FUNCTIONAL ASPECTS OF THE EVOLUTION OF RODENT MOLARS

by

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SUMMARY

The wear facets of primitive rodents can be homologized with those of primitive primates and ungulates. As in primates, the jaw movement was ectental, with an increased anterior component in the lingual phase (phase II). The buccal phase (phase I) in rodents approaches the horizontal and it tends to be reduced in importance in comparison with the lingual phase. In more advanced rodents the efficiency of grinding is increased by the development of additional cutting edges of enamel (e.g. enlargement of hypocone, development of mesoloph and lingual sinus). The buccal phase movement becomes lined up with the lingual phase movement to form a single oblique chewing stroke, resulting in planation of the crown. As the stroke becomes more longitudinal (propalinal) the enamel edges become more transverse. In Muridae propalinal chewing evolved before the loss of cusps, facets were reorientated and additional cusps developed.

Molar teeth provide direct evidence of their functioning in the form of attrition facets. These are areas of the tooth surface that are worn as a result of contact with opposing teeth during mastication. Not only do the facets show how the teeth fit together, but scratches on the surfaces of facets show the direction of the masticatory movements (Butler 1952). As far as I know, little attention has been given to this aspect of rodent molars. It is generally accepted that in the Sciuridae, as in the primitive Paramyidae, the chewing movement is largely ectental, essentially transverse, whereas in advanced rodents it has become propalinal, from posterior to anterior in the line of the tooth-row. This change must have had an effect upon the patterns of the teeth, and yet the voluminous literature on rodent molars gives very little information about the direction of the chewing movement. It has been necessary to get the evidence directly from specimens, and I have been gathering information on this topic for a number of years.

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I have examined a representative sample of fossil (mostly Eocene and Oligocene) and Recent rodents. Attrition facets are most clearly seen on lightly worn teeth. By turning the tooth so as to see it from different directions the facets are revealed as shiny areas of polished enamel. In many cases they are marked with striations, produced by gritty matter in the food. Having identified the facets on upper and lower molars of the same species (ideally, of the same individual, but this is seldom possible in the case of fossils), the occlusal relations were worked out. This was done by fitting teeth together, and by superimposing camera lucida drawings. Each facet on the upper molar must make contact with a facet on the lower molar (Butler 1973 ; fig. 1).

Evolutionary changes of upper and lower cusp patterns are coordinated in such a way as to retain the interrelations of the cusps during occlusion. For example, the hypoconid always occludes between the paracone and the metacone, and it bears facets on its anterior and posterior surfaces due to contact with those cusps. Just as cusps can be homologized in different mammals, so can the facets : homologous cusps carry homologous facets (Butler 1961). It is therefore not surprising that the facets of primates and ungulates can be recognized in paramyid and sciurid rodents (fig. 2), for the molars of all these mammals have been derived from the basic tribosphenic type.

The facets may be divided into three groups (fig. 1, 3) :

1/ Facets formed by contact between the buccal cusps of opposing teeth (protoconid and hypoconid with paracone and metacone) will be referred to as B-B facets.

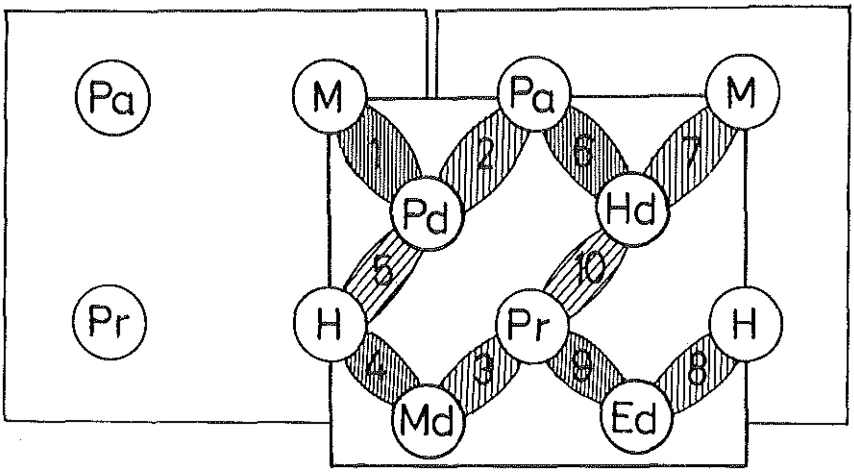


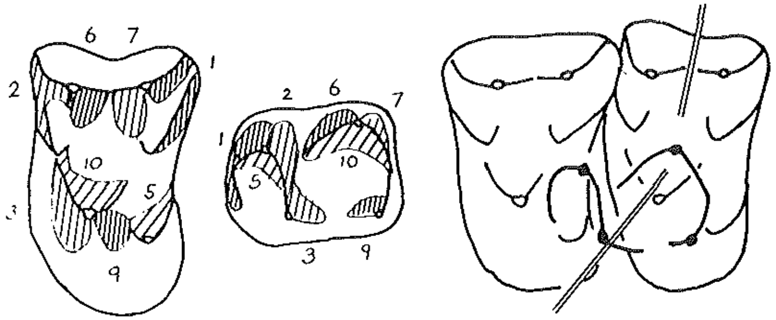
Fig. 1. — Facet nomenclature (Butler 1952, 1973). Facets 1, 2, 6 and 7 are due to contacts between the buccal cusps of opposing teeth (B-B facets) ; facets 4, 3, 9 and 8 are due to contacts between the lingual cusps (L-L facets) ; facets 5 and 10, are due to contacts between lingual upper cusps and buccal lower cusps during the lingual phase of occlusion (L-B facets). Facets 1, 4, 6 and 9 face posteriorly on upper molars and anteriorly on lower molars ; facets 2, 3, 7 and 8 face anteriorly on upper molars and posteriorly on lower molars.

