time during the day chewing, or they might chew more slowly, or both. These hypotheses are testable. Since it is a matter of common knowledge that small animals chew faster than large animals, it may be a reasonable hypothesis that the compensation occurs mainly via chewing rate. All else being equal, chewing rate should scale as $M^{-1/4}$ for comminution rate to scale with metabolic rate and ingestion rate as $M^1 \times M^{-1/4} = M^{3/4}$. Chewing cycle duration should then scale inversely as $M^{1/4}$.

The durations of various biological phenomena, for example, heartbeats and breaths, do in fact scale as $M^{1/4}$ in mammals (Peters 1983), but chewing cycle durations do not appear to have been investigated in this respect. Hiiemäe (1978) compiled a table of data then available, and concluded that no relationship exists between chewing rate and body size. However, her data were for mammals diverse in their taxonomy and diet, and any relationship might well

Table 8. Major axis regression of chewing cycle duration (ms) on body weight (kg). Log–transformed data from App. 6 (A) and Hendrichs 1965 (H).

Group	N	r	b	95 % CL (b)	log a
Fresh chewing (A)	12	0.91	0.23	0.16–0.31	1.15
Fresh chewing (A[1])	10	0.85	0.19	0.10–0.29	1.44
Fresh chewing (H)	16	0.79	0.13	0.07–0.19	1.67
Cud chewing (A)	12	0.91	0.22	0.15–0.29	1.46
Cud chewing (H)	16	0.86	0.16	0.10–0.21	1.58

[1] Rabbit and pig omitted.

be masked by factors unrelated to size. Even in single individuals, chewing cycle durations are influenced by the kind of food eaten, the time of day etc. (Hendrichs 1965, De Vree & Gans 1975). Hendrichs (1965) presented data on chewing rates for a wide range of ruminants, but about half of his larger species chew the cud at precisely one chew per second, suggesting that his data may not be sufficiently accurate for the present purpose. Analysing his data gives positive correlations of 0.79–0.86 between chewing cycle duration and body weight, and major axis slopes of 0.13–0.16 (Table 8).

Data on chewing cycle durations collected by myself at the Zoo of Helsinki (App. 6) give both higher correlations and higher slopes (Table 8). If data for rabbit and miniature pig taken from the literature are included, fresh chewing gives a correlation of +0.91 and a slope of 0.23. If rabbit and pig are omitted, lower values are obtained ($r = +0.85$, $b = 0.19$). Rumination probably helps to standardize conditions of chewing, and it is interesting that cud chewing gives a correlation of +0.91 and a slope of 0.22. (Table 8). Except for the data from Hendrichs (1965), which may not be sufficiently accurate, all the data sets give 95 % confidence intervals for the slope that contain the predicted value of 0.25. Considering that so many other factors must be involved, this is almost surprising. Certainly the hypothesis can not at present be rejected.

It is interesting to calculate that if processing capacity per stroke would scale as $M^{3/4}$, as predicted by Pilbeam & Gould (1974), and chewing rate as $M^{-1/4}$, volume processed per unit time would scale as $M^{1/2}$, leading to an immediate energy crisis in large animals with a metabolic rate scaling as $M^{3/4}$. This seems to falsify the hypothesis that volume comminuted per stroke scales with occlusal area, and thus the foundation of the hypothesis of direct 'metabolic' scaling of post-canine tooth area.

It seems, then, that isometry of occlusal area to body size is in fact also true metabolic scaling, and an acceptable 'null hypothesis' for comparisons. In the form in which it is presented here it is clearly distinct from the naive misconception criticized by Gould (1975), that geometric similarity as such would imply functional similarity. Geometric similarity prevails for reasons which may or may not be related to function (see below), and functional similarity is achieved through other than morphological means, as in this case through rates. It follows that it is impossible to consider the problem in terms of morphology and size alone, since that excludes a major part of the relevant information. The same applies to predictions, which may be quite specific, derivable from the present model. For example, one may predict that non-isometric scaling will be found when the diet of the animal consists of foods which cannot be manipulated as a plastic mass during chewing, or when the timing of the feeding is very restricted and/or chewing rate does not scale as $M^{-1/4}$. It would be interesting to investigate intraspecific scaling of chewing rate to find out whether or not it is related to the observed tooth size allometry. In particluar it might be rewarding to study chewing in carnivores and ungulates, to see whether the difference in tooth size allometry (negative in carnivores, positive in ungulates) tentatively noted in the previous section, corresponds to differences in chewing rate. Such a difference might, for example, reflect differences in mechanical properties of plant and animal foods.

3.1.4. Why is isometry so common?

Since ratios between parameters of different dimensionality change with isometric size change, isometry in the sense of geometric similarity can not be generally equivalent with functional similarity. For this reason, Gould (1971:129) considered it "a problem, not an expectation". I have tried to show above that functional similarity of isometrically scaled systems can be obtained by changes in the time dimension, and that this applies at least to the masticatory apparatus. In this section I will offer some speculation as to why isometry is so general in mammalian design.

Gould (1971) suggested two reasons for why isometric scaling would be common. First, that proportional size changes are commonly associated with simple genetic and hormonal changes which might permit rapid evolution of size in response to environmental change. Second, that it might improve functional performance, for example when functional similarity requires 'only' negatively allometric size increase of an organ (e.g. the brain). This second argument obviously cuts both ways since isometric size increase (or decrease) may equally well result in impaired function. In the brain, isometric size increase will improve 'encephalization', while isometric size decrease will impair it. If one accepts that animals are well designed as a rule, it seems unlikely that isometric size change would improve net overall functional performance.

D'Arcy Thompson (1917) pointed out that absolute jumping height in animals of similar design is independent of absolute body mass. Similarly, occlusal stress is independent of absolute size for isometrically scaled teeth and jaw muscles (Sect. 3.2.1). Given that required critical stress is determined by the food, it would seem that isometric scaling of the whole masticatory apparatus is to be expected, at least unless there is a systematic size-dependence of food strength. Such does not appear to be the case; grazers, for example, are found in all size classes. On the other hand, energy requirements (metabolic rate) would, ceteris paribus, require a negatively allometric scaling of tooth area. This points to a general problem of considerable theoretical importance: functional similarity in one sense (breakage) has different scaling requirements from functional similarity in another sense (rate of comminution). In other words, there is *no* scaling that will result in functional similarity at different sizes. In the case of food comminution, breakage requires a certain stress, and changes in timing can not alter this fundamental fact. In contrast, the rate of comminution can be altered by a changed chewing rate, and this is what is observed. It is conceivable that the principle could be generalized to cover size-dependent rates and durations in general, such as life span and metabolic rate, but that is not within the bounds of the present investigation.

The principle of nested growth, or the "production of parts in existing parts" (Woodger 1945:100), is another reason why general isometry in animals sharing a basic 'Bauplan' is to be expected. Spatial constraints during growth (and related phenomena such as the diameters of exit apertures) do not allow changes in proportions that would make the part nested inside another part relatively much larger. For surfaces, the well-known increase of folding offers an escape, but no such possibility is available for volumes. It follows that major size changes must be nearly isometric for nested organs (unless it is allometric in the other direction, which may then cause problems due to empty space). Of course, this principle would not apply to structures growing outside the body, such as horns and antlers, which do seem to be positively allometric to body size as a rule.

Growth and function of individual organisms is not so tightly constrained, however, as can be seen in the considerable variation in populations. One needs only to think of perfectly viable three-legged dogs or one-legged birds, or the variety of foods that can be successfully consumed by many animals, to realize that a considerable functional buffering or overcapacity is the rule during relaxed environmental circumstances, both among wild and captive animals. The constraints on proportions discussed above apparently apply to much greater size ranges than those normally covered by species or even genera. If the relationship exists at these levels it is obscured by other factors and by individual variation.

In summary, I propose that isometry at high taxonomic levels reflects two main circumstances. First, that *no* scaling of size alone will necessarily result in functional similarity at different sizes. Factors such as stress, which are ratios between equidimensional parameters (e.g. areas), are similar only with isometric scaling, while factors involving time can be altered by changing rates and durations. Second, that nested growth of organs precludes major changes in proportions without producing cascading effects on the whole body plan. (Such changes have probably occurred, but we may not recognize them as 'allometric'. Perhaps some morphological discontinuities between taxa correspond to this type of reorganization?) These principles apply to the higher taxonomic levels, or, perhaps more properly, to wide size ranges. The occurrence of proportional dwarfs due to simple mutations would result in isometric scaling, too (Gould 1971), but that mechanism predicts isometric scaling at lower levels also, which is not observed.

4.1.5. *Body size and spatial constraints on growth*

From fertilized ovum to full-grown adult, an elephant clearly has a longer way to grow than a mouse. This applies both to absolute mass increase and the number of mitoses (see e.g. Thompson 1917). It is also known that large mammals tend to have relatively smaller young than small mammals (Leitch et al. 1959). Peters (1983) compiled data from the literature giving least squares slopes between 0.71 and 0.95 for birth weight to adult body weight for mammals in general. For a sample of 21 species of ungulates taken from the literature, a major axis slope of 0.80 is obtained, significantly lower than the isometric 1.00 (Table 9). Since tooth size is isometric to adult body size, it should be positively allometric to birth size, and this is what is observed. Positive (though statistically insignificant) allometry is indeed found for all dental dimensions studied (Table 9). The same is true for skull size, which is interesting, since the brain grows with nega-

Table 9. Relationships between birth weight, adult weight, skull size and tooth size in a sample of ungulates (App. 1–2). Larger species have relatively smaller young, but adult skull size and tooth size is positively allometric to birth size. This presumably accounts for the isometry observed in adults. Abbreviations see p. 75.

W			*r*	*b*	95 % CL (*b*)	log *a*	Isom.
AWT	BWT	21	0.939	0.80	0.671–0.958	2.060	1.00*
BWT	CBL	22	0.950	0.35	0.299–0.408	3.007	0.33
BWT	SKA	22	0.926	0.72	0.595–0.826	0.450	0.67
BWT	TRUL	21	0.909	0.35	0.273–0.426	3.139	0.33
BWT	TRUA	21	0.901	0.77	0.606–0.969	1.250	0.67
BWT	M^1A	20	0.912	0.82	0.651–1.021	1.719	0.67
BWT	M^2A	20	0.903	0.81	0.633–1.020	1.676	0.67
BWT	M^3A	20	0.853	0.77	0.559–1.042	1.795	0.67

tive allometry to the body. Positive allometry of skull size to birth size suggests that the growth of the face and jaws is scaled to that of the teeth. Functional teeth are needed at weaning at the latest, and weight at weaning scales to adult weight at least squares slope 0.73 in mammals (Peters 1983).

One could thus hypothesize that the teeth of large mammals begin to grow in relatively smaller jaws than those of small mammals, and this might constitute a general constraint on the proportions of the dentition. A plausible specific hypothesis is that the teeth that begin to form first in the largest mammals should be most affected and the ones that begin to form last in the smallest mammals should be least affected, all else being equal. Thus, early forming teeth should be negatively allometric to late forming teeth in a sample of sufficient size range and unity of design for the constraint to have a measurable influence.

As noted above (Table 3), at the level of 'all ungulates' no such allometry is detected, nor is it within the bovid sample (unpublished data). But the data are not conclusive since they do not include height, which may be the critical dimension. Gingerich et al. (1982) found that in primates M1 is negatively and M3 positively allometric to body size, but did not consider growth constraints as a possible explanation.

If large mammals have relatively smaller young with relatively smaller jaws, this should affect the proportions between milkmolars and the premolars which replace them. Few researchers have bothered to measure milkteeth systematically, but Guérin (1981) gives data for six species of Plio-Pleistocene European rhinoceroses (see Table 10; "*Dicerorhinus*" *etruscus etruscus* and "*D.*" *e. brachycephalus* are perhaps distinct enough to be treated as species). Six species is too small a sample to allow great confidence, but the correlations are high and the major axis estimates plausible. Table 10 can be summarized as follows:

1. Taken as blocks the milkteeth are negatively allometric to the premolars ($b = 0.81$). The larger the animal, the relatively larger the premolars.

Table 10. Allometry between deciduous molar and premolar size (length × width) in six species of Plio–Pleistocene rhinoceroses: "*Dicerorhinus*" *megarhinus*, "*D.*" *etruscus etruscus*, "*D.*" *e. brachycephalus*, "*D.*" *hemitoechus*, "*D.*" *kirchbergensis*, *Coelodonta antiquitatis*. Data from Guérin 1980.

