

THE EVOLUTIONARY HISTORY

OF THE

SOUTH AMERICAN CRICETID RODENTS

by

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"If a man will begin with certainties, he shall end in doubts; but if he will be content to begin with doubts, he shall end in certainties."

Francis Bacon; The Advancement  
of Learning, I. v. 8.

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ABSTRACT.

The family Cricetidae is represented in the present South American fauna by 44 genera and 179 species, amounting to about 20% of the living species of mammals of this continent. The overwhelming majority of these genera and species are South American endemics. The most widely accepted hypothesis maintains that this impressive diversification took place in South America from a North American emigrant stock that entered South America by the Upper Pliocene as a part of the massive migration of Nearctic mammals following the establishment of the Panamanian land bridge. Recently, another hypothesis was proposed, which advocates an earlier arrival of the cricetids into South America.

To test these alternative views, this study surveyed the pattern of diversification of the South American cricetids; described a new and extensive fossil collection, mostly from the Plio-Pleistocene sequence of the Buenos Aires Province, Argentina, and explored the phylogenetic relationships and the major classification of the group.

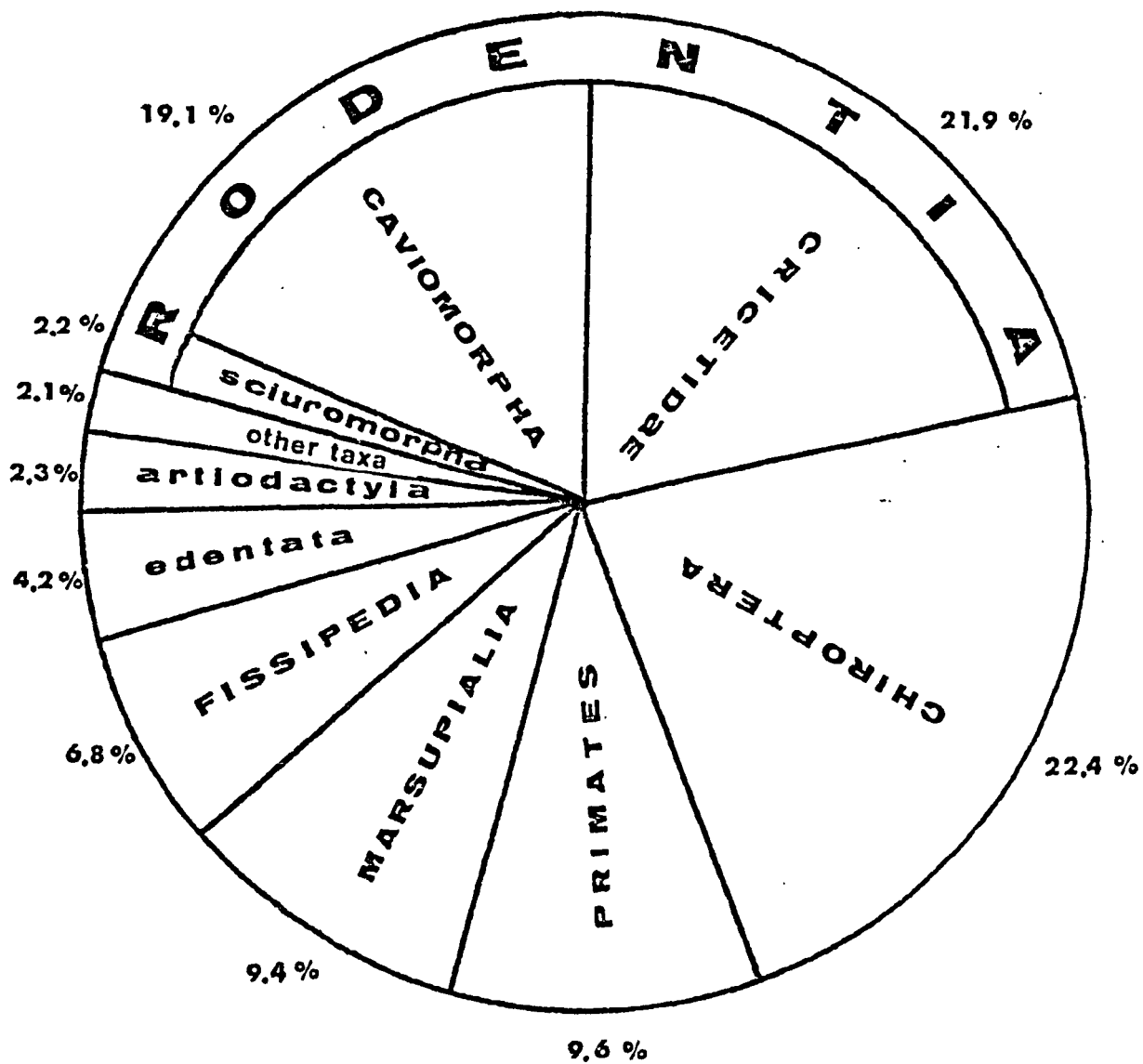
It was found that the South American cricetids belong mostly to a distinct subfamily, the Sigmodontinae. The 41 genera and 176 species of this subfamily can be grouped into seven clearly distinguishable tribes. One of them, the Oryzomyini, comprises very primitive cricetids, comparable to the Oligocene and Early Miocene cricetodontines of the Northern Hemisphere. Nineteen fossil taxa are described, among which there are eleven new species and two new genera. The earliest known fossil record of the Sigmodontinae is lower Late Pliocene, Montchermosian age. By those times, the living genera Bolomys and Phyllotis were already full-fledged, the latter represented



by an advanced species of the subgenus Auliscomys. In the immediately overlying, late Pliocene Chapadmalalan stage, other living genera and subgenera were found. The Early Pleistocene fossil forms belong mostly to extinct species related to living ones. From the Middle Pleistocene onwards, the living species predominate. One species is found in the whole sequence from the latest Pliocene to the Recent.

The modern character of the Upper Pliocene and Lower Pleistocene South American cricetid faunas, suggests an older in situ evolution of the Sigmodontinae than the fossil record indicates. The hypothesis holding that the cricetids are rather modern invaders in South America, is rejected as inconsistent with modern character of the Late Pliocene and Early Pleistocene fossils, and with the pattern of tribal, generic and specific diversification of the group in the living fauna. The origin of the Sigmodontinae is considered as dubious. The tentative hypothesis is advanced that they probably differentiated in South America from a cricetodontine ancestor, which entered the continent as a waif immigrant probably by Early Miocene times. This type of immigration is widely accepted for South American monkeys, caviomorph rodents and some procyonids. The absence of Sigmodontinae in the known deposits of the Miocene and Early and Middle Pliocene of South America can be explained by sampling bias. It is suggested that by those times the representatives of this subfamily evolved in areas of South America/<sup>which</sup> hitherto have not yielded an adequate fossil record of the history of mammals. As regards the geographical provenance of the early sigmodontinae stock, this is considered to be an open question. It is suggested that they might have originated either in North American or in African cricetodontines, so far not discovered.

Fig. 1. Diagram of the relative distribution of the major taxa of mammals of the living South American fauna (Data after Cabrera, 1961, modified by the author's revisions.)





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The illustrations have been made mostly by myself, but I received the invaluable help of Miss Eva Crawley in photographing my original drawings, and her skill and patience is here especially acknowledged.

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## 2. INTRODUCTION

About 22% of the living species of mammals of South America belong to the rodent family Cricetidae (Fig. 1). South America is, however, only a part of the geographical distribution of this family, which extends at present over all Middle and North America and the West Indies, the greater part of Eurasia, Africa and Madagascar.

The cricetids of Neartica and Palaeartica have been rather extensively studied, and many of the Ethiopian forms are reasonably well known. This is not the case with the Neotropical, and particularly, of the South American representatives of this family. As is also true with many other groups of mammals of this continent, they are still poorly known, even their taxonomy. Ellerman, in his monumental work on the families and genera of living rodents, stated that "directly Panama is passed, an enormous list of names described for the most part binomially and in appalling chaos, is reached" (Ellerman, 1941 : 327).

The knowledge of the South American cricetids which Ellerman so expressively described was mostly due at that time to the impressive work of Oldfield Thomas. Although after my incursion into the complexity of this group of mammals I am ready to endorse Ellerman's impression, I do not believe that any derogation to Thomas' outstanding contribution is here implied. In fact, the knowledge of the South American cricetids rests mainly on Thomas' work, who in a great number of papers described and identified hundreds of new species of a fauna almost completely unknown before his studies. The contributions of his predecessors and contemporaries were obviously minimal as compared with his overwhelming taxonomical achievement of classifying new and original kinds of rodents which

were continuously arriving on his desk at the British Museum from several local collectors during more than thirty years. This monumental work was by necessity a preliminary one, and it was carried out at a time when modern taxonomic practices and theory had not crystallised, and the separation into species was made on the subjective assessment of amount of morphological differences in a few skin and skull characters. Therefore, Thomas' heritage must be characterized as a pioneering effort to survey a sizable fauna on the tenets of the so-called alpha taxonomy, and as such it needs a thorough revision based on modern taxonomical concepts and procedures.

Revisions of this kind have been partially undertaken since Ellerman wrote the words quoted above and his work contributed a great deal to reorganize the available knowledge. Credit must also be given to Gyldenstolpe's (1932) previous attempt to survey the South American cricetids. However, the revisions of these authors did not involve a critical reassessment of the status of these rodents at the species level, and as much as they contributed to some clarification of the supra-specific taxa, they contented themselves with listing the "appalling chaos" of the binomially described forms of previous authors. Needless to say, it is essential to disentangle, at least in a preliminary way, the confusion of the nominal species, to achieve a reasonable understanding of the whole diversity of this group of mammals. This was attempted for a part of the South American cricetids by several outstanding contributions of Osgood (1925, 1943), Hershkovitz (1944 and following), Hooper (1952), Sanborn (1947), Pearson (1958, 1972) and others, and most of this revisionary work was incorporated into the corresponding sections of the Catalogue of South American Mammals of Cabrera (1961). However, and even when these con-

tributions helped a great deal to clarify the systematic position of these rodents, the South American cricetids are still, and in proportion to their relative importance, only fragmentarily known from a modern point of view. They are still whole highly polytypic taxa, as the Akodontini, and genera as much as two-thirds of the described species as Oryzomys and Thomasomys, which amount/have not received any comprehensive revision, and their status remains as Thomas left them.

To the same degree that the knowledge of the diversity of the living forms is still obscure, the evolutionary and phylogenetic picture of the South American cricetids is also poorly understood. Both situations are obviously closely related, as it is difficult to understand evolutionary patterns in a group the systematics of which is insufficiently known. In spite of this, the problem of the origin, antiquity and rate of evolution of this group of rodents has attracted the attention of several leading authors, and it has been recently the subject of opposing views. Notwithstanding the fact that this family contains so many of the living species of South American mammals, it has been usually thought of as a group of relatively late invaders of South America which reached this continent by the end of the Pliocene, as part of the alleged massive invasion of Nearctic mammals after the establishment of the Panamanian land bridge (Simpson, 1951, 1962, 1966; Hooper, 1949; Patterson and Pascual, 1968; Reig, 1962b, 1968a). In recent estimate, Hershkovitz (1969) gives the figures of 40 endemic genera and 179 endemic species of Neotropical sigmodontine cricetids, most of which are actually South American endemics. If the family really entered South America by the end of the Pliocene, the evolution of the cricetids in that part of the world would represent an outstanding case of explosive taxonomic diversification and of



a high rate of evolution.

The generally accepted view on the time of arrival of cricetids into South America was an inference from the known occurrence of their remains in the fossil record. With the exception of two species belonging to the living genera Reithrodon and Akodon (Ameghino, 1908; Roverto, 1914; Reig and Linares, 1969) which were found in Chapadmalalan stage currently considered as the uppermost Pliocene, all the remaining described fossil cricetids of South America were found in strata now placed in the Middle and Upper Pleistocene (Ameghino, 1889; Rusconi, 1931; Hoffstetter, 1963, 1968).

Doubts have been recently cast upon the idea that the cricetids are relatively recent invaders of South America. Hershkovitz (1966b, 1969) proposed that their radiation started on that continent much earlier than indicated by the fossil record, a contention that was also supported by Wenzel and Tipton (1966) on parasitological grounds. In fact Hershkovitz's new hypothesis on the origin and biogeographic history of South American cricetids is part of his thorough reappraisal of the historical biogeography of all the South American mammals as classically explained by Simpson (1951). Indeed, the Simpsonian theory of the history of South American mammals has been given extensive support and it is generally considered as a well established and soundly based "chef d'oeuvre" of modern biogeographic thought. The challenging of such authoritative theories has often led to an improved understanding of the basic problems, but the proponents of the new views must expect a contemptuous distrust at the beginning. However, science is based on facts and reasonable inference tested by appropriate methods, and the fate of Hershkovitz's new views, if they are supported by well grounded facts and soundly based inferences,

'could be a turning point for a new and deeper understanding of the evolutionary biogeography of the South American mammals.

Although we are loathed to accept the idea that the burden of the proof for hypothesis on the biogeographical history of a particular group of organisms must be taken mostly from the fossil record, we take for granted that a good knowledge of this record provides a great deal of the necessary evidence for these hypotheses. As for the opposing hypotheses on the biogeography of South American cricetids, it is evident that the available knowledge of the fossil record is at a very preliminary stage, a stage that hardly could afford an adequate test for the alternative existing views. Hooper (1949) emphasised that the fossil record was too inadequate to understand the history of the neotropical cricetids, and the situation has not much improved since then.

This is a curious situation, as during the last two decades the knowledge of other groups of fossil neotropical mammals has considerably increased. The lag in the increase in our knowledge of the fossil mice has multiple and obvious causes. First of all, remains of the mice are very scarce in the collections. This is due not only to the delicate nature of the bones of these tiny animals, which easily disintegrate before fossilization. A more important reason is that their small size requires a careful search and special techniques to recover their bones from the sediments, which up-to-date have been mostly explored in search of macrofossils. Secondly, vertebrate paleontologists have not been attracted by the study of material which is difficult to deal with, without a first hand knowledge of the living fauna. In fact, the greatest part of our information of the South American cricetids still comes from work of Ameghino who, without being an expert in this group of mammals, was

courageous enough to identify and describe the material available to him more than sixty years ago. Ameghino dealt with fossil cricetids in two papers (1889, 1908). After these, remains of fossil mice from South America have only been described by Roverto (1914), who merely redescribed some of Ameghino's specimens; Rusconi (1931) who added two nominal species of the Middle Pleistocene of Argentina; Hooijer (1967), who described Upper Pleistocene material from Curaçao, and Reig and Linares (1969), who gave a preliminary description of a new form from the Upper Pliocene of Argentina. The list is completed by the mention, but not the description, of cricetids in two deposits of the Upper Pleistocene of Bolivia by Hoffstetter (1963, 1968).

However, after Ameghino's work, increasing numbers of specimens of fossil cricetids have been added to the collections especially of the Argentinian museums. Until now the study of this new material has been postponed by the specialists deterred by the inherent difficulty of their study which demanded a full time study whilst new fossils of other groups were also in urgent need of attention. Most of the specimens of fossil mice are isolated mandibles, fragments of maxillae with cheek teeth, isolated teeth or isolated limb bones. The identification of this material requires a detailed knowledge of the corresponding parts of the living forms, and this knowledge was not fully available, as most of the neontological work on the South American cricetids lies on the external characters, the major features of the skull morphology and, in the taxa that have been better known, a preliminary knowledge of the tooth morphology particularly in the upper molars. Therefore, the specialist interested in identifying fossil material of mice, must start by gaining a first hand knowledge of the mandible and detailed teeth morphology of the score of known living genera and species, a task which takes

years of work. Besides this, and as it is obvious that the fossil specimens are usually closely connected with, if not belonging to, living genera and species groups, their correct identification requires in most of the cases the previous revision of the living forms which, as we have seen, are still in an "appalling chaos". These difficulties are liable to discourage the best intentions, and they explain why the cricetids have lagged back in the advancing study of the South American fossil mammals.

Due to a combination of favourable circumstances. I was able to attempt the study of this neglected group of fossil mammals. My previous work as a vertebrate paleontologist in Argentina allowed me to be familiar with the deposits where fossil mice occur, and to encourage some people, especially my good friend the active paleontologist. G. J. Scaglia, to search particularly for them in the mammal bearing strata of the rich succession of Plio-pleistocene deposits of the Chapadmalal region. After about fifteen years of careful collecting, a considerable amount of specimens have been made available for study. Second, my neontological field and laboratory work in the last ten years has been directed towards the study of the evolutionary cytogenetics and genetics of variation of South American rodents of Argentina, Venezuela and Chile, and these studies enabled me to gain a first hand knowledge of the diversity of some of the large taxa of the living cricetids of that continent. Finally, and thanks to the help of several bodies, I had on repeated occasions the opportunity to spend periods studying these mammals at most of the museums in the United States, South America and Europe where the more important collections of South American cricetids are deposited. Through these studies, mostly undertaken during the last five years, I have been able to

accumulate new information which has proved to be of the utmost value for the identification of the fossil material.

The identification and the evaluation of this material was completed after two years of concentrated work, and the results are the main bulk of the present contribution. It was also necessary to revise the classification of the family Cricetidae as a whole to dispose the South American representatives of this family in an appropriate classificatory and interpretative scheme. At the same time, it was necessary to clarify the question of the nomenclature to be applied to the different components of the morphology of the molar teeth of the cricetids, as it was found that the available systems of names were not completely satisfactory. The results of these two subsidiary works are also presented here. Finally, the results of the study of the fossil forms were by necessity tightly intermingled with revisions of the living forms, and the main conclusions of those revisions are also incorporated in the present work. The whole work was undertaken to gain a better understanding of the evolutionary history of the South American cricetids, and in my conclusions an attempt is made to further an explanation of the main facts of that history.

Nevertheless this work is only the starting point and a great deal of future work will be necessary before a good picture of the evolutionary history of the South American cricetids is obtained. The material available for study proved still too fragmentary and scattered, even when it appeared overwhelmingly abundant as compared with the previous known specimens. They come mostly from a succession of local faunules restricted geographically to a limited area of Argentina. Fossils from other areas were not available, or they were too young, geologically speaking, to be relevant to the main purposes of this study. Moreover, my

achievements in the study of the available material have been necessarily unbalanced. I had hoped to have arrived at definite taxonomic conclusions in the case of some groups, as the Akodontini, in which I had more significant material and a deeper familiarity with the living forms, or which were taxonomically simpler, as is the case of the Scapteromyini. Other groups proved to be more elusive, in part because of the still obscure taxonomy of the living forms, and in part because of the scarcity of the fossil material. Furthermore, I made no study of the postcranial remains present in my material. Their study proved to be almost impossible, and their description valueless, in the absence of comparative collections of skeletons of the living forms, which unfortunately are usually not preserved in the museum specimens.

I hope, however, that the general picture which results from these studies is explicit enough to attempt the testing of the mentioned alternative views on the evolutionary history of the South American cricetids, and to build up the framework of an explanation of the major events of that history. This explanatory attempt is here offered to provoke further work and thought and without any pretension of conclusiveness. I am aware that we are still far from a thorough understanding not only of the processes involved, but also of the major events of cricetid evolution in South America. I could not feel content uttering apodictic arguments in a field where the shadows of uncertainty still prevail. I hope, however, that some new light has resulted from my studies that this may eventually help to dissipate the dimmed atmosphere which still surrounds the evolutionary understanding of a fifth of the present mammalian fauna of South America.

### 3. MATERIAL AND METHODS.

The bulk of the descriptive part of this paper deals with the specimens of fossil mice. The necessary taxonomic information, reference to collections and descriptions are given under the corresponding systematic part of this work. Additionally, hundreds of specimens of living species of cricetids have been consulted, belonging to the collections of several museums and institutions. Their detailed record is not relevant to the purposes of this thesis, but some of the specimens of samples studied have been of necessity mentioned in the text, and in doing this, I recorded them under an abbreviation of the collection wherein they belong and their corresponding catalogue number. The following are the equivalents of the abbreviations used in the text:

- AMNH - American Museum of Natural History,  
New York.
- BMNH - British Museum of Natural History, London.
- FCM - Collection of Mammals of the Department  
of Biological Sciences, Faculty of Exact  
and Natural Sciences, University of  
Buenos Aires.
- MACN - Museo Argentino de Ciencias Naturales  
"Bernardino Rivadavia", Buenos Aires.
- MBUCV - Museum of Biology of the Institute of  
Tropical Zoology, Central University of  
Venezuela, Caracas.
- MHNP - Natural History Museum of Paris.
- MLP - La Plata's Museum, La Plata, Argentina.
- MMP - Municipal Museum of Natural History of  
Mar del Plata, Argentina.
- MVZ - Museum of Vertebrate Zoology, University  
of California, Berkeley, Cal. U.S.A.
- PVL - Laboroatory of Fossil Vertebrates, Miguel  
Lillo Institute, Tucumán, Argentina.
- USNM - United States National Museum - Smithsonian  
Institution, Washington, U.S.A.



The illustrations have been drawn by the author, with the help of the drawing tube of the M-5 Wild stereomicroscope. All the measurements were taken through the reticle eye-piece of the same microscope, which allowed measurement of the teeth to the closest 0.01 mm. The problem to define measurable limits on teeth was difficult in some cases. As a rule, only greatest length and width of teeth were taken, and the same convention to define the corresponding limits was followed in each compared set. Exceptions to this rule are given explicit mention when necessary. In the case of semi-hypsodont molar teeth as those of the Akodontini, the crown length of the molar rows proved to be less variable than the alveolar length, and it has been preferred for comparative purposes. All the measurements in the tables and graphs are given in mm.

4. THE CLASSIFICATION OF THE CRICETIDS.

Although the number of the living species of mammals can only be a matter of approximate calculation, the figure of 3,500 is generally accepted as a reliable estimate. This number of species is divided between 21 living orders of the Class Mammalia (accepting the relatively recent splitting of the Insectivora and Marsupialia).

But the remarkable peculiarity of the distribution into orders of the living species of mammals is that of the 21 living orders, there is one which comprises more than half of the whole number of mammalian species; this is the order Rodentia. Besides, the rodents are the most abundant mammals in numbers of individuals. Great numbers and such physiological and biodemographic features as a high rate of reproduction and a short life expectancy which determine rapid population turnovers, are indeed factors responsible for the enormous taxonomic diversity. Moreover, and by the same token, this diversity is in itself the result of an overwhelmingly intricate and usually rapid evolutionary process (Wood, 1947), based on populations with a high degree of genetic variation (Berry; 1970; Selander, 1970). On such grounds, natural selection found a wide range of possibilities to obtain remarkable adaptations, which frequently were achieved convergently by several unrelated evolutionary lineages.

The extensive occurrence of convergence, the relatively rapid tempo of speciation, the high phenotypic plasticity, the great genetic variability, and the inadequacy of the fossil record, all contribute to make difficult the study of the evolutionary relationships among the different groups of rodents. Consequently, the classification of the whole order

is very unsatisfactory and unstable.

The subordinal classification of the Rodentia is a clear reflection of this situation. Many attempts have been made to try to organize the considerable diversity of the rodent families into a comprehensive system. In fact, the goal seemed to be elusive, and there were so many cases which have been proved as not fitting in with the different proposed major groupings, that one is tempted to conclude that we are still far from having an acceptable major classification of the Rodentia. After surveying the various attempts to work out such a system by modern authors, the impatient student not directly involved in the subtleties of the many controversial points in the different attempts, is inclined to treat leniently the recognized shortcomings of such an early and old-fashioned, but simple and comprehensive system as Brandt's (1855). In this system, the whole order is divided into three suborders, the Sciuromorpha (squirrels and allies), the Myomorpha (mice and rats), and the Hystricomorpha (porcupines and cavy-like rodents. Brandt's tripartite system is basically adopted in Simpson's classification of mammals (1945), although he later (1959) changed this to accept one of the published and disputed modern systems.

I do not intend to discuss here in further detail the problem of the major classification of the Rodentia. The reader is referred to the thorough treatments and expositions of the topic in the classical works of Tullberg (1899), Miller and Gidley (1918), Winge (1924), Ellerman (1941) and Simpson (1945), and to the more modern discussions and proposals by Wood (1947, 1950, 1954, 1955, 1958, 1959, 1965), Wood and Patterson (1959, 1970), Schaub (1953, 1958), Lavocat (1951,

1956, 1962b, 1969), Landry (1957), Simpson (1959), Grassé and Dekayser (1955), Hoffstetter and Lavocat (1970). My concern here is limited to the place of the Cricetidae in the system and to explore the problems of the suprageneric classification within the limits of that family.

In Simpson's classification (1945), the Myomorpha are subdivided into three superfamilies: the Muroidea, the Dipodoidea and the Gliroidea. Following the first version of Wood's classification, he later (1959) included the Geomyoidea in the Myomorpha, and he treated the Gliroidea as cf. Myomorpha inc. sed. Wood later (1965) changed his original scheme to subdivide the Myomorpha into five superfamilies: Muroidea, Geomyoidea, Dipodoidea, Spalacoidea and Gliroidea. I shall not discuss here the four superfamilies other than the Muroidea. The position of some of them in this suborder is a matter of inconclusive discussion (see Ellerman, 1941; Grassé and Dekayser, 1955). I must however state here that I do not endorse Wood's proposed removal of the Spalacidae and Rhizomyidae from the Muroidea to a superfamily of their own, and therefore I shall keep the mole rats and their relatives within the muroids, in agreement with most of the modern authors. In any case, it is obvious that the Muroidea make the core of the concept of the suborder Myomorpha. Whatever the extension which is given to this taxon-concept, any successful assessment of the intension<sup>(1)</sup> of the concept of the

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(1) I here refer to my previous (Reig, 1970: 233) treatment of taxa as natural entities which we approach cognitively by means of the construction of taxon-concepts. As in any concept, the taxon-concepts have an extension and an intension. The extension of a taxon-concept is the set of subordinate taxa that belong to it. Its intension is the set of attributed that distinguish it from other taxon-concepts of the same hierarchical rank. The distinction between the extension and the intension of concepts goes back to the seventeenth century, and it was introduced by A. Arnauld and P. Nicole in their famous Port Royal Logic (1662). These authors used the French word 'compréhension' for what modern logicians now call 'intension'. The introduction of the latter goes back to the middle of the nineteenth century, and was due to Sir William Hamilton (see Kneale and Kneale, 1962: 318).

Myomorpha hinges on a good understanding of the Muroidea, which contain the overwhelming majority of the species of the suborder. Moreover, the Muroidea are by far the more important group, both in number of species and of individuals, of the whole order Rodentia. Ellerman (1941) provided the following approximate figures, which speak for themselves. He states that 192 valid genera containing 3,600 named forms (nominal species and subspecies) belonged to his family Muridae (which is roughly equivalent to what I here understand by Muroidea, see later), whereas 151 valid genera containing 2,773 named forms were distributed among the remaining 22 families of rodents he recognized.

It is to be expected that the difficulties in obtaining a satisfactory classification of the Rodentia as a whole also apply to their more diversified subordinate groups, and so it is. The nearly two hundred of presently recognized genera of muroids have been grouped in various ways, and it is only rather recently that some light has been shed on the understanding on their intricate interrelationships.

A few members of this superfamily are easy to differentiate by their extreme specializations from the scores of their generalized muroid relatives. They are the fossorial Eurasiatic mole-rats (Spalax), their also hypogeic African and Asiatic living and fossil relatives, the bamboo-rats (Rhizomys, Cannomys, Tachyoryctes, etc.), the again highly subterranean Asiatic 'sokhors' (Myospalax), and the peculiar crested hamsters of Africa (Lophiomys). They are usually grouped in suprageneric taxa of their own, although there is not still a full agreement as to the rank to be given to these groupings, and about the details of the interrelationships among them.

The remaining genera have been variously distributed

either into subfamilies of a single family Muridae, or into subfamilies and tribes of two families, Muridae and Cricetidae. The first attitude can be considered as the usually accepted one, supported as it was by such authorities as Thomas (1896), Hinton (1926), Ognev (1948) and Ellerman (1941). Moreover, the same view was taken by the authors responsible for most of the modern work on the muroids of the Western Hemisphere, as Hershkovitz, Allen, Osgood, Hooper, etc.

In spite of such an impressive support, it is becoming more and more evident that this view is in contradiction with the requirements of a classification aiming to differentiate phenetically distinctive entities with also distinctive patterns of distribution, resulting from distinguishable evolutionary histories. Therefore, a recognition of Cricetidae and Muridae as different families is increasingly accepted, specially since Simpson favoured this view in this classification of mammals (1945). In Simpson's classification, the Muroidea are arranged as follows:

Superfamily Muroidea

Family Cricetidae

Subfamily Cricetinae

Tribe Euyini

- .. Hesperomyini
- .. Cricetopini
- .. Cricetodontini
- .. Cricetini
- .. Myospalacini

Subfamily Nesomyinae

Subfamily Lophiomyinae

Subfamily Microtinae

Subfamily Gerbillinae

Family Muridae

Subfamily Murinae

Subfamily Dendromyinae

Subfamily Otomyinae

Subfamily Phlaemyinae

Subfamily Hydromyinae

Family Spalacidae

Family Rhizomyidae

As any comprehensive classificatory arrangement based on the tenets of the evolutionary taxonomy, this classification implies an assessment of different degrees of relativ-evolutionary relationships among the subordinate taxa. Several advances gained in the understanding of evolution of the cricetids since Simpson's arrangement of this family, turned the implied pattern of interrelationships therein in disagreement with more modern results. Moreover, the increasing knowledge of the systematics and morphology of several African genera currently considered as belonging to the Muridae as conceived by Simpson, introduced basic changes in our understanding of the limits of this family.

As regards the last point, the critical innovations started with Lavocat (1959, see also Lavocat, 1962a, 1964), when he claimed that the African tree-mice of the subfamily Dendromurinae (Dendromyinae) were not murids, but cricetids. The proposal of this author was further supported by detailed studies of the dentition by Petter (1966a, 1966b). This author also validated Robert's subfamilies Petromyscinae (Petter, 1967) and Cricetomyinae (Petter, 1964, 1966a), but he convincingly demonstrated that they must also be withdrawn from the Muridae to be allocated within the Cricetidae. These conclusions were endorsed by Missone (1969) and Dieterlen (1970). The latter also found that the peculiar and advanced African Otomyinae were not murids, and he proposed that they must be considered as more closely related to the cricetids. Furthermore, taking into



account the studies of Vorontzov (1966) which demonstrated that the African cricetid Mystromys is to be separated from its Eurasiatic relatives in a tribe of its own and the probable early origin of the Malagasy Nesomyinae, (Vorontzov, 1967, see later), the picture of the African Cricetidae is now completely renewed. This family seems to have undergone in Africa an extensive radiation which had probably started by Oligocene times (Lavocat, 1959; see also Cooke, 1968 : 248, Fig. 11), whereas the African Muridae probably represent a rather later invasion (Lavocat, 1967; Dieterlen, 1969; Misonne, 1969).

As regards Simpson's arrangement of the Cricetidae, an obvious implication of it is that the six taxa recognised as tribes subordinated to the subfamily Cricetinae are more closely related with each other than any of them with one or another of the remaining subfamilies. This view is now hard to be substantiated either on cladistic or patristic grounds. Contrariwise, the now available evidence on the evolutionary relationships, biogeographic history and phenetic affinity of the involved groups, strongly suggests the need of a thorough reassessment of the hierarchical arrangement of subordinate groups of the whole family. However, the work done on this subject since 1945 is far from affording unquestionable conclusions, and even when I am convinced that on the basis of that work, new proposals are needed so that there may be progress in our understanding of the group, I feel that the field is still a place for treading lightly, more than a subject for proceeding with confidence.

In spite of some recent attempts to clarify it, the classification of the fossil Oligocene and Miocene cricetids is still particularly obscure. However, some conclusions from recent studies are certainly well founded enough as to be

credited formal recognition. First of all, one fossil group, the Oligo-Miocene Melissiodontinae, placed by Simpson as ?Cricetodontini incertae sedis, now seems to deserve full revalidation with the rank proposed by Stehlin and Schaub (1951). The Melissiodontinae are characterized by brachyodont molars with a complicated enamel pattern, and the relationships of the Melissiodontinae with the Cricetidae seems to be firmly established. The Melissiodontinae, however, could also be related to a complex and divergent early radiation of the Cricetidae represented by genera as Eumysodon, Aralomys, and Selenomys (see Schaub, 1958; Vorontzov, 1963a, 1967), the position of which in the classification of the fossil cricetids is still not clear. The Melissiodontinae have been mostly found in Oligocene deposits of Asia and Europe. Cricetops, of the Oligocene of Mongolia, which Simpson made the basis of a tribe Cricetopini, could also be related to the same early radiation, and the taxonomic arrangement of the whole group may be better regarded as highly provisional, and still depending of a better understanding of the early Cricetodontinae.

As regards the Miocene Anomalomyinae of Stehlin and Schaub (op. cit.) which Simpson also placed as ?Cricetodontinae incertae sedis, they are revalidated as a full subfamily of the Cricetidae in a recent classification by Mein and Freudenthal (1971a). I follow them here, but not without doubts because of the resemblances pointed out by Viret and Schaub (1946) between Anomalomys and the Malagasy living genus Brachyuromys, and the suggestion advanced by Petter (1961) that Anomalomys, Brachyuromys and Spalax could be closely related. If these opinions were eventually substantiated by further evidence, the Anomalomyinae would be placed within the Spalacidae, instead as here allocated as a subfamily of the Cricetidae.

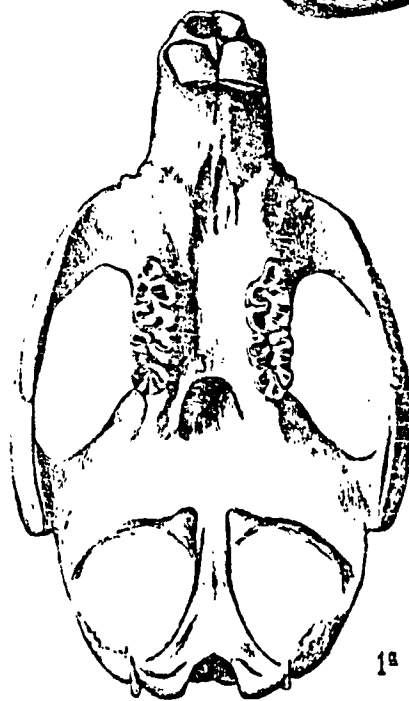
I also followed Mein and Freudenthal (op. cit.) in giving full subfamily recognition among the Cricetidae to the Platacanthomyinae, which Schaub (1958) placed as a tribe of the Cricetinae. As represented by the Miocene Neocometes (see Schaub and Zapfe, 1953; Fahlbusch, 1966) and their living Asiatic relatives Platacanthomys and Typhlomys, they are true cricetids in molar structure, but their crown pattern is somewhat specialized in a direction quite divergent from that of the Cricetinae.

As regards the Cricetodontinae, one of the first questions to be analyzed is whether the tribe Eumyini as proposed by Simpson based on Eumys (Fig. 2) and including most of the Oligocene and Miocene North American cricetids, which Stehlin and Schaub (1951) and Schaub (1958) prefer to give full subfamily rank, is really distinguishable from the Eurasiatic Cricetodontinae, either as different tribes within one single subfamily or as two different subfamilies. I believe that there is a strong case that the distinction is valueless and unfounded beyond the generic level, and in some cases, even within that level. Recently Alker (1966, 1967, 1968), basing his study on a detailed investigation of the variation of the molar teeth in large fossil samples, synonymized most of the described species of Eumys under Eumys elegans Leidy. He recognized Eumys exiguus Wood (with Eumys blacki Macdonald as a synonym) as a valid species, but he placed it in the genus Paracricetodon, so far only described as an Oligocene European Cricetodontinae. He also placed Paracricetodon the species alicae Bläck, type of the genus Cotimus of the Late Miocene to Early Pliocene of Montana (Black, 1961). Fahlbusch (1964) had previously referred to Cotimus two species of the Miocene of Europe formerly allocated in Cricetodon, the type genus of the Cricetodontidae. In a recent revision, moreover, Mein and Freudenthal (1971a) considered Paracricetodon as

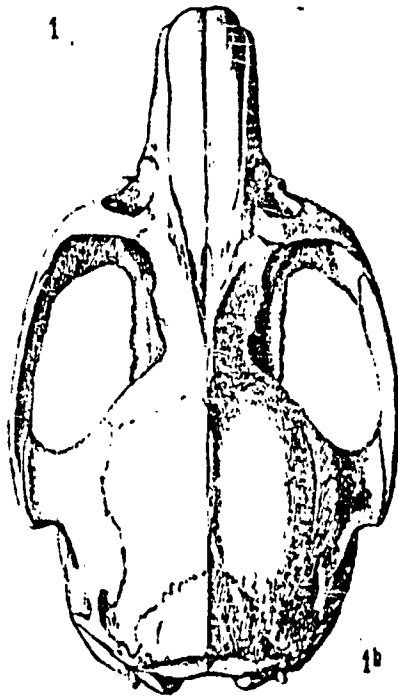
Fig. 2. Skull of Eumys elegans, Leidy, in lateral (1), ventral (1a) and dorsal (1b) aspects. From Wood (1937).



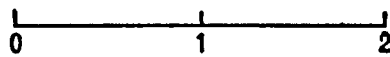
1.



1a



1b



the basis of a new subfamily of Oligocene European cricetids.

Although the fate of these rearrangements will only be settled after a careful and much needed restudy of the North American and European Oligocene and Miocene cricetids in conjunction, based on a thorough consideration of the concept of morphological variation in molar patterns; they are clearly a reflection of the lack of grounds for the distinction of the Eumyini or Eumyinae as a separate group of fossil cricetids. It is very likely that most of the North American and Eurasiatic fossil cricetids other than the Melissiodontinae, the Anomalomyinae, the Cricetopini, and the above mentioned specialized genera probably allied to them, represent a single closely related group, and that a certain amount of migration of the cricetid fauna of Nearctica and Palaeartica occurred in both directions during Oligocene and Miocene times (see Wilson, 1968). Besides Paracricetodon and Cotimus, there are other cases of the common occurrence of fossil cricetids in the two areas. If Alker's assessment is correct, Schaubeomys grangeri of the Early to Middle Miocene of North America, has a counterpart in the two species of the Late Oligocene or Early Miocene of the Aral Sea in the Asiatic U.S.S.R. described by Argiropolu (1939) as Schaubeomys woodi and Schaubeomys aralensis<sup>(1)</sup>. Another striking case was recognized by Galbreath (1966) and confirmed by Fahlbusch (1967, 1969). They found that Democricetodon Fahlbusch, of the Miocene of the United States, which is also found in the Early and Middle Pliocene (Clark, Dawson and Wood, 1964), and currently considered as a direct ancestor of the living genera

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(1) Stehlin and Schaub (1951) and Schaub (1958) claimed that Schaubeomys Wood, as based on S. grangeri Wood, was a member of the subfamily Sicistinae of the Zapodidae, but that S. woodi Arg. and S. aralensis Arg. were true cricetids. Therefore, Schaub (1958) proposed the new generic name Argyromys for the Asiatic species. Alker (1967) did not find grounds for such distinction, and he maintained the three species under Schaubeomys, placing this genus in the Cricetidae.

Peromyscus.

There exist, however, opinions which disagree with the occurrence of the same genera of fossil cricetids in Palaearctica and Nearctica. Freudenthal (1965) said that it is "unsicher" that the European species referred to Cotimus actually belonged to that genus, and he disregarded the value of the similarities in crown pattern of the molar teeth which were the basis of Fahlbusch's (1964) conclusion. Thaler (1966) created Eumyarion as a new subgenus of Cricetodon, to group in it the species of the Miocene of Europe referred to Cotimus by Fahlbusch, even when he recognized a great similarity between Eumyarion and Cotimus. Mein and Freudenthal (1971a) redefined Eumyarion as a full genus, but they considered that the problem of its synonym with Cotimus was unsettled. In the same paper, they ascribed to parallelism the similarities found by Galbreath and Fahlbusch between Democricetodon and Copemys. Certainly, the argument of convergence and parallelism can be misapplied, and Mein and Freudenthal do not appear as very convincing in their rejoinder to Fahlbusch's views. They allude to cranial differences between Democricetodon and Copemys, concluding that the resemblances in molar structure between them is due to convergence. They point out that Copemys has incisive foramina penetrating the palate beyond the anterior borders of the first molars, as in "Hesperomyines", whereas Democricetodon is characterized, as in the cricetines, by short incisive foramina. Actually I found that the relative development of these foramina, which Mein and Freudenthal take as a diagnostic character for the splitting of some suprageneric taxa of fossil cricetids, is more variable at the generic level than the molar structure. This is evident, among other well studied cases, in Akodon and Bolomys (see later). Moreover, the main evidential source for the



knowledge of the fossil cricetids is afforded by the enamel pattern of their molar teeth, and the characters provided by this pattern proved to be highly diagnostic in the definition of the living genera of cricetids. Therefore, Fahlbusch, Galbreath and Alker based their conclusions of the common occurrence in Palaearctica and Nearctica of various genera of Oligocene and Miocene cricetids on very legitimate grounds, and their results must be credited as convincing as most of our present knowledge of the systematic of fossil and living cricetids. Certainly, these results demonstrate that during Oligocene and Miocene times, the Cricetidae evolved in Eurasia and North America as a tightly interrelated, though complexly diverse, main major lineage, and for this lineage a single taxon concept, the Cricetodontinae, seems to be the best issue to be proposed. And even when subdivisions of the Cricetodontinae in tribes could prove to be convenient, there are not cogent reasons for erecting a subdivision for the North American cricetodontines as opposed to their Eurasiatic counterparts. Everything seems to indicate, therefore, that the concept of the Eumyini or Eumyinae, must be thoroughly discarded, and that Eumys, Scottimus, Leidimys and the North American Paracricetodon are to be allocated into a single subfamily Cricetodontinae with their Eurasiatic relatives. Recently, Mein and Freudenthal (1971a) offered a new arrangement of the Cricetidae of the Tertiary of Europe, in which they split the Cricetodontinae as originally conceived by Schaub (1925) into three different subfamilies, namely Cricetodontinae, Paracricetodontinae and Eucricetodontinae. The Cricetodontinae are further subdivided into three tribes. The basis of this classification is founded on a few cranial characters. In fact the cranial morphology of the fossil cricetids is still poorly known and the available material is too scarce to afford convincing information

about their variation at different taxonomic levels. Additionally, the classification proposed by these authors goes too far in the splitting attitude for the requirements of a balanced system of the whole family. The three subfamilies erected by Mein and Freudenthal instead of the classical Cricetodontinae, may prove to be distinct tribes within a single subfamily, as I provisionally envisage them here, but even so, they must be redefined on a more extensive set of characters.

A discussion is now necessary of the living groups of the Cricetidae grouped in Simpson's classification as the "Hesperomyini" and the Cricetini of the Cricetinae. I propose that the living representatives of this family grouped by Simpson as two tribes of one subfamily, are better classified as three different taxa, each of them of subfamily rank, namely the Eurasiatic Cricetinae (Simpson's Cricetini), the mainly South American Sigmodontinae and the mainly North American Peromyscinae (both a single group, the "Hesperomyini" in Simpson's classification).

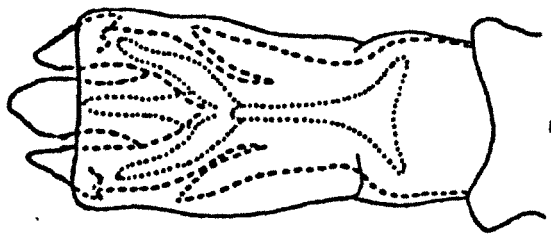
The name "Hesperomyini" as a tribe, of "Hesperomyinae" as a subfamily name, is inadequate, as it is based on mistake and on a now clearly invalid generic name. Unfortunately, it is still used in the modern literature (see, for instance, Mein and Freudenthal, 1971a : 32). Hershkovitz (1966b : 746) had already convincingly demonstrated that its use is untenable. Its original proposal as a subfamily name by Murray was based on a set of North American Cricetids none of which was actually congeneric with Hesperomys bimaculatus, the type-species of Hesperomys, Waterhouse 1939. By the other hand, the latter is a mere junior synonym of Calomys Waterhouse 1937, which is a member of the phyllotine group of South American Cricetids. Hershkovitz also indicates that the name Sigmodontinae as a

subfamily and Sigmodontini as a tribe name, are available as the correct ones for American cricetids. He also advanced that if the North American cricetids should be regarded as taxonomically distinguishable from the South American ones, the name Sigmodontini should be restricted to the latter, and he proposed the name Peromiscini as an available name for tribal distinction of the North American Group. In a later paper (Hershkovitz, 1969), he went straight ahead with this issue, and decided to distinguish as Sigmodontini the mainly South American group from the Peromiscini, a mainly North American group, regarding them as distinct tribes of the subfamily Cricetinae of the Muridae. I believe that there are strong reasons to accept the taxonomical formalization of the distinction between these two groups. However, invoking a need of balance in the whole system of the Muroidea, and the high probability that the two groups are only related by very early links of common ancestry, I propose to accord full subfamily categorical level to the two involved taxa.

The main reason for the splitting of these taxa was the existence of a clear-cut difference between the two in the morphology of the penis. After the studies of Hooper (1958, 1959, 1960, 1962) and Hooper and Mussett (1964), supplemented by the critical revision of this work by Hershkovitz (1966a, 1966b), it is now evident that the whole group of the South American cricetids is characterized by a complex-type penis with a three-digitate baculum, whereas the North American peromiscines show essentially a simple-type penis with an undivided, simple and elongated baculum (Fig. 3). Hooper and Mussett (1964) demonstrated that the complex-penis type is the primitive one, and that the simple type is derived from this.

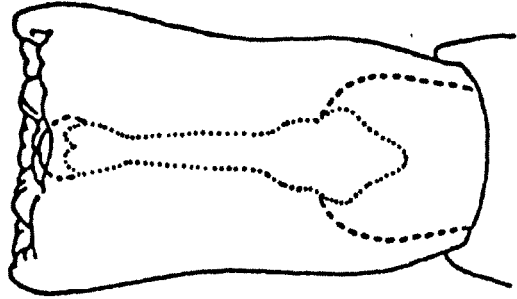
Additional support to the idea of a sharp distinction

Fig. 3. Simple and complex types of phalli and bacula of  
Cricetidae. A. Baiomys musculus; B. Phyllotis  
darwini. (From Hershkovitz, 1962).



B

COMPLEX



A

SIMPLE

between the North American and the South American cricetids was given by the work of Arata (1964) on the accessory glands of the male reproductive tract of the muroids. This author found that the South American group, as represented by Sigmodon, Akodon, Nectomys, Oryzomys, Oecomys (here considered as a subgenus of Oryzomys) and Phyllotis, is characterized by the presence of the full set of accessory glands (preputial, bulbo-urethral, vesicular, ampullary, anterior, dorsal and ventral prostates), resembling in this condition the Old World cricetines, the microtines (= arvicolids), and the murids. The North American group, on its part, is not homogeneous in this respect, and shows the frequent absence of one or the other of the accessory glands. Arata connects these observed differences with the previous results of Hooper on the structure of the penis, to draw, in a scheme of relationships among the examined muroid genera (op. cit., Fig. 9), two major divisions of this group of rodents: one including the North American genera Neotoma, Peromyscus, Reithrodontomys, Tylomys, Ochrotomys, Baiomys and Onychomys, and one other including the above mentioned South American genera, the arvicolids and the murines.

Another source of evidence to substantiate the dichotomy of Simpson's "Hesperomyines", was afforded by the myological studies of Rinker (1954). This author based his studies on the analysis of 228 identifiable muscles of Peromyscus, Neotoma, Oryzomys and Sigmodon. He found that 111 muscles were similar in the four genera, but that a sharp distinction was evident in the myology of Peromyscus and Neotoma, by one side, and Oryzomys and Sigmodon by the other side in the remaining 117 muscles, whereas each of these couples of genera showed a strong similarity for the same muscles. His conclusion was that Sigmodon and Oryzomys were more closely related to each other than any of them

to Neotoma or Peromyscus, and that the latter were as closely related to each other as Sigmodon to Oryzomys. Unfortunately, this study was based on a small number of genera, but the conclusion of Rinker, which is supported by a careful quantitative analysis, is clearly suggestive of a sharp distinction between the North American and the South American cricetids.

Furthermore, recent studies have demonstrated that the two groups are also distinguishable in microscopic hair structure. Stewart and Goerlich, (M.S), in an unpublished paper which I was allowed to read by the kindness of Dr. J. Kirsch, studied the hair scale patterns in 35 species belonging to 4 genera of peromiscines, 8 genera of sigmodontines and 6 genera of arvicolid. They found that the sigmodontines had a very characteristic and distinctive scale pattern, representing a great departure from the peromiscine pattern, and that the arvicolid form a similar distinct group as regards the two other groups. These results are in agreement with the recent statement of Hooper, when he said that "several kinds of evidence....indicate that in the New World there may be three major phyletic groups of murid rodents. These are the microtines, South American cricetines, and neotomines-peromyscines. These three are of about equal taxonomic rank, and may be approximately equidistantly related to the Old World cricetines and groups of murines." (Hooper, 1968 : 33). It is to be taken into account, moreover, that Wenzel and Tipton (1966 : 718) found that the sigmodontines are parasited by fleas and mites of essentially South American relationships, but which are strongly different from the ectoparasites of the peromiscines. They are inclined to conclude that the parasitological evidence suggests an earlier differentiation of the two groups than is indicated by the fossil record.

As I shall discuss in further detail later, sigmodontines



and peromiscines can be thought of as having independent origins and a separate evolutionary history since rather early in the history of the family. This has been anticipated by Hibbard (1968) who said that if the two groups were descendants from a common ancestor, their separation must be placed in the Oligocene or earliest Miocene.

As a consequence of their probably early separation, the two groups show various hierarchical levels in their supra-specific diversity. This fact demands the establishment of suprageneric groupings which have been proposed rather informally, distinguishing "clusters" of genera, or "groups" of genera (see Hershkovitz, 1944, 1962, 1966a, 1969; Hooper, 1968; Hooper and Musser, 1964), but that Vorontzov (1959) correctly expressed in proposing various tribal formal names. The mere fact that each of the groups must be given tribal subdivisions, demands subfamily status for the taxa of higher rank. Therefore, the conclusion of the splitting of the old "hesperomyines" into two taxa of subfamily rank, the Sigmodontinae and the Peromiscinae, is the necessary consequence of their morphological distinction based on several kinds of characters, inferred distinct evolutionary history, additional parasitological evidence, and a requirement of balance in the hierarchical classification.

As regards the Eurasiatic group of living genera and their close fossil relatives, grouped in Simpson's classification as the tribe Cricetini, subfamily rank seems also to be mandatory for them, as proposed by Stehlin and Schaub (1951) and accepted by most European authors. If not by other reason, their subfamily status is necessary just to keep them in good balance with the classification of the genera of the New World. But, and as I shall discuss in the next pages, it is quite probable that their splitting from a common cricetodontine ancestor goes back to about

the same time of the separation of the peromyscines as a distinct group. After the studies of Vorontzov on the African cricetids Mystromys (Vorontzov, 1966), it seems convenient to distinguish two main groups among the Old World cricetines: a tribe Cricetini for the Eurasiatic genera, and a tribe Mystromyini, for the African Mystromys.

As regards the seven living genera of cricetids of Madagascar, I follow here the orthodox view of grouping them all into a single subfamily Nosomyinae, in accordance with the classical point of view of Tullberg (1899) and Simpson (1945), recently supported by Vorontzov (1967). This is a highly diversified group showing a high degree of divergence in molar structure (Petter, 1962; Vorontzov, 1967), morphology of the stomach and the intestines (Vorontzov, op. cit.). Because of its extreme diversity, Ellerman (1941) concluded that it is not a natural taxonomic unit, and distributed its various genera into the Microtinae (= Arvicolidae) (Brachytarsomys), the Tachyoryctinae (= Rhizomyinae) (Brachyuromys), the Murinae (Eliurus), the American "Cricetinae" (Nesomys, Hypogeomys, Macrotarsomys), and a new subfamily Gymnuromyinae (Gymnuromys). Therefore, Ellerman thoroughly expunged the concept of Nesomyinae, and assorted the several Malagasy genera previously placed in it, into five suprageneric taxa of the most diverse geographic distribution. This issue is obviously hard to accept-if not for other reasons-on pure biogeographical grounds. The great diversification of the Malagasy nesomyines was interpreted by Simpson (1945) as an example of adaptive radiation in an insular situation by a single original immigrant stock, which found plenty of empty niches to display its evolutionary potentialities. There is the alternative possibility, suggested by Petter (1962), that the Malagasy cricetid fauna resulted from several cricetid lineages which invaded the island by

rafting on different occasions. If this alternative is true, the Nesomyinae should be regarded as a polyphyletic assemblage, and not as a natural taxon. However, both Petter (op. cit.) and even in more detail Vorontzov (op. cit.) demonstrated that the various molar patterns found in the different genera of the nesomyines, could be derived from a primitive cricetodontine molar pattern. Vorontzov summarises his conclusions stating: "On the basis of the knowledge of the dental system, it can be said that the Nesomyinae are a genetically unitary group" (op. cit. : 93)<sup>(1)</sup>. Later on in the same paper, and after discussing the anatomy of the stomach in members of this group, he concluded: "The resemblances in the structure of the stomach of Macrotarsomys, Gymnuromys, Eliurus and Brachyuromys with the Cricetinae, the Microtinae, the Gerbillinae and the Murinae do not afford any basis to draw any of those genera close to any of the mentioned subfamilies" (op. cit. : 144-145)<sup>(1)</sup>. And after studying the morphology of the intestines of the same group of genera, he concluded: "From the structure of the intestines, the Nesomyinae appear as a widely divergent group, but at the same time, and without any doubt, as a closely related group of forms of monophyletic origin" (op. cit. : 173)<sup>(1)</sup>. This results are in close agreement with Simpson's interpretation of the Malagasy cricetids, and they led me to conclude that they must be included in the system of the Muroidea as a single subfamily.

The arrangement resulting from the above arguments poses, however, several problems. One is the question of the vertical limits of each of the living subfamilies as regards the ancestral Cricetodontinae from where they are derived. It seems quite likely that the North American Peromyscinae descended from North American cricetodontines of Eurasiatic origin. It is even clearer than the Cricetinae were derived from Eurasiatic Cricetodontinae. Though the

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(1) Translation of the author.

origin of the South American Sigomodontinae is still obscure, as it will be later analyzed in this paper, there is also a strong case to maintain that they derived from the Cricetodontinae. The details of the involved phylogenies are less than clear so far, but some better understood cases furnish some clues of a picture the whole details of which would probably be adequately known after much new evidence has been discovered.

After the studies of Hartenberger (1965), Freudenthal, (1967), Mein and Freudenthal (1971a) and specially of Fahlbusch (1969), it appears that some Miocene European genera currently classified as Cricetodontinae, are more likely to be placed as Cricetinae. Fahlbusch established that this is especially the case of Copemys (Democricetodon) and Megacricetodon, and that the Pliocene genera Rotundomys, Kowalskia and Ruscinomys were closely related to the direct ancestry of such living genera as Cricetus, Phodopus, Allocricetus and Calomyscus. Formal allocation of some of the above mentioned fossil genera within the Cricetinae is therefore highly probable. Although here again the details of the actual phylogenetic relationships are a matter of differences of opinion (see Mein and Freudenthal, 1971a; Fejfar, 1970), there seems not to be a clear-cut limit between some of the Miocene "cricetodontines" and the true cricetines, and the transition between the two groups was probably a gradual one within a complicated pattern of intergeneric relationships still not completely well understood. In very general terms, the available evidence suggests as the more acceptable picture that by Early Miocene times Eucricetodontini derivatives reached a level of evolution leading to the Copemys-Democricetodon grade by Late Miocene times. From this grade, the Eurasiatic Cricetinae evolved from a Democricetodon-like ancestor, whereas at the same time, Copemys differentiated as a subgenus which migrated to North America to give rise there to the

peromiscines. In fact, limits between Copemys and the early Peromyscus in North America seem hard to establish, and a gradual transition between the two genera is likely to have occurred. Peromyscus russelli, described as a Peromyscus by James (1963) for instance, was considered a true Copemys by Clark, Dawson and Wood (1964). On the basis of the result of those authors, and of Askell (1967), it seems also probable that the Valentine Miochomys, quite likely a derivative of Copemys, may be the ancestor of the living Onychomys, and it could also be supposed that other North American peromiscines, as Reithrodontomys, Baiomys and Neotoma, could be eventually proved to have a common root in a Copemys-like ancestor. This is certainly a tentative, and probably also an oversimplified picture, but it seems to be a likely one in gross terms and, as such, a basis for considering that the Peromiscinae and the Cricetinae shared a common ancestor of Eurasiatic origin, which lived by Early Miocene times. Thus we come back to assessing, the unitary nature of the North American and Eurasiatic Pre-miocene cricetids, which we before proposed to group into a single subfamily Cricetodontinae. This subfamily was also the source of a previous Oligocene radiation not directly connected with the ancestry of the living North American and Eurasiatic cricetids. Among the several branches of that still poorly known radiation, the origin of the African scores of different cricetids probably took place.

In the following classificatory scheme I summarize the results of the former discussion. I incorporate into this scheme the recognition of the Arvicolidae<sup>(1)</sup> as a distinct family, following the view of several modern European authors. It is quite

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(1) I prefer the name Arvicolidae Gray 1821 to Microtidae Cope 1891. Although priority is not mandatory for family names, most European authors have lately been giving increasing endorsement to the previous name given to this group by Gray, and a glance at the recent literature indicates that Gray's name, either as a family or as a subfamily name, is now more favoured than Cope's name.

probable that the voles evolved as a geologically rather modern offshoot of the cricetid radiation (Reopening, 1968). Therefore, on strictly cladistic grounds, they ought to be classified as no more than a subfamily of the Cricetidae. However, the group was affected by a very rapid evolution since its separation from the main stem, achieving a high degree of differentiation as a evolutionary unit (see Guthrie, 1971). On the tenets of the very progressive/evolutionary systematics (Mayr, 1965) degree of differentiation and speed of evolution are at least as important as closeness of descent from a common ancestor. Accepting these principles, as I do, it seems to be mandatory to give full family status to the group of the voles and vole-like rodents. Moreover, the same argument may be applied to the murids, which are also a rather modern offshoot of the cricetid stem, and which evolved equally at a rapid tempo to attain a high degree of differentiation in molar structure, although in quite another direction. Therefore, if murids are recognized as a different family from the cricetids, the same attitude must be held for the arvicolids.

By the same reasons, the Gerbillidae, Spalacidae and Myospalacidae are given here full family status. In their cases, moreover, this view is additionally supported by the likelihood of their earlier differentiation from the main original cricetid stock. However, in the case of Rhizomys and related genera, I preferred to follow Thomas (1896) and Schaub (1958), and to arrange them as a subfamily Rhizomyinae of the Spalacidae. Rhizomys and Spalax are very close in molar structure and in general specializations, and their divergence from a common ancestor was not probably an early event.

In Table 1 I develop the classification of the Muroidea which I propose as a result of the previous discussion. As regards the subdivisions of the Muridae, I followed here the authoritative recent revision of Misonne (1969). I believe that a further sub-

division of the Murinae into tribes would be convenient, but I did not attempt such an enterprise because I am not familiar enough with this group. As regards the Peromyscinae and the Sigmodontinae, I followed as much as possible Vorontzov's proposals for tribal subdivisions. However, I followed Hooper (1968) in recognizing only two main subdivisions of the peromyscines, and I introduced several modifications to Vorontzov's classification of the South American forms, which I shall discuss in detail in the corresponding systematic parts of this paper. As for our main subject, the Sigmodontinae, a more detailed classification, including the genera recognized here and the number of species of each genus, is shown in Table II. The reasons for our conclusions as regards generic recognition and the arrangement in tribes will be dealt, also, under the corresponding systematic treatments in the succeeding parts of this paper.

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Superfamily Muroidea, Miller and Gidley, 1918.

Family Cricetidae Rochebrune, 1883.

Subfamily Cricetodontinae, Stehlin and Schaub, 1951.

Tribe Paracricetodontini, new name (as subfamily Paracricetodontinae, Mein and Freudenthal, 1972; including Eumyini, Simpson, 1945).

Tribe Eucricetodontini, new name (as subfamily Eucricetodontinae, Mein and Freudenthal, 1972).

Tribe Cricetodontini, Simpson, 1945 (including Megacricetodontini and Fahlbuschini, Mein and Freudenthal, 1971).

Tribe Cricetopini, Simpson, 1945.

Subfamily Melissiodontinae, Stehlin and Schaub, 1951  
(=Melissiodontidae, Schaub, 1958).

Subfamily Platacanthomyinae, Alston, 1876.

Subfamily Anomalomyini, Stehlin and Schaub, 1951.

Subfamily Cricetinae, Murray, 1866.

Tribe Cricetini, Simpson, 1945.

Tribe Mystromyini, Vorontzov, 1956.

Subfamily Peromyscinae, new name (as tribe Peromyscini in Hershkovitz, 1966).

Tribe Reithrodontomyini, Vorontzov, 1959 (including Onychomyini, Vorontzov, 1959, and "peromyscines" Hooper, 1968).

Tribe Neotomyini, Vorontzov, 1959 (= "neotomyines" Hooper, 1968).

Subfamily Sigmodontinae, Thomas, 1897 (Sigmodontes, Baird, 1857; Coues, 1877, = Sigmodontini Hershkovitz, 1969).

Tribe Oryzomyini Vorontzov, 1959 (= Oryzomyine group + Thomasomyine group in Hershkovitz, 1962, 1966).

Tribe Akodontini, Vorontzov, 1959 (= Akodont or Akodontine group + Oxymycterine group in Hershkovitz, 1962, 1966).

Tribe Scapteromyini, new name (= Scapteromyine group in Hershkovitz, 1966).

Tribe Sigmodontini, Vorontzov, 1959 (not Hershkovitz, 1969, in part equivalent to "Sigmodont rodents" in Hershkovitz, 1955).

Tribe Ichthyomyini, Vorontzov, 1959.

Tribe Wiedomyini, new tribe.

Tribe Phyllotini, Vorontzov, 1959 (including Reithrodontini, Vorontzov, 1959; almost completely equivalent to Phyllotine group Hershkovitz, 1962).

Subfamily Nesomyinae, Major, 1897.

Subfamily Dendromurinae, Lavocat, 1959.

Subfamily Cricetomyinae, Roberts, 1951.

Subfamily Petromyscinae, Roberts, 1951.

Subfamily Lophyomyinae, Thomas, 1897.

Subfamily Otomyinae, Thomas, 1897.

Family Arvicolidae, Gray, 1821.

Family Muridae, Gray, 1821.

Subfamily Murinae, Murray, 1866 (including Pseudo-



myinae, Simpson, 1961, Phlaemomyinae,  
Alston, 1876).

Subfamily Hydromyinae, Alston, 1876.

Subfamily Rhynchomyinae, Thomas, 1897.

Family Gerbillidae, Stehlin and Schaub, 1951.

Family Myospalacidae, new rank (= Myospalacinae Miller and  
Gidley).

Family Spalacidae, Thomas, 1896.

Subfamily Spalacinae, Thomas, 1896.

Subfamily Rhizomyinae, Thomas, 1896.

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Table I. A suggested classification of the Muroidea.

Family Cricetidae

Subfamily Sigmodontinae

Tribe Oryzomyini

- Genus Oryzomys (39)
- " Thomasomys (25)
- " Rhipidomys (5)
- " Neacomys (3)
- " Necotmys (2)
- " Phaenomys (1)
- " Chilomys (1)
- " Scolomys (1)

Tribe Scapteromyini

- Genus Scapteromys (1)
- " Kunsia (2)

Tribe Sigmodontini

- Genus Sigmodon (2)
- " Holochilus (2)
- " Reithrodon (1)
- " Neotomys (1)

Tribe Akodontini

- Genus Akodon (29)
- " Oxymycterus (6)
- " Bolomys (6)
- " Chelemys (3)
- " Notiomys (3)
- " Microxus (3)
- " Lenoxus (1)
- " Blarinomys (1)
- " Podoxymys (1)

Tribe Phyllotini

- Genus Phyllotis (18)
- " Euneomys (5)
- " Calomys (4)
- " Zygodontomys (3)
- " Eligmodontia (2)
- " Pseudoryzomys (1)
- " Galenomys (1)
- " Andinomys (1)
- " Chinchillula (1)
- " Irenomys (1)

Tribe Wiedomyini

- Genus Wiedomys (1)

Tribe Ichthyomyini

- Genus Ichthyomys (2)
- " Rheomys (1)
- " Anotomys (1)
- " Neusticomys (1)
- " Daptomys (1)

Sigmodontinae inc. sed.

- Genus Rhagomys (1)
- " Punomys (1)

Subfamily Peromiscinae

Tribe Reithrodontomyini

- Genus Tylomys (1)
- " Aporodon (1)
- " Reithrodontomys (1)

Table II. A synopsis of the classification of the rodents of the family Cricetidae of the living South American fauna. Figures between parentheses following each generic name indicate the number of species tentatively recognized. The estimated number of species of the Oryzomyini, Ichthyomyini and Peromiscinae are taken from Cabrera (1961). For the Scapteromyini, the Sigmodontini and partially the Phyllotini, I have followed Hershkovitz. The Akodontini are recorded species numbers after my own revisionary studies.

5. THE STRUCTURE OF THE MOLAR TEETH OF THE CRICETIDAE AND THE NOMENCLATURE OF THEIR ENAMELLED COMPONENTS.

All cricetids are characterized by a dental formula of  $I \frac{1}{1}, M \frac{3}{3}$  (1). 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 of the known variants in 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.4) (Schaub, 1925; Stehlin and Schaub, 1951; Petter, 1966c, etc.). A few rather well established phylogenetic sequences, as the one represented by Eucricetodon-Cotimus-Democricetodon-Kowalskia-Cricetus (Fahlbusch, 1969) or the other by Cricetodon sansaniensis-Ruscinomys europaeus (Freudenthal, 1966), 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.

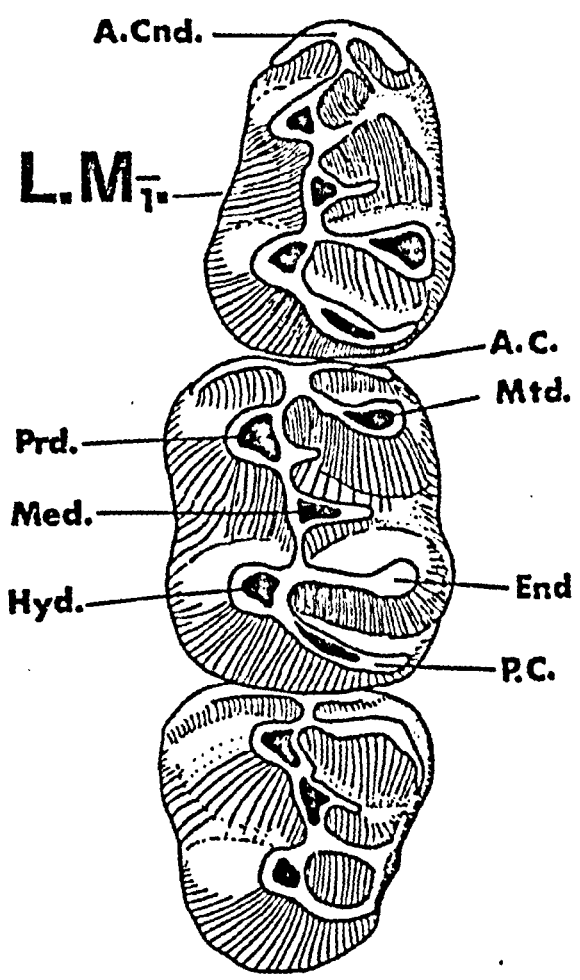
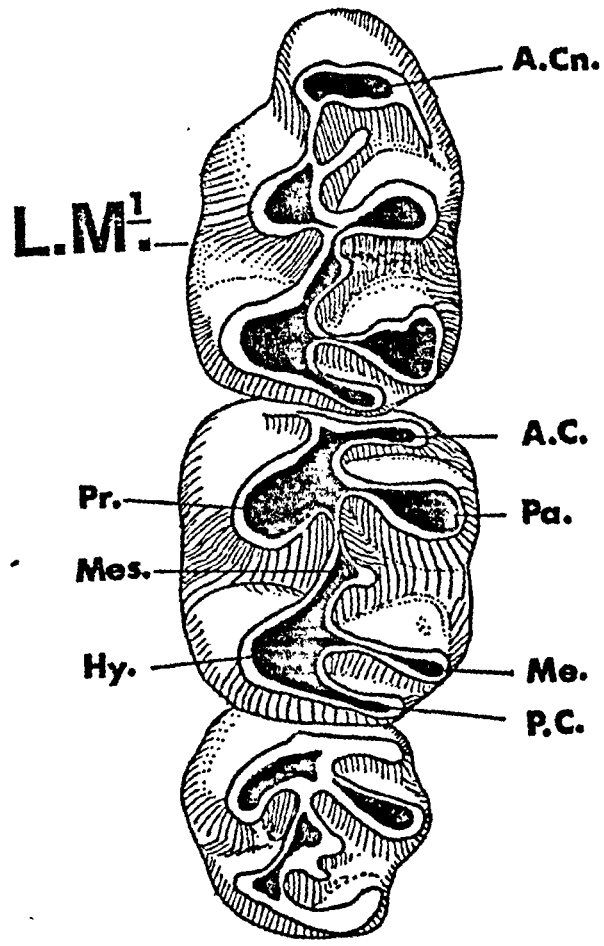
With small variations, the cricetodontine pattern of molar structure is also found in the more primitive of the tribes of the South American Sigmodontinae, namely the Oryzomyini (Fig.6). It is characterized by a relatively complex system of cusps, ridges connecting the cusps, and valleys or folds in between the cusps and ridges. These elements are developed in the crown surface of brachyodont, cuspidate, bunodont molars, in

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(1) 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  $I \frac{I}{I}, DP \frac{4}{4}, M \frac{I-2}{I-2}$ . This view was convincingly refuted by Wilson (1956). Alker (1967) also contributed to substantiate the interpretation accepted here.

