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Concepts of Functional, Engineering and Constructional Morphology*

Feeding specializations in Rodents

With 11 Figures

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Abstract

The particular pathway of evolution of the mammalian order of the rodents as compared to the other herbivorous mammals is described. In their dentition the most important change consisted in the replacement of the primitive molar plan of the pantotherian ancestors by completely new dental structures. The new evolutionary options acquired by this, are one of the reasons for the particular evolutionary success and the great diversity of niches formed by this group. The newly developed family-specific dental patterns soon became genetically fixed, to the effect that functional optimizations – that means adaptive evolution – could only be realized through allometric change of shape and proportions. This was possible in connection with increasing hypsodonty. New descriptive parameters allowing to characterize the divergent adaptations are defined. Among them the relative amount of enamel within the occlusal surface is the most reliable indicator of feeding specialization. A comparison reveals that the small rodents in their hypsodont evolution mostly diminished the crowding in their dental patterns, whereas in the evolution of several very large mammalian herbivores quite the contrary occurred. The functional reasons for this are discussed. Arguments are brought forward that the morphological optimization of the molar dentitions of rodents can attain degrees not realizable in large hypsodont herbivores.

Key words: Feeding specialization, Rodents, evolution

Introduction

The origination of new morphological structures and gradual change of shape and proportions of these, are two different evolutionary processes. One of the best known examples for this is the formation of the internal bony structure of the fins of the crossopterygians and the many secondary changes this pattern later underwent within the tetrapods under various functional needs. Thereby it revealed that the anatomical structures behaved in a highly conservative manner, whereas shape and proportions varied following particular environmental and adaptive contexts. Largely the same can be said of the evolution of the vertebrate skull. Probably one of the latest incidents of the formation of new morphological structures in evolution is the origin of the molar patterns in the mammalian order of the rodents. Also in this case manifold secondary change of

shape and proportions occurred in the subsequent evolution. Thanks to a good fossil documentation and the existence of many living species the rodent example can be investigated in much detail. Since they are frequently found in fossil sites in great numbers they are particularly suitable for quantitative comparative investigations on a statistical basis. Due to their typically very low body weight, rodents were able to form many different feeding niches, which is reflected in a multiplicity of divergent secondary changes of their molar teeth. In addition to this, in many cases the fossil species are well documented as evolutionary lineages over millions of years so that morphologic changes can be followed step by step. All this makes them particularly appropriate for evolutionary studies. In the following exclusively the herbivorous specializations are

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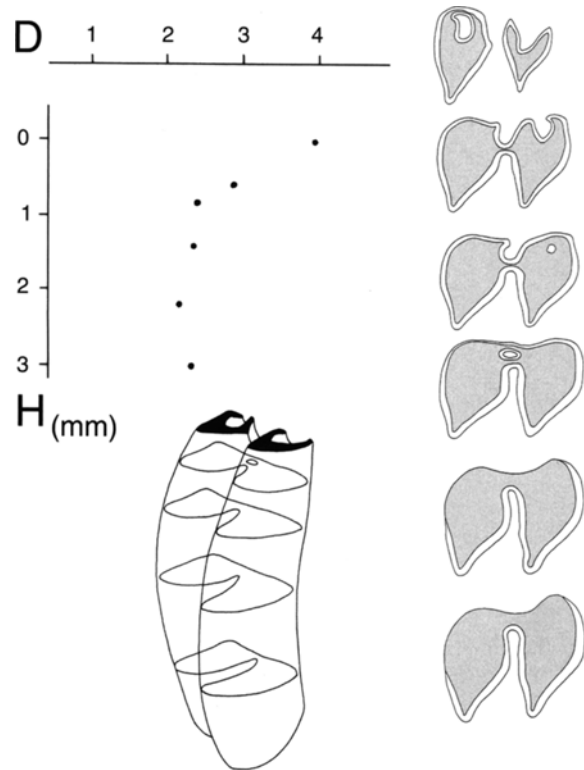
considered. Secondary piscivore and insectivore niches were formed as well but are rare and as to the morphology of the dentition do not show much particularities.

Degeneration of the inherited molar plan and formation of new dental structures

The primitive molar pattern originally shared by the marsupials and placentals was formed in the Cretaceous during the evolution of the pantotherians. Its characteristic arrangement of cusps and crests is generally called the tuberculosectorial or tribosphenic plan. Cheek teeth of this type were particularly suitable for breaking up insect food which very probably formed the main pantotherian alimentation source. When the radiation of mammals started, the tribosphenic molar plan revealed to be easily transformable for the needs of carnivorous specializations through rather simple allometries. Not the same can be said, however, as to the formation of vegetarian niches, because the cusps and crests of the plesiomorphic molar morphology were too steep as to allow high pressures between opponent dental surfaces during tooth occlusion. In most herbivores, as for instance the ungulates and New World notoungulates but also the lagomorphs, the original pattern was mainly conserved. Cones got reduced in height and crests became more prominent and only in the upper teeth few morphological elements were added. Therefore the plesiomorphic structure of the molars mostly is still discernible in the unworn teeth of even highly specialized descendants. Thanks to these modifications the molars became appropriate for disintegrating leaf material as the most abundant vegetarian food resource of the early Tertiary. Only later, that means in the Neogene, grass became another prevailing dietary basis.

Very different from this main stream development was the pathway of molar specialization of the rodents. In these the original tribosphenic pattern became largely dissolved to give free way to the formation of new occlusal structures. Looking for an explanation of this particular specialization history, two main reasons can be found. 1) Thanks to the possession of highly modified strong incisors, rodents were able to open up seeds and fruits covered by strong ligneous envelops. The exclusive access to this food resource could provide an essential part of their energy budget, given their typically very low body weight, and brought them a niche advantage not disputed by concurrents from other groups. 2) As supplement to this, due to their ability of living on trees, further soft and nourishing plant tissues could be acquired, such as burgeons and berries. In order to disintegrate such kind of food, molar surfaces with very low relief were most suitable, because more vertical pressure could be developed between their occlusal surfaces. From an evolutionary point of view such types of molars could easily be acquired through morphological atrophy of the plesiomorphic occlusal elements. As a result, occlusal surfaces with rounded cones and low and strongly variable surface shrinkles were formed, as can be found in many Lower to Middle Eocene representatives of the rodent order. However, with the evolutionary success of rodents and the increasing number of species very capacities of the characterized particular feeding niches were no longer sufficient very soon. As a consequence, increasing selective pressure towards the formation of niches with less restricted alimentary resources arose. This led to the many secondary specializations to more fibrous, less nourish-