Teeth (W:Y)	*r*	*b*	95 % CL (*b*)	log *a*
Premolars:milk molars	0.98	0.81	0.59–1.08	0.84
P^2:D^2	0.61	0.98	–	0.10
P^3:D^3	0.93	0.59	0.30–0.97	1.12
P^4:D^4	0.85	0.78	0.15–2.40	0.78
D^4:D^3	0.90	0.91	0.38–2.01	0.42
P^4:P^3	0.99	1.23	0.99–1.54	–0.67

2. P^2, which is a small, incompletely molarized terminal tooth, is isometric to dm^2.

3. dm^3 is strongly (and even at this sample size significantly) negatively allometric to P^3 ($b = 0.59$), whereas dm^4 is much less ($b = 0.78$) negatively allometric to P^4. As noted above (Sect. 3.4.2), the first cheek teeth to erupt in rhinoceroses are dm^3 and dm^2; dm^4 erupts distinctly later and grows in a larger jaw.

4. dm^3 is slightly negatively allometric or isometric ($b = 0.90$) to dm^4, which suggests that the growth constraint on the milkteeth is not strongly size dependent.

5. P^3 is positively allometric to P^4 ($b = 1.23$), indicating that the main change involved is an increase in the size ratio P^3/P^4 relative to dm^3/dm^4. Why P^3 should be more constrained in smaller forms than in larger ones is unclear, and this result is in conflict with the prediction. It must be noted, however, that the sample includes part of what is either a lineage or a series of closely related forms, and other interpretations are possible.

It is not necessary to postulate a general size relationship for spatial constraints on growth. Kingdon (1979) has argued persuasively that the increase in relative size of M3 from brachydont to hypsodont in the pigs *Potamochoerus porcus*, *Hylochoerus meinertzhageni* and *Phacochoerus aethiopicus* is related to growth constraints. Gould (1975) noted the greatly enlarged last molar of the capybara (*Hydrochoerus hydrochoeris*), and suggested that it was large in order to produce "enough tooth area". The pattern seems to be fairly common among hypsodont ungulates, suggesting that relative tooth size (height) is a more important factor than absolute size. A strong subjective impression (which I share with many colleagues) is that sheep and goats have relatively large third molars; in the fossil record a more obvious example is the stenomyline camels (see e.g. Frick & Taylor 1968). The small, hypsodont toxodontid notoungulate *Nesodon ovinus* also had relatively very much enlarged third molars compared with the larger, less hypsodont and better known *N. imbricatus*. The hypsodont equids are apparently a counterexample, and the principle, if it applies, is clearly less than universal.

An example involving a strong size factor would be the Ursidae, which have unusually small neonates (e.g. Eisenberg 1981), and wide teeth set in narrow jaws. Kurtén (1976) illustrated the relative increase in size of M_3 in the morphological series *Ursavus elmensis* – *Ursavus depereti* – *Ursus etruscus* – *Ursus arctos* – *Ursus spelaeus*, which corresponds to a marked increase in absolute size. Kurtén favoured the functional interpretation of increased herbivory, but the ontogenetic explanation is an alternative possibility. Nothing, of course, precludes that both are involved. Within the species *Ursus spelaeus* M_3 is strongly positively allometric to M_2, with a reduced major axis slope of 1.62 (Kurtén 1967). The similarity of ontogenetic and phylogenetic relationships could be read as evidence that ontogenetic constraints have influenced evolution.

I argued previously (Fortelius 1982) that hypsodont rhinoceroses have relatively larger last molars than brachydont ones because the last molars are better positioned for "grinding" grass, but the positional argument has been shown to be geometrically suspect by Greaves (1978), and I would now favour the ontogenetic explanation of growth constraints affecting the anterior molars more than the posterior ones.

4.2. Relative tooth width and functional categories

4.2.1. Rationale

Given that opposing surfaces are required for food comminution, one can predict that the greater the component of lateral movement is during the power stroke, the greater will be the difference in width between upper and lower teeth. In principle, either the upper or the lower teeth might be wider, but in practise it is almost always the uppers. This probably ultimately reflects the functional demand to keep the mandible as light as possible, although other explanations are conceivable (for example in terms of food circulation).

Recall that relationships exist between the path of movement during the power stroke and the proportions of muscle masses (Sect. 3.3). Thus the possibility exists that simple relative width of teeth might distinguish quantitatively not only between dental morphological categories but also, or perhaps primarily, between functional categories in the design of the whole masticatory apparatus.

4.2.2. Materials and methods

In order to investigate this possibility, I obtained width data for upper and lower molars from a sample of 483 species of recent and fossil 'herbivorous' mammals (details in App. 5). In order to be able to use data from the literature, I had to use maximum basal width, which is clearly not an ideal estimate of occlusal width. Yet for two reasons it may be better than might at first appear. First, in many ungulates at least, occlusal width is clearly related by gradual wear to basal width. Second, the widest parts of serially homologous teeth tend to occlude with each other. For example, in a typical rhinoceros such as *Diceros bicornis*, the upper molars are widest over the protoloph and the lower molars over the talonid, which are roughly the parts that occlude. In the case of M3 this second point is not always true, however. I did not use relative widths of premolars for this preliminary study because the varying degree of molarization introduces complications which would be difficult to handle at this stage. I chose M2 rather than M1 simply because the number of samples was larger. For macropod marsupials I used M3, which has the analogous position to M2 in placentals. (Sometimes I had to substitute M2 when data for M3 were not given.) For proboscideans I used M3 because very few data were available for other teeth. For manatees I used the last erupted tooth but one. I do not consider that this will affect the results in any relevant way.

The relative width of upper and lower teeth can be expressed as a simple index, obtained by dividing upper with lower width. I propose to call this the 'index of anisodonty' (*ADI*). Thus:

$$ADI = W_u / W_l,$$

where *W* is maximum tooth width and the subscripts refer to upper (u) and lower (l) serially homologous teeth, respectively. The derivation of the name is by analogy with anisognathy, which refers to unequal spacing of upper and lower toothrows (see below). Surprisingly enough, the term does not appear to be

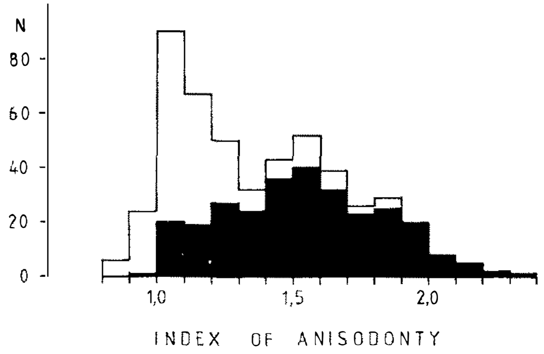

Fig. 27. Distribution of the index of anisodonty (ADI) in the whole sample. The distribution in the ungulate subsample is shown in black. N = number of species. See Table 11 for taxa included.

in earlier use. Anisodonty thus signifies unequal width of upper and lower teeth. The special case of equal width can be called isodonty (*ADI* = 1), while wider upper teeth will be referred to as positive anisodonty (*ADI* > 1) and wider lower teeth as negative anisodonty (*ADI* < 1). Because of the nature of the data one cannot expect any particular distribution of *ADI*, so statistical testing is difficult. However, the results are, on the whole, sufficiently unambiguous for interpretation even without the support of statistics.

4.2.3. Relative tooth width

Fig. 27 shows the distribution of *ADI*(M2) in the whole sample, and separately for ungulates. The whole sample has a trimodal distribution, with peaks at the 1.00–1.09, 1.50–1.59 and 1.80–1.89 classes. The same three peaks are distinguishable in the ungulate sample, and in addition there is a fourth peak at the 1.20–1.29 class. The distribution of *ADI* within selected groups shows that these peaks correspond to recognized morphological categories (Fig. 28). Thus the 1.00–1.09 peak mainly consists of forms that have molars with distinct transverse cutting edges and palinal chewing (Group I in Fig. 28). The 1.20–1.29 peak includes a considerable range of bunodont and bilophodont forms (Group II in Fig. 28). The two are not separated by *ADI*, and indeed in the whole material the first two peaks are united, showing that in terms of translation the bilophodont-bunodont group and its modifications are one complex. In contrast, the third peak at 1.50–1.59 stands out clearly and is shown to consist largely of selenodont artiodactyls (Group III in Fig. 28). The fourth peak, at 1.80–1.89, is made up of the various trilophodont and ectolophodont forms (Groups IV and V in Fig. 28). It is possible to distinguish subgroups: the equids and palaeotheres, which tend towards seleno-lophodonty, peak at 1.70–1.79, while the ectolophodont rhinocerotids (Group V) peak at 1.90–1.99.

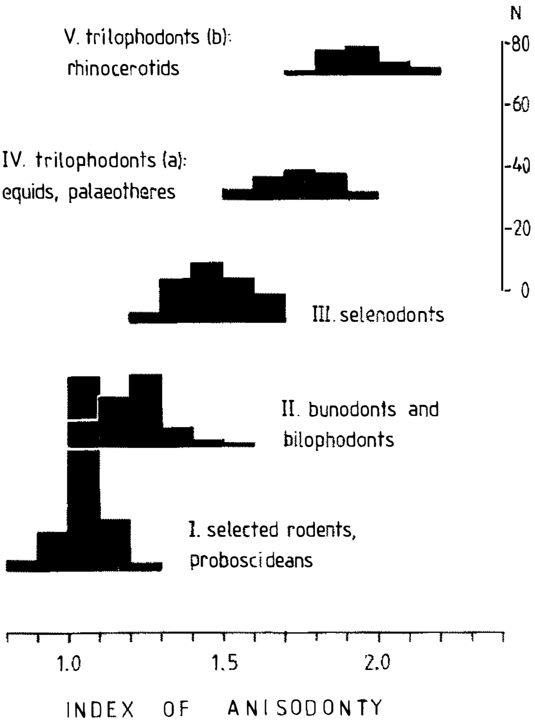

Fig. 28. The distribution of the index of anisodonty (ADI) in selected groups. N = number of species. The taxa included in the different groups are:
I. Heteromyidae, Cricetidae, Muridae, Proboscidea
II. Macropodidae, Diprotodontidae, Ursidae, Suidae, Tayassuidae, Tapiriidae, Dinocerata, Sirenia
III. Camelidae, Giraffidae, Cervidae, Bovidae
IV. Equidae, Palaeotheriidae
V. Rhinocerotidae

Table 11 gives the mean values of ADI(M2) for the taxa included in this analysis. Readers familiar with the groups will note several interesting features. Thus the most primitive forms (the 'condylarths' and the microsyopid, plesiadapid and adapid primates) have values clustering about 1.4–1.6. The strongly ectolophodot forms (rhinocerotoids, astrapotheres and some of the subungulate families) all have high values, at about 1.8–2.1. The trilophodont tapiroids (Lophiodontidae, Helaletidae) have an ADI-mean in the 1.7 region (together with chalicotheres, palaeotheres, equids, litopterns and procaviid hyraxes), while the bilophodont Tapiridae have a mean at 1.4 (corresponding to that of indriid primates, various suiform families, coryphodonts and sirenians). It is probably prudent to be conservative about interpretation of details at this stage, however.

Table 11. The index of anisodonty for second molars, ADI(M2), for selected taxa. N = number of species. Data see App. 5.