Fig. 4. Upper and lower molars of a representative of the Cricetodontinae, Querey, 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., pyoconid. L.M<sup>1</sup>, left first upper molar. L.M<sub>1</sub>, left first lower molar. Med., mesoconid. Mes., mesocone. Mtd., metaconid. Pa., paracone. P.C., posterior cingulum. Pr., protocone. Prd., protoconid.



0 1 2 mm

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 and 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 antero-lingual 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<sup>(1)</sup>. Therefore, we found in them an anterolabial protoconid, a posterolingual 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

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(1) 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 and 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.

protoconid and the hypoconid. Furthermore, the first lower molar also shows the addition of an anteromedian anteroconulid 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 "Längsrat" by Schaub (1925) but 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 individual cusps are better defined as enamel ridges than as lophs or lophids. From this stage, various degrees of hypsodonty, correlated with increasing lophodonty 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, 1960b, 1963b, 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. But the modifications involved are characteristic of several direct or indirect derivatives of the cricetodontines, as Neotoma and relatives among the peromiscines, the phyllotines and the sigmodontines among the Sigmodontinae, the Arvicolidae, etc.

Stehlin and Schaub (1951), Schaub (1958), Petter (1962, 1966c, 1967, etc.), Vorontzov (1960b, 1967), Hershkovitz (1962) and Vandebroek (1966) have described in detail the various transformations which occurred during dental evolution of the Muroidea, and the involved morphological processes.<sup>(1)</sup> 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,

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(1) For the nomenclature of the latter, I have followed in the text Hershkovitz (1962) in the use of such terms as the different types of hypsodonty, plication, lamination, involution, etc.

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. In fact, several different systems of names are being used at present for those structures, leading to confusion and making it appallingly difficult to compare the descriptions in the works of the various authors. I have found eleven different nomenclatures for the cusps, crests and valleys of the molar teeth of the cricetids from 1925 up to now. The relevant citations are Schaub (1925, see also Stehlin and Schaub, 1951; Schaub, 1958), Viret (1929; but see also Viret, 1955), Wood and Wilson (1936), Winge (1941, but actually originally Winge, 1924, and still earlier, Winge, 1888) Herschkovitz (1944, but see especially Herschkovitz, 1962), Jones (1963), Vandebroek (1966), Fahlbusch (1966), Alker (1967), Vorontzov (1967) and Mein and Freudenthal (1971b).

The very fact of the existence of so many proposed nomenclatures for just one kind of morphological structure might be a reflection of the dissatisfaction that the individual authors found in their practical work when trying to apply some of the previous proposed systems of names. These could have been found thoroughly unsatisfactory on general grounds, or not adequately fitted to the peculiarities of the structures to be described. This latter difficulty may result from a too strong attachment of the proponents of particular nomenclatures to the distinctive variants of their own material, or to a neglect of the convenience of a unifying general language for their descriptive purposes. It is easy to realize, for instance, that the European students working with cricetodontines or cricetines have not taken very much into

account the peculiarities of the molar structure of the peromiscines or the sigmodontines. The reverse case is also evident, as the nomenclatorial systems proposed for cricetids of the Western Hemisphere did not take into account that the fossil and living cricetids of the Europe, Asia and Africa show details in their molar patterns which must also be named. This omission of a comprehensive grasp of the whole cricetids, could be another source of the fact that a nomenclatorial system satisfying the whole group of specialists has not yet arrived.

The eleven different nomenclatures that I found in the literature 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' proposals, which differ from each other only in points of details. However, other systems of names are completely different, to the extent that a table of equivalences is required to follow the descriptions based on them. This is the case of the nomenclature of Winge, Wood and 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 teeth.

Winge's nomenclature is probably the first that everybody could agree now in 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 presently valid nomenclature.

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

Vandebroek's nomenclature differs from any other system, as 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 nomenclature starting from cusp names different from the widely endorsed Cope-Osbornian ones. The latter are so deeply incorporated to 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 and Wilson's system is also based on the Cope-Osbornian designation of mammalian molar cusps, and it is probably the more accurate and a reasonable attempt to adapt the Cope-Osbornian nomenclature to the distinctive structures of rodents in general, and cricetids in particular. In one or another way, it is the basis of several other proposals 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 be given names as much as the cusps and lophs, though the latter are thoroughly described and named in Wood and Wilson's system. James and Alker use nomenclatures that differ only in details from Wood and Wilson's. They introduce variants, however, which could be convenient for their own material, but which are not applied to other cricetids. Moreover, they also do not provide names for the valleys and folds.

During the last twenty 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 and Fornes, 1965c; Reig and Linares, 1969). Giving Cope-Osbornian names for the major cusps, this is mainly an objective and topographic system of names for cusps, styles and valleys or folds, but it does not provide names for several of the main lophs and lophids. The designations employed for the folds are complex of two or three combined anglicized Latin names describing the position and inferred relative morphological importance of the infoldings of a plicated surface. The procedure requires the employment of 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 and 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 here advance further in this attempt, though 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 elements of the crowns of cricetid rodents, and many of its proposals are worthy of being incorporated to any unifying nomenclatorial attempt. Vorontzov took much advantage of Hershkovitz nomenclature in proposing his own one. His proposal has the inconvenience, however, of still not providing names for the major crests, and in following 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.

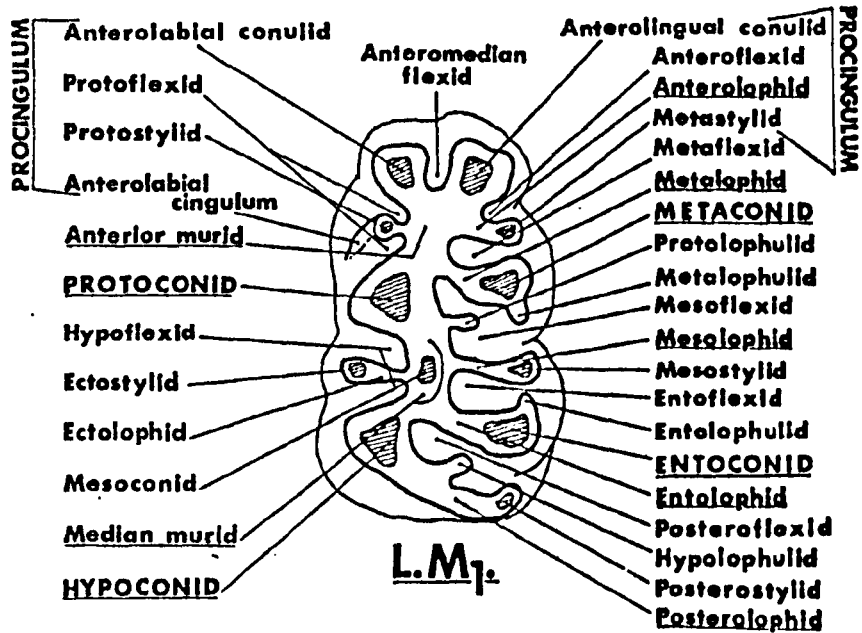
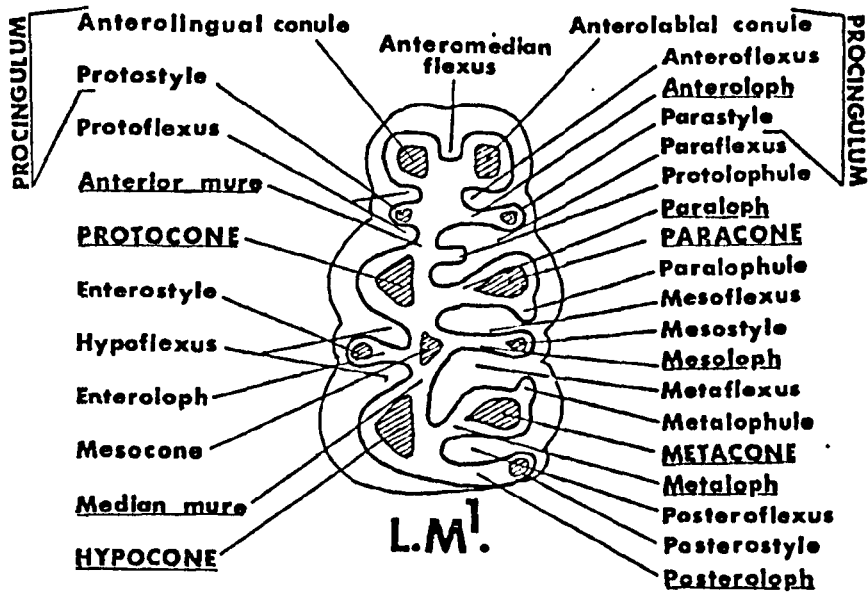
The nomenclature offered recently by Mein and Freudenthal (1971b) is probably one of the most complete so far proposed. It is mostly based in Wood and Wilson, but it is completed with names for the valleys between the tubercles not provided by the latter authors, which are an adaptation of Schaub's early 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). These names were adopted by Wood and Patterson (1959) for caviomorphs, and by Vorontzov (1967) for cricetids. Additionally, Mein and Freudenthal introduce some new names for certain lophs and ridges when names for the same structures were already available and in widespread usage. Furthermore, its strict fidelity to the cricetodontine variety of the cricetid molar pattern turns the whole system insufficient for describing some of the features found in other groups of the same family.

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 simple enough, comprehensive, detailed and universal as to be worthy of general acceptance, and that this is probably the main reason of the very existence of so many of them. Hence, the need of 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, its outcome is also urgent. I therefore decided to attempt the proposal of 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 already available systems of names. My proposal is therefore not actually to invent a new nomenclature but one in which the best contributions of the various authors are combined in a unified system. Judgements as to the value of those contributions are indeed unavoidable, and in such a delicate duty, I followed as much as possible the consensus of the implicit or explicit decisions of other authors.

I believe that the main tenets of such a unifying new proposal would be: 1) Agreement with the overwhelmingly accepted Cope-Osbornian names for the cusps of the tribosphenic molar pattern; 2) Agreement with a cogently supported hypothesis of the homologies of the cusps in the primitive cricetid molars; 3) Overall applicability: the nomenclature should be detailed enough and complete as 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;

Fig. 5. 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.





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.

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 and 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. 5, pictures of a generalized ideal crown pattern of a first upper and the first lower cricetid molars are given. They show the bidimensional topography of the different enamelled components which can be found in 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 rather 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 the same prefix that applies 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 called following the Cope-Osbornian nomenclature.

The styles and styliids 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 lophi 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 and Wilson. This applies to the crest of lophid which develops from the entoconid towards the hypoconid or the longitudinal crest, and which is named by these authors and many others the hypolophid. 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, as Paracricetodon (Alker, 1967) and Cotimus (fide Fahlbusch, 1964). The same structure was called "Hypoconidenhinterarm" by Schaub (1925), and hypolophid II by Alker (op. cit.). 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 (op. cit.) This is equivalent to Wood and 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 (op. cit.). 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, from 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 and Patterson (1959) for caviomorphs, and introduced by Mein and Freudenthal 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 structure in the literature on cricetids molars and their variation.

I also found 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 also 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 and Freudenthal (1971, but see also 1972: 11), and to the "rückwärtiger 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 of the 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 only 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 process of loss of individuality of the mesoloph or mesolophid by coalescence with the paraloph or hypolophid was suggested by Vandebroek (1966), though using a quite different nomenclature. It is also nicely exemplified in the

akodontine and scapteromyine sigmodontines. The resulting median transverse loph or lophid is therefore complexive in origin and in some cases, noticeably in the scapteromyines, it is very strong and has a more or less bifurcated distal border (Fig. 32 ). 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 call them, as already anticipated, flexi and flexids following Stirton (1935) and other authors (see for instance Wood and Patterson, 1959; Pascual, 1967). I followed the rule of greatest mnemonic value, of 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 "procinguloflexus", a rather cumbersome word, by Vorontzov. Therefore the fold separating the two conules of the procingulum is named anteromedian flexus, adapting the way it is called by 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 anteroflexid the

fold called procinguloflexid by Vorontzov, 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 any modification Vorontzov's terminology. The names here given to the flexi and flexids are not equivalent to the ones used by Wood and 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 and 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 and Schaub (1951) and to Hoffstetter and Lavocat (op. cit.)

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 widely agreed theory.

Moreover, I feel that other cautions must here be expressed about the 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 constructs to understand 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. Those 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), Wolfe and Layne (1968) 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 dare to 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.



6. STRATIGRAPHY

Most of the specimens of fossil mice described in the systematic part of this paper come from the Late Cenozoic sequence of the Chapadmalal region which out crops at the Atlantic cliffs and slopes in the coast between the cities of Mar del Plata and Miramar, Buenos Aires Province, Argentina. Some other specimens were found in the extension of the same deposits north of Mar del Plata and south of Miramar. Additionally, two very significant specimens come from the classical Monte Hermoso beds west of the city of Bahia Blanca, in the same Argentinian province, and a small collection was also seen, coming from a Bolivian Pleistocene deposit: the Tarija beds of southern Bolivia.

Knowledge of the Late Cenozoic mammal-bearing deposits of Buenos Aires Province goes back to Darwin (1851) and Bravard (1857). Darwin first observed the geology and collected in the Monte Hermoso beds and in Pleistocene strata close to the city of Bahia Blanca. Bravard made more extensive geological observations and collecting in the Pleistocene deposits elsewhere in the same province. The geologically more complete Chapadmalal sequence was discovered later.

But the first systematic work on the stratigraphy and paleontology of those deposits is due to the work of F. Ameghino (see especially, 1887, 1888, 1889, 1906, 1907, 1908, 1910). Ameghino is responsible, as it is well known, not only for the pioneering study of the Late Cenozoic geology and paleontology of Argentina, but of the whole mammal-bearing Cenozoic sequence of Argentina, one of the most complete and rich the world over.

The Late Cenozoic of Argentina as represented in the

deposits of Chapadmalal, Monte Hermoso, and the various outcrops of Pleistocene age in the Pampean region, is extraordinarily rich in fossil mammals. It is not surprising, therefore, that after Ameghino's work, several authors contributed with hundreds of scientific papers to its paleontological and stratigraphic study. Even a very brief summary of those contributions would be out of place here. Suffice it to say that the stratigraphy was worked out in more detail, after Ameghino, by Frenguelli (1921, 1928, 1950), Roth (1921), J. Kraglievich (1952), Gonzales Bonorino (1965), Pascual, Ortega Hinojosa, Gondar and Toni (1967), just to mention the more important contributors. Also the paleontological studies of this part of the Argentinian Cenozoic sequence were given special attention in what can be called the post-Ameghinian period (1911-1935), by Rovereto, L. Kraglievich, Castellanos and Rusconi. After this period scores of authors contributed to enrich our knowledge of the fossil mammals of this age and place.

One interesting aspect has to be noted as regards many of these contributions. Due to the alleged discovery of remains and artifacts of early men in the Monte Hermoso beds (Ameghino, 1907; Lehman-Nitsche, 1907) and the Chapadmalalan beds (Ameghino, 1911; Frenguelli and Outes, 1921; Vignati, 1922, 1941) as well as in later strata (Ameghino, 1909)<sup>(1)</sup>, the problem of the correlation of those strata with the European standard geological column became highly controversial and coloured of ideological prejudices. Ameghino, in accordance with his general tendency to make the Cenozoic strata of Argentina one epoch older than is now

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(1) A complete account, though unfortunately a very biased one, on the alleged early man in Argentina, can be found in Castellanos, 1937.

generally accepted, placed the deposits of Monte Hermoso and Chapadmalal in the Miocene, and the Ensenadan stage, which is now considered Middle Pleistocene, in the Pliocene. Needless to say, the discovery of hominids or their artifacts in South America in strata of these ages, would be scientifically astonishing. Consequently, scholars became divided into two opposing fields as regards the relative chronology of the corresponding strata, and this division pervaded for years the work of stratigraphers and paleontologists. Ameghino's followers, usually participant of naturalistic or positivistic philosophies, grouped to defend the Tertiary age of the geological beds involved, whereas authors with opposing views, tended to make them as young as possible within the Pleistocene. The evidence for the supposed hominids was eventually discarded or thoroughly reinterpreted (see, for instance, Bordas, 1942; J. Kraglievich, 1959) but even then, the controversies about the Tertiary or Quaternary age of the Monte Hermoso and Chapadmalal beds outlived in Argentina their origins, and in some contexts they resulted in a topic of acrimonious dispute which produced some oddly militant pieces of scientific literature.

Most of the controversies which took place during the first four decades of the present century on the relative chronology of the Cenozoic sequence of Argentina, may now be considered as basically settled. This was certainly the result of a new outlook coming from a new generation, but, it must be recognized, the important land mark in obtaining a consensus of opinion is Simpson's well-balanced and authoritative surveys of the mammal-bearing Tertiary of South America and its fossils. Simpson's papers on this general subject are too many to be summarized here, but probably the more influential one in this

EPOCHS		P R O V I N C I A L A G E S :			
		Europe	North America	South Amer. (Argent.)	
PLEISTOCENE	U	Versilian	Rancholabrean	Lujanian	
	M	Tirrenian Sicilian	Irvingtonian	Ensenadzan	
	L	Calabrian	Blanquian	Uquian	
PLIOCENE	U	Astian		Middle Lower	Montehermosian
	M	Plaisancian	Hemphillian	Huayquerian	
	L	Pontian	Clarendonian	Chasicoan	
MIOCENE	U	Sarmatian	Barstovian	Friasian	
	M	Vindo- bonian	Tortonian Helvetian	Hemmingfordian	Santacruzian
		Burdigalian	Arikareean		
	L	Aquitanian		Colhuehuapian	
OLIGOCENE	U	Chattian	Whitneyan		
	M	Rupelian	Orellian	Hiatus	
	L	Sannoisian	Chadronian	Deseadan Hiatus	
EOCENE	U	Ludanian	Duchesnian	(Divisaderan)	
		Bartpnian	Uintanian	Hiatus	
	M	Lutetian	Bridgerian	Mustersan	
	L	Cuisian Sparnatian	Wasatchian	Hiatus Casamayoran	
PALEOCENE	U	Thanetian	Clarkforkian Tiffanian	Riochican	
	M	?	Torrejonian	?	
	L		Dragonian Puercoan		

Table 3. Cenozoic epochs and corresponding Provincial ages of South American, as compared with the Provincial Ages of Europe and North America.

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The fossiliferous strata cropping out at Monte Hermoso are the basis of the concept of the Montehermosian stage and provincial age. Their fauna has always been considered as slightly older than the fauna of the Chapadmalalan beds, which are the type rock-unit of the Chapadmalalan stage and provincial age (Ameghino, 1908; Rovereto, 1914; L. Kraglievich, 1934; Reig, 1958). Therefore, the Chapadmalalan has been generally considered as a distinct stage from the Montehermosian. There is still disagreement between those who consider that the Chapadmalalan represents the Early Pleistocene, and the advocates of its Late Pliocene age. Moreover, it has been recently proposed to lump the Chapadmalalan completely into the Montehermosian.

As regards the first point, the main argument of the proponents of a Pleistocene age of the Chapadmalalan, is the alleged extensive occurrence in the Chapadmalalan beds of mammals of North American origin, whereas mammals of this kind are not found in Monte Hermoso. The previous assumptions of this argument are indeed reasonable: the massive migration of Nearctic mammals into South America was an event which took place necessarily from the Early Pleistocene, as it was only possible after the establishment of the Panamanian land bridge. There are strong reasons to believe that the establishment of this bridge was a consequence of orogenic movements of the Andean belt which occurred at the Plio-Pleistocene boundary (Harrington, 1962). Therefore, if the first extensive representation of Nearctic mammals is found in the Chapadmalalan beds, the latter should be considered as corresponding to the beginning of the Pleistocene.

Indeed, there is some oversimplification in the whole argument. The establishment of a land connection between

North and South America is far from being a matter of accurate geological assessment either as precise age or as correlation with orogenic events. Moreover, even when the scale of geological timing allows some indulgence, the locality of the Chapadmalal beds is a long way from the place where the first Nearctic mammals entered South America, and adequate time must be assumed to allow the Recent invaders to expand from what is now northern Colombia to the Pampean region. The Chapadmalalan should be considered, therefore, not as the earliest Pleistocene, but as somewhat after the Early Pleistocene, which, in view of the prevalent Pliocene character of its whole fauna, would be hard to maintain.

The whole argument is more fundamentally challenged by the fact that it is now clear that there was no such thing as an extensive occurrence of Nearctic mammals in the Chapadmalal beds. After the detailed stratigraphical survey of J. Kraglievich (1952), it is now generally accepted that Ameghino's "Chapadmalense" was a complex entity, and that he placed together in it strata of truly Pliocene age and others of later age. It was thereafter found that most of the fossils of Nearctic origin supposedly belonging to the Chapadmalalan fauna, had in fact been obtained from Early Pleistocene strata overlying the typical Chapadmalal beds. In my 1958 paper I offered the first "purified" list of the Chapadmalalan mammals, which resulted in a mostly "Pliocene" assemblage with the addition of only three mammals of North American provenance: a peccary, Platygonus marplatensis (= Argyrohyus chapadmalensis, see J. Kraglievich, 1959), a skunk, Conepatus altiramus, and a cricetid rodent, Reithrodon chapadmalensis. This was indeed a meagre representation of mammals of Nearctic origin as compared with those previously

, attributed to the Chapadmalalan. Additionally, procyonids of the genus Cyonasua, which also occur in the Chapadmalalan, are known from Montehermosan and Huayquerian deposits (see Kraglievich and Reig, 1954), and after the studies reported in this paper, we now know that cricetids were already present in the Montehermosan, and that they are probably an earlier component of the South American faunal assemblages. Therefore, there are reasons to suppose that the massive irruption of mammals of Nearctic origin into South America in the Pleistocene, was anticipated by several waves of waif immigrants, which reached the continent before the establishment of a firm land bridge, if this bridge was not really in existence before the end of the Pliocene (Reig, 1962a, 1962b, 1968a). Therefore, and taking into account the basically "Pliocene" character of the Chapadmalalan fauna, the presence of a few elements of Nearctic origin in it, is not a reasonable basis to shift it from the Pliocene to the Early Pleistocene. In support of this conclusion, it may also be pointed out that the sequence overlying the Chapadmalal beds in the region between Mar del Plata and Miramar, gave evidence of cyclic sedimentary changes which have been correlated by J. Kraglievich (1952) and Groeber (1952) with the climatic changes and the epeirogenetic consequences of the intra-Pleistocene movements of the Andean orogenesis, whereas the Chapadmalal beds properly, are excluded of these cyclic phenomena.

As regards the lumping of the Chapadmalalan stage into the Montehermosian stage, it can be regarded as a consequence of the thorough reassessment of the immigrant component of the former. The faunal differences between the two stages are thereby greatly reduced, and the remaining ones

are taken as merely reflecting a distinction of an ecological nature, rather than as an indication of evolutionary differences requiring their separation into distinct stages (Pascual et al., 1967: 179).

It cannot pass without remark here, that the argument of merely ecological differences between the Montehermosian and the Chapadmalalan was refuted by a detailed, though obviously outdated study of L. Kraglievich (1934). The conclusions of this author should be confirmed by an examination of the more modern now available evidence, but they cannot be ignored. Kraglievich convincingly demonstrated a clear evolutionary faunal difference between the Chapadmalalan and the Montehermosian, after a meticulous analysis of the components of the fossil assemblages of each stage.

Moreover, partial modern revisions support the idea of a true difference, even when not a strong one, in evolutionary stage of some of the components of the two faunas. The study of J. Kraglievich (1965) on the genus Eumysops, Simpson's (1970, 1972) revisions of the argyrolagids and didelphids, and Reig and Simpson (1972) study of the peculiar didelphid Sparassocynus may be cited in this connection. The present study also proves a difference between the cricetids of the two stages, though this could actually be a more ecological or geographical difference than an evolutionary one. As we have recently indicated (Reig and Simpson, op. cit.) there is clear evidence that the fauna of the Chapadmalal formation is much more closely related to that of the immediately overlying Early Pleistocene strata (Barranca Lobos and Vorohuë) than is that of the Monte Hermoso formation. Our conclusion was that the Chapadmalal fauna is similar to, but more advanced than the Monte Hermoso fauna.



But even if this conclusion is a valid one, there is still a convincing case for the lumping of the Chapadmalalan into the Montehermosian as a major age and chronostratigraphic unit. The Chapadmalal and the Monte Hermoso faunas are more closely related to each other than either of them to local faunas referred to the Huayquerian stage. It can be demonstrated that the combined Monte Hermoso and Chapadmalal faunas differ from the Huayquerian faunas to the same extent that the Huayquerian and the Chasicuan faunas differ from each other. Therefore, a tripartite division of the Argentinian "Pliocene" seems advisable, and for these three divisions the names Chasicuan, Huayquerian and Montehermosian are appropriate. However, these must be taken as major chronological and rock-time units which can be further subdivided, when they are required by inferred evolutionary differences in their faunal components. As we have seen, this is actually the case between the Monte Hermoso and the Chapadmalal faunas.

The inescapable conclusion is that there are good reasons for agreeing with Pascual et al. in considering the Chapadmalal and Monte Hermoso faunas as closely related enough to form a single major chronological and chronostratigraphical unit, the Montehermosian stage, which is probably roughly equivalent to the Early and Middle Blancan of North America. At the same time, the differences between the two faunas can be shown in some cases to represent evolutionary stages; also ecological differences may have existed although these have not been demonstrated yet. Therefore, my proposition is to recognize a Montehermosian stage subdivided into two distinct substages, a lower Montehermosian s.s. (roughly equivalent to the Early Blancan),

and an Upper Chapadmalalan substage (roughly equivalent to the Middle Blancan).

As regards what we now consider the Post-Pliocene part of the general stratigraphic column, it comprises a series of chronostratigraphic units which belong to what Ameghino distinguished as "Pampeano" and "Postpampeano". Ameghino's Pampean refers to a body of sediments which in the La Plata River basin and other parts of the Pampean region overlies a sand formation called the Puelche sands, or "Puelchense". The Postpampean of Ameghino is a set of rather thin deposits overlying the Pampean "formation". The subdivision of the Pampean and Postpampean into stages in Ameghino's system is as follows:

	Aymaran	
Post-pampean	Platian	
	Querandinian	
	Lujanian	
	Bonaerian	
Pampean	Belgranian	Upper Ensenadan
	Ensenadan	Inter-ensenadan
	Pre-ensenadan	Lower Ensenadan

Table 4. Subdivisions of the Pampean and and Post-pampean "formations" in Ameghino's system.

Ameghino placed the beginning of the Quaternary after the Ensenadan, but now the generally agreed view is to consider the whole Pampean as Pleistocene, and the Post-Pampean as Holocene. In any case, the nomenclature proposed by Ameghino, is the basis of the chronostratigraphic divisions of the whole Argentinian territory, whatever the different modifications introduced by latter authors.

The more widely agreed rearrangements of Ameghino's scheme can be summarized as follows: 1) recognition of the Inter-ensenadan, Belgranian and Querandinian as merely marine equivalents of the continental Ensenadan, Bonaerian and Platian, respectively; 2) disregard of the Aimarian as a distinctive lithostratigraphic or chronostratigraphic unit; 3) recognition of a Samborombonian marine equivalent of the Lujanian; 4) abandonment of the use of the term Pre-ensenadan, and its substitution by other chronostratigraphic names.

Moreover, Ameghino's nomenclature, and its implied subdivisions of the "Pampean" into stages, is now considered as formally incorrect from the point of view of the presently accepted principles of lithostratigraphic, chronostratigraphic and geochronological nomenclature and taxonomy (see specially the discussion in Pascual et al., 1967). Kraglievich (1952) was probably the first to introduce the distinction of rock units and time units into the Plio-pleistocene sequence of Argentina, and after him it has been a general trend to recognize different "formations" in the Pliocene and Quaternary of Argentina, and to distinguish them as regards a system of chronological or chronostratigraphic units. A concensus of opinion about this classification has not been obtained so far, and the usage of names of rock units and their correspondence with provincial ages and stages, is still unstable and uncertain. A complete discussion of the problems involved is out of place here, and the reader is referred to the modern contributions on this topic by Pascual et al. (op. cit.) and Bonorino (1965). A brief comment on the major issues connected with this subject, is, however, necessary.

As regards the Plio-Pleistocene sequence of the Chapadmalal region, Ameghino (1908) only recognized an

Ensenadan stage overlying therein the Chapadmalalan stage. Kraglievich (1952) demonstrated that the sequence is much more complex, and he distinguished there the following rock and time units:

ROCK UNITS ("Formations")	Provincial ages	Sub-epochs
Santa Isabel/Cobo	Lujanian	Neopleistocene
Arroyo Seco	Bonaerian	
Miramar	Ensenadan	Mesopleistocene
San Andrés	Sanandresian	
Vorohué	Vorohuean	
Barrabca Lobos	Uquian	Eopleistocene
Chapadmalal	Chapadmalalan	Neopliocene

Table 5. Rock units and provincial ages of the Late Cenozoic sequence at the Mar del Plata region, after Kraglievich (1952).

It has been alleged that Kraglievich went too far in distinguishing as "formations" the different rock units of a sequence which is hardly differentiable on strictly lithological grounds (see Teruggi et al., 1957; Gonzales Bonorino, 1965). Actually if "formation" is defined as a major mapeable lithologically uniform unit, it is probable that the whole series of the Pampean region beginning with the early Pliocene Chasicó beds, and finishing with the uppermost Pleistocene deposits, might be considered as a single formation. However, I agree with Pascual et al. (op. cit. : 172, note 10; 181 -185) that Kraglievich's "formations", even when not precisely

.definable on petrological grounds, are in most cases readily distinguishable in the field and useful for most practical purposes. Their distinction is one of colour of the sediments, type of bedding, and stratigraphic position as regards erosion surfaces of rather extensive occurrences, as I had the chance to confirm when assisting Kraglievich in his stratigraphic survey and in my later field work in the area. These different stratigraphic units are probably not formations as this term is conveniently defined, but they are distinguishable members of a complex stratigraphic column, and it has proved very useful to be able to differentiate them with local names. They agree, moreover, with the less stringent definition of the word "formation" given recently by Simpson (1972 : 4) : "a strictly stratigraphic unit defined as a recognizable body of rock". Therefore, and in agreement with my previous work (Reig, 1956, 1957, 1958a; Reig and Simpson, 1972) I shall continue using Kraglievich's rock-unit names.

As regards the geochronological subdivisions proposed by Kraglievich, Pascual et al. (op. cit.) sweepingly neglected as "inexistent" the ages recognized by the former between the Chapadmalalan and the Ensenadan, adding: "Nobody has proven until now with enough proof, that the Vorohuean is actually a distinct age as regards the Uquian. Therefore, we accept the Uquian age as the intermediate one between the Montehermosian and the Ensenadan, disregarding the others which have been proposed" (:179)<sup>(1)</sup>.

I agree that it is probably wise not to recognize within the South American Pleistocene more than three major provincial ages. This attitude would be in good keeping with

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(1) Translation of the author.

the recognition of three major units in the Pleistocene of North American (Upper Blancan, Irvingtonian and Rancho-labrean) and with a similarly tripartite division of the underlying South American Pliocene. However, this agreement does not imply that subdivisions of each of the major South American Pleistocene provincial ages would not be advisable, when well defined subages could be recognized on the basis of evolutionary distinctions in the involved faunas. Pending of confirmation coming from more comprehensive revisions of the corresponding faunas, I believe that distinctions of this kind have already been reported (Kraglievich, 1965; Reig, 1956, 1957), and they are further corroborated by the results of the present study. In fact, this was implicitly recognized by Pascual et al. in their Table II (op. cit., : 174), when they subdivided the Eopleistocene subepoch into a lower and an upper part, the first corresponding with the "Barranca de los Lobos Formation" and the second with the "Vorohué Formation" (including the San Andres formation).

The abandonment of a Sanandresian age or subage seemed forced by its proponent, when Kraglievich (1959;6) placed his San Andres formation as a mere member of his Vorohué formation. Pascual et al. (op. cit., foot note 15, page 179) took for granted that this lumping implied a disclaimer of the Sanandresian age by Kraglievich himself. That this is not necessarily the only possible interpretation is warranted by the independence of rock units as regards time units, a point about which Kraglievich was very clear. Moreover I have collected intensively in both Vorohué and San Andrés beds and I am convinced that these two rock units, which are easily recognizable in the field, have different faunal compositions, as will be partially demonstrated also in

this study. Therefore, I tentatively accept Pascual et al.'s subdivision of the Argentinian Pleistocene into three major provincial ages, but I shall subdivide their Uquian age into three subages: Uquian s.s. (including the Barranca Lobos, Puelche and Uquia "formations"), Vorohuean (including the Vorohué "formation"), and Sanandresian (including the San Andrés "formation").

As regards the Lujanian age, I also believe that there is a good case for proposing it be subdivided into a lower, Bonaerian subage, and an upper, Lujanian s.s. subage. Even when Pascual et al. are right in assessing that a clear-cut distinction between the faunas of Bonaerian and Lujanian provenance has not been demonstrated, the different stratigraphic units that have been referred to the Lujanian stage have been always fluvial or lacustrine strata deposited over an erosion surface excavated on the terrace made by the Buenos Aires "formation" or its equivalents. Therefore, the Lujanian strata are indeed younger than the underlying Bonaerian beds, and a distinction is here necessary, even though it has not been warranted so far by detailed faunistic evidence.

The general scheme of the Argentinian typical Late-Cenozoic sequence as represented in the Buenos Aires Province, and as here understood, is given in Table 6 :

**TEXT BOUND INTO  
THE SPINE**



.7. SYSTEMATICS

In this chapter I shall describe the fossil taxa of Sigmodontine rodents which constitute the evidential framework of this paper. However, the larger part of this chapter will deal with a revisionary discussion of the related living genera and species, as it was necessary to undertake a detailed study of the living forms in order to assess taxonomic conclusions about the fossil material. Moreover, I shall begin the treatment of the fossil forms with an initial brief discussion of the corresponding tribes, and thereby, I shall try to substantiate my general conception of the classification of the Sigmodontinae, as summarized in Table 2 (page ).

I must assert from the outset that the systematics of the Sigmodontinae is still at a very incomplete stage. For the overwhelming majority of the taxa of this subfamily, there is no information available at all about their ecology, biochemistry or comparative cytology or physiology. The knowledge of their morphological characteristics is also very incomplete for most of the organ-systems, and the variability of the morphological features used in practical taxonomy has not been given adequate attention. Even the geographical distribution of most of the species is only fragmentary known. On this frail groundwork it is impossible to surpass the level of a first approximation in the search of systematic relationships, and the reader must be aware that this is the intention of my attempt here.

Moreover, the species concept so far used when dealing with the South American cricetids, was certainly for the vast majority of the cases the morphotypic species concept (Reig, 1968b). The concept of species I use here is the morphological

one, understood as an approach, based on merely morphological evidence, to the biological species concept, which with the available evidence can only be taken as a framework of theoretical reference.

7.1. TRIBE ORYZOMYINI, Vorontzov, 1959.

After the early work of Thomas (1906, 1917) it became evident that the genera Oryzomys, Thomasomys and Rhipidomys are closely related as regards other genera of cricetids of the New World. These three genera, which comprise more of one third of all the species of the subfamily Sigmodontinae, are the basis of the concept of the "Oryzomine (sic) genera of rodents" of Tate (1932g), in which he included other actually or supposedly related genera as Nyctomys, Neacomys, Rhagomys, Phaenomys, Zygodontomys, Chilomys and Scolomys, besides a number of taxa that are now placed under Oryzomys or Thomasomys (some of them with subgeneric recognition). The allocation of Zygodontomys hereby was a matter of discussion which has not been completely settled so far. Moreover, Nectomys was later included as a relative of Oryzomys.

HersHKovitz (1944, 1960, 1962) proposed to split this group of genera into two assemblages, namely the Oryzomyine group (including Oryzomys, the recently extinct West Indian Megalomys, Neacomys, Scolomys and Nectomys), and a Thomasomyine group (including Thomasomys, Phaenomys, Rhipidomys and the Central American Nyctomys and Otonyctomys. Rhagomys was not placed by HersHKovitz in any of the two groups though it was considered by Thomas (1917) as a member of his "Oryzomys-Oecomys series". Vorontzov (1959) proposed the name of the tribe Oryzomyini as here understood, lumping under a single formal taxon concept the Oryzomyine group and the Thomasomyine group of HersHKovitz. However, Hooper and Musser (1964) maintained HersHKovitz's subdivision of the Oryzomyini into a Oryzomyine group and a Thomasomyine group, with some minor changes, as a result of their studies on the morphology of the

penis.

Actually, I found that the thomasomyines and the oryzomyines are closely related in cranial and dental morphology, and the data afforded by Hooper and Musser do not provide a clear-cut indication of a distinction of the two groups in phalic morphology. Moreover, according to Hershkovitz, the main distinction between them would center on the characters of the palate, which is long in his oryzomyine group, and short in his thomasomyine group. Otherwise, members of the two groups are unique in having a primitive type of molar teeth (Fig. 6) with fully persistent mesolophs and mesolophids, brachyodont and clearly cuspidated crowns and a crested or bi-level crown surface. In fact, they are set apart by Hershkovitz (1962) as a major subdivision of the whole group of the South American cricetids: an older sylvan stock opposed to the remaining more progressive, "pastoral" groups. It must be pointed out that the difference in palatal morphology accounted by this author are no greater than those found among some genera of the Akodontini usually recognized as closely related; and even among subgenera of Akodon (see below). Therefore, I prefer to treat the oryzomyine and thomasomyine groups of Hershkovitz as a single taxonomic group of tribal rank, as proposed by Vorontzov.

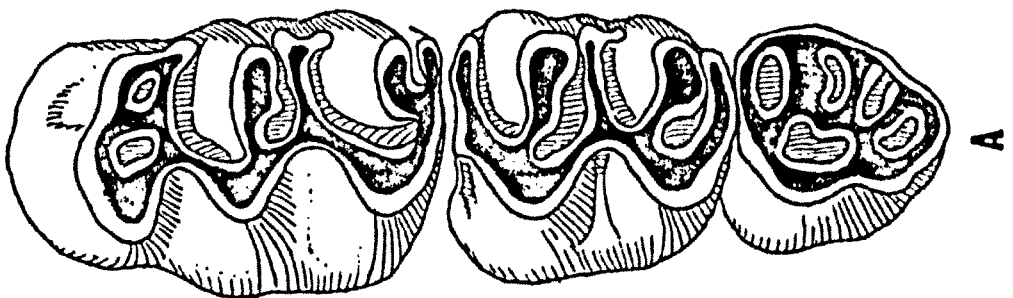
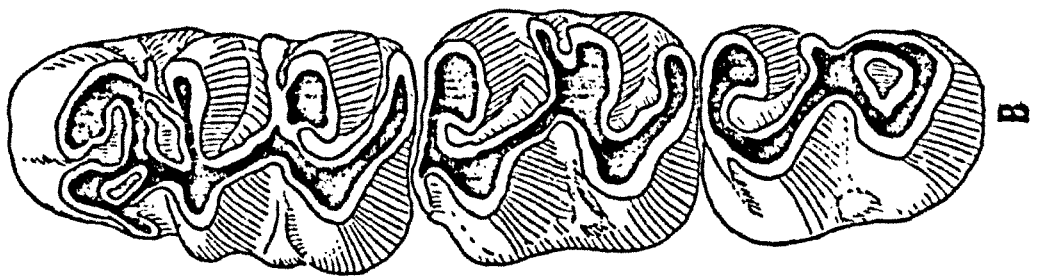
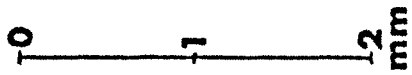
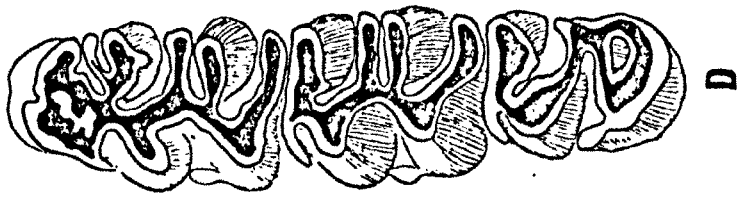
As regards the extension of the taxon-concept of the Oryzomyini, I include in it the genera Oryzomys, Thomasomys, Rhipidomys, Neacomys, Nectomys, Phaenomys, Chilomys and Scolomys of mainly South American distribution, plus the endemic genera of Central America Nyctomys and Octonyctomys, and the extinct West Indian Megalomys. Some other genera placed elsewhere in this classification have been postulated as more closely linked to Oryzomys than to the genera of the tribes where they

Fig. 6. Occlusal view of upper and lower molars of representatives of the Oryzomyini.

A, Left upper molars, and B, left lower molars of Oryzomys angouva Fischer. Female individual, BMNH 4.1.5.16. Sapucay, Paraguay.

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.



are here allocated, and one genus placed here as incertae sedis was supposed to be closely related to Oryzomys. This is the case of Holochilus, Zygodontomys and Rhagomys. Following Hershkovitz (1955, 1962), I place Holochilus within the Sigmodontini, and Zygodontomys within the Phyllotini. In adopting this issue, I am not giving my definite conclusion. In fact, I am not completely convinced that Zygodontomys is a phyllotine, though I believe that the evidence is stronger, in cranial and dentary morphology, to maintain that Holochilus is closely allied to Sigmodon. Zygodontomys, as Calomys, are morphologically intermediate forms between the phyllotines and the Akodontines. In any case, the available evidence is not conclusive as regards a definite allocation of both Holochilus and Zygodontomys, and other kind of information, viz. serological tests of affinity, would be necessary to settle their final tribal membership. Until this information is available, I prefer not to change the results of the careful revisions of Hershkovitz.

Scolomys is here only tentatively kept in the Oryzomyini. Though it resembles Neacomys in external characters, its cranial and dental characters are peculiar, so much that I was tempted to place it as Sigmodontinae incertae sedis. I did not hesitate, however, in withdrawing Rhagomys from the Oryzomyini and placing it as Sigmodontinae incertae sedis. Rhagomys is very peculiar in molar structure, and in some skull characters. The incisive foramina are tiny, as they are in some cricetodontines. This resemblance to the Cricetodontinae is also suggested by the molar teeth, which are extremely primitive by cricetid standards in being very brachyodont, almost exclusively bunodont with a merely incipient development of transverse and longitudinal ridges. Unfortunately, this

genus is still very poorly known. All the available material consists of the type specimen. the skull of which is partially broken, and another specimen also having a damaged skull and which, in addition, is of dubious geographic origin.

As regards the intension of the taxon-concept of the Oryzomyini, its assessment can only be approximatively reached. A definition of the Oryzomys group s.s. was given by Hershkovitz on two occasions (Hershkovitz, 1944, 1960). These definitions, or better, these assessments of the character-states of the Oryzomyine group, were mostly based on his revisions of the genus Nectomys and of the subgenus Oecomys of Oryzomys. Oryzomys is a highly diverse genus, and the species of its subgenus Oecomys are only a minor part of this diversity. All the remaining species of Oryzomys and the whole of the genera Thomasomys and Rhipidomys are badly in need of revision. And this means the vast majority of the taxa of the Oryzomyini. Therefore, an adequate understanding of the intension of the concept of the Oryzomyini would only be approached after these revisions are performed. A provisionsal, and synthetic definition of the Oryzomyini is provided here:

"Sigmodontine cridetids with a digestive system of a mostly omnivorous and insectivorous type, without specializations for plant feeding. Molar teeth typically brachyodont, never distinctly hypsodont, with main cusps relatively low and persistent with wear. Molar crown surface crested or terraced, never plane in unworn or moderately worn teeth. Main cusps of each side of upper and lower molars symmetrically opposed, not alternating in position. Loph and lophids well marked, but usually low and narrow, never laminated and rarely involuted. Mesoloph and mesolophid fully developed, usually united with mesostyle and mesostylid. Metaloph well developed, and usually



linked to the posteroloph; a posteroflexus constantly present in moderately worn teeth, or at least present as a posterofossetus. Procingulum well developed and complex, biconulate. Procingulum of  $M^1$  with well marked anteromedian flexus and deeply infolded anteroloph. Procingulum of the  $M_1$  with well marked anteromedian flexid, anterolophid and usually proto-stylid. Paralophules and entolophulids usually present. Enterolophs, enterostyles, ectolophids and ectostylids frequently present. Third upper and lower molar not reduced, usually maintaining a complicated enamel pattern. Incisive foramina well developed, but usually not passing backwards beyond the level of the first molars. Zygomatic plate normally short and high, comparatively slender, with a straight anterior border."

As emphasised by Hershkovitz (1962) the Oryzomyini (his Thomasomyine plus Oryzomyine groups) are mostly sylvan, as opposed to the remaining mostly "pastoral" South American cricetids. In fact, this distinction is only valid in gross terms. It is true that most of the taxa of the Oryzomyini are inhabitants of broad-leaf forests of tropical and subtropical South America, but exceptions are not rare. For instance, several species of Oryzomys invaded savannas and grazing prairies, where they can be found together with species of akodontine or phyllotine genera. Other species of Oryzomys succeeded in living in high altitude paramos, above the level of the tropical mountain forests, and the same happened with some species of Thomasomys. One genus, Nectomys, invaded the semiaquatic niche and occurs close to lakes, swamps and the banks of rivers of wooded areas, but also lives in open lands. These departures from the probably original forest habitats exemplified in the living fauna, are likely to have played a primary role in the evolution of the other tribes, most of

-which probably originated in oryzomyines that shifted from their original habitats.

In fact, there are reasons to believe that the Oryzomyini represent the most primitive Sigmodontinae. They show a primitive molar pattern closely comparable to that of some Oligocene and Early Miocene Cricetodontinae. In other aspects of their anatomy, they are also very generalized muroids (see Vorontzov, 1967). But the origin of the Oryzomyini, as I shall discuss later, is still obscure.

Our fossil material is extremely poor in representatives of this tribe. In fact, specimens of only one individual, referred to the genus Nectomys, belong here among the sizable collection from the Plio-Pleistocene of the Buenos Aires province which I studied.

7.1.1. GENUS NECTOMYS, PETERS

The Neotropical water rats of the genus Nectomys are probably the most advanced and specialized of the living Oryzomyini. They are very large by cricetid standards, and they are characterized by their large webbed hind feet, their long tail and short ears, and their relatively hypsodont molars. They live in most of South America from the parallel 30° northwards, and they also occur in Central America up to northern Nicaragua. Ellerman (1941) lists thirteen different nominal species, described by six different authors. The genus was revised by Hershkovitz (1944, 1948), and this large list of nominal species has been arranged by him into two polytypic species : N. squamipes Brants and N. alfari Allen.

Genus Nectomys, Peters

- 1861, Nectomys, Peters; Abh. k. Akad. Wiss. Berlin, 1860: 151.
- 1867, Holochilus, Fitzinger; Sitz. math.-nat. Klasse k. Akad. Wiss. Wien, 56 : 89 (in part).
- 1872, Potamys, Liais; Climates, géol., faune et géograph. botanique du Brasil, Paris. : 505.
- 1873, Hesperomys, Hensel; Abh. k. Akad. Wiss. Berlin, 1872 : 28 (in part).
- 1896, Holochilus, Thomas; Proc. Zool. Soc. London, : 1020.
- 1897, Sigmodontomys, Allen; Bull. Amer. Mus. Nat. Hist. 9 : 38 (valid as a subgenus).
- 1912, Oryzomys, Miller; Bull. U. S. Nat. Mus., 79 : 171 (in part).
- 1917, Oryzomys, Elliot; A check list of the Mammals of North America Continent, etc. Publ. Amer. Mus. Nat. Hist. : 58 (in part).

Type species:

Mus squamipes Brants, as designated by Miller (Bull. U. S. Nat. Mus. 79 : 180; 1912).

Distribution:

Tropical and subtropical regions of South and

Central America, from north Nicaragua to central Bolivia by the east; north and south of Venezuela and the Guiana region; the Amazonian basin; the upper Parana basin, Paraguay and Misiones (Argentina), and the southeast of Brazil to the parallel 30°.

Cranial and dental character-states:

Skull large, heavily built, somewhat elongated, specially in the frontal and post-frontal region. Rostrum thick and relatively deep. Supraorbital borders strong and ridged, divergent posteriorward, extending over parietals as distinct temporal ridges. Zygomata rather slender, fairly expanded behind and convergent anteriorward. Nasals shorter than frontals, narrowing backward from their anterior part, and usually extending beyond the fronto-premaxillary suture. Fronto-parietal suture forming an oblique angle at midline. Interparietal well developed. Zygomatic plate comparatively strong, higher than wide, its antero-posterior width less than combined length of  $M^1$  and  $M^2$ ; its anterior border straight and vertical, and its upper anterior corner rounded or slightly pointed. Antorbital foramen directed forward and upward, visible when viewed from above. Palate broad and long, extending backwards well beyond the posterior borders of  $M^3$ . Surface of the palate sharply grooved from the incisive foramina posteriorward, with posterolateral portions pitted and excavated as shallow fossae. Posterior border of the palate rather wide and concave. Incisive foramina relatively short, not reaching behind the level of the anterior borders of the  $M^1$ . Bullae strongly built, only moderately inflated. Mesopterygoid fossa broad; parapterygoid fossae relatively shallow. Lower jaw heavily built. Horizontal ramus very deep anteriorly, but its lower border very oblique and converging

. backwards towards the alveolar line. Lower and upper masseteric crests fairly well marked, converging anteriorly to a point between the anterior border and the middle of the  $M_1$ . Symphysis low, the anterior median point of the lower diastema well below the level of the alveolar row. Coronoid process high, with an anterior border sloping obliquely backwards and upwards from the middle of the  $M_2$ . Capsular projection of the incisor base distinct, but not forming a strong process. Sigmoid notch high and shallow. Condylod process higher than coronoid process, and projecting backwards beyond the level of the angular process.

Upper incisors opsithodont, robust, ungrooved. Molars broad and robust, with moderate coronal hypsodonty, but with low crests. Molar surface bi-level, tending to be plane with advanced wear. Mesoloph and mesolophid well developed, lower than paracone and entoconid in moderately worn teeth, free or united to mesostyle or mesostylid, respectively. Mesostyle very close to the paracone; mesostylid very close to the entoconid. Mesoflexus and posteroflexus rapidly transformed into mesofossetus and posterofossetus, entoflexid and metaflexid into, entofossetid and metafossetid, with wear. Paraflexus and metaflexus, mesoflexid and posteroflexid, wide and oblique in position, transformed into enamel islands in adult dentitions. Hypoflexus and protoflexus of similar development in  $M^1$ , but protoflexus usually absent in  $M^2$  and  $M^3$ . Procingulum of  $M^1$  broad, with anteromedian flexus only present in very young dentitions, transformed into a wide anteromedian fossetus after early wear; anteroloph wide and united to parastyle; anteroflexus only distinct as a narrow fold in unworn dentitions. Protoflexid moderately developed in  $M_1$ , frequently obsolete in  $M_2$  and  $M_3$ . Procingulum of  $M_1$  with anteromedian

flexid only present in unworn teeth, transformed into a fossetid with wear; anteroflexid deep in young dentitions, rapidly transformed into an anterofossetid with wear. Anterolabial cingulum well developed in  $M_1$ , less so in  $M_2$  and  $M_3$ . Third upper and lower molar usually only moderately reduced in size, and repeating with some simplifications the pattern of the second molars.

Included species:

squamipes and alfari (for diagnosis and subspecies, see Hershkovitz, 1944.)

Nectomys cf. squamipes Brants

MLP 62.VII.27.95.d. : Left and right  $M^1$ ; left  $M^2$ ; left  $M_1$  and  $M_2$ . All of them isolated, and belonging to a very young individual (Fig. 7B, D.). Found in association with specimens of Reithrodon auritus (see page 370), Akodon cf. cursor (see page 247) and other rodents, in a bone conglomerate probably representing a set of fossil owl pellets. The conglomerate was extracted from a rocky block which had fallen down from the Atlantic cliffs 5 Km north of Colonia Camet (about 15 Km north of the city of Mar del Plata), Buenos Aires Province, Argentina. The cliffs at this point expose sediments of the Miramar Formation, and this geological provenance can be assumed for the fossils found in the fallen block.

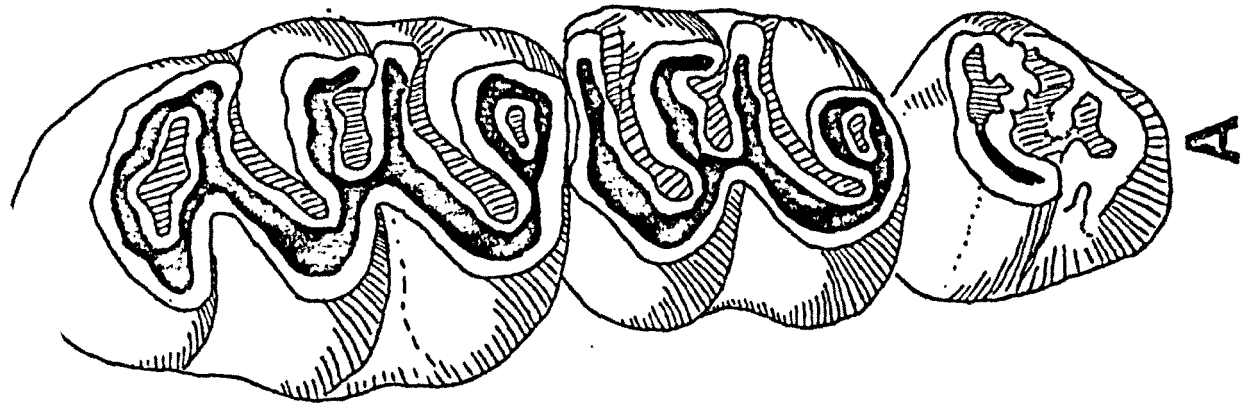
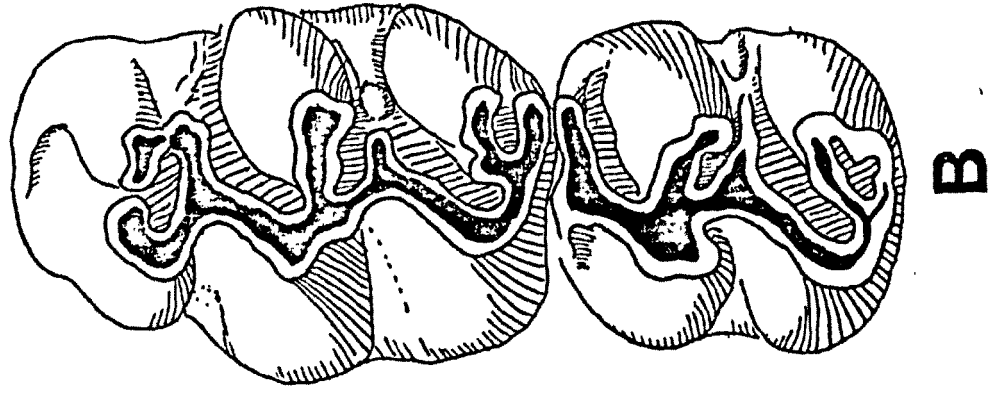
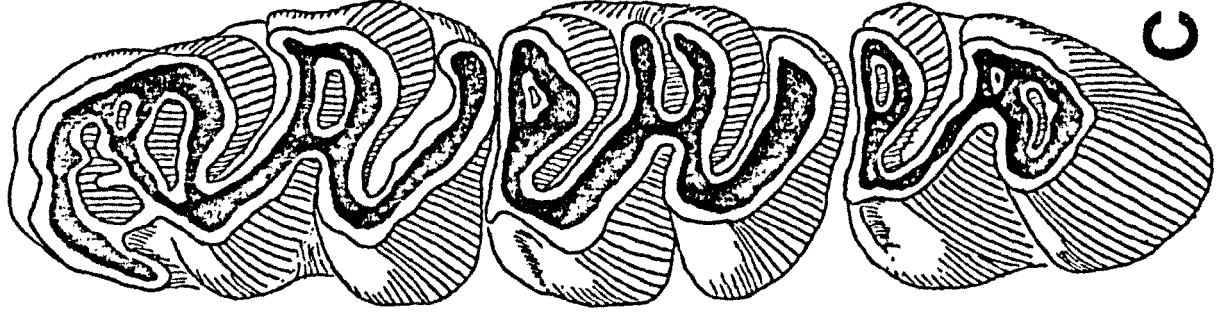
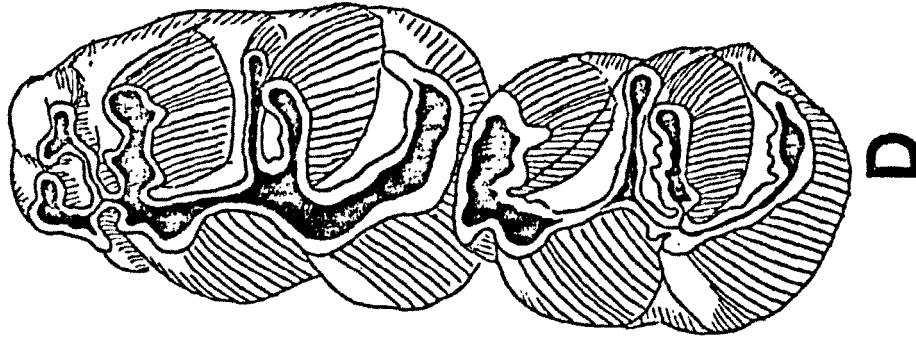
Comments:

The isolated teeth illustrated in Fig. 6B, D, belong obviously to a single very young individual, with recently erupted molar dentition. In the collection of the British Museum of Natural History I did not find specimens of living Nectomys of an equivalent young age. However, the specimen BMNH 3.9.4.53 (Fig. 7A; C), and the illustrations of young

Fig. 7. Occlusal aspect of upper and lower molar teeth of living and fossil Nectomys.

A, Left upper and left lower molars rows of Nectomys squamipes, probably N. s. aquaticus Lund. Fairly young female, BMNH. 3.9.4.53. Eugeneiro Reeve, Espiritu Santo, Brazil.

B, Left M<sup>1</sup> and M<sup>2</sup>, and D, left M<sub>1</sub> and M<sub>2</sub> of Nectomys cf. squamipes Brants, MLP. 62.VII.27.95.d. Miramar Formation, (Ensenadan stage, Middle Pleistocene), 5 Km. north of Colonia Camet, Mar del Plata, Buenos Aires Province, Argentina.





dentitions in the paper by Hershkovitz (1944, Fig. 4, 5) allow comparison with our material. There is no reasonable doubt that the fossil specimens belong to Nectomys, as they agree with all the character states of the molar teeth of this genus, as described above. In size, they are only comparable to N. squamipes, the different forms of the other living species, N. alfari, being much smaller. The available material does not allow one to believe that the fossil specimens could belong to an extinct species different from squamipes. But this possibility cannot be completely ruled out, and it could only be ascertained by the further discovery of additional specimens showing other characters. A comparison with the different subspecies of N. squamipes recognized by Hershkovitz (1944, 1948) and Cabrera (1961) is out of place here, in view of the scarcity and juvenile character of the fossil specimens. Suffice it now to establish the similarity of the latter with the living N. squamipes, and to assert that it is highly probable that its remains belong to a fossil form of this species.

But the striking point about these fossil specimens lies that they demonstrate a much more southern distribution of Nectomys in the Pleistocene than in Recent times. The locality where they have been found is in the close vicinity of the place where the 38° parallel passes, and the southernmost recorded locality of the living squamipes is Porto Alegre, Brasil (Hershkovitz, 1944), which is immediately south of parallel 30°. In a straight line, Camet is 1050 Km southwest of Porto Alegre. In view of the tropical and subtropical nature of the present distribution of Nectomys, the occurrence of a representative of this genus in the Middle Pleistocene of the southeast of Buenos Aires Province can be taken as an

indication of a more subtropical climate in the Pampean region in Ensenadan times. The occurrence of Akodon cf. cursor in association with the fossil Nectomys squamipes, which I shall mention below (see page 247) is an additional support for this inference, as this species of Akodon is also limited to a more northern and subtropical distribution in the living fauna. For additional reports of fossil Nectomys, see the note on page 379.

Specimen Variate	<u>Nectomys squamipes</u> , MLP 62.VII.27.95.(d) Miramar Ftion, Camet, North of Mar del Plata, Buenos Aires prov., Argent.	<u>Nectomys squamipes</u> , BMNH 3-9-4.53. Female Espiritu Santo, Brazil
Length of the M <sup>1</sup> .	3.16	2.98
Width of the M <sup>1</sup> .	2.23	2.10
Length of the M <sup>2</sup> .	2.17	2.11
Width of the M <sup>2</sup> .	1.89	1.75
Length of the M <sub>1</sub>	2.73	2.69
Width of the M <sub>1</sub>	1.74	1.79
Length of the M <sub>2</sub>	2.29	1.98
Width of the M <sub>2</sub>	1.74	1.70

TABLE 7. Measurements (in mm) of fossil and living Nectomys squamipes

.7.2. TRIBE AKODONTINI, Vorontzov

The concept of akodont rodents as a group of taxa of South American cricetids arose from the studies of Thomas. Both in intension and in extension, however, it is still a rather vague taxonomic concept. In 1916, Thomas wrote on the taxonomic status of a group of related species, which he distributed in seven different genera, namely Zygodontomys, Akodon, Thalpomys, Thaptomys, Bolomys, Chroeomys and Abrothrix. Subsequently, he added to the same group the genera Hypsimys and Deltamys. He recognized that other supraspecific taxa, as Blarinomys, Geoxus, Notiomys, Chelemys, Microxus, Oxymycterus and Lenoxus were also related to the above group. Osgood (1925) was probably the first author to revise Thomas' akodont genera, when he proposed to lump Notiomys, Chelemys and Geoxus under a single genus Notiomys, a contention which was criticized by Thomas (1927b). The monotypic genus Podoxymys was later added to the akodont group by Anthony (1939). A preliminary revision of the whole group which introduced the designation of "akodont rodents", is due to Tate (1932h). Tate's work, as his other revision of South American rodents, is a useful and careful historical and bibliographical review of the involved taxa, more than a revision based on a study of the actual collections but unfortunately it did not result in a clarification of the intension of the concept of the group. He recognized full generic rank to most of Thomas' supraspecific groups but he followed Osgood as regards Notiomys, and he introduces the innovation of withdrawing from the akodont group Zygodontomys, which he placed (1932g) in the oryzomine (sic) group.

The next comprehensive study of the whole group is due to Gyldenstolpe (1932), who did not treat the corresponding genera as a separate group, but involves them in his comprehensive concept of South American "sigmodont rodents", which is equivalent to my subfamily Sigmodontinae. Gyldenstolpe recognized full generic status to all the taxa of akodont rodents created by Thomas, and he contributed to afford rather complete definition of all of them. One point to emphasize here is that Gyldenstolpe agreed with Thomas in postulating full generic rank to Notiomys, Geoxus and Chelemys.

A thorough reappraisal of Thomas' akodont genera came with Ellerman (1941). He claimed that most of the genera created by Thomas in 1916, and the later Hypsimys and Deltamys may best be treated as subgenera of Akodon. He excluded Zygodontomys in this lumping which he regards as a full genus related to Akodon. He, however, retained Microxus, Oxymycterus, Lenoxus and Notiomys as full genera, the latter, according to Osgood, including Geoxus and Chelemys. Ellerman's balanced judgement and overall experience influenced the work of subsequent authors, and his concept of the akodont group of genera is essentially followed by Cabrera (1961).

Vorontzov (1959) coined the name Akodontini, for a tribe containing Akodon (as understood by Ellerman) Zygodontomys, Microxus, Podoxymys, Lenoxus, Oxymycterus, Blarinomys and Notiomys. As regards Zygodontomys, Hershkovitz (1962) did not hesitate in withdrawing it thoroughly from any relationships with the akodonts, and placed it in his phyllotine group, close to Calomys.

Hooper and Musser (1964) in their discussion of the bearing of phallic morphology in the interrelationships between cricetids and allied genera, arrived at the conclusion

That Oxymycterus is distinct enough in the characters of the glans penis as to support the recognition of an oxymycterine group distinct from the akodont group, although allied to it. Moreover, they stated that Notiomys stands as apart of Akodon as does Oxymycterus, that Zygodontomys is annectent between akodonts and oryzomyines and not closer to the phyllotines as claimed by Hershkovitz and that Calomys, and especially Eligmodontia, are to be placed near Akodon. Many of the conclusions of these authors have been seriously objected to by Hershkovitz (1966) on methodological grounds. He says that phallic evidence coming from a too narrow sample of taxa, each of them represented by a few individuals, should not be the basis for introducing major changes in a picture of intergeneric relationships which is based on a complex of character states from different organ systems and a large number of genera. Hershkovitz, however, followed Hooper and Musser in splitting the oxymycterines, (including Oxymycterus, Podoxymys, Lenoxus and Abrothrix, Microxus he considers to be a synonym of Abrothrix) from the akodont group and he gives a precise morphological definition of the oxymycterine group. A further basis for the splitting of Oxymycterus from the akodonts seems to be provided by its specializations on the stomach and intestines for an insectivorous diet, as illustrated in the detailed studies of Vorontzov (1967), (see also Tullberg, 1899; Echave Llanos and Vilches, 1964). However, the anatomy of the digestive system is only known in a few genera of this group, and no definite taxonomic conclusion can be allowed from fragmentary evidence.

To complete the picture of the status of the Akodontini, I must mention that Massoia and Fornes (1967) have

proposed a new genus, Cabreramys for a group of species of Akodon which, in a sense, they allege to be transitional between akodontine and phyllotine cricetids,

The Akodontini are therefore one of the most obscure groups of South American rodents. There is agreement neither as to its extension (v.i. Zygodontomys), to the rank to attribute to their different supraspecific groupings, nor even as to its unity as a suprageneric group. This situation is obviously due to the lack of extensive comparative studies and to the failure of the various authors to draw conclusions from the partial evidence.

Although I am convinced that we are far from the goal of achieving an acceptable knowledge of this group, I hope that certain conclusions at which I have arrived in studying some of the akodont genera can serve to improve our knowledge of this complex of sigmodontine rodents.