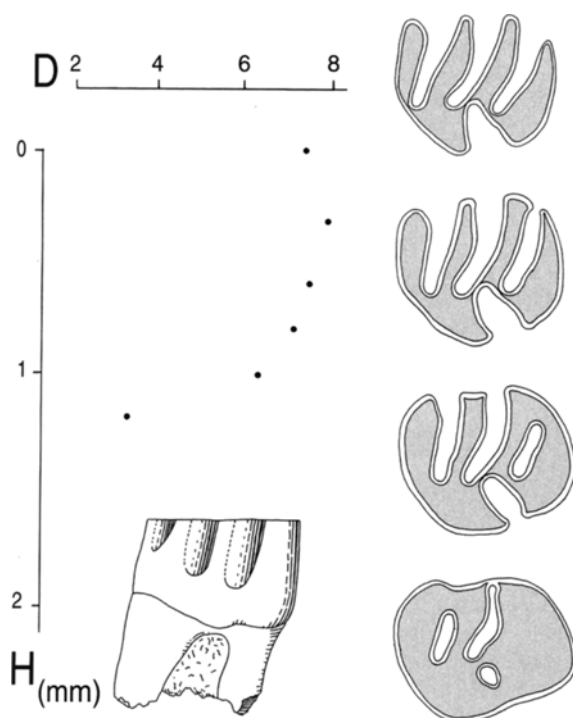
ing food. However, for the disintegration of these materials molar surfaces with more relief elements were required. This is why during a phase of secondary structuration new arrangements of crests were formed on the molars. These at the beginning were submitted to considerable variation but with further evolution soon became freezed to the group-specific patterns found in most rodent families since the Upper Eocene. In the following radiation, rodents with very low body weight formed numerous particular feeding niches, many of them not available to larger plantivorous mammals. In these niches the functional requirements for breaking up food were very different and as a consequence many divergent specializations formed. These, however, were not acquired by structural changes of the teeth in a proper sense, because the dental structures had already become genetically fixed in the preceding evolutionary phase. The modifications instead were realized through allometric changes of the tooth crown. This was possible in many groups in connection with a development generally known as increasing hypsodonty.



Text-fig. 1. Hypsodonty as result of exclusive vertical stretching of the base of the tooth crown; example of a lower molar of *Issiodoromys limognensis* from Pech du Fraysse, Upper Oligocene, Quercy, France. The parameter values were obtained by artificial abrasion of an individual tooth. D: structural density = degree of lobation of the tooth pattern; H: abraded crown height.

Progressive hypsodonty is a means of compensating the increasing rate of abrasion of the teeth during their function. At the same time it opens up the possibility of modifying the proportions of the tooth crown itself. In fact, hypsodonty could be realized in different ways as a result of particular ontogenetic growth programs. A closer look shows that the vertical elonga-

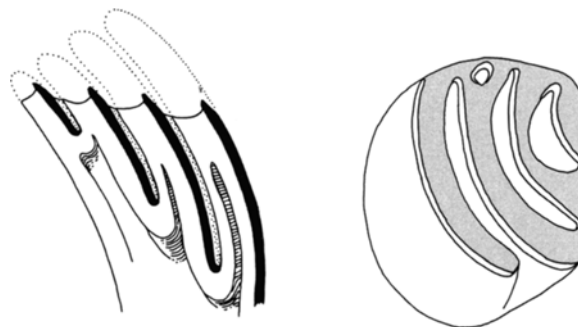
tion of the tooth crowns could be attained in four different ways: 1) through proportional stretching of all its parts (e. g. palaeotherians, *Parahippus*), 2) stretching of only the basis of the crown as shown in text-fig. 1 in the example of *Issiodoromys* (also found in cylindrodontids and bathyergids), 3) stretching of only the relief of the tooth as shown in text-fig. 2 in the example of *Spaniomys* (also found in many other caviomorphs and in arvicolidids), 4) asymmetrical stretching of the relief and expansion of the size of particular elements of the tooth crown on the costs of other elements (which become reduced or lost), as shown in text-fig. 3 in the example of pattern change from *Blainvillimys* to *Archaeomys*. As a result of these diverging allometries occlusal patterns with wear can either largely conserve their properties or become simplified or be changed through distortion or due to the loss of some of its elements.



Text-fig. 2. Hypsodonty as result of exclusive vertical stretching of the occlusal relief of the tooth crown; example of a lower molar of *Spaniomys riparius*, U. Miocene, Santa Cruz Formation, Patagonia, Argentina. The parameter values were obtained by artificial abrasion of an individual tooth. D: structural density = degree of lobation of the tooth pattern; H: abraded crown height.

Due to the effect of tooth abrasion the rather modulated primary relief of crests and cusps of the unworn tooth secondarily transforms into a horizontal plane exhibiting a pattern of dentinal areas surrounded by enamel bands and sometimes also cimentum areas outside the loops of enamel bands. Horizontally worn occlusal patterns can easily be quantified so that a more objective data basis for formulating and rejecting functional hypotheses becomes available. First attempts in this direction have been undertaken by RENSBERGER (1975, 1986) and RENSBERGER et al. (1984). Modern facilities of digital pattern analysis in the meantime allow the definition of new functionally relevant parameters, as proposed in the present

approach. Hence, two aims are envisaged in the following: a discussion of methodical points of view of pattern description and, based on this, a general functional analysis of food disintegration in herbivorous mammals.



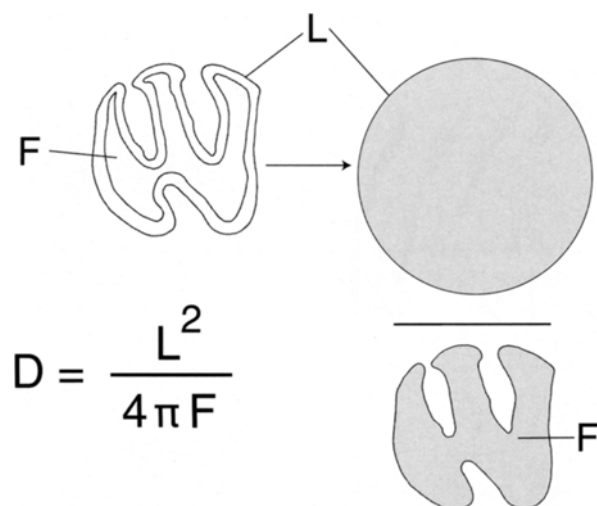
Text-fig. 3. Hypsodonty as result of unequal vertical stretching of different parts of the tooth crown; below: weakly advanced hypsodonty; many structural elements of the occlusal pattern are still present; example of an upper molar of *Blainvillimys blainvilli* (redrawn after VIANEY LIAUD et al. 1995); above to the right: advanced hypsodonty; original structural elements of the tooth crown were pushed aside or completely reduced to give free way to the elongation of functionally important enamel crests; example of an upper molar of *Archaeomys quercyi* (redrawn after MÖDDEN 1993). above to the left: section through an upper molar of *Archaeomys* perpendicular to the orientation of the functional enamel crests.