2/ L-L facets are formed by contact between the lingual cusps (metaconid and entoconid with protocone and hypocone).
3/ L-B facets are formed when the protoconid meets the hypocone and the hypoconid meets the protocone.

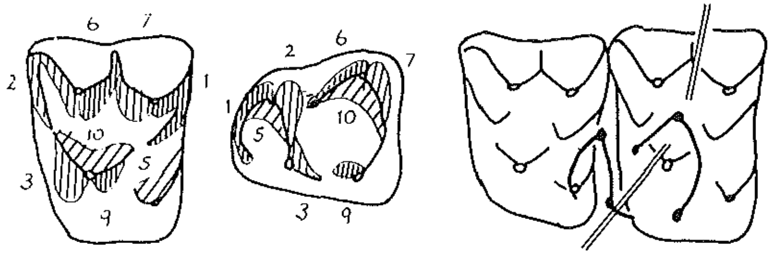
B-B and L-L facets are produced in the buccal phase (Mill 1955) (= phase I, Kay & Hiiemae 1974), when the lower teeth are moving approximately transversely (more exactly, about 10° forward from the transverse direction). L-B facets are formed in the lingual phase (= phase II), when in rodents, as in primates, the lower teeth are moving obliquely forward. In *Sciurus* the lingual phase movement is inclined forward from the transverse direction at an angle ranging from 35° on P4/ to 55° on M3/ (fig. 4).

Differences of molar pattern result in differences in the relative size and orientation of the facets. The molars of rodents are tilted, buccally in the upper jaw, lingually in the lower jaw. This tilting seems to be associated with the posterior position of the teeth in relation to the zygoma and coronoid process, for in primates the last molars are often tilted in a similar manner, resulting in a helical twist of the occlusal surface of the cheek dentition. One effect of the tilting is that movement of the lower molars in the buccal phase of occlusion, primitively steeply inclined at an angle of about 45°, becomes in rodents much more horizontal, with an inclination of 15° or less (fig. 3). The paracone and metacone have lost their primitive shearing function and are low and blunt. The hypoconid travels lingually through the wide valley between the paracone and metacone, first crushing food against the buccal surface of the protocone and then grinding the food during the obliquely forward movement of the lingual phase. At the same time the protoconid travels along the wide anterior cingulum of the upper molar and then grinds against the posterior cingulum and hypocone of the more anterior tooth. The mesostyle, which develops at the buccal end of the path of the hypoconid, parallels the parastyle which functions against the protoconid.

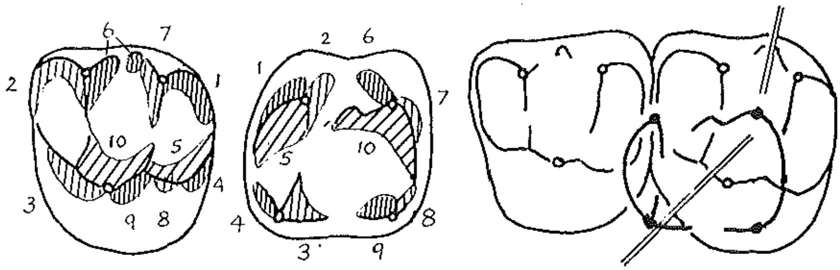
If molars of *Paramys* or *Sciurus* are compared with those of primitive primates such as *Palaechthon* it is seen that the lingual phase (L-B) facets occupy a larger area of the tooth, while the buccal phase (B-B and L-L) facets are reduced. The talonid of the lower molar is enlarged at the expense of the trigonid, in which the paraconid is represented only by an anterior cingulum and the metaconid has been displaced to the anterior edge of the tooth. The lower molar is also wider in proportion to the upper molar. In *Palaechthon*, when the protoconid meets the parastyle at the beginning of the chewing stroke, the metaconid is near the paraconule, and as the tooth moves lingually the metaconid wears a transversely extended facet on the anterior side of the protocone-paraconule crest. In rodents, with broader lower molars, the metaconid meets the upper molar nearer to the protocone, the paraconule is more lingual and the facet is less extensive (fig. 3). Contact of the protoconid with the paracone is also reduced, and hence the middle part of the protoconid-metaconid crest is lacking. The metaconid of rodents touches the hypocone, or that part of the posterior cingulum from which the hypocone will arise ; this contact is absent in *Palaechthon*, where owing to the presence



