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A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia)

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(With 4 figures in the text)

The primitive topography of the enamelled surface of molar teeth of the Cricetidae is described as expressed in the fossil Cricetodontinae. Morphological variations in the molar structure of different subgroups among the Cricetidae are interpreted as derivations from this cricetodontine pattern. Eleven available naming systems for such components are surveyed, and a new unifying nomenclature is proposed, based on the Cope-Osborn cusp homologies for mammals. Names for enamel cusps, cuspules, styles, lophs, folds and islands are given, in an attempt to include in an overall general nomenclature the advantages of the most valuable, already available, nomenclatorial systems. The system purports to apply to all modifications of the cricetid crown molar pattern, and it claims to fulfil the need for a uniform nomenclature.

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Introduction

The morphology of the enamelled components of the crown topography of the cheek-teeth of the cricetid rodents affords a source of information of paramount importance for the study of these mammals. Most of our knowledge of the phylogenetic history of cricetid muroids is based on the study of their molars, as these organs are well preserved in the fossil record; in many cases they form the only known elements of several extinct taxa. Diagnoses of subfamilies, tribes, genera and even species of living cricetids are increasingly being based on the structure of their molar teeth. This move facilitates attempts to compare the fossil and living representatives of the family. Moreover, the variations in components of the molar teeth of muroids have been shown to be governed by the laws of genetic variation, as demonstrated by the work of Grunneberg (1965), Hooper (1957), Bader (1959, 1965) and others. As such, they provide us with valuable genetic markers for studies of population genetics and genetics of variation, since there may exist up to about 30 character states per tooth.

As they are important for so many different purposes, it is regrettable that the names of components of the crown of these organs, are in a state of confusion and ambiguity. This stems from the fact that several different naming systems are being used for these features. I have found 11 different nomenclatures for the cusps, crests and valleys of the cheek-teeth of the cricetids in the literature from 1925 to the present. This not only leads to confusion, but also makes the comparison of descriptions in the work of different authors difficult.

The existence of so many proposed nomenclatures for one kind of morphological structure perhaps reflects the dissatisfaction that individual authors experience when trying to apply one or other of the previously proposed systems. The systems may have been unsatisfactory on general grounds, or they may not have accommodated the peculiarities of the structures to be described. This latter difficulty may result from too strong an attachment by the proponents of a particular nomenclature to the distinctive variants of their own material, or to a neglect of the convenience of a unifying general language for descriptive purposes. It is easy to see, for instance, that European students working with fossil cricetodontines or living and fossil cricetines, have not taken into account fully the peculiarities of the molar structure of the American peromiscines or sigmodontines. The reverse case is also true, as the proposed nomenclatorial systems for living cricetids of the Western Hemisphere failed to realize that the fossil and living cricetids of the Old World show details in their molar patterns which should also be named. This lack of a comprehensive grasp of the whole cricetids, may be another reason why a nomenclatorial system satisfying the whole group of specialists has not yet been produced.

To overcome the above-mentioned difficulties, I propose below a new nomenclature which adapts several of the current systems, which prove most convenient, into a unifying and widely applicable vocabulary. This proposal results from our failure to be able to apply one or another of the available nomenclatures in our practical work of describing a collection of fossil cricetids of South America, and of giving new and detailed diagnoses of the subordinate taxa of the South American sigmodont cricetids, which will be published in forthcoming papers.

Primitive morphology of the crown of cricetid cheek-teeth

All cricetids are characterized by a dental formula of $I\frac{1}{1}$, $M\frac{3}{3}$*. The cheek-teeth are usually complex in structure, and they show a considerable variation in the arrangement and relative development of their component parts. However, all known variants of molar structure of the different arrays of the members of this family can be thought of as modifications from a primitive common pattern, as represented in the early Cricetodontinae (Fig. 1) (Schaub, 1925; Stehlin & Schaub, 1951; Petter, 1966; Argiropulo, 1972, etc.). A few rather well-established phylogenetic sequences, such as the one represented by *Eucricetodon-Cotimus-Democricetodon-Kowalskia-Cricetus* (Fahlbusch, 1969) or the other

*Hinton, (1923, 1926) and other authors, have suggested that the first cheek-tooth of the cricetids was a deciduous premolar and not a true first molar, and therefore, that their dental formula should be $I\frac{1}{1}$, $DP\frac{4}{4}$, $M\frac{1-2}{1-2}$. This view was convincingly refuted by Wilson (1956). Alker (1967) also contributed to substantiate the interpretation accepted here.

by *Cricetodon sansaniensis-Ruscinomys europaeus* (Freudenthal, 1967), and the probable sequence of the North American forms leading to *Peromyscus* from *Copemys*, contribute to give palaeontological support to the above conclusion, which was based mostly on the logic of the comparative-anatomical type of inference.