New descriptive parameters

Indentation index *D*

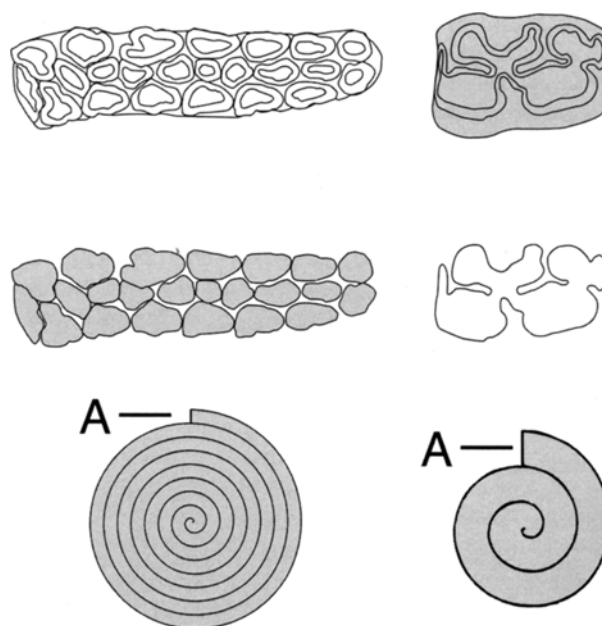
A basic descriptive parameter called structural density or indentation index (*D*) was introduced by SCHMIDT-KITTLER (1984) and subsequently used for pattern analysis in different groups of herbivorous mammals (SCHMIDT-KITTLER 1986, GAD 1987, SCHMIDT-KITTLER & VIANEY-LIAUD 1987, KULLMER 1999, HERRMANN 2002). Though its definition can be found in these articles, as a matter of completeness it is repeated here: The parameter expresses the ratio of the overall length of the enamel band occurring on a worn occlusal pattern (*U*) to the overall area of dentine surfaces (*F*) surrounded by them. Graphically the parameter can be represented as a quotient of two surfaces: the numerator of the quotient is formed by the circular area (F_x) whose perimeter equals the measured overall length of the enamel band (*U*). The denominator of the quotient is formed by the measured area of the occlusal surface including all dentine and enamel areas, but not the cimentum

(text-fig. 4). In the case of the simplest pattern, which is the circle, the parameter takes on the value 1. This is to say that the circle represents the basic unit of pattern density and all other pattern types are expressed by multiples of this unit.



Text-fig. 4. The structural density of an occlusal pattern is defined as the ratio of two areas: the numerator is formed by the area of the circle whose perimeter corresponds to the measured total length of the enamel band; the denominator corresponds to the measured area of the occlusal surface.

The herewith characterized parameter revealed to be an appropriate tool of analysing molar patterns of herbivorous species in regard of morphological/biostratigraphical and also functional questions. Its use is normally possible without meeting methodical biases. There are, however, particular approaches where this kind of parameter extraction can lead to inconsistencies. This appears when representatives of very different herbivorous groups are to be compared including also molar teeth which secondarily became strongly elongated together with multiplication of the primarily present elements of the occlusal pattern. Examples for this are the modern elephants, the Plio-Pleistocene East African suids of the *Phacochœrus*-group or the fossil and Recent species of *Hydrochoerus* etc. The reason for the problem is that the parameter D is based on the comparison of a particular pattern with the circle, that means with a closed geometrical figure. If we take multiples of it (which corresponds to the elongation and multiplication of pattern elements of a molar) and compare this newly formed set of a number of patterns once more with the circle the value is much higher though no change in the properties of the patterns themselves occurred. The consequence is that in approaches with a very extended scope including all types of dental specializations (as is needed for instance in an overall investigation of the functional significance of herbivorous tooth morphologies in general) the parameter D expresses sometimes different things and, thus, can not always be applied.

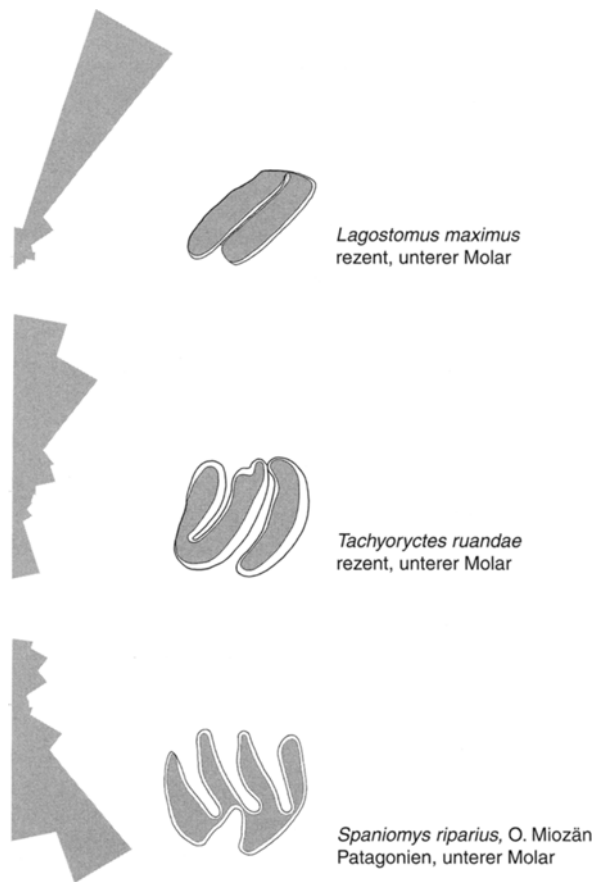


Text-fig. 5. The average density of crowding of the structural elements of a pattern can also be quantified using the Archimedean spiral as geometrical figure of reference. In the both examples shown, the density of the patterns is expressed by the crowding of the windings of corresponding spirals, which is measurable as the distance between the windings A. left side: occlusal pattern of the last upper molar of the East African pig *Phacochœrus aethiopicus*. right side: occlusal pattern of a lower molar of *Equus przewalskyi*, Pleistocene, Rhine Valley; the cimentum surrounding the enamel band is included in the calculation of the surface of the occlusal pattern.

Absolute crowding parameter A

In order to overcome the mentioned possible methodical bias a parameter is needed which basically expresses the same as the index D but is not dependent upon the extension or number of multiplied elements of patterns. The geometrical figure of reference in this case evidently cannot be a closed curve like the circle. It must be open and at the same time exhibit an isotropic property as a basis of parameter definition. The only regular geometrical curve performing this is the Archimedean spiral. It is distinguished from the other types of spirals by the fact that the distance between its windings has a constant value. In order to characterize an arbitrarily chosen pattern, the measured overall length of its outline in a first step must be transformed into the shape of an Archimedean spiral. Doing this, many options are left, because we have the choice between transforming it either into a small spiral with many turns or a bigger one with less turns. Therefore in a second step we must choose the only one spiral that in the overall length of its turns not only equals the measured outline but at the same time in the surface it covers is equivalent to the measured surface of the pattern. The winding height of this particular spiral (A) can now be taken as a measure of the absolute crowding of the lines within the pattern. In text-fig. 5 two occlusal patterns of herbivorous mammals are shown. Their measured occlusal surface and the overall length of the enamel bands are expressed by the corresponding Archimedean spirals exhibiting the same surface and possessing windings with the same length.