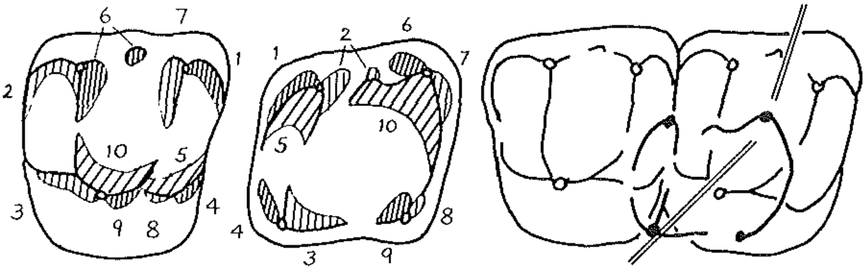
Palaechthon



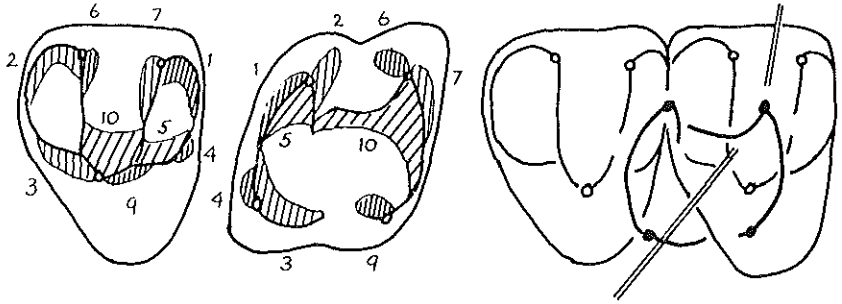
Mixodectes



Paramys



Sciurus



Marmota

of the paraconid the metaconid is placed too far back.

During the lingual phase oblique movement of the hypoconid carries its tip posterior to the paraconule and anterior to the tip of the protocone ; the posterior crest of the hypoconid crosses the anterior crest of the protocone. In this movement the hypoconid is preceded by the mesoconid, which provides an extra cutting edge. Efficiency of the grinding function is improved in many early rodents by the development of wrinkles and folds on the lingual surface of the hypoconid and the buccal surface of the protocone.

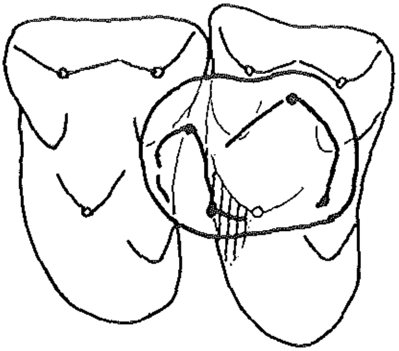
Many of the characters of primitive rodents are present in, or are approached by, the molars of other early placentals. Thus a nearly horizontal transverse jaw movement developed in condylarths and some primates. It was frequently associated with an increased importance of the lingual phase of occlusion, shown by enlargement of the talonid and compression of the trigonid. In *Uintasorex*, for example, the buccal cusps of the upper molar are low, and on the lower molar the talonid is large and the metaconid is displaced anteriorly. *Mixodectes* (fig. 2) has a mesostyle and a mesoconid as well as a wide talonid, but it is more primitive than rodents in the steeper buccal phase movement and the retention of the cutting function of the buccal cusps. In searching for rodent ancestors among primitive placentals, resemblances in molar teeth should be treated with great reserve, as the dentition is notoriously subject to parallel evolution. In the combination of their characters, however, the molars of primitive rodents are unique, and it is likely that the possession of such molars was one of the factors that led to the subsequent success of the order.

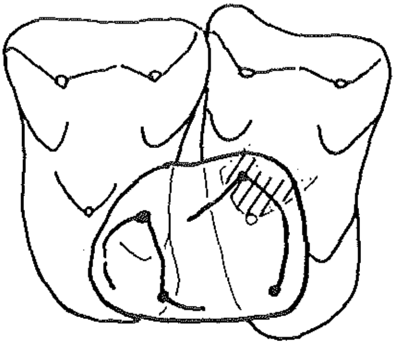
The primitive rodent molar pattern has given rise to a great variety of more specialized forms. I will discuss only a few representatives which illustrate some of the commoner trends.

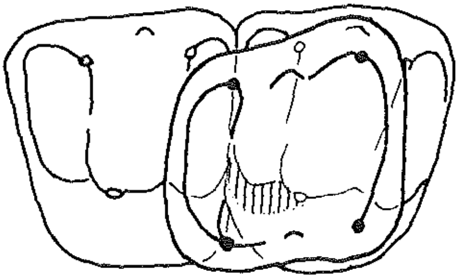
Prosciurus (Aplodontidae) (fig. 5) has departed from the paramyid condition in its buccally extended hypoconid, separated by a deep bay from the mesoconid. The enamel edges of these cusps cross the protocone during the oblique movement of the lingual phase. On the upper molar the anterior surface of the paraconule and the posterior surface of the metaconule extend as ridges which provide additional contacts in the buccal phase : the paraconule occludes with the mesolophid and the metaconule occludes with the elevated posterior cingulum of the lower molar. At the lingual end of the mesolophid is the metastylid which occludes with the tip of the protocone. The hypocone remains low and cingulum-like.