With small variations, the cricetodontine pattern of molar structure is also found in the more primitive of the tribes of the South American Cricetidae, namely the Oryzomyini (Fig. 2). It is characterized by a relatively complex system of cusps, ridges connecting the cusps and valleys or folds in between the cusps and ridges. These elements are developed in the crown surface of brachyodont, cuspidate, bunodont molars, in which four main cusps in both the upper and the lower teeth are easy to recognize. These cusps are readily homologized with the cusps of a modified tribosphenic type of mammalian molar tooth (Stehlin & Schaub, 1951; Vandebroek, 1966).

The first molar, both upper and lower, is usually the largest and the more complex of the row, and the third molar is, in the two rows, normally the smallest and the more simplified. Therefore, the second molar is more useful for a characterization of the morphological details of the crown surface of the cheek-teeth of these rodents.

In the upper molars, the main cusps are an anterolingual protocone, a posterolingual hypocone, an anterolabial paracone and a posterolabial metacone. This quatritubercular pattern is supplemented, in some cricetodontines, by the presence of a cuspule on the lingual side placed between the protocone and the hypocone, namely, the mesocone. Additionally, the M^1 shows in all the cricetids an anteromedian conule, which may be simple or subdivided into an anterolabial conule and an anterolingual conule. In the lower molars, the paraconid of the original tribosphenic molar pattern, is absent in the Muroidea.* Therefore, we found in them an anterolabial protoconid, a posterolabial hypoconid, an anterolingual metaconid and a posterolingual entoconid. As in the upper molars, some primitive cricetids also show a mesoconid on the labial side, between the protoconid and the hypoconid. Furthermore, the first lower molar also shows the addition of an anteromedian conulid which, when subdivided, gives rise to an anterolabial conulid and an anterolingual conulid. This tuberculated structure is supplemented in both upper and lower molars by an anterior cingulum which links with the protocone (or protoconid) and eventually becomes a transverse anterior loph (or lophid), and by a posterior cingulum connected with the hypocone (or hypoconid) and becoming a transverse posterior loph (or lophid). The anteroconule of the first upper, and the anteroconulid of the first lower molars can be interpreted as originally arisen as a thickening of the corresponding anterior cingula.

The peculiar feature of the cricetid molar pattern, especially as opposed to the murid pattern, is that a mainly longitudinal crest develops, uniting in the upper teeth the hypocone with the protocone (and in the midway the mesocone, when it exists), and in the lower ones the hypoconid with the protoconid (here again via the mesoconid when it exists). This longitudinal crest or ridge was named "Langsrat" by Schaub (1925) but

*Wood (1937), and following him most of the American authors, claims that the paraconid is altogether lost in the earliest rodents. The main argument for this conclusion is the absence of a paraconid in the Eocene genus *Paramys*. Stehlin & Schaub (1951) and Schaub (1958) maintain that a paraconid is present in the Oligocene sciurids and in the theridomyids. Therefore, they claim that the molars of *Paramys*, which lack or have a merely vestigial paraconid, cannot be considered as the more primitive rodent molar teeth. In any case the authors agree in the absence of a paraconid in the early cricetids and their descendants.

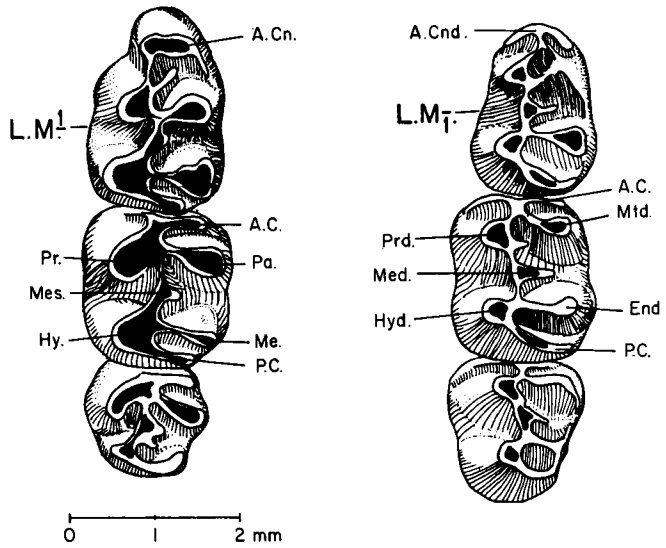

FIG. 1. Upper and lower molars of a representative of the Cricetodontinae, Quercy, France. "*Cricetodon*" gergovianus Gervais, Basel Museum Q.U. 807 and Q.U. 792. (Redrawn from Schaub, 1925, Lam. I, Fig. 19 and Lam. IV, Fig. 1.)

Abbreviations: A.C. anterior cingulum; A.Cn. anteroconule; A.Cnd. anteroconulid. *End.*, entoconid. *Hy.*, hypocone. *Hyd.*, hypoconid. L.M.^{1} left first upper molar; L.M.$_1$. left first lower molar; Med. mesoconid; Mes. mesocone; Mtd. metaconid; Pa. paracone; P.C. posterior cingulum; Pr. protocone; Prd. protoconid.