The newly defined crowding parameter A in its properties is complementary to D. As opposed to the latter, it is size dependent (having the absolute dimension of a length) and its value decreases with increasing crowding of lines within a pattern. While parameter D characterizes a pattern independently of its absolute size, the crowding index A changes if a pattern of a given absolute dimension becomes zoomed up to a greater size. In short, while D is a shape parameter, A is a textural parameter. The fact that index A is size dependent is not a disadvantage. On the contrary, it makes it particularly suitable for morpho-functional studies, because biophysical investigations are always connected to absolute dimensions.



Text-fig. 6. Distribution of frequencies of tangent orientations obtained by measuring the changing direction of the enamel band of a tooth pattern. The tangent values correspond to the interval of $0^\circ - 180^\circ$. Above: lower molar of *Lagostomus maximus*; middle: lower molar of *Tachyoryctes ruandae*; below: lower molar of *Spaniomys riparius*, U. Miocene, Argentine.

Parameter A is also suitable for studies beyond the scope of the present paper. It is of particular advantage in cases where patterns of very different sizes are to be analyzed. Frequently, as simplest method, the densities of patterns are expressed as overall length of lines found within an arbitrarily chosen surface of reference. Data gathered through this method are comparable with each other as long as the chosen surface of reference is the same. This normally is the case in the studies of one individual investigator but is not automatically guaranteed within a community of scientists which not all are closely cooperating with each other. Beyond of this, in approaches of more general scope there can be the need for comparison of patterns of very different sizes. In this case the limitations of defining pattern densities on the basis of a surface of reference is evident: It may be that the smallest surface of reference providing representative density values in a large pattern is much too big to be applicable to smaller patterns which form part of the same investigation. Also, in case the external shapes of patterns are very different, problems for using a reference surface can arise.

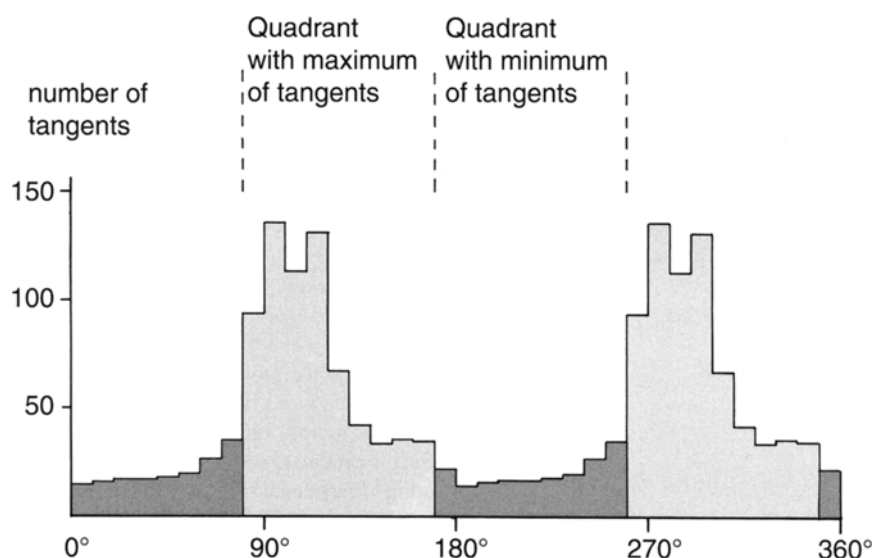
Orientation parameter G

The functional importance of the relative frequencies of particular enamel edge orientations on the molar surfaces of herbivores was already recognized by RENSBERGER et al. (1984) and RENSBERGER (1986). At that time the facilities of digital image processing were still not developed to the extent that an easily applicable parameter could be defined. This now is made in the frame of the present article. The degree of uniformness of orientation of the lines within a pattern can be expressed through counting the numbers of tangents of a certain direction constructed along the lines in short regular distances. Appropriate computer programs for taking the measures are available. The result can be represented e. g. in a rose diagram as seen in text-fig. 6 (only the half rosediameter is used there) or in a histogram as demonstrated in text-fig. 7. In the latter the two 90° quadrants possessing the greatest and smallest number of tangents respectively can be chosen for defining the following quotient:

(eq 1)

$$G = \frac{\text{quadrant with max. number of tangents}}{\text{quadrant with min. number of tangents}}$$

The orientation index G in the case of the circle equals 1 and takes on larger values with increasing predominance of a particular direction.



Text-fig. 7. Histogram showing the frequencies of the tangent values measured along the enamel band of the lower molar of *Tachyoryctes* of fig. 6. The considered interval is the complete rose of 360°. Within this two quadrants containing the maximum and minimum number of tangents respectively can be discerned. The quotient of the maximum number and minimum number of tangents can be taken as a parameter indicating the degree of orientation (G) of the lines in a pattern.

Functional specializations in hypsodont molars

Different kinds of mechanical disintegration of plant material

From a biophysical point of view on tooth surfaces basically two types of breaking down plant material can be distinguished. These are disintegration on the contact of surfaces fitting to each other, such as corresponding wear facets, or disintegration along edges gliding upon each other. In the first case the direction of movement leading to the contact of the corresponding surfaces may be vertical to them or be combined with a more or less marked component parallel to the surfaces so that they glide upon each other. Corresponding to this the disintegration effect is due only to pressure or to a combination of pressure with a shearing component. Through this the liquid content of the food as well as soft tissues are squeezed out and pushed away, that means transported to the margins of the surface contact. This type of food disintegration is typically found in low crowned (brachydont) teeth.

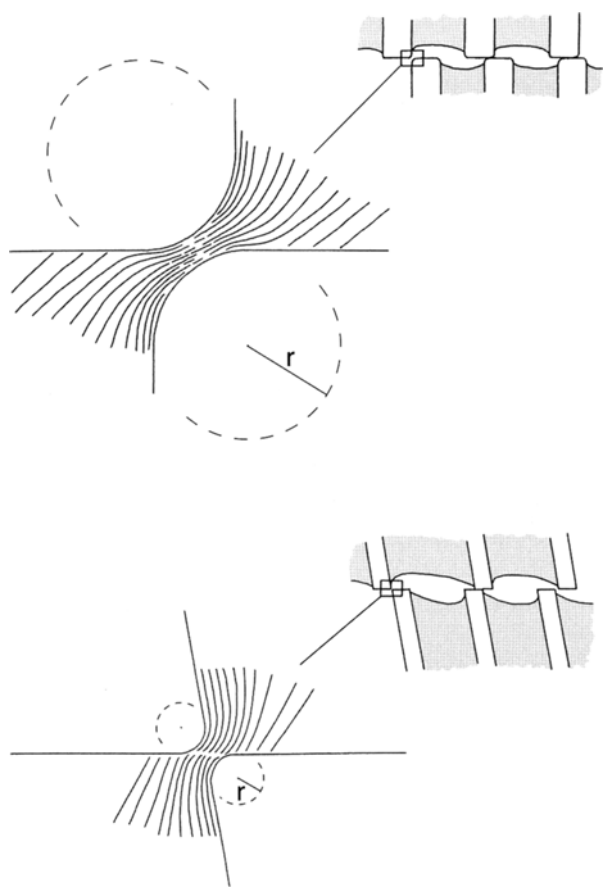
In the second type of food disintegration fibres or tissues are separated at small contacts through high punctual pressures and shearing forces along opposed edges gliding on each other. Depending upon the angle and the degree of sharpening or rounding of the edges the produced effect reaches from what can be called cutting separation to what can be called blunt separation (text-fig. 8), with all transitional stages between them. Both effects are found on low crowned as well as hypsodont molars.