First are the results of chromosomes studies undertaken by the present author and his associates. They demonstrate that species of Akodon, Bolomys, Abrothrix and Oxymycterus (Fig. 8) share an overall resemblance in their karyotype make-up (Bianchi, Reig, Molina and Dulout, 1972; and Reig and Spotorno, unpublished data for Oxymycterus), but that Zygodontomys stands quite apart from the former (Kiblisky, Lobig and Reig, 1970). The first group is characterized by a karyotype of no more than 56, mostly telocentric chromosomes. The latter is exceptional for mammals, but close to the Oryzomyini (Oryzomyini (Kiblisky, 1971), in having a karyotype of 84, mostly subtelocentric chromosomes. This result is strongly suggestive of the unity of oxymycterine and akodontine genera in a single group. (Oxymycterus and Akodon-olivaceous have very similar chromosome complements), and

of the splitting of Zygodontomys from the Akodontini. The chromosomic evidence, however, is not so conclusive as to place Zygodontomys close to the Oryzomyini as also suggested by the results of Hooper and Musser, and I prefer not to innovate here and to keep it within the Phyllotini, as proposed by Hershkovitz (1962).

Second are the results of the systematic survey of a great part of the specimens of Akodontini in the British Museum (Natural History) and in the collections of several North and South American museums. These studies reinforce many of the ideas of Ellerman as regards subgeneric recognition to a great deal of the supraspecific taxa treated by Thomas as full genera. However, I cannot agree with all the results of Ellerman. The genera of Akodontini here recognized are those listed in Table II. The reasons for the rearrangement are given under the corresponding genera, in the following taxonomic part. However, I shall not discuss here all the genera, just because only a part of them are represented in the material. But the only point not discussed below which must be explained is connected with Notiomys and its relatives. From my studies of the types and series of specimens referred to this group in the British Museum, I concluded that Osgood went too far as a lumpers, and that not three, as claimed by Thomas, but two genera must be distinguished here. These are Notiomys (including Geoxus) and Chelemys. The differences between both are as great as the differences between Akodon and Oxymycterus, and I did not find any evidence of an intergrading series of forms between the two, if the skull and teeth are carefully studied.

As it is often the case, the assessment of the extension



Fig. 8. Karyotype of Oxymycterus rufus, male individual from "Baliza San Andrés", Partido de General Pueyrredón, Buenos Aires Province, Argentina. From bone marrow. Giemsa stain.

AA AA AA AA AA AA AA

AA AA AA AA AA AA AA

AA AA AA AA AA AA

AA AA AA AA AA AA AA

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.of the concept of the tribe Akodontini precedes the achievement of a clear cut intensional definition of this taxon. To arrive at this definition it would be necessary to complete a revision of the whole group and of other related groups. However, one can approach such a definition for a few characters: "Sigmodontine cricetids of small to medium size, with omnivorous to insectivorous digestive system, usually without specializations for plant feeding. Molar teeth subhypodont to mesodont, crested, terraced or secondarily plane; mesoloph and mesolophid reduced or vestigial when present, often fully or partially coalesced with paraloph or entolophid and only shown as terminal remnants usually united with mesostyle or mesostylid. Posteroloph coalesced with metaloph and posteroflexus usually obsolete. Zygomatic plate little to moderately developed, never very high and strongly projecting before the antorbital bridge. Incisive foramina usually reaching backwards beyond the anterior plane of the  $M^1$ . Palate broad, short to moderately long."

The Akodontini are indeed more advanced than Oryzomyini, and they are quite probably a group directly derived from the latter. Some of them became rather specialized for an insectivorous diet, and they did not invade specially the herbivorous niches, which were particularly exploited by their probable derivatives, the Phyllotini. Although most of them are inhabitants of open land and they are found only occasionally in forest habitats, some of their genera, specially Blarinomys, Notiomys and Chelemys, exploited the subterranean-insectivore niche, and might be considered as the South American counterparts of the moles Shrews.

7.2.1. Genus Bolomys, Thomas.

There are several species currently placed in, or originally described as Akodon which have been thought of as more closely related to Zygodontomys. Some other species of the same group have been lately transferred to an alleged new genus.

The first move in this direction was probably Tate's (1932g) action in referring the South Brazilian, "Hesperomys" arviculoides (Wagner), a species currently classified as a typical Akodon, to the genus Zygodontomys, to which he also assigned, as previously suggested by Thomas (1902), Mus lasiurus Lund and "Hesperomys" brachyurus Wagner, also from Brazil.

HersHKovitz (1962), in a provisional revision of Zygodontomys, grouped several Brazilian and Paraguayan nominal forms under Z. lasiurus with tentative subspecies recognition to some of them, as Z.1. lasiurus (Lund), Z.1. fuxinus (Thomas), Z.1. pixuna Moojen, Z.1. brachiurus (Wagner), Z.1?. languarum (Thomas) and Z.1?. tapirapoarus J.A. Allen. This group of species is called by them "Southern Group" of Zygodontomys, as apposed to a "Northern Group" represented by the typical "Z. brevicauda Akodon arviculoides is maintained in Akodon. However, HersHKovitz does not seem to be quite certain about the systematic position of this group of species when he states that "Zygodontomys is an annectent form between phyllotine and akodont rodents, (:202)", and before: "No sharp line can be drawn between Zygodontomys and the nominal species Akodon varius Thomas, A. arviculoids Wagner and A.obscurus Waterhouse", (:201). Following his own data, it is clear that the more "Akodon like" forms of Zygodontomys are those he put in his "Southern Group". As regards "A. obscurus, in studying

specimens assigned to this species from S.E. Buenos Aires Province, I had the occasion to compare them with specimens of Z. lasiurus pixuna, and I found so many resemblances in skull and dental morphology, that I did not hesitate in placing obscurus in Zygodontomys (Reig, 1964).

In fact, and as I shall demonstrate later, most of these taxonomic statements came from a misinterpretation of the limits of Zygodontomys on one hand, and Akodon on the other. Actually, the involved species does not belong to any of them.

This was partially, but incorrectly grasped by Massoia and Fornes (1967), when they erected the then new genus Cabreramys with "Akodon" obscurus Waterhouse as the type-species, and including Akodon benefactus Thomas and Akodon languarum Thomas. These two species had been recognized by Thomas (1898, 1918) as closely related to A. obscurus, as it was A. dolores (Thomas 1916), a species not discussed by Massoia and Fornes. These authors failed to recognize that if obscurus, benefactus and languarum are to be grouped in a genus different from Akodon, and Zygodontomys, the extension of this distinct genus should be broadened to include the whole "Southern Group" of Hershkovitz' Zygodontomys as well as other Brazilian and Andean forms. They also failed to realize that it was not necessary to propose a new name for such a genus, as in the same group should also be included the Peruvian species "Akodon" amoenus, which Thomas (1916) made the type-species of Bolomys.

Apart from the type-species, Thomas erected Bolomys to include also A. albiventer and A. berlepschi also from the Andean highlands. Moreover, in 1918 he created the species Akodon lactens from the mountains of N.W. Argentina. He later referred lactens to Bolomys together with negrito, a form from the highlands of Catamarca (Thomas, 1926a). The possibility

'of a close connection between Bolomys and forms referred by Massoia and Fornes to Cabreramys, was actually anticipated by Thomas himself when, commenting on specimens of "Akodon" lenguarum found in Carapari, Bolivia, he held that the latter is linked with A. obscurus and A. benefactus by its proodont incisors, adding: "The buffy-washed A. lectens and orbis also have this character, and no doubt belong to the same group" (1925: 579). Akodon orbis had been created by him in 1919, as a form allied to lacteus.

Bolomys remained, however, as a dubious taxon and, in fact, it was a compound genus since the beginning. It is now easy to demonstrate that albiventer and its allied (and probably conspecific, see Thomas, 1902) berlepschi do not belong here. The composite nature of Bolomys was broadened by Tate (1932h). Tate included in Bolomys, apart from the species assigned to it by Thomas, four other species of Andean akodonts: A. andinus Philippi, gossei Thomas, orbis Thomas and jucundus Thomas. Osgood (1943) was struck by the heterogeneity of the whole group. He remarked that the skull of andinus (including gossei and jucundus) showed similarities to that of albiventer, "but it is widely distinguishable from that of lactens." He adds that andinus (and impliedly albiventer and berlepschi) is better retained in Akodon, and he concluded that Bolomys must be held for redefinition "as to its limits and perhaps also as to its validity" (1943: 179).

I had the opportunity to examine the type specimens and original material of most of the involved taxa and I have arrived at the following conclusions:

- 1°) Bolomys, as redefined on the basis of its type-species Akodon amoenus, is a good and distinctive genus;
- 2°) Akodon amoenus and Akodon obscurus are closely

related and inseparable at the generic level; therefore, Cabreramys Massoia and Fornes 1967 is a junior synonym of Bolomys Thomas 1916;

3°) Akodon albiventer and A. berlepschi do not belong to Bolomys and they are closely related to Akodon andinus;

4°) A. lactens (including negrito, orbus and leucolimnoeus, see Cabrera, 1957-62) is a well differentiated species of Bolomys.

5°) Hershkovitz "Southern Group" of Zygodontomys, as well as Akodon arviculoides are also to be included under Bolomys.

Thus Bolomys is a broadly distributed and polytypic genus of akodont rodents. Moreover, the fossil material demonstrates that it was already differentiated by Pliocene times and that it had fossil relatives now extinct, (see below).

Due to the composite nature of Thomas' concept of Bolomys, his diagnosis (Thomas, 1916) is now misleading and insufficient. Massoia and Fornes' characterization of Cabreramys is, moreover, rather vague and somewhat contradictory. Therefore, a new amended descriptive account of the characters of the genus is badly needed. In the following formal description I include the formal taxonomy resulting from the discussion, and shall provide a description of the skull and dental characters thereby supporting the identity of Bolomys as a genus.

Genus BOLOMYS, Thomas 1916

1916. BOLOMYS, Thomas, Ann.Mag.Nat.Hist. (8), 18: 339  
(in part).
1932. BOLOMYS, Tate, Amer.Mus.Novit.Nr. 582: 2, 22 (in part).
1941. AKODON (BOLOMYS), Ellerman, The families and genera of  
living rodents, II: 415 (in part).
1961. AKODON (BOLOMYS), Cabrera.
1962. ZYGODONTOMYS, Hershkovitz, Fieldiana,Zool. 46:206  
(in part).
1964. ZYGODONTOMYS, Reig, Publ.Mus.Munic.C.Nat.Trad.Mar del  
Plata 1: (in part).
1965. ZYGODONTOMYS, Reig, Physics, 25: 208.
1967. CABRERAMYS, Massoia and Fornes, Acta.Zool.Lilloana,  
23: 418.

TYPE SPECIES - Akodon amoenus Thomas 1900, by original  
designation.

INCLUDED SPECIES - Bolomys amoenus, lactens, obscurus,  
lasiurus, scagliarum, n.sp. bona-  
partei, n.sp.

KNOWN DISTRIBUTION - Grasslands and scrublands of temper-  
ate South America, from the south of  
the Pampean region in Argentina, north  
into the Chacoan region of Paraguay  
and Bolivia, the savannas of South-  
Eastern Brazil, west into the Andean  
and the caatingas regions of Ceara  
highlands, "Sierras Pampeanas", of Peru,  
Bolivia and Andes and northwestern  
Argentina.

GEOLOGICAL DISTRIBUTION - Upper Pliocene (Montehermosian)  
to Recent.

CRANIAL CHARACTERS - Skull moderately heavily built, with  
a broad brain-case, a short occipital region and a moderately  
or slightly elongated rostrum markedly tapering forwards in  
lateral view. Upper profile of the skull gradually sloping  
forwards from the middle of the parietals. Zygomata moderately  
expanded, convergent anteriorly; widest distance between them  
less than length from posterior border of nasals to anterior



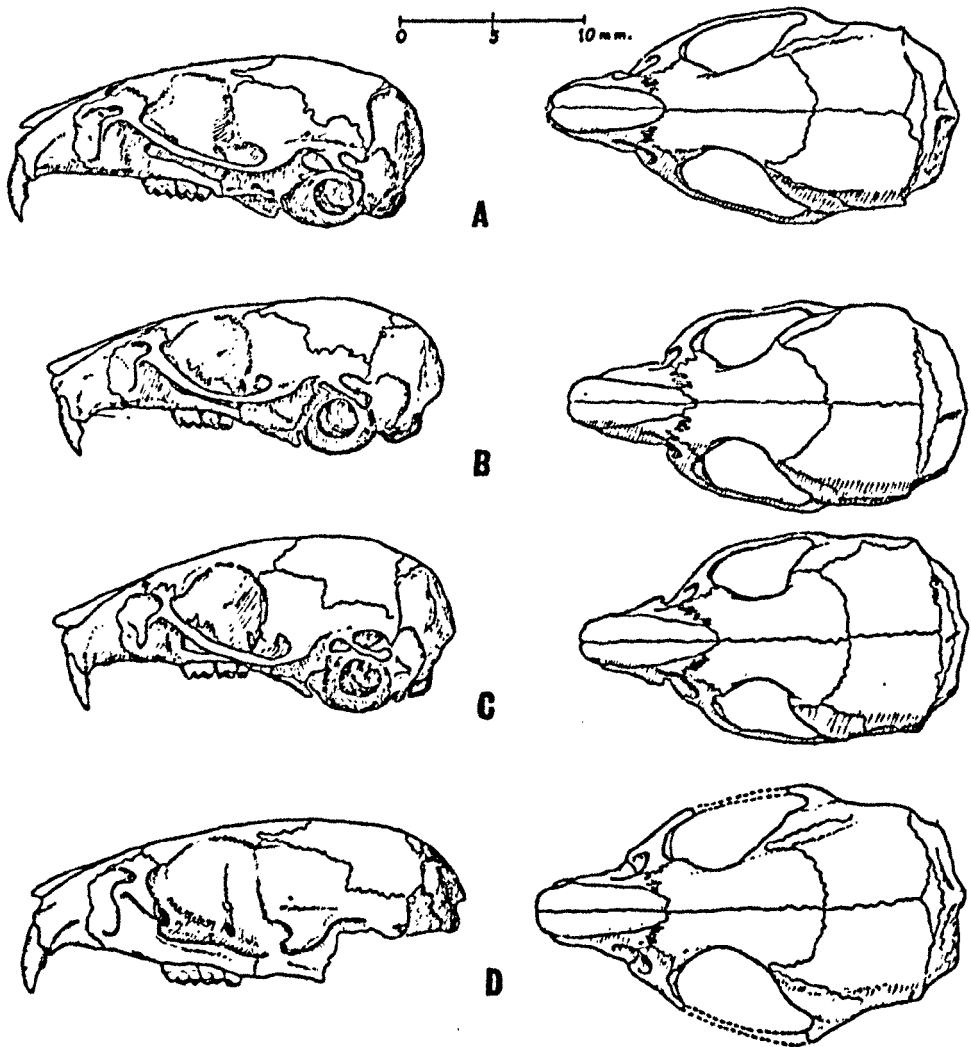
border of interparietal. Nasals shorter than frontals, their anterior borders well posterior to the level of the anterior border of the incisors, and never produced forward to form a trumpet; their posterior border usually not extending beyond the fronto premaxillary suture. Frontals rather long, with a moderately narrow interorbital region. Supraorbital region posterior to the interorbital constriction slightly convex in cross-section, with divergent sides, the borders not beaded but forming slightly marked supraorbital ridges continued by incipient temporal ridges. Fronto-parietal suture crescentic in outline. Parietals short, their length in the midline less than half the length of the frontals, extending anterolaterally by means of elongated spines between frontal and temporal. Interparietal moderately to greatly reduced anteroposteriorly and transversely. Zygomatic plate rather strong, with lateral surface plane; its anterior border descends abruptly and it is usually partially perpendicular to the diastema; its upper corner is rounded. Incisive foramina rather short, shorter than diastema; their posterior border pointed and passing beyond the anterior border of the first molars, but not reaching the level of their protocones. Posterior palatal region moderately long and slightly wide, the median posterior border of palatines slightly behind the posterior plane of the third molars. Distance between inner borders of first molars slightly wider than the length of the first molars. Palatal surface slightly pitted, with shallow and narrow lateral grooves and without a median ridge. Mesopterygoid fossa narrow, its width at the anterior base of the pterygoid processes as wide as the narrow parapterygoid fossae. Bullae moderately small, its anteroposterior length,

less tubes, clearly less than alveolar length of molar rows. Mastoids moderately inflated. Occipital region short, its posterior outline truncated when viewed from lateral aspect. Mandible moderately strong. Symphysis not much upturned, its antero-superior point not reaching the level of the alveolar row. Height of the horizontal ramus at the middle of the  $M_1$  equal or slightly larger than diastema length. Lower masseteric crest smooth, but clearly developed, reaching forwards the level of the anterior border of  $M_1$ , but not going beyond this level. Upper masseteric crest short and moderately developed. Coronoid process well developed, not projected far backwards, its anterior border oblique and moderately upturned. Condylod process high, elongated, slightly projected backwards. Capsular projection of the incisor base well developed, its central point lying behind the middle of the sigmoid notch. Angular process moderately deep and blunt.

DENTAL CHARACTERS : Upper incisors protodont to orthodont, never opisthodont or grooved. Molar rows parallel-sided. Molar mesodont, terraced in moderately worn state, planate with advanced wear, relatively broad and robust, moderately lophodont and involuted.  $M^1$  four-rooted. Upper molars with the lophs almost completely transversal, the individual cusps of each side almost completely opposed, the lingual ones only slightly anterior to the labial ones.  $M^1$  and  $M^2$  usually trilophodont, the latter secondarily bilophodont in worn teeth. Mesoloph usually completely coalesced with paraloph, and metaloph united to posteroloph, so that the posteroflexus is almost completely absent in moderately worn teeth. Paraflexus and meta flexus moderately directed

Fig. 9. Skulls of Akodont rodents. Left row, lateral view,  
right row, dorsal view.

- A. Bolomys anenus. Male. BMNH 1.1.1.12, Sangero,  
Puno, Peru.
- B. Akodon andinus Philippi. Female, type of Akodon  
gossel Thomas, N.M.N.H. 98.3.21.5, Puente del Inca,  
Mendoza, Argentina.
- C. Akodon albiventer Thomas. Male, BMNH 21.11.1.51,  
Sierra de Zenta, Jujuy, Argentina.
- D. Bolomys obscurus Waterhouse, Lectotype, BMNH 55.  
12.24.161, Maldonano, Uruguay.



backwards, hypoflexus and protoflexus slightly directed forwards, but the opposite flexi do not alternate with each other. Enterostyle and enteroloph normally absent. Mesostyle often present in  $M^1$  and  $M^2$  free or united with a short and weak lingual remnant of the mesoloph when it is present.  $M^2$  usually longer than wide.  $M^3$  reduced in size, bilophodont or cylindriform in moderately worn teeth. Procingulum of  $M^1$  simple, transverse or moderately oblique in position, transversely elongated and subelliptical in outline, connected to the protocone through an anteroposteriorly oriented or slightly oblique anterior mure; protostyle and anteroflexus normally absent; anteromedian flexus absent or very slightly indicated. Protoflexus of  $M^2 - M^3$  very weakly developed in moderately worn teeth, absent with further wear. Lower molars with lingual cusps somewhat anterior to the labial ones; metalophid usually transverse, entolophid and posterolophid more oblique in position. Mesolophid remnants and mesostylid usually absent. Ectolophid normally absent in  $M_2$  and  $M_3$ , very rarely present, but never well developed in  $M_1$ . Ectostylid sometimes present in  $M_1$  and  $M_2$ , more rarely in  $M_3$ . In  $M_1$  and  $M_2$  hypoflexid broad and transverse in position, mesoflexid moderately directed obliquely forwards; posteroflexid well developed, rather transverse in position in  $M_1$  and  $M_2$ , absent in moderately worn  $M_3$ , never directed backwards in  $M_2$ .  $M_1$  tetralophodont, with a simple, ovate procingulum defined by usually shallow metaflexid and protoflexid; anteroflexid completely absent, protostylid very rarely, and anteromedian flexid normally absent.  $M_2$  trilophodont, longer than wide, with protoflexid very reduced in scarcely worn teeth, completely absent in moderately worn

state.  $M_3$  about three fourths the length of  $M_2$ , with protoflexid completely obsolete, bilophodont and sigmoid shaped in moderately worn teeth, 8-shaped with more advanced wear.

DISCUSSION - That Akodon albiventer is more closely related to Akodon andinus than to species of Bolomys is obvious from Fig. 9. These two species share in common a broad brain-case, enlarged bullae, nasals and premaxillae produced forward over the incisors; incisors slightly opisthodont, zygomatic plate rather weak and low, nasals as long or slightly longer than frontals, projecting behind the fronto premaxillary suture, wide interorbital region, mandible without a strong capsular projection, to mention the most noticeable features. In all these characters albiventer, as well as andinus are quite distinct from Bolomys as represented by the type species, B. amoenus. In most of these characters, they agree with such atypical Akodon as A. boliviensis, the type-species of the genus (Fig. <sup>12,20</sup> 13). They differ from those of boliviensis and its close relatives only in the enlarged bullae, but these can hardly be a basis for generic distinction, at least at the degree to which the difference is shown. All seems to indicate, therefore, that Thomas was wrong in placing albiventer (and his closely connected allied berlepschi, see Thomas, 1902) in the same genus (Bolomys) with amoenus, andinus, gossei and jucundus (which Osgood, 1943, convincingly took as a single species: andinus). As for the validity of Cabreramys, I could not find any basis to separate Akodon obscurus (the type-species of that alleged new genus by Massoia and Fornes' description) from Akodon amoenus (the

type-species of Bolomys by Thomas' original description) at the generic level. Fig. <sup>9</sup>10 and Fig. 11 allow comparison between the skull and dental morphology of the type and representative specimens of both. A. obscurus agrees with amoenus in such typical and distinctive characters as the procumbent incisors, the short nasals and parietals, the presence of parietal "horns", the retracted anterior nasal border, the tapering of the rostrum, the shortness of the occipital region the strength of the zygomatic plate, the shape of the incisive foramina, the simplification of the molar pattern, the depth of the ramus and the development of the capsular projection of the mandible. Differences which can be found in relative depth of the incisors, backwards extension of the incisive foramina, etc., are certainly less significant and are to be attributed to species distinction. As here redefined, Bolomys appears as a very distinctive genus, easily separable from Akodon and Zygodontomys, two genera with which it has been repeatedly confused. Actually, close resemblances with any of those genera is based in misidentifications, and the three genera become more easily distinguishable as soon as the redefinition of Bolomys allows one to identify various species currently now classified as Akodon and Zygodontomys as belonging to it.

.7.2.1.1. The living species of Bolomys

As here conceived the genus Bolomys comprises several low-land and high-land species of akodont rodents. At first sight, it is clear that there are many more names available for such species than the actual number of species that exist.

A conclusive assessment of the living species of Bolomys will probably only be possible in the future, after a careful revision of all the material available at present, further collecting, and the consideration of other biological and ecological data so far almost completely ignored. It is both possible, and convenient, however, to attempt a preliminary elucidation of the confusing array of the different nominal taxonomic entities which exist in connection with this genus.

From the species assigned to Bolomys by Thomas, only amoenus, lactens, orbis and negrito remain for consideration. The type specimen of B. amoenus comes from the Rio Colea, north of Sumbay, some 100 Km. west of Titicaca Lake, in South Peru. Three other specimens in the British Museum (Nat. Hist.) which are indistinguishable from the type, come from the same general region, and a fourth, also inseparable from the latter, is labelled as coming from Huarconda, probably Huaraconda, which is some 300 Kms. north, in Cuzco. B. amoenus is a high-land form from the Peruvian "Altiplano" and it is the smallest of the known species of Bolomys. The three other nominal species come from northwest Argentina. B. lactens was originally described (Thomas, 1918) from one specimen from Leon, Jujuy, the "Sierra Pampeanas" at 1500 m.a.s.l. Specimens from further south,



Fig. 10. Ventral view of palatal region of skull in two species of Bolomys.

- A. Bolomys amoenus Thomas, BMNH 1.1.1.12, Sangero, Puno, Peru.
- B. Bolomys obscurus Waterhouse, lectotype, BMNH 55.12.24.161, Maldonado, Uruguay.

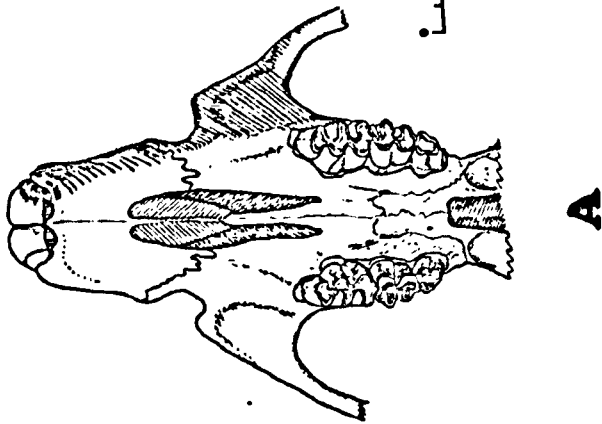
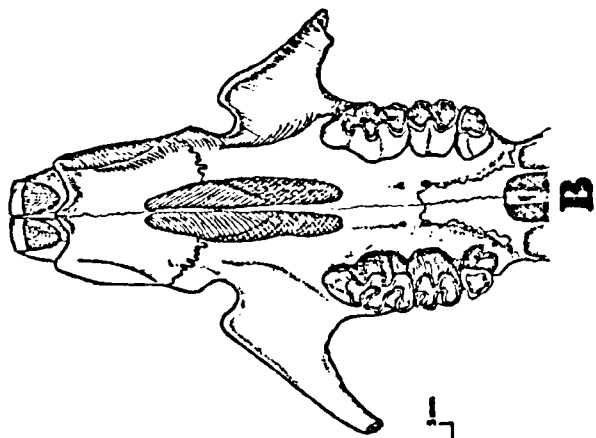
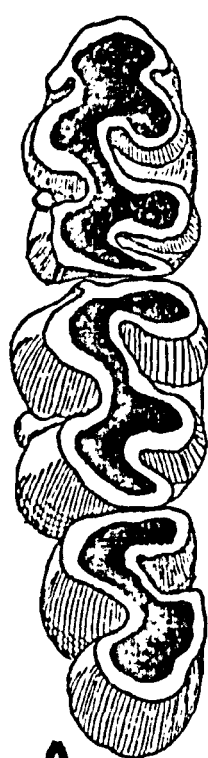
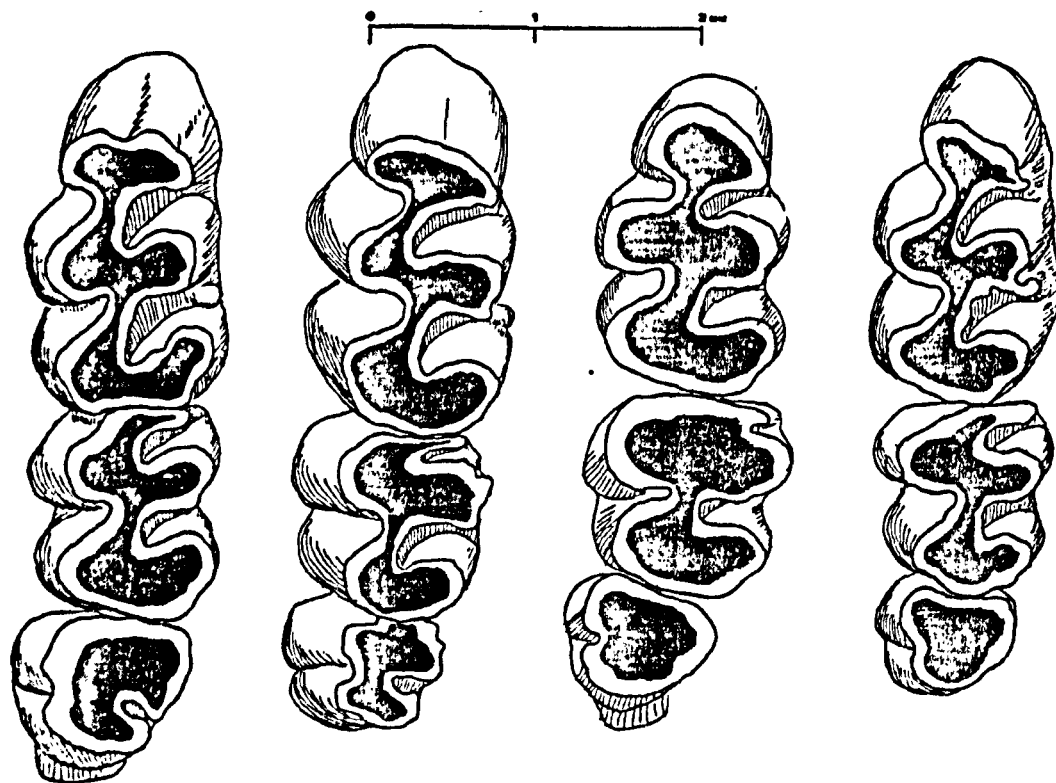
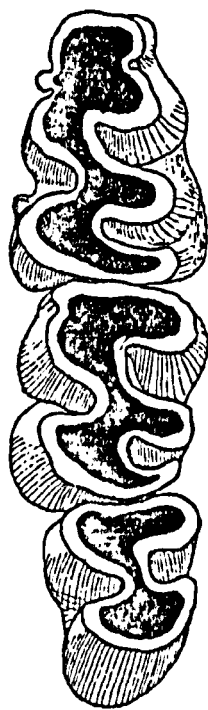


Fig. 11. Molar teeth of Bolomys. Upper row, left upper molar series. Lower row, left lower molar series.

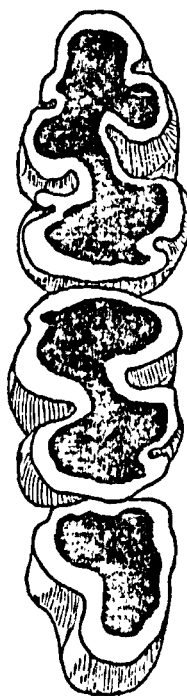
- A. Bolomys obscurus Waterhouse. Lectotype, BMNH 55.12.24.161, Maldonado, Uruguay.
- B. Bolomys obscurus Waterhouse, type specimen of Akodon benefactus Thomas, BMNH 16.10.3.35, Bonifacio, Guaminí, Argentina, Prov. de Buenos Aires.
- C. Bolomys amoenus Thomas, type specimen, B.M. O.10.1.77. Rio Colca, North of Sumbay, Peru.
- D. Bolomys amoenus Thomas, BMNH 22.1.1.97, Huarconda, Peru.



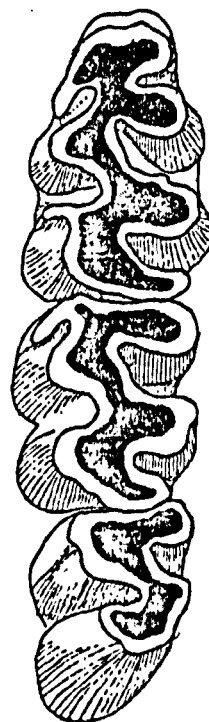
A



B



C



D

-Tucuman, were later referred to it (Thomas, 1926b).

B. orbus was based in material from Chumbicha, Catamarca, closely allied to lactens (Thomas, 1919), and B. negrito was created for a few dark specimens from the Aconquija range, in Tucumán (Thomas, 1926a). The validity of orbus and negrito as regards lactens is dubious. Both agree with lactens in size, accentuated proodonty and long diastema, and they are distributed in the same general region. Thomas himself suspected that negrito was nothing else but a "dark or semimelanoid race of lactens" (1926b: 605). Gyldenstolpe (1932: 119) probably misinterpreted this passage and suggested that negrito might be a melanic variety of albiventris. Cabrera (1961: 454) included both negrito and orbus without any hesitation in the synonymy of Akodon lactens lactens. Moreover, he recognized Akodon lactens leucolimnaeus as another sub-species, based on his Akodon leucolimnaeus from the highlands of Northern Catamarca.

Cabrera (1961) expressed the suspicion that the forms grouped by him under lactens might merely be southern subspecies of amoenus. Although I tentatively accept Cabrera's arrangement of the forms he refers to lactens, I believe that it is almost certain that amoenus and lactens are distinct biological species. They show clear cut differences in size, morphology of the cheek, teeth, incisors procumbency, and diastema length. In fact, lactens looks like a well differentiated and rather specialized species which exaggerated, in a sense, some of the morphological distinctions found in other species of the genus. Some of their characteristics seem to represent specializations for a more fossorial life. Therefore, from the forms referred

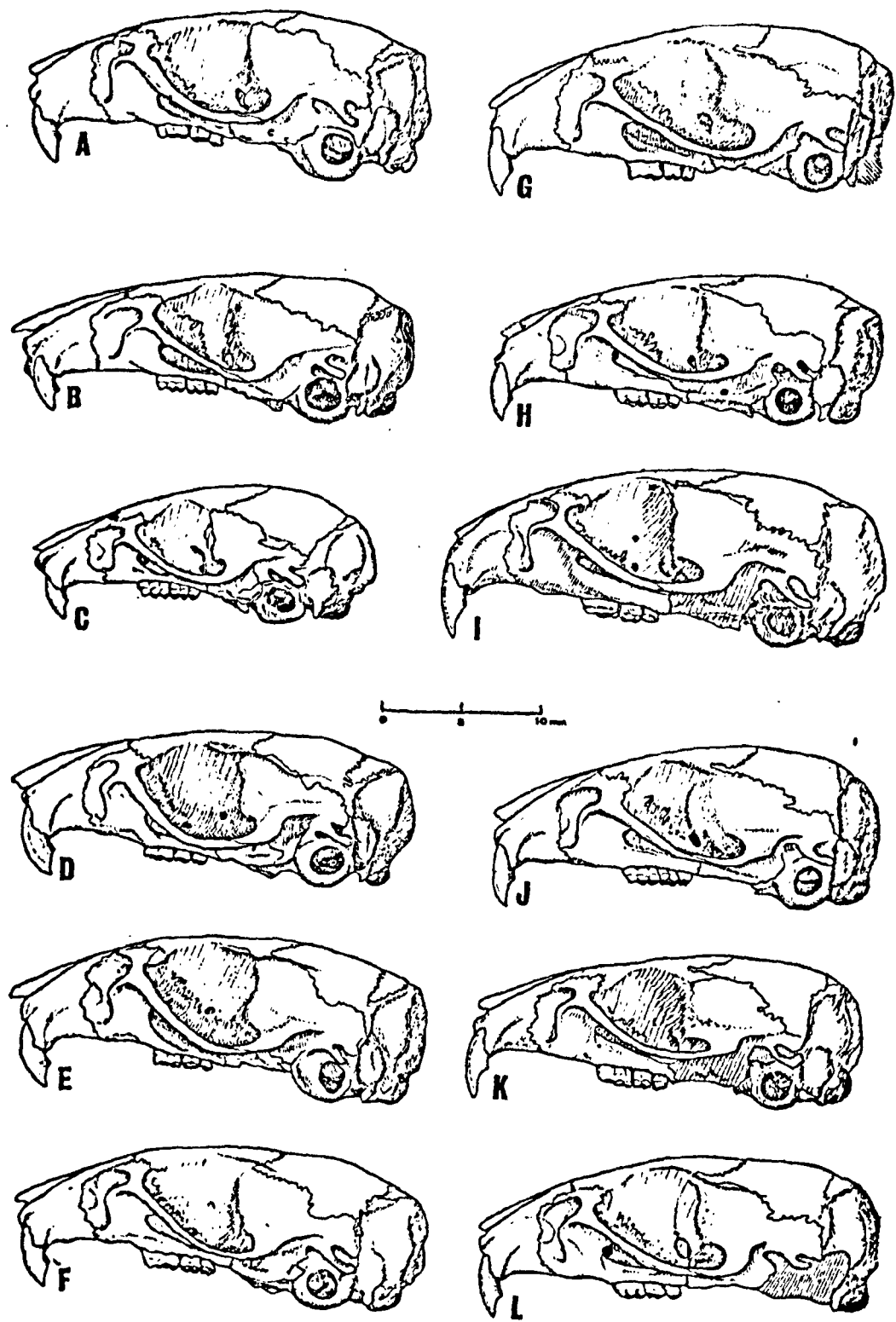
to Bolomys by Thomas, only amoenus and lactens are likely to stand as valid species.

Massoia and Fornes recognized A. obscurus Waterhouse and A. benefactus Thomas as distinct species and they also accepted in his alleged new genus "A. lenguarum Thomas, though casting doubts on its validity as a full species. Akodon obscurus was originally based on specimens from Maldonado, Uruguay, collected by Darwin and described by Waterhouse (1837). I have examined the lectotype designed by Thomas (1927) and several specimens from different localities of Uruguay and one from Goya, Corrientes, Argentina, which proved to be inseparable from the type specimen. It must be mentioned, however, that the latter is atypical in having a concave anterior border of the zygomatic plate (Fig. 9D), a feature which is certainly to be considered as an individual variant without taxonomic significance. Bolomys obscurus is a species easily distinguishable from amoenus and lactens in size, fur colour and several characters of the skull which I shall summarize later.

"Akodon" benefactus was based in specimens from Bonifacio, Guamini, West Buenos Aires Province (Fig. 12J). Massoia and Fornes referred to its specimens from other localities in the West and North of Buenos Aires Province. Cabrera (1961) and Crespo (1966) treated benefactus as a subspecies of obscurus. I have compared the type specimens and representative series of obscurus and benefactus in the British Museum (Nat. Hist.) and I have been unable to find any significant difference either in morphological features or in size between them. I conclude that obscurus, as represented by the Uruguayan material, and benefactus are

Fig. 12. Skulls in lateral view of species of Bolomys, Akodon and Zygodontomys.

- A. Akodon dolores, Male, Type specimen, BMNH 16.1.6. 38. Villa Dolores, Cordoba, Argentina.
- B. Akodon cursor, Female, BMNH 66.1874. Puerto Gisela, Misiones.
- C. Akodon boliviensis tucumanensis Thomas, Type specimen, female. San Miguel de Tucuman, Argentina, BMNH 0.7.9.13.
- D. Zygodontomys thomasi Allen, Female, BMNH 14.9.1. 60. El Trompillo, Carabobo, Venezuela.
- E. Zygodontomys microtinus Thomas, Female, type specimen, BMNH 66.8.11.10. Surinam.
- F. Akodon varius varius Thomas, Female, type specimen, BMNH 2.1.1.67. Cochabamba, Bolivia.
- G. Bolomys lasiurus lasiurus Lund, Topotype, B.M. 88. 1.9.4. Lagoa Santa, Brazil.
- H. Bolomys lasiurus fuscinus Thomas, Male, Type specimen, BMNH 97.4.1.3. Marajo.
- I. Bolomys scagliarum, Male, FCM 1399. Arroyo Corrientes, W. of Mar del Plata, Buenos Aires Prov., Argentina.
- J. Bolomys obscurus Waterhouse, type specimen of Akodon benefactus Thomas BMNH 16.10.3.35, Male, Bonifacio, W. Buenos Aires Province, Argentina.
- K. Bolomys lactens Thomas, Female. Type specimen, BMNH 18.1.1.37. Leon, Jujuy, Argentina.
- L. Bolomys lengururum Thomas, Type specimen B.M. 98. 5.14.4. Waikthlatingmayalwa, northern Chaco, Paraguay.

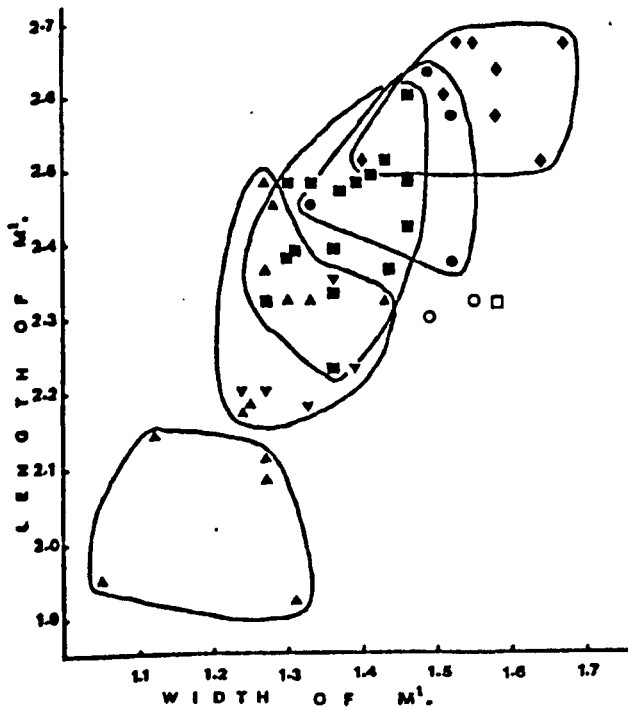
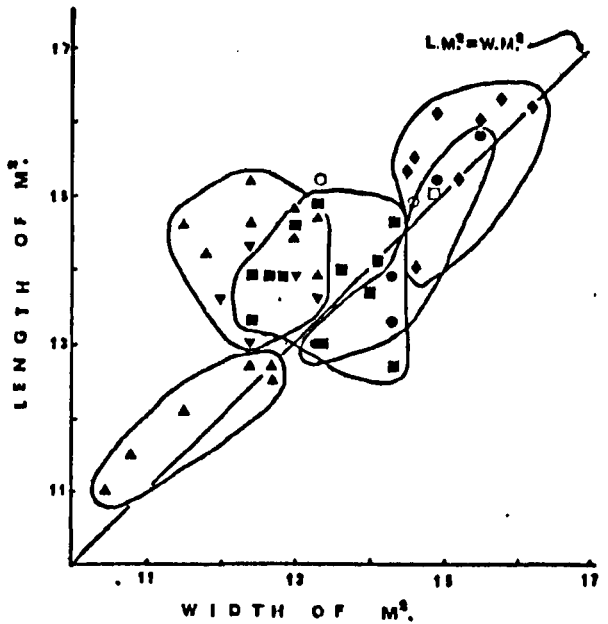
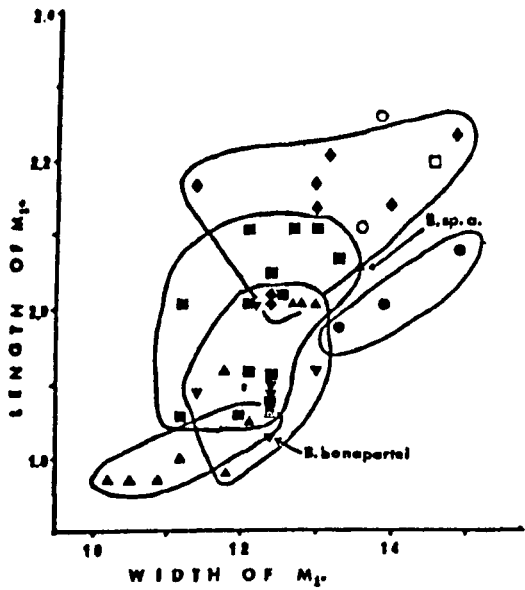




conspecific. It is to be noted, however, that Massoia and Fornes found significant size differences between benefactus and the specimens of obscurus they studied. These authors reported a few measurements based on a sample of 19 (for external characters) and 8 - 10 (for skull characters) individuals from Miramar referred to obscurus, and a sample of 5 - 7 individuals from two different populations of benefactus. In spite of statistical tests of significance not being given, the data seem to indicate significant differences for several variants. It is of interest to realize, in this connection, that the lower molars of specimens from Miramar illustrated by Massoia and Fornes (1967: Fig. 10) show distinctly a mesolophid remnant and a mesostylid in 4 out of 5 individuals (the sixth in the Table has the molars too worn off to check for this feature), whereas such structures were not found in the 'Cabreramys' of Uruguay and Bonifacio examined by me.

In view of these conflicting results, I examined the hypothesis that the typical obscurus and benefactus are conspecific, but that the populations of S.E. Buenos Aires Province referred to obscurus (Reig, 1964, 1965; Fornes and Massoia, 1965; Massoia and Fornes, 1969; Bianchi et al, 1972) may represent a different geographic race, or even a distinct as yet undescribed living species. Unfortunately, I have been unable to obtain samples large enough from the three areas involved so as to arrive at a conclusion statistically soundly based. However, the material seems to indicate a clear cut distinction from the Bolomys obscurus of S.E. Buenos Aires Province (Figs. 13, Table 8), and the differences found are of the degree which usually reflect only

Fig. 13. Scattergrams of measurements of molar teeth in  
species of Bolomys and Dankomys.



- ◆ *B. scagliarum*
- *B. lactens*
- *B. lenguarum*
- ▲ *B. obscurus* (Maldonado)
- ▼ *B. obscurus* (Bonifacio)
- ▲ *B. amonius*
- *D. verchvensis*
- *D. simpsoni*

species distinction among akodont rodents. Therefore, I distinguish the Southern form as Bolomys scagliarum (1) n.sp. (Type FCM. 2036), a short diagnosis of which will be provided later (Page 151). The formal description of this new living species will be provided elsewhere.(

Bolomys scagliarum is one of the largest species of Bolomys, and it is only comparable in size with Bolomys lactens from which it differs in the less simplified molar teeth, shorter diastema, stronger incisors and darker colour.

As regards lenguarum, (Fig. 12L; Fig. 14C), I have studied a sample of 15 individuals from North Paraguay and East Bolivia which includes the type specimen, and found that it is different from both obscurus and scagliarum, in several metric variables. It is also lighter in colour. It also differs from amoenus and lactens in several morphological characters of skull and dentition, as stated later. I tentatively consider lenguarum as a full species of Chacoan distribution. I provisionally synonymize it with "A". tapirapoanus Allen 1916 ( for wrong and contradictory statements about this nominal form by Cabrera, see Massoia and Fornes, 1962). Specimens in the British Museum (Nat. Hist.) from Buena Vista, Bolivia, referred by Hershkovitz (1962: 207) to tapirapoanus are inseparable from lenguarum.

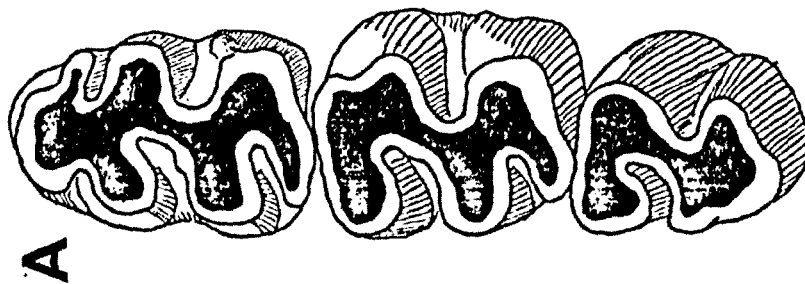
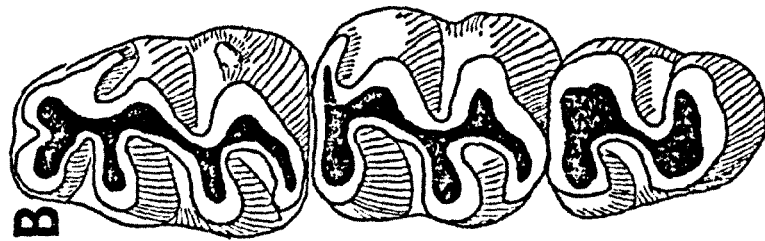
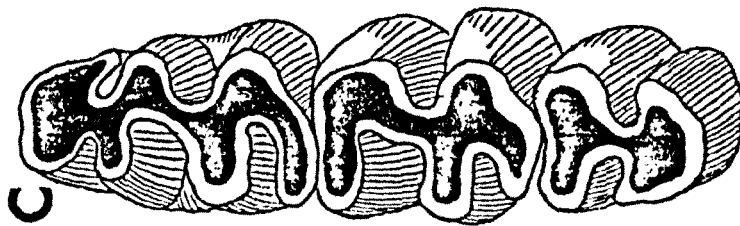
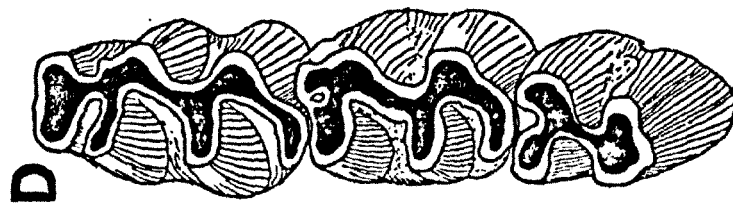
As already said, lenguarum and tapirapoanus have been placed by Hershkovitz under the generic name Zygodontomys, as probable subspecies of Z. lasiurus. The question arises, therefore, as to the connection of the other forms placed by Hershkovitz under Z. lasiurus, to Bolomys. They are

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(1) The species name is in acknowledgement of the work of Lorenzo, Galileo and Orlando Scaglia, members of three generations of naturalists of Mar del Plata, thanks to whom this species was discovered.

Fig. 14. Right lower molar series of living and fossil Bolomys.

- A. Bolomys scagliarum, n. sp. FCM 2036. Arroyo Corrientes, Partido de General Pueyrredon, Prov. de Buenos Aires, Argentina.
- B. Bolomys, sp. A. MLP 50.10.4.30 b. Fcion San Andres, Lower Pleistocene of Miramar, SE Buenos Aires Province, Argentina.
- C. Bolomys languarum Thomas. BMNH 26.12.4.60. Buena Vista, Bolivia.
- D. Bolomys obscurus Waterhouse, BMNH 16.10.3.37. Bonifacio, Guamini, W. Buenos Aires Province, Argentina.



lasiurus Lund, brachyurus Wagner, fuscinus Thomas and pixuna Moojen. I have examined the British Museum topotype of "Z". lasiurus (B.M. 88.1.9.4) (Fig. 12G.), the holotype of A. fuscinus (B.M. 97.4.1.3) (Fig. 12H) and specimens identified by Moojen as "Z". pixuna, now in the collections of the Faculty of Sciences of the University of Buenos Aires, and concluded that these species can be referred to the genus Bolomys without any serious doubt. Actually, misidentification of Hershkovitz' Southern Group of taxa as Zygodontomys has been the source of some confusion about the limits of the genus Akodon, and the alleged existence of transitional forms between the two genera. Actually, Zygodontomys, restricted in extent to cover the "Northern Group" of Hershkovitz which must include at least two good species Z. brevicanda and Z. microtinus (Fig. 12E), is an easily distinguishable taxon characterized by strong and apisthodont upper incisors, elevated forward, not tapering rostrum, nasals much longer than frontals, long parietals and well developed interparietals, well developed postorbital ridges, well long posterior plate, incisive foramina, widely opened and ovate in outline, extremely wide mesopterygoid fossa, high mandibular ramus with up-turned symphysis and incisors and well marked lower masseteric crest, opposite cusps of the upper molars transversely placed, total absence of mesoloph: and mesostyle, mesolophid and mesostylid, lophs and lophids transverse, median and anterior mure quite longitudinal, to mention only a few diagnostic character states.

In all the above features, the "Southern Group" of Hershkovitz' Zygodontomys is clearly different comparing like characters from Bolomys as defined above. But although it

. seems safe to conclude that this group of nominal taxa must be included in Bolomys it is not clear if it represents one or more species. B. lasiurus and brachyurus have typical localities in Mines Geraes and Sao Paulo respectively, in South Eastern Brazil. Wagner (1845) suggested that the latter could be identical with lasiurus, as described by Lund a few years before. Cabrera (1961) followed that suggestion proposing the synonym of brachyurus under "Z". lasiurus lasiurus.

Akodon fuscinus was described by Thomas on material from the Marajo Island, in the mouth of the Amazonas, Para, northern Brazil. "Z". pixuna comes from Ceara, in North Eastern Brazil. Both are treated as distinct subspecies of lasiurus by Cabrera and Hershkovitz. I have not access to adequate material of the Brazilian forms and, in the lack of new evidence, I prefer not to innovate and tentatively accept the criterion of these authors, which seems reasonable on geographical grounds.

There are still other species to be considered for possible inclusion in the genus Bolomys.

In his description of Akodon dolores, Thomas (1916) mentioned that this species "looks as if it were allied to A. obscurus and lengurarum." Referring to its skull, he says that it is "of somewhat similar build to that of A. obscurus", though in the same page (335) it says it "is perhaps most like that of A. varius." As I have said before, the latter species and A. arviculoides were mentioned by Hershkovitz (1962) with A. obscurus as making a group which he considered as difficult to separate from Zygodontomys. This poses the question of the relationships of



arviculoides, dolores and varius with obscurus and related species, and of the possible inclusion of the former in Bolomys.

I have examined the holotype and several additional specimens of dolores (Fig. 12A), varius (Fig. 12F) and several forms referred by Thomas (1926), Gyldenstolpe (1932) and Cabrera (1962) as synonyms or subspecies of the latter (neocenus, simulator, glaucus, toba, tartareus). Besides confirming the justification of including the latter under varius I found that dolores and varius are distinct but allied species which are not related to Bolomys at all, and that they are inseparable from Akodon as represented by such typical members as bolivianus and azaræ. Akodon dolores resembles certain species of Bolomys, especially Bolomys obscurus, in the simplification of the cheek teeth, and the robustness of the zygomatic plate, but it is quite Akodon-like in the strongly opsithodont incisors, the anteriorly elongated nasals, the longer occipital region, the non-tapering muzzle (Fig. 12A) the morphology of the mandible, etc. As regards varius (Fig. 12F), it is even more typically Akodon in skull and molar structures, and there is no reason to think that it has any close relationships with Bolomys. The chromosome evidence recently reported by Bianchi, Reig et al (1971) points to the same conclusion as the karyotype of varius as represented by varius simulator and varius neocenus, is identical with that of A. boliviensis. Akodon dolores has peculiar polymorphic karyotypes as different from those of varius as from those of representatives of Bolomys (see later). The species arviculoides was described by Wagner (1842) as a Hesperomys, according to the broad use of this unvalidated generic name by the early authors. It was considered a true

- Akodon by Thomas (1913) who described montensis as a subspecies he compared with cursor, Winge, 1888. Tate (1932g) regarded montensis as a true Akodon but he considered arviculoides as a Zygodontomys.

Latterly, Massoia and Fornes (1962) referred with some doubts material from Misiones, Argentina, to A. a. montensis, and later the group was discussed by Ximenez and Langguth (1970). These authors, after the study of the types of arviculoides, cursor and montensis, arrived at the conclusion that the two latter are very closely related and presumably only different at the subspecific level. But they consider cursor and arviculoides as different species of the genus Akodon and they argue that arviculoides was a Zygodontomys is untenable because it does not agree with the latter in having a long palate and a large interparietal and lacking of a "paralophule" in the M<sup>1</sup>.

The photograph of the type of "A. arviculoides" illustrated by Ximenez and Langguth (1970) provides a possibility to compare some skull and mandible characters with those of the species attributed to Bolomys. A. arviculoides agrees with the latter in having: a broad brain case, a rather short and tapering muzzle, in the outline and breadth of the zygomatâ; in the short nasals and in the absence of a trumpet-like forward expansion of nasals and premaxillae; in the width and ridges of the supraorbital region, in the wide fronto parietal suture; in the anterolateral "horns" of the parietals, in the greatly reduced interparietal, in the strong zygomatic plate and the shape of its anterior border, in the development and outline of the incisive foramina, in the scarcely long and wide posterior palate, in the high

mandibular ramus, in the morphology and relative development of the condyle and the development and position of the capsular projection. The only significant difference lies in the greater development of the parietal region, which is relatively a little longer than in all the studied specimens referred to Bolomys. The structure of the molar teeth cannot be appreciated in the illustration given by Ximenez and Langguth (1970), but they agree with those of Bolomys in general outline and relative size. The presence of a mesolophe remnant ("paralophule") in  $M^1$  indicated by those authors, is occasionally found in Bolomys. The chromosomes of A. arviculoides have been described by Yonenaga and Ricci (1969) - a previous description of the karyotype of A. a. cursor by Cestari and Imada (1968) being probably based on another animal - and this description was recently confirmed by Bianchi, Reig et al (1972). These authors found that the chromosomes of arviculoides are exactly the same, both in number and structure as those of obscurus from the vicinity of Miramar and Chasicó, here referred to Bolomys scagliarum. All seems to indicate, therefore, that arviculoides is a Bolomys.

The problem now arises of the validity of arviculoides as a good species as regards lasiurus, described by Lund, one year before. The illustration given by Winge (1888) of one of the types of lasiurus in the Museum of Copenhagen, and the study of the <sup>no</sup>type specimen in the British Museum (Nat. Hist.) (BM No. 88.1.9.4) suggests that they are closely related, but they can be distinguished by the longer parietal region of arviculoides. This difference is of little value in the absence of statistical studies based in good samples but they suggest that at least it would

be wise to retain arviculoides as a <sup>sub</sup>species of lasiurus until more material is available. Therefore my preliminary conclusions lead me to recognize six living species of Bolomys: a highland Bolomys amoenus inhabiting the Peruvian Altiplano; a likewise highland form, Bolomys lactens inhabiting the Pampean Sierras of Northern Argentina; a lowland species living in the grasslands of Southern Buenos Aires Province: B. scagliarum; a likewise grassland form of Uruguay, Northern and Western Buenos Aires Province and probably Entre Rios and Corrientes in Argentina (B. obscurus); a scrubland, Chacoan species (B. lenguarum) and a Northern, Northeastern and Southeastern Brazilian species (B. lasiurus).

Needless to say, this arrangement is tentative, and it is particularly provisional for the Brazilian forms. For the purpose of determining our fossil material, one needed to have a definition of the recognized species mostly on dental morphology. To this end, I have attempted a diagnosis of the six "species" as follows:

Bolomys amoenus:

Size small, crown length of  $M^1 - M^3$  4.0 mm, of  $M_1 - M_3$  4.3 mm. Incisors weak, the upper clearly protodont, diastema moderate.  $M^1$  relatively very short with a moderate procingulum without any indication of anteromedian flexus. Mesostyle almost always present, but mesolophe indistinct.  $M^2$  usually as wide as long without indication of styles or mesolophe.  $M_1$  relatively narrow, with a small procingulum showing a shallow trail of anteromedian flexid sometimes present, metaflexid and protoflexid well defined, mesostylid and mesolophid remnants absent, an ectostylid, free or united with a weak ectolophid, very often present; postero-

·lophid oblique.

Bolomys lactens:

Size large, mean crown length of  $M^1 - M^3$  4.9 mm, of  $M_1 - M_3$  5.1 mm. Incisors moderately developed, the upper strongly proodont; diastema long.  $M^1$  relatively long and broad, with a broadened procingulum apparently without any trace of anteromedian, but young specimens are not available. Mesostyle and lingual remnant of mesoloph rarely present in  $M^1$  and  $M^2$ .  $M^2$  usually as long as wide.  $M_1$  with a moderately well developed procingulum, without anteromedian flexid, and a shallow metoflexid and protoflexid. Mesostylid, mesolophid remnants, ectostylid and ectolophid apparently completely absent, but sample is too small to ascertain normal absence, posterolophid transversal.

Bolomys obscurus:

Size medium. Mean crown length of  $M^1 - M^3$  : 4.4 of  $M_1 - M_3$  : 4.6 . Incisors strong, the upper orthodont to proodont, diastema moderate.  $M^1$  short and narrow with a broad and short procingulum, frequently with a shallow anteromedian flexus. Mesostyle frequently present, but remnant of mesoloph absent or very rare.  $M^2$  relatively narrow, longer than wide without styles or mesoloph remnant.  $M_1$  relatively short, with small procingulum rarely with an anteromedian flexid and with very shallow metoflexid and protoflexid, mesostylid and mesolophid remnants only exceptionally present; a free ectostylid may or may not be present; ectolophid never present. Posterolophid somewhat oblique.

Bolomys lenguarum:

Size intermediate between lactens and obscurus. Mean crown length  $M^1 - M^3$  4.7 ,  $M_1 - M_3$  4.9 . Incisors moderate, the upper proodont. Diastema moderate.  $M^1$

relatively broad; procingulum wide and short, without anteromedian flexus. Mesostyle and lingual remnant of mesoloph frequently present.  $M^2$  relatively broad, but only occasionally wider than long; with missing styles or mesoloph remnants.  $M_1$  relatively long, with a broad procingulum lacking any trace of anteromedian flexid and metoflexid and protoflexid moderately marked; mesostylid may or may not be present, mesolophid remnant totally absent, ectostylid and weak ectolophid usually present.  $M_2$  relatively short, without mesostylid, mesolophid traces or ectostylid; posterolophid somewhat transversal.

Bolomys scagliarum, n. sp. :

Size: largest of the genus. Crown length of  $M^1 - M^3$  : 5.2 ; of  $M_1 - M_3$  : 5.3 . Incisors strong, the upper orthodont to moderately proodont. Diastema moderate,  $M^1$  relatively wide, with a broad and short procingulum without any trace of anteromedian flexus. Mesostyle and lingual portion of the mesoloph almost always present both in  $M^1$  and in  $M^2$ .  $M^2$  wide, but usually longer than wide.  $M_1$  relatively narrow, with a rather strong procingulum with anteromedian flexid very shallow, when present, and metaflexid and protoflexid moderately marked; mesostylid and lingual portion of the mesolophid usually distinct on  $M_1$  and  $M_2$ ; ectostylid and ectolophid rarely present on them.  $M_2$  long with a transverse posterolophid.

Bolomys lasiurus (based on the topotype BM. 88.1.9.4):

Size intermediate. Crown length of  $M^1 - M^3$  : 4.5 mm; of  $M_1 - M_3$  : 4.6 mm. Incisors moderate, the upper ones orthodont. Diastema moderate.  $M^1$  wide, with a relatively large procingulum without an anteromedian flexus. Mesostyle and mesoloph remnant present.  $M^2$  wide, without

styles or remnants of mesolophæ.  $M_1$  relatively short, with a broad procingulum without anteromedian flexid. Mesostylid and lingual portion of mesoloph, ectostylid and ectolophid present on  $M_1$ .  $M_2$  short and wide, with a mesostylid and an ectostylid. Posterolophid rather oblique.

7.2.1.2. The fossil remains of *Bolomys*.

*Bolomys bonapartei*<sup>(1)</sup>, n. sp.

Holotype: PVL 2396. Fragmentary right lower jaw including most of the symphysis, the horizontal radius  $M_1$  and  $M_2$ , the incisors and the  $M_1$  and  $M_2$  (Fig. 15G,H,I). Monte Hermono Formation, Member 3, Atlantic Coastal slopes of Southern Buenos Aires Province, 60 Km. East of Bahfa Blanca. Upper Pliocene, Montehermosian subage of Montehermosian age.

Hypodigm: The holotype only.

Diagnosis: A small species of *Cabreramys*, of the size of *B. amoenus*, with a reduced procingulum in the  $M_1$ , rather well defined by reentrant protoflexid and metaflexid, and more strongly alternating lingual and labial cusps in  $M_1$  and  $M_2$ .

Description:

The available fragment of mandible agrees with the mandibular rami of *Bolomys* in the deep horizontal ramus, which reaches 3.78 mm below the  $M_1$  and was certainly deeper than the diastema length. The border of the ramus immediately in front of the  $M_1$  descends abruptly towards the upper border of the symphysis, which is moderately high, not reaching in its anterior border the level of the alveolus of the  $M_1$ . In lateral surface, the upper masseteric crest is well defined, stronger than the lower masseteric crest, and reaches anteriorly the level of the anterior border of the  $M_1$ .

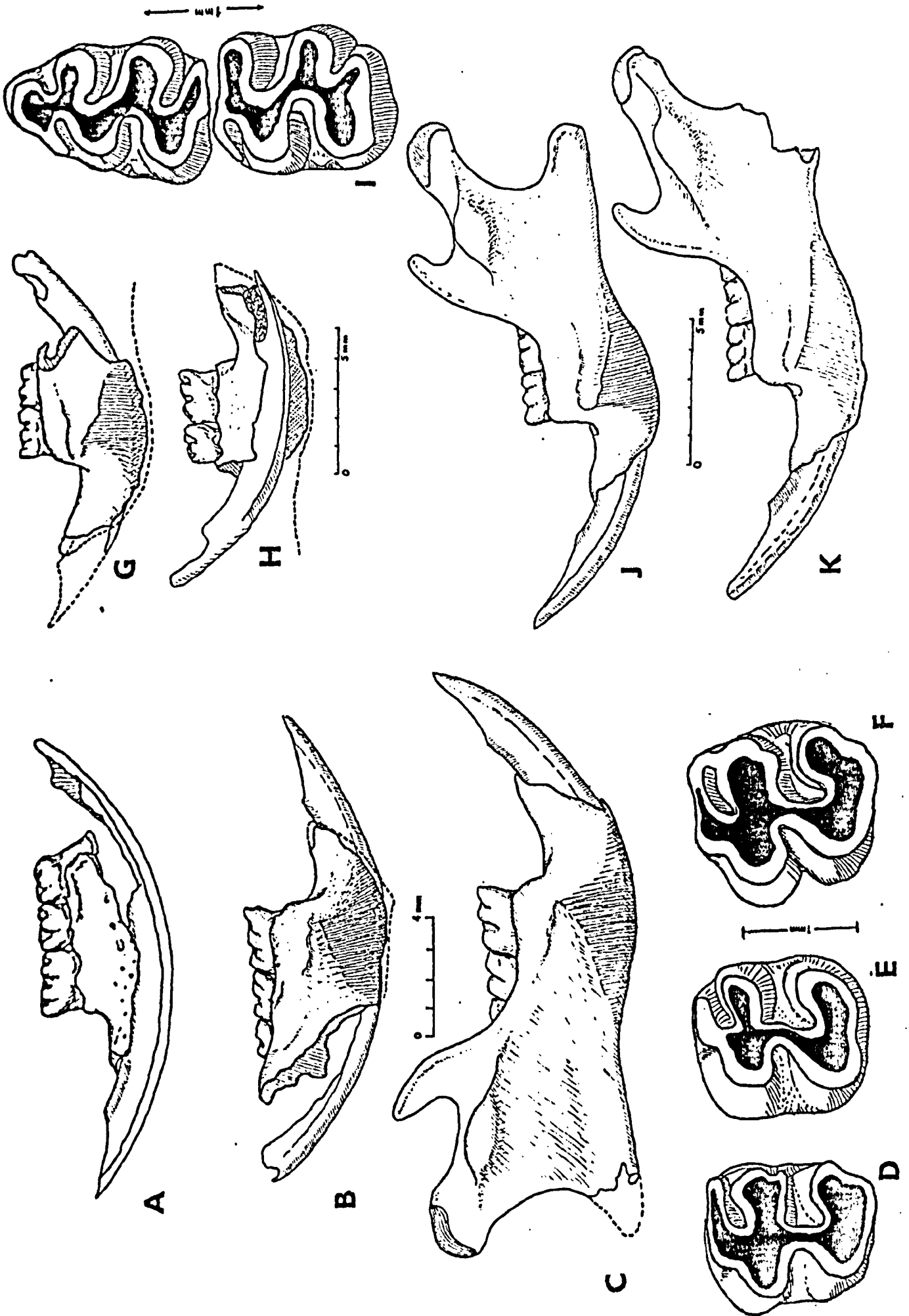
The incisor is 1.28 mm in depth and

1. The species name is given for Mr. J.F. Bonaparte, who discovered the single specimen referred to it.



Fig. 15. Teeth and mandibles of fossil and living Bolomys.

- A. Internal view, and B. external view of the left incomplete lower mandible of Bolomys sp. A.M.L.P. 52-10-4-30, San Andres Formation, Miramar. (Lower Pleistocene).
- C. External view of left lower jaw of Bolomys scagliarum, n. sp. Male. FCM 2036, Arroyo Corrientes, Partido de General Pueyrredon, Prov. de Buenos Aires. Living.
- D. Occlusal view of left  $M^2$  of Bolomys languarum Thomas, Female, BMNH 29.12.4160. Santa Cruz, Bolivia. Living.
- E. Occlusal view of left  $M^2$  of Bolomys sp., MMP M-1157. Miramar Formation, Santa Helena, Mar Chiquita, Prov. de Buenos Aires (Middle Pleistocene).
- F. Occlusal view of left  $M^2$  of Bolomys scagliarum n. sp. FCM 2036. Other data as in C.
- G. Lateral view of the mandible, H. internal view of the mandible and I, occlusal view of  $M_1$  and  $M_2$  of Bolomys honapartai, n. sp. Monte Hermoso Formation, south of Buenos Aires Province, Argentina (Upper Pliocene).
- J. External view of the left lower mandible of Bolomys amaenus Thomas, Type specimen, BMNH O.10.1.77. Rio Colca, North of Sumbay, Peru. Living.
- K. External view of the left lower mandible of Bolomys obscurus (Waterhouse). Type specimen. BMNH 55.12.24.161. Maldonado, Uruguay. Living.