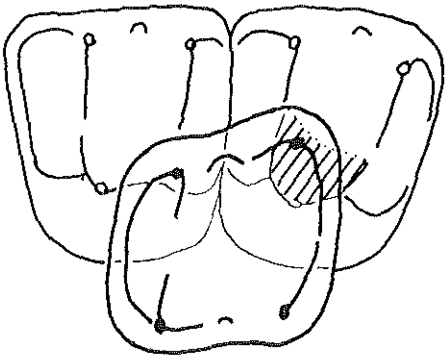
Fig. 2. — Facets on M2/ and M/2, and occlusal diagrams showing M/2 in centric occlusal relation with M1-2/. The straight lines on the occlusal diagrams indicate the path of the hypoconid during the buccal and lingual phases of occlusion. Anterior is to the left.

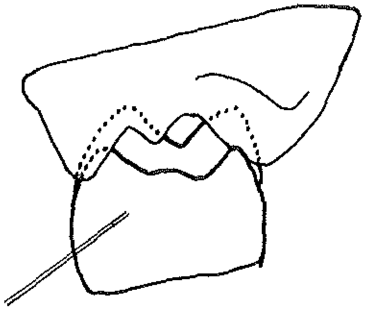
There is an essential similarity between a primate (*Palaechthon*), an « insectivore » (*Mixodectes*), a paramyid (*Paramys*) and sciurids (*Sciurus*, *Marmota*).

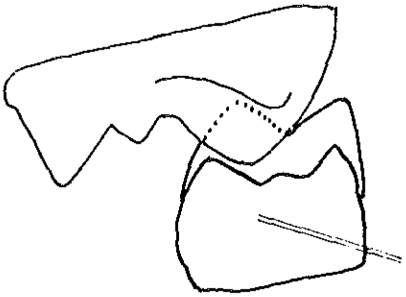


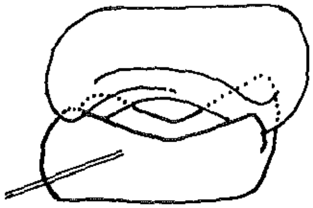


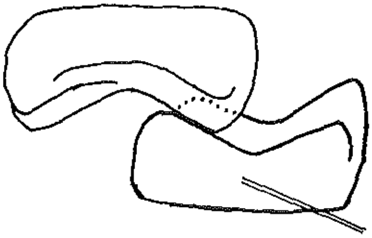












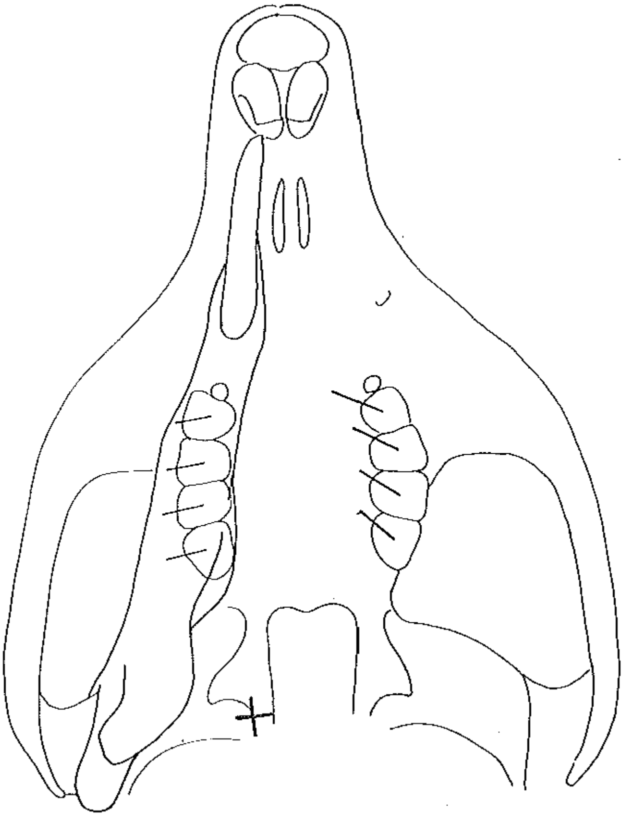


Fig. 4. — *Sciurus carolinensis*. Palatal view, showing the direction of striations on facets produced during the buccal phase (left side of figure) and the lingual phase (right side). The centre of rotation is indicated by + . A lower jaw is drawn in a position it occupies early in the buccal phase.