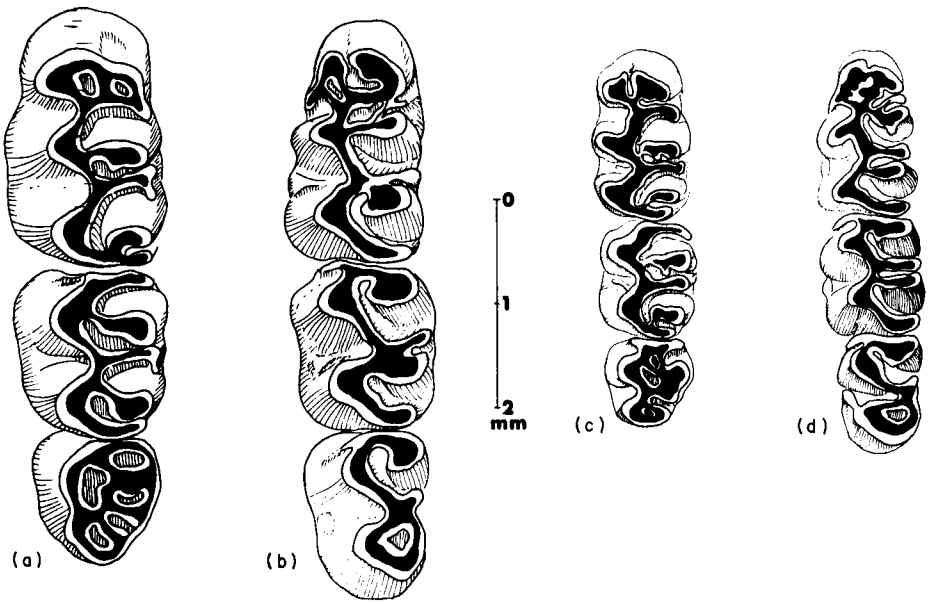

FIG. 2. Occlusal view of upper and lower molars of representatives of the Oryzomyini. (a) Left upper molars and (b) left lower molars of *Oryzomys angouya* Fischer. Female individual, BMNH 4.1.5.16. Sapucay, Paraquay. (c) Left upper molars and (d) left lower molars of *Thomasomys gracilis*, Thomas. Male, BMNH 22.1.1.74. Torontoy, Peru. All figures at the same scale.

differently by other authors. Moreover, transverse or more or less oblique ridges develop from the paracone and the metacone to the lingual enamelled components of the upper molars, and from the metaconid and entoconid to the enamelled structures of the labial side of the lower molars. These ridges may link with the opposing cusps or with the connecting longitudinal ridges in different ways, but whatever the case they define, in combination with the anterior and posterior cingula, three main transverse or somewhat oblique valleys in the crown topography, which open to the labial side of the upper, and to the lingual side of the lower molars. The middle valley is usually further subdivided by a transverse ridge taking its origin on the longitudinal crest, which is currently named the mesolophe in the upper, and the mesolophid in the lower teeth. This accessory ridge is little developed in several cricetodontines, but from the early steps of the evolution of that group, it soon reaches the status of a full-fledged crest, which unites frequently with a mesostyle (or a mesostylid). The fate of the mesoloph (lophid) varies with the evolution of the different lineages, but in most advanced cricetids it becomes usually secondarily reduced or coalesced with the more adjacent major ridge. On the lingual side of the upper and on the labial side of the lower molars a single major valley develops between the protocone and the hypocone or the protoconid and the hypoconid, respectively, which is limited mesially by the longitudinal ridge. At the bottom of this major valley, a transverse ridge can develop which may unite with a style or stylid emerging at the outermost middle point of the valley. Additional styles and stylids usually develop in front of the protocone and the paracone, the protoconid and the metaconid, and from them secondary minor ridges may or may not develop to the main adjacent enamelled component already mentioned. Other minor aberrations in the topography of the crown may also occasionally occur, as a minor ridge opposed to the protocone and partially dividing the anterior part of the middle lingual valley or a similarly minor ridge arising from the hypoconid and penetrating into the posterior lingual valley of the lower molars.

At the cricetodontine and oryzomyine stage, the molars are brachyodont and the crown is mainly bunodont, so that the crests linking the individual cusps are better defined as enamel ridges than as lophs or lophids. From this stage, various degrees of hypsodonty, correlated with increasing lophiodonty and plication (Hershkovitz, 1962) develop. These changes are connected with a shift from an omnivorous diet (see Landry, 1970) to specializations for more abrasive vegetarian, including cellulosic, diet (Vorontzov, 1960, 1963, 1967). The wear surface of the molars, as a result of an increasing masticatory action, develops structures more resistant to abrasion, together with an increasing time of growth of the teeth. The ridges therefore transformed into true lophs and lophids and eventually into transverse or more or less oblique prisms or laminae which with wear show enamelled walls and a dentine internal component. With increasing hypsodonty, the enamel folds also penetrate more and more deeply into the base of the molars. As a consequence of these processes, the individual cusps lose a topographical distinction, and they are only able to be identified by their position. Some cricetodontines of the Miocene show this trend at various stages of development, and specializations in the same direction have also been demonstrated as part of the still obscure Oligocene radiation of the subfamily. However, the modifications involved are characteristic of several direct or indirect derivatives of the cricetodontines, e.g. *Neotoma* and relatives among the peromiscines, the phyllotines and the sigmodontines among the Sigmodontinae, the Arvicolidae, etc.