In hypsodont dentitions separation of fibres and tissues along edges gliding on each other is by far the most important way of breaking down plant food. This is due to the fact that their occlusal surfaces with few exceptions (*Capromys* and

Geocapromys) possess a permanent relief formed by the more prominent harder enamel ridges on the one side and the less resistant surfaces of dentine and cimentum on the other. As to the pathways of specialization of these secondary occlusal surfaces, some major divergencies can be found between small species such as rodents and large species e. g. ungulates. This is due to the fact that the relation between mastication force and consistency of the food, and also the dimensionality of the chewing apparatus compared to the body weight, are very different in these animals (see below).

Enamel thickness as controlling factor of tooth abrasion and function

The rate of tooth abrasion is, of course, dependent upon the kind of food and also eventual admixtures of dust or soil. But an even more important factor is the thickness of the enamel. The latter not only influences the abrasion rate of the tooth but also the degree of sharpening of the enamel crests and, hence, their function. Since the enamel is markedly more resistant against wear than the dentine and cimentum, its share on the occlusal surface is the main controlling factor of the rate of tooth abrasion. If the ratio between the enamel surface and the entire occlusal surface (E/F) is high, wear is prograding rather slowly and there is no selective pressure towards very advanced hypsodonty. As a consequence molars with an E/F ratio higher than about 0,35 with very few exceptions (e. g. *Pedetes*) are moderately hypsodont and possess roots (diagram text-fig. 9). Opposite to this, teeth with an enamel thickness index lower than about 0,35 are rootless. This at least applies to the extant rodents. In fossil rodents it reveals that the decrease



Text-fig. 8. Separation of fibrous plant material along the enamel edges of the occlusal surface; above: blunt separation; enamel edges relatively rounded; large amount of fibres torn apart by shearing forces produced within the food material by the increasing pressure between the approaching enamel ridges. below: cutting separation; enamel edges sharpened; fibres disrupted altogether by a high and punctually acting shearing force between the approaching enamel ridges.

of enamel thickness can go faster than the development towards hypsodonty. Detailed investigations of the evolutionary lineage of *Issiodoromys* showed (Schmidt-Kittler & Vianey-Liaud 1987) that a low E/F value was attained rather rapidly at a semihypsodont stage of hypsodonty and then remained unchanged for the rest of the evolution of this genus. At the same time increase of hypsodonty went on to reach the state of rootlessness of the teeth only very late. This indicates that in the evolution of hypsodonty further factors can be involved. In the particular case of *Issiodoromys* the fossil record shows (Lavocat 1951, Vianey-Liaud 1976) that the advanced species of the lineage turned to bipedal saltatorial locomotion. As Rensberger (1975) argued, this type of movement requires much more energy and, hence, consumption of more food, which in turn leads to increased wear of the molar dentition and, hence, to more advanced hypsodonty. In the extant rodents the index E/F of about 0,35 with only few exceptions marks the limit between rooted and rootless molars. This seems to indicate that most living species have attained an equilibrium of optimization of their dental apparatus.

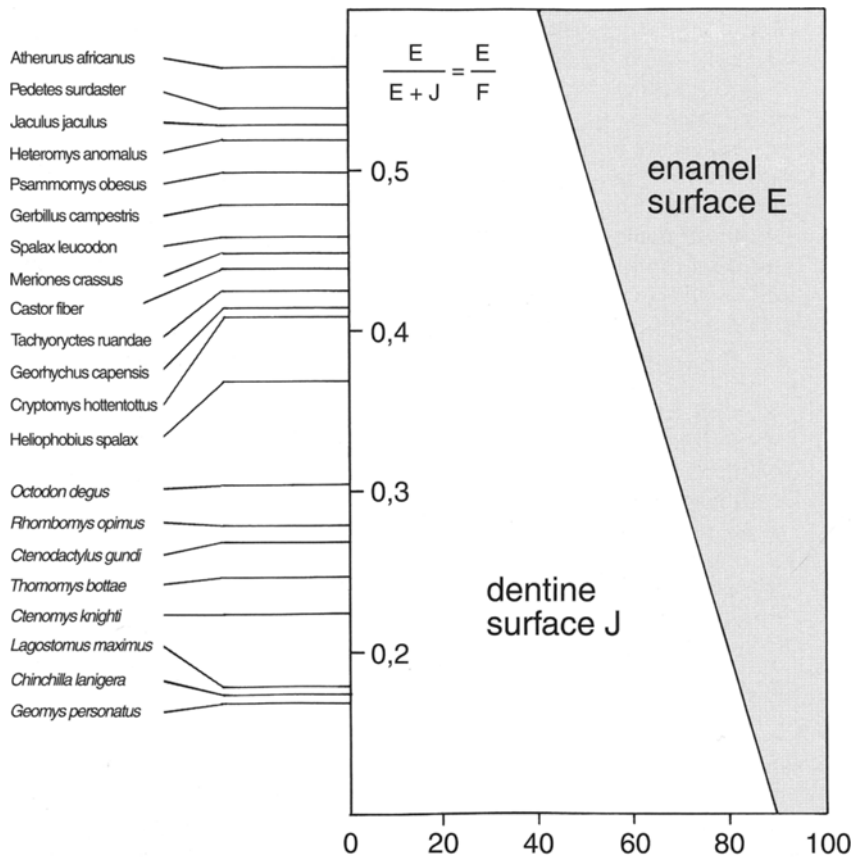
In case the enamel occupies a considerable part of the entire occlusal surface, pressures on the prominent enamel sur-

faces are lower and enamel-food-enamel contacts play a relatively important role, compared to direct enamel-enamel contacts with attrition. Tooth abrasion is prograding rather slowly so that there is enough opportunity for damages to be caused on the edges of the enamel crests through e. g. soil particles occasionally taken up with the food. As a result the enamel ridges become rounded and are not appropriate to exert very high punctual pressures, so that 'blunt' subdivision of fibres is the prevailing type of food disintegration. However, in case the percentage of the enamel is low, punctual pressures on the enamel crests are very high and tooth attrition through direct enamel-enamel contacts becomes a very important factor. Tooth abrasion is accelerated and the incidents of damages compared to the progress of wear diminish in relative number. As a consequence, with decreasing enamel thickness (corresponding to E/F values of 0,25 or below) a self sharpening effect is produced on the enamel crests to the effect that a high cutting efficiency is acquired and maintained (see text-fig. 8).