	N	ADI	*CV*
Marsupialia (ADI(M2,3))	19	1.22	6.5
Macropodidae	13	1.18	4.5
Diprotodontidae	6	1.29	6.4
Primates	42	1.43	15.8
Microsyopidae	5	1.61	3.9
Plesiadapidae	10	1.54	2.4
Adapidae	5	1.60	4.3
Indriidae	8	1.29	11.5
ibid. excl. *Archaeolemur*	5	1.36	3.9
Hominoidea s.l.	10	1.14	7.8
Australopithecus + *Homo*	3	1.06	0.9
Rodentia	147	1.06	8.7
Paramyidae	8	1.14	2.7
Ischyromyidae	6	1.15	9.1
Sciuridae	12	1.12	6.0
Castoridae	3	0.90	4.0
Heteromyidae	18	1.01	9.9
Theridomyidae	6	1.19	7.7
Gliridae	10	1.11	5.0
Cricetidae	33	1.03	3.9
Muridae	24	1.08	5.4
Hystricidae	6	0.94	6.8
Carnivora			
Ursidae	7	1.20	5.1
Artiodactyla	108	1.41	5.1
Dichobunidae	3	1.48	4.9
Leptochoeridae	2	1.50	–
Entelodontidae	3	1.45	4.3
Anthracotheriidae	2	1.58	–
Hippopotamidae	4	1.32	6.8
Suidae	12	1.23	6.4
Tayassuidae	9	1.12	8.0
Agriochoeridae	3	1.60	1.3
Merycoidodontidae	2	1.47	–
Oromerycidae	4	1.72	12.3
Camelidae	11	1.38	6.9
Protoceratidae	5	1.53	4.6
Tragulidae	2	1.60	–
Hypertragulidae	2	1.58	–
Leptomerychidae	2	1.61	–
Cervidae	13	1.46	10.0
Giraffidae	2	1.41	–
Bovidae	28	1.44	5.6
"Condylarthra"	14	1.52	9.1
Arctocyonidae	7	1.51	8.2
Phenacodontidae	2	1.44	–
Hyopsodontidae	3	1.54	1.9
Meniscotheriidae	2	1.63	–
Tillodontia			
Esthonyx	2	2.02	–
Tubulidentata			
Orycteropus	3	1.00	0.6
Litopterna	8	1.70	8.8
Proterotheriidae	6	1.72	5.7
Macraucheniidae	2	1.67	–
Notoungulata	16	1.81	22.7
Oldfieldthomasiidae	3	2.19	14.7
Isotemnidae	2	2.14	–
Homalodotherium	1	1.89	–
Leontinidae	2	2.14	–
Notohippidae	2	1.52	–
Toxodontidae	2	1.30	–
Hegetotheriidae	2	1.33	–
Astrapotheria	2	2.11	–
Perisodactyla	75	1.79	9.6
Tapiroidea excl. Tapiriidae	14	1.70	6.7
Tapiriidae	3	1.44	5.6
Hyracodontidae	2	1.73	–
Rhinocerotidae	24	1.94	5.3
Amynodon	1	2.11	–
Equidae	17	1.72	4.7
Palaeotheriidae	11	1.77	7.7
Chalicotheriidae	2	1.77	–
Pantodonta	8	1.82	10.6
Pantolambdidae	2	1.88	–
Barylambdidae	5	1.88	4.5
Coryphodon	1	1.40	–
Dinocerata			
Tinoceras	1	1.27	–
Sirenia			
Trichechus	2	1.30	–
Proboscidea (ADI(M3))	19	1.07	4.6
Gomphotheriidae	3	1.08	1.9
Zygolophodon	1	1.04	–
Stegodontidae	2	1.14	–
Elephantidae	13	1.06	4.8
Hyracoidea			
Procaviidae	10	1.61	6.6
Kvabebihyrax	1	2.00	–

4.2.4. Anisodonty and chewing mechanics

In chewing it is of course the movement in three dimensions that is of interest, rather than the component of lateral movement resolved into the horizontal plane. A major distinction exists between forms in which the occlusal surfaces dip towards buccal all the way (corresponding to a continuously dorsally plunging path of the power stroke), and forms in which such is not the case (Fig. 13). As discussed by Becht (1953) and Greaves (1980), the reason is that when the occlusal surfaces dip towards buccal the animal can use both working- and balancing-side masseters throughout the power stroke (see above Sect. 3.3.2). When the surfaces are horizontal, and particularly when there are lingually dipping phase II surfaces, this is not the case, and the pterygoids assume a crucial function. For the latter group the point beyond which the mandible cannot be pulled further towards mediad must be determined by the working angles of the pterygoids, but no similarly distinct limit needs to exist in the former (essentially selenodont artiodactyls plus *Equus* of the living ungulates). It follows that increased lateral movement

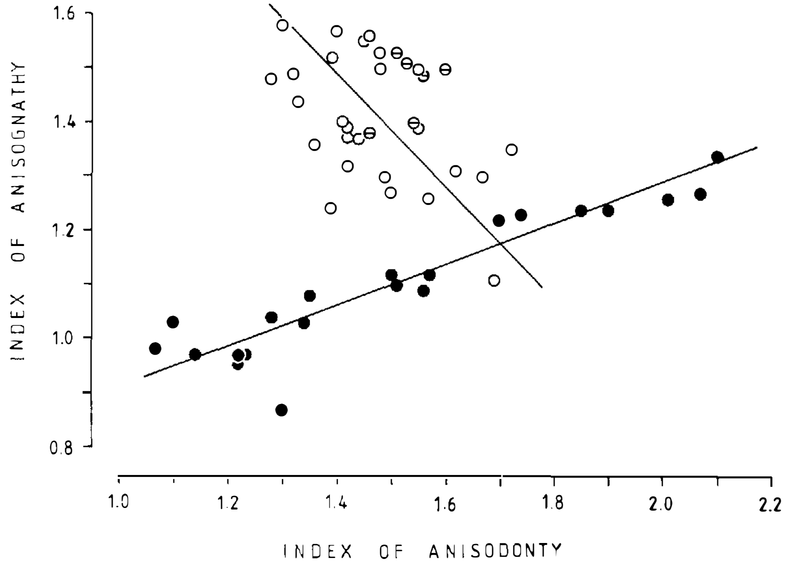

Fig. 29. Major axis regression of the index of anisognathy (AGI) on the index of anisodonty (ADI) for two groups of ungulates. Black circles are bunodont forms and lophodont forms with a two-phase occlusal morphology. Empty circles are selenodont artiodactyls. Split circles are *Equus*. Discussion in text.

can come about in different ways in the two groups: whereas the 'unlimited' group can expand the upper tooth either buccally or lingually, the 'pterygoideus-limited' group can only expand the upper tooth towards buccal to increase lateral movement. A specific prediction is that a strong positive correlation between anisodonty and anisognathy (the relative spacing of the toothrows) will be found in the latter, but no in the former group.

To test this prediction we need a measure of anisognathy. To measure spacing independently of tooth width we may take the distance between the buccalmost parts of left and right teeth, and subtract one (= two halves) toothwidth from that. The index of anisognathy (*AGI*) is the ratio of upper to lower spacing of serially homologous teeth. Formally:

$$AGI = D_u - W_u \,/\, D_l - W_l,$$

where D is buccal-to-buccal distance between left and right teeth, W is tooth width and the subscripts refer to upper (u) and lower (l) jaws and teeth. I used first molars, which are usually the most widely spaced teeth in the upper toothrows of ungulates, but other molars ought to give a similar result if the hypothesis is correct.

Fig. 29 shows a plot of *ADI*(M1) against *AGI*(M1) for a sample of ungulates (App. 2). It is immediately obvious that the prediction is gloriously fulfilled: the correlation for the heterogeneous group excluding selenodont artiodactyls and *Equus* is +0.92 ($P < 0.001$), while the selenodont plus horse group has a correlation of –0.44 ($P < 0.05$) (Table 12). None of the four dimensions included in *ADI* and *AGI* is significantly allometric to any of the others, nor to skull size or body size (unpublished data), and the result is unlikely to reflect some trivial relationship external to the argument. Neither can it be an artefact of incorrectly measured spacing of lower teeth in forms with an unossified mandibular symphysis, since the horses and camels plot with the other selenodonts. If the negative correlation in this group is a real phenomenon it has interesting implications beyond the original hypothesis (see below).

To understand the result in more detail, it is useful to consider the influence of the 'correction term' (i.e. tooth width) included in *AGI*. If this term is eliminated and the 'uncorrected' buccal-to-buccal distances are used as such, the negative correlation is decreased to insignificance in the selenodont-plus-horse group, while the positive correlation is somewhat increased in the other group (Table 12). The most parsimonious explanation of this pattern is that anisodonty changes by buccal expansion or reduction in the bunodont-lophodont forms, but by lingual expansion or reduction in the selenodont-plus-horse group. Increased *ADI* thus leads to increased *AGI* in the former (the ratios between distances and between widths both increase), but to decreased *AGI* in the latter (buccal-to-buccal distance remains unchanged but the ratio between the 'correction terms' is increased).

As in the case of tooth size relationships, the strong correlation between *ADI* and *AGI* in lophodonts is a phenomenon of extended size ranges and/or higher taxonomic levels. An intraspecific plot of *ADI* against *AGI* for *Diceros bicornis* gives no significant correlation ($N = 28$, $r = -0.29$). The nature of the pterygoideus-vector hypothesis, used above to explain the observed relationships, is such that it must exist at all taxonomic levels. Either individual

Table 12. Relationships between relative width and spacing of upper and lower molars in ungulates. ADI = index of anisodonty, AGI = index of anisognathy. See discussion in text.

Group/index	*N*	*r*	*P*(*r*)	*b*	95 % CL (*b*)
Bunodonts and lophodonts (excluding *Equus*)					
AGI:ADI	21	0.92	<0.001	0.38	0.31–0.46
'buccal-to-buccal':ADI	21	0.96	<0.001	0.50	0.44–0.57
Selenodonts plus *Equus*					
AGI:ADI	32	–0.44	<0.05	–0.98	–2.58– –0.37
'buccal-to-buccal':ADI	32	–0.24	–	–0.35	–1.54– –0.33

variation occurs within limits which are wide enough to obscure the functional pattern that is apparent at higher levels, or the hypothesis is false. The present data are not sufficient to decide between these alternatives.

4.2.5. Evolutionary significance

It is possible to use the results discussed above to interpret evolutionary changes in dental morphology in relation to chewing mechanics.

The cheek teeth of primitive representatives of most placental orders were quite similar, not far removed from the tribosphenic type but with some beginning differentiation between carnivores with more vertical wear facets and herbivores with more horizontal ones (Butler 1972). One of the latter is the Late Cretaceous condylarth *Protungulatum*, which is probably close to the origin of all ungulates, at least morphologically. Later condylarths and early representatives of at least artiodactyls and perissodactyls have basically similar cheek teeth, with varying stages of development of a hypocone. The molars are brachydont, with more or less separate cusps partly connected by ridges, and with both phase I and phase II wear facets present. *ADI* values cluster about 1.5 (Table 11). Occasionally they are referred to as bunodont, but they are not bunodont in the same sense as those of later suiforms and hominoids, for example, which have *ADI* values in the 1.0–1.3 range and reduced buccal facets (see below). Later lophodont, selenodont and bunodont teeth must have evolved from such an ancestry.

The artiodactyls apparently arose from arctocyonid or hyopsodontid condylarths (discussion in Van Valen 1971), and the 'stem artiodactyl' *Diacodexis* is not much different from either. *ADI* is in the region of 1.5–1.6 in both these condylarths and the early artiodactyl families (Table 10). Later selenodont families have slightly lower *ADI*, about 1.4–1.5, which may relate to increased crown height and correspondingly less prominent basal projection of the lingual cusps of the upper teeth. The basic plan of the molars, with longitudinally flattened cusps, is little changed, but primary is replaced by secondary occlusal morphology. Apparently in this process the phase II facets are lost and the single-phase occlusal surfaces which dip gently towards buccal are developed. It is interesting to consider that present-day selenodont artiodactyls all ruminate, and that rumination affects the structural and mechanical properties of foods but cannot reduce wear due to inorganic inclusions. In other words, one rather expects to find differences in crown height, but not in occlusal morphology, as noted in Sect. 3.2.2.

The derivation of bunodont teeth in artiodactyls seems to proceed via a bunoselenodont stage such as is seen in anthracotherids, for example (Thenius 1976), by reduction of the distance between buccal and lingual cusps in the upper tooth. A basin between buccal and lingual cusps of the upper tooth is required for steeply dipping anteroposteriorly striking phase I facets. If it is lost the lower tooth cannot move into it and more horizontal contact surfaces result. It was suggested (and perhaps demonstrated) above, that the buccal cusps are displaced towards lingual rather than vice versa, presumably because the limit of movement towards lingual is set by the angle of the pterygoideus vector. A bilophodont condition (as in *Listriodon splendens* or various peccaries) can evolve from a bunodont one by secondary development of basins between pairs of anterior and posterior cusps. This makes possible a high occlusal relief without changing the anatomy of jaws and muscles.

The radiation in molar morphology seen in the Perissodactyla can be similarly understood. The earliest representatives of equoids, tapiroids and chalicotheroids are all similar to each other, although with characteristic differences in detail (Radinsky 1969). Of these, the equoid, *Hyracotherium*, is closest to the ancestral phenacodontid condylarths, and is generally considered the most primitive (Radinsky 1966). The mean *ADI* of phenacodontids in Table 11 is 1.44, but the sample is small, so a true value of about 1.5 may be more likely.