Discussion of the different available nomenclatures

Stehlin & Schaub (1951), Schaub (1958), Petter (1962, 1966, 1967, etc.), Vorontzov (1960, 1967), Herschkovitz (1962) and Vandebroek (1966) have described in detail the various transformations which occurred during dental evolution of the Muroidea, and the involved morphological processes.* In any case, and whatever the degree of modification achieved, all the resulting structures can be easily derived from the above described general primitive pattern of cricetid molar teeth, already developed in the Oligocene cricetodontines. It is to be expected, therefore, that a uniform nomenclature should be applied to the enamelled components of the crown structure of all cricetids. However, this is far from true. I have found 11 different nomenclatures for the cusps, crests and valleys of the molar teeth of the cricetids from 1925 until now. The relevant citations are Schaub, 1925 (see also Stehlin & Schaub, 1951; Schaub, 1958), Viret (1929; but see also Viret, 1955), Wood & Wilson (1936), Winge (1941, but originally Winge, 1924, and still earlier, Winge, 1888), Hershkovitz (1944, but see especially Hershkovitz, 1962), James (1963), Vandebroek (1966), Fahlbusch (1966), Alker (1967), Vorontzov (1967) and Mein & Freudenthal (1971).

These 11 different nomenclatures do not necessarily represent as many incompatible alternatives. In fact, some of them are more or less equivalent. This is the case of Schaub's, Viret's and Fahlbusch's proposals, which differ from each other only in points of details. However, other systems are completely different, to the extent that a table of comparisons is required to follow the descriptions based on them. This is the case for the nomenclature of Winge, Wood & Wilson and Vandebroek, which have little, if anything, in common, being based on different general theories of the evolution and homologies of the components of the mammalian molar tooth.

Winge's nomenclature is probably the first that everybody could agree now to discarding. Though it was based on a theory of cusps homologies of the mammalian molar teeth which was remarkably similar to the original Cope-Osbornian tritubercular theory, it failed to propose a successful system of names for the main cusps of the molars of the mammal in general, and in this sense, it was thoroughly overthrown by the success of the Cope-Osbornian tritubercular nomenclature. Furthermore, its failure to be adopted by any subsequent student of rodent molars is in itself a reason to rule it out in our search of a valid nomenclature.

Schaub's nomenclature in German, developed in Stehlin & Schaub (1951) and adapted with variants by Viret (1929, 1955) and Schaub himself (1958) to French, is based on the Cope-Osbornian cusp names universally adopted during the last 70 years. These nomenclatures are useful for cricetodontids, but they emphasize some structures which are not common to the cricetids as a whole, and lack technical names of Latin origin for many details of the crown surface.

Vandebroek's nomenclature differs from any other system, in that it is based on the author's particular views of the evolution of mammalian molar teeth (see Vandebroek, 1961), the homologies of their cusps, and consequently, the names of the main cusps of the original tribosphenic molar. Whatever the value of any new hypothesis on cusp evolution and homologies, I strongly believe that it is highly inconvenient to adopt a

*For the nomenclature of the latter, I found it useful to follow Hershkovitz (1962) in the use of such terms as the different types of hypsodonty, plication, lamination, involution, etc.

nomenclature starting from cusp names different from the widely endorsed Cope-Osbornian ones. The latter are so deeply incorporated in the language of modern mammalogy, and it is so unnecessary to modify them even on more up-to-date theoretical grounds, that any innovation would be unwelcome.

Wood & Wilson's system is also based on the Cope-Osbornian designation of mammalian molar cusps, and is probably the most accurate and reasonable attempt to adapt the tritubercular nomenclature to the distinctive structures of rodents in general, and cricetids in particular. In one way or another, it is the basis of several other systems which have been employed by various modern authors. Its major shortcoming is that it does not provide names for the valleys and folds, which for descriptive purposes must have names as much as the cusps and lophs, the latter being thoroughly described and named in Wood & Wilson's system. James & Alker used nomenclatures that differ only in details from Wood & Wilson's. They introduce variants, however, which could be convenient for their own material, but which are not applicable to other cricetids. Moreover, they also do not provide names for the valleys and folds.

During the last 20 years or more, the nomenclature proposed by Hershkovitz in 1944 has been generally adopted by most North American students, and it has also been followed or adapted by some South American authors (Massoia & Fornes, 1965; Reig & Linares, 1969).