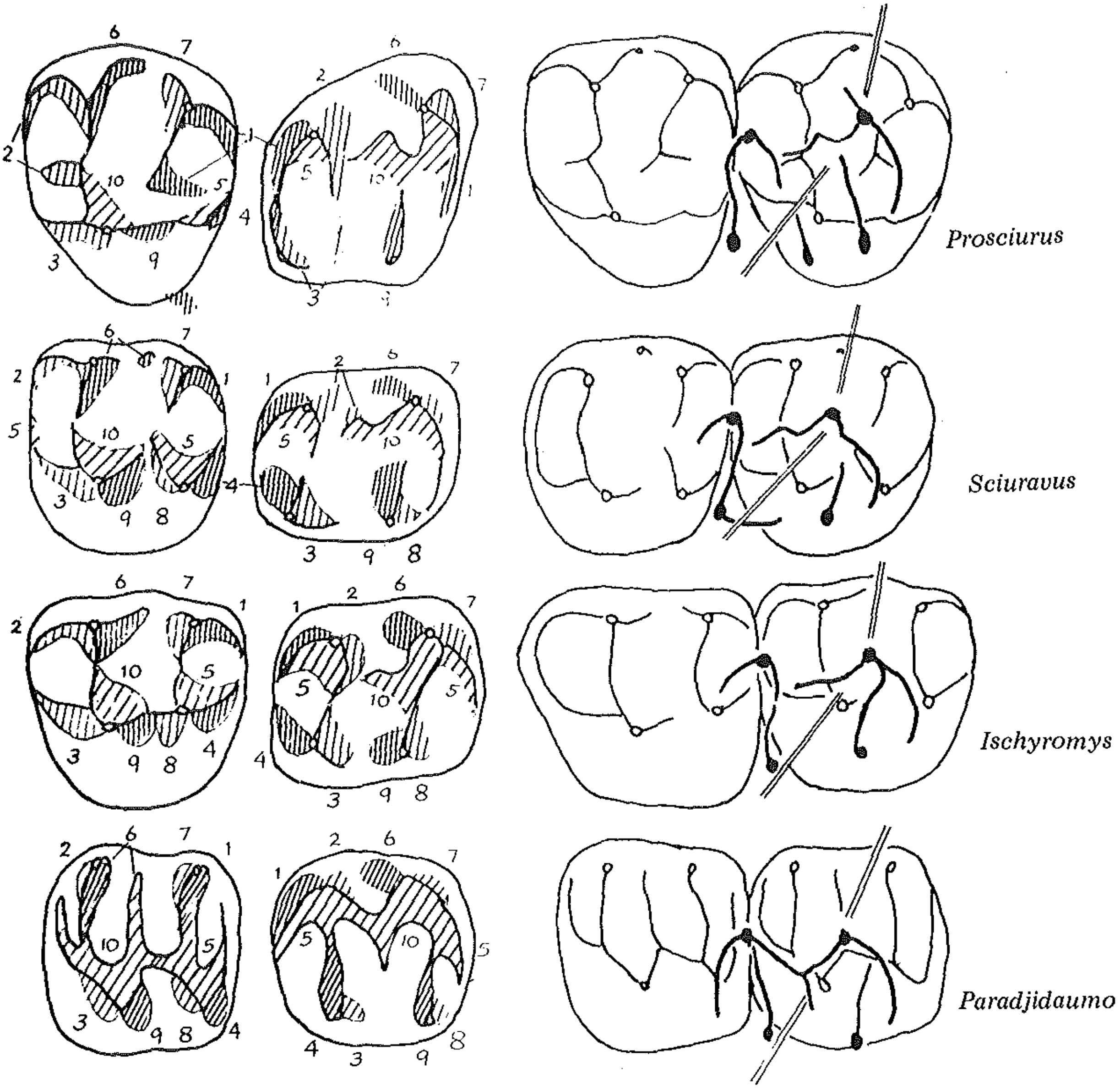
Fig. 3. — Above, *Palaechthon* and *Sciurus* with M/2 in the buccal phase (left) and lingual phase (right), illustrating the formation of facet 3 (anterior surface of protocone) and facet 5 (buccal surface of protocone). The greater relative width of the lower molar of *Sciurus* reduces the transverse extent of facet 3.
Below, M2/ and M/2 in posterior view. Movement in the buccal phase is more horizontal in *Sciurus* than in *Palaechthon*.

In *Sciuravus* (Sciuravidae) (fig. 5), on the other hand, the hypocone is as large as the protocone and resembles it in shape : an anterobuccal ridge, occluding with the protoconid, resembles the ridge on the protocone that occludes with the hypoconid. On the lower molar the high entoconid is connected with the base of the hypoconid by a transverse ridge ; this bears on its anterior surface a facet for the protocone, similar to the facet on the metaconid for the hypocone. A smaller facet on the posterior surface of the entoconid is produced by the hypocone. Space for the hypocone is provided by the broad posterior cingulum which displaces the entoconid from the posterior end of the tooth.

Ischyromys (Ischyromyidae) (fig. 5) resembles *Sciuravus* in the enlargement of the hypocone and entoconid. The entoconid is still more anteriorly placed and the ridge that joins it to the ectoloph is higher, giving the tooth a more bilophodont structure. On the upper molar transverse lophs connect the buccal and lingual cusps. Although the teeth are still cuspidate, their crowns are higher and the facets are confined to near the tops of the crests. All the facets of the primitive molar can nevertheless still be recognized.