0.72 mm in width, agreeing in size and shape with B. obscurus, and differing markedly from Bolomys amoenus, where the incisors are weaker (1.08; 0.65).

The molars agree with those of other species of Bolomys in their simplified enamel pattern, the disposition in echelon of the cusps, the transverse metolophid and only moderately oblique entolophid and posterolophid and the relatively transverse posteroflexid. Resembling in this respect Akodon, the disposition in echelon of the labial cusps with respect to the lingual ones is even more pronounced than in the living species, the protoconid being at a level well posterior to the metaconid and the hypoconid to the entoconid. As it is usually the case in the living species, mesolophid remnants and mesostylids are lacking in  $M_1 - M_2$ . The  $M_1$  is small, its length being slightly longer than the mean length in B. amoenus and most individuals of B. obscurus and the other species of Bolomys examined (Fig. 13, Table 8). But if by its size it is within the range of variability of B. amoenus and even B. obscurus, it differs from them in the details of structure so far discussed and, particularly, in the scarcely developed but well defined cingulum, which seems to be formed from a simple anteroconid and has a rounded anterior border without any trace of anteromedian flexid. In all the living species of Bolomys the procingulum is better developed in width, though usually less well defined by the

infolding of metaflexid and protoflexid. In little worn teeth of B. obscurus, and usually in amoenus, moreover, a more or less developed shallow anteromedian flexid may be present, marking the distinction of an anterolabial and an anterolingual conulid. The metaflexid and protoflexid are well defined in C. bonapartei, as it is the case in some individuals of amoenus and in the species of Dankomys (see later), but as in amoenus instead of defining a somewhat transverse constriction, as in this genus, they are obliquely oriented the metaflexid being more anterior than the opposite flexid. As occasionally occurs in B. obscurus, a free ectostylid is present on the floor of the hypoflexid of  $M_1$ . In B. amoenus and B. languarum it occurs more often than in B. obscurus, and it is usually connected with a poorly developed ectolophid.

The  $M_2$  is shorter than in any individual of B. obscurus from the sample, and it approaches more the proportions of this tooth in B. languarum and B. lasiurus (Fig. 13). It has a well defined protoflexid, and is somewhat square in outline, due to the posterior position of the hypoconid and the transverse position of the metalophid and entolophid. The posterolophid is less developed than is usual in the other species and the posteroflexid is short and it faces a little backwards.

#### Discussion:

The inclusion of bonapartei in Bolomys is ascertained by a comparison with all the

relevant genera of South American cricetids. Because of the combination of enamel pattern, absence of mesolophid remnant, and the simple-shaped procingulum of the  $M_1$ , Akodon, Microxus, Notiomys, Oxymycterus and related akodont genera must be ruled out as candidates for generic allocation, as is any member of the Oryzomyini and Scapteromyini, which are quite different in molar structure. Only some Phyllotines, and Bolomys remain. Among the former, some resemblance is found with Calomys in the overall pattern of the lower molars. However, Calomys is easily discarded by its stronger mandible, more tuberculate molars and much more developed procingulum of the  $M_1$ , which is bipartite and united with the metolophid by a long, antero-posterior anterior murid. Eligmondontia must also be discarded by the same dental characteristics, and the genera of the Phyllotis section of Hershkovitz' phyllotines are clearly set apart by the more planate and high crowned molars. Species of Zygodontomys agrees with bonapartei in simplification and terraced molar teeth and in the simple, individual procingulum. This is, however, much better developed in Zygodontomys which also strikingly differs in the enamel pattern, showing more opposite labial and lingual cusps and opposed, not interlocking hypoflexid and mesoflexid. The mandible of Zygodontomys moreover is much more robust and has a more up-raised symphysis.

In all those characters which do not allow the placing of bonapartei in any of the above mentioned genera except Bolomys, it fully agrees with the latter, and at least to the extent of the evidence available from the present material, little doubt can be cast to its allocation to this genus.

Within Bolomys, the validity of bonapartei, founded on a single specimen, may raise objections from the point of view of modern taxonomic procedures. It can be argued, for instance, that the characters found in the single available individual may be an extreme case of individual variation within the limits of a known living species, as amoenus or obscurus. Though on theoretical grounds this may be possible, I believe that this is very improbable, and the objection is not soundly based on the overall variation found in the available samples of living species of Bolomys. Designation of new species on single individuals and, even worse, fragmentary ones, is not an ideal procedure, but it is certainly convenient in fossil material for most practical purposes, when it is backed by clear cut differences, (which quite probably are a reflection of genetic discontinuities), ascertained after an exploration of the pattern of variability in the other members of the genus where the new species is located.

The distinction of B. bonapartei from the other species of Bolomys are given in the above

description of the new species. It seems to be related to amoenus and/<sup>it</sup>shares some of the characters of B. obscurus, <sup>(living at present</sup>~~the Andean cricetids (which now live~~ ~~xxx~~ in the Pampean region) and B. lasiurus (distributed far in the North of the former, in the Chacoan region), but because of the small size and simple procingulum of the M<sub>1</sub> it looks as more primitive than this species. This points to an interpretation of the phylogenetic significance of simple, as against complex procingula. The problem whether a simple undivided p-ocingulum with a single anterocone, is the more primitive character, or if it is a simplified condition from a more complex, biconulate, primitive condition, is considered as dubious by Hershkovitz (1962: 75), though he is clearly in favour of the second alternative. In fact, South American cricetids with full-fledged mesolophs and mesolophids and primitive cus<sup>p</sup>pidate molars, as the Oryzomyini have complicated, biconulate procingula. The exception is Rhagomys, which has exceedingly primitive cuspidate - pentalophodont molars, but a simple anterocone and anteroconid. As this is the usual situation in the Oligocene and Miocene Cricetodontines, it is safe, and more logical, to assume that this is the primitive character state for the Sigmodontinae.

This being the case, the question arises of the phylogenetic significance of B. bonapartei, one of the earliest taxa from the known fossil record of South American cricetids. It is possible that

B. bonapartei represents an ancestral population which gives rise to both B. scagliarum (which now lives in the same general area) and to B. obscurus. Whether or not it is also ancestral to other species of living Bolomys is at the present state of knowledge, a point of mere speculation.



Bolomys sp. A.

M L P - 52 x 4.30 a. Left incomplete lower jaw with the whole dentition (Fig. 14B, Fig. 15A). Found by the late Dr. J. Frenguelli in association with remains of Reithrodon sp. in his "Prebelgranense" (= San Andrés Formation) of the vicinity of Miramar, Buenos Aires Province.

Description:

The preserved portion of the diastema and ramus, as well as the size, position and shape of the incisors, agree with Bolomys more than with any other sigmodontine cricetid, as so do the molar teeth. The lower masseteric crest is noticeably slightly stronger than in the specimens of Bolomys I have examined, but in any case, it is less strong than in Zygodontomys or Calomys.

In absolute size and in proportion of the molars, this specimen matches well with specimens of B. scagliarum now inhabiting the same region (Fig. 13, 14, Table 8), but it could hardly be assigned to this species in view of the enamel pattern and the proportions of the incisor. In the fossil specimen, the incisor is markedly less deep than in scagliarum. The depth measures 1.36, close to the value of B. lenguarum (see Table 8). In the type of scagliarum it measures 1.43, and the mean value in a sample of eight specimens is 1.50.

In the structure of the molars, the fossil specimen is characterized by a relatively large procingulum divided in front by a well defined

anteromedian flexid, separated from the metolophid by a deeply re-entrant metoflexid, whereas the protoflexid is shallow as is usual in Bolomys. A strong obliquely oriented anterolabial cingulum is also visible. A shallow anteromedian flexid in the  $M_1$  is often present in B. amoenus, less frequently in obscurus and scagliarum, but it is not found in B. lasiurus or lactenss. In B. languarum it is normally absent. I observed a well infolded anteromedian flexid in one specimen only from Buena Vista, Bolivia, (BMNH. 26.12.4.61) which is otherwise anomalous in molar structure. A deeply re-entrant metaflexid opposed by a shallow protoflexid is unusual in any species of Bolomys. A similar structure is found in one out of fifteen specimens of B. obscurus from the collection of the BMNH (BMNH. 16.10.3.37) which seems to be anomalous for this character. Whether the similar characteristic in our fossil specimen is also anomalous or a regular occurrence in its population is a question that cannot be settled now. Neither are any traces of the mesolophid nor mesostylids present in the molars of this specimen, as is normally the case in B. languarum, B. obscurus and B. lactens. These accessory structures are present in the topotype of lasiurus and are frequent in scagliarum. A reduced free ectostylid is seen in the  $M_1$ , but it is absent in the  $M_2$ , as is often the case in other species of the genus.

The entolophid and posterolophid are

rather oblique in direction and the posteroflexid is well developed, both in  $M_1$  and  $M_2$ . The protoflexid of the latter is well defined, but not so much as in B. bonapartei. The  $M_3$  is sigmoid in outline, with interlocking and similarly developed hypo- and mesoflexid, and lacks any trace of the protoflexid.

Discussion:

The individual described shows that a species of Bolomys was living as early as the uppermost Pleistocene in the South East of Buenos Aires Province; this is to be expected as the genus is found in the Upper Pliocene of Monte Hermoso and has its present distribution in the same general area. The possibility that the San Andrés specimens may belong to Dankomys, a related genus which reaches the underlying Vorohué Formation, (see later), does not seem to be sustained by the evidence available. The lower molars of Dankomys have characteristically much more re-entrant hypoflexids and protoflexids, and more diagonal entolophids and posterolophids. D. voroh uensis has also a reduced posteroflexid and no anteromedian flexid at all. Moreover, its  $M_3$  is larger than in the San Andrés specimen.

The problem of the allocation of the only available individual to a known species cannot be convincingly settled on the basis of the present evidence. Quite certainly, this specimen does not belong to B. bonapartei or B. amoenus, from which it differs markedly in size. In size, it approaches

B. lactens and especially B. scagliarum, but in molar morphology it seems more closely related in some respects to B. obscurus and in others to B. lenguarum. In the proportions of the molar teeth, the  $M_1$  is within the lowest values found in scagliarum (see Fig. 13), but it is as long and wide as in the largest specimens of lenguarum as it is clearly distinct than obscurus. The  $M_2$  is within the range of scagliarum and lactens. It is as long as in the largest lenguarum and close to the length values with the greater frequency in obscurus (which is characterized by proportionally long  $M_2$ ), but it is definitely wider than in the two latter. The length of the  $M_3$  as compared with the length of the  $M_2$ , approaches the values found in scagliarum and lactens; and the  $M_3$  is therefore relatively longer than what is usual in obscurus, lenguarum and amoenus and the examined topotype of lasiurus. The characteristics of the procingulum of this individual are peculiar, but they match better with B. obscurus than with lenguarum and scagliarum, as is also true of the relative size of the  $M_2$ . It must be noticed, however, that it even differs from the living population of B. scagliarum in the same area, lacking any trace of mesolophid and mesostylid, although these structures may also be absent in some specimens of scagliarum. The discovery of more material may prove it more convenient to separate the San Andrés Bolomys as a distinct species, allied to scagliarum but the

available evidence does not allow such a distinction, and I believe that in this case it is wiser not to propose a new name for this isolated specimen.

Bolomys sp. B.

MMP M- 642 (b). Isolated left  $M^2$  (Fig. 15E). Found by G. J. Scaglia in association with Reithrodon auritus, in strata of the Miramar Formation, at Santa Elena, Ptdo. de Mar Chiquita, Prov. de Buenos Aires, Argentina. This isolated upper molar quite probably belongs to a member of Bolomys. It agrees in all the morphological features with  $M^2$  of members of that genus studied, and it is distinguishable from other akodontines by lack of any trace of mesoloph, the transversal position of the cusps and their proportions. It cannot be excluded, however, that it may belong to an Akodon with simplified enamel pattern, or even to a Zygodontomys, though this last possibility is quite improbable on biogeographical grounds.

On the tentative, but quite likely allocation to the genus Bolomys, it is easily distinguishable by size from amoenus and bonapartei, but it agrees in size and proportion with B. lenguarum more than with B. obscurus (see Table 8). It is definitely smaller than B. scagliarum and lactens. Because of these size characteristics, it is improbable, though not impossible, that it represents the same species as

that to which the mandible from the San Andrés Formation belongs.

Specimen	<u>B. bonapartei</u> , TYPE PVL 2396. Monte her moso Ftion.	<u>Bolomys</u> sp. MLP 52- X-4-30 (b). San An- drés Ftion.	<u>Bolomys</u> sp. MMP M- 1157. Miramar Ftion.	<u>B. amoenus</u> . TYPE BMNH 0.10.1.77	<u>B. obscurus</u> , TYPE BMNH 52-12-21-61	<u>B. lenguarum</u> , TYPE BMNH 92.5.14.4	<u>B. lactens</u> , TYPE BMNH 18.1.1.37	<u>B. scagliarum</u> , TYPE FCM 2036
Variate								
Length diastema	3.11	3.20	----	3.09	3.46	----	3.42	3.64
Depth of mandible at the middle of M <sub>1</sub>	3.78	3.88	----	3.14	3.78	----	3.33	3.90
Alveolar length M <sub>1</sub> -M <sub>3</sub>	----	5.31	----	4.54	4.83	4.60	5.37	5.31
Coronal length M <sub>1</sub> -M <sub>3</sub>	----	5.25	----	4.41	4.61	4.51	5.06	5.12
Length of M <sub>1</sub> .	1.83	2.05	----	1.80	1.78	1.89	2.01	2.02
Width of M <sub>1</sub>	1.24	1.36	----	1.12	1.18	1.24	1.39	1.24
Length of M <sub>2</sub>	1.46	1.58	----	1.39	1.49	1.45	1.55	1.64
Width of M <sub>2</sub>	1.27	1.43	----	1.08	1.27	1.17	1.30	1.46
Length of M <sub>3</sub>	----	1.58	----	1.21	1.39	1.21	1.39	1.52
Width of M <sub>3</sub>	----	1.25	----	0.99	1.14	1.08	1.12	1.20
Depth of incisor	1.28	1.36	----	1.08	1.30	1.32	1.27	1.43
Width of incisor	0.72	0.99	----	0.65	1.15	1.01	1.10	1.11
Length of M <sup>2</sup>	----	----	1.46	1.27	1.46	----	1.30	1.61
Width of M <sup>2</sup>	----	----	1.37	1.34	1.15	----	1.33	1.39

TABLE No. 8 Measurements of the lower jaw and of the dentition of fossil specimens of Bolomys and the types of some of the living species of the same genus.

7.2.2. GENUS DANKMOYS, N. GEN.

Among our fossil material there are several remains which belong to an akodontine relatively closely allied to Bolomys, but which differ sufficiently from the known species of this genus, to require a new generic name.

Dankomys, n. gen. (1)

Type species:

Dankomys vorohuensis, n. sp.

Referred species:

The type species and Dankomys simpsoni, n.sp.

Known distribution:

Chapadmalalan, Uquian and Vorohuean sub-ages, Uppermost Pliocene and Lower Pleistocene, South East of Buenos Aires Province, Argentina.

Diagnosis:

A relatively large, advanced akodont rodent allied to Bolomys. Zygomatic plate deeper and stronger; incisive foramina longer, as wide anteriorly as posteriorly. Capsular projection of the mandible weak, not forming a strong process; horizontal ramus deeper. Molar more robust and broader, moderately hypsodont, with occlusal surface slightly terraced in moderately worn teeth, which plane with advanced wear. Mesoloph and mesolophid remnants, as well as mesostyles and mesostylids, completely absent. Enteroloph and enterostyle absent; ectolophid absent, ectostylid normally absent. Procingulum of the  $M_1$  well defined by opposed protoflexid and metaflexid.  $M_3$  almost as long as  $M_2$ . Upper molars with

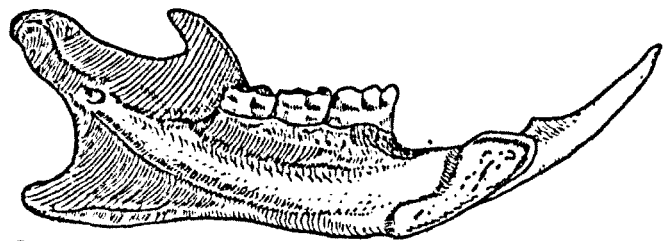
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(1) The generic name is given for Danko Bruncic, the leading South American evolutionary biologist, whose remarkable work on genetics and evolution of South American Drosophilae have inspired the author's study of evolutionary processes.

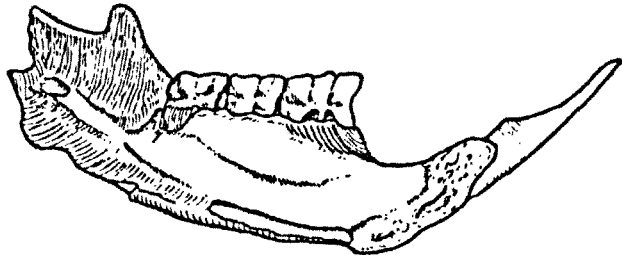


Fig. 16. Lower jaws of Bolomys and Dankomys.

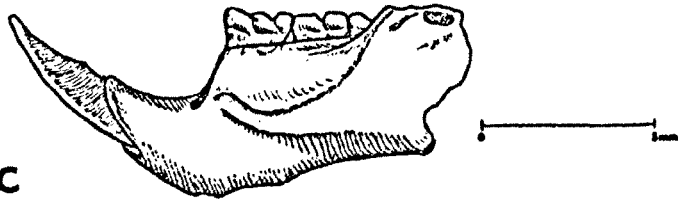
- A. Bolomys obscurus, Maldonado, Uruguay, BMNH 55.12.24.160, internal view of left lower jaw.
- B. Dankomys vorohuensis. Type MMP M-1064, internal view.
- C. External view, and D. internal view of Dankomys vorohuensis, MMP M-1066.



A



B



C



D

labial and lingual main cusps clearly opposed to each other. Paraflexus and metaflexus only slightly directed backwards, incipiently alternating with hypoflexus and protoflexus in the M<sup>1</sup>.

Dankomys vorohuensis, n. sp. (1)

Holotype:

MMP M-1064 (Fig. 16B, 17, 18C): Both incomplete maxillae and premaxillae with the upper incisors and  $M^1 - M^2$ : both lower jaws, each with the complete dentition, but lacking angular and condyloid processes; half of the atlas; right humerus without the proximal epiphysis; distal half of left humerus; most of the right tibia; a fragment of pelvis; proximal half of right cubitus; proximal fragment of a femur; one caudal vertebra; one metacarpal; one proximal fragment of a metatarsal and one ectocuneiform, the two latter and the atlantal fragment probably not corresponding to the same individual or species. Found by Galileo J. Scaglia in the lower beds of Vorohué Formation, about 1 Km south of Punta Lobería, Atlantic cliffs of the coastal region of Partido de General Pueyrredón, Buenos Aires Province, Argentina.

Hypodigm:

The type and:

MMP M-1077 (Fig. 18B): Incomplete left maxilla with  $M^1 - M^3$ , a portion of the pelvis, two fragments of the lower jaws without teeth. Found in association with the holotype and therefore, same collector, and geological and geographic provenance.

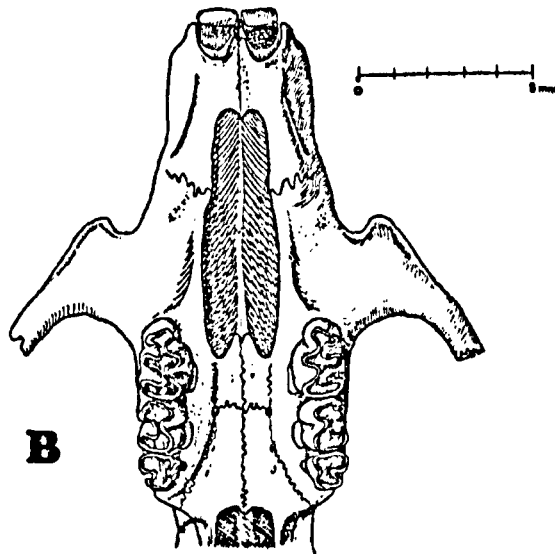
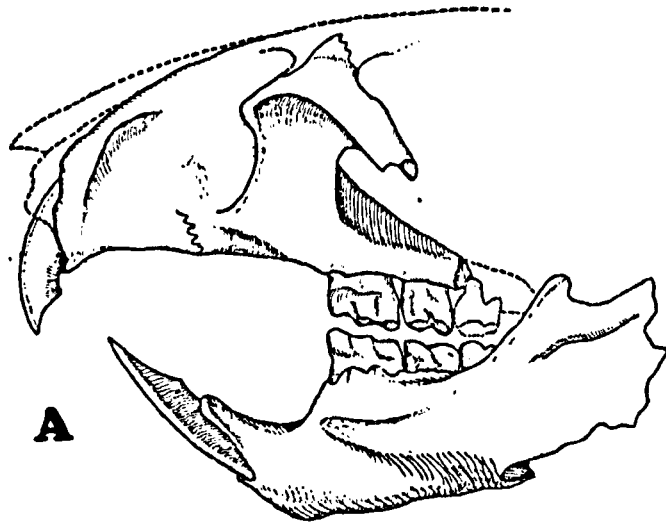
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(1) The species name is given for the geological provenance of the type and associated specimens: Vorohué Formation. Vorohué is a toponym of Araucanian origin.

Fig. 17. Dankomys vorohuensis, type specimen, MMP M-1064.

A. Lateral view of skull and lower jaw.

B. Partially reconstructed view of the ventral aspect of the skull.



MMP M-1066 (Fig. 16C, 18E): Left lower jaw without condyloid, coronoid and angular processes, with the entire dentition; left humerus lacking the proximal epiphysis; proximal half of right femur; right and left tibiae; one caudal vertebra. Found by G.J. Scaglia in the lower levels of Barranca Lobos Formation, at "Bajada Barranca Lobos", Atlantic cliffs of the Partido de General Pueyrredón, S.E. Buenos Aires Province, Argentina.

Diagnosis:

A Dankomys species with a moderately deep mandibular ramus, and a relatively slender symphyseal region. Zygomatic plate relatively slender.  $M^1$  and  $M_1$  without any indication of anteromedian flexus or flexid. Entolophid and posterolophid of  $M_1$  and  $M_2$  markedly obliquely directed backwards. Postero-flexids little developed in  $M_1$  and  $M_2$ . Protoflexid of  $M_2$  little developed or completely absent in moderately worn teeth.

Known distribution:

Uquian and Vørøhucan subages of the Uquian age, Lower Pleistocene, South East of Buenos Aires Province, Argentina.

Dankomys simpsoni, n. sp.<sup>(1)</sup>

Holotype:

MMP M-1153 (Fig. 18A,D; Fig. 19A,B,C,D): Left maxilla including the zygomatic plate, the posterior palate and the three molar teeth; portion of the right maxilla with the molar teeth; incomplete left lower jaw including broken incisor and

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(1) The name of the species is given for George G. Simpson, in honour of his remarkable contributions to the knowledge of the Argentinian fossil mammals, including those of the Chapadmalal formation, where this fossil species occurs.

M<sub>1</sub> - M<sub>2</sub>; proximal half of a right humerus; caudal vertebra and three unidentifiable skull fragments. (The humeral portion has a different type of fossilization, and may belong to another animal). Chapadmalal formation, Atlantic cliffs between Mar del Plata and Miramar, S.E. of Buenos Aires Province, Argentina (collector unknown; transferred from the Museum of La Plata, where it originally belonged, in exchange from the Museum of Mar del Plata).

Hypodigm:

The holotype is the only known individual of the new species.

Diagnosis:

A Dankomys species with a deep mandibular ramus, strong symphyseal region and wide zygomatic plate. M<sup>1</sup> with a well-marked anteromedian flexus; M<sub>1</sub> with a shallow anteromedian flexid. M<sub>1</sub> and M<sub>2</sub> with more transversely directed entolophids and posterolophids, and well developed posteroflexids or a rather transverse position. Protoflexid of M<sub>2</sub> well developed.

Known distribution:

Chapadmalalan subage of the Montehermosian age, Uppermost Pliocene; South East of Buenos Aires Province, Argentina.

Description of the specimens of Dankomys:

Skull:

The best specimen of Dankomys is the holotype of D. vorohuensis, MMP M-1064, found in association with MMP M-1077. The type specimen shows a great deal of the skull and mandible



characters, and it is mostly on the basis of this specimen that the concept of the new genus arose. The right maxilla and premaxilla of the holotype of vorohuensis are fairly complete and in a good state of preservation. The premaxilla, however, was misplaced during preparation in a way that could only be corrected now with danger of damage to the whole specimen. However, the whole anterior lateral view of the skull can be reconstructed safely as indicated in Fig. 17. The left maxilla and premaxilla are less complete, but they helped a great deal to make the reconstruction possible, as did the occurrence of the left maxilla of the other specimen associated with the type.

In lateral view (Fig. 17A), the antorbital region of the skull shows that the rostrum tapers forwards much as in Bolomys, differing thereby from Zygodontomys, Akodon or Calomys, which show a rostrum much higher anteriorly. As in various species of Bolomys, the incisor is clearly orthodont, whereas in Zygodontomys, Akodon, Calomys and Phyllotis it is usually opsithodont. The more anterior point of the premaxillae is broken in all the available specimens, but these bones certainly did not extend in front of the incisors, as is also the case in Bolomys. In fact, the rostrum of Dankomys is very similar to that of Bolomys. The only important distinction between these two genera in this region lies in the zygomatic plate, which is clearly deeper in Dankomys, which approaches the condition found in the phyllotines. In Dankomys vorohuensis the zygomatic plate defines an area of insertion of the pars profundus of musculus masseter lateralis, which is clearly higher than wide, as it is in Phyllotis and Calomys, whereas in Akodon, Bolomys and Zygodontomys, this area is wider than

high and does not reach so high in the lateral view of the skull. The anterior border of the zygomatic plate has a long concave outline, as its upper corner is pointed and slightly projected forwards. This is very similar to the condition found in the type specimen of Bolomys obscurus (BMNH 55.12.24.161) (Fig. 9), but this specimen is exceptional for the standards of Bolomys, including other specimens of the same species, in this respect, and must be considered anomalous. In all the other specimens of obscurus available, and in all the other specimens of Bolomys (Fig. 12), the anterior border of the zygomatic plate is plane or very slightly concave (specially in Bolomys scagliarum, see Fig. 12I), and has a rounded upper corner not projected forward. This is also the usual condition in Akodon, in which the zygomatic plate can even be much less deep and in some cases shows an anterior border gradually slanting backwards.

A distinction occurs in the zygomatic plate of the two species of Dankomys recognized here, as the single known specimen of simpsoni shows this plate as high as in vorohuensis, but clearly wider than deep. The phylogenetic significance of the zygomatic plate and associated structures in the cricetids has been discussed by Vorontzov (1963b, 1967). According to his conclusions, Dankomys might be considered as more evolved in masticatory specializations than Bolomys, an inference which is also supported by its molar modifications.

In ventral view (Fig. 17B), the type specimen of vorohuensis shows long and wide incisive foramina, which are almost as wide posteriorly as anteriorly, whereas in Bolomys they are usually narrower behind. These foramina reach farther forwards than in Bolomys, and are relatively longer than in

any of the species of the latter. As in Bolomys their posterior borders pass beyond the anterior borders of the  $M^1$ , but in Dankomys vorohuensis they reach to a point slightly more posterior than in Bolomys, and they are at the same level as the protocone of the  $M^1$ . In D. simpsoni, the incisive foramina, even when passing beyond the anterior border of the  $M^1$ , do not reach to their protocone, being in this respect more similar to those of Bolomys.

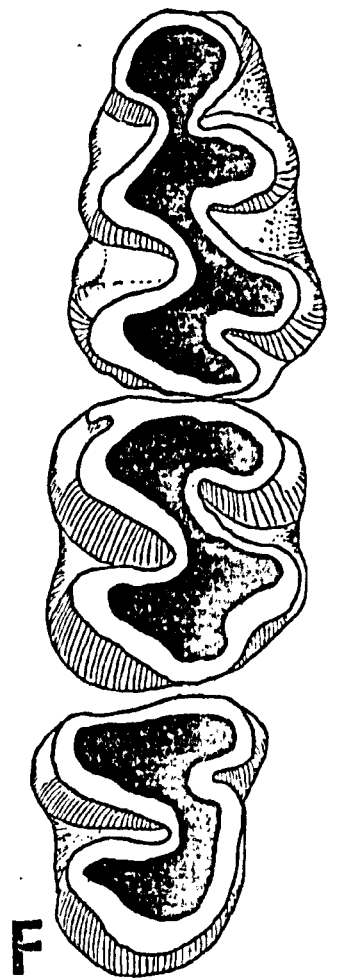
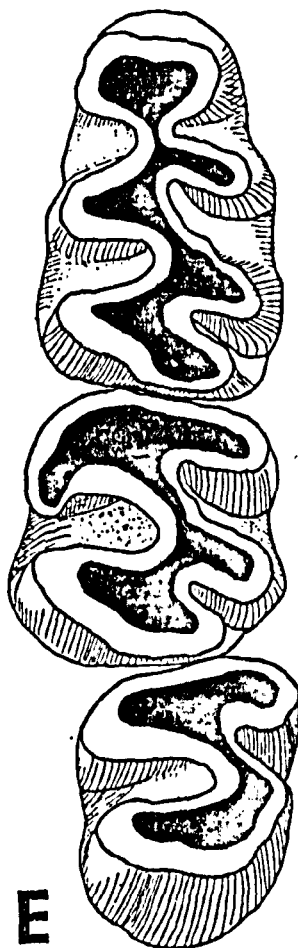
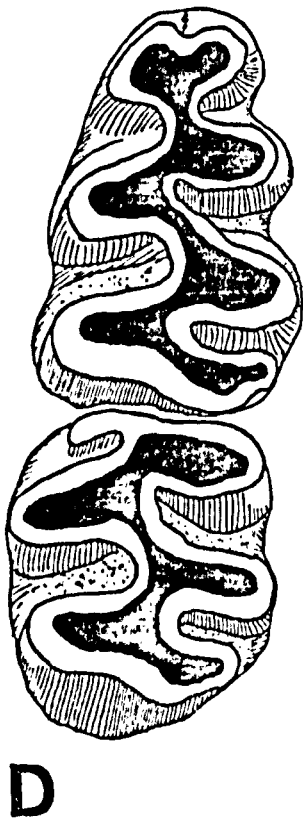
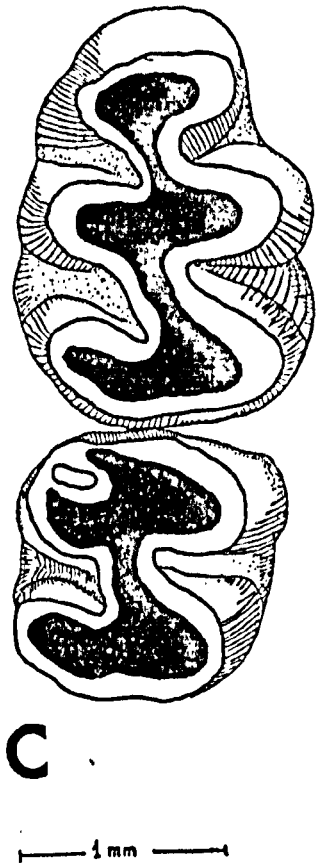
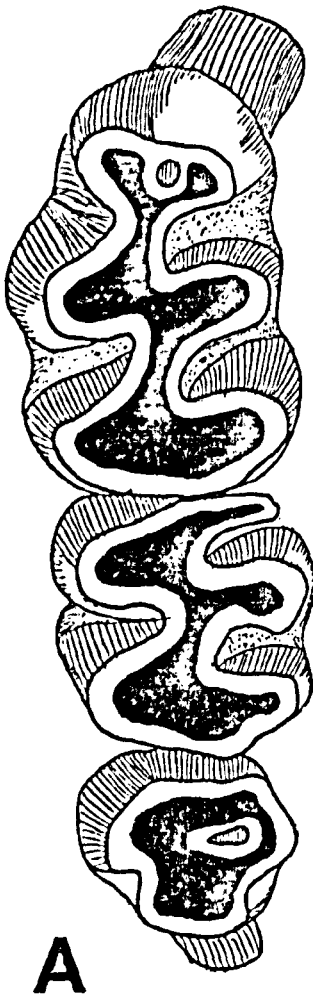
The posterior palate is very similar to Bolomys. It can be accurately reconstructed from the available specimens of vorohuensis, and the details which can be observed in the specimen of simpsoni are not different. The molar rows are slightly diverging posteriorwards, whereas in Bolomys they are roughly parallel to one another. The space between the internal borders of the  $M^1$  is definitely longer than the total length of the  $M^1$ , so that the palate is wide, as defined by Hershkovitz (1962). As regards its length, it can be defined as moderately long: the median posterior border of the palate lies behind the posterior border of the  $M^3$ , more so than in Bolomys, but less so than in Zygodontomys. A medial ridge is not observed, but a narrow and shallow groove goes forwards at each side from the anterior palatal foramen to the incisive foramina. From what can be inferred from the incomplete preservation of this region, the mesopterygoid fossa was large, and probably wider than the parapterygoid fossae.

#### Mandible:

The lower jaw of D. vorohuensis is known from the two incomplete lower jaws of the holotype and from specimen MMP M-1066 (Fig. 16, 17). The condyloid and angular processes are not preserved in any of them. The horizontal ramus is

Fig. 18. Upper and lower molar teeth of Dankomys simpsoni, n. gen., n. sp., and Dankomys vorohuensis, n. gen., n. sp.

- A. Left upper molar series of Dankomys simpsoni, n. gen. n. sp. Type, MMP M-1153 Chapadmalal Ftion. Atlantic cliffs between Mar del Plata and Miramar. (Upper Pliocene).
- B. Left upper molar series of Dankomys vorohuensis, MMP M-1077. Lower Vorohue Ftion. Partido de General Pueyrredon, Province de Buenos Aires, Argentina.
- C. Right  $M^1$  and  $M^2$  of Dankomys vorohuensis n. gen., n. sp. Type specimen, MMP M-1064. Lower Vorohue Ftion., other data as in B.
- D. Left  $M_1$  and  $M_2$  of Dankomys simpsoni n. gen., n. sp. Type specimen, MMP M-1153 (Other data as in A.).
- E. Left lower molar series of Dankomys vorohuensis, n. gen., n. sp. MMP M-1066. Lower Barranca Lobos Ftion., Partido de General Pueyrredon, Prov. de Buenos Aires, Argentina.
- F. Left lower molar series of Dankomys vorohuensis, type specimen, MMP M-1064. (Other data as in C.).



robust and high, as in Zygodontomys, relatively deeper than in Bolomys and the subgenera of Akodon. The height of the ramus at the middle of the  $M_1$  is noticeably longer than the length of the diastema, whereas in Bolomys it is merely slightly longer than the diastema. The border of the ramus immediately in front of the  $M_1$  slants downwards forming an obtuse angle with the upper border of the symphysis, whereas in Bolomys, Zygodontomys, and several species of Akodon, it descends abruptly, almost perpendicular to the symphysis. The symphysis is moderately long, and relatively low, the antero-superior point of the diastema being at a level lower than the alveolar row. The lower masseteric crest is moderately well marked, more so than in Bolomys and Akodon, but less than in Zygodontomys. As in the latter, its most anterior point lies somewhat before the level of the anterior border of the  $M_1$ . Here it joins a moderately developed upper masseteric ridge, which first runs parallel to the lower masseteric crest, to diverge upwards behind the level of the entoconid of  $M_1$ . The mental foramen is normally developed and it is visible in lateral view. The coronoid process is not very high and does not project backwards, its anterior border being almost straight and gradually sloping backwards from the anterior part of the  $M_3$ . The capsular projection of the base of the incisor is only slightly developed, and the posterior tip of the incisor reaches slightly behind the coronoid process. In internal view, the symphysis looks rather strong and its posterior point lies perpendicular to the anterior border of the root of the  $M_1$ , or a little behind this point. The ramus is high, has a moderately concave surface, and the capsule of the incisor is not visible behind the  $M_3$ . The mandibular ramus of D. simpsoni agrees with

the above description, but it is clearly deeper and has a stronger symphysis, which extends somewhat farther backwards than in vorohuensis.

Teeth:

The upper incisors of D. vorohuensis are very similar to those of Bolomys, both by their being orthodont and by their form and relative development. They are, however, relatively weaker than in most species of Bolomys. The same can be said of the lower incisors, as is indicated both by their relative size and by the development of the capsular projection of the mandible. The lower incisors of D. simpsoni are evidently stronger than those of vorohuensis.

The molar teeth in the two species of Dankomys show a moderate coronal hypsodonty, and the masticatory surface is slightly terraced in moderately worn teeth, becoming plane with more advanced wear. The molars are remarkably broad and robust, clearly more so than in Bolomys and Zygodontomys, and differing sharply from the more slender and narrow molar teeth of species of Akodon. Both the upper and the lower first molar have four roots.

The enamel pattern is simplified beyond the condition found in Bolomys, being in this respect more comparable to Zygodontomys and Calomys, and clearly different from that in most of the species of Akodon. In D. vorohuensis, the lophs of the upper molars are transverse in position, and the area of the main cusps of each side well opposed to each other. The mesoloph is completely fused with the paraloph, and no evidence of it is left. The metaloph is also completely coalesced with the posteroloph, not being any indication of the posteroflexus in the M<sup>1</sup> and the M<sup>2</sup>, merely a slight one

in the  $M^2$ . As in Bolomys, the paraflexus and the metaflexus are moderately directed backwards, and the hypoflexus and the protoflexus (the latter only in the  $M^1$ ) are slightly inclined forwards, so that the opposite flexi incipiently alternate with each other. In Zygodontomys and Calomys are distinctly opposed to each other, and they do not alternate. As in Bolomys, the median mure is, in Dankomys slightly oblique, so that the hypocone is more directly connected to the internal part of the paraloph than to the protocone. In Zygodontomys and Calomys this diagonal trend is not seen, and the median mure is quite in an anteroposterior position. Mesostyles, enterostyles and enterolophs are completely absent in all the available specimens.

The  $M^1$  and  $M^2$  are trilophodont in the type specimen, but specimen MMP 1077 has a bilophodont  $M^2$  by the disappearance of the paraflexus and parafossetus, certainly because of more advanced wear.  $M^1$  and  $M^2$  are markedly broader than in Bolomys (Fig. 11). In absolute size, the  $M^1$  is as short as in the shortest  $M^1$  of B. obscurus, and it is always shorter than in specimens of B. lenguarum. But in width, the  $M^1$  of D. vorohuensis is clearly broader than in all the examined specimens of Bolomys, excepting one individual of B. lenguarum and a few specimens of the larger species B. lactens and B. scagliarum (see Fig. 13).

The procingulum of the  $M^1$  is simple in the two available specimens; it is transverse in position and sub-elliptical in outline; an anteromedian flexus, as well as a protostyle and an anteroflexus are completely lacking, as is usually the case in the species of Bolomys. Again as in the latter, the anterior mure is slightly oblique in position,



whereas in Zygodontomys it is distinctly anteroposterior in direction.

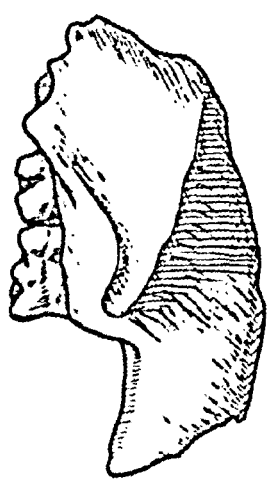
MMP M-1064 has the  $M^2$  clearly longer than wide, but in MMP M-1077 it is slightly longer than wide. In both cases, however, the absolute width of the tooth is visibly greater than in most of the examined specimens of Bolomys, the only exception being some individuals of B. scagliarum and B. lactens. The protoflexus is completely absent in  $M^2$  and  $M^3$  in the two specimens. The  $M^3$ , known only from specimen MMP M-1077, is bi-lophodont, roughly 8-shaped and relatively less reduced in size than in Bolomys (Fig. 11, 18).

In the single known specimen of D. simpsoni the upper molars show a stage of wear similar to that of MMP M-1064, and they agree with the molars of this specimen in size and in most of the character states, as described above. The  $M^1$ , however, has a well-defined anteromedian flexus, and the procingulum is more oblique in position. The  $M^2$  is wider than long and is clearly trilophodont. The  $M^3$  is cylindrical, its paraflexus being isolated as a parafossetus, and its metaflexus and hypoflexus being poorly developed, not defining an 8-shaped outline as in D. vorohuensis.

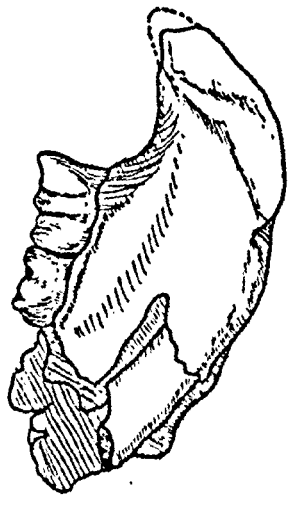
The lower molars of Dankomys vorohuensis have the lingual cusps at a more anterior position than the labial ones, as is the case in Bolomys and most of the akodonts, but the enamel pattern differs from that of Bolomys in several respects. In the  $M_1$  and the  $M_2$ , the metalophid is slightly directed forwards from the area of the metacone to the anterior murid, and the entolophid and the posterolophid are even more inclined in the same direction. Therefore, the mesoflexid and posteroflexid are noticeably oblique and more directed

Fig. 19. Mandible, Upper jaw and upper dentition of Dankomys simpsoni, n. gen., n. sp., and internal view of upper molar series of Dankomys, Bolomys, Calomys and Zygodontomys.

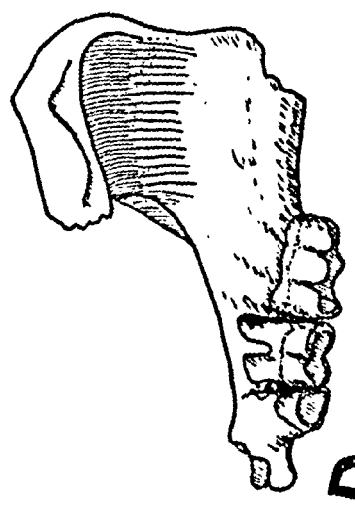
- A. External view and B. internal view of left incomplete lower jaw of Dankomys simpsoni, n. gen., n. sp. Type specimen, MMP Chapadmalal Formation, Atlantic cliffs between Mar del Plata and Miramar, SE Buenos Aires Province, Argentina (Upper Pliocene)
- C. Ventral view and D, lateral view of portion of right maxilla of Dankomys simpsoni, n. gen., n. sp. Type specimen, MMP (Other data as in A and B)
- E. Internal view of right molar series of Zygodontomys thomasi Allen. Female, BMNH 14.9.1.60. El Trompillo, Carabobo, Venezuela.
- F. Internal view of right molar series of Calomys venustus Thomas. Female, BMNH 25. 13. 13.31. Concepcion, Tucuman, Argentina.
- G. Internal view of left upper molar series (inverted) of Dankomys vorohuensis MLP Lower Vorohue Formation, Partido de General Pueyrredon, Prov. de Buenos Aires, Argentina (Lower Pleistocene).
- H. Internal view of left upper molar series (inverted) of Dankomys simpsoni, n. gen., n. sp. Type specimen MMP (Other data as in A. and B.).



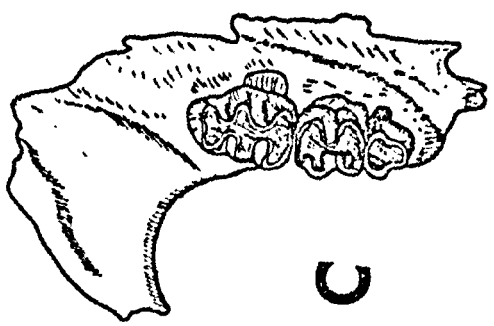
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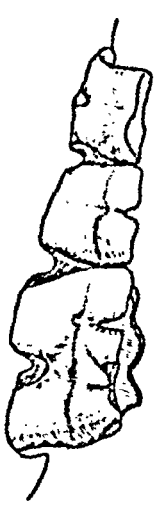
**B**



**D**



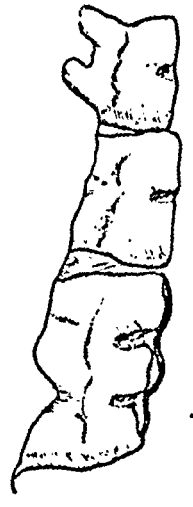
**C**



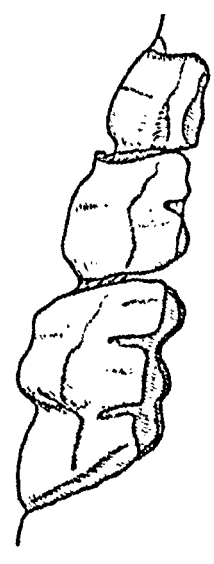
**E**



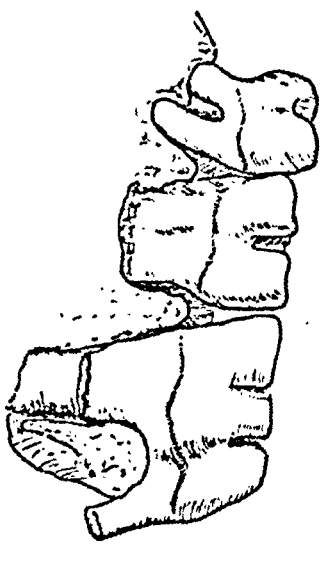
**F**



**G**



**H**



**I**

'backwards, the latter being rather reduced in depth, recalling the condition in Zygodontomys, specially in the  $M_2$ . The hypoflexid is large and wide in all three molars, more re-entrant than is usual in Bolomys. The area of the protoconid is triangular in outline and opposes the mesoflexid. The median mure is short and wide, and is oblique in direction, connecting the hypoconid with the internal part of the entolophid. There is no trace of the mesolophid in all three molars, and absent are also the mesostylid and the ectolophid. An ectostylid is present in the  $M_2$  and the  $M_3$  of the two known specimens, but it occurs in the  $M_1$  of the type specimen, although absent in MMP M-1066. Ectostylids are very rare in the  $M_1$  of Bolomys obscurus, but they are often present in B. lenguarum and in other species of this genus.

The  $M_1$  is tetralophodont, and has a simple procingulum which lacks any trace of an anteromedian flexid, and which is ovate in outline in MMP M-1066, more rounded in the type specimen. Anteroflexid, protostylid and metastylid are completely absent in the two specimens, and there is neither an indication of the anterolabial cingulum, which is often present in Bolomys. Another outstanding difference in the procingulum as regards the latter genus, is its greater anteroposterior development, and its separation from the rest of the tooth by a well marked "neck" defined by deeply infolded and fairly opposed protoflexid and metaflexid. Zygodontomys and Calomys resemble Dankomys in this character, but the procingulum of Bolomys is much less clearly defined because the corresponding flexids are rather shallow.

In absolute size, the  $M_1$  of the two specimens are wider than is usual in Bolomys. The length of the  $M_1$

of the type specimen of vorohuensis is larger than in MMP M-1066, and the two specimens are only surpassed in length by the largest species of Bolomys (Fig. 11, 14).

The  $M_2$  is bilophodont in MMP M-1066, as in it the posteroflexid was worn off, but this flexid, although reduced and directed outwards and backwards much as in Zygodontomys, is present in the type specimen. The  $M_2$  is relatively shorter and wider than in most species of Bolomys (Fig. 11, 13, 14). In absolute size, the length of the  $M_2$  of the two specimens can be equated with large individuals of B. obscurus, or with small individuals of B. lenguarum, but in width they surpass any Bolomys. Here again, a superficial resemblance is found with Zygodontomys, which  $M_2$  is also relatively shorter than in Bolomys. The protoflexid is very reduced in MMP M-1064, completely worn-off in MMP M-1066. Resembling in this respect Pseudoryzomys, Wiedomys and some species of Phyllotis, D. vorohuensis is distinguished from Bolomys, most species of Akodon and Zygodontomys, by its large  $M_3$ , which is almost as long (MMP M-1064) or even a little longer (MMP M-1066) than the  $M_2$ . In the two specimens, the enamel figure is sigmoid, resembling some species of Phyllotis. In these moderately worn teeth there is not trace of the protoflexid. The hypoflexid is more deeply infolded than the mesoflexid and the two flexids are clearly involuted.

The single known individual of D. simpsoni is clearly distinguishable from D. vorohuensis in the morphology of  $M_1$  and  $M_2$ . In being robust, broad and with a well marked procingulum in the  $M_1$ , they agree with vorohuensis, but the labial flexids, as well as the labial lophids, are clearly more transverse in position, and the posteroflexid is deeper

in the two molars. Moreover, the procingulum of the  $M_1$  is less developed anteroposteriorly, and bears a shallow, but clearly distinguishable anteromedian flexid. The  $M_1$  and the  $M_2$  are even wider than in vorohuensis, and there is a well marked protoflexid in the  $M_2$ .

Affinities:

From the above description, I believe that there is a strong case to assume that Dankomys is a distinct genus of the Akodontini, allied to Bolomys. It is more advanced than Bolomys in molar specializations, probably connected with more herbivorous feeding habits. In this respect, Dankomys parallels most closely the dental evolution of some of the phyllotines, particularly Phyllotis. The possibility that it actually may be placed in the Phyllotini, does not seem to be supported by the available evidence. In skull characters, Dankomys closely agrees with Bolomys, and it differs from the phyllotines in the tapering rostrum and in palatal structure. Moreover, the molar teeth, though convergent to those of Phyllotis in the relatively high crowns, involution, and tendency to flattening of the crown surfaces with moderate wear, are less markedly evolved in all these respects than the molars of Phyllotis, and they differ additionally from Phyllotis in lacking any trace of the anterolabial cingulum, which is always well developed in the species of this genus.

Probably Bolomys and Dankomys are patristically closely connected, and the latter may be conceived as a lineage which departed from a Bolomys-like ancestor approximately by Middle Pliocene times, to become more adapted to an herbivorous diet. Dankomys may represent, therefore, a

lineage of the akodontines which shifted in feeding habits, but which did not succeed in surviving, probably because of the competition of the phyllotines. It cannot be conceived, as an ancestral form of the phyllotines. Actually, true representatives of Phyllotis were contemporaneous and even older than Dankomys, and the advanced phyllotines comparable to Dankomys in molar structure, are probably derived from more primitive phyllotines, resembling Calomys, and having a common ancestor with the akodontines in much earlier, probably Miocene, times.

Variate Specimen	Dankomys voro- huensis, TYPE MMP M-1064. Vo: rohú Ftion.	Dankomys voro- huensis, MMP M- 1077. Vorohú formation.	Dankomys voro- huensis, MMP M- 1066. Bca. Lo- bos Ftion.	Dankomys simpso- ni, TYPE, MMP M- 1153. Chapadma- lal Ftion.
Length upper diastema	8.31	-----	-----	-----
Length incisive foramina	7.24	-----	-----	-----
Width zygomatic plate	2.69	-----	-----	3.84
M <sup>1</sup> -M <sup>3</sup> , alveolar length	-----	5.25	-----	5.06
M <sup>1</sup> -M <sup>3</sup> , coronal length	-----	5.18	-----	4.88
M <sup>1</sup> , length	2.32	2.30	-----	2.32
M <sup>1</sup> , width	1.55	1.49	-----	1.58
M <sup>2</sup> , length	1.49	1.52	-----	1.50
M <sup>2</sup> , width	1.46	1.33	-----	1.49
M <sup>3</sup> , length	-----	1.19	-----	1.02
M <sup>3</sup> , width	-----	1.21	-----	1.24
Upper incisor, depth	1.46	-----	-----	-----
Upper incisor, width	0.87	-----	-----	-----
Length mandible, sym- physis- M <sup>3</sup>	10.05	-----	9.57	-----
Length lower diastema	3.84	-----	3.71	-----
Depth of mandible below M <sub>1</sub>	4.48	-----	4.35	4.74
M <sub>1</sub> - M <sub>3</sub> , alveolar length	5.82	-----	5.44	-----
M <sub>1</sub> - M <sub>2</sub> , coronal length	5.63	-----	5.25	-----
M <sub>1</sub> , Length	2.26	-----	2.11	2.20
M <sub>1</sub> , width	1.39	-----	1.36	1.46
M <sub>2</sub> , length	1.61	-----	1.49	1.55
M <sub>2</sub> , width	1.49	-----	1.47	1.55
M <sub>3</sub> , length	1.63	-----	1.55	-----
M <sub>3</sub> , width	1.27	-----	1.30	-----
Lower incisor, depth	1.24	-----	1.23	1.61
Lower incisor, width	0.74	-----	0.74	0.99

TABLE No. 9. Measurements (in mm) of the known specimens of Dankomys.



7.2.3. GENUS AKODON, MEYEN

7.2.3.1. A REASSESSMENT OF THE GENUS AKODON AND ITS  
SUBGENERA

Akodon is the most polytypic of the akodontine sigmodontines, and is undoubtedly the most confusing and less understood of them all. However, once the species grouped here under Bolomys are kept apart, the limits of Akodon appear more precise. One gains the impression that all the remaining forms usually grouped under Akodon, Abrothrix, Chroeomys, Deltamys, Hypsimys, Thalpomys and Thaptomys, represent a complex array of allied species, more closely connected with each other than with any species of the remaining genera of akodont rodents (Bolomys, Oxymycterus, etc.). This impression supports the idea of a large central genus, Akodon, within which it may prove convenient to distinguish some distinctive single species or set of species as subgenera.

This was basically Ellerman's (1941: 406-410) conception of Akodon. I must admit that in the first steps of my revisionary studies of the akodont cricetids, I was reluctant to agree with Ellerman's lumping of Thomas' full genera under Akodon. Therefore, I expressed (in Reig, Kiblisky & Linares, 1971; Bianchi, Reig, Molina and Dulout, 1971) my tentative acceptance of full generic status for most of the various taxa included under Akodon by Ellerman. In fact, some of the arguments of Ellerman on this matter were hard to accept, and one had the impression that he was inclined to act as too much of a 'lumper'.

However, as I advanced in the knowledge of the confusing array of species in this group, I became more and

more convinced of the convenience of treating them as a single evolutionary unit under a single genus-concept. Therefore, and on other grounds, I arrived at conclusions rather closely in agreement with Ellerman's concept of Akodon, resulting from my proposals as to the limits of Bolomys and from other reinterpretations.

The first major change is, indeed, the complete withdrawal of the species of Bolomys, as here understood, from the extensions of Akodon, and the inclusion under the latter genus of albiventer and berlepschi (see later). The second is that I do not recognize Thaptomys as a distinct subgenus. I could not find any relevant difference, going distinctly beyond the limits of variation occurring within Akodon s. s., to keep A. nigrita Licht, the type and the single species of Thaptomys (see Cabrera, 1961; Massoia, 1964), as a separate subgenus. Cranially and dentally, nigrita is a typical Akodon and its alleged fossorial adaptations are too incipient to deserve any special taxonomic treatment.

Thalpomys is here only tentatively recognized as a separate subgenus. Thalpomys is more easily distinguishable from Akodon than Thaptomys, but is too poorly known for me to be able to come to any convincing conclusion as to the degree of its differentiation. Chroeomys, I believe, is still nebulous as to its limits. Chroeomys is certainly a differentiated offshoot of the Andean akodonts, but it is difficult to assess the species to be included here. It is quite possible that some species of Akodon s. s., which have been incorrectly associated with Bolomys (see Tate, 1932h), may be proven as better placed within Chroeomys. Deltamys, Hypsimys and Abrothrix, contrariwise, are clearly distinguish-

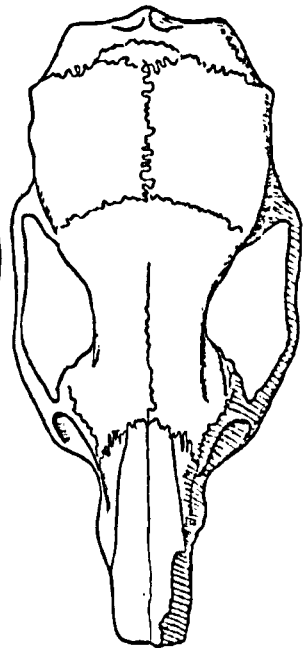
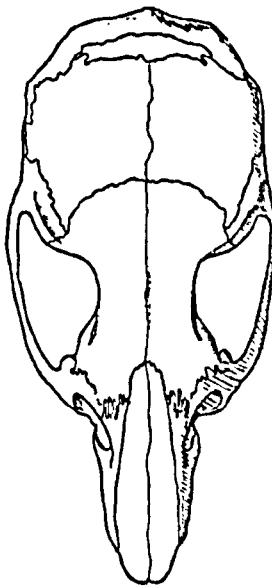
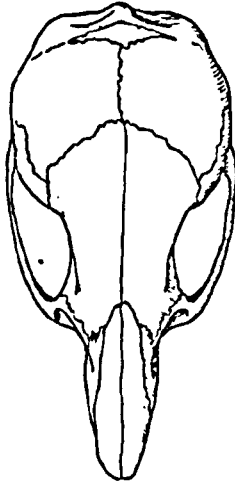
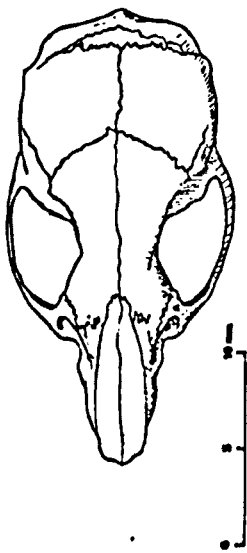
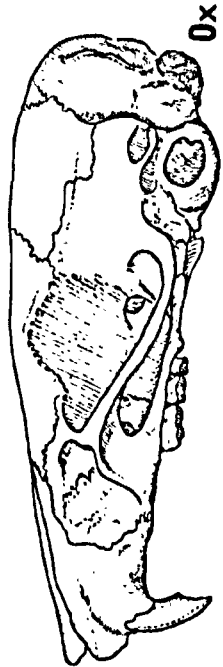
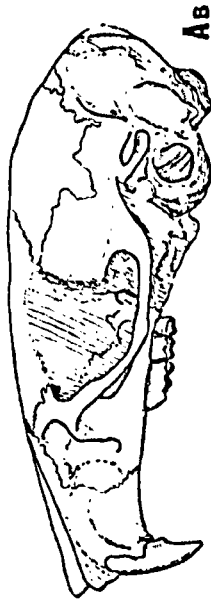
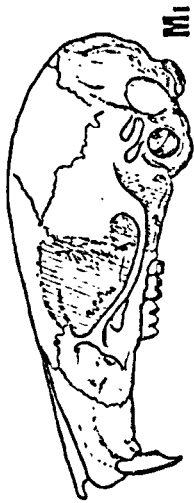
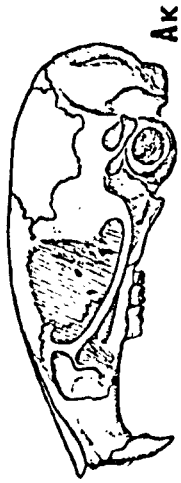
Fig. 20. Skulls of typical representatives of Akodon, Microxus,  
Abrothrix and Oxymycterus. Left row, lateral views;  
right row, dorsal views.

AK Akodon boliviensis boliviensis, MBUCV 1.1889.  
30 Km. NW Ollantaytambo, Cuzco, Peru.

MI Microxus minus Thomas, Female, Type specimen,  
BMNH 1.1.1.48, Limbane, Puno, Peru.

AAB Abrothrix longipilis Thomas, Male, BMNH 98.8.2.2.  
Valparaiso, Chile.

OX. Oxymycterus rufus Desmarest, Male, Type speci-  
men of Oxymycterus platensis Thomas, BMNH 99.  
10.4.1.



able subgenera in diagnostic features and also in extension.

A point of clarification is still necessary as regards Abrothrix. Recently, Hershkovitz (1966: 96, 127) included Microxus under Abrothrix on the argument that M. minus, the type species of Microxus, is an Abrothrix. Actually, this statement could hardly be supported by a close comparison of the type specimens of M. minus (Fig. 20), with a typical representative of longipilis (the type-species of Abrothrix). Microxus, as represented by its type-species and by M. bogotensis, is a genus quite distinct from Abrothrix in skull and in molar morphology (Fig. 20). As already recognized by Thomas (1909), Microxus is much more closely related to Oxymycterus, to the extent that the species iheringi, which looks like an intermediate form between the two, has been erratically placed in one or other of those genera. By the same reasons, I do not support Cabrera (1961), who treats Microxus as a subgenus of Akodon.

A redefinition of Akodon on the basis of cranial and dental characters now seems quite essential.

Genus Akodon, Meyen

- 1833. Akodon, Meyen. Nova Acta Leopold. 16, pt.11: 599
- 1837. Abrothrix, Waterhouse. Proc.Zool.Soc. London: 21 (accepted as a subgenus)
- 1839. Hesperomys, Wagner. Schreber. Säugeth. Suppl. 3: 516 (in part)
- 1886. Habrothrix, Thomas. Pro.Zool.Soc. London: 450
- 1887. Hesperomys; Leche. Zool.Jahrb., 1: 687 (in part)
- 1916. Chalcomys, Thomas. Ann. Mag. Nat. Hist. (8) 18: 338.

1916. Chrocomys, Thomas. Ann. Mag. Nat. Hist.  
(8) 18: 340 (accepted as a subgenus).
1916. Bolomys, Thomas. Ann. Mag. Nat. Hist.  
(8) 18: 339 (in part, not including  
the type species).
1916. Thalpomys, Thomas. Ann. Mag. Nat. Hist.  
(8) 18: 339 (provisionally accepted as  
a subgenus).
1916. Thaptomys, Thomas. Ann. Mag. Nat. Hist.  
(8) 18: 339
1917. Deltamys, Thomas. Ann. Mag. Nat. Hist.  
(8) 20: 98 (accepted as a subgenus).
1918. Hypsimys, Thomas. Ann. Mag. Nat. Hist.  
(9) 1. 190 (accepted as a subgenus)

Type species.

Akodon boliviensis Meyen, by original designation.

Distribution:

Temperate zone meadows, grasslands and brushlands of Argentina, Chile, Uruguay, Paraguay, Bolivia and South Eastern Brazil. Andean valleys, highlands and fringes of mountain forests of Argentina, Chile, Bolivia, Peru, Ecuador, Colombia and Venezuela.

Included species:

Twenty-nine living species grouped in six subgenera: Abrothrix, Akodon, Chrocomys, Deltamys, Hypsimys and Thalpomys (see names of recognized species under each subgenus).

Cranial character-states:

Skull usually slender, with a typically fairly narrow and rounded brain case, a fairly elongated occipital region and a rostrum of regular shape, not tapering forwards in lateral view. Upper profile of the skull sloping forwards and backwards from the posterior part of the frontals. Zygomata slightly expanded and not markedly convergent anteriorly. Nasals usually longer than, or as long as, the frontals, their anterior

border passing forward beyond the anterior plane of the incisors, but not projected or expanded to form a trumpet-shaped opening. Posterior borders of the nasals usually tapering backwards and projecting beyond the fronto-premaxillary suture. Frontals long, usually with a narrow and transversely convex interorbital region with more or less sharply squared edges not forming a well defined supraorbital ridge. Fronto-parietal suture angular or crescentic in shape. Parietals relatively long, their length, in the midline, usually more than half the length of the frontals, not extending forwards through lateral processes between frontals and temporals. Interparietal moderately reduced in width and length. Zygomatic plate moderately developed, relatively narrow and low, but usually with anterior border vertical, straight or slightly concave, not slanting gradually backwards from its lower root to the upper border. Upper corner of the zygomatic plate rounded, not projecting forwards. Incisive foramina wide and elongated, narrow behind, usually penetrating between the level of the first molars well beyond their anterior plane, to reach or slightly surpass the level of the protocone of  $M^1$ . Posterior palate long and wide, its median posterior border usually slightly behind the posterior plane of the  $M^3$ . Palatal surface relatively simple, without marked ridges and with shallow grooves. Mesopterygoid fossa narrow and less than width of parapterygoid fossa. Bullae usually small, less frequently moderately large. Mastoid not noticeably inflated. Occipital region somewhat elongated, its posterior border rounded and continuous with the line of the brain case when viewed from the lateral side.

Mandible somewhat slender, its height at  $M_1$

usually shorter than diastema length. Lower masseteric crest present, but not strong, reaching forward to the level of the anterior half of  $M_1$ . Upper masseteric crest rather long and usually as strong as the lower one. Coronoid process rather short, with anterior border gradually slanting backwards. Condylod process relatively low, elongated and projected backwards. Articular surface of the condyle extending dorsally and slightly posteriorly. Capsule of incisor root normally not projected as a well developed tubercle, lying on the anterior half of the sigmoid notch. Angular process longer than high.

Dental character-states.

Upper incisors usually opisthodont, less frequently orthodont, never protodont. Molar rows parallel-sided. Molars relatively small, usually with moderately developed cusp hypsodonty, with crested and with bi-level occlusal surface in slightly worn teeth, terraced with advanced wear.

$M^1$  four rooted. Upper molars with labial (paracone-metacone) main cusps only slightly posterior to the level of the lingual ones (protocone-hypocone), and main lophs transverse in position.  $M^1$  and  $M^2$  usually trilophodont in moderately worn teeth. Mesoloph reduced, usually only partially fused with the paraloph, so that a lingual remnant of it is usually present, forming a bifurcated broad median loph marked by a shallow mesoflexus in  $M^1$  and  $M^2$ . Metaloph united with the posteroloph and not reaching the hypocone, almost completely coalesced with posteroloph, so that posteroflexus is very narrow or completely absent in moderately worn teeth. Paraflexus and metaflexus somewhat directed backwards, hypoflexus



and protoflexus somewhat forwards, the opposite flexi slightly alternating. Enterostyle and enteroloph usually completely absent. Mesostyle often present in  $M^1$  and  $M^2$ , usually united with the remnant of mesoloph.  $M^2$  usually much longer than wide.  $M^3$  much reduced, cylindrical in moderately worn teeth. Procingulum of  $M^1$  moderately simple, slightly oblique in position, usually clearly biconulate by the presence of a well-developed anteromedian flexus. Procingulum united to protocone through an anteroposteriorly oriented anterior mure. Protoflexus absent undivided by a protostyle, anteroflexus usually present but not deeply infolded. Anteroloph well defined and usually united to paratsyle. Protoflexus of  $M^2$  evident in moderately worn teeth, absent on  $M^3$  of similar stage of wear.

Lower molars with lingual cusps (metaconid and entoconid) placed fairly anterior to the labial ones (protoconid-hypoconid), with metalophid, as well as entolophid and posterolophid usually oblique, directed slightly forwards from the lingual border to the labial one. Mesolophid almost completely fused with entolophid, but a weak lingual remnant, usually united with a mesostyle, is often present in most of the species. Ectolophid and ectostylid frequently present in  $M_1$ , occasionally in  $M_2$ , rarely in  $M_3$ . In  $M_1$  and  $M_2$ , hypoflexid broad and transverse, mesoflexid directed obliquely forwards from outside. Posteroflexid well developed, oblique and parallel to the mesoflexid, absent in  $M_3$ .  $M_1$  tetralophodont, with a somewhat complex procingulum, defined by a usually well defined, well-infolded metaflexid and protoflexid, anteroflexid normally absent. Protostylid and anterolabial cingulum usually present. Anteromedian flexid normally well developed

in moderately worn teeth.  $M_2$  trilophodont, well longer than wide, with protoflexid usually well marked in moderately worn teeth.  $M_3$  relatively large, but ever smaller than  $M_2$ , usually bilophodont and sigmoid-shaped in outline, with protoflexus frequently present in moderately worn teeth.

Remarks.