Giving Cope-Osbornian names for the major cusps, it is mainly an objective and topographic system of names for cusps, styles and valleys or folds, but does not provide names for several of the main lophs and lophids. The designations employed for the folds are compounded of two or three anglicized Latin names describing the position and inferred relative morphological importance of the infoldings of a plicated surface. This procedure uses such combinations as "first secondary fold", "second primary fold" or "second secondary fold". After several years of studying Hershkovitz papers and of working with cricetid molars, I found such combinations confusing and very difficult to memorize. I attempted (in Reig, Kiblisky & Linares, 1971) to indicate the equivalences of such terms with the already available names for flexi and flexids as introduced by Stirton (1935) for beavers, and adapted for cricetids by Vorontzov (1967). I shall continue this attempt here, although in a somewhat different way, as I shall state later. Besides the cumbersome fold nomenclature, the Hershkovitz system has the shortcoming already mentioned of not providing names for several of the main lophs and lophids. However, it introduced a refreshing objectivity in the naming of the details of the crowns of cricetid rodents, and many of its proposals are worthy of being incorporated into any unifying nomenclatorial attempt. Vorontzov took advantage of the Hershkovitz nomenclature in proposing his own. His proposal, however, still does not provide names for the major crests, and follows a wrong homologization of the major cusps of the lower molars, in which the true metaconid is confused with the paraconid, and the true entoconid is misinterpreted as the metaconid.

The nomenclature offered recently by Mein & Freudenthal (1971) is probably one of the most complete so far proposed. It is based mostly on Wood & Wilson, but contains names for the valleys between the tubercles not provided by the latter authors, which are an adaptation of Schaub's early German names, here named sinuses and sinusides. The introduction of these designations for the valleys and folds is actually unnecessary, as they had previously been called flexi and flexids by Stirton for castorids (Stirton, 1935).

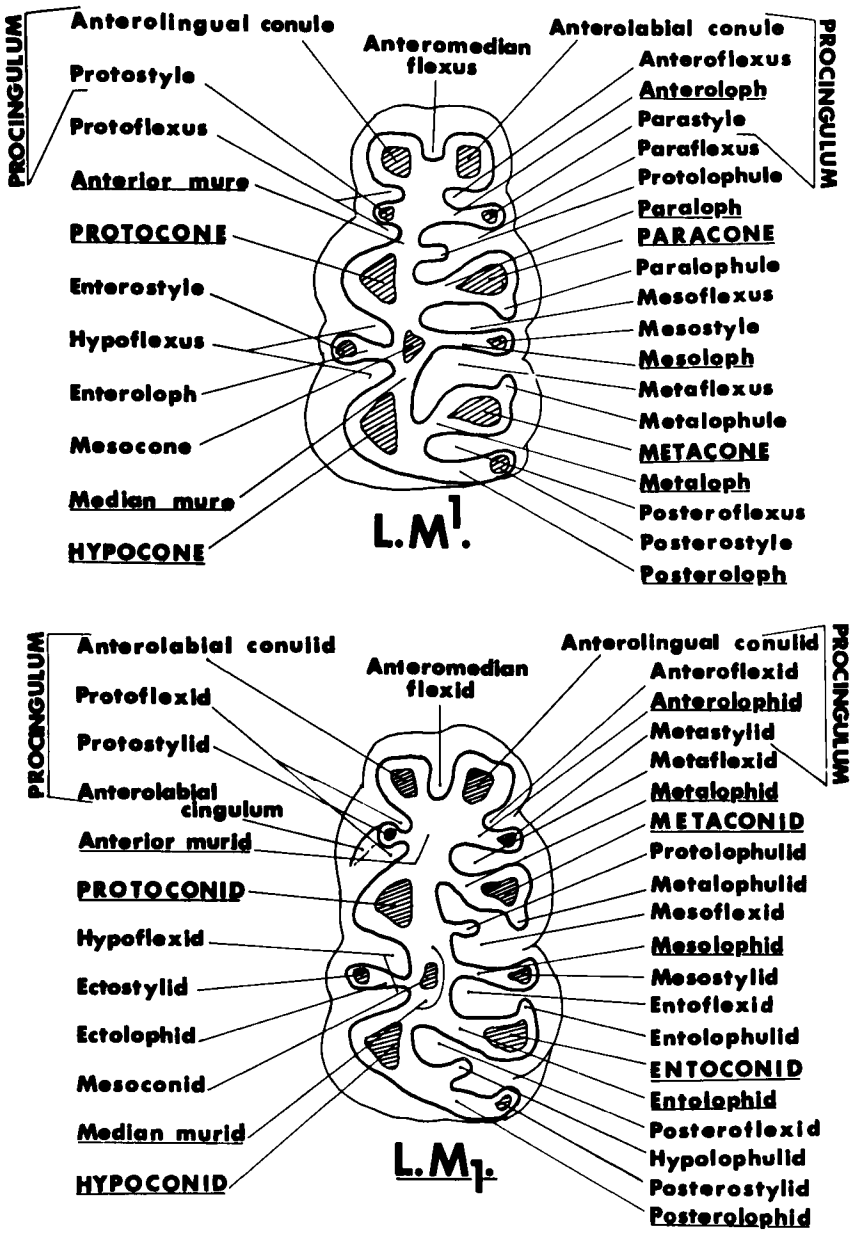

Fig. 3. Master plan of the occlusal surface of an idealized first upper and lower molar of the family Cricetidae, showing all possible elements present in the crown surface and their corresponding suggested names.