Fig. 30. Ventral views of skulls of *Diceros bicornis* (left) and *Ceratotherium simum* (right). Note the widely spaced zygoma of the ectolophodont *Diceros* and the narrow zygoma of the plagiolophodont *Ceratotherium*. Both skulls from TE.

Hyracotherium can be called buno-lophodont, with phase I facets both buccally and across the cross lophs, and phase II faces in the usual positions (Butler 1952a). The molars of later perissodactyls are modifications of this type, involving (at least initially) a stronger development of lophs and increased occlusal relief. From various trilophodont forms more specialized bilophodont and ectolophodont types are derived. From the latter plagiolophodont teeth with serial anteroposteriorly striking cutting edges and secondarily reduced occlusal relief occasionally evolve. The purest bilophodonty is found in the tapiroid families Tapiridae and Deperetellidae. Other tapiroids are variously trilophodont, and rhinocerotoids presumably arose from such forms, perhaps paraphyletically (Radinsky 1969). In the Ceratomorpha (tapiroids and rhinocerotoids) the cusps are suppressed and the lophs are smooth. This is in contrast to the Hippomorpha (equoids, chalicotheroids, brontotheroids), in which cusps tend to retain more of their individuality. This is probably related to the tendency towards dilambdodonty (with a W-shaped ectoloph) in the latter group, but the differences are not clearly reflected in *ADI*.

Rhinocerotids and amynodontids, however, have *ADI* values that are distinctly higher than those of other trilophodont perissodactyls, which probably reflects the extreme ectolophodonty of these hypsodont forms. To maintain a secondary two-phase occlusal morphology a wide 'basin' between the buccal and lingual edges of the upper tooth is required. To load the buccally displaced phase I facets, the masseter vectors must have a marked component towards lateral, which proably is why rhinoceroses have such widely spaced zygomatic arches. In plagiolophodont forms this does not apply, and it is striking that in such rhinoceroses (*Coelodonta*, *Ceratotherium*) the zygoma are much narrower (Fig. 30).

Plagiolophodonty seems to require anteroposteriorly striking medial and lingual cutting edges (seleno-lophodonty), and the functional morphology is analogous to selenodonty. In the modern equids this is observed as a lack of the positive correlation between *ADI* and *AGI*, but *Ceratotherium* still plots with the other rhinoceroses. Perhaps this is because *Ceratotherium* developed plagiolophodonty very recently and is still very much like a 'typical' rhinoceros in its anatomy?

4.3. Tooth shape and enamel structure

4.3.1. Introduction

The patterns of stress distribution must be different in differently shaped teeth, and the differences in shape must reflect differences in development. Similarly, the fine structure of the dental tissues, particularly enamel, directly reflect developmental processes on one hand and affect the mechanical properties of the teeth on the other. It is thus reasonable to expect that relationships will exist between morphology, development, function and evolution, although these relationships need not be simple.

An outline of the relationships between enamel development and structure was given in Section 3.1.2., and the relationships between enamel structure and wear properties were discussed in Section 3.4.1. In this section I will deal with relationships at one particular level of organization, namely that of the orientation of the zones of decussating enamel prisms or Hunter-Schreger bands (HSB:s). This question has received little attention until recently, and a comprehensive synthesis is not within reach (Rensberger & von Koenigswald 1980, Rensberger 1983, Fortelius 1984, Boyde & Fortelius in press). A discussion of the problem is nevertheless clearly required in the present context.

Technical problems loom large. Particularly, there is no method available to image the HSB:s over more than small areas of the crown at a time, which makes mapping tedious and uncertain. Nevertheless, these problems do not affect the theoretical issues. A discussion of materials and methods as well as technical data are given in Appendix 7.

4.3.2. Hunter-Schreger bands and wear relief

Historically, the discovery of vertically oriented Hunter-Schreger bands with vertical prism decussation is due to the striking effect this arrangement has on wear relief. Rensberger & von Koenigswald (1980), in their original description of the phenomenon, stated that they wished to know how the curious tiny ridges and valleys observed on rhinoceros enamel came about. They found that the relief corresponds to radially arranged vertical HSB:s, one set of bands forming ridges separated by valleys corresponding to the other set.

As a matter of fact, all HSB:s are potentially capable of producing such a relief. Ordinary horizontal HSB:s with horizontal decussation frequently give rise to a concentric wear relief, as for example in the suid *Potamochoerus porcus* or the desmostylian *Desmostylus hesperus* (Fig. 31). The relationship involved is simply that prisms of different HSB:s are intercepted by the wear surface at different angles, and are consequently unequally resistant to wear (see Sect. 3.4.1.). Vertical decussation maximizes this difference for horizontal wear surfaces, and consequently gives rise to a higher relief. It is also highly probable that relief is more distinct when decussation is between distinct zones (i.e., involves little gradual transition in prism direction) than when zones intergrade into each other, although this has not been investigated.

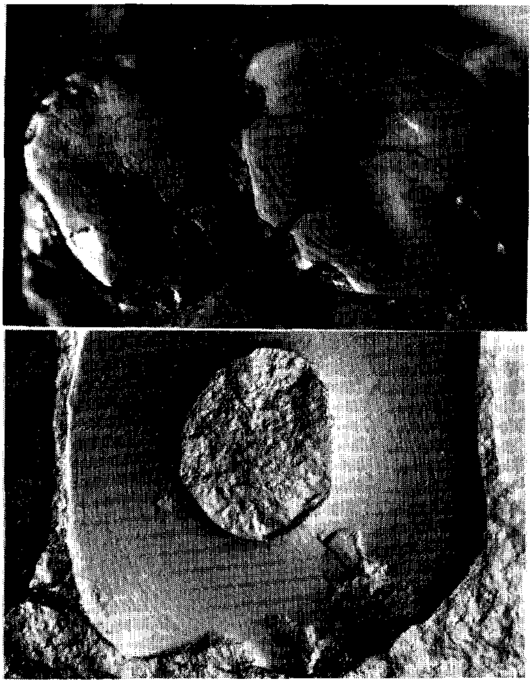

Fig. 31. Concentric wear relief in thick-enamelled forms with horizontal decussation. – Above: *Potamochoerus porcus*, entoconid and hypoconulid of second lower molar (ST 130a, Cameroun). Field width 11 mm. – Below: *Desmostylus japonicus*, one cusp on holotype specimen (TO). Field width 18 mm. Light micrographs of transparent epoxy casts (App. 7.1).

The relief on true facets is relatively low, and the highest relief develops where occlusal contact does not occur (Fig. 18). Why this is so is not entirely clear, but it indicates that the differential wear is mainly due to low energy processes of food 'polish' rather than to events associated with high stress. The relief developed on one facet may cause a distinct relief on the facet with which it occludes. For example, on the buccal phase I facets in rhinoceroses or astrapotheres, where the ridges on the ectoloph edge wear troughs into the buccal facets of the lower teeth (which are situated mainly on outer enamel with little decussation) (Fig. 32).

One might argue that such wear-induced ridging is a functional feature associated with cutting tough

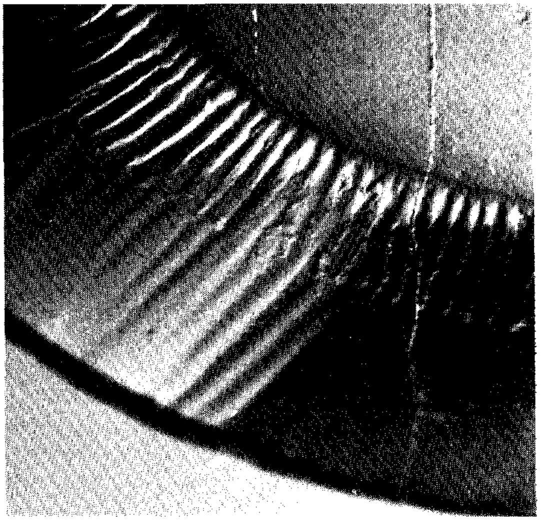

Fig. 32. Wear relief due to two different causes on *Rhinoceros sondaicus* lower premolar buccal edge (facets 3 and 4). The relief on the upper part (inner enamel) is due to differential wear resistance (vertical decussation), while the relief in the lower part (outer enamel) is due to the relief on the antagonist (which in turn is again due to vertical decussation). Light micrograph of transparent epoxy cast (App. 7.1). Field width 5 mm.

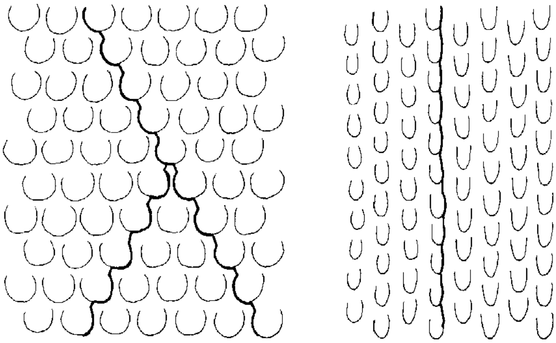

Fig. 33. Crack propagation in enamel with different prism packing patterns. Cracks 'jump' from one prism boundary discontinuity to the next. Based partly on Boyde 1976b and partly on personal communication with Alan Boyde (1983—84). The directions shown are typical but not the only ones that occur.

food materials, just as the crenellated canines of sabre tooth cats are said to have been designed to cut through tough skin. The weakness of this argument is that the relief (unlike on the canines) is developed parallel to the direction of relative movement, at least at the main cutting edges. Because of this they cannot function as stress concentrators, which is the functional principle involved in all crenellated and saw-toothed cutting devices (which are usually single blades, not blade pairs).

Rensberger & von Koenigswald (1980) argued that the relief, as such, is of little functional relevance, and that the functional advantage of vertical decussation is that it increases overall wear resistance. They described an experiment in which two pieces of rhinoceros enamel where glued together with the HSB:s vertical in one piece and horizontal in the other, and abraded by sandblasting. Under these experimental circumstances the piece with vertical HSB:s was the most resistant one. This result, however, is easily explained in terms of prism (rather than HSB) orientation (see Sect. 3.4.1.). When a portion of enamel with vertical prism decussation is turned on its side and cut parallel with the HSB direction, all the prisms are exposed longitudinally; i.e., in the orientation of least wear resistance. This is not the case when it is cut transverse to the HSB direction, when (depending on the angle of decussation) at least one, and in all but one orientation both sets of bands have prisms cut at an angle. Nor is it the case in real horizontal decussation, where prisms in both left- and rightslanting zones apparently always have an inclination towards occlusal and are therefore intercepted at an angle by a horizontal surface.

Thus there are no grounds for regarding vertical decussation as increasing wear resistance. Indeed, if only wear resistance is considered, non-decussating enamel is the ideal. Hardness of enamel is proportinal to density (Karlström 1931), and for simple geometrical reasons parallel prisms can be more closely packed than decussating prisms. It is indeed the case that the outer, little-decussating enamel of rhinoceroses is more resistant to wear than the inner, strongly decussating enamel (Boyde & Fortelius in press).

4.3.3. Hunter-Schreger bands and crack propagation

Enamel is not an isotropic material, and cracks are preferentially propagated from one prism boundary discontinuity to the next at locations where crystals are stressed transverse to their c-axes (i.e., separated from each other rather than broken in tension) (Boyde 1976b). Such crack propagation is determined by the prism packing pattern, but cracks may also follow the boundaries of zones of decussating prisms, at least when the change in prism orientation is abrupt, as in rhinoceroses (Boyde & Fortelius in press). At least two levels of structural organization thus influence crack propagation: prism pattern and HSB orientation.

Pattern 3 enamel cracks preferentially in such a way that prism boundary discontinuities are joined diagonally across the rows (Boyde 1976b), while Pattern 2 enamel cracks along the rows (along the 'inter-row sheets') (Alan Boyde, pers. comm. 1984) (see

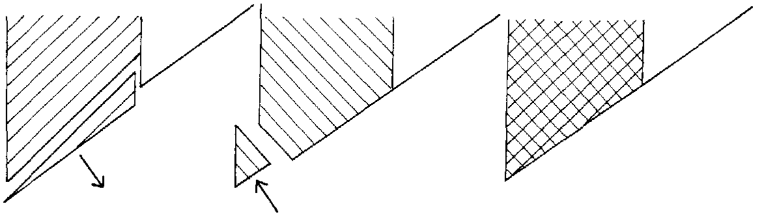

Fig. 34. Hypothetical scheme to show advantage of vertical decussation when enamel is loaded away from the dentine. The vertically 'laminated' structure prevents massive cleavage in planes parallel to the prism boundaries and occlusal surfaces. See text.