The above morphological description of the character-states of Akodon is intended to apply to the whole genus. Akodon is, however, rather varied and, as already mentioned, the distinction of various subgenera seems here to be appropriate. Therefore, in all those cases where exceptions to the above description are known, the corresponding character-states have been qualified as usually present. Departures from those states are indicated in the diagnosis of the subgenera which are provided in the following pages. These diagnoses must be taken as provisional as they are not based on a thorough revision of all or most of the species of each subgenus. They are mostly based on the characters of the type-species of each, and checked through the examination of series of at least 70% of the included species.

Subgenus Akodon, Meyen

1833. Akodon Meyen, Nova Acta Leopold. 16, pt. 11: 599.
1839. Hesperomys, Wagner, Schreber. Säugeth. Suppl. 3: 516 (in part).
1884. Habrothrix, Thomas, Proc. Zool. Soc. London : 450
1886. Hesperomys, Leche, Zool. Jahrb. 1: 687 (in part)
1916. Chalcomys, Thomas, Ann.Mag.Nat.Hist. (8) 18: 338

1916. . Thaptomys, Thomas, Ann.Mag.Nat.Hist.  
(8) 18: 339
1916. Bolomys, Thomas, Ann.Mag.Nat.Hist.  
(8) 18: 339 (in part)

Type species: Akodon boliviensis Meyen (by original designation)

Known distribution:

As for the genus.

Included species:

aerosus, andinus (a Chroeomys?),  
albiventer (a Chroeomys?), azarae, boliviensis, chacoensis,  
cursor, dolores, iniscatus, molinae (?), nigrita, nucus (?),  
olivaceous, orophilus pacificus, puer, serrensis, surdus,  
tolimae, urichi, varius, xantorhynchus. (additionally, two  
fossil species described in the following pages. Akodon  
lorentzini, n. sp., and A. johannis, n. sp.)

Characters.

Skull normally built and usually somewhat elongated behind. Nasals longer to slightly shorter than frontals. Zygomatic plate normal, with anterior border usually vertical in position. Brain case moderately long, usually not broadened, its breadth as large or slightly shorter than 1/2 the condylobasal length. Interorbital region usually fairly narrowed, without supraorbital ridges. Anterodorsal frontal sinuses not inflated. Interparietal normally to much reduced. Bullae usually not enlarged. Incisive foramina usually reaching the protocone of M<sup>1</sup> or slightly before it. Posterior border of palate behind the posterior border of M<sup>3</sup>. Mandible relatively high and stout, more slender in the smaller species, with masseteric crest normally developed and reaching forward the middle of the M<sub>1</sub>. Incisor capsule usually not

projected as a definite tubercle. Upper incisors normally opisthodont, less frequently orthodont. Molars not markedly elongated and narrowed, with a moderately developed tubercular hypsodonty. Molar crowns usually bi-level, terraced to planate with wear, cusps neither noticeably tuberculate, nor with noticeably inclined enamel walls.  $M^1$  usually with an anteromedian flexus and an anteroflexus. Paraflexus of  $M^2$  directed lingually, the anteroloph of normal position. Mesoloph remnants usually united to mesostyle, typical on  $M^1$  and  $M^2$ . Entoconid wide, but not noticeably bulging laterally in  $M_1$  and  $M_2$ . Mesoflexid and posteroflexid of  $M_1$  and  $M_2$  normally inclined and well developed. Anteromedian flexid of  $M_1$  frequently present, but only exceptionally deeply infolded, metaflexid moderately to scarcely infolded. Mesolophid remnants, ectolophids, ecto- and mesostylids frequently present.  $M_3$  long, but clearly shorter than  $M_2$ .

Subgenus Abrothrix Waterhouse

1837. Mus (Abrothrix) Waterhouse, Proc. Zool. Soc. London. 21 (proposed as a subgenus of Mus)
1843. Habrothrix Wagner, Schrebers Saugeth. Suppl. 3. (in part)
1895. Acodon Thomas, Ann.Mag.Nat.Hist. (6) 14: 369 (in part)
1916. Abrothrix Thomas, Ann.Mag.Nat.Hist. (8) 18 (considered as a full genus)
1941. Akodon (Abrothrix), Ellerman, The families and gen. of living rod. Vol. 2: 409,416. (proposed as a subgenus of Akodon)
1943. Akodon (Abrothrix), Osgood, Field Mus. Publ. Zool. 30: 184-198 (revision of most of the living species).

Type species: Akodon (Abrothrix) longipilis Waterhouse (by

original designation).

Distribution:

Low lands and mountain valleys of southern and central Chile; Andean slopes and low valleys of Argentina from southern Santa Cruz to Mendoza; mountain valleys of Tucuman, Argentina.

Included species:

illuteus, lanosus, longipilis and sanborni (additionally, two fossil species described in the following pages. A. kermackii, n. sp., and A. magnus, n. sp.

Characters.

Skull strong and elongated, with a rather long and slender muzzle. Nasals well longer than frontals, exceeding backwards the fronto-maxillary suture and slightly projecting forwards. Zygomatic plate relatively deep and short, with anterior border vertical or slightly inclined backwards. Brain case relatively long, rounded and slightly broadened, its breadth as large as  $1/2$  the condylobasal length. Interorbital region of median breadth, without supraorbital ridges and with smoothly rounded edges. Anterodorsal frontal sinuses slightly inflated, its dorsal surface rounded. Interparietal normally reduced. Incisive foramina elongated but scarcely reaching the protocone of  $M^1$ . Posterior border of the palate well behind the posterior border of the  $M^3$ . Bullae not enlarged. Mandible moderately low and elongated, with upper masseteric crest better marked than the lower masseteric crest, slightly surpassing forwards the middle of the  $M_1$ . Incisor capsule projected as a comparatively fairly developed tubercle. Upper incisors orthodont, rather strong. Molars comparatively broad, with a moderately well developed tubercular hypsodonty

and a slight crown hypsodonty. Molar crowns bi-level, terraced to planate with advanced wear. Cusps not noticeably tuberculate, with somewhat inclined enamel walls. Antero-medial flexus of  $M^1$  completely obsolete or barely noticeable. Anteroflexus present, but shallow. Paraflexus of  $M^2$  directed lingually, anteroloph normal. Mesoloph remnants usually united to mesostyles in  $M^1$  and  $M^2$ . Mesoflexid and posteroflexid of  $M_1$  and  $M_2$  well developed, the former scarcely inclined and the latter smaller and nearly transversal in position. In  $M_1$  and  $M_2$  entoconid typically bulging lingually.  $M_1$  with anteromedian flexid obsolete or occasionally present in an incipient stage as a shallow and open notch, metaflexid little to moderately infolded. Mesolophid remnants constant on  $M_1 - M_3$ , but poorly developed and projecting from the antero-lateral border of the entoconid, usually connected with mesostylids. Ectolophids completely absent, ectostylids sometimes present on  $M_1$ , very rarely so in  $M_2$ .  $M_3$  long, but smaller than  $M_2$ .

Subgenus Deltamys Thomas

1917. Deltamys Thomas, Ann.Mag.Nat.Hist. (8)  
20: 99 (proposed as a full genus)
1941. Akodon (Deltamys) Ellerman, The families  
and genera of living rodents, Vol. 2  
: 409, 414

Type species: Deltamys kempii, Thomas, by original designation.

Distribution:

Delta region of Parana River and Rio de La Plata, and adjacent areas of Argentina and Uruguay.

Included species:

Only the type species.

Characters:

Skull elongated and narrow. Nasals slightly

longer than frontals. Zygomatic plate weak and low. Brain case long, rounded and narrow, its breadth less than 1/2 the condylobasal length. Interorbital region slightly narrowed, without supraorbital ridges. Anterodorsal frontal sinuses moderately inflated. Interparietal very reduced in width. Bullae not enlarged. Incisive foramina reaching the level of the protocone of the  $M^1$ . Posterior border of the palate anterior to the border of the  $M^3$ . Mandible low and elongated, masseteric crests scarcely defined. Incisor capsule projected as a comparatively well developed tubercle. Upper incisor ppisthodont, moderately strong. Molars fairly elongated and narrowed, with comparatively fairly developed tubercular hypsodonty. Molar crowns crested to bi-level, the cusps slightly tuberculate with enamel walls of upper molars inclined posteriorly, of lower molars inclined anteriorly.  $M^1$  with a well defined anteromedian flexus and anteroflexus. Paraflexus of  $M_2$  directed forwards, the anteroloph not reaching the lingual border of the tooth. Mesoloph remnants evident on  $M^1$  and  $M^2$ , united to mesostyles. Lower molars with deeply inclined forward meso- and posteroflexids. Entoconid moderately bulging laterally on  $M_1$  and  $M_2$ . Mesolophid remnants, ectolophid, ecto- and mesostylids absent. Anteromedian flexid of  $M_1$  usually obsolete, metaflexid of  $M_2$  normally well developed,  $M_3$  almost as long as  $M_2$ .

Subgenus Chroeomys Thomas

1916. Chroeomys Thomas, Ann.Mag.Nat.Hist. (8) 18: 340 (proposed as a full genus)
1941. Akodon (Chroeomys), Ellerman, The families and genera of living rodents, Vol. 2 : 409, 415.
1947. Akodon (Chroeomys), Sanborn, Fieldiana, Zool. 31: 137 (revision)

Type species. Akodon pulcherrimus Thomas (= Akodon (Chroecomys) jelskii pulcherrimus, fide Sanborn), by original designation.

Distribution.

The high Andes north of Jujuy, Argentina, up to Central Peru.

Included species.

Following the revision of Sanborn (1947) the five species recognized by Thomas are to be lumped into a single polytypic species: jelskii. It is possible, moreover, that albiventer and andinus may belong here.

Characters.

Skull enlarged and broadened behind. Nasals longer than frontals. Zygomatic plate not weakened, but with a rounded anterior border scarcely projecting forwards. Brain case not noticeably long, but broad and rounded, its breadth more than 1.2 the condylobasal length. Interorbital region fairly narrowed, with smoothly rounded edges, without supraorbital ridges. Anterodorsal frontal sinuses not inflated. Interparietal slightly reduced. Bullae enlarged and moderately swollen. Incisive foramina scarcely reaching the level of the protocone of the  $M^1$ . Posterior border of the palate at a line with the posterior border of  $M^3$ . Mandible relatively strong and high, with masseteric crests slightly developed and reaching the middle of the  $M_1$ . Incisor capsule weak and not projected at all as a tubercle. Upper incisors slightly opisthodont. Molars comparatively broad, with a relatively well developed tubercular hypsodonty. Molar crowns bi-level, with cusps slightly tuberculate and with enamel walls slightly inclined.  $M^1$  without a distinct anteromedian flexus, but with a well developed and deeply infolded antero-



.flexus. Paraflexus of  $M^2$  directed lingually, the anteroloph short, but of normal position. Mesoloph remnants and mesostyle absent or very small on  $M^1$  and  $M^2$ . Entoconid of  $M_1$  and  $M_2$  broad but not bulging laterally. Mesoflexid and posteroflexid of  $M_1$  and  $M_2$  normally inclined and well developed, rather open. Anteromedian flexid and metaflexid of  $M_1$  very deeply infolded. Mesolophid remnants, ectolophid, ecto- and mesostylids absent.  $M_3$  not enlarged, clearly smaller than  $M_2$ .

Subgenus Hypsimys Thomas

1918. Hypsimys, Thomas, Ann.Mag.Nat.Hist. (9) 1: 190.

1941. Akodon (Hypsimys), Ellerman, The families and genera of living rodents, Vol. 2: 409, 414.

Type species: Hypsimys budini Thomas, by original designation.

Distribution:

Mountains of northwestern Argentina, in the Province of Jujuy.

Included species:

The type species only. After a comparison of the type specimens, I agree with Cabrera (1961) that deceptor Thomas 1921 is a synonym of budini Thomas 1918.

Characters:

Skull broadened behind. Nasals as long or slightly shorter than frontals. Zygomatic plate normal, but with a somewhat inclined backwards anterior border. Brain case long, rounded and broad, its breadth more than 1/2 the condylobasal length. Interorbital region not noticeably narrowed, without supraorbital ridges. Anterodorsal frontal sinuses not inflated. Interparietal normally reduced.

Incisive foramina reaching slightly behind the level of the protocone of  $M^1$ . Posterior border of the palate anterior to the posterior border of  $M^3$ . Bullae not enlarged. Mandible slender, with upper masseteric crest better defined than the lower masseteric crest. Incisor capsule projected as a slightly developed tubercle. Upper incisors orthodont, moderately strong. Molars strongly elongated and narrowed, with a comparatively well developed crown hypsodonty. Molar crowns <sup>i1</sup> bevelled to terraced with more advanced wear, the cusps neither noticeably tuberculate, nor with the enamel walls noticeably inclined.  $M^1$  without an anteromedian flexus of an anteroflexus. Paraflexus of  $M^2$  directed lingually, the anteroloph of normal position. Mesoloph remnants evident on  $M^1$  and  $M^2$ , mesostyles absent or very low. Entoconid of  $M_1$  and  $M_2$  not bulging laterally. Mesoflexid and posteroflexids of  $M_1$  and  $M_2$  strongly inclined forwards and rather shallow. Anteromedian flexid of  $M_1$  very shallow and open, metaflexid normally well developed. Mesolophid remnants, ectolophid, ecto- and mesostylids absent.  $M_3$  long, but clearly shorter than  $M_2$ .

Subgenus Thalpomys Thomas

1916. Thalpomys Thomas, Ann.Mag.Nat.Hist. (8), 18: 336. (proposed as a full genus)
1941. Akodon (Thalpomys) Ellerman, The families and genera of living rodents, Vol.2: 409, 914.

Type species:

Mus lasiotis Lund (by Thomas, designation)

Distribution:

Lagoa Sants, southwestern Minas Geraes, Brasil.

Included species:

The type species only.

Characters: (based on BMNH 88.1.28.4. and illustrations by Winge, 1888).

Skull rather elongated and narrow. Nasals slightly shorter than frontals. Zygomatic plate normal, with anterior border vertical in position. Brain case moderately long and not broadened, its breadth slightly less than  $1/2$  the condylobasal length. Interorbital region rather wide, with strong supraorbital ridges with distinctly overhanging ledges. Anterodorsal frontal sinuses very moderately inflated. Interparietal not reduced. Incisive foramina much narrowed behind and reaching the protocone of the  $M^1$ . Posterior border of palate behind the posterior border of  $M^3$ . Bullae not enlarged. Mandible slender, with almost unnoticeable masseteric crests reaching forward the anterior border of the  $M_1$ . Incisor capsule not projected as a definite tubercle. Upper incisors orthodont. Molars not specially elongated or narrowed, with moderate tubercular hypsodonty. Molar crowns terraced in the worn teeth.  $M^1$  with a distinct anteromedian flexus and anteroflexus. Mesoloph remnants and mesostyles evident in  $M^1$  and  $M^2$ .  $M_3$  strongly reduced, much shorter and narrower than  $M_2$ .

7.2.3.2. THE FOSSIL REPRESENTATIVES OF THE GENUS AKODON

Akodon (Abrothrix) kermacki<sup>(1)</sup>, n. sp.

Holotype: MMP S-321: Right and left almost complete lower jaws with the whole lower dentition; portion of the left maxilla including the three upper molars (Fig. 21A,E; Fig. 22A). Collected by G.J. Scaglia in stratum IX of the Chapadmalal Formation, 500 m north of "Bajada del Vivero" (Punta Loberfa), Atlantic cliffs of the Partido de General Pueyrredon, S.E. Buenos Aires Province, Argentina. Figured by Reig and Linares (1969, Fig. 1A and B) as Akodon sp.

Hypodigm: The holotype and the following:

MMP S-222: Almost complete left mandibular ramus, with the whole dentition. Collected by G.J. Scaglia in stratum VIII or IX of the Chapadmalal Formation, 650 m north of "Bajada del Vivero" (Punta Loberfa) (other data as in the holotype). Figured by Reig and Linares (1969, Fig. 2), as Akodon sp.

MMP M-1067: Anterior part of left lower jaw with the whole dentition. Collected by G.J. Scaglia and Mr. Prima in stratum IX of the Chapadmalal Formation, at "Bajada del Vivero" (Punta Loberfa) (other data as in the holotype).

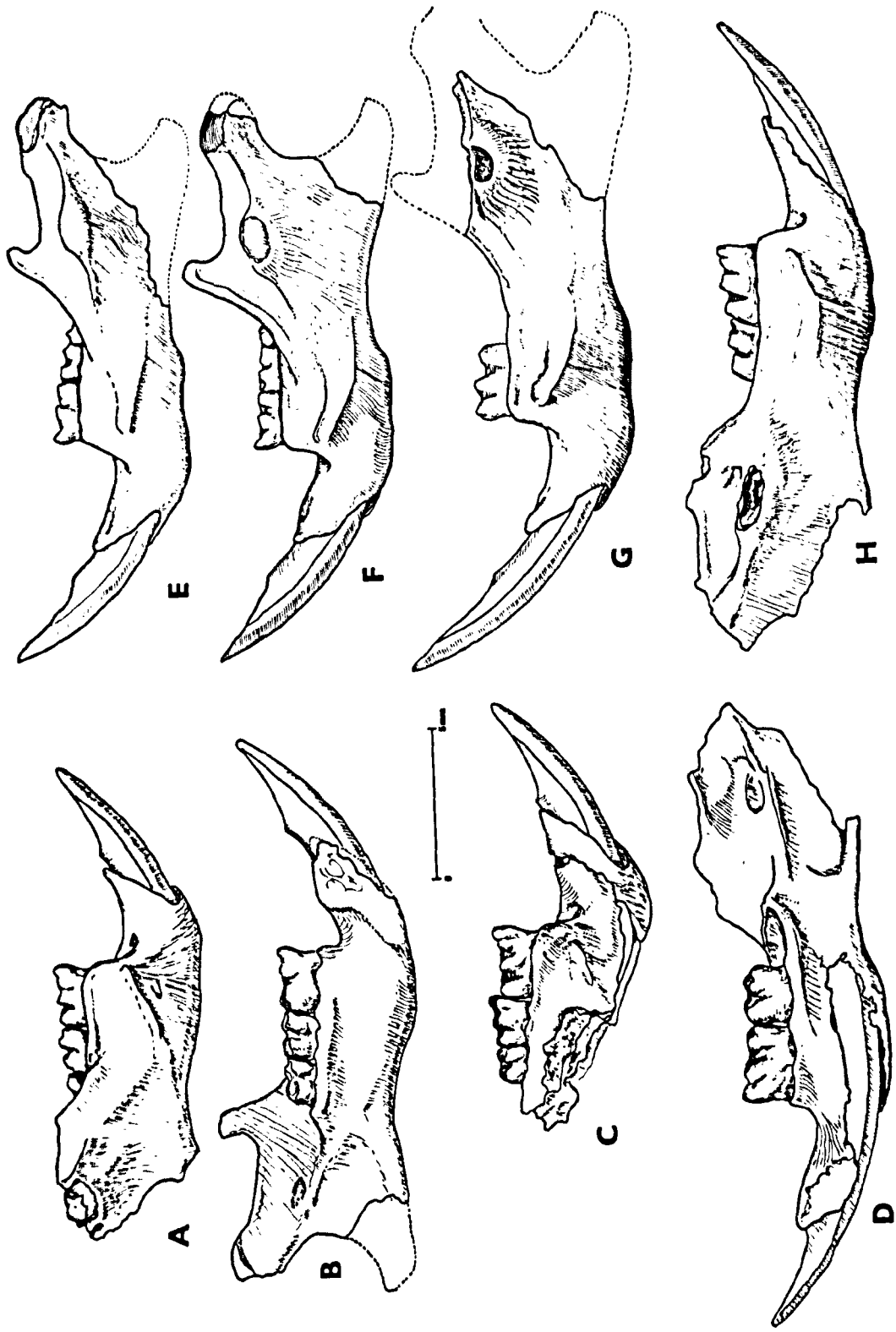
MMP M-1071: Anterior part of right lower jaw with the whole dentition. Collected by G.J. Scaglia in the lower levels of Barranca Lobos Formation, in the cliffs north of "Bajada del

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(1) The species name, kermacki, is given for Dr. Kenneth Kermack for his help and advice, and in homage to his outstanding contributions to the study of the early mammals.

Fig. 21. Lower jaws of Akodon (Abrothrix) Kermacki, n. sp. and Akodon (Abrothrix) magnus, n. sp.

- A. Akodon (A.) Kermacki, external aspect of left lower jaw, and E, of right lower jaw of the holotype, MMP S-321.
- B. Internal aspect and F, external aspect of MMP S-222, A. (A.) Kermacki.
- C. External view of MMP M-1071, A. (A.) Kermacki.
- D. Internal view of right lower jaw, H, external view of the same, and G, external view of left mandible of the type of A. (A.) magnus, MMP M-551.



Vivero" (Punta Lobería) (other data as in the holotype).

MLP 62.VII.27.84: Almost complete left lower jaw with the whole dentition. Collected by G.J. Scaglia in association with the holotype. Data as in the holotype.

MMP M-1154: Incomplete right lower jaw with the whole dentition. Collected by G.J. Scaglia in association with the holotype. Data as in the holotype. (Note: specimens MLP 62.Vii.27.84 and MMP M-1154 are mentioned in Reig and Linares, 1969: 634, as belonging to a single individual, bearing the catalogue number MMP S-321b. It was found later that because of size differences and differences in degree of wear, they belonged to two distinct individuals. Additionally, they were submitted to exchange and recataloguing).

Known distribution:

Chapadmalal and Uquian subages, South east Buenos Aires Province, Argentina.

Diagnosis:

A species of Abrothrix close to A. longipilis; size larger than in A. longipilis longipilis. Incisor stronger and deeper,  $M^1$  with a shorter and wider, noticeably oblique procingulum, with a visible, though weakly developed, antero-median flexus.  $M_1$  relatively shorter and  $M_3$  larger than in A. longipilis longipilis.  $M^3$  without any evidence of a meta-fossetus. Lower jaw with the capsular projection for the base of the incisor more developed than usual in the subgenus.

Description:

The only known part of the skull: a piece of left

maxilla including the cheek teeth which belongs to the type specimen, is too fragmentary to afford useful information about the structure of the palate. Moreover, it does not include any part of the usually diagnostic zygomatic plate. From the bone tissue preserved posterointernal to the  $M^3$  it can be inferred that the posterior border of the palate was behind the posterior border of the last upper molar, as it is in Abrothrix.

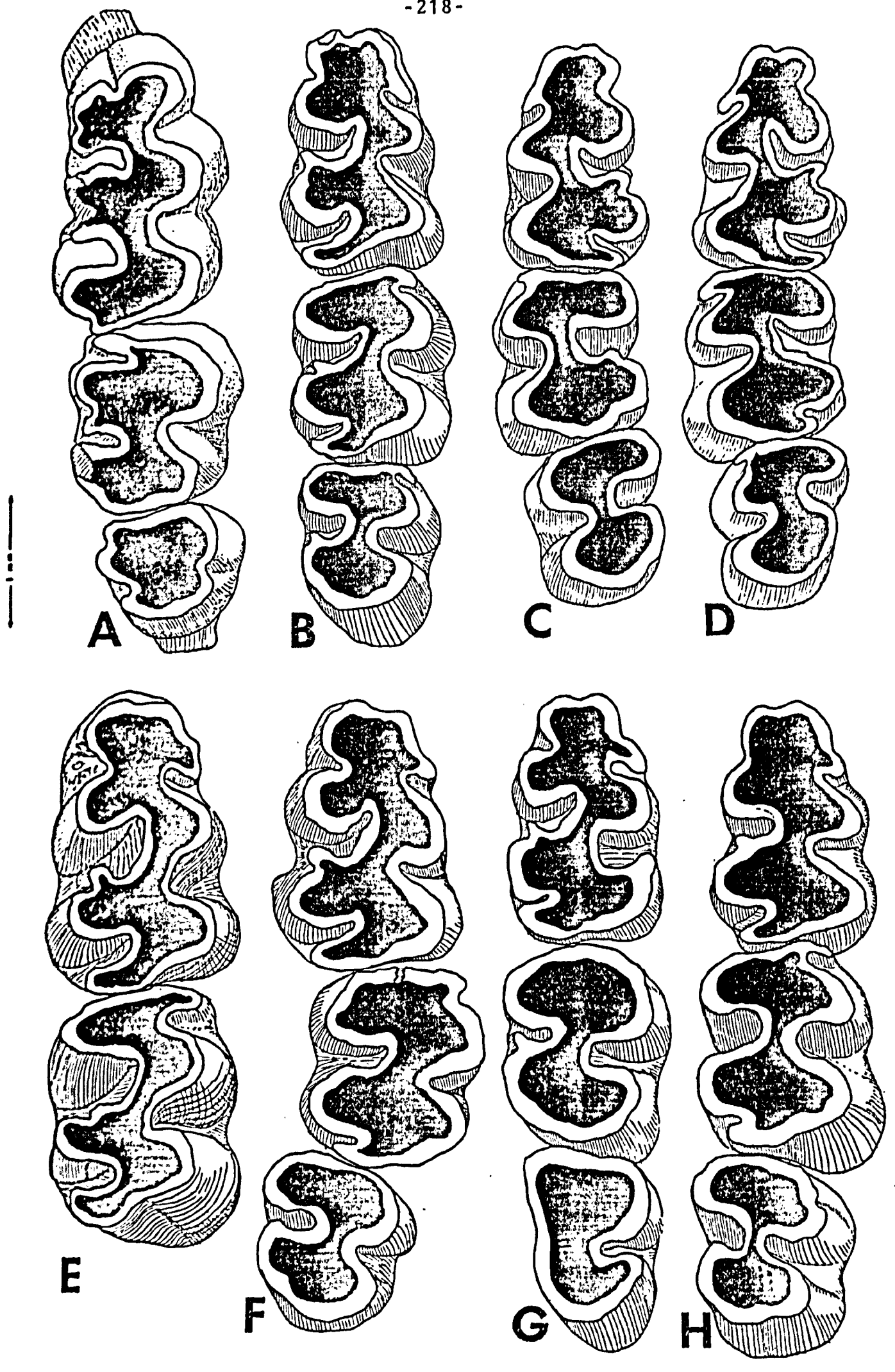
The mandible (Fig. 21) is very well preserved in the holotype and associated specimens and in S-222. It is relatively slender, moderately low and elongated, as it is in Abrothrix and some species of Akodon s.s., as A. cursor. The diastema has approximately the same length as the combined length of  $M_1$  and  $M_2$ , and the depth of the horizontal ramus below the  $M_1$  is less than the diastema length in all the specimens but in M-1071, in which it is slightly larger. The lower border of the ramus bends gently upwards and backwards behind the level of the middle of the  $M_2$ , and descends again behind the level of the  $M_3$ , shaping a concave line, as is usual in Abrothrix. The border of the ramus immediately in front of the  $M_1$  descends rather abruptly downwards, making with the upper border of the symphysis a slightly obtuse angle. The symphysis is relatively long and moderately low, and the uppermost anterior point of the diastema is almost at a level with the alveolar row. The lower masseteric crest is smooth, but well marked, rather high in position, and better developed than is usual in A. longipilis; it reaches to a level anterior to the middle of the  $M_1$ , but posterior to its anterior border. The upper masseteric crest is not so well defined as the lower one, and is less developed than in A. longipilis. The mental



Fig. 22. Upper and lower molar teeth of Akodon (Abrothrix)

kermacki, n. sp. and Akodon (Abrothrix) magnus, n.sp.

- A. Right upper molar series and B. right lower molar series of A. (A.) kermacki, Type specimen, MMP S-321. Chapadmalal Formation, Partido de General Pueyrredon, Prov. de Buenos Aires, Argentina (Upper Pliocene).
- C. Left lower molar series of A. (A.) kermacki, n. sp. M-1153. Chapadmalal Formation. Found in association with S-321.
- D. Left lower molar series of A. (A.) kermacki, n. sp. Chapadmalal Ftion., Partido de General de Pueyrredon, Prov. de Buenos Aires, MMP S-222.
- E. Right  $M_1$  and  $M_2$  of A. (A.) magnus, n. sp., Type specimen, MMP M-551. Vorohue Formation (Lower Pleistocene), Chapadmalal region, Partido de General Pueyrredon, Prov. de Buenos Aires, Argentina.
- F. Right lower molar series of A. (A.) kermacki, n. sp. MMP M-1067. Chapadmalal Ftion, Partido de General Pueyrredon, Prov. de Buenos Aires, Argentina.
- G. Right lower molar series of A. (A.) kermacki, n. sp. MMP M-1071. Lower levels of Barranca Lobos Ftion., (Lowermost Pleistocene), Partido de General Pueyrredon, Buenos Aires Province, Argentina.
- H. Right lower molar series of A. (A.) kermacki, n. sp. MMP M-1154. Chapadmalal Formation. Found in association with S-321 (A-B) and M-1153 (C).



foramen is normally developed and opens on the dorso-lateral surface of the diastema. The anterior edge of the coronoid process originates at the level of the middle of the  $M_2$  and slopes gradually upwards, with most of the  $M_3$  visible in lateral view when the mandible is seen perpendicular to the plane of the symphysis. The coronoid process is relatively short, and the condyloid process is low and elongated, slightly projected backwards, resembling closely the situation found in A. longipilis. The capsular projection, which lies at the level of the anterior part of the sigmoid notch, is stronger than is usual in Abrothrix, reaching a development similar to Deltamys, but it is less developed than in species of Bolomys.

The greater development of the capsule of the incisor root is obviously a consequence of the relatively more strongly developed lower incisor. This is unusually deep for the standards of Akodon sensu lato, and it is absolute and proportionally noticeably deeper than in the living species of Abrothrix. In all the available specimens of kermacki the mean depth of the incisor is almost as large as the length of the  $M_3$  (length  $M_3$ . 100/ depth incisor = 0,993), and in half of the available individuals it surpasses the  $M_3$  (see Table 10, Fig. 24 ). In a sample of 19 A. l. longipilis from Valparaiso, Chile, in the British Museum (Nat. Hist.), the same index is 0,927, and the length of the  $M_3$  is in all the individual cases longer than the depth of the incisor.

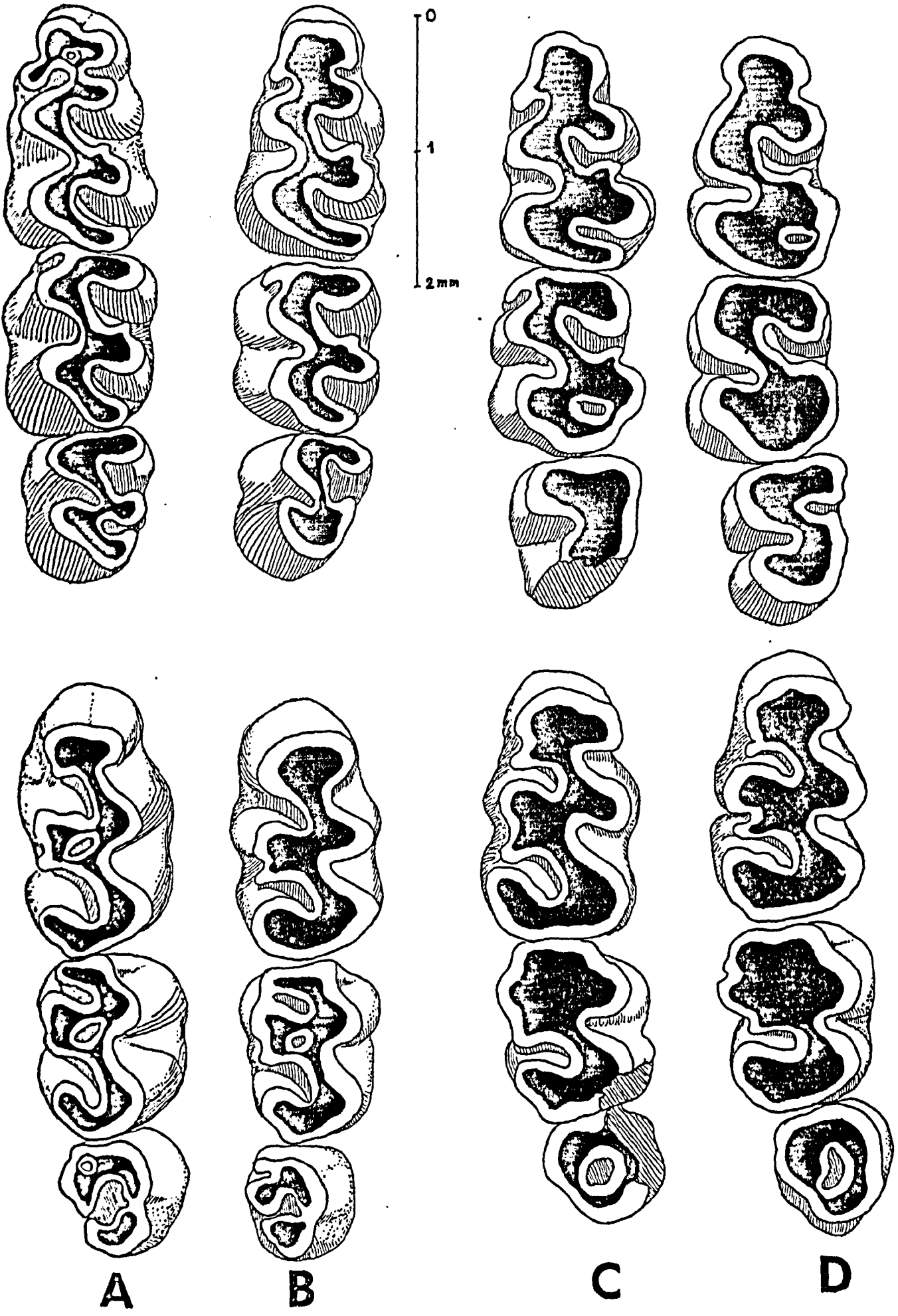
The molar teeth agree in all respects with the characters of Abrothrix as stated in the diagnosis of this subgenus given above. In all the six known specimens the masticatory surface shows an appreciable, but little advanced, degree of wear, corresponding to wear stages 2-3 of Akodon

azarae as described by Pearson (1967). Therefore, most of the details of the enamelled structures of the crown can be observed. The upper dentition is only known from the type specimen. The total length of the upper molar row (4.91 mm in crown length). places A. kermacki among the largest species of Akodon s.s. (A. urichi, A. varius) and within the range of variation in the available sample of A. longipilis longipilis from Valparaiso, which is the largest subspecies of longipilis. In morphology, some differences are apparent, which might be of diagnostic value.

In  $M^1$  and  $M^2$  the main cusps are nearly opposed, the paracone and metacone being only slightly posterior to the protocone and hypocone, respectively. As in Abrothrix and in Akodon s.s., the  $M^2$  is clearly longer than wide, and the  $M^1$  is strong and comparatively broad. The procingulum of the  $M^1$  is short and wide, more so than is usual in A. longipilis and A. illuteus, and it is more strongly oblique in position than in these species, the anterolingual conule being more anterior than the anterolabial conule. The anteromedian flexus is distinct, though it is only very slightly infolded; its presence is also indicated in the anterior surface of the crown by a shallow groove descending up to the alveolus. The anteroloph is barely defined by a very shallow anteroflexus, much as in the type specimens of A. longipilis longipilis and A. illuteus (Fig. 23C, D). As in them, the protoflexus is wide and moderately infolded to the centre of the tooth, its innermost point reaching a level anterior to the level of the innermost point of the opposed paraflexus. The metaflexus is rather transverse in position, scarcely inclined backwards, and it is at a level posterior to the main axis of the hypoflexus, which

Fig. 23. Molar teeth of representative species of living Akodon of the subgenus Abrothrix. The upper row are right upper molars. The lower row are left lower molars of the same individuals of the upper row.

- A. Akodon (Abrothrix) longipilis longipilis (Waterhouse). Male, BMNH 97.5.1.6. Valparaiso, Chile. A rather young specimen of the studied sample of 20 individuals, showing interna remnants of the mesoloph in M<sup>1</sup> and M<sup>2</sup> in the form of a persisting mesofossetus, and a persisting metaflexid in the M<sub>3</sub>.
- B. Akodon (Abrothrix) sanborni (Osgood). Male, MBUCV 1-2025. Mehuin Valdivia, Southern Chile. Rather young specimen showing persisting mesofossetus on M<sup>1</sup>.
- C. Akodon (Abrothrix) longipilis longipilis (Waterhouse). Type specimen, BMNH 55.12.24.177, Coquimbo, Chile.
- D. Akodon (Abrothrix) illuteus Thomas, Female, Type specimen, BMNH 28.10.14.2. Aconquija, Tucuman, Argentina.



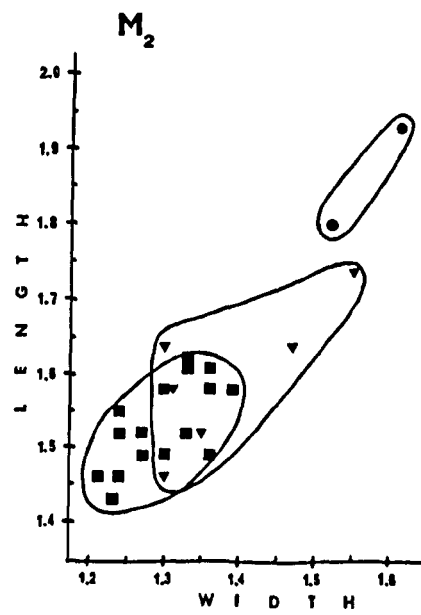
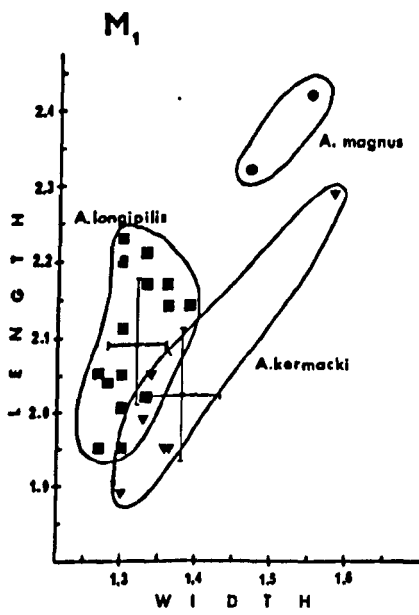
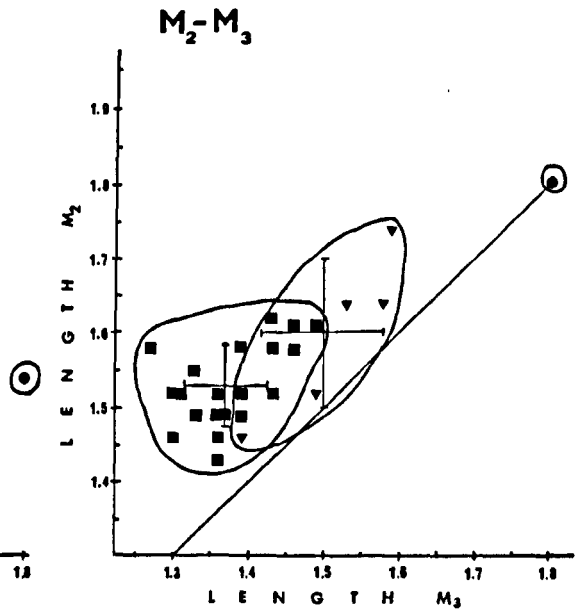
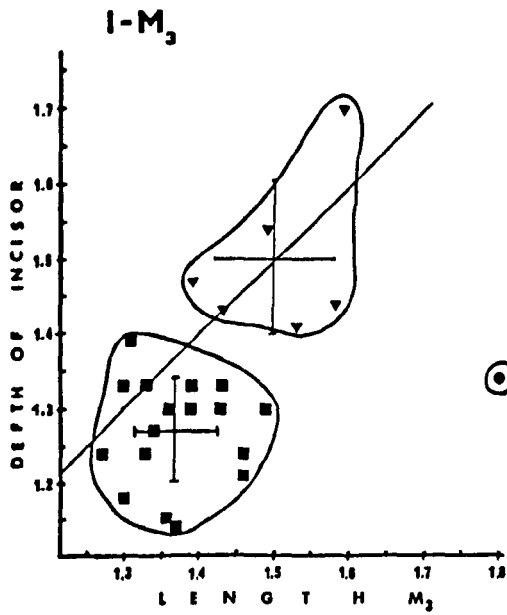
is wide and slightly oriented forwards. The lingual surface of the crown is partially broken at the walls of the medial loph (paraloph + mesoloph), but the presence of a free lingual remnant of the mesoloph is clearly indicated, though it cannot be checked if a mesostyle was also present. In the  $M^2$ , the mesoloph remnant is evident, but there is not distinguishable mesostyle. The protoflexus is obsolete both in the  $M^2$  and the  $M^3$ . The  $M^2$  is very similar to the homologous tooth in the types of illuteus and longipilis, but the paraflexus is better indicated, probably because of less advanced wear, though the metaflexus is less re-entrant than in those specimens. The  $M^3$  is subcylindrical in outline, though it maintains traces of the lingual flexi. There is no trace, however, of a metafossetus in this tooth, whereas such an internal enamel island is present in the type specimens of the above mentioned species, in the types of A. l. hirtus and A. l. nubilus, and in all the specimens of the above mentioned sample of longipilis from Valparaiso. Even in the most worn-down  $M^3$  of the observed Abrothrix, the presence of a metafossetus is constant, and because of this, its absence in A. kermacki is a diagnostic feature.

The lower molars can be studied in the six available specimens. They are typical Abrothrix lower molars in the bulging of the entoconid and the small, anteriorly directed mesolophid remnant and the elongated and oblique median murid of  $M_1$  and  $M_2$ . As it is usual in Akodon s. l., the main cusps are disposed nearly in echelon and the metaconid and entoconid are placed at a level anterior to the protoconid and hypoconid, respectively. The procingulum of the  $M_1$  is wider than is usual in Abrothrix and bears a very shallow, but distinguishable,

anteromedian flexid in 5 out of the 6 available individuals (83.3%). In the studied sample of A. 1. longipilis from Valparaiso, it was observed only in 25.0% of the cases, and then only as a very shallow notch. There is a well developed anterolabial cingulum, similar to that in other species of Abrothrix, and, as in them, there is no evidence of a division of the protoflexid into an anterior and a posterior portion, though the lateral surface of the crown at the procingulum shows a pronounced concavity anterior to the anterolabial cingulum in some cases. As in other Abrothrix, the mesoflexid is obliquely directed anteriorly from the outside in  $M_1$  and  $M_2$ ; and the posteroflexid is less oblique, almost completely transverse with more advanced wear. In all the specimens, a well defined, but weak mesolophid remnant connected with a mesostylid is apparent in the  $M_1$ . It grows out from the anterior border of the entolophid, and directs forwards and outwards, defining a very shallow entoflexid. In the  $M_2$ , this structure is even weaker, to the extent of being obsolete in three out of the 6 known specimens. This development and disposition of the mesolophid remnant is also typical of other species of Abrothrix. As is also the case in other species of this subgenus, the ectolophid is absent in all the observed specimens, and the ectostylid is present in the  $M_1$  in only one of the six specimens, but in none of them was there any evidence of it in the  $M_2$ . In the observed type specimens of the living species of Abrothrix, there is no trace of ectostylid either on  $M_1$  or  $M_2$ , and in the studied sample of A. 1. longipilis from Valparaiso, an ectostylid was found in 8 of the 19 cases in the  $M_1$ , and in 2 out of 19 cases in the  $M_2$ . However, no specimens showed any trace of an ectolophid. The ectolophid



.Fig. 24. Scattergrams of measurements of different teeth in .  
living and fossil species of Akodon (Abrothrix).



- A. (Abrothrix) l. longipilis
- ▼ A. (Abrothrix) kermacki
- A. (Abrothrix) magnus

Table N.10. Measurements (in mm) of the known specimens of Akodon (Abrothrix) magnus, n. sp. and of Akodon (Abrothrix) kermacki, n. sp. (Some of the specimens of A. kermacki were reported with slightly different values for some of the measurements, in Reig and Linares, 1969. The new values given here result from applying conventions to define the limits of the measured items, which are used in the present study.

Variate	Akodon magnus, type MMP M-551, Vorohué Ftton.	Akodon magnus, MMP S-407, Vorohué Ftton.	Akodon kermacki, type, MMP S-321 (r) Chapadmalal Ftton.	Akodon kermacki MLP 62-7-25-84 Chapadmalal Ftton.	Akodon kermacki M.MP M-1154. Cha- padmalal Ftton.	Akodon kermacki MMP S-222, Chapad- malal Ftton.	Akodon kermacki, MMP M-1067, Chapad- malal Ftton.	Akodon kermacki, MMP M-1071, Bca. Lobos Ftton.
mand. condyl.-symph.	-----	-----	17.00	16.55	-----	16.80	-----	-----
length low. diastema	4.22	4.61	4.03	4.03	-----	3.99	4.42	3.65
length ramus at middle M <sub>1</sub>	3.96	4.48	3.71	3.78	-----	3.82	4.03	3.84
- M <sub>3</sub> (alveolar)	6.40	6.14	5.06	5.04	5.57	5.25	5.69	5.57
- M <sub>3</sub> (coronal)	-----	6.02	5.03	4.86	5.38	4.93	5.63	5.31
length	2.42	2.32	1.98	1.89	1.95	1.95	2.29	2.05
width	1.55	1.47	1.33	1.30	1.36	1.37	1.58	1.33
length	1.93	1.80	1.58	1.46	1.64	1.52	1.74	1.64
width	1.61	1.52	1.31	1.30	1.47	1.35	1.55	1.30
length	-----	1.80	1.43	1.39	1.58	1.49	1.59	1.53
width	-----	1.25	1.15	1.12	1.20	1.14	1.39	1.12
length lower incisor	1.36	1.34	1.43	1.47	1.44	1.54	1.70	1.41
width (thickness) l. incisor	0.87	0.77	0.86	0.87	0.82	0.84	0.99	0.87
- M <sup>3</sup> (alveolar)	-----	-----	5.37	-----	-----	-----	-----	-----
- M <sup>3</sup> (coronal)	-----	-----	4.91	-----	-----	-----	-----	-----
length	-----	-----	2.45	-----	-----	-----	-----	-----
width	-----	-----	1.39	-----	-----	-----	-----	-----
length	-----	-----	1.49	-----	-----	-----	-----	-----
width	-----	-----	1.30	-----	-----	-----	-----	-----
length	-----	-----	1.05	-----	-----	-----	-----	-----
width	-----	-----	1.12	-----	-----	-----	-----	-----

is usually present in the species of Akodon s. s., which could be compared with kermacki by size. Following our records, the presence of an ectolophid in the  $M_1$  has a frequency of 92% in Akodon tolimae (N=40), 83% in Akodon urichi saturatus (N=48), 100% in Akodon urichi venezuelensis (N=27) and 64% in Akodon azarae (N=58). An ectolophid is completely absent, however, in some small species of Akodon as A. iniscatus.

In the  $M_2$  the protoflexid is well defined, though it may be completely eroded by wear (c.f. M-1071). It disappears earlier by wear than in the  $M_3$ . This tooth varies from sigmoid-shaped to nearly figure of eight-shaped with wear. In one case (M-1071), the mesoflexid is completely obliterated by advanced wear. In size, the  $M_3$  is relatively longer than the  $M_2$  in A. l. longipilis (Fig. 23) and, from what can be inferred from the type specimens, than in the other forms of the subgenus.

As regards metrical differences of A. kermacki in comparison with A. l. longipilis and large sized species of Akodon s.s., Figs. 24 and 25, and Tables 10, 11, 12 and 13, show the corresponding data.

Variate	<u>A. (A) . longipilis - A. (A) . kermacki</u> d.f. = 23	
Alveolar length $M_1 - M_3$	t= 1.62	P > 0.05
Coronal length $M_1 - M_3$	t= 1.59	P > 0.05
Length of $M_1$	t= 1.36	P > 0.05
Length of $M_2$	t= 1.91	P < 0.05
Length of $M_3$	t= 3.94	P < 0.001
Depth of incisor	t= 5.41	P < 0.001

TABLE 11. Student's test for the statistical significance between the means in six selected variates of Akodon (Abrothrix) longipilis and Akodon (Abrothrix) kermacki, n. sp. From the statistics in Table 10 and Table 13.

Discussion:

From the morphological characteristics of the molar teeth and the mandible, it seems mandatory to place A. kermacki in the subgenus Abrothrix. It matches all the studied character states of this subgenus, and the differences found are merely indicative of a clear-cut distinction at the species level. As regards the metrical analysis, the evidence is conclusive for statistical differences in some of the studied variables, but not in all of them, as it is to be expected in this kind of analysis. Metrically, kermacki, is quite distinctive as regards the depth of the incisor, the relative shortness of the  $M_1$  and the relative longer  $M_3$ . These two differences are complementary, and the result is that the mean crown length of the molar row is not statistically significant as regards the living A. l. longipilis, which is a good example of the care which has to be taken when dealing with overall statistical significances in inferring systematic kinship or differences. Combining the results of the morphological studies and the metrical analysis, there can be little doubt that we are dealing with a distinctive species of Akodon (Abrothrix).

The fossil species seems to be more closely related to the living longipilis and illuteus than to sanborni and lanosus which are much smaller. In size, it is slightly larger than the largest living representatives of longipilis, namely A. l. longipilis, and it belongs, with A. varius simulator and A. urichi saturatus to the group of the largest species of Akodon s. l. Its size is only surpassed, within the limits of the genus Akodon, by the new species I shall describe next.

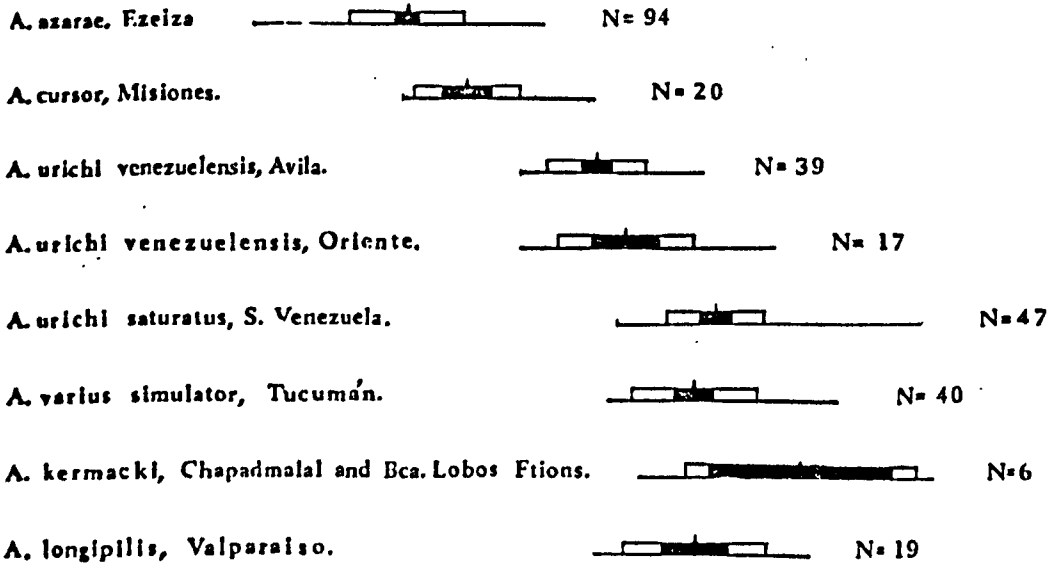
In the larger size of the incisor and the correlated greater development of the capsular projection of the incisor base, kermacki shows a more modified state of characters than in the living species. If this is an indication of a definite evolutionary divergence, kermacki could not be the ancestor of any of the living species of Abrothrix. But this conclusion could hardly be based on such frail evidence, and it would be necessary to await for more specimens and thereby allowing further study of other characters, to evaluate the evolutionary significance of this fossil species.

In any case, it is of interest to realize that the occurrence of Abrothrix in the Upper Pliocene and lowermost Pleistocene of S.E. Buenos Aires Province extends for those times near one thousand km eastwards of the present distribution of members of this subgenus. Actually, the living representatives of Abrothrix are now limited to the lowlands and low valleys of Central Chile and the eastern Andean slopes of Mendoza and Patagonia, up to Tierra del Fuego, plus the isolated A. illuteus of Tucuman.

This difference in distribution between the living and the fossil Abrothrix can be taken as an indication of a reduction of the range of Abrothrix to its present limits from an earlier much more extended area, a phenomenon which could have been caused by the climatic changes that occurred during the Pleistocene. The case of Abrothrix is not isolated, and the presence in the Upper Pliocene of Buenos Aires Province of mammals presently restricted to Chilean or Andean distributions, is also indicated by other known cases. One is the fossil caviomorph Pithanotomys, which is hardly separable from the living Aconaemys, restricted now to a few isolated popula-

Fig. 25a. Dice-grams of the variation in the length of the lower molar row (coronal length) in various species of Akodon of medium and large size.

The arrow indicates the sample mean ( $\bar{x}$ ) value, as regards the scale in mm herewith. The heavy horizontal line shows the observed range of variation. The black portion of the bar represents two standard errors to each side of the mean (95% confidence limits) ( $2s_x$ ). One sample standard deviation ( $s$ ) to each side of the mean is indicated by the corresponding part of the black bar plus the white bar.



LENGTH M<sub>1</sub>-M<sub>3</sub>. (CROWN)



Species, subspecies and locality	Statistic				
	N	range	$\bar{x}$	s	$s\bar{x}$
<u>Akodon puer</u> (Perú and Bolivia)	14	3.58-4.36	3.76	0.176	0.046
<u>Akodon iniscatus</u> (Chubut)	20	3.39-4.22	3.97	0.186	0.041
<u>Akodon azarae</u> (Ezeiza, Bs.As.)	94	3.84-4.60	4.24	0.154	0.014
<u>Akodon cursor</u> (Misiones, Arg.)	20	4.23-4.73	4.40	0.138	0.031
<u>Ak. urichi venezuelensis</u> (Avila)	39	4.54-5.02	4.74	0.128	0.019
<u>Ak. urichi venezuel.</u> (Oriente)	17	4.54-5.21	4.82	0.179	0.043
<u>Ak. urichi saturatus</u> (Tepuyes)	47	4.80-5.50	5.06	0.135	0.019
<u>Ak. varius simulator</u> (Tucumán)	40	4.38-5.39	5.01	0.167	0.023
<u>Ak. l. longipilis</u> (Valparaiso)	19	4.73-5.31	5.01	0.186	0.042
<u>Akodon kermacki</u> (Plioc., Bs.As.)	6	4.86-5.63	5.19	0.299	0.118

TABLE No. 12 Statistics of the coronal length of  $M_1$ - $M_3$  in ten different ~~num~~ samples of different species and subspecies of Akodon

tions in southern Chile and in a high valley of southern Mendoza. Abrocoma, also a caviomorph, is now only known from the Andes from Central Chile up to southern Perú and the mountains of N.W. Argentina. In the late Cenozoic, however, this genus has been reported from the Province of Buenos Aires as a fossil, and I identified in the collection of the Museum of Mar del Plata undescribed specimens which prove that Abrocoma outlived in that area up to the San Andresian age. Other instance is afforded by the discovery of coenolestids in Montehermosian strata of the Buenos Aires Province (Reig, 1955), whereas representatives of this family are now restricted, for southern latitudes, to the Valdivian forest of southern Chile.

Variate	<u>Akodon (Abr.) kermacki</u> Upper Pliocene and low- ermost Pleistocene, S.E. Buenos Aires Prov. N=6			<u>Akodon (Abr.) longi- pilis</u> . Sample of the BMNH from Valparaiso N=19		
	range	$\bar{x}$	s	range	$\bar{x}$	s
M <sub>1</sub> -M <sub>3</sub> (alveol)	5.04-5.69	5.35	0.28	4.80-5.57	5.18	0.21
M <sub>1</sub> -M <sub>3</sub> (coronal)	4.86-5.63	5.19	0.30	4.73-5.31	5.02	0.19
M <sub>1</sub> Length	1.89-2.29	2.02	0.14	1.95-2.23	2.09	0.08
M <sub>1</sub> width	1.30-1.58	1.38	0.10	1.27-1.39	1.32	0.04
M <sub>2</sub> Length	1.46-1.74	1.60	0.10	1.43-1.62	1.53	0.05
M <sub>2</sub> Width	1.30-1.55	1.38	0.10	1.21-1.39	1.30	0.05
M <sub>3</sub> Length	1.39-1.59	1.50	0.08	1.27-1.49	1.37	0.05
Depth incisor	1.41-1.70	1.50	0.11	1.14-1.39	1.27	0.07
M <sup>1</sup> -M <sup>3</sup> (alv)	-----	(5.37)	----	4.67-5.69	5.13	0.24
M <sup>1</sup> -M <sup>3</sup> (cor.)	-----	(4.91)	----	4.35-5.18	4.79	0.20

Table 13. Statistics of the sample of Akodon (Abrothrix) kermacki compared with a sample of Akodon (Abrothrix) longipilis from a living population at Valparaiso, Chile.

Akodon (Abrothrix) magnus, n. sp.

Holotype:

MMP M-551 (Fig. 21D, H, G; Fig. 22E): Left lower jaw with the incisor, M<sub>1</sub> and M<sub>2</sub>, lacking the M<sub>3</sub> and the condyloid, coronoid and angular processes; right lower jaw with incisor and M<sub>1</sub>, lacking M<sub>2</sub> and M<sub>3</sub>, coronoid and condyloid processes; left femur broken in the middle of the shaft; right calcaneus (the two latter bones are only tentatively associated with the mandibles). Found by G.J. Scaglia in the Vorohué Formation, at the Atlantic slopes of the Chapadmalal region at Baliza San Andrés, Partido de General Pueyrredón, Buenos Aires Province, Argentina. These specimens were found in association with MMP M-867 and MMP M-868 (Akodon lorenzinii, n. sp., see later), and MMP M-869 (Cholomys pearsoni, n. gen., n. sp., see later).

Hypodigm: The holotype and :

MMP S-407: Right fragmentary mandible of an old individual, bearing the incisor and the three molar teeth, the latter greatly worn. Found by G.J. Scaglia in the Vorohué Formation, in the sector of the Atlantic slopes which stretches from south of Arroyo Lobería, Chapadmalal region, Partido de General Pueyrredón, Buenos Aires Province, Argentina.

Diagnosis:

A very large species of Abrothrix, exceeding in size A. kermacki. Mandible slender; incisor relatively much

weaker;  $M_1$  with a distinct metastylid.

Known distribution:

Vorohuean subage of the Uquian age, Lower Pleistocene of S.E. Buenos Aires Province, Argentina.

Description:

The description is based on the holotype, as specimen MMP S-407 is only tentatively included in the species.

The mandible is distinctly larger than that of A. kermacki, but it is more slender. The diastema is, however, a little shorter, its length being less than the space occupied by the two first molars. The horizontal ramus is shorter, as its height is less than the diastema length, and its lower border bends slightly upwards from the level of the anterior part of the  $M_2$ . The border of the ramus immediately in front of the  $M_1$  is as in A. kermacki, but the upper border of the diastema is slightly more concave. The symphysis, though it is shorter, is lower and more slender. The lower masseteric crest is somewhat higher in position than in A. kermacki. The mental foramen is as this species. The anterior border of the coronoid process is only partially preserved, but it is clear that it originates further posteriorly than in kermacki, at the level of the middle of the alveolus of the  $M_3$ . The condyloid process is not preserved, but the remaining parts of the ascending ramus shows a great deal of the sigmoid notch and allow the inference that the condyle was rather low and well projected backwards. The capsular projection has broken walls in the two mandibles of the holotype specimen, and it is slightly less pronounced than in kermacki, the root of the incisor lying further forwards, in between the place of the coronoid process and the beginning of the sigmoid notch.

The incisor is much weaker than in kermacki and

its proportions, are as normal in A. longipilis. Its absolute size in depth is less than in kermacki, even when magnus shows greater values for all the remaining measurements of the dentition.

The  $M_1$  and  $M_2$  are very similar to those of kermacki, the main distinction being one of absolute size. However, the  $M_1$  shows clearly a metastylid, a character which has not been observed in any other specimen of Abrothrix examined by me, and which may be considered as a diagnostic character for this species. However a larger sample would be necessary to check the constancy of this character in the new species. As it is typical of kermacki and of other Abrothrix, the mesolophid remnant is weak and grows out from the middle of the entolophid in the  $M_1$ , and the entoconid makes a noticeable bulge on the lingual face of the tooth. In the  $M_2$  the mesolophid remnant is rudimentary, but the protoflexid is better marked than in the known specimens of kermacki. The roots of the  $M_3$  shows that this tooth was large, probably relatively larger than in kermacki. This is confirmed by the very worn down  $M_3$  of specimen MMP S-407.

#### Discussion:

Although the main distinction of A. magnus as regards A. kermacki is one of size, the slender mandible and weaker incisor confirm that we are dealing with a different species. The difference in absolute size is obvious at first sight (Fig. 21, 22), but looking at the diagram of Fig. 21 one is tempted to wonder whether this specimen could not be thought of as an extreme case of large size within the size range of A. kermacki. One specimen of A. kermacki (MMP M-1067) from the Chapadmalal Formation is close in  $M_1$  length to specimen

MMP S-407, attributed to A. magnus. The Chapadmalal specimen, however, has a much shorter  $M_2$ , and agrees with kermacki in mandible and relative size of the incisor. Another specimen of kermacki from the Chapadmalal Formation (MMP M-1154) has a  $M_2$  which approaches the size of the  $M_2$  in specimen S-407, but its  $M_1$  is much shorter and it also agrees with kermacki in incisor and mandible characters. In any case, there is no overlapping in absolute size in any of these specimens, and the species distinction seems to be well validated by the sum of all the studied characters.

It could be alleged, however, that the reported cases of transition in size between the two species might be a reflection of a real transition between the two taxa, and that a process of phyletic speciation is here involved. Such cases of phyletic speciation have been described in the echimyid rodent Eumysops from the same sequence (J. Kraglievich, 1965), and surmised in the case of the didelphids Thylatheridium (Reig, 1958b) and Sparassocynus (Reig and Simpson, 1972) also from the same sediments. Though the answer to this possible interpretation can only be given by more material, I believe that the greater development of the incisor in kermacki does not support the idea that this species would be the direct ancestor of magnus. Moreover, the single specimen of kermacki known from the intermediate Barranca Lobos Formation (MMP M-1071), does not show intermediate character states, but it is closer to the type specimen of kermacki in size than some other specimens referred to the same species. In any case, and even when it can eventually be demonstrated that there is a direct phyletic link between the two species, there would still be enough basis for maintaining magnus as a dis-

distinct species, as its size differences as regards the typical kermacki could hardly be compatible with the known range of size variation in species of the subgenus Abrothrix.

Akodon (Akodon) johannis<sup>(1)</sup>, n. sp.

Holotype:

MMP M-742 (Fig. 25F, H, J): Right lower mandible with incisor and  $M_1$ - $M_2$ , lacking the coronoid and the angular processes; left lower mandible with  $M_1$  and  $M_2$ , with broken incisor and lacking the same processes; left maxilla with  $M^1$ - $M^3$ ; portion of right maxilla with  $M^1$ - $M^3$ ; the two tibiae, the right incomplete; incomplete right and left femora; right humerus and cubitus; portions of scapula and of left pelvis; two vertebrae. Found by G.J. Scaglia in the Miramar Formation, at the Atlantic slopes S. of "Bajada San Andrés", Chapadmalal region, Partido de General Pueyrredón, Province of Buenos Aires, Argentina.

Hypodigm:

The type only.

Diagnosis:

A small species of Akodon s. s. of the size of Akodon andinus or Akodon nigrita; moderately strong mandible with a low symphysis, a relatively deep incisor and a fairly well developed capsular projection. Incisive foramina almost at the level with the anterior borders of  $M^1$ . Zygomatic plate strong, wider than the length of the  $M^1$ , with a rounded and slightly projecting forward anterior border. Molars relatively broad.  $M^1$  with a wide and oblique procingulum show-

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(1) The species name, johannis, is given for Juan Brkljacic, a close collaborator of G.J. Scaglia's work in the Museo de Mar del Plata, responsible for a great deal of the progress of that institution during the last few years.



ing a moderately developed anteromedian flexus, but without anteroflexus. Lower molars without mesolophid remnants and mesostylids; ectolophids and ectostylids also absent.

Known distribution:

Ensenada age, Middle Pleistocene of S.E. Buenos Aires Province, Argentina.

Description:

Of the skull, only the maxilla and the middle palatal region can be studied. The palate is long and wide; the space between the internal borders of the crowns of the  $M^1$  is greater than the length of the  $M^1$ . There is no direct evidence of the position of the posterior border of the palate, but the maxillary bone surrounding the  $M^3$  clearly indicates that the border was slightly behind the posterior border of the  $M^3$ . The posterior limit of the incisive foramina (Fig. 25J) are clearly indicated in the two portions of maxillae. The foramen scarcely surpass the anterior border of the  $M^1$ , and they are even less expanded behind than in Akodon nigrita, a living species with rather short incisive foramina. In fact, the position of the posterior border of these foramina resembles the condition found in Notiomys and Microxus, (in which they scarcely surpass the anterior border of the  $M^1$ ) more than the usual condition in Akodon s.s., in which they usually reach the level of the protocone of the  $M^1$ . In the zygomatic plate, however, johannis stands quite apart from Notiomys and Microxus, and shows an unusually strong and wide plate, with an anteroposterior length greater than the length of the  $M^1$ , as is also the case in Akodon nigrita and Akodon andinus. In most species of Akodon of small size other than the two latter, the length of the  $M^1$  exceeds the antero-

posterior diameter of the plate, as is the case in A. puer, A. boliviensis and A. azarae, or the two measurements are roughly equivalent, as is the case in A. iniscatus. The anterior border of the zygomatic plate is quite upright, and it slightly projects forwards at its rounded upper corner, and it is not sharply cut-off above, the upper corner being very slightly turned into the anterior border.