In the forms mentioned so far the jaw movement is of the primitive ectental type, with an increased forward component in the lingual phase. In many rodents however the buccal phase movement has become more oblique, so as to bring it more directly into line with the lingual phase. An example is *Eumys* (Cricetodontidae) (fig. 6). The forward movement of the buccal phase produces most wear on the anterior surfaces of lower cusps and the posterior surfaces of upper cusps ; the buccal phase facets that are best developed are paracone-hypoconid, metacone-protoconid, protocone-entoconid and hypocone-metaconid. A large part of the tooth is occupied by L-B facets ; these form a flat surface from which project the upper buccal cusps or the lower lingual cusps. Such teeth in the Cricetidae were described as « terraced » by Hershkovitz (1967). This effect is due to the fact that, although the buccal phase and lingual phase movements are aligned when seen in occlusal view, there is still a difference in the vertical direction : the lower molar moves horizontally or slightly upwards in the buccal phase, slightly downwards in the lingual phase. A a result, buccal phase (B-B and L-L) facets do not lie in the same plane as lingual phase (L-B) facets. Besides Cricetidae, the terraced pattern can be seen in Eomyidae (fig. 5) and Zapodidae. Lavocat (1973) noticed buccal phase facets with oblique striations on the lower molars of *Paraphiomys* (Thryonomyidae).

Fig. 5. — Facets on M2/ and M/2, and occlusal diagrams showing M/2 in centric occlusal relation. *Prosciurus* has mesolophid, enlarged conules and buccaly extended hypoconid. *Sciuravus* has enlarged hypocone and entoconid. *Ischyromys* is bilophodont. *Paradjidaumo* (Eomyidae) has pentalophodont pattern, lingual sinus and oblique buccal phase movement.


6 7 2 1 10 5 4 3 9
6 2 7 1 5 10 1 3 8
Prosciurus
6 7 2 1 5 10 5 4 3 9 8
2 6 7 1 5 10 4 3 9 8
Sciuravus
6 7 1 2 10 5 3 9 8 4
1 2 6 7 5 10 5 4 3 9 8
Ischyromys
2 6 7 1 10 5 3 9 8 4
2 6 7 1 5 10 5 4 3 9 8
Paradjidaumo

Another feature of *Eumys*, widespread in rodents, is the presence of a lingual valley, or sinus, between the protocone and the hypocone. The sinus passes to the buccal side of the protocone which is extended posterolingually. When worn the protocone has two cutting edges of enamel, arranged perpendicularly to the direction of movement of the lower molar. The crest which originally joined the hypocone with the protocone is displaced towards the centre of the crown, providing additional cutting edges. On the lower molar the protoconid-mesoconid-hypoconid crest is displaced lingually in a similar manner. Short transverse crests branching from the central crests of the upper and lower molars increase the efficiency of the grinding function.

In *Theridomys* (Theridomyidae) (fig. 6) the occlusal surface has become almost flat : the upper buccal cusps and the lower lingual cusps project very little, and the buccal phase facets lie only slightly out of the plane of the lingual phase facets. The chewing action has been simplified to a simple oblique movement, at about 45° to the axis of the tooth row, in which grinding takes place by the crossing of ridges on the opposing teeth. There is a deep lingual sinus on the upper molar and a similar buccal sinus on the lower molar. The protocone, hypocone, protoconid and hypoconid form oblique ridges, lying approximately at right angles to the direction of motion. The anterior and posterior cingula of the upper molar, together with the mesoloph, are of similar height to the paracone and metacone, producing a pentalophodont pattern ; on the lower molar the posterior cingulum and the mesolophid are similarly elevated. The facets which primitively developed on the posterior surfaces of lower cusps and the anterior surfaces of upper cusps are no longer present.

A number of rodents, in different families, agree with *Theridomys* in having flat-topped molars that function in an oblique chewing movement. In *Hystrix*, *Erethizon* and *Myocastor*, for example, the movement (measured on M2/) makes an angle of about 45° to the mid-line of the palate, as in Theridomyidae and most Cricetidae. In other genera chewing is more propalinal, making a smaller angle with the mid-line, e.g. 33° in *Spalax*, 25° in *Castor*, 20° in *Rhizomys* and 10° in *Capromys*. In *Cavia* the angle is 30°, but the tooth-rows converge anteriorly, so that the lower teeth move directly along the line of the upper teeth. As the propalinal condition is approached the enamel ridges of the teeth change from an oblique to a transverse arrangement, always lying across the direction of relative motion (fig. 6). For discussions of the function of these enamel ridges in grinding see Greaves (1970) and Rensberger (1973, 1975).