Fig. 33). Pattern 3 enamel cracks diagonally across the HSB:s; Pattern 2 enamel along them. Both may presumably crack between HSB:s at sharp zone boundaries. Irrespective of prism pattern, vertical decussation would thus reduce the tendency of the enamel to flake off parallel to horizontal surfaces. This would be particularly critical when the enamel is stressed in shear in a direction away from the supporting dentine, as on the steeply dipping buccal and lingual facets of trilophodont teeth (Fig. 34).

Composite materials with fibres (or whiskers) in a matrix are stronger in tension along rather than across the fibres (see e.g. Gordon 1968). von Koenigswald (1980) discussed the enamel structure of rodent molars in terms of tensile and compressive stress, and it may be that the aspect is important. Conditions of prolonged tensile stress are probably rare in teeth, but might occur during chewing of very sticky foods. More important is perhaps elastic deformation and rebound during and after compression, which may induce local tension and cracking. If such deformation is mainly along an axis normal to the occlusal surface (which is reasonable if load is normal to that surface), enamel with prisms (more properly: crystals) parallel to the surface will crack more easily than enamel with prisms normal to it. Again, the steeply dipping buccal and lingual facets of trilophodont upper teeth are the ones where prisms are most parallel to the surface in non-decussating and horizontally decussating enamel (in which all prisms are inclined towards occlusal) (Fig. 34). Vertical decussation means that the prisms in alternate bands are nearly normal and nearly parallel to the surface in both upper and lower teeth. If decussation patterns are functionally important and if they are related to crack propagation, one would thus expect vertical decussation primarily in association with a pronounced two-phase occlusal morphology (high relief transverse to the direction of the power stroke).

4.3.4. *The occurrence of decussation modes*

Among living ungulates, vertical decussation is found only in rhinoceroses, while all others have horizontal decussation (in which the zone boundaries may be abrupt or gradual). In the fossil record, however, vertical decussation is not a rare phenomenon, but is commonly found in large lophodont forms, though apparently never in bunodont or selenodont ones. Horizontal HSB:s can, however, be variously bent and tilted, and it is necessary to make explicit distinctions between decussation modes. Table 13 summarizes prism packing patterns and decussation modes in the lophodont forms considered in this investigation.

Horizontal decussation

Horizontal decussation develops as concentric zones about the origin(s) of enamel secretion, usually the cusp tip(s), and usually but not always parallel to the developing front (Boyde & Fortelius in press, and below). The pattern usually resembles a spiral, and spirals are extremely common in structures formed by incremental growth (Thompson 1917). I assumed earlier (Fortelius 1984) that it is in fact a spiral and still consider that likely, but the question has not been properly investigated. In any case the arrangement is concentric.

On flat, high cusps which join to make a loph there is a tendency of the HSB:s to bend towards the loph crest between cusp tips (Fig. 35A). The same pattern results if one squeezes plasticine model cusps flat,

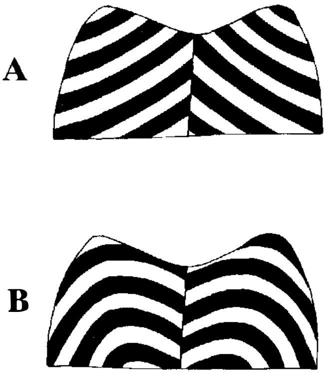

Fig. 35. Modified horizontal decussation patterns: Concave horizontal decussation (above), where HSB's bend towards the loph crest between cusps, and convex horizontal decussation (below), where the HSB's follow the occlusal relief. Highly schematic.

Table 13. Decussation and prism packing patterns (PP) in some lophodont ungulates. See App. 7 for methods.

	Species studied	HSB orientation	PP	Methods
Pantodonta				
Pantolambdidae	*Pantolambda bathmodon*	none (vertical?)	1,3	TSRLM, LM
Coryphodontidae	*Coryophodon* sp.	vertical (irregular)	3	TSRLM, LM, SEM
Dinocerata				
Uintatheriidae	*Uintatherium* sp.	vertical (irregular)	3	TSRLM, LM
Litopterna				
Macraucheniidae	*Macrauchenia patachonica*	horizontal (convex)	2	TSRLM, LM
Notoungulata				
Toxodontidae	*Nesodon imbricatus*	horizontal	2	TSRLM, LM, SEM
	Toxodon platensis	horizontal	2	TSRLM, LM, SEM
Astrapotheria				
Astrapotheriidae	*Astrapotherium* sp.	vertical (regular)	3	TSRLM, LM, SEM
Pyrotheria				
Pyrotheriidae	*Pyrotherium* sp.	vertical (irregular)	3	TSRLM, LM, SEM
Perissodactyla				
Lophiodontidae	*Lophiodon rhinocerodes*	horizontal (concave)	?	LM
Helaletidae	*Hyrachyus* sp.	horizontal (concave)	?	LM
?Helaletidae	*Chasmotherium minimum*	horizontal (concave)	?	LM
Deperetellidae	*Deperetella* sp.	vertical (regular)	2	TSRLM, LM
Tapiridae	*Tapirus indicus*	horizontal (concave)	3(2)	TSRLM, LM
Hyracodontidae	*Hyracodon nebrascensis*	vertical (regular)	?	LM
Rhinocerotidae	many species	vertical (regular)	3	TSRLM, LM, SEM
Amynodontidae	*Amynodon* sp.	vertical (regular)	?	LM
Equidae	*Mesohippus bairdi*	horizontal (convex)	3,2	TSRLM, LM, SEM
	Anchitherium aurelianense	horizontal (convex)	3,2	TSRLM, LM, SEM
	Merychippus primus	horizontal	2	TSRLM, LM
	Equus caballus	horizontal	2	LM, SEM
Palaeotheriidae	*Palaeotherium magnum*	horizontal (concave)	2(3)	TSRLM, LM, SEM
	Plagiolophus sp.	horizontal	3	TSRLM, LM
Brontotheriidae	*Lambdotherium* sp.	horizontal (concave)	?	LM
	Menodus prouti	horizontal (concave)	?	LM
	Titanotherium sp.	horizontal (concave)	3	LM, SEM
Chalicotheriidae	*Nestoritherium sivalense*	horizontal (concave)	?	LM
	Schizotherium pilgrimi	horizontal (concave)	?	LM
	Chalicotherium goldfussi	horizontal (concave)	?	LM
Artiodactyla				
Suidae	*Listriodon splendens*	horizontal (concave)	2	TSRLM, LM
Proboscidea				
Dinotheriidae	*Prodinotherium* sp.	irregular	3	LM, SEM
Hyracoidea				
Geniohyidae	*Titanohyrax ultimus*	horizontal	3(2)	TSRLM, LM
Embrithopoda				
Arsinoitheriidae	*Arsinoitherium zitteli*	vertical (irregular?)	2	TSRLM, LM, SEM

and the pattern may at least partly be a simple mechanical consequence of flattening. However, it means that HSB:s are intercepted nearly transversely along the loph crest, and wear relief similar to that in genuine vertical decussation is developed. This situation, which I will refer to as 'horizontal concave' HSB:s, is found in palaeotheres, brontotheres, and in many tapiroids. The HSB:s in this arrangement are parallel to the perikymata.

A curious modification of horizontal decussation is what appears to be the reverse of the above, namely that the HSB:s curve down along cusp walls. This arrangement is found along the buccal enamel of upper teeth in selenodont artiodactyls, on the ectoloph of equids (Fig. 35B) and possibly also in *Macrauchenia.* The orientation of the HSB:s is nearly transverse to the perikymata; i.e., they are curved in opposite senses. I have been unable to reconstruct the three-dimensional arrangement of the HSB:s in this mode, which I will refer to as 'horizontal convex' HSB:s.

In all horizontal decussation the HSB:s are sectioned in a basically concentric pattern by a horizontal wear surface, but inclined bands and/or surfaces may cause varying degrees of radial orientation and corresponding wear relief. Such relief is maximized when the HSB:s are concave and minimized when they are convex (Fig. 35).

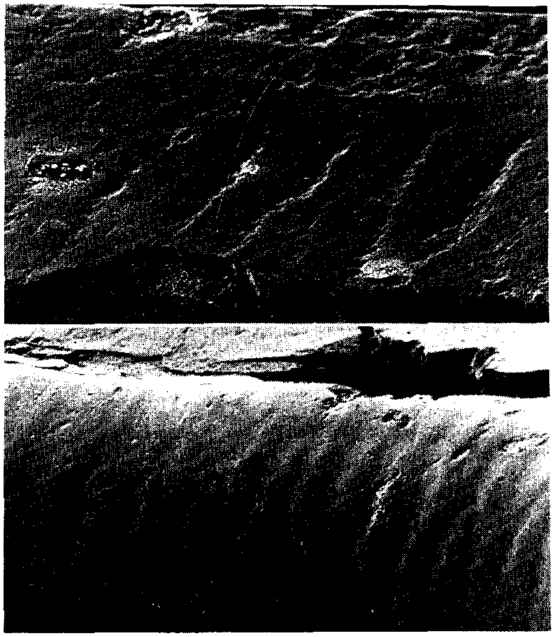

Fig. 36. Wear surfaces of forms with irregular vertical decussation. The grooves correspond to narrow zones of prisms parallel with the occlusal surface; on these inclined surfaces these are either occlusal- or cervical-slanting prisms. – Above: *Coryphodon* sp. (Pantodonta, Eocene) protoloph (facet 1) of M^3 (HP P1109). – Below: *Uintatherium* sp. (Dinocerata, Eocene) premolar protoloph wear surface (non-facet) (BM M3815). The enamel-dentine junction is towards the bottom (above) or towards the top (below). SEM images of epoxy casts, field width of both images 1.7 mm.

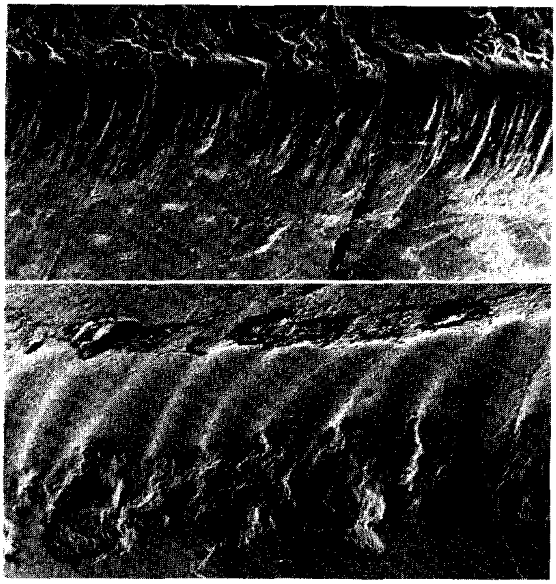

Fig. 37. Wear surfaces of forms with (irregular?) vertical decussation more pronounced than of those in Fig. 36. Grooves and valleys are of about equal width. – Above: *Arsinoitherium zitteli* (Embrithopoda, Oligocene), hypolophid (facet 4) of lower molar (HP P788). – Below: *Pyrotherium* sp. (Pyrotheria, Oligocene), cross loph of (upper?) molar (HP P868). Enamel dentine junction towards top in both. SEM images of epoxy casts, field width of both images 2.1 mm.

Vertical decussation

In rhinoceroses, at least, vertical decussation develops radially; i.e., transverse to the formative edge from the beginning of enamel secretion (Boyde & Fortelius in press). It is thus transverse to the perikymata, and the HSB:s do not depart from their vertical course at or between cusps. Two grades of organization can be distinguished, which I will refer to as 'irregular' and 'regular'.

In irregular vertical decussation many prisms have horizontal inclinations, but the strongly inclined prisms are inclined vertically (towards occlusal or cervical). Focussing up through such enamel (with the TSRLM; see App. 7.3) in a surface-parallel view one can see prisms feeding in from both sides to join a vertical zone of steeply inclined prisms. The developmental situation must have been that in a field of more or less random, moderate translatory movement, some groups of ameloblasts translated rapidly through the 'crowd' in vertical directions. The result is an enamel which is not neatly divided into adjacent HSB:s, but in which vertical zones exist in a less decussating 'matrix'. This kind of arrangement is found in coryphodontids and dinocerates (Fig. 36). More documentation is needed to decide whether the irregular vertical decussation seen in *Pyrotherium* and *Arsinoitherium* (Fig. 37) is of the same nature.