These names were adopted by Wood & Patterson (1959) for caviomorphs, and by Vorontzov (1967) for cricetids. Mein & Freudenthal (1971) introduced some new names for certain lophs and ridges when names for the same structures were already available and in widespread usage. Furthermore, its restriction to the cricetodontine variety of the cricetid molar pattern makes the whole system insufficient for describing some of the features found in other groups of the same family.

Need for a uniform, unifying nomenclature

My conclusion is, therefore, that none of the available nomenclatures for the designation of the enamelled components of the crown of the cricetid molars is sufficiently simple, comprehensive, detailed and universal to be worthy of general acceptance. Hence, the need for a unifying nomenclature is obvious. In view of the increasing literature on problems connected, in one way or another, with the teeth of the cricetid rodents, it is also urgent. I, therefore, decided to propose a new unifying nomenclature which might be applied to the molar teeth of all cricetids, giving as much credit as possible to the valuable contributions of the systems already available. Judgements as to the value of those contributions are indeed unavoidable, and in such a delicate duty, I followed as much as possible the concensus in the implicit or explicit decisions of other authors.

I believed that the main tenets of such a unifying new proposal would be: (1) agreement with the overwhelmingly accepted Cope-Osbornian names for cusps of the tribosphenic molar pattern; (2) agreement with a cogently supported hypothesis of the homologies of cusps in the primitive cricetid molars; (3) overall applicability: the nomenclature should be detailed and complete enough to be able to cope with the description of the different variants of the cricetid molar pattern; (4) unifying value: the system should give adequate credit to the names already established by the use of the various students during the last decades; (5) mnemonic value: the proposed system should be simple and able to assist memory; (6) completeness: the system should include names for all cusps, styles, crests and folds, and (7) linguistic universality: the system should be based on names of Latin or latinized Greek origin easy to translate as neologisms to any of the scientific languages.

A proposed unified nomenclature

To my pleasure, I found that such tenets could be satisfied without introducing many major changes to the most valuable preceding systems but, in a way, complementing them. The resulting proposal could be thought of as a derivation of the nomenclature of Wood & Wilson, supplemented by an adaptation of Stirton's names for the folds, plus several of the contributed proposals of Hershkovitz and Vorontzov, and by a few other innovations introduced by other authors.

In Fig. 3, pictures of a generalized ideal crown pattern of a first upper and the first lower cricetid molar are given. They show the bidimensional topography of the different enamelled components which can be found in the crown of these organs, and their proposed names. For the purpose of simplifying as much as possible an already quite complicated structure the enamel islands which occur often in the molar surface of certain groups of cricetids are omitted from the figure. These structures are normally a result of the invagination of the different flexi or flexids as a consequence of wear of the crown surface. When they exist, they can be adequately named by calling them fossetus in the case of the

upper, and fossetids of the lower molar, adding to these general names of the same prefix that apply to the flexi and flexids from which they are derived.

The names applied to all the crown elements are derived as much as possible from the names of the primary cusps, which are named following the Cope-Osbornian nomenclature. The styles and stylids are named following the current use in most of the discussed authors, and their names have no implication whatsoever as regards homologies with similar structures in other mammals. The names of the transverse lophs and lophids are almost always derived from the name of the main cusp from where they take their origin.

This is of mnemonic value, and it made necessary some changes in the nomenclature proposed by Wood & Wilson. This applies to the crest of lophid which develops from the entoconid towards the hypoconid or the longitudinal crest, and which is named the hypolophid by these and many other authors. This name is also inconvenient because the comparative anatomy demonstrates that it actually develops from the entoconid, and not from the hypoconid. I use, however, the name hypolophulid for the accessory crest which emerges from the hypoconid in the valley between the entoconid and the posterolophid in some cricetodontines, such as *Paracricetodon* (Alker, 1967) and *Cotimus* (fide Fahlbusch, 1964). The same structure was called "Hypoconidenhinterarm" by Schaub (1925), and hypolophid II by Alker (1967). In agreement with the same principles, I call the crest which develops from the paracone towards the protocone, the paraloph, as also proposed by Alker (1967). This is equivalent to Wood & Wilson's "protolophule I". The name protolophule is here restricted to the occasional ridge that in some cricetodontines emerges from the protocone to extend laterally, usually only for a short distance, in the floor of the valley between the paracone and the anteroloph. This is equivalent to the "Protoconusvorderarm" of Schaub (1925). Consequently, I call protolophulid Schaub's "Protoconidenhinterarm", which is named by Alker "protolophid II", and this refers to an occasional ridge which in some cricetids emerges from the protoconid anterior to the mesolophid. I believe that following this notation we shall prevent any further confusion with the use of the name protoloph or protolophid which have been variously used by the different authors.