The cutting effect of the sharpened enamel ridges is further strengthened through the fact that they do not sit on the occlusal surface in upright position but are tilted towards the direction of movement of the opposite tooth. With this the angle of the cutting edges becomes less than 90° and the punctual pressures during function are even more increased. Tilting of the enamel crests can be found in all rodent molars exhibiting E/F values below 0,25.

Only in case the percentage of the enamel surface is diminished further, the difference of the abrasion rate on the enamel and the dentine or cimentum surfaces finally disappears so that the relief of the occlusal surface turns to become a plane without any prominent elements. This is found in the Recent rodents *Capromys* and *Geocapromys*. With this a secondary grinding surface is attained.

It is quite interesting to realize on this occasion that the shape of the occlusal relief and with this its ability of exerting a particular function, is not a property of the tooth *per se* but the result of a dynamic process within which the kind of food and the enamel thickness play the role of indirect controlling factors. Considered in more detail, the enamel bands frequently also change in thickness within the occlusal patterns themselves, depending upon their orientation and also their distance from each other. This can be seen e. g. in *Tachyoryctes* (see text-fig. 6) or *Blainvillimys* (see text-fig. 3) and also in many arvicolids (HERRMANN, this volume). Similar phenomena are also found in large herbivores, for instance in horses (see Kaiser, this volume). It indicates that the functional importance of the enamel bands on the occlusal surfaces in many cases must be studied even more specifically in the context of particular taxonomic groups. In the rodent family Chinchillidae for instance the total length of the functionally relevant enamel band is halved through the fact that it becomes completely reduced on all upward sides of the pattern (see *Archaeomys* in text-fig. 3). As a consequence of this, also the E/F value is diminished by factor 2 and the average distance of the shearing crests is doubled. Parallel to this the remaining enamel crests become stretched and orientated in a way that increases their cutting efficiency. The same can be found in rodents belonging to other extant groups (e. g. *Otomys*) and also in the fossil *Blainvillimys*- and *Archaeomys*-lineages of the European Oligocene.

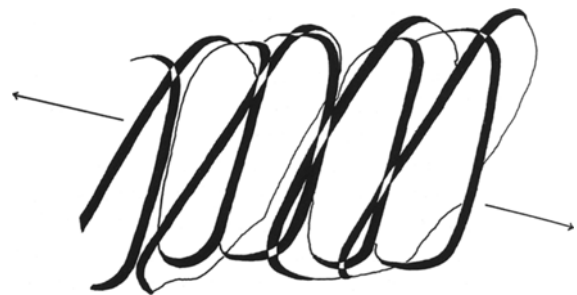


Text-fig. 9. Relative thickness of the enamel bands of the occlusal patterns of various extant rodents expressed as ratio of the enamel surface and the entire occlusal surface (E/F). Species with fossorial life habit and seed feeders are found at the upper end, leaf and grass feeders are placed at the lower end of the scale.

Orientation of the enamel crests

Occlusal surfaces with a relief consisting of numerous small elevations and depressions, like a rasp, can produce a grinding effect anyway. This is largely independent of the particular shape and orientation of the surface elements. Because of this, also random windings of enamel crests with very low orientation parameters G can lead to relevant food disintegration. Occlusal surfaces of this type are particularly suitable for breaking up soft plant material with or without admixture of a certain amount of soil (many subterranean rodents, e. g. spalacids or bathyergids), but also rather hard material such as grains or xerophytic sprouts in desertic environments (e. g. gerbillids, dipodids, hystricids). However, if there appears the need of cutting fibres and tissues, elongate ridges are more advantageous and also their orientation in regard of the direction of the stroke can no longer be arbitrary. Angles of enamel crests in the upper and lower molars of rodent dentitions exhibiting pronounced shearing specialization vary between 20° and 30° (measured in SCHMIDT-KITTLER 1984; see also the example of *Lagostomus* in text-fig. 10). In case the angle is considerably greater, food material is pushed aside but not obstructed between the shearing edges. If the angle is very low tending

even towards zero, much material is jammed along large parts of the edges at the same moment, to the effect that high pressure peaks appear whenever two of the many crests of the upper and lower molars meet. As a result more muscular force must be applied in mastication than really needed. This means that the measured angles are the result of evolutionary optimization for cutting disintegration of food.



Text-fig. 10. Occlusal scheme of the upper and lower molars of *Lagostomus maximus* as functional example of a highly optimized chewing apparatus. The straight and uniformly oriented enamel edges form angles of about 20°.

Distances between the crests

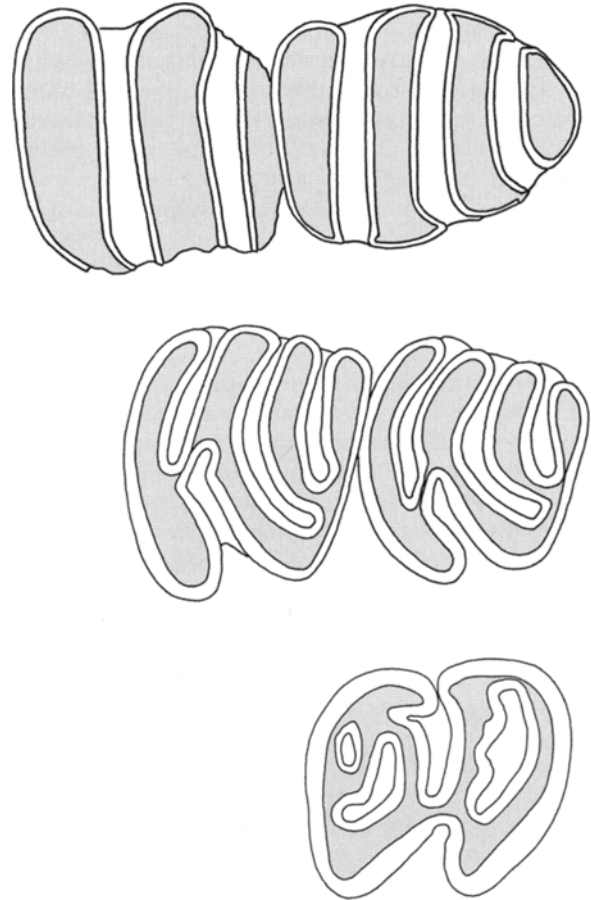
Enamel crests developed on the occlusal surface of a molar in order to produce a good desintegration effect should be distributed more or less equally. In brachyodont and weakly hypsodont teeth this is often not the case but there are many fossil examples where regularity of distribution of the occlusal elements increases with progressive hypsodony. Most clearly this development can be found in rodent lineages optimizing the shearing function of their molars, e. g. in Eocene/Oligocene theridomyids (the *Blainvillimys*-type leading to the *Archaeomys*-type, see text-fig. 3) Oligocene to Pliocene castorids (the *Chalicomys*- and *Stenofiber*-type leading to the *Castoroides*-type, text-fig. 11), Miocene to Recent murids (the *Stephanodon*-type leading to the *Otomys*-type), and also Miocene to Recent chinchillids and hydrochoerids etc.. Distances between the parallel oriented crests are not exactly the same in upper and lower molars (see HERRMANN, this volume), which may as well be explained as a means of distributing jamming effects during the stroke as equally as possible. In secondarily elongated dentitions, like that of *Hydrochoerus*, the distance of crests slightly decreases in caudal direction, that means towards the side where mastication pressure becomes higher. This leads to the assumption that in rodents under favourable circumstances adjustments of functionally relevant tooth parameters can attain very high degrees.