The mandible is also characterized by its low symphysis, and the very procumbent incisor. This is reflected by the position of the anterior median point of the diastema, which is well below the level of the alveolar row, even more so than in Akodon cursor (Fig. 25A) a species with a particularly low symphysis. In Akodon (Deltamys) kempi and in Akodon nigrita (Fig. 25E) and Akodon andinus (Fig. 26D) the symphysis is also low, but less markedly so than in A. johannis, whereas in most of the other species of Akodon s. l. the symphysis is more up-turned and consequently, the incisor is less procumbent. The mandibular ramus is relatively deep: although the depth of the ramus at the  $M_1$  is less than the diastema length, the ramus is higher than in similarly sized species, as A. nigrita, A. iniscatus and A. puer, and it is greater than the combined length of  $M_1$  and  $M_2$ . The lower masseteric crest is high and moderately marked, more clearly so than the upper masseteric crest, and the two crests reach forwards to close to the anterior border of the  $M_1$ . The tip of the coronoid process is broken in the two mandibles, but its anterior border is partially preserved and it slopes backwards somewhat abruptly. The condyle is well posterior and fairly high in position, and the capsular projection is well developed, as compared to what is usual

Fig. 25. Lower jaws, maxillaries and molar teeth of Akodon

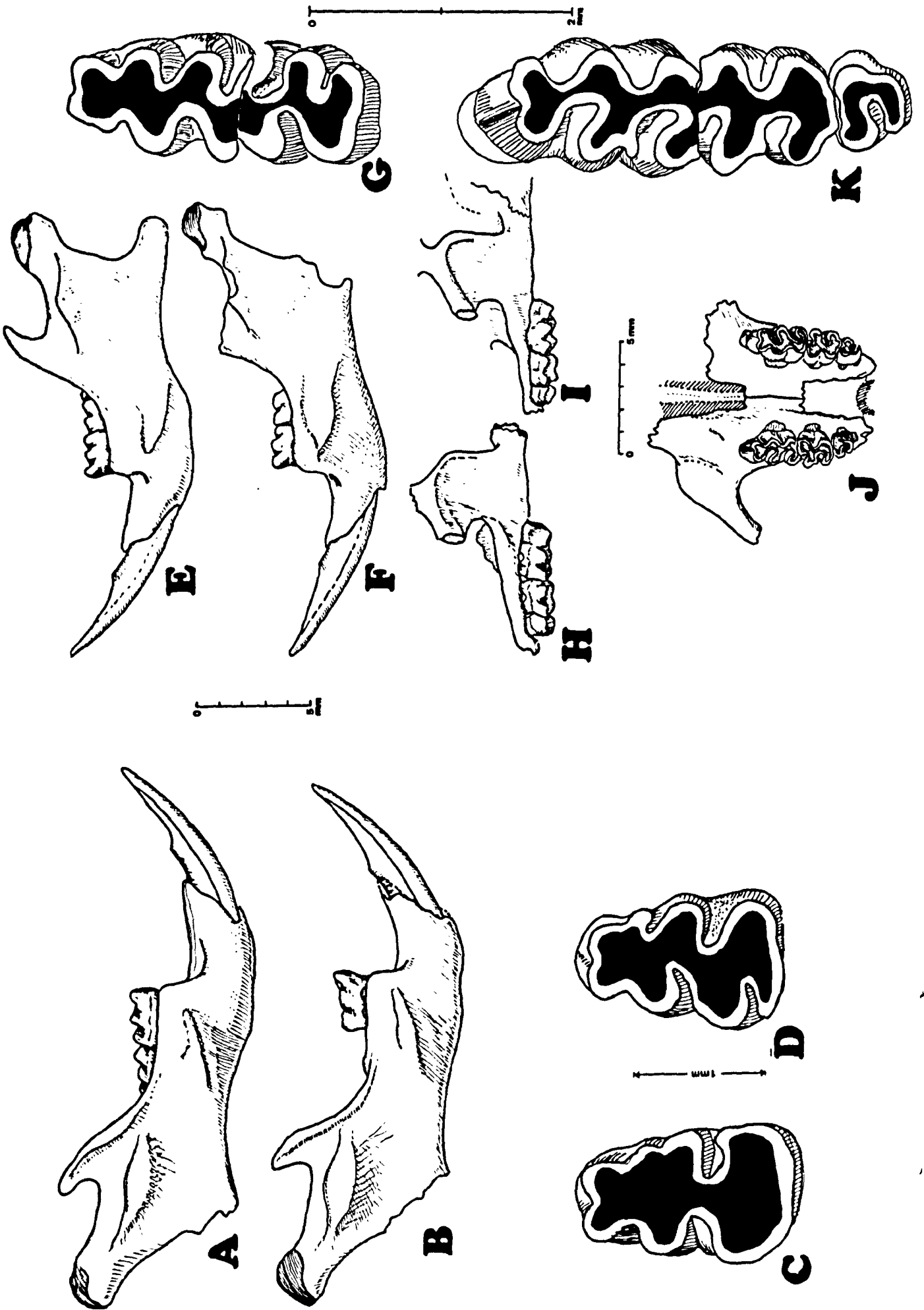
(Akodon) cf. cursor (Winge), and Akodon (Akodon)

johannis, n. sp., in comparison with the living

Akodon (Akodon) cursor montensis Thomas, and Akodon

(Akodon) nigrita (Lichtenstein).

- A. Lateral view of left lower jaw of A. (A.) cursor montensis Thomas, Female, BMNH 1874. Puerto Gisela, Misiones, Argentina. Living.
- B. Lateral view of left lower jaw of A. (A.) cf. cursor (Winge). MLP 66.VII.27.95 (a). Miramar Formation (Ensenadan stage), Vicinity of Camet, Partido de Mar Chiquita, S.E. Buenos Aires Province, Argentina (Middle Pleistocene).
- C. Crown view of left  $M_1$  of A. (A.) cf. cursor (Winge) MLP 66.VII.27.95. Other references as in B.
- D. Crown view of left  $M_1$  of A. (A.) cursor montensis Thomas. Type specimen, BMNH 4.1.5.3.36. Sapucay, Parahuay. Living.
- E. Lateral view of right lower jaw of Akodon nigrita Licht. Male, BMNH 3.7.1.74. Roca Nova, Parana, Brazil. Living.
- F. Lateral view of right lower jaw of Akodon (Akodon) johannis, n. sp., Type specimen, MMP M-742. Miramar Ftion. (Ensenadan stage), Chapadmalal Region, Partido de General Pueyrredon, Buenos Aires Province, Argentina (Middle Pleistocene).
- G. Crown view of right lower  $M_1$  and  $M_2$  of A. (A.) johannis, n. sp., Type specimen, MMP M-742 (Other data as in F).
- H. Lateral view of left maxilla of A. (A.) johannis, n. sp., Type specimen, MMP M-742 (Other data as in F).
- I. Lateral view of left maxilla of A. (A.) nigrita. BMNH 3.7.1.74. (Other data as in E).
- J. Palatal view of left and right maxillae of A. (Ak.) johannis, n. sp., Type specimen MMP M-742 (Other data as in F).
- K. Crown view of upper molar series of A. (Ak.) johannis, n. sp., Type specimen, MMP M-742 (Other data as in F).



in Akodon s.s. .

The incisor is comparatively strong, markedly more so than in nigrita, andinus and puer, and it is comparable in relative depth to the incisor of iniscatus (Fig. 26A). As already indicated, it is characteristically procumbent. The molar teeth (Fig. 25G, K.) are broad and rather short, and they look similar, though they are a little more heavily built than the molars of nigrita. They differ from that species, however, in the lack of any indication of remnants of mesolophids and ectolophids and ectostylids in  $M_1$  and  $M_2$ , but the upper molars are more closely comparable between the two species in morphology and proportions, and in the advanced reduction of the  $M_3$ . Both in the upper and in the lower molar series, the posterior border of the first molars is partially cut-off, and so is, though less markedly, the anterior border of the second molars. This is probably an individual anomaly.

Discussion:

Akodon johannis appears to be clearly distinct species showing a characteristic combination of character states that distinguish it clearly from the living small-sized species of Akodon s. l. It is obviously distinct from the contemporary Akodon cf. cursor, which I shall describe next. Among the living species, it seems to be more closely related to Akodon nigrita than to any of the other species with which it has been compared. It is beyond any reasonable doubt that it is to be allocated in the subgenus Akodon s.s., and it probably represents an extinct lineage among the extensive diversification of the subgenus. The dubious Necromys conifer Amegh, which Ameghino (1889)

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mentions as being represented in the coetaneous Ensenadan stage of the north of Buenos Aires Province, does not seem to have anything in common with A. johannis. Though the illustrations and the description are very obscure, the drawings given by Ameghino (op. cit., Atlas, Table IV, figs. 17 and 18) show a mandible with an up-turned symphysis and a non-procumbent incisor. Hershkovitz (1962) considers Necromys a mere synonym of Calomys, a contention which I cannot accept, having regard to Ameghino's poor illustrations.

Akodon (Akodon) cf. cursor (Winge)

MLP 62.VII.27.95 (a) (Fig. 25B, C): left lower jaw with the incisor and the  $M_1$  of an old individual; (b): right lower jaw with the incisor and the alveoli of the molar teeth; (c): fragment of right lower jaw with extremely worn  $M_1$  and  $M_2$ . These three specimens found in association with each other and with remains of other rodents, (Reithrodon auritus, Nectomys squamipes, Ctenomys sp. etc) in a bone conglomerate probably representing a set of fossil owl pellets. The bone conglomerate was extracted from a block of sediments fallen down from the Atlantic cliffs 5 Km N. of Camet (some 15 Km N. of Mar del Plata City) (for other data, see under Nectomys squamipes, page 103).

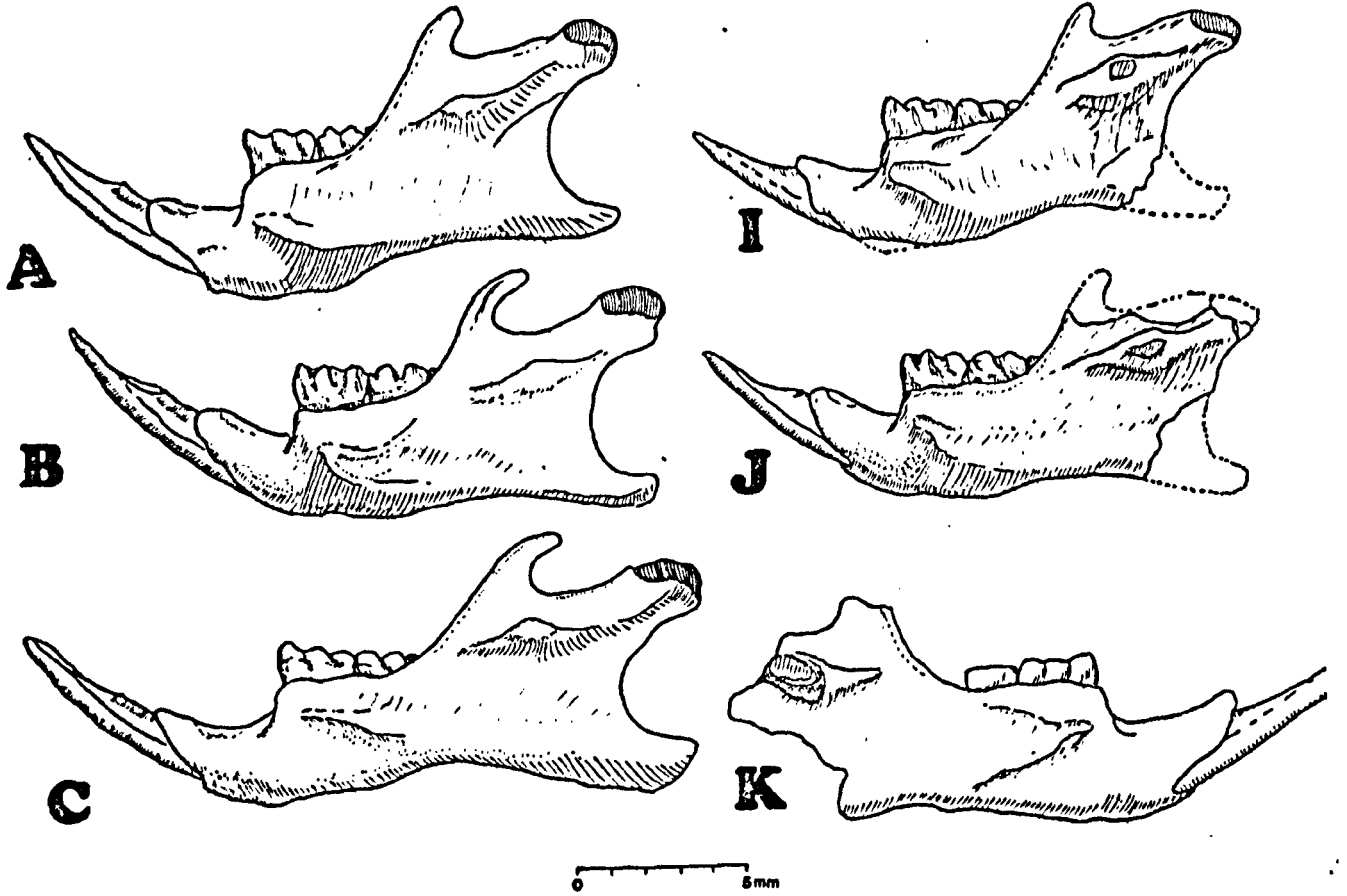
Description:

The morphology and measurements (Table 14) of the mandibles indicate that we are dealing with a representative of Akodon closely allied, if not identical, to the living species Akodon (Akodon) cursor (Winge). As in this latter species, the mandible is elongated and slender by the standards of the other species of Akodon of this intermediate size. The symphysis is elongated and low, the anterior median point of the diastema being at a level below that of the alveolar row. The length of the diastema is as long as the space occupied by  $M_1$  and  $M_2$ , and the depth of the ramus below the  $M_1$  is slightly greater than the diastema length. The lower border of the ramus is gently concave behind the  $M_1$ . The lower masseteric ridge is relatively well marked and

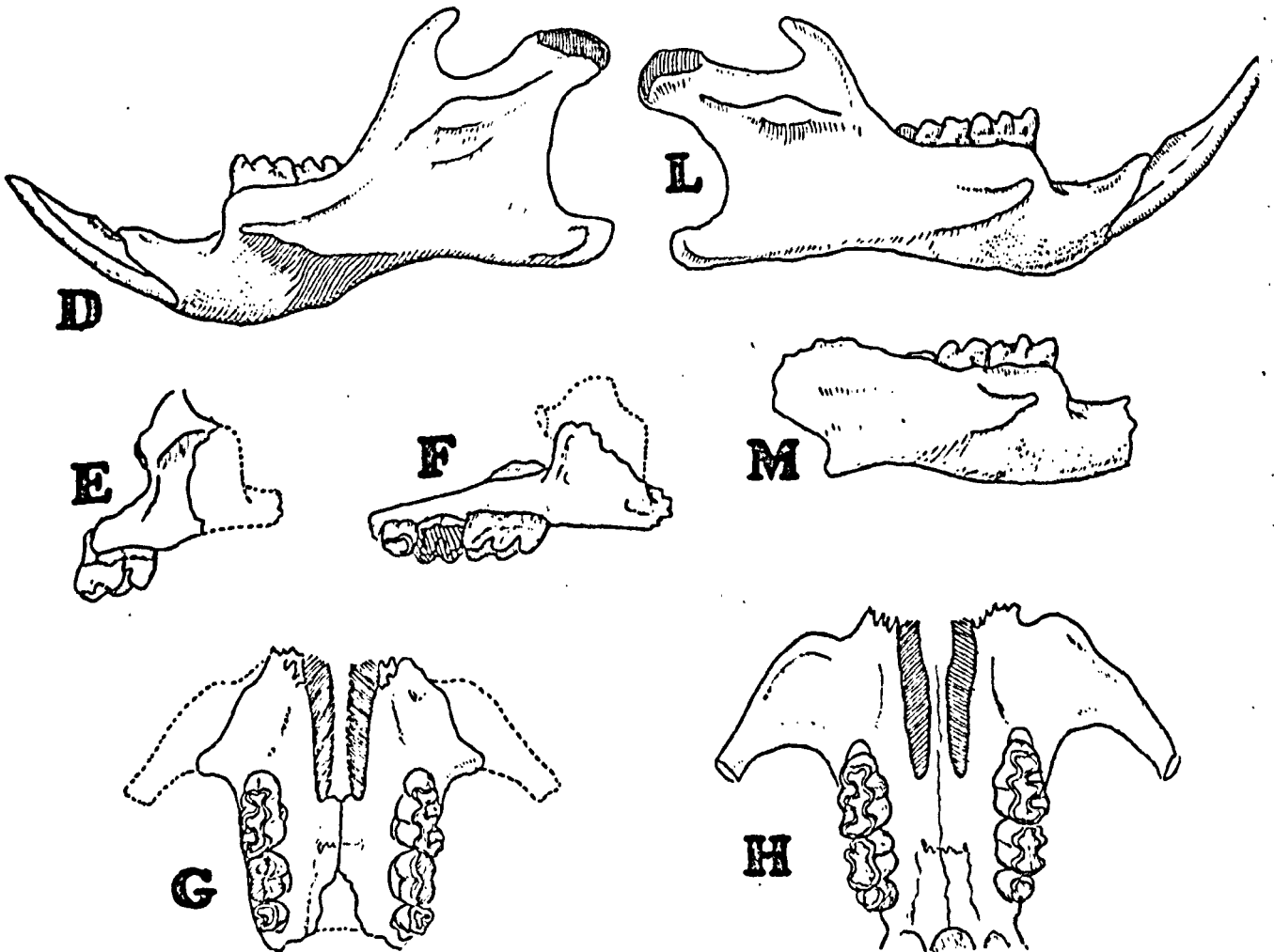
Fig. 26. Lower jaws and maxillae of Akodon (Akodon) lorenzini n. sp. and Akodon (Ak.) cf. iniscatus of the Lower Pleistocene, compared with related living species.

- A. External view of right mandible of Akodon iniscatus Thomas. Type specimen, Female, BMNH 3.7.9.64. Lago Blanco Valley, Chubut, Argentina. Living.
- B. External view of right mandible of Akodon albi-venter (Thomas). Male, BMNH 21.11.1.51. Sierra de Zenta, Jujuy, Argentina. Living.
- C. External view of right mandible of Akodon puer Thomas. Type specimen. BMNH 2.1.1.78. Female, Choquecamate, Bolivia.
- D. External view of right lower mandible of Akodon andinus (Philippi), type specimen of Akodon gossei Thomas. Female, BMNH 98.3.21.5. Puente del Inca, Mendoza, Argentina. Living.
- E. External view of fragment of left maxilla with M<sup>1</sup> of Akodon lorenzini, n. sp. MLP 52.X.4.44 (a) San Andres Ftion. Miramar, Prov. de Buenos Aires, Argentina. (San Andresian, Uppermost Lower Pleistocene).
- F. External view of incomplete left maxilla with molar teeth of Akodon lorenzini, n. sp. MMP M-867 Vorohue Formation, Chapadmalal region, Partido de General Pueyrredon, S.E. Buenos Aires Province, Argentina/Vorohuean (Lower Pleistocene).
- G. Reconstructed palatal view of Akodon lorenzini n. sp., based on MMP M-867 (the right half is an inverted drawing of the original left half.) Other data as in F.
- H. Palatal view of the skull of Akodon iniscatus Thomas, Male. BMNH 13.11.1.5. Pampa Central, Argentina. Living.
- I. External view of left mandible of Akodon lorenzini, n. sp., type specimen. MMP M-1081. San Andres Ftion., Barranca Parodi, Miramar, Prov. de Buenos Aires, Argentina. Sanandresian, (Lower Pleistocene).
- J. External view of left mandible of Akodon lorenzini, n. sp., MMP M-868. Found in association with MMP M-867. Other data as in F.
- K. External view of right mandible of Akodon cf. iniscatus. MMP S-640. Vorohue Ftion. S. Arroyo Loberia, Chapadmalal region. Other data as in F.
- L. External view of right mandible of Akodon iniscatus Thomas. Male. BMNH 13.11.1.5. Other data as in H.
- M. External view of incomplete mandible of Akodon lorenzini, n. sp. M:L.P. MLP. 52-X.4-44 (a). Other data as in E.





0 5mm



rather high in position, the upper masseteric ridge being scarcely noticeable and somewhat parallel to the alveolar border. The coronoid process is low and its anterior border slopes upwards very gently. The condyloid process is also low and projected well backwards. There is a fairly well developed capsular projection of the base of the incisor, slightly stronger than is usual in living specimens of cursor examined, but the difference is not really very marked. The incisor is, as in cursor, well developed, and its depth is a little greater than that of the type specimen of A. cursor montensis and other specimens examined.

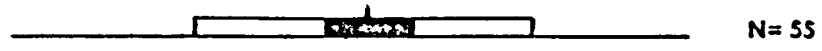
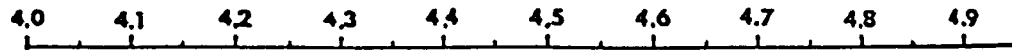
The molar teeth are too much worn down to show many details of their structure. However, the  $M_1$  of specimen (a) is slightly less worn (Fig. 25C) and shows a clear indication of an anteromedian flexid, and an overall shape and development of the procingulum which matches perfectly with the features of the procingulum of cursor. A well marked anteroflexid is present in the type of A. cursor montensis (Fig. 25D), and in all the individuals of a sample of 15 animals from Puerto Gisella, Misiones, attributed to the same subspecies. The shape of the enamel walls at the hypoflexid permits the inference that an ectostylid was present. An ectostylid is absent in the type of A. c. montensis, but it is present in 7 out of 14 specimens of the above mentioned sample. From the enamel wall of the mesoflexid, it could be assumed that no mesolophid remnant was present in this fossil specimen. This structure is present in 80% of the cases in the comparative sample studied but it is almost completely absent in the type of A. c. montensis. In length and width, the  $M_1$  falls within the limits of variation in a sample of the living cursor (Fig. 27), and

there is also a complete correspondence between the fossil specimens and the living sample in the length of the molar series (Fig. 27).

Discussion:

Apart from Akodon cursor, the only alternative which could be considered for relationships of these remains, is Akodon azarae, now living in the same locality where the fossils were found (Reig, 1964; additionally, I have collected a good sample of Akodon azarae, now in the collection of the Department of Biological Sciences of the University of Buenos Aires, at Santa Clara del Mar, a few Kms from Camet, in the same general coastal region). Akodon azarae agrees with the fossil specimens in being a medium-sized species with a rather elongated mandible. It is, however, significantly smaller than the fossil specimens (Fig. 27) and has a stronger mandible. A sample of 55 A. azarae from Ezeiza, close to Buenos Aires City, now in the Museum of Mar del Plata, shows an alveolar length of the lower series significantly smaller ( $P < 0.001$ ) than the studied sample of Akodon cursor from Puerto Gisella, Misiones (Fig. 27), whereas the alveolar molar length of the three fossil specimens here described has exactly the same mean value than the latter. Moreover, azarae is characterized by narrower molar teeth, as it is evident for the  $M_1$  in the diagram of Fig. 27. In view of these facts, I believe that the idea of a close relationship of the fossil specimens with azarae must be ruled out. The morphological resemblance and the agreement in size with cursor is such, that I have no doubt that the fossils from Camet represent a form very probably conspecific with the living cursor. This species was first described by Winge (1888) from living and subfossil

Fig. 27. Dice-grams and scattergram fro measurements of the dentition of species of Akodon (Akodon).



A. (Akodon) azarae

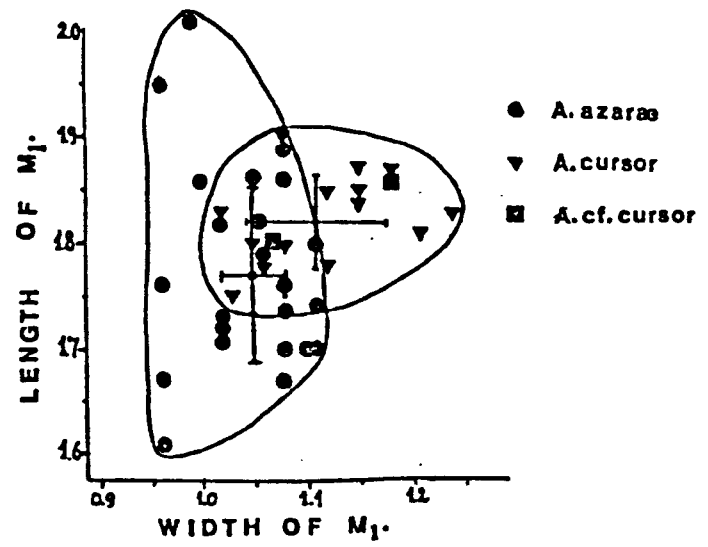


A. (Akodon) cursor



A. (Akodon) cf. cursor

LENGTH  $M_1-M_3$  (A L V.)



specimens from Lagoa Santa, Minas Geraes, Brazil, as a member of "Habrothrix" (Thomas had proposed earlier, 1884, to place under "Habrothrix" all Akodon-like South American mice). Thomas (1902) places cursor in Akodon, and later (1913) he described Akodon arviculoides montensis, which he compared with cursor. As already discussed (page     ), arviculoides is not an Akodon, but a Bolomys, and montensis, as proposed by Ximenez and Langguth (1970) is to be considered as presumably a subspecies of cursor. Therefore, it is likely that two subspecies of cursor should be recognized, namely A. cursor cursor (Winge), which following Vieira (1955) extends over Minas Geraes, Espiritu Santo, Guanabara (Rio de Janeiro), Sao Paulo and Paraná; and A. cursor montensis which is known from Paraguay (Thomas, 1913), Misiones (Massoia and Fornes, 1962) and Central Uruguay (Ximenez and Langguth, 1970). These subspecies are not, however, well defined so far, and even if they were, our fossil sample is too small in number and represented by too fragmentary material either to attempt a comparison with the nominal living subspecies or to decide if it could be placed in a fossil subspecies of its own. The best that can be done on the basis of the present evidence, is to identify the fossil remains as Akodon cf. cursor. It is of great interest to realize that these remains indicate that the distribution of cursor extended by Middle Pleistocene times at least 600 kms south of the southernmost known limit of the living populations (see additional comments under Nectomys squamipes, page     ).

Akodon cf. cursor from the Miramar Formation cannot be confused with Akodon johannis, found also in the

TABLE 4. Measurements of mandible and lower molars of fossil and living specimens of Akodon (Akodon) cursor.

Specimen	Akodon cf. cursor MLP 62-VII-27-95 (a) Miramar Ftion.	Akodon cf. cursor MLP 62-VII-27-95 (b) Miramar formation.	Akodon cf. cursor MLP 62-VII-27-95 (c) Miramar formation.	Akodon c. montensis Type, BMNH 4.1.5.35	Akodon c. montensis Female, BMNH 66- 1874. Misiones, Arg.	Sample of <u>Akodon c. montensis</u> in the BMNH from Puerto Gisella, Misiones, Argentina N=15		
						range	$\bar{x}$	s
length mandible condyle-a.b.diastema	14.20	13.60	-----	14.12	14.41	-----	-----	-----
length from condyle ant. border of M <sub>1</sub>	11.39	11.39	-----	-----	10.99	-----	-----	-----
length diastema	3.20	2.94	3.32	-----	3.46	-----	-----	-----
length condyle-post. under alveolus M <sub>3</sub>	6.46	5.82	-----	-----	6.21	-----	-----	-----
width of mandible the M <sub>1</sub>	3.26	3.26	3.27	-----	3.07	2.56-3.64	3.01	0.36
M <sub>3</sub> (alveolar)	4.67	4.74	4.54	4.55	4.61	4.35-4.93	4.65	0.18
length	1.86	-----	1.80	1.77	1.71	1.75-1.90	1.82	0.04
width	1.18	-----	1.02	0.99	1.08	1.02-1.24	1.11	0.06
length	-----	-----	1.39	1.43	1.37	1.33-1.49	1.40	0.05
width	-----	-----	1.03	0.99	1.05	0.99-1.22	1.09	0.07
length	-----	-----	-----	1.24	1.24	1.22-1.49	1.31	0.08
width	-----	-----	-----	0.93	0.99	0.87-0.99	0.94	0.04
width, low. incisor	1.19	1.05	-----	1.08	1.04	-----	-----	-----

same strata. The latter is much smaller, has a relatively stronger mandible and a relatively deeper incisor, a more up-turned and higher coronoid process, and a much lower symphysis. Its  $M_1$  is proportionately much wider than broad and the procingulum lacks a well defined anteromedian flexid. The differences between these two species are as great as the differences between living representatives of Akodon cursor and Akodon nigrita in their areas of sympatry.



Akodon (Akodon) lorenzini<sup>(1)</sup>, n. sp.

Holotype:

MMP M-1081 (Fig. 26I; Fig. 28H): The two lower jaws with incisors and molar teeth. Found by Mr. S. Lorenzini in the Atlantic slopes 5 Km. north of the City of Miramar classically known as "Barranca Parodi", Buenos Aires Province, Argentina. The fossil was found in strata of the San Andrés Formation, as confirmed in the field by G.J. Scaglia and J. Zetti.

Hypodigm:

The type specimen and :

MMP M-867 (Fig. 26G; Fig. 28G): Incomplete right maxilla with M<sub>1</sub>, broken M<sub>2</sub> and M<sub>3</sub>, and partially broken zygomatic plate. Found by G.J. Scaglia in the Vorohué Formation at the Atlantic slopes of the Chapadmalal region close to Baliza San Andres, Partido de General Pueyrredón, Buenos Aires Province. Found in association with the next specimen and with MMP M-551, type of Akodon (Abrothrix) magnus, n. sp. and MMP M-869, type of Cholomys pearsoni, n. gen., n. sp., (see later).

MMP M-868 (Fig. 26J): Left lower jaw with the incisor and all the molar teeth, lacking partially the coronoid, condyloid and angular processes. Found in association with maxilla Nr. MMP M-867. The possibility that M-867 and M-868 belong to the same individual is not excluded, but the molar teeth of the mandible look more worn than

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(1) The species name, lorenzini, is given for Mr. S. Lorenzini, discoverer of the type specimen and of other remarkable fossil cricetids, and an active collaborator of the Museum of Natural History of Mar del Plata.

the upper molar teeth, and therefore, I prefer to treat them as belonging to two different individuals.

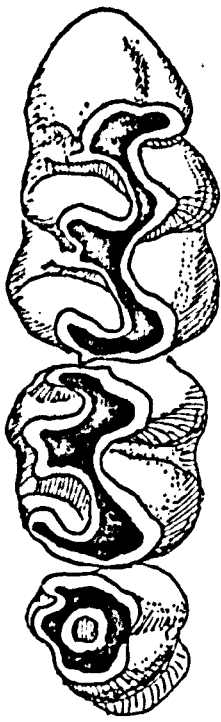
MLP 52-X-4-44 (a): Greater portion of right lower jaw (Fig. 26M) broken in front of the middle of the symphysis and at the posterior processes, with broken incisor and  $M_1$ - $M_3$ , the  $M_2$  partially broken; fragment of right maxilla including the  $M^1$  and the posterior half of the zygomatic plate; left femur; portion of the left tibia; right upper incisor. Found by J. Frenguelli in association with MLP s2-X-4-44 (b), referred to Scapteromys herskovitzi, in beds of San Andres Formation (= "Prebelgranense" in Frenguelli's stratigraphic nomenclature) in the Atlantic slopes extending south of Punta Hermengo, Miramar, Partido of General Alvarada, S.E. Buenos Aires Province, Argentina.

Diagnosis:

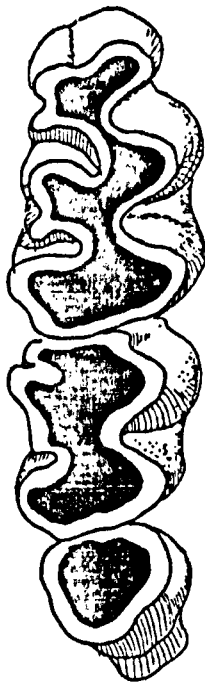
A small species of Akodon of the size of Akodon puer. Mandible relatively short and high. Zygomatic plate moderately wide. Incisive foramina well beyond the anterior border of the  $M^1$ , but not reaching their protocones. Upper first molars with a well-marked anteromedian flexus, a shallow anteroflexus and a projecting, narrow mesoloph remnant united to a mesostyle. Lower molars relatively narrow, without any indication of mesolophid remnants, mesostylids or ectolophids, and with somewhat oblique entolophids and posterolophids. Procingulum of  $M_1$  narrow, with a shallow anteromedian

Fig. 28. Crown views of right upper and left lower molar teeth of living and species of Akodon (Akodon) and of the Lower Pleistocene Akodon (Akodon) lorenzini, n. sp.

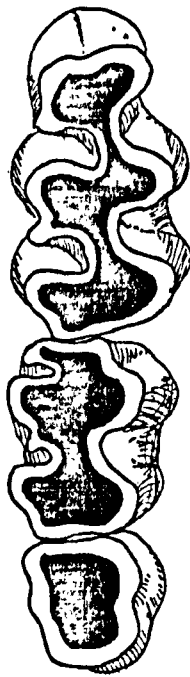
- A. Upper and B, lower molars of Akodon andinus (Phil.). Type of Akodon gossei Thomas, Female, BMNH 98.3.21.5. Puente del Inca, Mendoza, Argentina. Living.
- C. Upper and D, lower molar teeth of Akodon puer, Thomas. Type specimen, female, BMNH 2.1.1.78. Choquecamata, Bolivia. Living.
- E. Upper, and F, lower molar teeth of Akodon iniscatus, Thomas, Type specimen. Female. BMNH 3.7.9.64. Valle del Lago Planco, Chubut, Argentina.
- G. Upper molar teeth of Akodon lorenzini, n. sp. Vorohue Ftion., Lower Pleistocene, Partido de General Pueyreedon, Province de Buenos Aires, Argentina. MMP M-867.
- H. Lower molar teeth of Akodon lorenzini, n. sp. Type specimen, MMP M-1081. San Andres Ftion., Barranca Parodi Miramar, Partido de General Alvarado, Prov. de Buenos Aires, Argentina. Lower Pleistocene.
- I. Right M<sup>1</sup> of Akodon lorenzini, n. sp., M.L.P. 52-X-4.44 (a) San Andres Ftion., South of Punta Hermengo, Miramar, S.E. Buenos Aires Province, Argentina. Lower Pleistocene.
- J. Lower molar teeth of Akodon lorenzini, n. sp. MMP M-868 Found in association with MMP M-867, other data as in G.



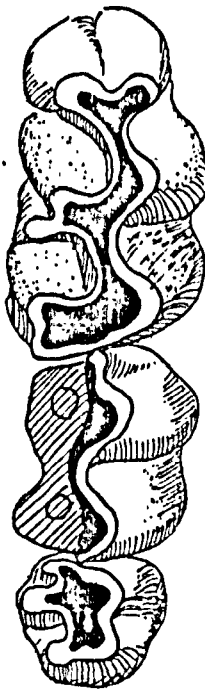
**A**



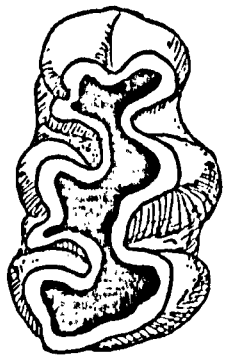
**C**



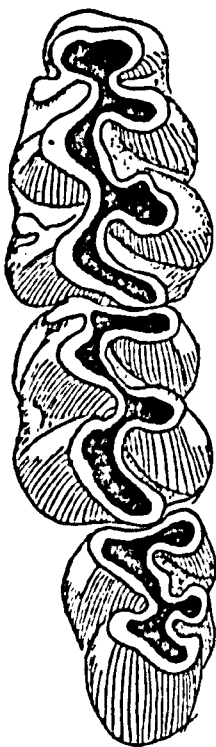
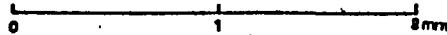
**E**



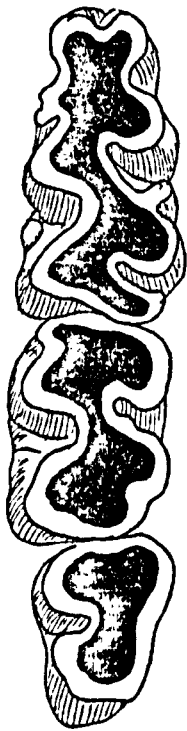
**G**



**I**



**B**



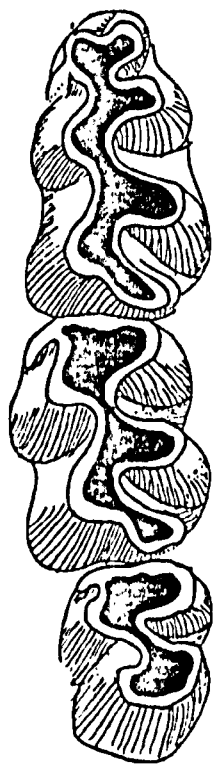
**D**



**F**



**H**



**J**

flexid and a well marked metaflexid.  $M_3$  relatively small.

Known distribution:

Vorohuean and San Andresian subages, Lower Pleistocene, South East of Buenos Aires Province, Argentina.

Description:

The skull fragments of specimens MMP M-867 and MLP 52-X-4-44 (a) only afford a few indications of the maxillary and palatal region. They show that this species had a rather robust zygomatic plate, probably wider than in A. iniscatus and as wide as in A. puer. The anterior border of the zygomatic plate is not preserved in neither of the two specimens, but its anterior lower limit can be observed in specimen MMP M-867, thus enabling one to deduce its relative width, which is slightly longer than the length of the  $M_1$ . The incisive foramina (Fig. 26G) are far more expanded backwards than in johannis, and they extend to the middle of the protoflexid of the  $M^1$ , not reaching to the protocone. In this respect, lorenzinii resembles iniscatus and andinus more than puer, in which the incisive foramina extend slightly behind the protocone of the  $M^1$  in all the 20 individual from different localities I examined.

The mandible (Fig. 26I, J) is much shorter than in puer, iniscatus, andinus or johannis. It differs markedly from the slender and elongated mandible of puer (Fig. 26C) and in proportions it is closer to the mandible of iniscatus, though it is noticeably smaller than the latter. The symphysis is fairly well up-turned, as the middle anterior point of the diastema reaches the level of the molar alveolar rows, differing also in this respect from puer, and obviously from johannis, to approach more the condition found in iniscatus. The masseteric crests are in a rather middle

position in the height of the ramus, as is also the case in iniscatus, whereas in puer and andinus they are placed at a higher level. They are less marked than in iniscatus, and the lower one is smooth, though even so, it is stronger than the upper one. The depth of the mandible at the  $M_1$  is greater than the diastema length, but it is less than the combined length of  $M_1$  and  $M_2$ . In iniscatus, the depth of the mandible is less than both the diastema length and the combined length of the first two molars, whereas in puer the diastema is longer than the depth of the mandible. The coronoid process slopes rather abruptly backwards, more or less as in iniscatus, and more so than in puer. The process itself is short and low, so that the condyle is at a level higher than the tip of the coronoid process. The condyloid process is high and it is not markedly projected backwards. The capsular projection is moderately developed, but it is stronger than in puer and andinus, even a little stronger than in iniscatus.

The incisor is comparatively deep, clearly more so than in puer, and it is also slightly deeper than in iniscatus. Its depth equals or exceeds the length of the  $M_3$  (Fig. 26).

The upper molars of MMP M-867 show little wear, while the  $M^1$  of MLP 52-X-4-44 (a) is moderately worn. They are very similar in morphology to both puer and iniscatus which share a great similarity in upper molar morphology. The only significant difference lies in the mesolophid remnant which unites to the mesostyle in the two available specimens and is projected further laterally than in the other species mentioned. In this respect, lorenzinii resembles more closely Akodon andinus, but it differs from the

latter in the stronger procingulum of the  $M^1$ , which has a well marked anteromedian flexus and a less projecting parastyle. The  $M^2$  is broken in its external half in the only specimen that shows this organ (MMP M-867), but it is evident that it was relatively narrow, as it is the case in puer and iniscatus.

The lower molars are more distinctive in showing a little marked anteromedian flexid and a rather narrow procingulum in the  $M_1$ , without any indication of a protostylid. There is, however, a well developed anterolabial cingulum, but it does not contribute to the shape of the crown enamel pattern of the procingulum as in the other species. The metaflexid is also more re-entrant than in puer and iniscatus. As in them, there is no trace of a mesolophid remnant or a mesostylid, and the simple entolophid is rather oblique in position, especially in the  $M_1$ . The posterolophid is even more oblique, so that the posteroflexid is noticeably wide. A protoflexid is well marked in the three lower molars, and the  $M_3$ , which, as in puer, is relatively small, has a sigmoid shape. No trace of ectolophid is shown in any of the three lower molars, but a tiny ectostylid is observed in the  $M_2$  or the type specimen.

Discussion:

Akodon lorenzinii is a very small species of Akodon showing a distinctive combination of characters. It seems to be more related to A. puer and A. iniscatus than to any other species of the subgenus Akodon, and the balance of similarities would favour a closer relationship with iniscatus. This is also to be expected on biogeographic grounds. In fact, puer is a wide-spread species, but re-

stricted to the Andean and Pampean mountains from Perú to north west Argentina. Thomas originally described puer from specimens of Chaquecamata, in west central Bolivia, and he subsequently identified as puer specimens which I have examined from south and central Perú. He later (1918) described coenosus from the mountains at Leon, Province of Jujuy, in the north west of Argentina, as a subspecies of puer. However, in a later publication (1920) in which he records more specimens from the city of Jujuy, he proposed full species status to coenosus, as did Cabrera (1961). However, after the examination of the corresponding types and of all the specimens referred to puer and coenosus in the British Museum (Nat. Hist.), I could not find any reasonable basis to accept species or even subspecies recognition for coenosus, and I therefore treat it as a junior synonym of puer.

Akodon iniscatus is based on an animal caught in the Andean region of Patagonia, south west of Chubut Province, but Thomas referred to is specimens from northern Patagonia to central Pampa Province and he says (1919: 205) that it extends to the south of Buenos Aires Province. A. iniscatus collinus was described by Thomas (1919: 206) as a subspecies from north western Patagonia, and Akodon nucus, described as a full species by Thomas (1926) from specimens of western Neuquen and southern Mendoza, was also considered as a subspecies of iniscatus by Cabrera (1961) Following my examination of the type specimen and a fairly large series in the British Museum (Nat. Hist.), Akodon nucus is obviously different from the typical iniscatus. It is a much larger form, and I surmise that it must be retained as



a distinct species. The subspecies distinction of collinus as regards the typical iniscatus is not at all evident, and I prefer to treat the two forms as a binomen. I suspect that Akodon molinae Contreras, described from specimens from the south of Buenos Aires Province, belong close to iniscatus and nucus, and that it may even be a synonym of one of the other of these species. I examined specimens in the collection of the British Museum (Nat. Hist.) from Central Pampa Province, which match perfectly with the type of A. iniscatus, and I am therefore inclined to give credit to the opinion of Thomas that there is a widespread distribution of iniscatus reaching north east to the south of Buenos Aires Province.

Therefore, the presence of a form apparently related to iniscatus in the Lower Pleistocene of south eastern Buenos Aires Province is not surprising. Whether lorenzinii can be thought of as a form related to the ancestry of iniscatus or as a member of an independent, though related lineage, is a matter that cannot be solved with the available evidence. The second alternative is more likely since a form more closely related to the living iniscatus than lorenzinii, was contemporaneous with the latter, as I shall discuss next.

Akodon (Akodon) cf. iniscatus Thomas

MMP S-640 (Fig. 26K): Right lower jaw with the incisor, and the very worn  $M_1$  and  $M_2$ , broken at the tip of the coronoid process and lacking the condyloid and angular processes. Found by G.J. Scaglia in stratum II of Vorohué Formation at the Atlantic slopes south of Arroyo Loberia,

Variate	Specimen											
	<u>Akodon lorenzini</u> <u>nii</u> , TYPE, MMP M-1081	<u>Akodon lorenzini</u> <u>nii</u> , MMP M-868	<u>Akodon lorenzini</u> <u>nii</u> , MMP M-867	<u>Akodon lorenzini</u> <u>nii</u> , MLP 52-X-4-44(C)	<u>Akodon johannis</u> TYPE MMP M-742	<u>Akodon cf. iniscatus</u> , MMP S-640	<u>Akodon iniscatus</u> Male, BMNH 13- 11-1-5.	<u>Akodon nigrita</u> Male BMNH 3.7- 74.	<u>Akodon puer</u> TY BMNH 2.1.1.78. Female	<u>Akodon andinus</u> (TYPE of A. gos) BMNH 98.3.21.5	<u>Akodon iniscatus</u> TYPE BMNH 3.7.9.64	<u>Akodon coenosu</u> TYPE BMNH 18.1.1.38
Length mandible, condyle-diastrama	10.85	11.39	-----	-----	-----	-----	13.27	13.00	12.80	12.73	13.01	13.27
L. Mand., cond.-M <sub>1</sub>	8.90	-----	-----	-----	-----	-----	10.05	9.91	9.91	9.65	-----	9.78
Length low. diastrama	2.37	2.49	-----	-----	3.26	3.26	3.07	3.00	2.75	2.94	-----	2.94
Depth mandible at M <sub>1</sub>	2.59	2.68	-----	2.75	3.07	3.01	2.75	2.57	2.62	2.88	3.11	2.54
Length M <sub>1</sub> - M <sub>2</sub>	2.75	2.80	-----	-----	2.56	2.88	2.88	2.69	2.75	2.69	2.85	2.75
Length M <sub>1</sub> -M <sub>3</sub> (alveolar)	3.70	3.90	-----	4.03	3.87	4.22	3.97	3.71	3.58	3.84	3.76	3.78
Length M <sub>1</sub> -M <sub>3</sub> (coronal)	3.66	3.90	-----	3.90	-----	-----	3.97	3.71	3.66	3.71	3.73	3.78
Length of M <sub>1</sub>	1.55	1.59	-----	1.58	1.49	1.64	1.67	1.53	1.58	1.55	1.64	1.56
Width of M <sub>1</sub>	0.99	1.07	-----	0.99	1.08	1.12	1.02	0.94	0.90	1.05	0.99	0.89
Length of M <sub>2</sub>	1.24	1.36	-----	1.18	1.15	1.24	1.21	1.18	1.15	1.21	1.21	1.18
Width of M <sub>2</sub>	0.97	1.02	-----	0.97	1.12	1.12	0.93	0.93	0.87	1.02	0.99	0.90
Length of M <sub>3</sub>	0.91	0.90	-----	1.08	-----	1.08	1.05	1.02	0.90	0.90	0.99	0.96
Width of M <sub>3</sub>	0.71	0.78	-----	0.83	-----	-----	0.74	0.83	0.72	0.77	0.77	0.77
Depth lowe incisor	0.94	0.97	-----	-----	1.05	1.02	1.02	0.99	0.84	0.97	1.01	0.85
Length M <sup>1</sup> -M <sup>3</sup> (alveolar)	-----	-----	4.03	-----	3.99	-----	4.16	3.58	3.71	3.84	-----	3.84
Length of M <sup>1</sup> -M <sup>3</sup> (coronal)	-----	-----	3.88	-----	3.78	-----	3.84	3.39	3.45	3.52	3.61	3.65
Length of M <sup>1</sup>	-----	-----	2.01	1.83	1.92	-----	2.01	1.74	1.74	1.78	1.80	1.89
Width of M <sup>1</sup>	-----	-----	1.08	1.08	1.21	-----	1.08	0.96	1.05	1.05	0.90	1.00
Length of M <sup>2</sup>	-----	-----	1.21	-----	1.21	-----	1.21	1.16	1.05	1.08	1.12	1.12
Width of M <sup>2</sup>	-----	-----	-----	-----	1.15	-----	1.08	0.99	1.02	0.99	0.87	0.93
Length of M <sup>3</sup>	-----	-----	0.77	-----	0.71	-----	0.65	0.62	0.68	0.71	0.71	0.65
Width of M <sup>3</sup>	-----	-----	0.87	-----	0.87	-----	0.77	0.84	0.74	0.87	0.68	0.81

TABLE 15. Measurements of Akodon lorenzini, n. sp., Akodon johannis, n.sp, and Akodon cf. iniscatus in comparison with types and selected specimens of related living forms.

Chapadmalal region, Partido de General

Peuyrred6n, Buenos Aires Province, Argentina.

Description and discussion:

This specimen cannot be included either in the coeval species A. lorenzini, or A. cf. cursor or A. johannis which immediately follows it in the succession. It differs from the former mostly in size and by all the characters I discussed in comparing lorenzini with iniscatus. It cannot be confused with johannis because of its somewhat greater size and more up-turned symphysis. In all the observed character states, this specimen matches in every detail with the studied mandibles of iniscatus so as to make it very plausible that it must be referred to the living species. The alveolar length of the lower molar row is, however, somewhat greater (Table ) than in the type of iniscatus, but the difference obviously falls within the range of variation of the sample of living iniscatus pooled from various localities, which I measured (Fig. ). Here again Akodon azarae must be considered as a possible candidate for relationship to the fossil specimen. Though a close relationship with azarae could be eventually demonstrated by new material, I believe that it is unlikely, and the present evidence does not support such relationships. A. azarae shows a less marked capsular projection, a more elongated mandibular ramus, a less up-turned symphysis and a relatively deep incisor; and in all these characters, specimen MMP S-640 agrees closely with iniscatus (Fig. 26L). Unfortunately, the molar teeth are too worn to show details of the enamel pattern, which is quite different in azarae and iniscatus,

Fig. 29. Dice-gram and scattergram of measurements of molar teeth in different species of Akodon (Akodon).



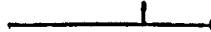
*A. iniscatus* N=20



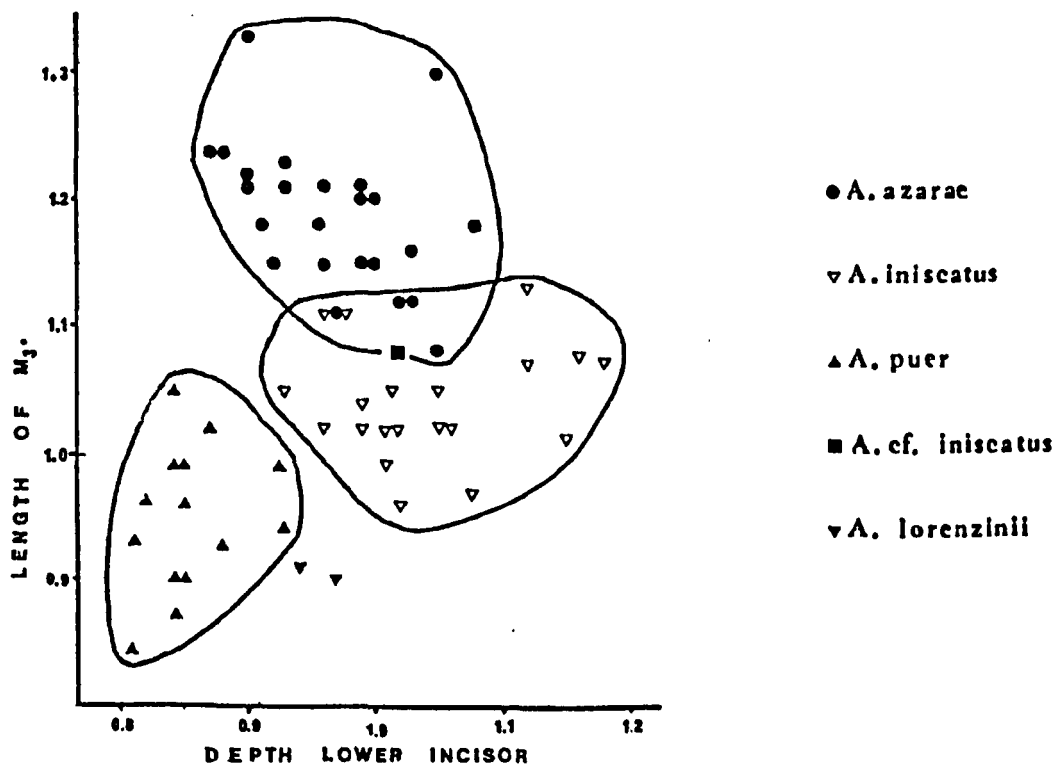
*A. puer* N=14



*A. lorenzinii* N=3



LENGTH  $M_1-M_3$  (CROWN)



as is shown by the high frequency in the former of ectolophids and ectostylids, mesolophid remnants and mesostylids, which are almost completely absent in the latter. The  $M_2$  of the fossil specimen, although very worn down, shows the external border of the mesoflexid fairly clearly, which does not show any trace of a mesolophid remnant or of a mesostylid, thus confirming a closer resemblance to iniscatus.

7.3. TRIBE SCAPTEROMYINI NOV. (= Scapteromyine group,  
Hershkovitz, 1966)

The scapteromyine sigmodontines have been recently revised by Hershkovitz (1966a). Following this revision, no more than three species grouped in two genera, Scapteromys and Kunsia, are to be recognized. However, many more nominal species have been described. Their taxonomic history is summarized in Tate (1932d), Massoia and Fornes (1964) and Langguth (1965). Hershkovitz proposed to separate S. tomentosus Lichtenstein<sup>(1)</sup> under the generic name Kunsia, and included S. gnambicuarae M. Ribeiro as a synonym. He recognizes the fossil S. principalis a subspecies of tomentosus (see also Massoia and Fornes, 1965a). He also recognizes S. fronto Winge (including S. chacoensis Gyldenstolpe as a subspecies), as a second species of Kunsia. Scapteromys is therefore limited to S. tumidus (including S. aquaticus Thomas).

Although rather closely related, Scapteromys and Kunsia are clearly distinct and easy to distinguish in size, morphology, ecology and distribution. The first is a rat-like, long-tailed inhabitant of the stream banks and marshes of the Rio de la Plata Basin, distributed in Uruguay, Southern Rio Grande do Sul in Brazil, Entre Rios, Corrientes, eastern Santa Fé and northern Buenos Aires Province in Argentina.

Kunsia is a stouter, much larger (it is the

---

(1) This species was known very vaguely until Hershkovitz's work, and its geographic provenance was a matter of doubt. After Langguth (1965) and Hershkovitz (1966) discussions of the subject, there is now little doubt that the type specimen did not come from Uruguay, but from the Rio Uruguay, in Southern Brazil. References to this species from localities in Argentina and Uruguay (including Langguth's own reference) are misidentifications based on specimens of S. tumidus.

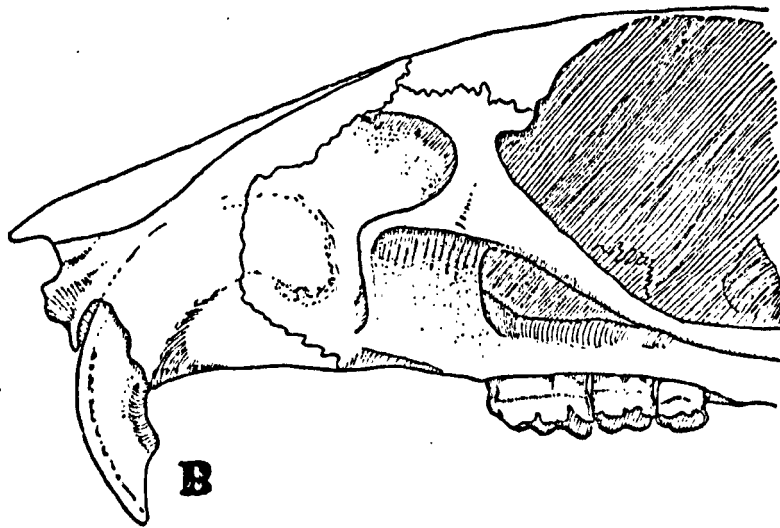
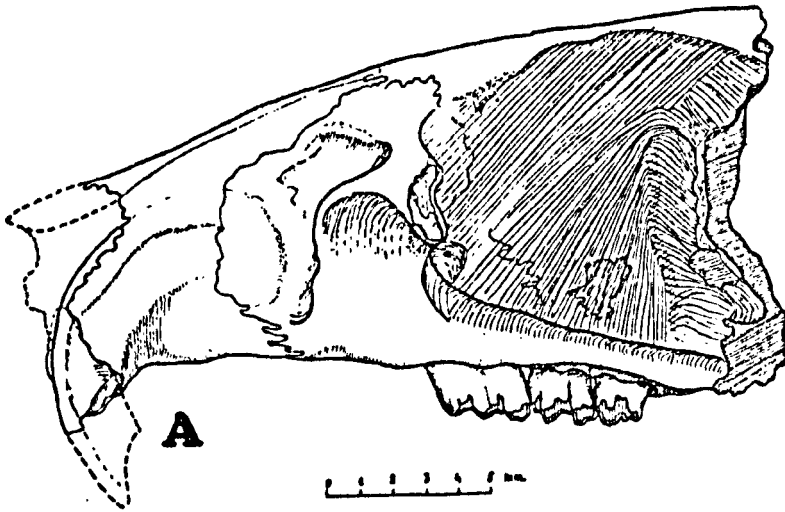
.largest living cricetid), shorter-tailed rodent of fossorial habits inhabiting the savannas and highlands of Matto Grosso and Minas Geraes the uplands of Beni and the northern Chacoan region.

The two recognized species of Kunsia are represented in the Upper Pleistocene and sub-recent cave deposits of Lagoa Santa, in Minas Geraes. Scapteromys, more generalized in morphology and adaptation, has not yet been described as a fossil. The origin and evolutionary history of the group is therefore obscure.

Although a strongly differentiated group, the Scapteromyines are also of dubious relationships. Tate (1932d) treated Scapteromys in a group of unrelated genera in which large size was the only common character. Ellerman (1942) places Scapteromys near Akodon, but states that it is very distinctive and of unclear relationships. Vorontzov (1959) placed Scapteromys as Akodontini incertae sedis, without any comments. Hooper and Musser (1964) found that Scapteromys is extremely distinctive in penis morphology and noticed some resemblances with the neotomyines, especially the Central American Nyctomys. However, these resemblances are balanced by an overwhelming amount of similarities with the penes of the South American cricetids, and they are better considered as convergences. Hershkovitz, formalized the distinction of Scapteromys in separating it as a group of its own, and suggested that they arose, together with the phyllotines and Oxymycterus from a common akodont stock (1966: 96). In his included dendrogram (op. cit. figs. 3 and 4) the Scapteromyines appear as cladistically more closely related to Oxymycterus than to any other group, including Akodon. A close relation-



Fig. 30. Skull, in lateral aspect of A. Scapteromys herskovitzi, n. sp., MMP M-853. B. Scapteromys tumidus Waterhouse, FCM-493, Punta Lara, La Plata, Buenos Aires Province.



ship of Scapteromys with Oxymycterus had been suggested by Baird as early as in 1859 (Tate, 1932d; 9). However, it is hard to find convincing support for such a close relationship, as in skull and dentition, digestive system phallic morphology and chromosomes, Oxymycterus and Scapteromys are set well apart. They are more likely to be regarded as two separate lineages evolving in different directions, though with a common ancestor at not very early times in the history of the sigmodontines.

The idea of an origin in the Akodontini does not seem also to be very convincing. Scapteromys has rather well developed mesoloph and mesolophids which in Akodontines are usually less evident or coalesced with their neighbour crests at a more advanced stage. The ancestry of Scapteromys must be sought in a full-fledged pentalophodont group, namely the Oryzomyini. In fact, the molar teeth of Scapteromys resemble very closely those of some species of Thomasomys or Oryzomys, which differ mostly in their tuberculate or crested to bi-level condition. Hershkovitz (1966a) provides a detailed description of the characters of the Scapteromyine group and the reader is referred to this work for thorough information on them at the tribal and generic level, as well as for the synonymies and other taxonomic detail. A shorter definition, centering on the diagnostic characters of the skull and dentition is as follows:

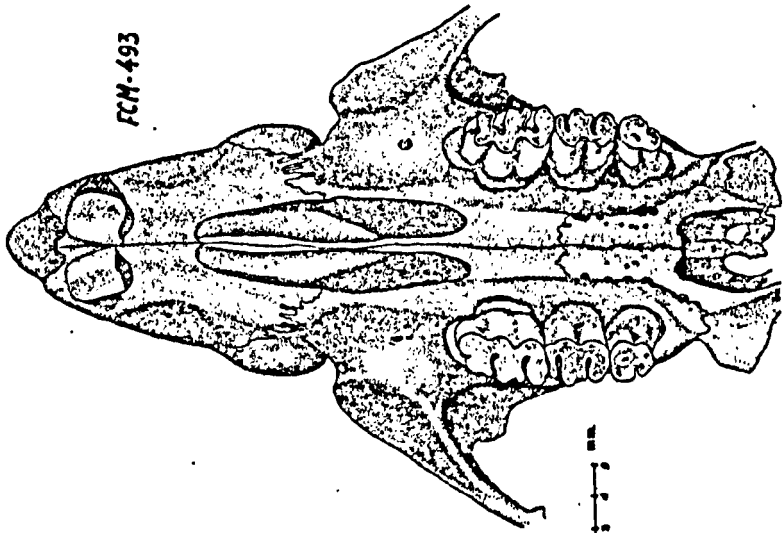
Sigmodontine cricetids of omnivorous to insectivorous feeding habits, without specializations for plant feeding. Molar teeth subhysodont; terraced when unworn, rapidly becoming plane with wear. Mesoloph and meso-

lophid well developed or obsolete in unworn teeth, when present partially or completely fused with paraloph or entolophid in worn teeth. Posteroloph vertical in unworn, completely fused with metaloph in worn teeth. Procingulum of  $M_1$  wide and biconulate with well developed anteromedian flexus and shallow anteroflexus. Ectolophid rarely, enteroloph never present.  $M_3$  as long or slightly longer than  $M_2$ . Zygomatic plate well developed, high, wide and projecting well forward the antorbital bridge.

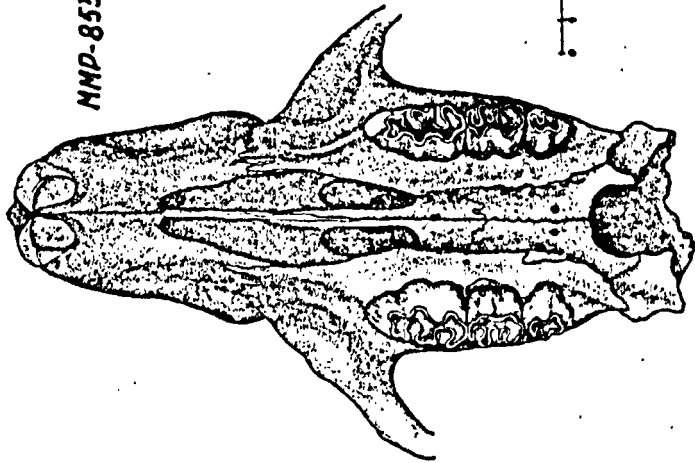
Accordingly I give the following definition of the two included genera.

Fig. 31. Skull, in ventral view of Scapteromys hershkovitzi,  
n. sp. type, MMP M-853, and scapteromys tumidus,  
FCM -493 (other data as in Fig. 30).

FCH-493



NMP-853



7.3.1. GENUS. SCAPTEROMYS, Waterhouse

DIAGNOSIS: A moderate-sized scapteromyine, skull not strongly crested. Rostrum comparatively long and slender. Zygomatic plate well separated from the internal wall of the intra-orbital foramina. Mandibles rather weak and elongated with comparatively low horizontal ramus and ascending processes. Capsular projection of the inciseve not forming a tubercular process. Unworn molar teeth terraced, with distinct mesoloph and mesolophid,  $M^2$  and  $M_2$  distinctly longer than wide.

TYPE SPECIES: Mus (Scapteromys) tumidus Waterhouse, by original designation.

INCLUDED SPECIES: Only Scapteromys tumidus. Scapteromys aquaticus Thomas 1920 has been proved (Massoia and Fornes, 1964; Hershkovitz, 1966) to be inseparable from the type species. Other designated species have been referred by Hershkovitz to this genus Kunsia, a proposal with which I fully agree. I found that a fossil Scapteromys from the Lower Pleistocene of Buenos Aires Province differs so much from the single living species as to deserve its being a new species.

Scapteromys herskovitzi<sup>(1)</sup>, n. sp.

Holotype: MMP M-853 (Fig. 30A, Fig. 31, Fig. 32B): Fragmented skull missing most of the brain case, the zygomatic archs and the anterior tip of nasals and premaxillae. San Andrés Formation, Atlantic cliffs of S.E. Buenos Aires Province,

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(1) The species is named for Philip Hershkovitz, as an homage to his remarkable contributions to the better knowledge of the South American mammals.

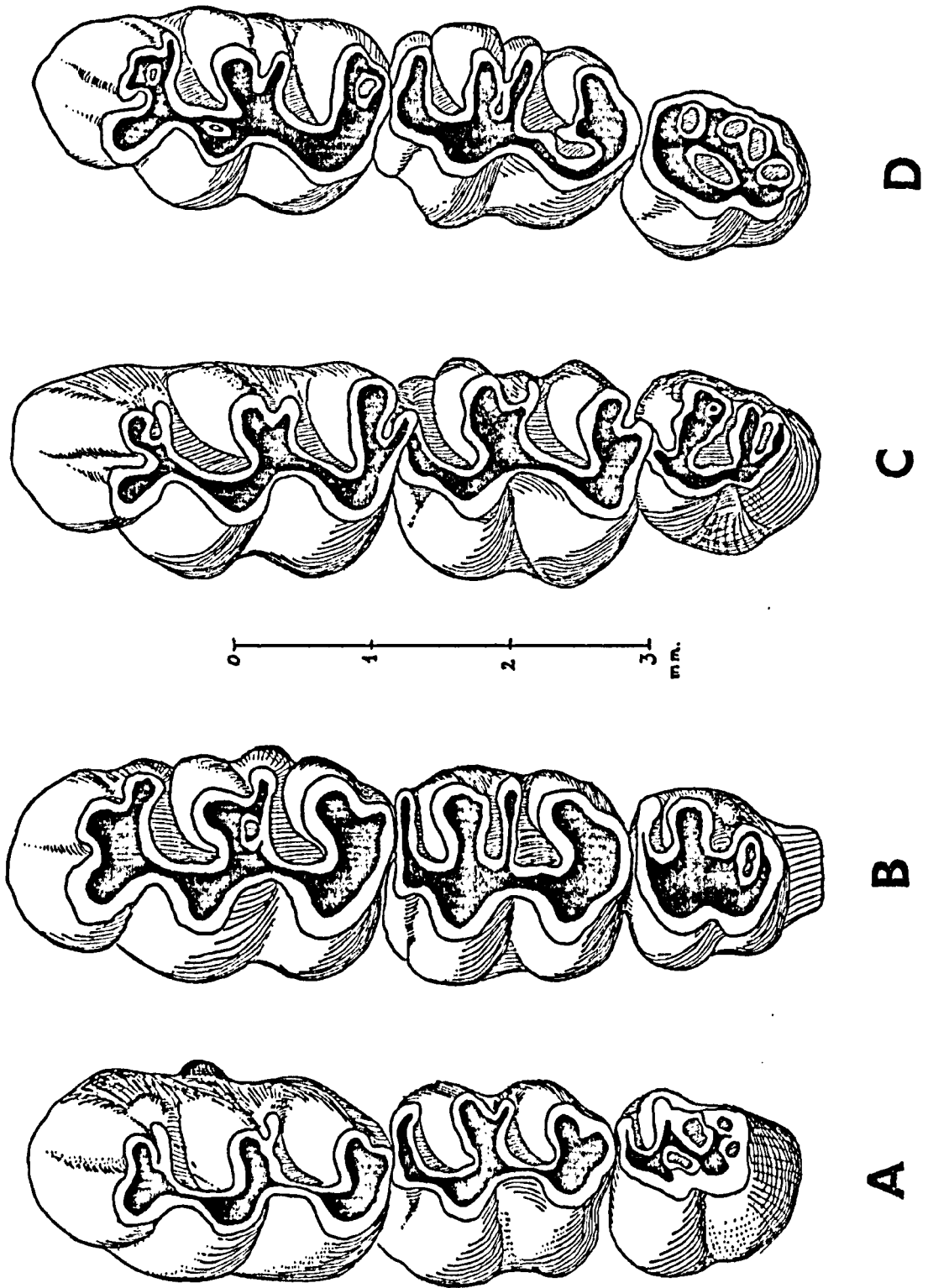
Fig. 32. Upper molar teeth, in occlusal view of living and fossil Scapteromys.

A. MMP M-1079, S. herskovitzi, n. sp.

B. MMP M-853, S. herskovitzi, n. sp.

C. and D. Two specimens of Scapteromys tumidus, Waterhouse, from Uruguay.





Argentina, close to Punta San Andrés, Partido de General Pueyrredón, Buenos Aires Province, Argentina.

Hypodigm:

The holotype and MMP M-1079 (Fig. 32A, Fig. 33B, C, E): Left maxilla with M<sup>1</sup>-M<sup>3</sup>; right maxilla with M<sup>1</sup>-M<sup>2</sup>; right lower jaw missing the M<sub>3</sub> and the angular and ascending processes; left mandibular ramus missing the M<sub>2</sub> and M<sub>3</sub> and the angular and ascending processes, fragmentary right pelvis. Lower Vorohué Formation, Atlantic cliffs of S.E. Buenos Aires Province, 1/2 K south of "Arroyo Loberia", Partido de General Pueyrredón.

DIAGNOSIS: A Scapteromys of size slightly smaller than S. tumidus. Incisive foramina extended backwards to the middle of the M<sup>1</sup>; posterior border of the nasals truncated, zygomatic plate high and relatively narrow, with rounded anterior corner. Mandibular ramus relatively slender with anterior point of the symphysis distinctly lower than alveolar border.

KNOWN DISTRIBUTION: Lower Pleistocene (Vorohuan and San Andresian subages of the Uquian age) South Eastern Buenos Aires Province, Argentina.

DESCRIPTION: The concept of Scapteromys hershkovitzi is based on the holotype. The other specimen is tentatively referred to the same specimen but it shows differences in morphology which could be an indication that we are dealing with another form. Therefore, it will be des-

cribed separately.