As regards the longitudinal crest, I have followed the current usage by calling it a mure in the upper molars, and I agree with James (1963) in distinguishing a central mure, which I call the median mure, for the crest uniting hypocone and protocone, and an anterior mure for the crest uniting the latter with the anterior cingulum or the anterior conules. The latter is called protoloph I by Alker. For the longitudinal ridge of the lower molars, I followed the same issue, though innovating by introducing the modified name "murid" instead of "mure". This innovation seems necessary to keep the whole system in agreement with the distinction of all the elements of the lower molars by the addition of the suffix "id" as compared with similar elements of the upper molars. Again in agreement with James, I have here distinguished an anterior murid and a median murid. The name ectolophid for the longitudinal crest of the lower molars is here discarded. It was used by Stirton (1935) for castorids, by Wood & Patterson (1959) for caviomorphs, and introduced by Mein & Freudenthal (1971) for cricetids. Unfortunately, the same name was applied by Hershkovitz (1962) and Hooper (1957) to the secondary transverse lophid in the middle of the labial main flexid of the lower molars, and it is now widely used for such a structure in the literature on cricetids molars and their variation.

I also found it useful and convenient to adopt Hershkovitz' name "procingulum" for

the complex of structures anterior to the protocone and paracone of the first upper molar, and anterior to the protoconid and metaconid of the first lower molar. However, I have found unnecessary the application of the same name to the other molars. Names for secondary crests or lophs budding occasionally from some of the major cusps or lophs are here adopted from Hershkovitz. These are the paralophule and metalophule of the upper molars, the metalophulid and entolophulid of the lower ones. The paralophule is obviously equivalent to the posterior ectolophe of Mein & Freudenthal (1971), and to the "ruckwartiger Paraconussporn" of Fahlbusch (1964), a character which seems to have taxonomic importance in some cricetodontines. However, I disagree with Hershkovitz in applying the names paralophule and entolophulid to similar structures in most peromiscines and sigmodontines. In most of the cases, I have interpreted these structures in those rodents as remnants of the mesoloph or the mesolophid, respectively. I have taken for granted that the mesoloph and the mesolophid are primitive components of the molar teeth of the ancestors of the two groups, and that when these structures disappear, the process involved is most frequently their partial or total coalescence with the paraloph or hypolophid, respectively. Therefore, I believe that in most cases if a "paralophule" or an "entolophulid" exists in the peromiscines and sigmodontines, they are merely structures indicating an incomplete fusion of the mesoloph or mesolophid in their terminal portions. That this is actually the case is often additionally supported by the presence of a mesofossetus or a mesofossetid.

Such loss of individuality of the mesoloph or mesolophid by coalescence with the paraloph of hypolophid was suggested by Vandebroek (1966), though using a quite different nomenclature. It is also exemplified in the akodontine and scapteromyine sigmodontines. The resulting median transverse loph or lophid is therefore complex in origin and in some cases, noticeably in the scapteromyines, is very strong and has a more or less bifurcated distal border (Fig. 4). As it is not one of the main transverse lophs or lophids, but the result of the fusion of one of them with the mesoloph or mesolophid, it was found convenient to refer to it as the median loph or the median lophid.

As regards the names for the valleys or folds, I named them, as already anticipated, flexi and flexids following Stirton (1935) and other authors (see for instance Wood & Patterson, 1959; Pascual, 1967). I followed the rule of greatest mnemonic value in deriving the name for each of them from the name of the loph or lophid or the cusp or cuspid, which define them posteriorly. The resulting nomenclature differs in some respects from the nomenclature of flexi and flexids applied to cricetids by Vorontzov (1967). The names for the flexi of the upper molars, however, agree almost completely with the names given by him. The only exceptions are that I name anteroflexus the fold which develops in front of the anteroloph, which is called "prociguloflexus", a rather cumbersome word, by Vorontzov. Therefore the fold separating the two conules of the procingulum is named anteromedian flexus, adapting the name from Hershkovitz. For the lower molars, however, we ought to depart in several respects from Vorontzov because some of the names he used are based on a misinterpretation of the homologies of the two major lingual cuspids. Therefore, the flexid in front of the entoconid is here called entoflexid, and not metaflexid, and the flexid in front of the metaconid is here called metaflexid, and not paraflexid. Additionally, I call the fold called procinguloflexid by Vorontzov, anteroflexid, and anteromedian flexid the anteroflexid of this author. For the names of the folds of the lingual side of the upper molars, and of the labial side of the lower ones, I follow without