Propalinal chewing is approached in some Cricetidae with flat-topped molars, such as *Sigmodon* (angle 25°) and *Holochilus* (15° ; fig. 6), indicating how the microtid condition could have arisen. The Muridae must have developed propalinal chewing in a different manner, for cusps are retained and the facets do not lie in a plane. If a typical murid such as *Apodemus* (fig. 7, A) is compared with *Mystromys* (fig. 7, M) it is not difficult to homologize the facets. In both genera the hypoconid makes contact with the paracone and the protocone, and the protocone makes contact with the entoconid

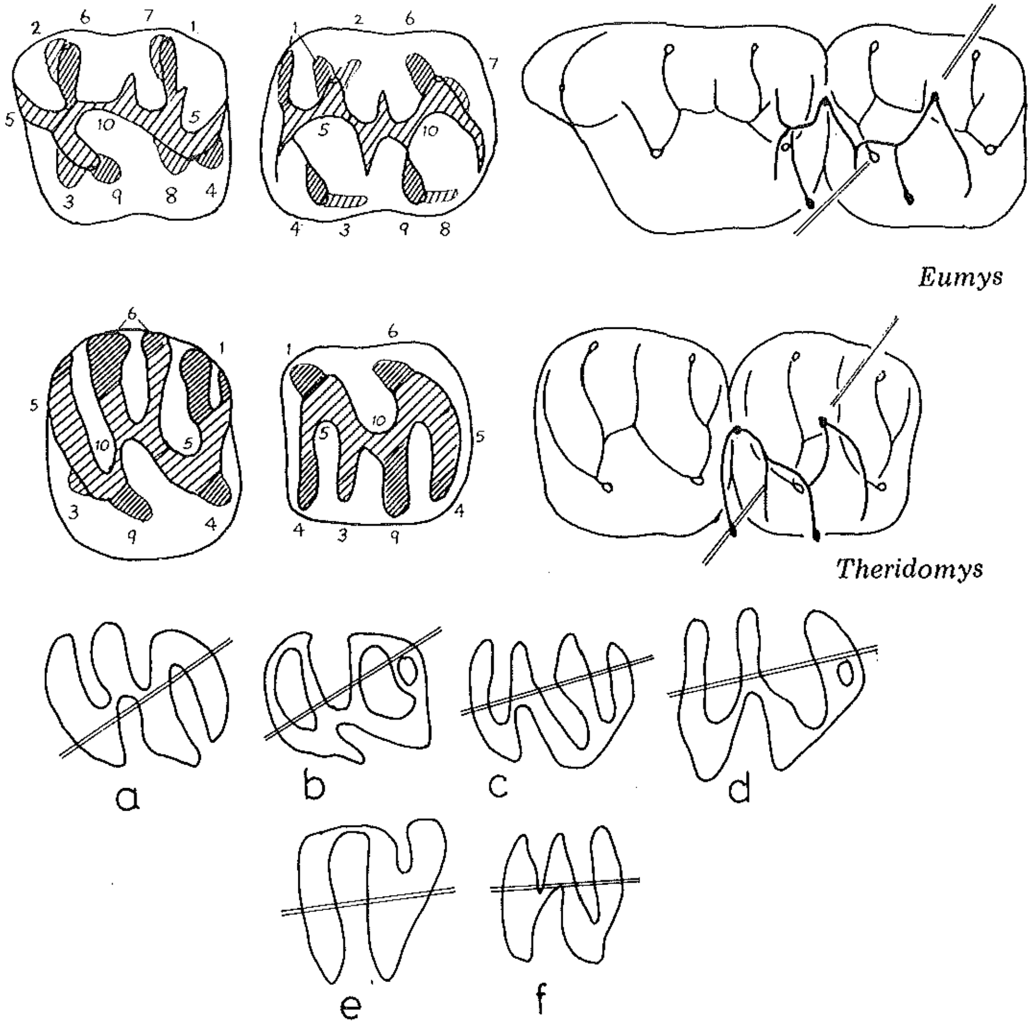


Fig. 6. — Facets on M2/ and M/2 of *Eumys* and *Theridomys*, with occlusal diagrams showing M/2 in centric occlusal relation. In *Eumys* the buccal phase movement is oblique, there is a deep lingual sinus, and additional transverse ridges are present. In *Theridomys* the buccal and lingual phase movements are nearly in line, the crown is almost flat, and facets 2, 3 (except on the mesolophid), 7 and 8 have disappeared.

Below, examples of enamel patterns of upper molars to show that as the movement becomes more propalinal the ridges become more transverse. a : *Myocastor* ; b : *Erethizon* ; c : *Castor* ; d : *Holochilus* (Cricetidae) ; e : *Cavia* ; f : *Capromys*.