The preserved part of the skull agrees with the diagnostic characters of Scapteromys in all the observed characters. The rostrum is slender, comparatively long and less deep and robust than in Kunsia. The incisors are broad at the level of the alveoli, but they can be reconstructed as orthodont to slightly opisthodont, as in S. tumidus. In the lateral view the striking difference between the living and the fossil species lies in the zygomatic plate. The fossil skull shows this plate strongly inclined laterally and with its anterior part well separated from the medial wall of the antorbital foramina, as it is diagnostic of Scapteromys. The plate is, however, higher and shorter than in S. tumidus, does not project so far anteriorly as in this species, and has a concave anterior border and a widely rounded dorsal corner. In S. tumidus the anterior border is slightly concave or straight, and the dorsal corner is more pointed than rounded. Dorsally, the antorbital foramina shows an ovate outline and it is widely exposed, as in S. tumidus, but it is abruptly truncated and does not show any median spine, as it does in Kunsia tomentosus. The supra-orbital region is narrow, but it is slightly less constricted than in tumidus. The anterodorsal frontal sinuses are less inflated than in tumidus, but they are distinctly more inflated than in K. tomentosus. The supraorbital edges are smooth but evident, and a rudimentary postorbital process may be distinguished.

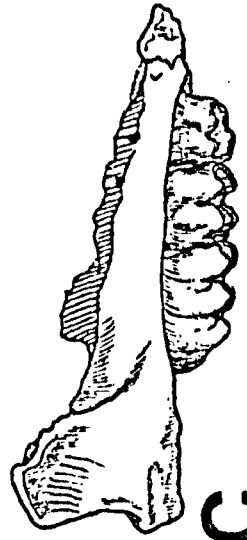
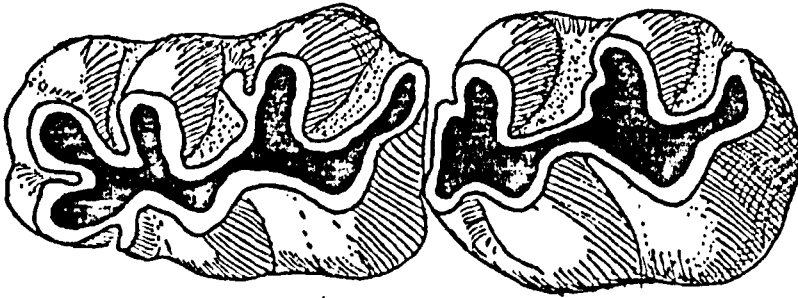
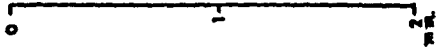
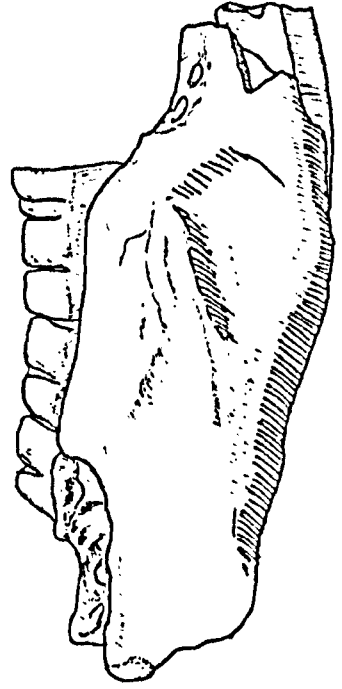
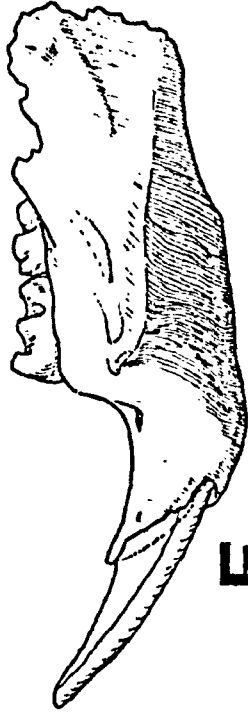
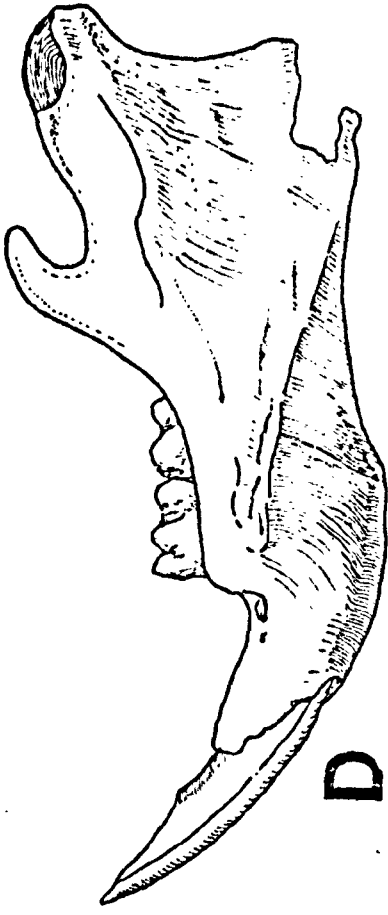
The incisive foramina are elliptical in outline and comparatively well-open, differing from those of tumidus in being much wider. They project backwards much further than in any other scapteromyine, reaching to the middle of the M<sup>1</sup>.

In tumidus they reach to the anterior border of the M<sup>1</sup> or slightly posterior to that border. The palate is long and wide and extends beyond the posterior border of the M<sup>3</sup> in a rounded posterior border not showing any median spine. The posterolateral palatal pits are less numerous and smaller than in tumidus and there is no evidence of posterolateral palatal fossae.

The stage of wear of the cheek teeth indicates a young adult individual, and much of the enamelled elements of the crown surface are clearly shown. The molars are very similar to those of individuals of tumidus of equivalent degree of wear (Fig.32). The occlusal surface is slightly terraced. The procingulum of the M<sup>1</sup> is noticeably wide and has a rather distinct anteromedian flexus. The anterolabial conule is stronger than the anterolingual conule, and the anteroloph is fused to a distinct parastyle, whereas the anteroflexus is merely indicated as a notch anterior to the parastyle. No anterofossetus is visible, whereas this element is often evident in similarly worn M<sup>1</sup> of tumidus. The mesoloph is incompletely fused with the paraloph, forming a distinct mesofossetus and shaping a median loph bifurcated into a large paraloph and a smaller mesoloph united with a strong mesostyle. The meta-loph is oblique in position and connects backwards with the posteroloph, though both elements are almost completely confluent, the posteroflexus being represented merely by a shallow notch posterior to the metacone. The hypoflexus is well open and there is no indication either of an enteroloph or an enterostyle. The M<sup>2</sup> repeats the main features of the M<sub>2</sub>, but it has a completely independent and full-fledged mesoloph separated from the paraloph by a deep and complete mesoflexus.

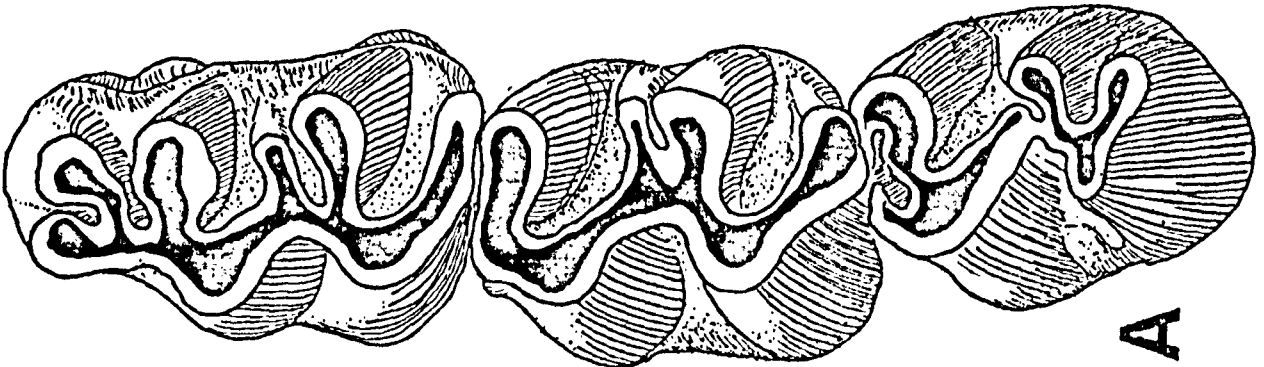
Fig. 33. Lower molars, mandibles and maxilla of living and fossil Scapteromyini.

- A. Right lower molars of Scapteromys tumidus Waterhouse, BMNH 24.9.1.65. Soriano, Uruguay.
- B. Right M<sub>1</sub> and M<sub>2</sub>, AnC, external aspect of left maxilla, and E, lateral<sup>2</sup> aspect of left lower jaw of Scapteromys hershkovitzi, n. sp., MMP M-1079.
- D. Lateral view of left lower jaw of same specimen as in A.
- F. Lateral view of right lower jaw of Kunsia fronto, Winge. MINP TAR-1.



B

C



A

Both the anteroloph and the mesoloph are transversal and narrower than the paraflexus, which is somewhat more oblique. The mesoloph shows this diagonal trend more strongly marked and is completely fused with the posteroloph, not being any indication of the posteroflexus. Labial lophs and styles are absent. The  $M^3$  shows a deep paraflexus and a mesoloph not fused with a well developed mesostyle.

Specimen MMP M-1079 (Fig. 32A, 33B, C, E) agrees in size and in basic morphology with the holotype. It shows, however, differences, the significance of which cannot be evaluated with the material at hand.

The skull fragments show a lower and shorter zygomatic plate (see measurements in Table 16) with a somewhat concave anterior border and a rounded dorsal corner. The palate is shorter, as its hind border lies at the same level of the posterior border of the  $M^3$ . The posterior points of the incisive foramina, on the contrary, reach as far backwards as in the type specimen. The upper molar teeth are less worn than in the holotype and therefore the occlusal surface is more strongly terraced and the lophs are narrower. In spite of that, the mesoloph is almost completely fused with the paraloph in the  $M^1$  and  $M^2$ . In the former, it is only visible as a narrow spur projecting from the posterobuccal corner of the paracone, and connected with a mesostyle. In the latter it is somewhat stronger and it is defined by a shallow mesoflexus which has the shape of a notch separating the end of the paraloph from the buccal remnant of the mesoloph. This makes a clear cut difference with the condition in the holotype, already described. However, differences of the same magnitude are observed between individuals of S. tumidus

(Fig.     ).     .

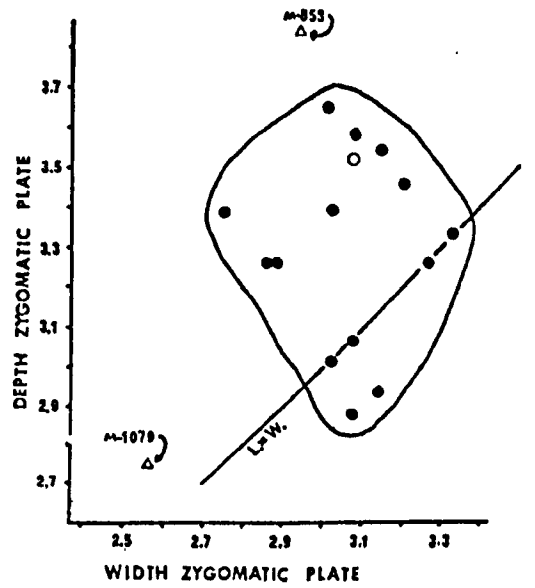
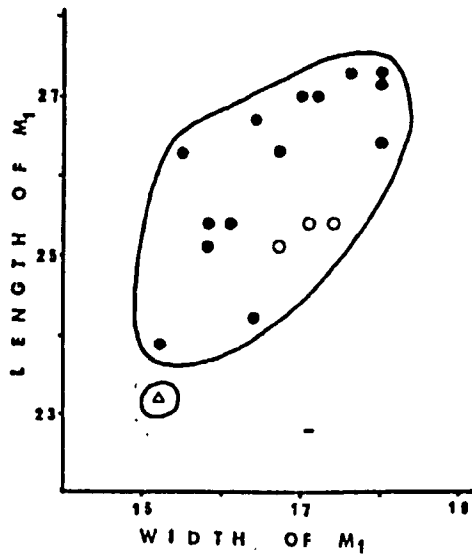
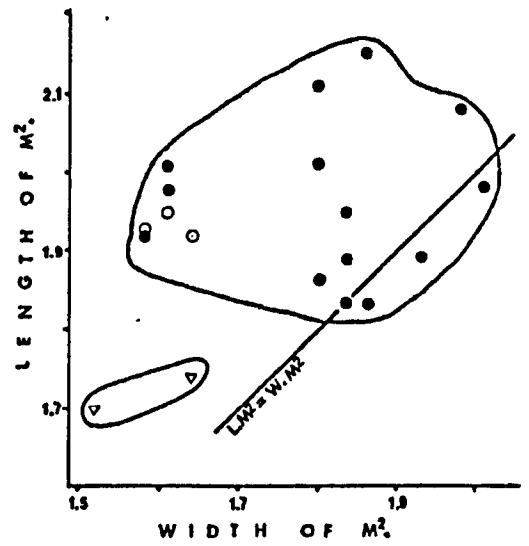
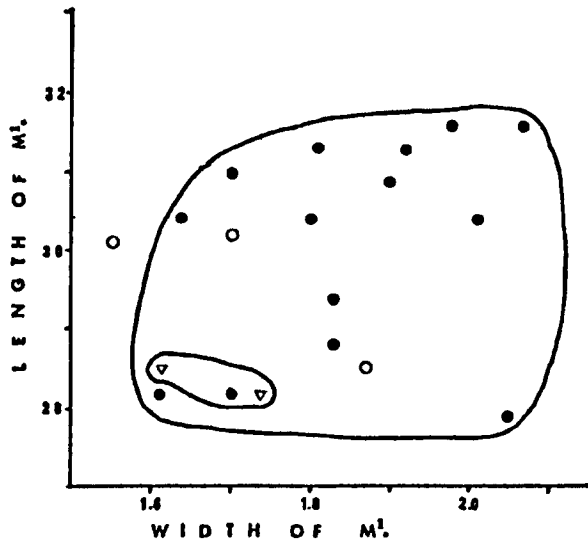
The mandibular fragments (Fig. 33E) of this specimen closely resemble the mandibles of individuals of similar age (as inferred from tooth wear) of S. tumidus. The horizontal ramus is, however, slightly more slender, and the symphysis is less uprightly directed, its uppermost anterior point not reaching the level of the alveolar plane. Moreover, the masseteric ridges join anteriorly at a point which lies below the anterior border of the  $M_1$ , whereas in S. tumidus this point is situated well behind that border.

The incisor is very weak as compared with those of the living species (see Table 16). The  $M_1$  is shorter and narrower than in S. tumidus (Fig. 33). It has a well developed procingulum made of subequal conulids separated by deeply re-entrant metaflexid and a protoflexid. In the latter a distinct anterior cingulum is present. The metalophid and entolophid are slightly oblique and of subequal development and the mesolophid is rudimentary, merely represented by a spur projecting forwards and inwards from the middle of the entolophid. The posterolophid is narrow and does not end on a distinct posterostylid. Neither in the  $M_1$  nor in the  $M_2$  is there any indication of ectostylid or ectolophid. The  $M_2$  is relatively short, but it is as wide as it is usual in S. tumidus. It shows a distinct procingulum, well defined both by a shallow labial protoflexid and a shallow lingual metaflexid. The mesolophid is here also rudimentary and represented by an even shorter and blunt outgrowth from the middle of the anterior border of the entolophid. The posterolophid is comparatively narrow and very oblique in position.



Fig. 34. Scattergrams of measurements of the molar teeth and of the zygomatic plate of living and fossil Scapteromys.

- *S. tumidus* (Paraná Delta)
- *S. tumidus* (Soriano, Uruguay)
- ▽ *S. hershkovitzi*



DISCUSSION:

There is little doubt about the proposal that the skull from the San Andres Formation represents a species of Scapteromys different from the living S. tumidus. The differences supporting its separation are not evident in the morphology of the molar teeth, but are clear in the characters of the zygomatic plate, the fronto-nasal suture and the shape and backwards extension of the incisive foramina. The species distinction is further supported by the characters of the referred specimen from the underlying Vorohué Formation which shows distinctive characters in the mandible, the lower incisor and the lower molar teeth. It is possible, however, that this second specimen may represent another species, different both from S. tumidus and from S. hershkovitzi. The shorter palate and the differences in the zygomatic plate are suggestive of this, but they could also be attributed to variation within the limits of one species. At least the differences observed between the San Andrés and the Vorohué specimens in the morphology of the upper molars are within the range of the variabilities observed in samples of the living S. tumidus. The latter species does not show the same amount of variation in the morphology of the palate and the zygomatic plate (Fig. 34), but it can not be extrapolated from this that the fossil specimens belong to different species. Though this possibility must be kept in mind, it can only be demonstrated on the basis of larger samples of fossils from the two formations.

In any case, the described specimens of the Early Pleistocene do not show any character state which could convincingly be considered ancestral to the states of the

Variate \ Specimen	<u>Scapteromys her-</u> <u>shkovitzi</u> , TYPE MNP M-853. San Andrés formation.	<u>Scapteromys her-</u> <u>shkovitzi</u> . MMP M-1079. Voro- rohué formation.	<u>Scapteromys tu-</u> <u>midus</u> , female, BMNH 24.9.1.65, Soriano, Uruguay.
Length Incisor - M <sup>3</sup>	17.31	-----	18.49
Length upper diastema	9.38	-----	10.05
Length of nasals	13.40	-----	15.81
Length of frontals	8.98	-----	12.46
Width of rostrum at fronto-premaxillary suture	6.83	-----	6.97
Length incisive foramina	8.44	-----	8.58
Palatilar length	15.89	-----	16.70
Length posterior palate	5.76	-----	6.29
Width of palate between M <sup>1</sup>	3.58	-----	2.68
Depth zygomatic plate	3.84	2.75	3.52
Width zygomatic plate	2.94	2.56	3.07
Minimal interorbit. width	5.50	-----	5.18
Alveolar length M <sup>1</sup> -M <sup>3</sup>	6.53	6.27	6.46
Coronal length M <sup>1</sup> -M <sup>3</sup>	6.14	6.02	6.08
Length M <sup>1</sup>	2.82	2.85	2.85
Width M <sup>1</sup>	1.74	1.61	1.87
Length M <sup>2</sup>	1.74	1.70	1.92
Width M <sup>2</sup>	1.64	1.52	1.64
Length M <sup>3</sup>	1.46	1.46	1.46
Width M <sup>3</sup>	1.37	1.33	1.46
Depth upper incisor	2.04	-----	2.14
Width upper incisor	1.05	-----	1.21
Length mandible symphysis-M <sub>3</sub>	-----	11.00	12.43
Length symphysis	-----	4.03	4.93
Depth mandible at M <sub>1</sub>	-----	-----	4.48
Alveolar length M <sub>1</sub> -M <sub>3</sub>	-----	6.27	6.91
Coronal length M <sub>1</sub>	-----	2.32	2.54
Width M <sub>1</sub>	-----	1.49	1.71
Length M <sub>2</sub>	-----	1.86	1.98
Width M <sub>2</sub>	-----	1.46	1.70
Depth lower incisor	-----	1.02	1.67
Width lower incisor	-----	0.74	1.12

TABLE No. 16 Measurements, in mm of Scapteromys  
hershkovitzi, n. sp., and one individual  
of the living Scapteromys tumidus

same characters found in the living species. It is true that the slightly smaller size and the more generalized zygomatic plate can be regarded as indications of ancestry, but this is not so with the morphology of the molar teeth and the shape of the incisive foramina which can be considered as advanced or even more advanced in the fossils than in the living species. Scapteromys herskovitzi seems rather to be a distinct extinct relative of S. tumidus, and both species are better considered as descendants of a common ancestor, than as linked to each other by direct ancestry.

It is of interest to realize that S. herskovitzi is found in a geographic area located beyond the limit of distribution of the living scapteromyines. Scapteromys tumidus was reported by Hershkovitz (1966: 100, Map Fig. 1) as extending southwards to the coast of the Samborombón Bay in N.E. Buenos Aires Province. Massoia and Fornes (1965c) had reported to have found five specimens of this species on a Southern locality, on the Atlantic coast at the Partido de Castelli, which agrees with Hershkovitz southern limit. The species occurs, however, further south, as Contreras (pers.comm.) found one specimen in the vicinity of Santa Clara del Mar, some 150 Km south of the Samborombón Bay, and only some 40 km north of San Andrés, the place where the fossils were found.

7.3.2. GENUS KUNSIA, Hershkovitz

Diagnosis:

A large scapteromyine with a robust and well-ridged skull. Rostrum heavy, short and deep. Zygomatic plate proximally pressed to the internal lateral wall of the intraorbital foramen. Mandible deep and robust, with high horizontal ramus and high ascending processes. Capsular projection of the incisor forming a prominent tubercular process. Unworn molar teeth plane, without or with a merely vestigial mesoloph. Mesolophid totally or almost completely fused with entolophid.  $M^2$  and  $M_2$  about as wide as long.

Type species: Mus tomentosus Lichtenstein (By Hershkovitz's designation).

Included species:

fronto and tomentosus.

Comments on the included taxa:

As indicated above Hershkovitz (1966a) recognized two species and four subspecies of Kunsia, namely:

Kunsia tomentosus tomentosus (Lichtenstein) 1830  
(= Scapteromys gnambicuarae Miranda Ribeiro)

Kunsia tomentosus principalis (Lund) 1839

Kunsia fronto chacoensis (Gyldenstolpe) 1932

Kunsia fronto fronto (Winge) 1888.

This separation into subspecies must be taken as provisional, as the two species are only known by so few specimens, and it is based mostly on geographical grounds. K. t. principalis and K. t. fronto are only known from the holotypes, fragmented skulls from the Upper Pleistocene de-

posits of Lagoa Santa, in south eastern Brazil. K. f. chacoensis is also only known from the type specimen, a skin and skull from Chaco, Argentina. Hershkovitz mentions that he has seen only four specimens of K. t. tomentosus. In spite of the scarcity of their known representatives in the collections, the two species are well established, and little doubt can be cast about the validity of their distinction. They show a clear-cut size difference, tomentosus being larger than fronto and the largest known living cricetid (it can reach 445 mm of total length, and its skull length reaches more than 50 mm).

K. fronto has a relatively shorter tail, and it is also different in having a vestigial mesoloph, which is completely absent in tomentosus. Moreover, fronto has more elongated nasals which taper acutely backwards, whereas the nasals of tomentosus have truncated proximal ends, as also happens in S. herskovitzi.

One fragmentary lower jaw in the collection of the Museum of Natural History of Paris agrees with the characters of fronto and in fact represents the fourth known specimen of this rare species.

Kunsia fronto (Winge) 1888

1888. Scapteromys fronto Winge, E. Museo Lunds 1 (3):44

1932. Scapteromys chacoensis, Gyldenstolpe, Ark. Zool. Stockholm, 24B, No. 1:1

1966. Kunsia fronto, Hershkovitz, Z. f. Saugetierkunde 31:113.

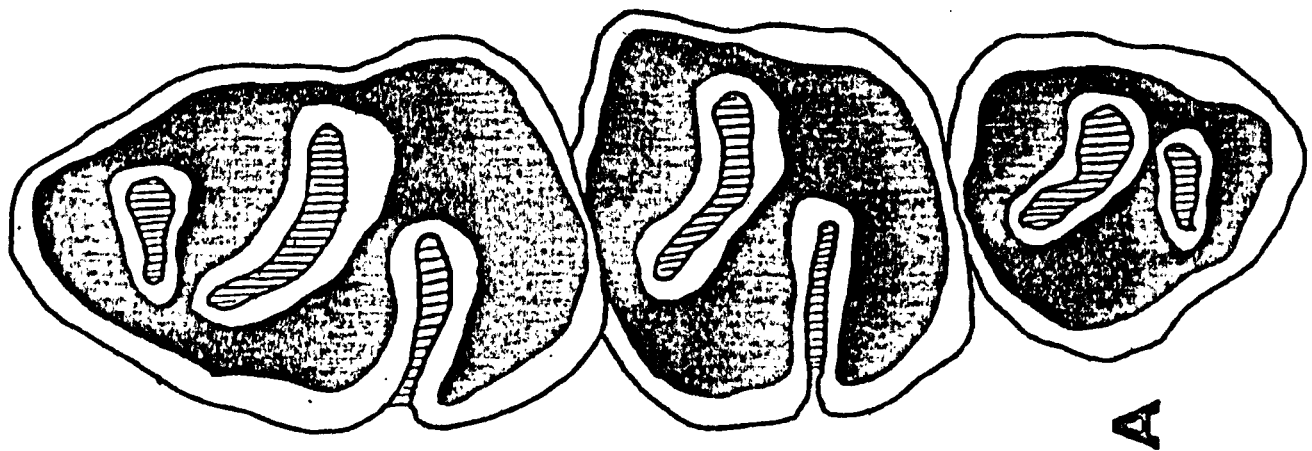
Referred specimen:

MHNP TAR-1 (Fig. 33F, Fig. 35C): Fragmentary left lower jaw with broken incisor and the three lower molars; the symphysis broken anteriorly, and lacking the angular, coronoid and condyloid processes. Found in the Tarija beds (Upper Pleistocene), at Tarija, southern Bolivia (see pages

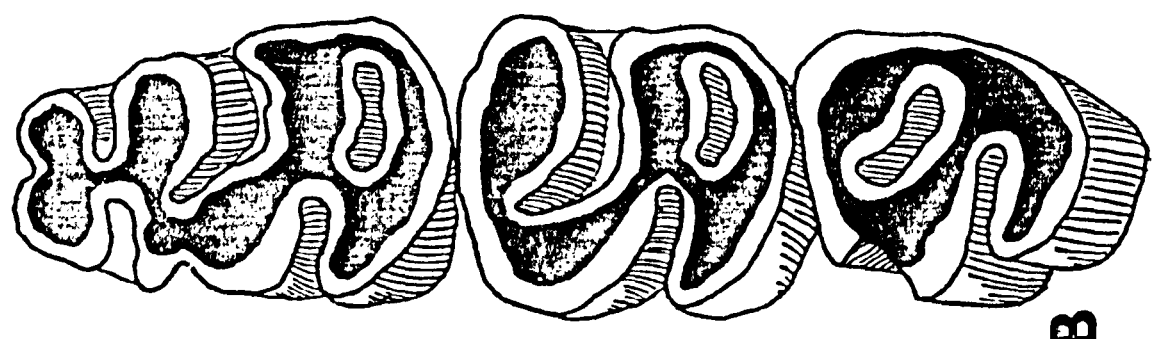
Fig. 35. Left lower molars, in occlusal view of Scapteromyini.

- A. Kunsia tomentosus (Lichtenstein). s/n San Joaquin, Beni, Bolivia. Drawn after photograph in Hershkovitz (1966 a).
- B. Kunsia fronto (Winge), Type of S. chacoensis Gyldenstolpe, RNHMS Nr.26. Rio de Aro, Chaco, Argentina.
- C. Kunsia fronto (Winge), Tarija beds, Bolivia, MHNP TAR-1.
- D. Scapteromys tumidus. BMNH, Isla Ella, Paroná Delta, Argentina.

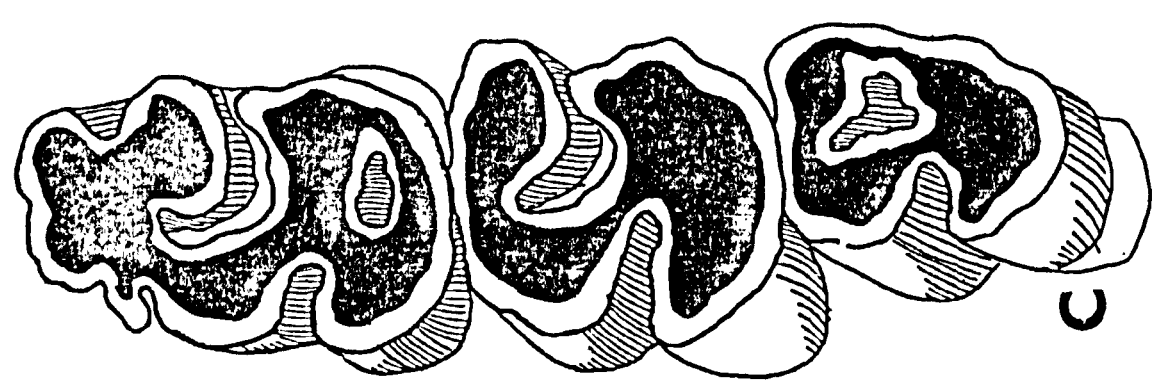




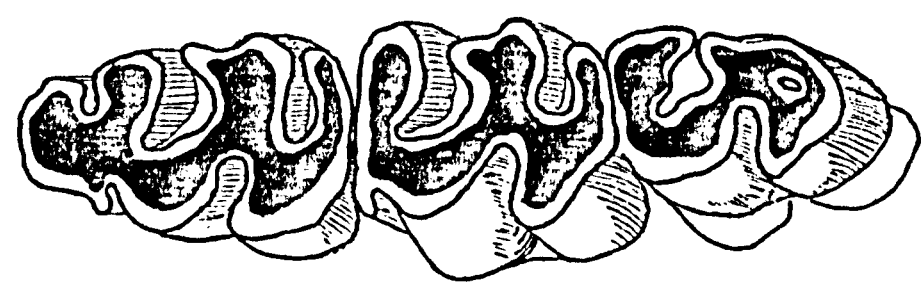
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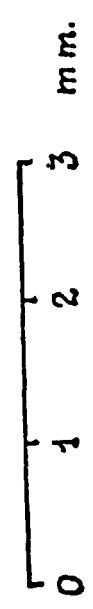
B



C



D



for other associated cricetid remains),

Description:

The specimen belonged to an adult individual of an advanced age, judging from the degree of wear of the molar teeth. However, the wear is not advanced enough as to have erased the enamelled structures of the crown. Both in size (Table ) and in the structure of the mandible and the molars, it matches in every detail the mandible of K. fronto using the photographs published by Hershkovitz of the type specimen of S. chacoensis. The other known mandible of this species, the one mentioned by Winge (1888: 44) has not been illustrated.

This mandible has a double mental foramen, a character which is neither shown in the photographs of K. fronto illustrated by Hershkovitz, nor known in any other scapteromyine. This is probably an individual anomaly of no taxonomic value. The enamel pattern of the molars also shows some variations as regards the type specimen of chacoensis (Fig. ). The metaflexid and the protoflexid of the  $M_1$  are very shallow, and the anteromedian flexid is merely vestigial in the specimen from Tarija, whereas those elements are deeper in the specimen from Chaco. Similarly, the posterofossetid of the  $M_2$  is well developed in the latter, and completely absent in the fossil specimen, and there are also some minor differences in the shape of the  $M_3$ . That all these differences are merely due to different degree of wear of the crown surface, can be readily concluded after examining a series of Scapteromys tumidus including individuals of different ages. This is well demonstrated in the series from the Paraná Delta.

Both the fossil Tarijan and the living Chacoan specimens show in the  $M_1$  and the  $M_2$  an anteriorly projected

Variate \ Specimens	Kunsia fronto (Type of S. Cha- coensis.) RNHMS No. 26, Rio de Oro, Chaco, Ar- gentina.	Kunsia fronto MHP TAR-1, Pleis- tocene of Tarija, Bolivia	Kunsia tomentosus (without catalogue number) San Joa- quin, Beni, Boli- via.
Depth of mandible below M <sub>1</sub>	7.17	6.16	8.66
Alveolar length of M <sub>1</sub> -M <sub>3</sub>	8.09	7.79	----
Coronal length of M <sub>1</sub> -M <sub>3</sub>	7.68	7.45	9.26
Length of M <sub>1</sub>	3.12	3.05	4.26
Width of M <sub>1</sub>	2.02	2.09	2.79
Length of M <sub>2</sub>	2.39	2.35	2.87
Width of M <sub>2</sub>	2.09	2.09	2.98
Length of M <sub>3</sub>	2.17	2.06	2.57
Width of M <sub>3</sub>	1.87	1.80	2.32

TABLE No. 17 Measurements of the lower jaw and lower molars of specimens of Kunsia (The figures in the first and third row were calculated from Hershkovits's illustrations)

lingual spur of the medial loph which represent a mesolophid remnant united to a mesostylid. These features are not shown in Kunsia tomentosus which is also clearly different in size (Fig. 35, Table 17), and in having the  $M_2$  distinctly wider than long.

Discussion:

The presence of Kunsia fronto in the Upper Pleistocene of Bolivia is not a surprising occurrence, as the species was found in the Upper Pleistocene of south eastern Brazil and is living at present in the Chacoan region. Moreover, the other species of Kunsia, tomentosus, has been recorded as living in north eastern Bolivia. In any case, its discovery in the Pleistocene of Tarija extends the known distribution of the species far more westwards in the Quaternary than its probable present distribution as stated by Hershkovitz: "the Rio Paraná Basin from the Brazilian highlands to the Argentine Chaco" (1966: 113).

7.4. TRIBE WIEDOMYINI, NEW TRIBE.

Wiedomys was proposed as a generic name by Hershkovitz (1959) for a monotypic taxon based on Mus pyrrhorhinus Wied, 1826, a species, the systematic position of which has been a matter of doubt for years, having been referred to Mus, Oryzomys, "Hesperomys", Rhipidomys and Thomasomys (for a taxonomic history of Mus pyrrhorhinus see Tate, 1932e, and Hershkovitz, 1959).

In discussing the affinities of his new genus Wiedomys, Hershkovitz indicated the distinctions of Wiedomys as regards his oryzomyine and thomasomyine groups of genera, the akodontines and Phyllotis. He found that Wiedomys was close to Calomys and Eligmodontia in some characters, but a close relationship with these genera was discarded by him. He states (1959) that the new genus is very distinctive from the phyllotines in several respects, and in his further revision of the phyllotines (Hershkovitz, 1962) Wiedomys was not included at all, even to compare it with the various phyllotine genera. Actually, Hershkovitz did not indicate any close affinity of Wiedomys with any taxon of the South American cricetids, and the taxonomic relationships of his new genus was left tacitly as an open question.

On the basis of the material of pyrrhorhinus in the British Museum (Nat. Hist.) and of additional specimens more recently obtained by F. Petter in Brazil, and now belonging to the collection of the Museum of Natural History of Paris, I undertook a new study of the systematic relationships of Wiedomys, and I conclude that this genus shows a unique combination of characters which challenge its placing in any of the tribes of the subfamily Sigmodontinae recognized in

this paper. If I had not found amongst my fossil material a specimen representing a new genus which resembles closely Wiedomys in the morphology of the lower molars, I should have felt inclined to quote Wiedomys as Sigmodontinae incertae sedis. However, after realizing that Wiedomys was not alone in its distinctiveness, I concluded that I was justified in proposing a tribe of its own for Wiedomys and the new genus which I shall describe immediately.

Wiedomys is likely to be the only living representative of a distinct group of the Sigmodontinae which probably was much more diverse in the past. This group, the Wiedomyini, is likely to represent an early offshoot of the South American cricetid radiation, directly derived from a Thomasomys-like ancestor. It shows a remarkable association of primitive and rather advanced characters. On the basis of the two only known monotypic genera, but centered on the living Wiedomys, the new tribe can be characterized as follows:

Wiedomyini, new tribe

Type genus:

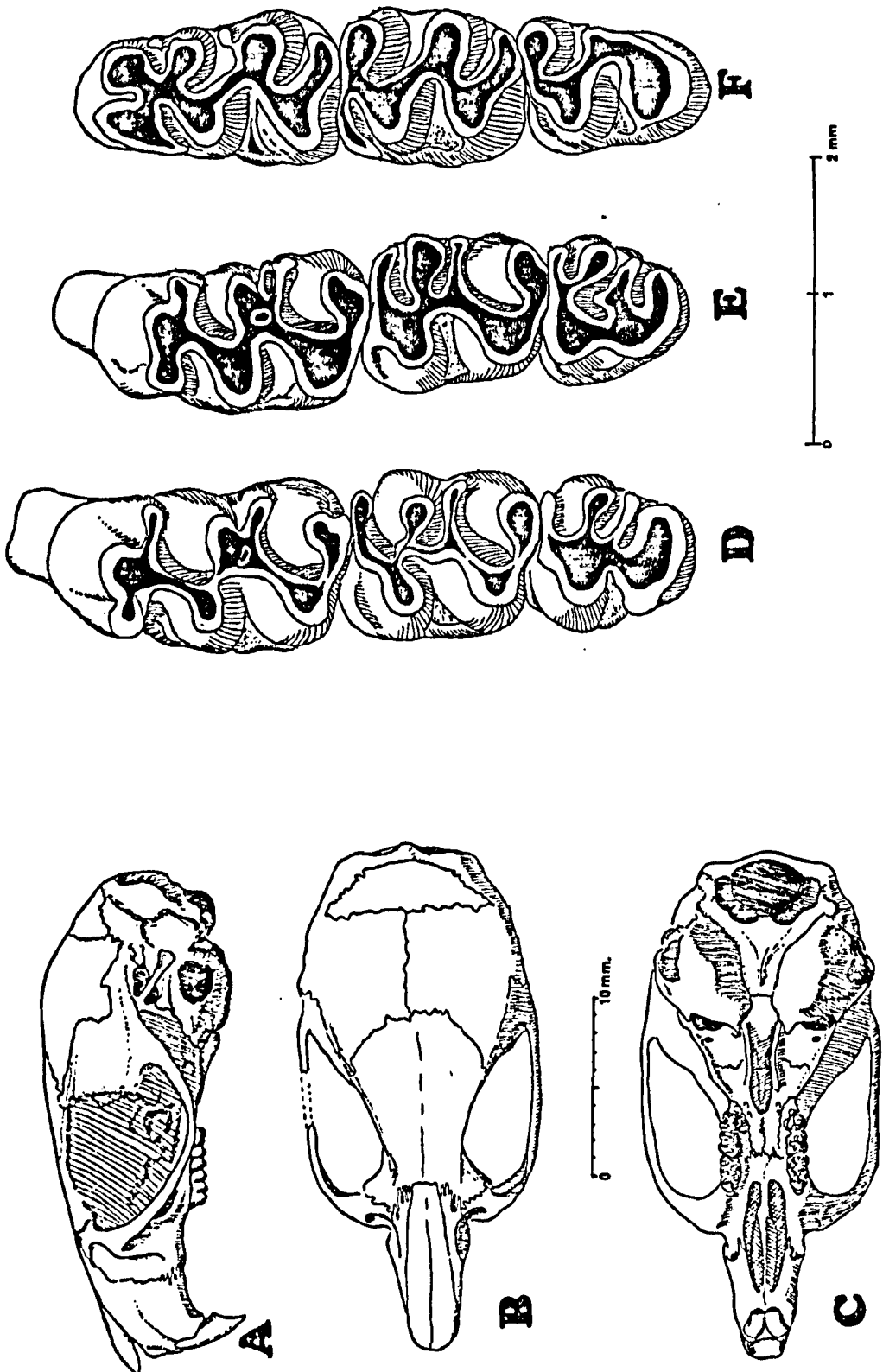
Wiedomys Hershkovitz, 1959

Diagnosis:

Sigmodontine cricetids with elongated brain case, narrow and deep rostrum and unexpanded zygomatic arches. Zygomatic plate short and high, not projecting laterally. Interorbital region with borders diverging backwards and with a well marked supraorbital ridge. Incisive foramina long and broad with their posterior borders passing well beyond the level of the anterior border of the M<sup>1</sup>. Posterior palate wide and moderately long. Interparietal large. Mesopterygoid fossa narrow, parapterygoid fossae much wider than mesopterygoid

Fig. 36. Skull and molar teeth of Wiedomys pyrrhorhinus (Wied).

- A. Left lateral aspect, B, dorsal aspect and C, ventral aspect of BMNH 3.9.5.63. Male, Lamarao, Bahia, Brazil.
- D. Occlusal aspect of left upper molar teeth of the same individual.
- E. Occlusal aspect of the left upper molar teeth, and F, of left lower molar teeth of MHNP 1970-247, Pernambuco, Brazil.





fossa. Mandible relatively strong, with low and short coronoid process and well developed masseteric crests. Molars brachyodont and bunodont, the upper crested to slightly bi-level, the lower bi-level. Individual cusps distinct, and the labial and lingual ones incipiently anternating in position. Mesoloph low, but clearly distinct in  $M^1-M^3$  and fused with mesostyle. Enteroloph absent, but enterostyle present in  $M^1-M^3$ , expanded as a median cingulum. An antero-lingual cingulum present on  $M^1-M^3$ . Anteroloph low, but well developed on  $M^1-M^3$ , fused with a parastyle. Procingulum of  $M^1$  biconulate, with anterolabial conule almost twice the size of the anterolingual conule; anteromedian flexus indicated, but shallow. Lower molars with mesolophid obsolete and a strong anterolabial cingulum. Ectolophid absent; mesostylid variable. Ectostylid elongated as a long mesolabial cingulum. Protoflexid well marked on  $M_1-M_3$ . Procingulum of  $M_1$  with subequal conulids; metaflexid deeply infolded, opposing the protoflexid at the middle of the tooth. Third molar well developed, the lower as long or longer than the  $M_2$ , and sigmoid-shaped.

Known distribution:

At present limited to north eastern Brazil and probably north eastern Bolivia. During the Lower Pleistocene known also in S.E. Buenos Aires Province, Argentina.

Included genera:

Wiedomys, Hershkovitz, and Cholomys, n. gen.

CHOLOMYS<sup>(1)</sup>, n. ge.

Type species:

Cholomys pearsoni, n. sp.

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(1) This new generic name is not created with regard to classical purity, but for euphony, shortness and simplicity, and in the honour of Galileo J. Scaglia, discoverer of the single known specimen of this remarkable rodent. Cholomys is made from "Cholo", the nick name of the discoverer, and  $\mu\upsilon\sigma$ , Greek for mouse.

Diagnosis:

A wiedomyine sigmodontine cricetid with a strong and thick lower incisor, a robust mandible with short and strong symphysis and, probably, a strongly projecting capsular process. Lower molars as in Wiedomys, but with incipient coronal hypsodonty, mesostylid absent, and ectostylid present and forming a mesolabial cingulum in  $M_1$  and  $M_2$ , but absent in  $M_3$ .

Known distribution:

Vorohuean subage, Lower Pleistocene, South East of Buenos Aires Province, Argentina.

Included species:

Only the type species is known.

Cholomys pearsoni<sup>(1)</sup>, n. sp.

Holotype:

MMP M-869 (Fig. 37A, 38C, E, F, J): Incomplete right lower jaw including the incisor and the three lower molars perfectly preserved, broken slightly behind the molar row, so that the coronoid, condyloid and angular processes are missing. Found by Galileo J. Scaglia in association with MMP M-551 (Akodon Abrothrix magnus) MMP M-867 and M-868 (Akodon Akodon lorenzinii) in the Vorohué Formation at Baliza San Andrés, Atlantic slopes of the Chapadmalal region, Partido de General Pueyrredón, Buenos Aires Province, Argentina.

Hypodigm:

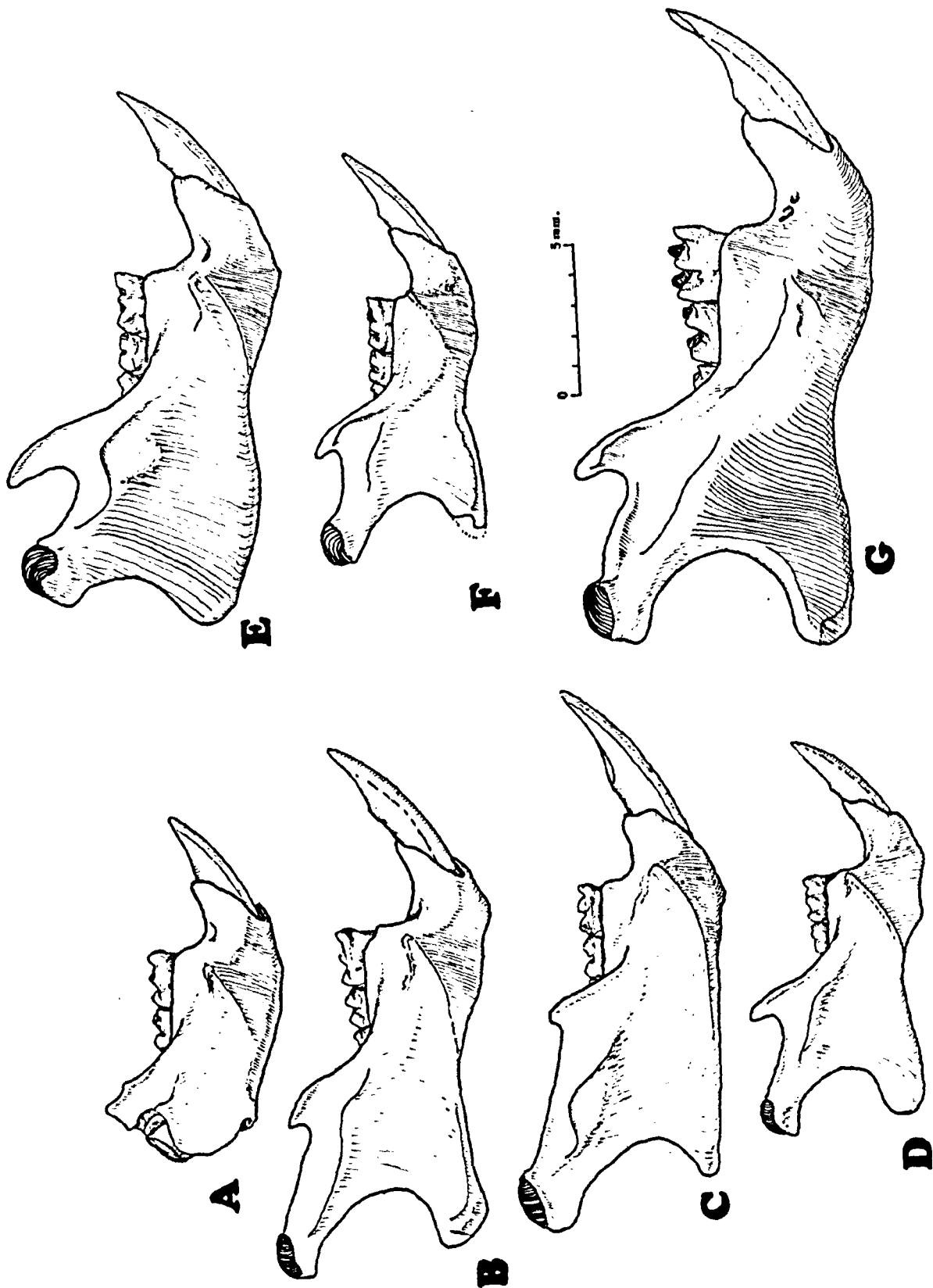
The type is the only known specimen referred to

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(1) The species name, pearsoni, is made in honour to Dr. Oliver P. Pearson, for his first rate contributions to the knowledge of the South American rodents.

Fig. 37. Lateral views of right lower jaws of several  
Sigmodontinae.

- A. Cholomys pearsoni, n. ge., n. sp., Type, MMP M-869. Vorohue Ftion. (Lower Pleistocene), Baliza San Andres, Coast of Partido de General Pueyrredon, Buenos Aires Province, Argentina.
- B. Wiedomys pyrrhorhinus (Wied.) Male, BMNH 3.9.5.63. Lamarao, Bahia, Brazil.
- C. Rhagomys rufescens Thomas, Type, BMNH 86.2.8.5. Rio de Janeiro, Brazil, Female.
- D. Calomys lepidus (Thomas), Type, BMNH 85.4.1.43. Junin, Central Peru.
- E. Pseudoryzomys wavrini (Thomas), Type, BMNH 20.12.18.16., male. Jesamatathla, west of Concepcion, Chaco Boreal, Paraguay.
- F. Phyllotis (Phyllotis) amicus Thomas, Type, male, BMNH O.3.1.94. Tolon, Cajamarca, Peru.
- G. Punomys lemminus Osgood, Male, MVZ 116195, 15 Km SSW of Limbani, Puno, Peru.



this species.

Diagnosis:

As for the genus.

Known distribution:

As for the genus.

Description and comparisons:

Unfortunately, there is only one incomplete specimen to describe the features of this interesting new rodent. The available fragmentary lower jaw is nicely preserved and permits the studying of several characters which proved to be particularly distinctive.

The mandibular ramus (Fig. 37A, Fig. 38E, F) is fairly robust and deep. Its depth below the middle of the  $M_1$  is much larger than the length of the diastema or the combined length of  $M_1$  and  $M_2$ . Its lower border is gently convex below the molar row, and the depth of the ramus does not decrease markedly backwards, as it occurs in Wiedomys, Calomys and Pseudoryzomys (Fig. 37). Differing also from the latter, the mandible of Cholomys does not show a sharp distinction of the posterior end of the symphysis, so that the lower border of the symphysis when viewed in lateral aspect (Fig. 37) continues the line of the lower border of the ramus, as it is also the case in Phyllotis amicus and Eligmodontia typus (see later). A noticeable difference between Calomys and Eligmodontia lies in the relative development and position of the masseteric crests. In Cholomys the crests are very similar to those in Wiedomys and Pseudoryzomys. The lower one is well defined, but not strongly marked as in Calomys and Eligmodontia, and it only reaches forward to a level slightly anterior to the  $M_1$ , whereas in those genera it goes forward to a level usually

beyond the anterior border of the  $M_1$ , projecting above the mental foramen. The upper masseteric crest of Cholomys is also well marked, but is very short and it descends backwards from its junction with the lower masseteric crest to disappear at the level of the posterior border of the  $M_1$ .

The symphysis is short and robust; it is also relatively low, as the anterior median point of the diastema does not reach the level of the tooth row, but it is distinctly more raised than in Wiedomys. The mental foramen is well developed and it lies on the posterior upper lateral surface of the symphysis, as is also the case in Wiedomys. Viewed from above, the diastema is remarkably broad, much broader than in Wiedomys, and recalling the condition in Punomys lemminus (Fig. 38H) and Phyllotis micropus. It has an anterior truncated border, as in Punomys.

From the size and trajectory of the incisor, and from its visible posterior end, it is obvious that it had to bulge in a projecting capsular projection for encasing its base. This capsular projection was probably similar in development to that in Böломys (Fig. 15) and Rhagomys (Fig. 37C), and much strongly developed than in Wiedomys.

The incisor is robust and thick, much stouter than in Wiedomys and as is usual in generalized incisors of Sigmodontinae. In this feature, it resembles again Phyllotis micropus and Punomys lemminus (Fig. 38H). The index incisor thick/incisor depth gives a value of 0.830 in Cholomys pearsoni, quite similar to the value of 0.834 in Punomys lemminus and of 0.813 in Phyllotis micropus, whereas in Wiedomys pyrrhorhinus it is 0.638. But apart from being thick and deep, the lower incisor shows a cutting edge rather

abruptly truncated and shovel-shaped, indicating a probable triturating type of upper incisor (HersHKovitz, 1962: 104) and some kind of gnawing specialization.

The lower molars (Fig. 38C, J) are bunodont, lophodont and moderately brachyodont, less so than in Wiedomys, as they show an incipient coronal hypsodonty as compared with the latter. However, in most details the molars of Cholomys and Wiedomys are remarkably similar. They also show many resemblances to the lower molars of Calomys and Eligmodontia, from which they differ in the bi-level instead of crested crown, and in having the cusp less tuberculate, as well as several other details of the enamel pattern that I shall mention next.

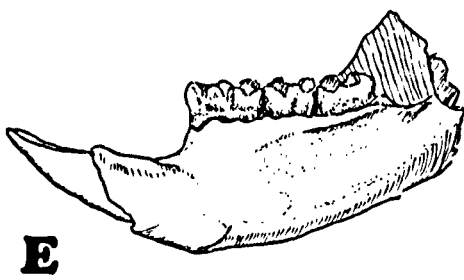
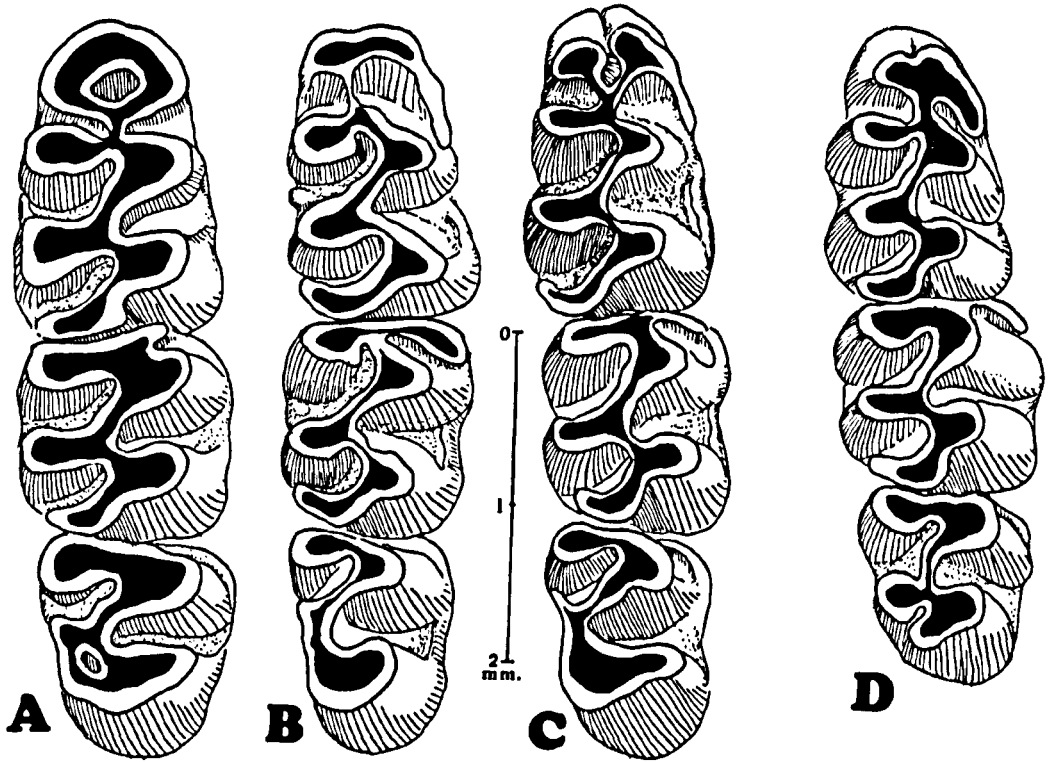
As in Wiedomys, the peculiar feature of the lower molar of Cholomys is the strong development of the external cingulum. It develops as a backward continuation of the antero-external border of the procingulum in the  $M_1$ , to form a lateral ledge encircling the basin-like floor of the protoflexid from outside. Additionally, the floor of the wide and strongly infolded hypoflexid is also limited laterally by a similar low cingulum, which can be thought of as derived from an elongated ectostylid. This mesolabial cingulum is well developed in  $M_1$  and  $M_2$ , as is also the case in Wiedomys, but, contrariwise to the latter, it is not present in the  $M_3$  of Cholomys pearsoni. No such structure was found either in Calomys or Eligmodontia in any of the three lower molars, but the development of a mesolabial cingulum is also observed in the lower molars of Rhagomys.

In relative size and proportions the three

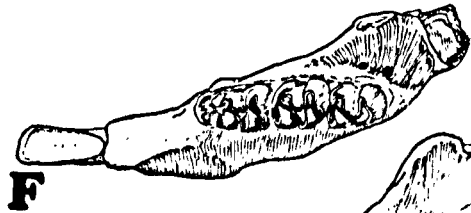
Fig. 38. Right lower molar teeth and mandibles of Pseudoryzomys, Wiedomys, Cholomys, Calomys and Punomys.

- A. Occlusal view of right lower molar teeth of Pseudoryzomys wavrini (Thomas), Type, BMNH 20.12.18.16, Male, Jasematathla, west of Concepcion, Chaco Boreal, Paraguay.
- B. Occlusal view of right molar teeth of Wiedomys pyrrhorhinus (Wied.), BMNH 3.9.5.63. Lamarao, Bahia, Brazil.
- C. Occlusal view of right lower molar teeth of Cholomys pearsoni, n. gen., n. sp., MMP M-869. Vorohue Ftion. (Lower Pleistocene) Baliza San Andres, Coast of Partido de General Pueyrredon, Buenos Aires Province, Argentina.
- D. Occlusal view of lower right molar teeth of Calomys callosus Pengger. BMNH 3.1.9.6. Female, Goya, Corrientes Province, Argentina.
- E. Internal aspect of right lower jaw of Cholomys pearsoni, n. gen., n. sp., Type specimen MMP M-869 (Data as in C.)
- F. Dorsal aspect of right mandible of Cholomys pearsoni, n. gen., n. sp., same individual as in E.
- G. Dorsal aspect of right mandible of Wiedomys pyrrhorhinus (Wied.), same specimen as in B.
- H. Dorsal aspect of anterior portion of right mandible of Punomys lemminus Osgood, MVZ 116036, Female, Huaylarco 90 Km ENE of Arequipa, Depto. of Arequipa, Peru.
- I. Buccal view of right lower molars of Calomys callosus Rengger. Same specimen as in D.
- J. Buccal view of right lower molar of Cholomys pearsoni, MMP M-869. Other data as in C.
- K. Buccal view of right lower molars of Wiedomys pyrrhorhinus, same specimen as in B.
- L. Buccal view of right lower molars of Pseudoryzomys wavrini (Thomas) Type, same specimen as in A.
- M. Buccal view of right lower molars of Punomys lemminus Osgood. Same specimen as in H.

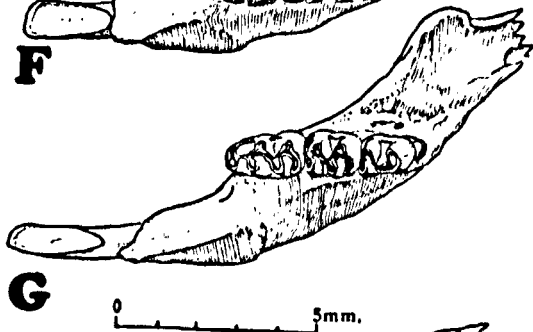




**E**



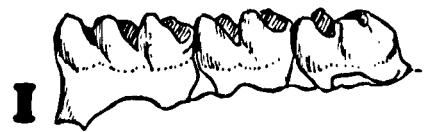
**F**



**G**



**H**



**I**



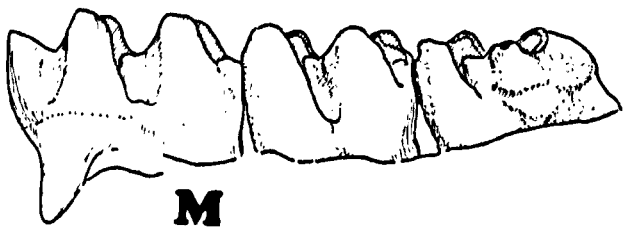
**J**



**K**



**L**



**M**

lower molars resemble closely those of Wiedomys (Fig. 36, 38B), and they are clearly narrower than in Calomys (Fig. 38D) or Eligmodontia (Fig. ). In the structure of the enamel pattern the procingulum of the  $M_1$  in Cholomys pearsoni differs noticeably from one of the specimens of Wiedomys pyrrhorhinus I have examined (Fig. 36, 38B). In the fossil species, the procingulum deeply bifurcates, the two subequal anteroconulids being separated by a deep and internally expanded anteromedian flexid, so that each conulid appears pedunculated, connected to the rest of the masticatory surface by a narrow bridge of enamel and dentine. With more advanced wear, this deeply infolded and expanded anteromedian flexid would probably become an anteromedian fossetid as one of the characteristics of Psuedoryzomys (Fig. 38A). In specimen BMNH 3.9.5.63 of Wiedomys pyrrhorhinus (Fig. 38B) the procingulum is much simpler and its enamel surface is wide and compressed anteroposteriorly. Dr. F. Petter (MHNP 1970-247) kindly lent me a specimen from Pernambuco, which agrees in all other details with the BMNH specimen above mentioned, in that the procingulum is quite similar to that of Cholomys pearsoni, though the anteromedian flexid is shallower and not so expanded in the middle. Another available specimen from Pernambuco has the molars too worn to illustrate the details of the enamel pattern. In Galomys the procingulum is much shorter and narrower, and also lacks a well-marked anteromedian flexid. There is not vestige of a metaflexid either in Cholomys or in Wiedomys, as is also the case in Calomys. Cholomys pearsoni lacks any trace of a mesostylid either in the  $M_1$  or the  $M_2$ . A mesostylid is present in the  $M_1$  and also, though much more reduced, in the  $M_2$  of the

studied specimens of Wiedomys pyrrhorhinus.

As in Wiedomys pyrrhorhinus, the protoflexid is well developed in the  $M_2$  of Ch. peasoni, more so than in Calomys, and the mesoflexid is quite open, oblique and its internal wall parallels the internal wall of the hypoflexid, so that the median murid is long, narrow and diagonal in position, quite in agreement with the condition found in Wiedomys pyrrhorhinus. In all three lower molars, the meta-lophids are transverse in position, but the entolophid and posterolophid, and specially the latter, are rather oblique and inclined backwards lingually. The  $M_3$  is very large, a bit longer than the  $M_2$  (Table 18) and shows a highly involuted sigmoid shape, lacking any trace of the posteroflexid which as such, or as a posterofossetid, is often present in Calomys and Pseudoryzomys. The shape and relative development of the  $M_3$  are highly similar in Cholomys and Wiedomys, whereas in Calomys, Eligmodontina and most other phyllotines, this tooth is usually much smaller than the  $M_2$ .

Discussion:

From the above description, I believe there is little doubt about the assessment of a close tribal affinity between Cholomys and Wiedomys. The resemblance in the structure of the molar teeth between these two genera is remarkable, and they indicate a peculiar type of molar teeth. Some similarities found with the lower molars of Calomys and its relatives are counterbalanced by important differences, so that it seems likely that they result from the sharing of some primitive traits combined with some evolutionary convergences.

But as much as Cholomys resembles Wiedomys

in the main characters of the lower molar teeth, it differs from it in the morphology of the mandible and of the incisor, which are quite peculiar to Cholomys. The reported differences in these characters, combined with the differences in details of the enamel pattern of the molars already described, are conclusive in suggesting that one is dealing with a fully distinctive genus. The similarities in symphysis and development of the incisors found between Cholomys, Punomys and Phyllotis micropus, are obviously convergent, as these three taxa are quite different in most other respects. The morphology of the incisors and related parts of the mandible indicate that Cholomys was more specialized than Wiedomys, and that it probably occupied a different food niche than their contemporaries and associated species Akodon s.s. and Akodon (Abrothrix).

Variate	Specimen							
	<u>Cholomys pearsoni</u> TYPE, MMP M-869 Vorohué formation.	<u>Wiedomys pyrrhorhinus</u> BMNH 3.9.5.63. Bahia, Brazil	<u>Pseudoryzomys wavrini</u> TYPE, BMNH 20-12-18-16 Jesematahla, W. of Con- ception, Paraguay.	<u>Calomys callosus</u> BMHN 3.1.2.9. Goya, Corrientes, Argentina	<u>Wiedomys pyrrhorhinus</u> , MHNP 1970-247. Female, Pernambuco, Brazil.	<u>Wiedomys pyrrhorhinus</u> MHNP 1970-151. Female, Pernambuco, Brazil.	<u>Punomys lemminus</u> , Male MVZ 116.195. 15 Km SSW of Limbani, Puno, Perú	<u>Punomys limminus</u> , Female, MVZ 116.036. Huaylarco, Arequipa, Perú.
Length of Mandible M <sub>3</sub> -anterior border of diastema	7.36	7.73	8.05	7.68	7.91	7.55	11.12	11.66
Length of diastema	2.50	3.20	3.46	3.20	3.20	3.20	4.09	4.55
Depth of mandibular ramus below M <sub>1</sub>	3.78	4.03	4.54	3.65	4.10	4.16	4.67	4.94
Alveolar length M <sub>1</sub> -M <sub>3</sub>	4.86	4.83	4.61	4.48	4.61	4.67	6.59	7.42
Coronal length M <sub>1</sub> -M <sub>3</sub>	4.93	4.80	4.83	4.35	4.58	4.48	6.53	7.10
Length of M <sub>1</sub>	1.98	1.99	2.08	1.77	1.92	1.89	2.64	2.76
Width of M <sub>1</sub>	1.16	1.17	1.33	1.15	1.08	1.13	1.77	1.92
Length of M <sub>2</sub>	1.47	1.43	1.44	1.22	1.38	1.30	1.98	2.29
Width of M <sub>2</sub>	1.20	1.16	1.38	1.27	1.13	1.12	1.70	1.95
Length of M <sub>3</sub>	1.49	1.39	1.43	1.15	1.30	1.33	1.96	2.14
Width of M <sub>3</sub>	1.12	1.05	1.27	1.09	0.95	0.99	1.55	1.74
Depth lower incisor	1.12	1.19	1.30	1.28	1.24	1.15	1.61	1.68
Width lower incisor	0.93	0.76	1.02	0.87	0.86	0.69	1.30	1.49

TABLE No. 18. Measurements of the mandible and the lower teeth of Cholomys pearsoni, n. gen., n. sp. compared with those of Pseudoryzomys wavrini, Calomys callosus, Wiedomys pyrrhorhinus and Punomys lemminus.

7.5. TRIBE PHYLLOTINI, VORONTZOV.

The sigmodontine cricetids of the tribe Phyllotini represent a specialized and highly diversified branch of the South American radiation of muroid rodents. They are represented in the living fauna by about 37 species distributed in 10 different genus, one of which, Phyllotis comprises almost half the number of the recognized species, and is susceptible to being subdivided into various subgenera. Most of the phyllotine species are vole-like in appearance and are adapted to a mainly herbivorous diet. The more primitive genera of the group, namely Calomys and Zygodontomys, show a low degree of modification for a vegetarian diet in the molar teeth, though both of them, and specially Zygodontomys are inhabitants of grassy prairies and savannas. The more advanced pastoral forms show varying degrees of hypsodonty, and a tendency to lamination and plication of the enamel folds and of flattening of the crown surface.

Calomys and Zygodontomys show many resemblances with the Akodontini, and they suggest that the phyllotines may have taken an origin in this tribe, rather than from the primitive oryzomyines. In fact, even the most primitive phyllotines show modifications in the molar teeth which surpassed or are equivalent to the more advanced developments of the akodontine molar morphology from the primitive pattern of the Oryzomyini.