Pathways of specialization

In brachyodont rodent molars the sheet of the enamel envelop of the dentine is normally rather thick compared to the size of the tooth. In the evolution towards hypsodony in most cases enamel thickness decreases to attain lower E/F values. A good example for this is seen in the evolution of the lineage *Issiadoromys* (see above). Only in few groups enamel thickness increased as compared to the plesiomorphic situation. This can be found in species feeding on subterranean parts of plants such as the extant Bathyergidae and Spalacidae or in some Oligocene Cylindrodontidae. It seems that in these groups development of a thicker enamel is a means of compensating the higher abrasion caused by inevitable soil admixtures in their food. In addition, tooth wear in these animals also seems to be reduced through the manner they are chewing their food, because no striations can be found on the enamel surfaces of their teeth. This leads to the assumption that the horizontal component of jaw movement is comparably unimportant. Probably the both factors together are fairly preventive since bathyergids and spalacids notwithstanding their particularly abrasive food never exceeded a state of medium hypsodony.

As to the main stream development in rodents, reduction of thickness of the enamel bands at first glance appears to be contra-productive because it raises the rate of tooth abrasion. There is, however, an important positive effect, because at the same time the surfaces of contact between the enamel bands of the upper and lower molars are diminished, to the effect that punctual pressures caused by the jaw musculature become higher and with this shearing along their edges becomes better. It is likely that this is the main driving factor in the development towards decreased E/F values, and that increased hypsodony in many cases is rather to be considered a consequence. Another advantage of this is the possibility that the whole tooth

crown, and together with it the occlusal pattern, can undergo allometrical changes in divergent directions and, thus, be adapted to the needs of particular feeding niches (leading to the different types of hypsodony as shown in text-fig. 1 – 3).



Text-fig. 11. Three species of castorid rodents exhibiting prograding degrees of specialization. It can be seen in the modifications of the enamel bands, as there are increasing uniformity of their orientation, increasing uniformity of their distances from each other and decreasing thickness. below: lower molar of *Chalicomys dehmi*, Upper Oligocene, Gaimersheim, Germany; middle: upper molars (M2 and M3) of the extant *Castor fiber*; above: upper molars (M2 and M3) of *Castoroides ohioensis*, Pleistocene, Florida. Not to scale.

Evidently the many different occlusal patterns found in hypsodont rodents, reaching from extremely simple to highly folded types, are the result of directed selective pressures acting in the context of particular niches. In these optimizations thickness and orientation of the enamel crests seem to play the most important role. They finally indicate to which degree a cutting effect on the molars is important or not important to a particular feeding habit. It should therefore be basically possible to distinguish between root eaters, grain eaters or leaf and grass eaters also on a quantitative basis. The most reliable indication can be drawn from the E/F value because it exclusively seems to reflect the effect of niche specific optimization. As to the orientation index, it basically says the same. However, it can more or less be biased by limited optimizability due to peculiarities of the inherited pattern, as is for instance the case in the arvicolids (see HERRMANN, this volume).

Extant rodents feeding on leaves and grass with no exception exhibit self sharpening shearing edges on their occlusal surfaces. In opposition to this in large hypsodont mammals depending on the same particular food, the enamel crests of the molars are predominantly rounded, with few exceptions in artiodactyles and horses. It seems that in large herbivores emphasis is not so much laid on the degree of food disintegration but rather on the quantity ingested (see below). This leads to the supposition that selective pressure towards optimization of the occlusal patterns was less stringent as compared to the rodents.

Microdontology and macrodontology

A specialization evidently connected to the enamel thickness and the orientation parameter is the relative size of the entire tooth row compared to that of the skull. It reveals that rodents specialized to feeding on subterranean parts of plants but also species feeding on seeds (that is exhibiting a high E/F ratio and a low orientation index) are distinguished by possessing comparably small molars. The ratio of the surface of the entire cheek dentition (both sides) and the surface of the cranium, seen from the ventral side, is very low (e. g. 0.019 in *Dipodomys merriami*, 0,020 in *Cryptomys hottentotus*, 0,021 in *Spalax leucodon*, 0,024 in *Ellobius fuscocapillus*). In opposition to this, species possessing molars with accentuated shearing specialization (indicated by a low E/F ratio and a high orientation index) have relatively larger cheek dentitions (e. g. 0,04 in *Lemmus lemmus*, 0,048 in *Cavia porcellus*). Further studies will be necessary to document more completely the differences between these two types of specialization, where for instance the microdont bathyergids, spalacids and gerbillids are opposed to macrodont specialization types like *Lemmus*, *Cavia* or *Hydrochoerus*. As to the explanation of microdontology there are possibly several factors involved. One main reason for it could be that with decreasing size of the molars the punctual pressures produced by the mastication musculature become higher. As to the macrodont molar dentitions, an explanation seems to be more easily at hand: In these, as a matter of functional optimization, the distances between the shearing crests on the occlusal surfaces typically take on particular average values. At the same time the quantity of food to be chewed is dependent on the number of cutting crests. This means that in order to increase the amount of food to be ingested the crests have to be multiplied, which automatically leads to more occlusal surface. Since large herbivores need relatively higher quantities of food than small species, their macrodontology should be more accentuated. This is in fact the case in nearly all large hypsodont herbivores (e. g. bovids, horses, rhinocerotids). *Equus* for instance is characterized by a macrodontology index of 0.043. Exceptions are the clearly microdont phacochoerines (*Phacochoerus* with an index equal to 0.019) and elephantines. Both are distinguished from the other large herbivores by the reduction of their dentition to only one molar, the M3. It would be highly interesting to study in more detail their particular evolutionary pathways.