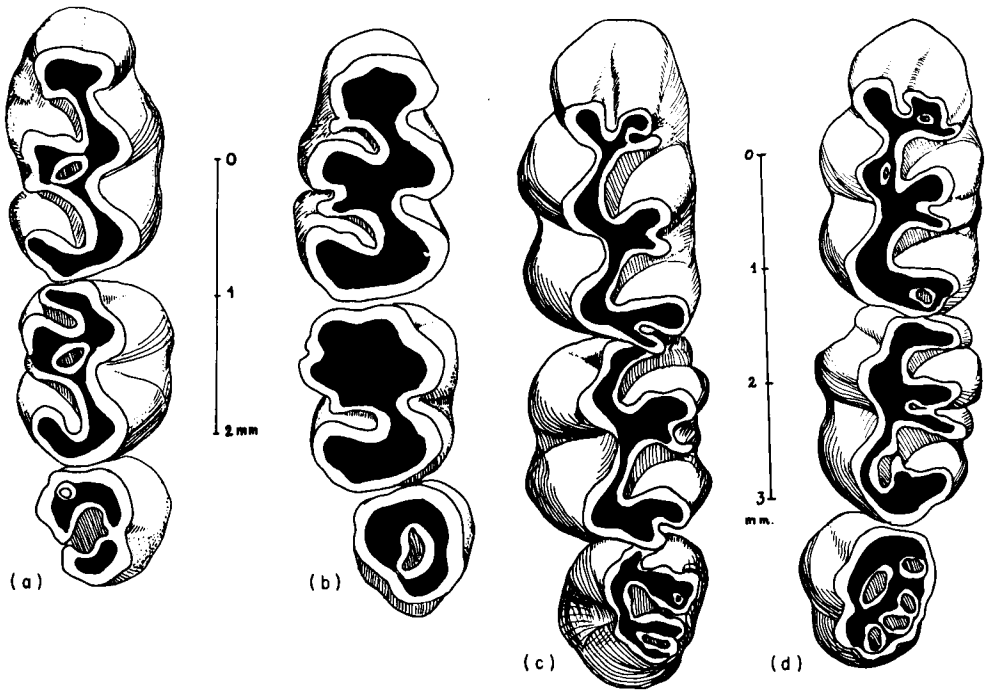

FIG. 4. Occlusal view of upper molars of *Akodon* and *Scapteromys*. (a) Left upper molar row of *Akodon* (*Abrothrix*) *longipilis* (Waterhouse). Male, BMNH 97.5.1.6. Valparaiso, Chile. A rather young specimen showing internal remnants of the mesoflexus in M^1 and M^2 in the form of a persisting mesofosettus. (b) Left upper molar row of *Akodon* (*Abrothrix*) *illuteus* Thomas. Female, type specimen, BMNH 28.10.14.2. A mesostyle and remnant of the mesoloph are clearly shown in M^1, defining a mesoflexus behind the paraloph. (c) and (d). Right upper molar rows of two specimens showing different degrees of wear of *Scapteromys tumidus* Waterhouse from Soriano, Uruguay, Col. BMNH. In the M^2 of D, a fully fledged mesoloph and mesostyle, defining in front a deep mesoflexus turning into a mesofosettus, is clearly shown. In the M^2 of C the complex of paraloph and mesoloph is better described as a median loph showing a mesostyle and mesoloph remnant.

any modification Vorontzov's terminology. The names here given to the flexi and flexids are not equivalent to the ones used by Wood & Patterson (1959) and by Pascual (1967) for caviomorphs. Actually the latter are based on an interpretation of the homologies of the major lophs and cusps of the molars of those rodents which is not at all a matter of complete agreement (see Hoffstetter & Lavocat, 1970). However, our nomenclature of the folds of the cricetid molars could be perfectly adapted to the caviomorphs if the homologies of the major crests and cusps of the latter are interpreted according to Stehlin & Schaub (1951) and to Hoffstetter & Lavocat (1970).

Some theoretical cautions

The nomenclature here proposed must be taken as an attempt to find a universal specialized system of names for descriptive purposes, more than as the linguistic expression of a particular theory. Obviously, and unavoidably, the nomenclature is referring to some well-established theories on cusp homologies and molar evolution. However, its purpose is not interpretative, but descriptive. I am aware, however, that description in

science is always connected with some sort of theoretical framework, but I want to emphasize here the need of a common language as a starting point to arrive at a widely agreed theory.

Moreover, I feel that caution should be shown in the use of words and the structures they refer to in a nomenclature system. A linguistic system is an expression of a conceptual system, and concepts, in science, are not fixed entities, but hypothetical constructions in understanding reality. Therefore, in applying this view to our subject, it is necessary to keep in mind that the enamelled structures of the molar teeth of the cricetids, as in other mammals, must be understood in their inherent objectivity, as explained by modern scientific theory. These structures are not an expression of invariant morphological markers with an immediate and essential significance for phylogenetic or taxonomic conclusions. As demonstrated by the studies of Bader (1959, 1965), Grunneberg (1965), Guthrie (1965), Hooper (1957), and others, these structures are genetically variable, and of probable polygenic origin. They are further affected by quasi-continuous (Grunneberg, 1952) or epigenetic (Berry, 1968, 1970) variation, besides environmental influences. Therefore, and whatever the need for a unifying system of names, a nomenclature for those structures should not be biased by any sort of commitment to the idea of giving names to fundamental or invariable patterns.

If these warnings are given adequate attention, I believe that some of the still controversial arguments as regards homologies or phylogenetic importance of certain features of the molar teeth of rodents, would probably be regarded as reminiscences of an old-styled typological outlook, more than as legitimate pieces of scientific controversy in our times or a pervading influence of the genetic and evolutionary theory.

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