Regular vertical decussation is found in rhinocerotoids, deperetellid tapiroids, and in astrapotheres (Figs. 38, 40). The (inner) enamel is entirely divided into HSB:s, and decussation is purely vertical. The bands may divide around each other to form 'Y-junctions' in both the surface-parallel and transverse senses (Boyde & Fortelius, in press), but are in principle continuous (Fig. 39).

4.3.5. Evolutionary relationships

The primitive mammalian condition is non-decussating, and probably non-prismatic, enamel (see Kozawa 1984 for a brief review and references), and it appears highly likely that decussation evolved independently several times. Until more is known

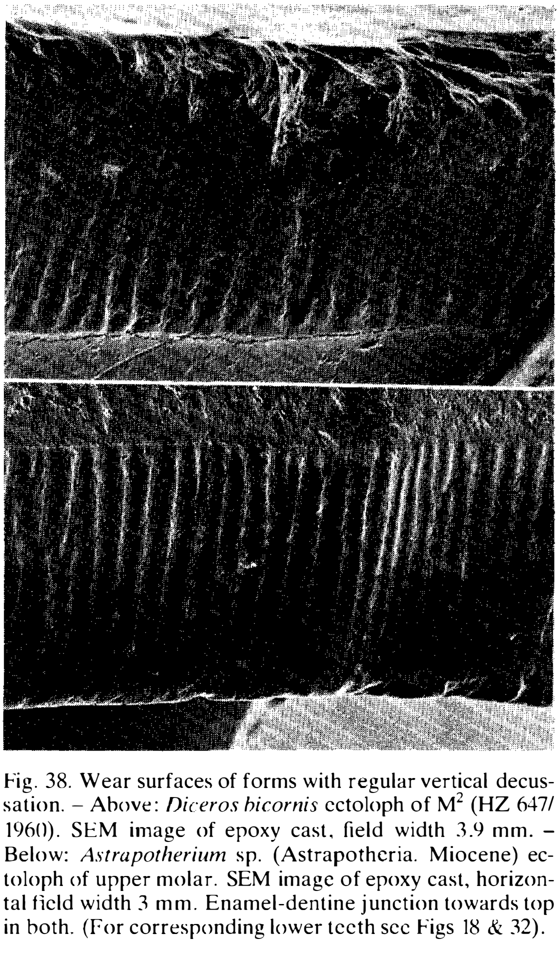

Fig. 38. Wear surfaces of forms with regular vertical decussation. – Above: *Diceros bicornis* ectoloph of M^2 (HZ 647/1960). SEM image of epoxy cast, field width 3.9 mm. – Below: *Astrapotherium* sp. (Astrapotheria. Miocene) ectoloph of upper molar. SEM image of epoxy cast, horizontal field width 3 mm. Enamel-dentine junction towards top in both. (For corresponding lower teeth see Figs 18 & 32).

Fig. 39. Y-junctions of HSB's on polished and airpolished (App. 7.2) protoloph enamel of *Astrapotherium* sp. (HP unregd. fragm.). Horizontal section, enamel-dentine junction towards bottom. SEM (BSE+SE) image, field width 1000 μm.

about the organization of enamel in fossil ungulates evolutionary scenarios must remain speculative.

True vertical decussation seems to unite the rhinocerotoids with the deperetellids (Fig. 40). The condition in the supposed helaletid ancestors of rhinocerotoids has not been sufficiently well studied, but the HSB distribution appears to be concave horizontal. The same appears to be the case in lophiodontids (Fig. 41). The data are very incomplete at the moment, and more documentation is needed before their significance can be evaluated. They do, however, lend some support to the proposal of Rensberger & von Koenigswald (1980) that vertical decussation in rhinocerotoids evolved by modification of a concave horizontal pattern. For ontogenesis this requires the destruction of the relationship between the decussation and the developing front: ameloblasts must move transverse rather than parallel to the front. The breaking-up is complete in rhinoceroses, and the very beginning of decussation is vertical with the HSB:s radial from the cusp tip (Boyde & Fortelius in press).

An alternative scenario, which is attractive ontogenetically but lacks phylogenetic support, is that vertical decussation arose directly out of non-decussation. It does not appear to be known whether the wholly irregular decussation of proboscideans (Boyde 1969) is primitive or derived, but irregular vertical decussation could easily arise from such a state by simple emphasizing of ameloblast movement in the vertical directions. Similarly, regular vertical decussation could be derived from irregular vertical decussation by a further increase in dominance of vertical movement to the exclusion of all other directions. At the moment the evolutionary sequence does not appear to have been established for a single lineage, and speculation beyond this point is of little avail. Nothing requires that the same sequence apply in all cases.

4.3.6. *Causal relationships*

In the absence of other options it is defensible to discuss possible causal relationships in terms of correlation, although it must be recognized that associations between factors may reflect relationships which are not included in the analysis. The main correlation between HSB orientation and crown shape is clearly the actual orientation of the HSB:s to occlusal surfaces on one hand and the height of occlusal relief on the other. In the buccal enamel of upper teeth where enamel is loaded in a direction away from the enamel-dentine junction, there is a particularly suggestive pattern.

Fig. 40. Vertical decussation in *Deperetella* sp. (Tapiroidea, Eocene). Occlusal (horizontal) surface of M_3 hypolophid (BM M12756). The light bands are due to reflection from prism sheaths lying more parallel to the surface (transverse to the light path) than those in neighbouring zones. The enamel-dentine junction is towards the bottom of the field; note how the light bands gradually disappear towards the non-decussating, outer enamel. This suggests that the light bands are zones of cervically inclined prisms, since all prisms in the outer enamel are inclined towards occlusal (at least in rhinoceroses and astrapotheres). TSRLM image (App. 7.3), field width 570 µm.

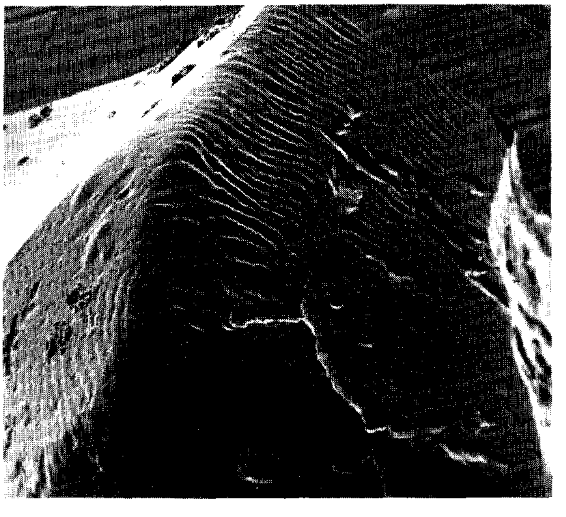

Fig. 41. Wear relief on M^3 protoloph (facet 1) of *Lophiodon lautricense* (Tapiroidea, Eocene; BM M8331). The appearance is much as in vertical decussation, but is apparently due to concave horizontal decussation (see text). SEM image of cut epoxy cast, field width 8.5 mm.

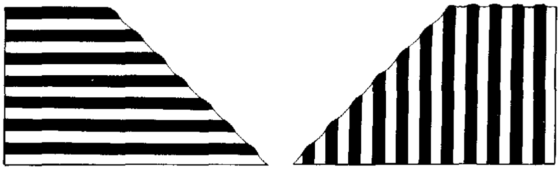

Fig. 42. How inclined facets intercept HSB's, irrespective of whether these are horizontal or vertical.

If there is no transverse occlusal relief (i.e., parallel to the direction of occlusal movement), then vertical HSB:s will be intercepted transversely and horizontal HSB:s longitudinally by the wear surface (Fig. 42). If transverse relief is present, the angle of interception will depend on the orientation of the HSB:s and that of the wear facet. Bands inclined in one direction will be intercepted more transversely and bands inclined in the other direction more longitudinally. In an idealized case of wear facets inclined 45 degrees, both straight vertical and straight horizontal decussation result in the same angle of the bands to the facets (Fig. 42). It is quite striking that high transverse relief accompanies concave horizontal decussation that produces the characteristic radial ridging in palaeotheres and titanotheres. True vertical decussation is found in forms with low transverse relief, such as rhinocerotoids, astrapotheres and arsinoitheres. In both cases the longitudinal occlusal relief (transverse to the direction of movement) is pronounced.

Of the lophodonts, equids are the ones which seem to have the lowest longitudinal occlusal relief (the least distinction between the phases of the power stroke). It is very suggestive that the arrangement of the HSB:s at the ectoloph in lophodont horses (e.g. *Anchitherium*) is convex horizontal, as it is in selenodont artiodactyls. This arrangement minimizes the angle between facets and HSB:s. A common feature of horses and selenodonts is also the relatively thin enamel with Pattern 2 prism packing (at least at the buccal facets concerned). The litoptern *Macrauchenia* seems to have the same structure, and toxodontid and homalodontid notoungulates have thin enamel, little transverse relief and straight horizontal bands, which also results in parallel orientation of bands and facets. These forms also have Pattern 2 enamel.

In other cases the relationship is less clear, but I know of no actual counterexample to the principle that HSB:s tend to be parallel to occlusal facets in thin-enamelled forms with Pattern 2 prism packing and low longitudinal relief. HSB:s transverse to occlusal facets are, on the whole, found in association with relatively thicker enamel and higher longitudinal relief, but with both Pattern 2 and Pattern 3 prism packing. Depending on transverse relief, the HSB:s may be either straight or concave horizontal. In other words, the prediction made above (Sect.

4.3.3.) is fulfilled; that vertical decussation, or more properly transversely intercepted HSB:s, would occur in association with high longitudinal relief.

It is much more difficult to suggest any unifying principle, however speculative, for crown shape and true ontogenetic decussation mode. This proves nothing, of course, and may simply reflect lack of imagination, but one might interpret it as evidence that decussation modes reflect functional demands rather than ontogenetic constraints. At the same time, if the functional relationships proposed are correct, an ontogenetic constraint is strongly implied at a secondary level. The decussation mode is the same over the whole crown, and in upper as well as lower teeth, although the functional advantage only applies to one (important but limited) set of facets. In other words, ameloblasts behave in one way or another, but not in several ways simultaneously in the same dentition.

5. Thesis: adaptations, exaptations, constraints and evolution

There can be no reasonable doubt that teeth function well because their evolution has been largely adaptive; i.e., under the control of natural selection. Dental morphology is highly heritable, and both natural and artificial selection do result in altered morphology (see review by Butler 1983). However, selection for other than morphological properties may also result in morphological change (Paynter & Grainger 1962, cited in Butler 1983), so all observed change in dental dimensions (for example, in successive age classes) is not necessarily a result of selection directed at the dimensions studied. This is true, for example, in cases where variance has been shown to decrease with increasing age (Kurtén 1953 and several papers since; see Butler 1983). The actual demonstration of selection is consequently problematic. After careful sifting of the evidence, Butler (1983) concluded that major differences between groups are related to specific functional demands (and hence are presumably adaptive), but that minor differences between closely related taxa may well be due to chance, and this conclusion appears plausible. Major functional types of (more or less interdependent) dentitions, muscular systems and jaw designs exist and can be identified (Sect. 4.2 above).

That teeth function well is not proof, however, that their evolution has been entirely adaptive. Gould & Vrba (1982) pointed out that there has been no term for functionally 'good' (aptive) features which are not the result of natural selection for their present purpose. They proposed the term 'exaptation' for features which 'happen to be' fit (aptus) by reason of (ex) their form; such exaptations have incidental effects, as opposed to adaptations which have functions resulting from selection. Both are 'aptations', and what has usually been known as preadaptations should be called 'preaptations'; i.e., potential but unrealized exaptations. Features which do not contribute to fitness are 'nonaptations'. I will adopt this terminology here despite the disadvantage of using unfamiliar terms, since I think that Gould & Vrba correctly identify the lack of appropriate terms as one reason for the ignoring of other features than 'adaptations' 'preadaptations' and 'nonadaptations'. Such other features clearly exist and appear important in evolution.

When attention is shifted from current function and evolutionary past to the evolutionary potential in the future, it becomes immediately clear that many aptations are also constraints; i.e., limit the adaptability of the functional system for new or altered tasks. Viewed from a hypothetical future functional state before any adaptation for the future function has occurred, only exaptations and nonaptations exist, and these determine the potential for change: current aptations are constraints on the future. (Constraints obviously have no specified relation to current functional performance, and may equally well be 'strengths' as 'weaknesses'. Thus both aptations and nonaptations may be constraints.)