Pattern density and body weight

The functional significance of the density parameter D (or the crowding parameter A respectively) can be seen in the fact that

they indicate the degree of folding of the enamel bands and with this the average number of enamel-enamel contacts during occlusion. The more contacts between the enamel crests of the upper and lower molars occur the more the mastication force is subdivided into partial pressure components. Given a particular most economic mastication force normally applied by a species, it is clear that in case the enamel contacts become more and more numerous a critical point will be reached where the punctual pressure components will no longer be high enough as to guarantee efficient shearing along the enamel edges. Mastication force depends upon the thickness of the masticatory muscular bundles (measured as cross sections) which in mammals is correlated in the second power to body size. As a consequence the described critical point of inefficiency will more easily be met in very small mammals, whereas larger mammals may hardly be confronted with this limitation.

A look at the many families of small rodents leads to the supposition that in these mastication force is in fact a limiting factor of molar function. In the various families the group specific brachydont occlusal patterns in most cases are rather complicated so that they produce rather high D values. But later, with growing hypsodontology a general tendency towards diminished D-values can be found (aplodontids, ctenodactylids, theridomyids, heteromyids, eomyids etc.) In large mammals, however, we find the opposite development. Due to the fact that their brachydont occlusal patterns are derived from the primitive tribosphenic molar plan, their occlusal surfaces are rather poorly provided with enamel crests. However, in many families or lineages developing towards advanced hypsodontology, the molar patterns become more crowded. This can be seen in the evolution of the elephants, horses and elasmotheriine rhinoceroses. But there are also exceptions as for instance the ruminant artiodactyles. These, however, cannot be understood as refutations because their nonconformity is due to other reasons. The artiodactyles in their evolution very early adopted a transversal jaw movement and in connection with this developed a very effective selenodont molar pattern. The latter would not have been transformable to another type of pattern without passing transitional stages with much lower functional efficiency.

If in the crowding of the occlusal patterns opposite evolutionary trends can be found in small and large mammals, there must also exist an intermediate body size where no advantage can be drawn from a change of the crowding of the occlusal pattern in neither direction. This seems to be the case with body sizes comparable to those of the suids. *Phacochoerus* and his Plio/Pleistocene fossil relatives for instance attained extreme hypsodontology without changing the degree of crowding of their molar patterns compared to their more primitive forerunners.

Another difference connected to the described trends is the possible degree of functional optimization of the molars in small and large species. In small hypsodont herbivores, e.g. rodents, decreasing crowding density of the molar patterns through selection can lead towards reduction of just those elements which are most unefficient. Linked to this, more space becomes available for enamel crests to adopt functionally more favorable orientations. As a result in the evolution of many rodent families there was much free space for the optimization of their molar patterns. In very large mammals, due to the trend

towards increasing crowding density, much less free space was available for appropriate pattern changes so that the patterns of the hypsodont teeth are not so much different from those of the earlier brachydont evolutionary stages. In horses for instance few supplementary elements occur in the upper molars, whereas in the lower ones the only change to be found is a certain elongation of the overall length of the enamel band and its

more homogeneous distribution over the occlusal surface. In elasmotherians there is nearly no pattern change but instead an intense folding of the enamel bands. In the elephantids the transversal series of cusps developed on the primitive molars of *Gomphotherium* became multiplied in number and compressed to form a more or less densely packed complex of tooth lamellae.

Conclusion

The evolution of the molar dentition of the rodents is exceptional in so far as no other example of structural revolution of similar kind has been described up to now. At first glance the example seems to refute the generally held opinion that anatomical structures, once integrated to form part of a Bauplan, remain stable in their essential properties, that means conserve the particular relationships between their elements (on the condition that these do not become reduced). A closer look at the early evolution of the rodents shows, however, that first many inherited pantotherian features of the molars disappear and only then new morphological structures become introduced to fill the unoccupied space, just like a *tabula rasa* can become structured by new elements. Thanks to this shift to new dental structures rodents were able to develop a lot of new niches, many of them not accessible to other mammals and, thus, came to form the most diversified radiation among herbivores. This becomes particularly evident if we compare them with the lagomorphs. Most Paleogene species of this mammalian order were comparable to rodents in body size and from this point of view could as well have been candidates for root eater (radicivore) or grain eater (granivore) niches. However, their molar dentition, though simplified, essentially conserved the ancient tribosphenic plan (which is particularly clear in the trigonid/talonid-subdivision of the lower molars). This means, there was not enough evolutionary plasticity for confronting the teeth with sensibly different functional requirements as a precondition to developing new alimentary niches.

Interesting enough the new molar structures of the rodents in turn became genetically fixed rather soon, that means in the Eocene, to form conservative patterns in the further evolution. This notwithstanding, many divergent functional specializations could be attained through allometric modifications of the shape and proportions of the elements of the occlusal patterns. However, it revealed that the patterns due to their accidentally acquired particular structural properties were modifiable to different degrees so that optimizations could become more or less accentuated. In the following Neogene history of the rodents further structural innovations in the molar patterns occurred only twice. This is the transition of the cricetid molar type to the arvicolid pattern of the voles and lemmings on the one side and to the stephanodont pattern of the murids on the other. In both cases the innovations were not acquired through structural change of existing elements in a proper sense but through multiplication of already present (arvicolids) or addition of new elements (stephanodontid type). As a whole, it revealed that in rodents the extent of optimization of

biomechanical food disintegration is dependent on the particularities of the inherited dental structure. The only dental parameter not biased in its optimization is the E/F value of the occlusal surfaces of the molars. It therefore is of particular paleoecological significance. It allows to distinguish quite clearly between root and seed eaters in the one extreme (high E/F values) and leaf and grass eaters (low E/F values) in the other extreme, with in between a large field of intermediate species accustomed to feed on different kinds of food (see also HERRMANN, this volume). As to the molars of the root- and seed eaters, their dental patterns with no exception are the result of simplification. This implies that they are not much biased by the inherited structure of the dental pattern. As a consequence also the D values can be ecologically indicative in these cases.

Optimization of molar patterns in the large herbivores is much weaker than in rodents. An explanation for this is that in rodents emphasis is laid on both the degree of food disintegration and the quantity to be broken up per time, whereas in large herbivores the need for quantity overrules that of disintegration quality: Given the need of a high amount of food to be ingested per day there is actually not much possibility of increasing the degree of food disintegration, though this would in principle be functionally realizable. The most important limitation is the time factor. Breaking down plant food to very small pieces can be realized on the condition that not much plant material is brought between the tooth rows per time. This means, the better the degree of disintegration, the smaller the overall quantity which can finally be taken in. Hence a critical point soon is reached where the advantage of facilitating the biochemical process of digestion is overruled by the disadvantage of not taking up enough plant material as to cover the energy requirements. This means that in large herbivores there is optimization of the molar dentition but not to the extent as it is possible in rodents. This another time underlines the relevance of the latter group to our attempts of better understanding processes of gradual evolution.

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