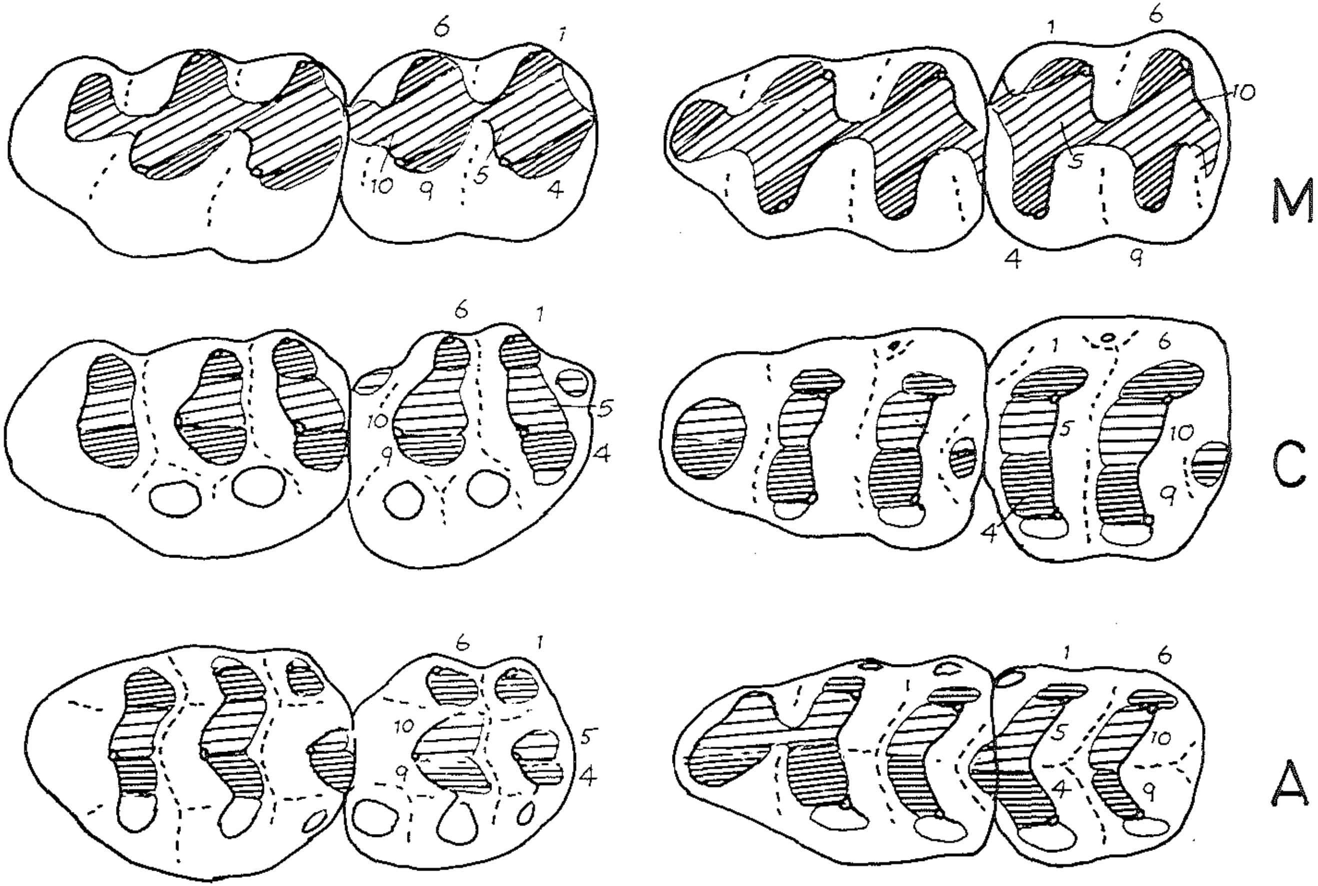


Fig. 7. — Wear facets on M1-2/ and M/1-2 of *Mystromys* (M), *Cricetomys* (C) and *Apodemus* (A). In *Mystromys* the movement is oblique ; in the others it is longitudinal, resulting in a different orientation of the facets. Additional cusps on the lingual side of the upper molars occlude with the metaconid and entoconid (unshaded facets).

and the hypoconid. However in *Mystromys* the movement is oblique, and the facet on the paracone for the hypoconid faces posterolingually, whereas in *Apodemus*, where the movement diverges from the sagittal direction by only about 15°, this facet is on the lingual side of the paracone. The protocone-entoconid contact also faces lingually in *Apodemus*. In Muridae there is an additional row of lingual cusps on the upper molar which occlude with the lingual surfaces of the metaconid and entoconid : t/1 with the metaconid and t/4 with the entoconid. Some Muridae also have buccal cusps on the lower molars which occlude against the buccal surfaces of the paracone and metacone. *Cricetomys* (fig. 7, C) is very similar to the Muridae, except for the more posterior position of the lingual cusps of the upper molars (Petter 1966). Accessory cusps developed in a parallel way in the Heteromyidae.

Although for reasons of space it has been possible to mention only a few among the bewildering variety of rodents, I hope I have shown that a study of attrition facets enables us to see, if only dimly and in broad outline, a functional meaning in the trends of rodent molar evolution. It would be interesting to carry the analysis to a deeper level, discussing the details that distinguish related genera and species. It would also be interesting to know how the different modes of jaw movement, revealed by tooth wear, are reflected in the musculature. Most evolutionary changes in the rodent dentition have taken place more than once, by parallelism. Phylogeny cannot therefore be based on the teeth alone, but cranial and skeletal characters must be taken into account. However, the fossil record of rodents is made up preponderantly of teeth, and it is desirable that we should extract the maximum of information from them.

ACKNOWLEDGMENTS

I first became interested in rodent molars during a visit in 1966 to Pittsburgh, Pennsylvania, where at the Carnegie Museum Dr Craig Black allowed me free access to the collections at that time under his charge, and gave me much-appreciated guidance. I have since examined specimens in several museums, and particularly the British Museum (Natural History), where I received much practical help from Dr J. Hooker of the Department of Palaeontology and from the staff of the Mammal Section.

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