The 'alveolar area hypothesis' (Sect. 3.4.2), if correct, is an example of this. Relative eruption pressure (and hence relative wear rate) of adjacent teeth is a function of the number of fibroblasts present in the periodontal ligament; i.e., approximately of the area of unerupted tooth left in the alveolus. This relationship follows from a general physiological principle and is thus an exaptation, not an adaptation. It has the functional effect of causing teeth of unequal height to wear at rates proportional to their height, so that the dentition wears out evenly. However, this levelling has only a limited effect, because the eruption pressure is only a fraction of the total occlusal pressure. Hence the mechanism can only compensate for moderate size differences, and may be said to act as a constraint on size gradients.

Similarly, the inclination of enamel prisms towards occlusal, which causes lower teeth to be more wear-resistant than upper at buccally dipping buccal facets and lingually dipping lingual facets (Sect. 3.4.1) is an exaptation (if it is an aptation at all), for it is present in all kinds of teeth, even non-occluding ones. It is difficult to come to grips with this problem, but the arrangement is perhaps best viewed as a constraint, a nonaptation that has been co-opted (Gould & Vrba 1982) into a functional system. In other words, it has partly channelled the evolution of that system. It is clear, however, that several adaptations also affect the relative dimensions of upper and lower teeth (particularly between chewing mode and occlusal relief), which makes theoretical analysis difficult.

A somewhat more simple case is the unequal wear resistance of the dental tissues which makes possible occlusal surfaces with proud enamel edges (blades) separated by hollowed-out areas of dentine and cement. It is almost certain that they have undergone adaptive evolution since first occlusion and later hypsodonty (and hence secondary occlusal surfaces) evolved (Sect. 4.3.6), but the original difference in wear resistance antedates both, and is clearly an exaptation with respect to them.

Because teeth begin to form at their tips and are finished at their bases increased crown height can evolve easily (Sect. 3.1.1), and this presumably constrains change in other directions. However, hypsodont (and hypselodont) teeth are only functionally meaningful with secondary occlusal surfaces. When the primary occlusal morphology cannot be replaced by a functionally similar secondary morphology (as in bilophodonts) hypsodonty is of little avail. No bilophodonts have ever become truly hypsodont (at least not while maintaining a high-relief occlusal surface); instead, at least in two cases (*Trichecus, Peradorcas*) they have evolved continuous replacement when faced with heavy dental wear. This seems to be a case of adaptations acting as constraints, since bilophodonty and trilophodonty (the latter is possible with secondary occlusal surfaces) arose from emphasis on different sets of facets. Because bilophodonty and trilophodonty have different muscular requirements, the two systems diverge by a process that might be called 'functional autocanalization': two components (occlusal surface morphology, musculature) of a functional system (the masticatory apparatus) constrain change in each other and thus of the whole system. In one case the extreme is continuous replacement, in the other continuous growth (hypselodonty).

The synchronization of the ontogenies of future anatagonists and the resulting buffering of the system against malocclusion due to genetic variation or environmental disturbance (Sect. 3.1.1), must greatly affect the evolutionary potential of the dentition. Changes will tend to result in altered but occluding dentitions, and such changes that do not will be strongly selected against. Until the matter is better understood it is useless to speculate on the evolutionary origin of this synchronization. At present it may be equally regarded as an adaptation to prevent malocclusion or as an exaptation with the same effect.

Tooth classes (whether due to intrinsic or extrinsic ontogenetic control) appear in many ways as the most distinct morphological and functional units of the dentition (Sect. 3.1.1). The differences between single teeth in a class are often small and gradual along the series, while the whole dentition in mammals rarely if ever can be regarded as one morphological or functional unit. Tooth classes may become very similar morphologically (particularly 'molarization' of premolars), but even in an extreme case such as *Equus*, isolated molars and premolars can generally be distinguished by specialists. In contrast, separation of P3 from P4 or M1 from M2 is difficult or impossible in many ungulates, for example, rhinoceroses which have much less uniform toothrows than that of a horse. It also appears that increasing hypsodonty of the molars may be associated with increasing hypsodonty of the premolars, as in most ungulates, but also with premolar reduction as in pigs.

Kurtén (1953) applied correlation analysis to the problem of the genetic control of dental morphology, and found that: (i) adjacent molars tend to have more highly correlated dimensions than more distant molars, and (ii) that occluding teeth show the highest correlations of all. In many of his diagrams (particularly Kurtén 1953, figs. 37) there is a suggestion of separate correlation maxima for occluding teeth which belong to the same class. However, in carnivores with well developed carnassials (*Vulpes, Felis*) the highest correlation in the cheek tooth row is between the carnassials, which belong to different classes (P^4, M_1). I suggested above (Sect. 3.1.1) that the carnassials of carnivores have 'escaped' from their classes, which might explain this obviously aptive feature. If this is true, then their strong correlation would seem to be an adaptation rather than an exaptation. It is a reasonable guess that the proximate cause of correlation patterns is synchronized ontogeny where several teeth share a substantial amount of genetic information. It is difficult, however, to decide whether this represents an adaptation or a constraint which has become co-opted into the functional system as an exaptation.

As shown above (Sect. 4.1.3), previous attempts to relate tooth size to body size via metabolic rate have failed to take into account the relevant time parameters (chewing rate, life span), and have therefore resulted in predictions at variance with the empirically observed data. If the time dimension is properly considered, predictions and observations largely coincide, but the problem as such becomes more complex. The isometric scaling of tooth size to body size results in 'metabolic scaling' of tooth performance and durability when chewing rate and life span are scaled to body size as they are, but whether the temporal scaling is cause or effect of the spatial scaling is impossible to decide. Perhaps one should see the whole pattern as a reflection of some basic physiological consequences of body size; i.e., (again) as interacting constraints co-opted into the functional system as exaptations?

This admittedly speculative review thus suggests that much of what might appear as obvious adaptations to the naive observer are either certainly or possibly exaptations, which can equally well be regarded as one-time constraints. These have determined the basic lines of evolution of the system, while modifications within the portion of morphospace defined by them may be largely adaptive (although minor variations may again be nonaptations due to drift rather than natural selection). Stated thus in the abstract, this conclusion sounds rather trivial, but it is worth noting that these different levels and features can at least partly be identified and investigated empirically, as shown above.

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Appendices

Appendix 1. Body weight data

All the data on body weight were taken from the literature. This was necessary because weight data were not recorded for the museum specimens on which skull and tooth measurements were taken. I used the following sources, in the order of preference: Kingdon (1979—1982), Siivonen (1982), Eisenberg (1981), Heptner et al. (1966). The weight data for the Rhinocerotidae were taken from Kingdon (1979), Groves (1982) and Laurie (1982). A list of species and sources is given after the next section (App. 2.).

For sexually dimorphic mammals the mean of the means for the sexes was used except when the cranial and dental measurements were only for one sex. In such cases the value for the appropriate sex was used. When only ranges were given, range midpoints were used as a substitute for means.

Birth weights were obtained from the same literature, particularly from Eisenberg (1981).

For body weights used in the chewing rate analysis see App. 6.

Appendix 2. Cranial and dental mesurements

The material was accumulated from several different collections. For most species only a few complete specimens were available, and it would not have been worth while to measure large samples in the few cases when this would have been possible, particularly as the weight data had to be taken from other sources anyway. Thus the data are at best only approximate, and insufficient for more refined analysis, but it would have been beyond my powers to collect much better data for this investigation.

Material was used from the following collections:

CA	Museum of Zoology, University of Cambridge (UK)
GB	Naturhistoriska Muset, Gothenburg (Sweden)
HZ	Zoologiska Museet, Helsinki (Finland)
KO	Zoologisk Museum, Copenhagen (Denmark)
LE	Rijksmuseum van Natuurlijke Historie, Leiden (The Netherlands)
ST	Naturhistoriska Riksmuset, Stockholm (Sweden)
TE	Koninklijk Museum voor Midden-Afrika, Tervuren (Belgium)
UZ	Zoologiska Institutionen, Uppsala (Sweden)

The measurements were taken with large calipers (when available) or steel tape for dimensions exceeding 160 mm. Smaller dimensions were measured with small dial calipers. Depending on how accurately the endpoints of the dimension could be determined, the small calipers were read to the nearest mm or the nearest 1/10 mm. Large calipers and tape were always read to the nearest mm.

Data for the following species were used in this investigation (*N* refers to number of specimens, occasionally one or several measurements could not be obtained from one or more specimens; species marked (*) were only used in the tooth width analysis; BW refers to body weight source: Eis = Eisenberg 1981, Gro = Groves 1982, Hep = Heptner et al. 1966, Kin = Kingdon 1971—1982, Lau = Laurie 1982, Sii = Siivonen 1976):

Species	*N*	Coll.	BW
PERISSODACTYLA			
Equidae			
Equus grevyi	2	KO	Kin
E. burchelli	2	KO	Eis
E. caballus	2	HZ	-
E. hemionus (*)	1	HZ	-
E. asinus (*)	1	HZ	-
E. onager (*)	1	HZ	-
Tapiridae			
Tapirus terrestris	3	ST	Eis
T. indicus	1	ST	Eis
Rhinocerotidae			
Dicerorhinus sumatrensis	2	KO	Gro
Rhinoceros sondaicus	3	KO	Gro
R. unicornis	2	KO,UZ	Gro
Diceros bicornis	24	TE,KO, ST,GB,LE	Kin
Ceratotherium simum	11	TE,KO	Lau
ARTIODACTYLA			
Suidae			
Sus scrofa	1	HZ	Sii
Potamochoerus porcus	4	ST	Kin
Hylochoerus meinerzhageni	2	ST	Kin
Phacochoerus aethiopicus	2	ST	Kin
Babirussa babirussa	4	ST	-
Tayassuidae			
Tayassu peccari	3	ST	Eis
T. tajacu	3	ST	Eis

Hippopotamidae			
Hippopotamus amphibius	2	ST	Kin
Camelidae			
Camelus dromedarius	2	HZ,ST	Eis
Tragulidae			
Tragulus spp.	6	ST,KO	Eis
Hyaemoschus aquaticus	2	ST,KO	Kin
Cervidae			
Moschus mosciferus	4	ST,KO	Eis
Muntiacus muntjak	3	ST,KO	Eis
Hydropotes inermis	3	ST,GB	-
Dama dama	1	HZ	Sii
Odocoileus virginianus	1	HZ	Sii
Rangifer tarandus	4	HZ	Sii
Alces alces	1	HZ	Sii
Capreolus capreolus	1	HZ	Sii
Giraffidae			
Giraffa camelopardalis	2	ST	Kin
Bovidae			
Litocranius walleri	1	ST	Kin
Sylvicapra grimmia	4	KO,ST	Kin
Madoqua saltiana	3	ST,UZ	Kin
Ourebia ourebi	1	KO	-
Rhaphicerus campestris	2	KO	Kin
Tragelaphus scriptus	2	KO	Kin
Beatragus hunteri	1	KO	Kin
Alcelaphus buselaphus	2	KO	Kin
Connochaetes taurinus	1	KO	-
Bos grunniens	2	ST	-
Syncerus caffer caffer	1	TE	Kin
S. c. nanus	1	TE	Kin
Taurotragus oryx	1	GB	Kin
Oryx beisa	1	KO	Kin
O. gazella	1	GB	Kin
Hippotragus equinus	2	ST,GB	Kin
H. niger	1	GB	Kin
PROBOSCIDEA			
Elephantidae			
Elephas maximus	1	HZ	Eis
SIRENIA			
Trichechidae			
Trichechus inunguis (*)	1	UZ	-
T. senegalensis (*)	1	UZ	-
HYRACOIDEA			
Procaviidae			
Procavia capensis	3	ST,GB	Kin
P. habessinica	3	ST	Kin
Heterohyrax spp.	3	ST	Kin
Denrohyrax dorsalis	1	ST	Kin
D. spp. (small)	4	ST,GB	Kin

Appendix 3. Fossil material

The fossil material mentioned in this paper is housed in the following institutions:

BM British Museum (Natural History), London (UK)
HP Paleontologiska Museet, Helsinki (Finland)
KO Zoologisk Museum, Copenhagen (Denmark)
MU Staatliche Sammlung für Paläontolgie und historische Geologie, Munich (German Federal Republic)
ST Naturhistoriska Riksmuset, Stockholm (Sweden)
TO National Science Museum, Tokyo (Japan)
UP Paleontologiska Institutionen, Uppsala (Sweden)

Appendix 4. Sectioned casts

For a qualitative illustration of the plunge of occlusal movement during the phases of the powerstroke, epoxy casts (see App. 7.1) of upper and lower teeth were sectioned in one vertical plane, the horizontal direction of which was determined by sighting along occlusal facets and/or striae. An example showing both the occlusal surface and the sectioned surface is Fig. 43. The sectioned surfaces were polished smooth and camera lucida drawings were prepared (Figs 14—16).

Fig. 43. An example of a sectioned molar replica (*Equus grevyi* M^3), showing both the occlusal surface and the profile.

Appendix 5. Tooth width data

Maximum basal tooth widths of fossil and recent 'herbivorous' mammals were taken from the ungulate sample (App. 2, 3), but mainly from the literature. All the relevant monographs, journals and reprints in the public and private libraries in the Division of Geology and Paleontology, Department of Geology, University of Helsinki were used. Data used met the minimum requirements of: (1) upper and lower teeth of at least one individual, or (2) at least three isolated specimens of each tooth from one locality. However, most species are represented by samples well above these minimum requirements (up to >100 specimens). Only M1 and M2 were used in this investigation, but the widths of all cheek teeth were recorded (see text). The species and sources are not listed here, but are available from the author. A family-level summary is given in Table 11.

In the analysis of anisodonty and anisognathy I used data from the ungulate sample (App. 2 above). The following species were included:

1) Bunodonts and lophodonts (excl. *Equus*):
Diceros bicornis, Ceratotherium simum, Dicerorhinus sumatrensis, Rhinoceros sondaicus, R. unicornis, Tapirus terrestris, T. indicus, Sus scrofa, Potamochoerus porcus, Hylochoerus meinerzhageni, Phacochoerus aethiopicus, Babirussa babirussa, Tayassu peccari, T. tajacu, Hippopotamus amphibius, Procavia habessinica, Heterohyrax spp., *Dendrohyrax dorsalis, D.* spp.

2) Selenodonts plus *Equus*:

Equus grevyi, E. burchelli, E. caballus, E. hemionus, E. onager, E. asinus, Camelus dromedarius, Tragulus spp., Hyaemoschus aquaticus, Giraffa camelopardalis, Moschus mosciferus, Muntiacus muntjak, Hydropotes inermis, Dama dama, Odocoileus virginianus, Rangifer tarandus, Alces alces, Capreolus capreolus, Litocranius walleri, Sylvicapra grimmia, Madoqua saltiana, Rhaphicerus campestris, Tragelaphus scriptus, Beatragus hunteri, Alcelaphus buselaphus, Syncerus caffer caffer, S. c. nanus, Taurotragus oryx, Oryx beisa, O. gazella, Hippotragus equinus, H. niger.

Appendix 6. Chewing rate measurements

The data were obtained at the Helsinki Zoo in March 1984. The chewing rates were calculated from timed sequences of rhythmic chewing (I used a stopwatch and counted until the animal stopped chewing). This was much easier for cud chewing than for fresh chewing, which in ruminants tends to consist of short bouts of about a dozen cycles. Depending on availability, between 20 and 500 cycles were timed for each species (mean 209, *SD* 125). Comparison of values obtained from different chewing bouts suggests that there is little variation in one individual but that individuals differ markedly in ways not obviously related to body size.

The body weights were estimated with the help of zoo records and the literature, particularly Eisenberg (1981). Is is obvious that they are only rough approximations but nothing else was available. The data obtained are listed below (CD = chewing cycle duration in milliseconds, BW = body weight in kilograms):

Species, sex	CD	BW
I. Fresh chewing		
Capra ibex	597	40
C. falconeri	581	64
Hemitragus jemlahicus	471	50
Oreamnos americanus	780	60
Ammotragus lervia	584	66
Bos grunniens	872	250
Bison bonasus	793	300
Camelus bactrianus	912	500
Equus hemionus	797	210
II. Cud chewing		
Capra ibex, subadult	821	40
C. falconeri	657	64
Hemitragus jemlahicus	628	50
Oreamnos americanus	846	60
Ovibos moschatus	1169	400
Bos grunniens	880	250
Bison bonasus	1145	500
Rangifer tarandus	864	125
Alces alces	1072	450
Odocoileus virginianus	779	80
Camelus bactrianus	1172	500

III. In addition, the following data from the literature were used (D&G = De Vree & Gans 1975, H&S = Herring & Scapino 1973, W&S = Weijs & Dantuma 1981):

Fresh chewing		
Oryctolagus cuniculus (W&D)	267	1.8
Sus scrofa (dwarf) (H&S)	330	22.3
Capra hircus (dwarf) (D&G)	520	20
Cud chewing		
Capra hircus (dwarf) (D&G)	500	20

Appendix 7. Preparation of samples for microscopy and imaging techniques

App. 7.1. High resolution replication and study of worn tooth surfaces

Replication

The teeth were cleaned with water and detergent, ethanol, acetone, or various combinations of these, depending on the circumstances. If facilities were available the teeth were rinsed in distilled water and air dried, but more often they were wiped dry with soft tissue. Two-stage silicone rubber molds were made of the cleaned teeth (Optosil hard and Xantopren blue, Bayer Dental, D-5090 Leverkusen, BRD). The molds were transported to Helsinki, cleaned when necessary and poured with a clear epoxy resin (UH Products, Porvoo 15, Finland). Bubbles were removed mechanically with a blunt needle, and the epoxy was allowed to set at room temperature and pressure. A useful discussion of replication problems and artefacts is given by Gordon (1984).

Light microscopy

Clear epoxy replicas are particularly suitable for light microscopy, as they (unlike the teeth themselves) can be illuminated by transmitted light so that surface reflections are eliminated. For low magnification study and documentation of wear surfaces, an ordinary stereo light microscope is thus a good alternative to a scanning electron microscope.

In this investigation I used a Wild M7 stereomicroscope with a fibre optics lightsource. The casts were placed on a transparent plastic box directly below the objective lens, and illuminated by light reflected obliquely from a white paper card underneath the box. The illumination thus achieved is either lightfield or darkfield, depending on the relative positions of light source, reflective surface and specimen. By adjusting these, a suitable illumination could generally be achieved without difficulty. It should be noted that this technique primarily resolves structures transverse to the direction of illumination, which may confuse the unwary.

Scanning electron microscopy

Epoxy replicas can, of course, be coated and examined in a scanning electron microscope. Depending on the quality of the replica, magnifications up to several thousand times can be used (see Gordon 1982). In this investigation the replicas were sputter-coated with gold and examined in the secondary electron mode at 10 kV acceleration voltage (see below).

App. 7.2. Enamel samples for scanning electron microscopy (SEM)

Minimum damage strategies in preparation of tooth samples for the SEM are discussed by Boyde & Martin (1982). Most of the samples used in this investigation were prepared by rather destructive techniques, since I was unaware of alternatives at the time. The specimens were cut in defined planes, polished, etched and coated. Polishing was variously on abrasive paper, on a glass plate with abrasive powder of successively finer grain, on 'jeweller's rouge' paper or on a soft lap with diamond paste. Chemical etching was with H_3PO_4, typically but not invariably 0.5 % for 60 seconds. For physical etching an 'airpolishing' unit (Dentsply/Cavitron Prophy-Jet, Dentsply International, York, PA 17405, USA) was used (at the Department of Anatomy and Embryology, University College London). Various working distances and treatment times were used, but an approximate norm was 2—3 mm and 60 secs. These and other preparation procedures are discussed in Boyde & Fortelius (in press).

The specimens were sputter coated with gold or gold-palladium and investigated in secondary (SE) and/or backscattered (BSE) electron modes at 10—20 kV acceleration voltage (depending on imaging mode). The microscopes used were Cambridge Stereoscans 1 and S4-10 (at the Department of Embryology and Anatomy, University College London), the latter with a 4 sector solid state backscattered electron detector, and a JEOL 135-C (at the Department of Electron Microscopy, University of Helsinki).

App. 7.3. The tandem scanning reflected light microscope (TSRLM)

The technical details of this optical scanning microscope are given in Boyde et al. (1983) and references cited therein. The microscope is able to focus on a very narrow optical plane, and to exclude any reflections from above or below this plane (including the strong reflection from the surface of the specimen, which is otherwise a major problem of reflected light microscopy). By moving the focal plane up and down through the specimen, one can obtain information about the three-dimensional structure of the tissue. Unfortunately this information is difficult to record in a form that could be published in a journal, and at the moment static light micrographs and verbal description have to suffice.

The microscope used in this study is one housed in the Department of Anatomy and Embryology, University College London (Prof. Alan Boyde); as of this writing (Dec. 1984) it is the only operational TSRLM outside Czechoslovakia. This particular instrument is designed to take standard light microscope objective lenses. For investigations of enamel structure, oil immersion lenses were found to be most suitable, but dry lenses and water and glycerin immersion lenses could also be used successfully.

The depth of penetration (i.e., the greatest depth from which enough light is reflected to form an image) varies, but 100 microns is not unusual for fossil enamel and visible light. A practical limit (which was occasionally reached) is set by the free working distance of the objective lens. For standard oil immersion lenses of 100 times magnification this is in the region of 200 microns. The thickness of the non-decussating outer enamel of many larger ungulates exceeds the depth of penetration, so that it is not possible to study the more 'diagnostic' or otherwise more interesting, decussating inner enamel from the surface. However, the problem can be partly overcome by inspecting occlusal and interstitial wear facets or broken surfaces which expose the inner enamel.

Despite some technical difficulties with TSRLM, it has several features which make it a most promising tool for paleontological fine structure research. No preparation of the specimen is required, very large specimens (on the instrument used in this study up to one metre in diameter) can be examined intact, and the specimens are not submitted to anything more drastic than intense visible light. Thus complete specimens (including holotypes!) can be examined without undue risk of damage. Any part of the specimen (within the limits of accessibility) can be examined, not just the fragments that happen to be available. It is to be hoped that this microscope will become part of the standard equipment of paleontological museums and laboratories. It would drastically reduce the drain on irreplacable material now lost in destructive ultrastructure research invloving cutting and etching.

Appendix 8. Statistical calculations

All more demanding calculations were performed on a Burroughs B7800 computer, located at the Computing Centre, University of Helsinki, using the 'Minitab' program system (Minitab Inc., 215 Pond Laboratory, University Park, Pa. 16802, U.S.A.). The major axis slopes, intercepts and confidence limits were calculated according to Sokal & Rohlf (1981); all other statistics according to programmes extant within the 'Minitab' system (Ryan et al. 1982).

Appendix 9. Abbreviations

Variables

AWT	adult body weight
BL	basal skull length
BRCL	braincase length
BWT	birth weight
CBL	condylobasal skull length
CPL	length of skull from condyles to anterior margin of second premolar
FEL	femur length
HBL	head and body length
M^1A, M^2A, M^3A	area (L × W) or upper molars
M_1A, M_2A, M_3A	area (L × W of lower molars
M^1L, M^2L, M^3L	length of upper molars
M_1L, M_2L, M_3L	length of lower molars
M^1W, M^2W, M^3W	width of upper molars
M_1W, M_2W, M_3W	width of lower molars
MAL	length of mandible
MRUL	length of upper molar row
P^4AL	alveolar length of P^4

SKA	skull "area" (CBL × WZY)
TRLA	area of lower postcanine toothrow (except for Table 2 calculated as TRLL × M_2W)
TRLL	length of lower postcanine toothrow
TRUA	area of upper postcanine toothrow (except for Table 2 calculated as TRUL × M^2W)
TRUL	length of upper postcanine toothrow
WZY	greatest zygomatic width (of skull)

Statistical parameters

a, b	empirical constants of the allometric equation $Y = aW^b$; b is slope and log a is intercept of the line $\log Y = b \log W + \log a$
CL	confidence limits
CV	coefficient of variation
l.s.q.	least squares slopes
m.a.	major axis slope
N	number of data points
P	probability of rejection of null hypothesis
r	coefficient of correlation
r.m.a.	reduced major axis slope
SD	standard deviation
W	(independent) variable
Y	(dependent) variable

Other abbreviations

ADI	index of anisodonty (def. p. 51)
AGI	index of anisognathy (def. p. 54)
HSB	Hunter-Schreger band

For crown morphology see caption of Fig. 2. Abbreviations of museum collections are given in App. 2–3. Further occasional abbreviations are given in the relevant figure and table captions.