The group was surveyed by Osgood (1947), Hershkovitz (1962) made a thorough revision, and there is an illuminating revision of most of the species of large genus Phyllotis by Pearson (1958). Hershkovitz included in

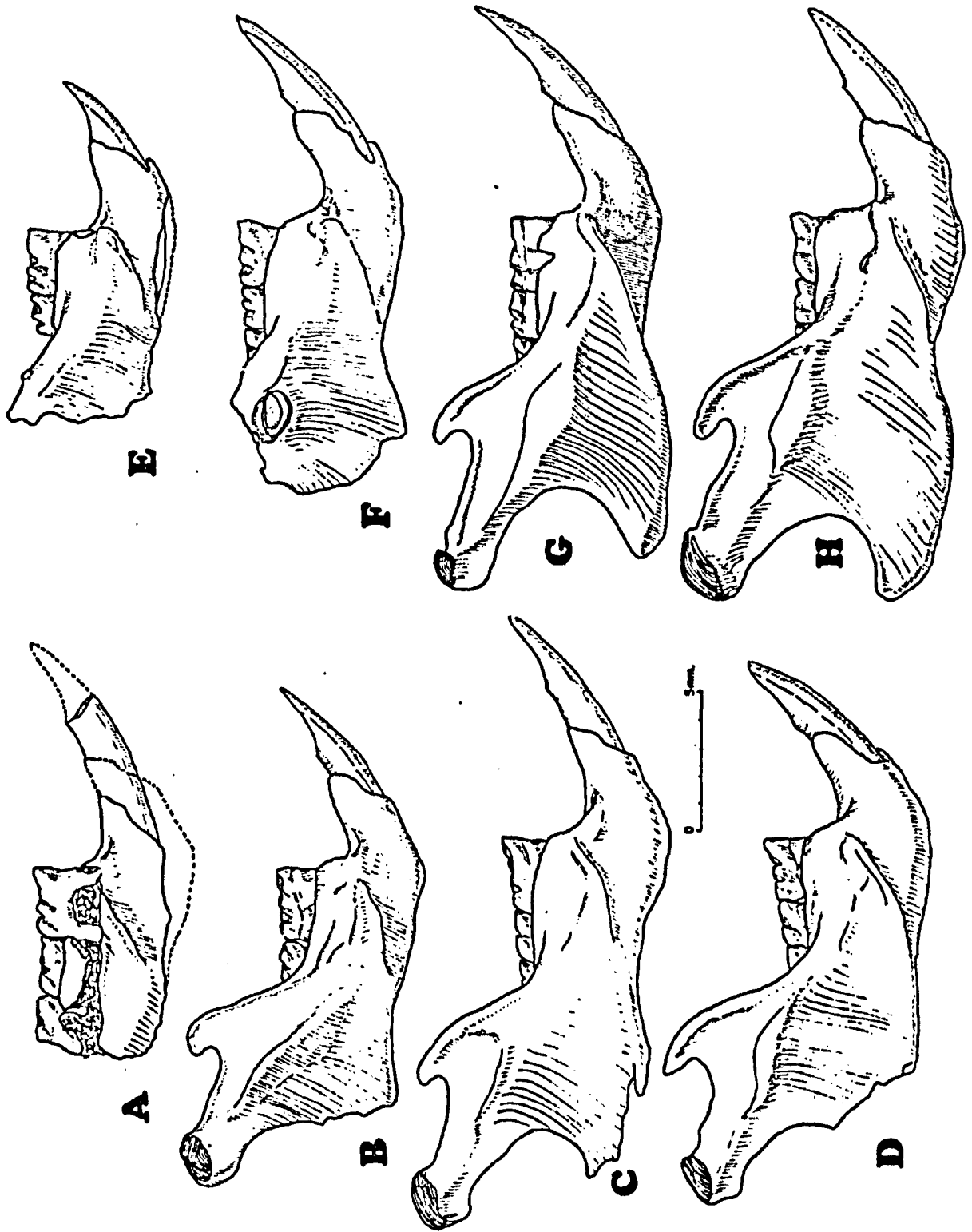
his "Phyllotine group" the genera Calomys, Eligmodontia, Zygodontomys, Pseudoryzomys, Phyllotis, Galenomys, Andinomys, Chinchillula and Euneomys. Previous surveys of members of this group (Gyldenstolpe, 1932; Tate, 1932b) recognized some other genera, which are now better lumped with some of genera recognized by Hershkovitz, or ranked as subgenera of Phyllotis. In proposing the tribal name Phyllotini, Vorontzov (1959: 136) included in it "Hesperomys", Eligmodontia, Graomys, Phyllotis, Punomys, Irenomys, Euneomys, Chelemyscus, Chinchillula and Andinomys, (Zygodontomys was placed by him in the Akodontini). As already stated, Hesperomys is a synonym of Calomys; Graomys was disregarded as a valid genus and even subgenus by Hershkovitz, and he placed the species referred to it under Phyllotis. I recognize Graomys as a distinct subgenus of Phyllotis, following Osgood (1947) and my own results. As regards Chelemyscus, I here follow the provisional decision of Hershkovitz (1962: 498) in considering it as but a mere synonym of Euneomys. As already said, I keep Zygodontomys among the Phyllotini, at least until more evidence is available. Vorontzov himself, in a later paper (1967: 76) seems to be inclined to follow Hershkovitz in placing Zygodontomys among the Phyllotini. As regards Irenomys and Punomys, two genera not included by Hershkovitz in his phyllotine group, I agree with Vorontzov in allocating the former within the Phyllotini, but after studying two specimens of Punomys from the Museum of Vertebrate Zoology, Harvard College, I found no reason to think of this genus as a member of the same group. Irenomys, although rather isolated and distinctive in molar morphology and in cranial characters, can be conceived as a specialized offshoot of the

Fig. 39. Lateral aspect of right lower jaw of species of

Phyllotis.

- A. Phyllotis (?Auliscomys) formosus, n. sp. Type, PVL 2397. Monte Hermoso Ftion., (Upper Pliocene), Monte Hermoso, 60 Km east of Bahia Blanca, Buenos Aires Province, Argentina.
- B. Phyllotis (Auliscomys) pictus, Thomas, Type, BMNH 85.4.1.34. Junin, Lima District, Peru.
- C. Phyllotis (Auliscomys) boliviensis, Waterhouse, Type, BMNH 45.11.18.9. Potosi, Central Bolivia.
- D. Phyllotis (Loxodontomys) micropus Waterhouse, Type, BMNH 55.12.24.179. Santa Cruz, Patagonia.
- E. Phyllotis (?Graomys) dorae, n. sp. Type, MMP M-743, Chapadmalal Ftion., Atlantic cliffs at Bajada Las Palomas, Partido de General Pueyrredon, Buenos Aires Province, Argentina. (Uppermost Pliocene).
- F. Phyllotis (Graomys) griseoflavus Waterhouse, Type, BMNH 55.12.24.184. Mouth of the Rio Negro, north Patagonia, Argentina.
- G. Phyllotis (Phyllotis) bonariensis Crespo, MACN 14914. Sierra de La Ventana, south Buenos Aires Province, Argentina. Male.
- H. Phyllotis (Graomys) domorum taterona, Thomas, Type, BMNH 26.1.1.166, Male, Tablada, Tarija, Bolivia.





phyllostine radiation. This is not the case with Punomys, which has a remarkably peculiar molar structure (see Osgood, 1943, and Figs. 38 and 39 ) and specialized skull and mandible. Its complicated molar teeth cannot be derived from the simplified molar patterns of even the more primitive phyllostines, and I believe that it is reasonable to agree with Osgood that Punomys is unique, and I do not hesitate in classifying it as Sigmodontinae incertae sedis.

The tribe Phyllotini can be characterized by the following synthetic diagnosis, as modified from Hershkovitz (1962):

"Sigmodontine cridetids of a vole-like or Mus-like appearance, usually pastoral and with various degrees of specialization for a herbivorous diet. Molars tuberculate and moderately hypsodont in the primitive forms, fully lophodont and relatively high-crowned in the more advanced forms; molar surface crested in the primitive forms, terraced to plane in most of the genera. Mesoloph and mesolophid obsolete or thoroughly coalesced with paraloph or entolophid, respectively. Ectolophid and enteroloph always absent. Metaloph usually coalesced with posteroloph; posteroflexus usually obsolete. Loph and lophids well developed and most frequently showing a tendency to lamination and involution. Procingulum of first molars usually broad and short, rather simplified, without an anteroflexus and anteroflexid, and with very reduced or obsolete anteromedian flexus and flexid. Skull moderately to very heavy, with a well developed, high zygomatic plate showing a vertical, straight or concave anterior border. Palate long. Incisive foramina long and normally extending posteriorly beyond the anterior borders of the first molars."

The fossil record of the Phyllotini until now was extremely poor. The only undoubtful member of this group recorder as a fossil was Bothriomys catenatus Ameghino (1889: 118), which Hershkovitz (1962: 500) correctly placed under the living genus Euneomys. It was described on the basis of a lower jaw from deposits of Bonaerian age from the city of Córdoba, Argentina. The validity of the species is still doubtful, but this record is conclusive in demonstrating that Euneomys lived by Upper Pleistocene times. The other doubtful nominal genus and species, Necromys conifer was described by Ameghino (1889: 120, pl. 4, figs. 17 and 18) from material found in strata of Ensenadan, "Belgranán" and Bonaerian age from the Province of Buenos Aires, Argentina. Hershkovitz (1962: 172) synonymized this form, with doubts, with Calomys callosus, but actually, the poor illustrations provided by Ameghino and his description do not allow any conclusion as to its affinities. The original material described by Ameghino could not be found in the Ameghino's collection when I recently examined it.

In the collection now available to me, there are a few, but very significant remains of phyllotine cricetids, belonging to the genus Phyllotis and Eligmodontia. Other phyllotine remains are mentioned in the note of page 379.-

7.5.1. GENUS PHYLLOTIS, WATERHOUSE.

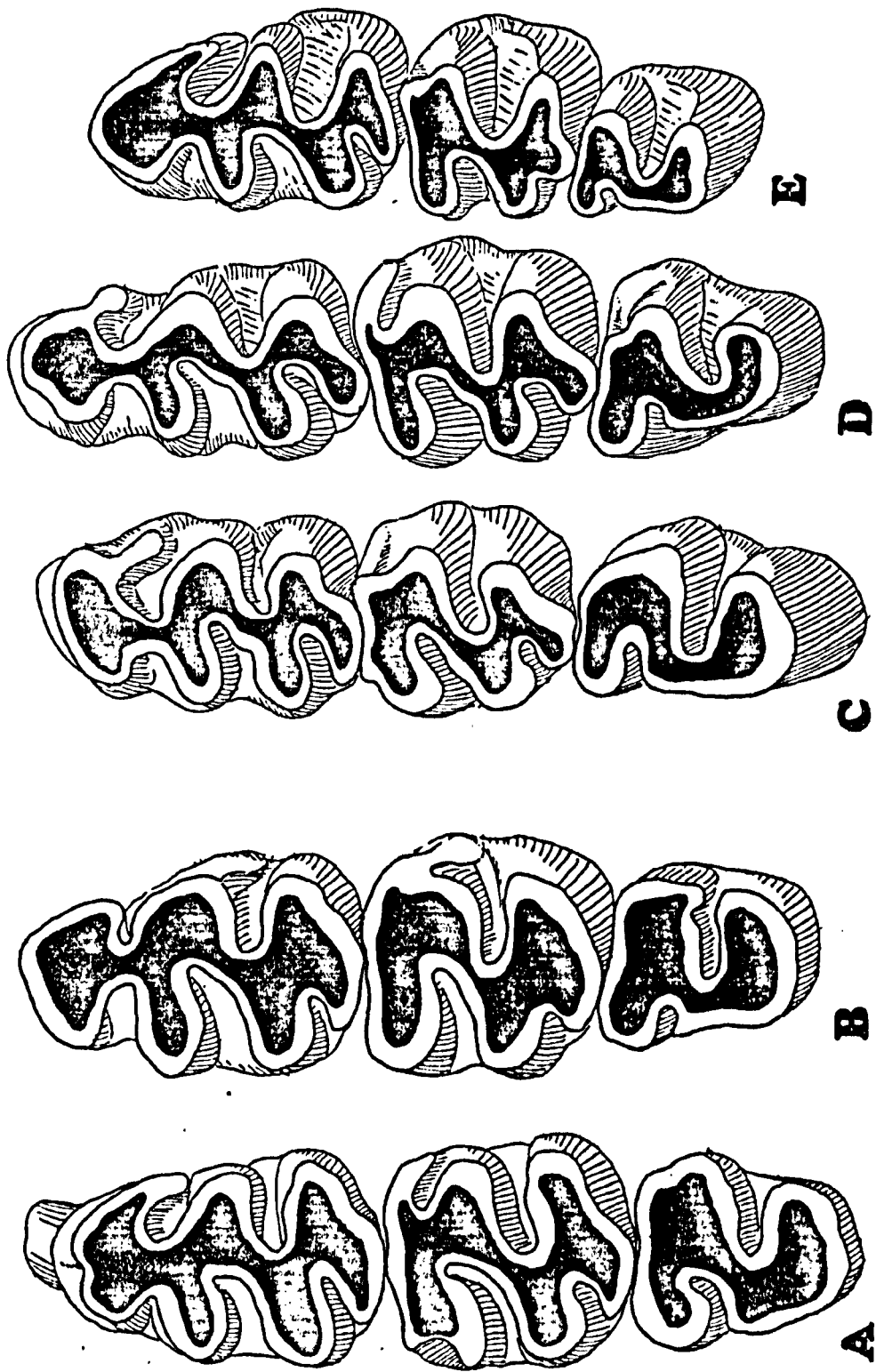
With 18 living species distributed in four different subgenera, Phyllotis ranks fourth amongst the more polytypic and widespread genera of living sigmodontines. It comprises pastoral forms living in open grassland, thornscrubs, mountain valleys and plains, and semidesertic stony areas, and it is usually very abundant where it occurs.

In cheek-teeth morphology, the members of this genus show a moderately advanced stage in plication and planation in moderately hypsodont molars adapted to an herbivorous diet, which is accompanied by an almost complete obsolescence of mesolophs and mesolophids. However, Phyllotis seems far from being an exclusively or even mostly herbivorous animal, as its digestive tract, and some available information on the stomach contents (Mann, 1944) indicate a greater contribution of insects and other animal food in its diet than in its more typically herbivorous relative Euneomys. Other phyllotines, as Euneomys, Andinomys and Chinchullula, show a more advanced stage in the transformations of the molar teeth correlated with a mainly herbivorous diet. Phyllotis can therefore be considered as a more generalized phyllotine, though already well advanced in pastoral adaptations as regards the more primitive genera Calomys and Zygodontomys. It is quite possible that Phyllotis represents the central main stem of the more typical evolutionary grade of the tribe. From this central stock several branches advanced in pastoral specializations as to deserve full generic treatment, as is the case of Euneomys, Chinchillula, Andinomys and Galenomys.

Within Phyllotis itself an extensive diversifi-

Fig. 40. Right lower molar teeth, in occlusal view of species of Phyllotis.

- A. Phyllotis (?Auliscomys) formosus, n. sp., Type PVL 2397. Monte Hermoso Formation, Upper Pliocene, Monte Hermoso, 60 Km west of Bahia Blanca, Prov. of Buenos Aires, Argentina.
- B. Phyllotis (Auliscomys) boliviensis Waterhouse, BMNH 2.2.2.22. Female, Potosi, Bolivia.
- C. Phyllotis (Loxodontomys) micropus, Waterhouse, Type, BMNH 55.12.24.179. Santa Cruz, Patagonia.
- D. Phyllotis (Auliscomys) pictus Thomas, Type, BMNH 85.4.1.34. Junin, Lima District, Central Peru.
- E. Phyllotis (Phyllotis) darwini darwini Waterhouse, Valparaiso, Central Chile. Female, BMNH 98.9.2.7.



0 1 2 mm

cation is observed which led to the recognition of subgenera, some of which have been treated as deserving full generic status, as I shall discuss later. The species of Phyllotis have been the subject of two modern and comprehensive reviews (Pearson, 1958; Hershkovitz, 1962). Therefore, it can be considered as one of the best understood genera of living sigmodontines on taxonomy and distribution. Lately, the study of the karyotypes of a rather extensive number of species (Pearson, 1972) contributed to a further understanding of the interrelationships of a great number of its species. Several points of interpretation are, however, still open as regards the taxonomy of the genus. Its evolutionary history has been hitherto only a matter of tentative speculations, in the absence of any record of fossil representatives. Close resemblance in cranial, phalic and dental morphology with the more generalized phyllotine Calomys, suggest that Phyllotis took its origin in a Calomys-like ancestor, which, by its side, may have evolved from one branch of the complex akodontine radiation. The fossil specimens described next, strongly suggest that the origin of Phyllotis must be thought of as taking place rather early in Neozoic times.

Genus Phyllotis, Waterhouse

1837. Mus (Phyllotis), Waterhouse, Proc. Zool. Soc. London, 1937: 28.
1843. Phyllotis, Gray, List Mammals British Mus: 112.
1839. Hesperomys, Waterhouse, Zool. Voy. Beagle, Mammals, : 75 (in part).
1884. Hesperomys (Phyllotis), Thomas, Proc. Zool. Soc. London: 449 (treated as a subgenus of Hesperomys, with Mus darwini designated as type species)

1896. Phyllotis, Thomas, Proc. Zool. Soc. London; 1020 (full generic recognition)
1898. Eligmodontia, Thomas (not Cuvier), Proc. Zool. Soc. London: 210 (in part).
1901. Euneomys, Thomas (not Coues), Ann.Mag. Nat.Hist. (8) 17:143 (in part).
1915. Auliscomys, Osgood, Field Mus. Nat. Hist. Zool. Ser. 10:190 (as a subgenus). Treated as a full genus by Thomas, 1926. Ann.Mag.Nat.Hist. (9) 17:317.
1916. Graomys, Thomas, Ann.Mag.Nat.Hist. (8) 17:141,
1926. Paralomys, Thomas, Ann.Mag.Nat.Hist. (9) 17: 315.

Type species:

Mus darwini, Waterhouse, designated by Thomas (1884).

Cranial and dental characters:

Skull usually rather strongly built, with a flat or slightly convex dorsal contour; deep and broad rostrum not tapered forward dorso-ventrally. Zygomatic well developed and usually moderately expanded. Brain case moderately broad. Zygomatic plate high and wide, with anterior border vertical, usually straight or concave, and cut sharply back above. Nasals long and broad, usually terminating close to the fronto-premaxillary suture. Interparietal well developed. Fronto parietal sutures crescentic in outline. Palate broad and long, with posterolateral portion pitted but not markedly excavated. Anterior palatal pits not distinct. Mesopterygoid fossa not narrowed, but less broad than parapterygoid fossae. Parapterygoid fossae not expanded laterally. Bullae not enlarged. Mandible moderately strong, with a rather deep ramus, a short coronoid process and a distinctly marked lower masseteric ridge reaching forward to the anterior



border of the  $M_1$ , but not projecting beyond that point as a tubercle. Base of incisor usually not forming a capsular projection, but defining a moderately developed ridge. Molar crowns moderately hypsodont, usually with flat occlusal surfaces. Main cusps not apparent, not tuberculate, usually laminated or compressed anteroposteriorly. Mesoloph and mesolophid completely or almost completely fused with paroloph or entoloph, respectively. Procingulum of first molars usually undivided, that of the  $M_1$  usually continued backwards by a strongly developed anterolabial cingulum. Protoflexus obsolete in  $M^2$  and  $M^3$ . Protoflexid usually well, to strongly, developed in  $M_2$ , frequently absent in  $M_3$ . Posterolophid normally shorter than entolophid in  $M_1$  and  $M_2$ .  $M^3$  usually with well developed para- and metaflexi;  $M_3$  large to moderately reduced, sigmoid shaped in outline.

Distribution:

"From the Ecuadorian Andes at the Equator, south along the Andes and coast of Perú and Chile to the Straits of Magellan, west over the Bolivian Andes into the Paraguayan Chaco and continuing southward through the Andes of Argentina; altitudinal range from sea level to over 5.500 metres above, or to limits of perpetual snow" (Hershkovitz, 1962: 217-219).

Included species:

amicus, andium, boliviensis, bonariensis, caprinus, darwini, domorum, edithae, gerbillus, griseoflavus, haggardi, hypogeicus, magister, micropus, osilae, pictus, sublimis and wolffsohni (arranged in subgenera as in Cabrera, 1961). Additionally, the fossil species formosus, n. sp., and dorae, n. sp., described immediately.

Phyllotis (Auliscomys) formosus, n. sp. (1)

Holotype:

PVL 2397: Broken left lower jaw (Fig. 39A) preserving the three lower molars (Fig. 40A), the broken incisor and a portion of the ramus and of the symphyseal region. Found by J.F. Bonaparte in stratum III of Monte Hermoso Formation at the typical deposits of Monte Hermoso, Atlantic slopes and cliffs some 60 Km. east of Bahía Blanca City, Buenos Aires Province, Argentina.

Hypodigm:

The type is the only known specimen.

Diagnosis:

A large species of Phyllotis of the size of Phyllotis boliviensis. Molars wide, with major lopids inclined obliquely backwards and outwards. Posterolophid of  $M_1$  and  $M_2$  moderately reduced in breadth. Procingulum of  $M_1$  short and wide, transverse in position, with a rudimentary anteromedian flexid, and a well developed anterolabial cingulum.  $M_2$  relatively robust, longer than wide, and with a well developed protoflexid.  $M_3$  sigmoid-shaped and fairly involuted, shorter than  $M_2$ . Incisor deep, not noticeably thickened.

Known distribution:

Montehermosian subage (early late Pliocene), south of Buenos Aires Province, Argentina.

Description:

The lower jaw was unfortunately broken after

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(1) The species name, formosus (Latin for beautiful) alludes to the geological and geographical provenance of the single known specimen, which comes from Monte Hermoso: (beautiful hill)

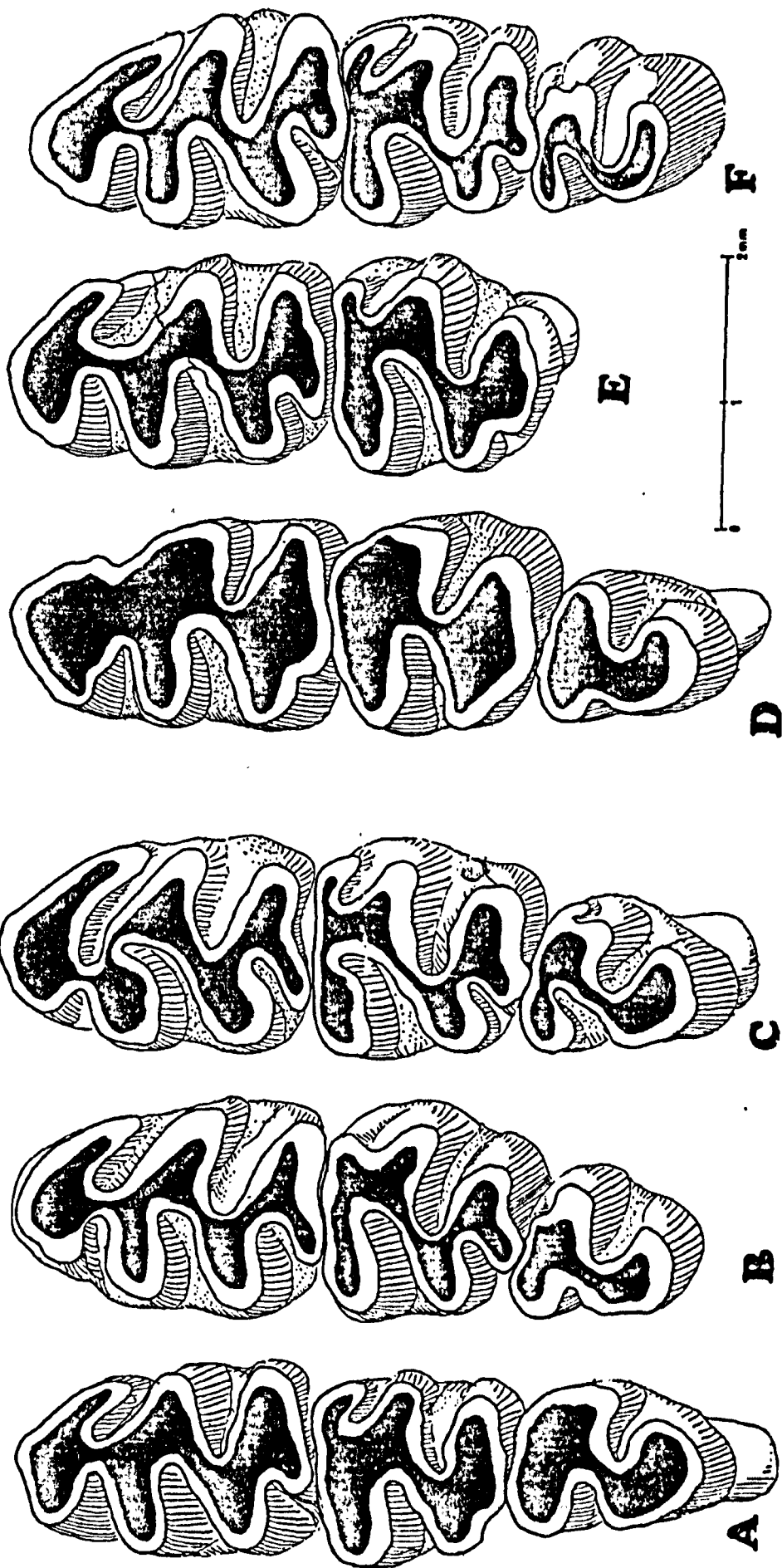
its extraction from the matrix and now little can be studied of the mandibular morphology. It was indeed a deep and robust mandible, as in species referred to the subgenera Auliscomys and Loxodontomys. The preserved portion of the external side of the ramus shows part of the lower masseteric crest, which is quite comparable to the position and development of it as in Ph. boliviensis (Fig. 39C). The preserved portion of the symphysis is conclusive in indicating a relatively low symphysis, different from the short and upturned symphysis of Ph. micropus (Fig. 39D), and more similar to boliviensis and pictus (Fig. 39D).

The incisor is relatively deep, more so than in the studied specimens of boliviensis and pictus, and comparable in depth to micropus. It is, however, much thinner than in the latter, which is characterized by particularly thick incisors (see Table 19). The lower incisor of formosus resembles more closely in proportions the incisors of boliviensis and pictus, but is slightly thicker.

The lower molars are closely comparable with those of boliviensis and pictus (Fig. 40) both in size, relative development and proportions (Table 19). In morphology they also match with the characters found in species of Auliscomys (pictus, boliviensis) and, to a lesser degree, to those of Loxodontomys (micropus). As in them, the molar crowns are rather low and plane, and the metalophid, the entolophid, and to a lesser degree the posterolophid of  $M_1$  and  $M_2$  are somewhat oblique in position and directed backwards and outwards, though less markedly so than in micropus. These lophids are parallel sided and fairly elongated, indicating an incipient trend toward lamination. Similarly, the protoconid

Fig. 41. Right lower molar teeth, in occlusal view, of member of Phyllotis.

- A. Phyllotis (Graomys) griseoflavus Waterhouse, Type, BMNH 55.12.24.184. Mouth of the Rio Negro, north Patagonia.
- B
- B. Phyllotis (Graomys) domorum, Thomas, Type BMNH 2.1.1.47. Tapacari, north Bolivia, Male.
- C. Phyllotis (Graomys) taterona Thomas, topotype, BMNH 26.1.1.21. Tablada, Tarija, Bolivia. Female.
- D. Phyllotis (Phyllotis) bonariensis Crespo., MACN 14918, Female, Sierra de la Ventana, south Buenos Aires Province, Argentina.
- E. Phyllotis (Graomys) dorae, n. sp., Type, MMP M-743. Chapadmalal Ftion., Atlantic cliffs at Bajada Las Palomas, Partido de General Pueyrredon, Buenos Aires Province, Argentina.
- F. Phyllotis (Graomys) lockwoodi Thomas, Type Male BMNH 18.1.1.6. Manuel Elordi, Rio Bermejo Salta Province, Argentina.



and hypoconid are transversely elongated and rather compressed anteroposteriorly. The metalophid is slightly shorter than the entolophid, as it is in micropus, boliviensis and darwini (Fig. 40), whereas in pictus it is even more markedly shorter. The posterolophid is well developed in  $M_1$  and  $M_2$ , though it is clearly smaller than the entolophid, resembling the condition found in darwini, boliviensis and pictus more than the state shown by micropus, in which the posterolophid is more developed and more oblique in position and the posteroflexid is deeper and strongly inclined backwards. The  $M_1$  is characterized by its short and wide procingulum, which is slightly subdivided by a very shallow anteromedian flexid, which shows a clearly transverse position and extends well backwards laterally by the well developed anterolabial cingulum. The procingulum of the  $M_1$  is different in the studied specimens of boliviensis, in which it is longer, narrower, subtriangular in shape and somewhat oblique, lacks any trace of an anteromedian flexid, and has a less developed anterolabial cingulum. In micropus, it is even more strongly oblique, but it has, as in formosus, a strong and well projected backwards anterolabial cingulum, whereas in pictus and darwini it is longer and narrower than in formosus, subovate in outline, and also lacks any trace of the anteromedian flexid. The shape of the procingulum of the  $M_1$ , therefore, seems to be diagnostic in formosus and, in a sense, it resembles remarkably the state of this character found in species of the subgenus Graomys (Fig. 41) from which it differs clearly in other traits of the molar structure.

The  $M_2$  is strong, proportionately so as in boliviensis, and relatively wide, although its length is still

greater than its width. It has a well marked protoflexid, differing in this respect from boliviensis, in which this fold is very reduced or obsolete in moderately worn teeth, and from darwini, in which it is also little developed. The relative development of the protoflexid of the  $M_2$  is in formosus as in micropus and pictus, and it is far from the strong and deeply infolded condition found in species of Graomys. The  $M_3$  shows an indication of very rudimentary protoflexid, but it has no trace at all of the posteroflexid, being sigmoid-shaped in outline. It shows an advanced stage of involution, the mesoflexid and hypoflexid overlapping slightly. In relative size, the  $M_3$  is as in boliviensis and pictus, clearly shorter than the  $M_2$ . In this respect it differs markedly from micropus; in which the  $M_3$  normally exceeds the  $M_2$  in length (see Table 19 and Fig. 42).

#### Discussion:

Although the available material is poor, it is evident that this fragmentary mandible which represents the earliest known fossil phyllotine, belong to a species of Phyllotis as advanced as the more advanced living species of the genus. Although a more thorough knowledge of the variation in lower molar teeth is required for a definite assessment of the relationships of this fossil form, it seems quite safe to make it the basis of a new species of Phyllotis. At a first glance, I was inclined to believe that it was closely related to the geographically nearer micropus, the only known species of the subgenus Loxodontomys. But a study of 20 assorted specimens of micropus from Chubut Province, Patagonia, proved that formosus, even when resembling micropus in several respects, was quite distinct from it in

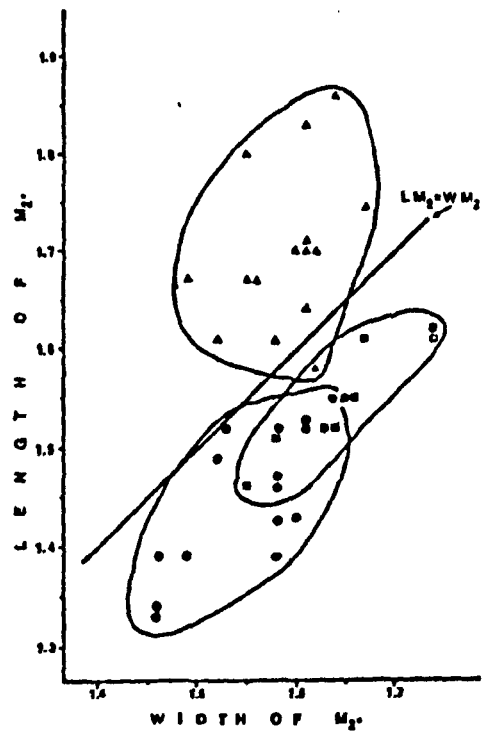
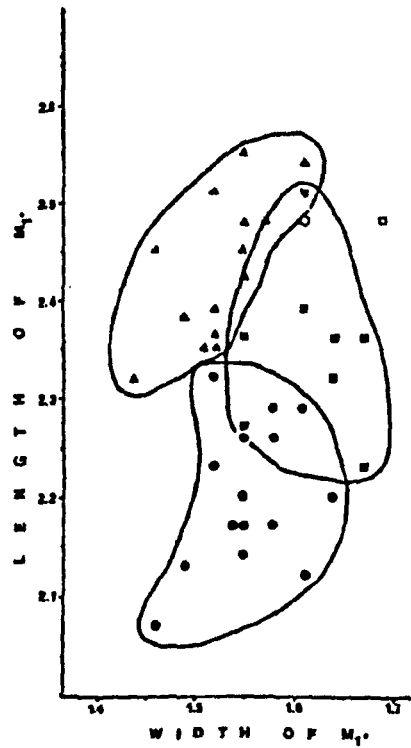
a great deal of characters. Just because of size similarities, formosus was then compared with the types and additional specimens of boliviensis and pictus, which occur far more distantly geographically, and which are currently referred to the subgenus Auliscomys (Osgood, 1915, 1943, 1947; Pearson, 1958). To my surprise, I found that formosus was closer to these species than to micropus. Comparisons with species of Phyllotis s.s. revealed a less close resemblance, even when Ph. wolffsohni was of a similar size. A subspecies of darwini, bonaeriensis, was described by Crespo (1964) for the region of the Sierra de La Ventana, close to Bahía Blanca, in the general area where formosus was found. Thanks to the kindness of Dr. J. Crespo, I had the opportunity to examine 3 specimens of this remarkable form. It is certainly a typical member of the subgenus Phyllotis but it differs sharply from darwini, both in size and in several skull characters. I believe that there is a strong case for proposing full species status for this form, which is also geographically isolated. It is not, however, related to formosus, from which it differs by its smaller size, relatively smaller  $M_3$ , more retracted posterolophid in the  $M_1$  and  $M_2$  and the obsolescence of the protoflexid of the  $M_2$ , in all these characters, bonaeriensis being a typical member of the subgenus Phyllotis.

In most of the details of the molar structure, in the size and relative proportions of the incisor, and in what can be observed of the mandibular morphology, formosus is most similar to boliviensis and pictus, and all the available evidence suggests that it must be classified as a distinct species of the subgenus Auliscomys.



Fig. 42.

Scattergrams of solar teeth in different species Phyllotia



- *Phyllotis griseoflavus*
- *Phyllotis daterona*
- ▲ *Phyllotis micropus*
- *Phyllotis dorae*
- *Phyllotis formosus*

Specimen Variate	Ph. formosus, TYPE, PVL 2397 Mte. Hermoso Ftn.	Ph. micropus TYPE MNH 55-12- 24-179.	Ph. pictus, XXRE, BMNH 26-2-1.50.	Ph. pictus, TYPE BMNH 85.4.1.34	Ph. boliviensis, TYPE, BMNH 45-11. 18.9.	Ph. boliviensis, BMNH 22.2.2.2.	Ph. darwini, Val- paraiso, BMNH 98.8.2.7.	Ph. micropus al- sus, Type
Coronal length M <sub>1</sub> -M <sub>3</sub>	6.21	5.95	5.81	5.89	6.08	6.24	4.92	6.02
Alveolar length M <sub>1</sub> -M <sub>3</sub>	6.32	6.08	5.96	6.21	6.46	6.42	5.15	5.82
Length of M <sub>1</sub>	2.48	2.36	2.48	2.54	2.60	2.57	2.32	2.48
Width of M <sub>1</sub>	1.61	1.52	1.50	1.55	1.67	1.63	1.33	1.55
Length of M <sub>2</sub>	1.95	1.61	1.83	1.74	1.89	1.92	1.39	1.74
Width of M <sub>2</sub>	1.64	1.52	1.62	1.64	1.74	1.72	1.42	1.67
Length of M <sub>3</sub>	1.70	1.64	1.70	1.61	1.78	1.74	1.30	1.86
Width of M <sub>3</sub>	1.43	1.30	1.29	1.30	1.37	1.33	1.18	1.43
Depth of incisor	1.46	1.41	1.19	1.21	1.30	----	----	1.46
Width of incisor	0.99	1.24	0.85	0.87	0.93	----	----	1.21

TABLE No. 19. Measurements of the lower dentition (in mm) of Phyllotis (Auliscomys) formosus, n. sp. and of living specimens of Phyllotis of the subgenera Phyllotis, Auliscomys and Loxodontomys

**Text cut off in original**

Auliscomys was originally erected as a subgenus of Phyllotis by Osgood (1915) but later, it was treated by Thomas (1926a, 1926b, 1927) as a full genus. The same view was held by Tate (1932b) and Gyldenstolpe (1932). Osgood (1943) was inclined to keep Auliscomys as a subgenus, and he suggested that micropus could belong here. He later (1947) made micropus the basis of a subgenus of its own, Loxodontomys. Both Auliscomys and Loxodontomys are recognized as subgenera of Phyllotis by Pearson (1958) and Cabrera (1961). However, Mann (1944) and later Hershkovitz (1962) did not recognize Auliscomys as a separate subdivision of Phyllotis. Recent studies by Pearson (1972), however, show that pictus and sublimis (another member of Auliscomys) are closely related to each other and quite apart from the other surveyed species (currently referred to the subgenus Phyllotis) in chromosome number and structure. His conclusion is explicitly emphasized when he says: "There is no simple route by which the karyotypes of the subgenera Phyllotis and Auliscomys can be related. Subgeneric, or even generic separation seems mandatory" (op. cit. : (15). It my conclusion that formosus is a member of Auliscomys is correct, Pearson's view is supported by a relatively ancient separation of the two groups.

Phyllotis (Graomys) dorae<sup>(1)</sup>, n. sp.

Holotype:

MMP M-743: Right incomplete lower jaw (Fig. 39E) with the incisor, the M<sub>1</sub> and the M<sub>2</sub> (Fig. 41E) and the alveolus of M<sub>3</sub>, lacking most of the

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(1) The species name, dorae, is given in honour of Dr. Doris Kermack, and in acknowledgement of her kind and friendly hospitality and help during the author's stay in London.

coronoid process, and the angular and condyloid processes. Found by V. di Martino in lower levels of the Chapadmalal Formation, in the Atlantic cliffs between Arroyo Corrientes and Arroyo Lobería, at "Bajada de las palomas", Partido de General Pueyrredón, Buenos Aires Province, Argentina.

Hypodigm:

The type is the only known specimen so far known.

Diagnosis:

A large species of Graomys of the size of the largest individuals of Ph. (Graomys) domorum taterona, with a short diastema and a relatively weak incisor. Lower molars robust and broad, with a rather advanced lamination and involution.  $M_1$  long, with a rather short procingulum.  $M_2$  relatively broad, highly involuted, with a short posterolophid and a very reduced posteroflexid.

Known distribution:

Chapadmalal subage (Latest Pliocene), south east of Buenos Aires Province, Argentina.

Description:

As it can be inferred from the preserved parts, the mandible was relatively slender. The depth of the ramus below the  $M_1$  could hardly have exceeded 4.5 mm, whereas in specimens of similar molar size of Ph. domorum it usually exceeds 5.1 mm, and reaches usually more than 6 mm. The well developed lower masseteric crest extends forwards to a point slightly anterior to the level of the anterior border of the  $M_1$ , and descends obliquely backwards defining a smooth

but well marked ridge. The symphysis is relatively short and the diastema length is less than the combined length of  $M_1$  and  $M_2$ , which is unusual for Ph. griseoflavus, but is the more common condition in the examined specimens of Ph. domorum. The symphysis is also relatively low, the anterior median border of the diastema being at a level lower than the plane of the molar alveoli. The same state is the regular one in domorum, whereas in griseoflavus, the anterior median point of the diastema is usually at a line with the alveolar plane, and the symphysis shows an overall more upturned position (Fig. 39).

The incisor resembles that of Ph. bonaeriensis in depth, but it is thinner. It is rather weak by Graomys standards and it is distinctly less deep than in griseoflavus and, particularly, less than in domorum taterona (Fig. 39H, Table 20). Its anterior border is ungrooved, and is also narrow and of an unspecialized type. The  $M_1$  is noticeably long and robust but not very broad (see Table 20), and has a plane and moderately hypsodont crown. It is as broad as it is regular in a series of griseoflavus examined by me (Fig. 42), but it is much longer than in any individual of this series. In absolute size and proportions, it is very close to the single known specimen of Ph. formosus, just described, and to Ph. bonaeriensis. But it differs in morphology from both to agree with the typical molar pattern of species of Graomys. As in them, the metalophid and entolophid are laminated, almost completely transverse flexids. Of these, the mesoflexid clearly overlaps forwards the transverse and deeply re-entrant hypoflexid, specially in the  $M_1$ , which therefore, shows a typically involuted pattern. Moreover, the posterolophid is strongly shortened

and retracted, more markedly so in the  $M_2$  than in the  $M_1$ . The procingulum of the  $M_1$  is oblique, short and wide, and its connection with the remaining of the crown surface is strongly constricted by deep opposing inner border of the metaflexid and the protoflexid. There is no indication at all of an anteromedian flexid. In fact, the  $M_1$  of Ph. dora resembles strongly the  $M_1$  of the type of Ph. griseoflavus (Fig. 41A), from which it differs mostly in absolute size. It differs from the examined specimens of domorum in the more deeply infolded metaflexid. The  $M_2$  is also more similar to the  $M_2$  of specimens of griseoflavus than to domorum in general shape, and specially in the reduction of the posteroflexid and the almost complete obsolescence of the posteroflexid in the moderately worn tooth. In domorum I found a lesser degree of transverse reduction of the posteroflexid, and a more persistent and infolded posteroflexid. However, the  $M_2$  of dora differs from the same tooth in griseoflavus both in absolute and relative size, and it is relatively wider than longer than in domorum taterona (Fig. 42), which shows broader  $M_2$  than griseoflavus. Due to the well developed and penetrant protoflexid, and the atrophy of the posteroflexid, the enamel pattern of the  $M_2$  of dora shows a shape which looks like a reverted normal sigmodontine  $M_2$ , with one main lingual fold (the mesoflexid) and two labial folds (protoflexid and hypoflexid); instead of the normal main lingual fold (hypoflexid), and the two main labial ones (mesoflexid and posteroflexid), which are characteristic of most of the sigmodontines with obsolete mesoflexids. This involuted reverted pattern of the  $M_2$  is characteristic of Graomys, and it is typically developed in the



fossil species. In this respect, Ph. dorae differs sharply from Ph. bonaeriensis, which has a  $M_2$  with the typical pattern of the subgenus Phyllotis: 8-shaped with wear by the obsolescence of the protoflexid.

Discussion:

There seems to be little doubt that the specimen described above must be referred to the subgenus Graomys of Phyllotis with the species of which it so closely agrees in their distinctive molar features. However, this specimen strikingly agrees in size and proportions of the teeth with Ph. bonaeriensis (Fig. 41D, Table 20), which now lives some 500 Kms SW of the Chapadmalal region (see page ). Moreover, this species also shows retracted posterolophids which give to the lower molars a certain resemblance to a species of Graomys. However, and as already stated, bonaeriensis is a typical member of the subgenus Phyllotis in cranial characters and in the other features of the molar teeth. The  $M_2$  is particularly different in the two forms, by the obsolescence of the protoflexid and the resulting 8-shaped pattern of the moderately worn teeth, which is a typical feature of darwini. Moreover, the involution of the flexids in bonaeriensis is not as advanced as in the species of Graomys, and these differences allow one to conclude that the fossil specimen is distinct from bonaeriensis both at the specific and subgeneric levels.

It is also beyond any reasonable doubt that the Chapadmalal fossil belongs to a distinct species than the other known Pliocene form of the Buenos Aires Province, Ph. formosus, the molar pattern of which is so close to that of the species of the subgenus Auliscomys. All the available evidence suggests,

, therefore, that, the subgeneric identity of Phyllotis goes back to before the early Upper Pliocene.

The species distinction of the Chapadmalal form as regards the living species of Graomys seems also to be warranted by a distinctive combination of character states. In molar pattern and development of the incisor, Ph. dorae seems to be more closely connected with griseoflavus, but in size, in the morphology of the lower jaw and in the relative proportions of the  $M_1$ , it is more alike the forms of the larger species Ph. domorum.

In fact, Hershkovitz (1962) did not recognize domorum as a distinct species, and treated it as a mere subspecies of griseoflavus. In my preliminary revision of the types and series of Graomys in the British Museum (Nat. Hist.) which was essential for the identification of the fossil material, I arrived at the conclusion that Hershkovitz went too far as a 'lumper' in treating the forms described by Thomas under Graomys, and that he also was not right in denying the validity of Graomys as a subgenus. Though I am convinced that a new revision of this group is urgently needed, I prefer to adopt here Osgood's (1947) criterion, and recognize two species, griseoflavus and domorum for the larger forms of Graomys, with subspecies provisionally arranged as in Cabrera (1961). Additionally, and here in agreement with Hershkovitz, I recognize under Graomys two other species of small size: edithae and hypogeicus.

As for the idea of the small Phyllotis amicus from the western part of north and central Perú, as an annectant form between Phyllotis s.s. and Graomys, proposed by Osgood (1947) and adopted by Hershkovitz (1962), I did not

find, after examining the types and additional specimens of amicus (Fig. 37F), any reasonable basis to endorse it. In fact, amicus can be thought of as a survivor of the primitive and original Phyllotis stock, which probably lived by late Miocene or early Pliocene times. It is very generalized in skull and dental characters, and of a size which would be expected in an ancestral Phyllotis. Moreover, Pearson (1972) recently found that amicus has a karyotype very similar to that of Ph. darwini and related forms of the subgenus Phyllotis s.s. Furthermore, following his tentatively suggested trend of chromosome evolution within Phyllotis (from low numbers of metacentric chromosomes to higher numbers of acrocentric chromosomes through Robertsonian rearrangements), amicus would have an ancestral primitive chromosome complement.

Although not a true fossil Phyllotis has been previously described as such, Bravard (1857) mentioned a Mus fossilis, which was later made a basis of Hesperomys bravardi by Burmeister (1879). This author mentions a left lower jaw with 2 molars as the original specimen of Bravard, and he adds that his H. bravardi was very close, if not identical, with griseoflavus. Ameghino (1889) places bravardi under Calomys, and he says that the original specimen was lost and that its geological provenance is unknown. Burmeister pointed out that it came from levels more recent than the Quaternary. Hershkovitz placed Hesperomys bravardi, probably on account of Burmeister's statements as its close affinity to the living form, under the synonym of Ph. griseoflavus. Needless to say, both this action and any further attempt to identify this taxon-name is unwarranted, as it is based on a lost specimen described without sufficient precision.

Variate \ Specimen	Ph. doraе, TYPE, MMP M-743. Chapadmalal formation.	Ph. griseoflavus, TYPE BMNH55.12.24.184. Rio Negro, Argentina	Ph. domorum taterona, TYPE, BMNH26.1.1.166. Tarija, Bolivia	Ph. domorum lockwoodii. TYPE, BMNH 18.1.1.6. Upper Bermejo, Salta, Argentina.	Ph. bonaerensis, Male MACN 14914. Sierra de la Ventana, Argentina	Ph. bonaerensis, female MACN14.918. Sierra de la Ventana, Argentina.	Ph. bonaerensis, male MACN 14.920. Sierra de la Ventana, Argentina
Alveolar length M <sub>1</sub> -M <sub>3</sub>	5.82	5.50	6.08	5.89	6.08	5.82	6.02
Coronal length M <sub>1</sub> -M <sub>3</sub>	-----	5.50	5.38	5.67	5.82	5.57	5.63
Length of M <sub>1</sub>	2.48	2.31	2.51	2.46	2.51	2.45	2.51
Width of M <sub>1</sub>	1.69	1.52	1.61	1.64	1.70	1.67	1.70
Length of M <sub>2</sub>	1.61	1.52	1.52	1.61	1.64	1.51	1.68
Width of M <sub>2</sub>	1.74	1.53	1.61	1.70	1.77	1.74	1.86
Length of M <sub>3</sub>	-----	1.46	1.43	1.48	1.58	1.39	1.43
Width of M <sub>3</sub>	-----	1.24	0.96	1.30	1.43	1.27	1.33
Depth of incisor	1.39	1.55	1.74	1.46	1.36	1.39	1.36
Width of incisor	0.74	0.81	0.90	0.74	1.02	0.96	1.02
Depth mandible at M <sub>1</sub>	4.50	4.29	6.30	5.09	4.16	4.35	4.29
Length of diastema	3.58	4.50	3.75	4.15	4.22	3.71	3.84

TABLE No.20, Measurements of Phyllotis (Graomys) doraе! of the types of some of the living species of the subgenus Graomys, and of three specimens of Phyllotis (Phyllotis) bonaerensis

7.5.2. GENUS ELIGMODONTIA, CUVIER

Eligmodontia is a small phyllotine allied to Calomys and skull and molar morphology, but quite distinct in its gerbil-like appearance, elongated hind-limbs and habitat preferences. It is a dweller in semidesert or desert mountain and lowland areas, though it is also found in the margins of the Pampean region, in more humid grassy plains. The living forms of this genus have been revised by Hershkovitz (1962) who lumped the ten nominal taxa of previous authors into a single species with two recognized subspecies: E. typus typus and E. typus puerulus. A less extreme attitude was taken by Cabrera (1961), who arranged the nominal forms into two species: a northern E. puerulus with two subspecies, and a southern E. typus, subdivided into five subspecies. Although I believe that the geographic forms of Eligmodontia are too little known for subspecies distinctions to be well grounded, I endorse Cabrera's view of recognizing two species. I arrived at these conclusions after examining the types and small series of this genus in the collection of the British Museum (Nat. Hist.).

Eligmodontia was reported to occur in the "Benson" Formation (Lower Pleistocene) of North America, and a fossil species was erected on the basis of this record: Eligmodontia arizonae Gidley (1922). However, this record was based on misidentification, and the species arizonae was later made the basis of a new genus, Bensonomys by Gazin (1942), which was eventually synonymized with Peromyscus by Alker (1967). No fossil representative of Eligmodontia as such has been described so far for South America. However, it is possible that some of the small specimens from the Upper Pleistocene and the

Holocene illustrated by Ameghino (1889), could belong to this genus. This is particularly quite probable in the case of the lower jaw (Ameghino, 1889, Plate IV, Fig. 7) referred to Calomys longicaudatus. However, it should be necessary to look at the actual specimens to confirm this possibility, and I was unable to find them in the Ameghino collection.

Eligmodontia is not represented in my material from the Upper Pliocene to the Middle Pleistocene. However, several specimens collected by personnel of the Museo de La Plata in strata of the Upper Pleistocene (Lujanian) age, of the south of Buenos Aires Province, prove to belong to this genus, and they represent the first fossil record of the genus.

Genus Eligmodontia, F. Cuvier

- 1837, Eligmodontia, F. Cuvier, Ann. Sci. Nat. Paris, Zool. (2) 7: 168
- 1841, Eligmodon, Wagner: Archiv f. Naturg., 1841, 1: 125
- 1843, Calomys, Gray: List Mamm. British Mus. :112
- 1846, Heligmodontia, Agassiz: Nomencl. Zool. Mamm. Addenda, 5, Index Univ. :136, 175
- 1896, Eligmodon, Thomas: Ann. Mag. Nat. Hist. (6) 18: 307

Type species:

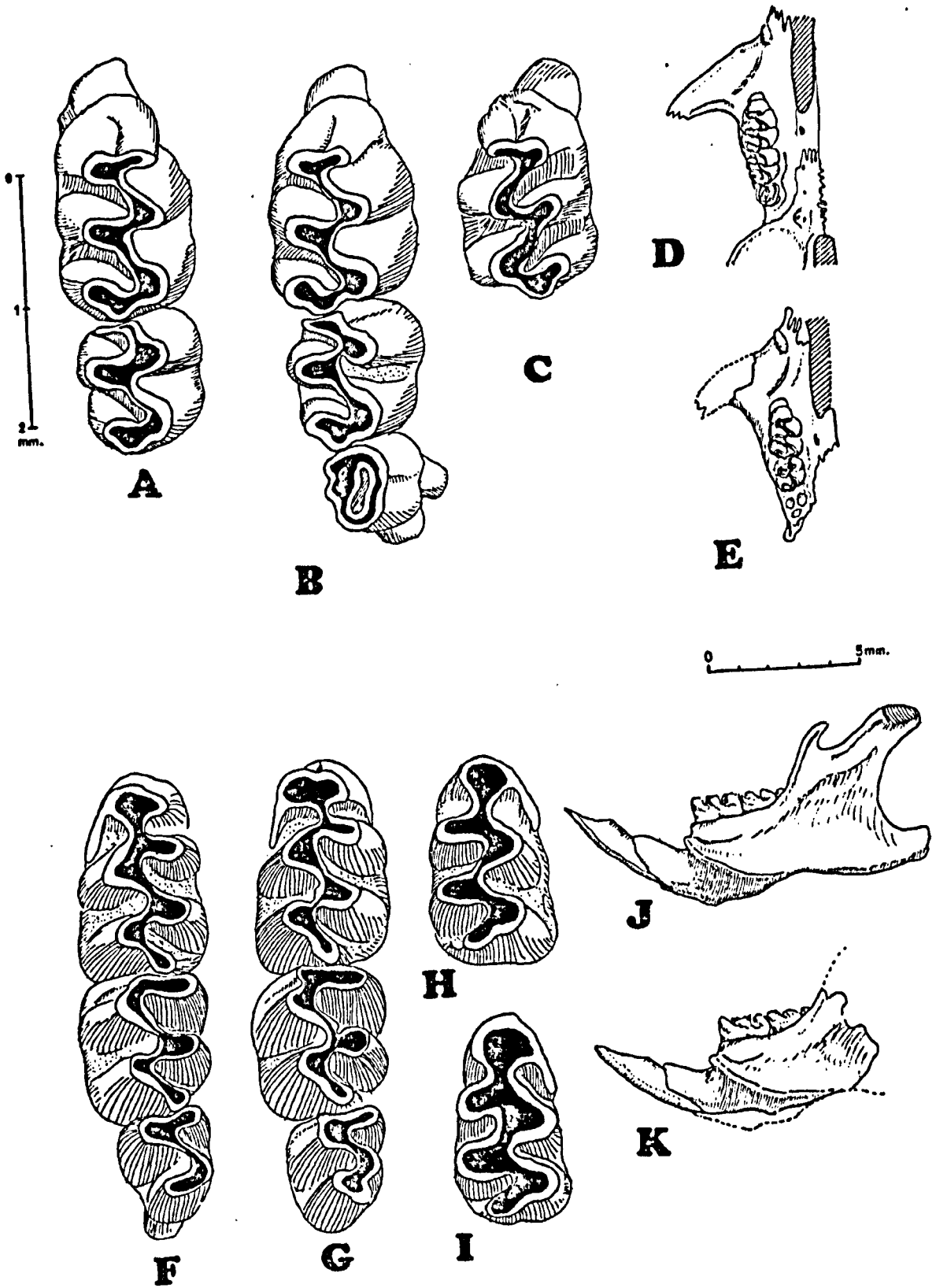
Eligmodontia typus F. Cuvier, by original designation.

Cranial and dental characters:

Skull lightly built, with a dorsal contour rounded posteriorly. Rostrum narrow and slender. Zygomata slender, roughly parallel-sided and not expanded. Brain case fairly broad. Zygomatic plate moderately high and wide, with straight or slightly concave anterior border, cut

Fig. 43. Molar teeth, mandibles and maxillae of living and fossil Eligmodontia.

- A. Occlusal view of right M<sup>1</sup> and M<sup>2</sup> of Eligmodontia cf. typus Cuvier, MLP 63-VI-10-14-e. Lujanian stage (Upper Pleistocene), Arroyo Indico Rioco, south Buenos Aires Province, Argentina.
- B. Right upper molar series in occlusal view of Eligmodontia typus Cuvier, Female, BMNH 66-1714. Chos Malal, Neuquén, Argentina.
- C. Left M<sup>1</sup> of Eligmodontia cf. typus Cuvier, MLP 64-VI-10-14-f. Lujanian stage (other data as in A).
- D. Ventral aspect of right maxillary and palatal region of Eligmodontia typus, BMNH 66-1714 (other data as in B).
- E. Ventral aspect of right maxilla of Eligmodontia cf. typus, same specimen and data as in B.
- F. Left lower molar series in occlusal view of Eligmodontia cf. typus, MLP 63-VI-10-44-a. Lujanian stage, other data as in A.
- G. Left lower molar series in occlusal view of Eligmodontia typus Cuvier, same specimen and data as in B.
- H. Right M<sub>1</sub> of Eligmodontia cf. typus, MLP 63-VI-10-44-c. Lujanian stage, other data as in A.
- I. Right M<sub>1</sub> of Eligmodontia cf. typus Cuvier, MLP 63-VI-10-44-d. Lujanian stage (other data as in A).
- J. Lateral aspect of left lower jaw of Eligmodontia typus Cuvier, same specimen and data as in B.
- K. Lateral aspect of left incomplete lower jaw of Eligmodontia cf. typus Cuvier, MLP 63-VI-10-44-a (other data as in A.)





sharply back above. Nasals long and relatively broad, terminating behind at the same level of the fronto-femaxillary suture varying from rather straight to slightly crescentic in outline. Palate moderately broad and very long, with posterolateral portion depressed and marked by a pit. A pair of anterior palatal pits present, each one behind the incisive foramina. Mesopterygoid fossa very narrow; parapterygoid fossae expanded sideways and little excavated. Bullae moderately inflated. Mandible relatively strong, with a high ramus marked, a strongly developed, diagonal placed lower masseteric crest reaching forward beyond the anterior border of the  $M_1$  and projected into a small knob. Capsular projection of the base of the incisor moderately developed. Coronoid process short. Molars with moderate coronal hypsodonty, bi-level occlusal surface, moderately tuberculate cusps tending to triangulation. Mesoloph and mesolophid completely absent, as well as mesostyle and mesostylid. Procingulum of first molars divided by an anteromedian fold in unworn or little worn teeth, which disappear with more advanced wear. Protoflexus weak in  $M^2$ , obsolete in  $M^3$ . Protoflexid rudimentary in  $M_2$ , obsolete in  $M_3$ . Posterolophid tending not to show reduction.  $M^3$  with little developed paraflexus and well developed metaflexus, tending to become a metafossetus.  $M_3$  sigmoid-shaped, relatively small.

Distribution:

Arid and semi-arid open lowlands and mountain valleys, from southern Patagonia in Chile and Argentina to the Pampean region of Argentina by the east, to the sub-Andean plains of central western Argentina by the west, continuing northwards along the Andes into northern Chile, western Bolivia and Southwestern Perú.

Included species:

puerulus and typus

Hligmodontia cf. typus, Cuvier

Referred specimens:

MLP 63.VI.10.44 (a): Incomplete left lower with incisor and  $M_1$ - $M_3$  (Fig. 43F), broken behind the alveoli and in the lower border of the ramus. This, and the following specimens have been found by J. Psiano, E.J. Ortega and E. Tonni in a layer of green clays referred to the Lujanian stage, cropping out at the right bank of the "Arroyo Indio Rico, Partido de Tres Arroyos, south east of Buenos Aires Province. They were associated with several remains of Reithrodon auritus and Ctenomys sp, catalogued under the same number.

MLP 63.VI.10.44 (b): Portion of right lower jaw with incisor and  $M_1$ - $M_2$  (Fig. 43), broken behind  $M_2$ . Found in association with the former.

MLP 63.VI.10.44 (c): Portion of right lower jaw with the  $M_1$  (Fig. 43H). Found in association with the former.

MLP 63.VI.10.44 (d): Portion of right lower jaw with the  $M_1$  (Fig. 43I). Found in association with the former.

MLP 63.VI.10.44 (e): Incomplete right maxilla with  $M^1$ - $M^2$ , the alveolus of the  $M^3$ , the palatal region, and part of the zygomatic plate (Fig. 43A). Found in association with the former.

MLP 63.VI.10.44 (f): Isolated left  $M^1$ . Found in association with the former.

Comment:

The above mentioned specimens have been compared with samples of Eligmodontia typus from Patagonia and from Buenos Aires Province, and I did not find any basis for separating them from the living species, which is known to live in the vicinity of the area where the fossils were found. I personally caught a specimen of Eligmodontia typus in 1964 close to the city of Necochea, in the dune belt of the Atlantic coast, and not very far from the Partido de Tres Arroyos.

Specimen Variate	E. typus. BMNH 66.1714. Chos Malals Neuquen, Argentina.	E. cf. typus, Luja- nian Stage, MLP 63.IV.10.44 (a)	E. cf. typus, Luja- nian stage, MLP 63.IV.10.44 (b)	E. cf. typus, Luja- nian stage, MLP 63.IV.10.44 (c)	E. cf. typus, Luja- nian stage, MLP 63.IV.10.44 (d)	E. cf. typus, Luja- nian stage, MLP 63.IV.10.44 (e)	E. cf. typus, MLP 63.IV.10.44 (f)
Depth mandible at M <sub>1</sub>	2.62	2.56	2.56				
Length of low. diastema	2.30	2.30	3.56				
Alveolar length M <sub>1</sub> -M <sub>3</sub>	3.99	3.97					
Coronal length M <sub>1</sub> -M <sub>3</sub>	3.84	3.73					
Length of M <sub>1</sub>	1.68	1.68	1.71	1.70	1.67		
Width of M <sub>1</sub>	1.09	1.05	1.08	1.04	0.96		
Length of M <sub>2</sub>	1.21	1.21	1.12				
Width of M <sub>2</sub>	1.08	1.03	1.07				
Length of M <sub>3</sub>	0.93	0.90					
Depth lower incisor	0.94	0.97	0.96				
Width lower incisor	0.53	0.57	0.60				
Alveolar length M <sup>1</sup> -M <sup>3</sup>	4.03					4.05	
Coronal length M <sup>1</sup> -M <sup>3</sup>	3.71						
Length M <sup>1</sup>	1.81					1.80	1.74
Width of M <sup>1</sup>	1.12					1.08	1.05
Length of M <sup>2</sup>	1.17					1.13	
Width of M <sup>2</sup>	1.12					1.05	

TABLE No.21. Measurements (in mm) of the lower jaw, lower and upper dentition of fossil and living Eligmodontia typus

7.6. TRIBE SIGMODONTINI, VOTONTZOV.

The idea that the genera Sigmodon, Holochilus, Reithrodon and Neotomys compose a natural and distinctive group of South American cricetids, was proposed by Hershkovitz (1955) which coined for them the name sigmodont group. These genera had been treated before in different ways, and no clear idea had emerged before Hershkovitz's work about their relationships. This author found that the four genera share in common several characters suggestive of a rather close relationship, both in the external features, and in the skull and dentition, and his paper is fairly convincing in demonstrating that as far as cranial and dental characters are concerned, the four genera seem more closely related to each other than any of them to genera of other groups.

However, the contention that these four genera make a closely knit group was challenged by Hooper (1962) and Hooper and Musser (1964), who find that Sigmodon was most peculiar in phallic morphology, and that for the same characters Holochilus was closely related to the oryzomyines and Reithrodon to the phyllotines. Neotomys was not included in this revision, but Hooper and Musser concluded that the sigmodont group should be restricted to Sigmodon and Sigmomys (the latter is correctly interpreted by Hershkovitz as a synonym of the former). Hershkovitz (1966a: 129-130) criticized these results, arguing that even when the phallic differences are real, they are counterbalanced by a fundamental combination of cranial, dental and external characters which demonstrate a close resemblance among the four genera, and that these resemblances cannot be ignored on account of differences

in the morphology of a single organ, which can be peculiar of each radiating genus of the group. His argument is convincing, and I believe that the controversy must be settled in favour of Hershkovitz's view, if not by other reasons, just because he based his conclusion on a larger number of characters.

Another disagreement with Hershkovitz conception of the extension of the sigmodont group was advanced by Vorontzov (1959), who included in his tribe Sigmodontini the genera Neotomys, Holochilus, Sigmodon and Sigmomys, but excluded explicitly from this group Reithrodon, which he made the basis of a tribe of its own, Reithrodontini (misspelled in his paper Reithrodonini, and including also Proreithrodon, Amegh., a junior synonym of Reithrodon). However, Vorontzov changed his mind in a later paper (1967), and here he treats Reithrodon, Sigmodon, Holochilus and Neotomys as closely connected to each other in molar morphology.

After re-examining the skull and dental characters of these genera, I found that there can be little doubt that Holochilus is closely related to Sigmodon. They agree in so many details of skull, mandible and dental characters, that it could hardly be admitted that these resemblances are not an indication of a close kinship. Reithrodon is much more modified in skull structure, and in some particulars it resembles more closely Neotomys than any of the two other genera. But the particularities of Reithrodon and Neotomys can be easily conceived as specializations from a Sigmodon-like skull, and these two genera agree with the other couple in most fundamental traits of the skull and dental anatomy. The whole group is probably an early offshoot of the Sigmodon-

tine radiation, and some features of the unworn dentition of Holochilus, along with the phallic resemblances pointed out by Hooper and Musser, suggest that the tribe may have derived directly from the Oryzomyini, probably in the early steps of the differentiation of the major groups of the subfamily. If this conclusion is true, the four living genera are to be considered as the living remnants of a major radiation, and the divergences found among them can be explained by a long evolutionary independent history. In fact, there are reasons from the fossil record to reinforce the idea that one is dealing with a relatively old group of genera. Sigmodon is known since the Upper Pliocene in North America (Hibbard, 1960; Martin, 1970) where it is most probably a descendant from a South American ancestor. The living species Reithrodon auritus was recorded from the Upper Pliocene of South America (see later). These records indicate a much earlier separation of the two genera.

The Sigmodontini are a typically pastoral group, and they show more advanced specializations for a plant diet in the dentition than do the Phyllotini. The stomach of Sigmodon, and specially its intestine tract, is well advanced in adaptations to a food containing much cellulose (Vorontzov, 1967). I have analysed the data on stomach contents of recently caught specimens of Reithrodon from Argentina and of Holochilus and Sigmodon from Venezuela, and I found mainly green vegetable material. Holochilus is well known as a pest in cane plantations. The tribe can be defined as follows:

"Sigmodontine cricetids of a moderately large to very large size adapted to a vegetable diet, with reduced outer hind toes; molars large and hypsodont, with flat or

terraced occlusal surface, with major lophs and cusps tending to lamination and flexi and flexids tending to be highly involuted. Mesoloph and mesolophid usually totally absent, exceptionally rudimentary and sometimes present in  $M^3$ . Posteroflexus rarely present in juvenile dentitions, usually metaloph completely coalesced with posteroloph. Mesostyle and mesostylid absent or extremely reduced; enteroloph, enterostyle, ectolophid and ectostylid absent. Procingulum of first molars usually extremely simplified, or showing peculiar patterns; anteromedian folds usually absent in adult dentitions; anteroflexus and anteroflexid absent. Skull heavily built, with a high and broad zygomatic plate, with a concave anterior border and an upper corner projected as a short and sharp spine. Palate wide and short to moderately long, with two pitted fossae in the posterior portion separated by a median ridge. Incisive foramina long to very long, usually narrow, reaching behind beyond the level of the anterior plane of the  $M^1$ . Bullae moderately to well-inflated."

As already stated, Reithrodon had been recorded as a fossil in South America. It is the only sigmodont represented in the collection from Buenos Aires Province. Records of Holochilus will be discussed later.



7.6.1. GENUS REITHRODON, WATERHOUSE.

Reithrodon is a widely distributed genus in the living fauna of Argentina, Uruguay and Chile. With its hare-like long ears, its specialized cranium is also remarkably cuniculoid in superficial appearance, its burrowing habits, its delayed gestation period and its almost completely vegetarian diet, it is probably one of the more specialized and interesting members of the South American radiation of muroid rodents. However, very little is known of its systematics, ecology and evolution, as it has not been the subject of a recent comprehensive revision.

Six nominal species have been proposed by the various authors, namely auritus Fischer 1814 (= physodes Olfers 1818), cuniculoides Waterhouse 1837, typicus Waterhouse 1837, pachycephalus Philippi 1900, hatcheri Allen 1903, and caurinus Thomas 1920. Moreover, six other names have been proposed as subspecies of cuniculoides, auritus and typicus, some of them having been doubted as valid taxa by their own proponents (see Tate, 1932a, for a taxonomic history of the named forms). Osgood (1943), after a revision of the literature supplemented by the examination of extensive series, expressed his conclusion that Reithrodon was monotypic and proposed to arrange all the named forms in one species, auritus, with five or six subspecies, differing from each other in shade of colour or in the extent of hairiness of the feet" (op.cit. :223). His conclusion was followed by Hershkovitz (1955), with the variation of using the name physodes Olfers 1818, instead of auritus Desmarest 1819, in his attempt to credit the validity of Olfers' names. However, as demonstrated by Langguth (1966),

the name auritus was proposed in 1814 by Fischer for Azara's "rat oreillard", and it is therefore the oldest available formal name for a species of Reithrodon, physodes becoming a junior synonym of auritus.

Osgood's concept of a single species of Reithrodon subdivided into several subspecies was also followed by Cabrera (1961). After examining the types and the series of this genus in the British Museum (Nat. Hist.), I am also ready to endorse Osgood's view, though I also concluded that subspecies recognition within Reithrodon auritus is merely nominal before a formal and thorough revision is undertaken.

Reithrodon is clearly the more abundant fossil cricetid in the Neocenozoic deposits of the Buenos Aires Province, and their remains are dominant in the fossil material available to me. Various generic and specific names have been proposed for fossil remains studied formerly by Ameghino (1889, 1908), Roverto (1914) and Rusconi (1932). Ameghino (1889) described Reithrodon typicus fossilis for the Lujanian, Ptyssophorus elegans, also for the Lujabian, and Tretomys atavus, of the Bonaerian. Ptyssophorus and Tretomys were later discussed by Merriam (1894), who noticed a striking resemblance in molar structure among these two named genera and Neotoma, proposing a new subfamily Neotominae (sic) for them. Actually, he merely noticed a striking case of convergence in molar structure between the North American Neotoma and the alleged new fossil genera of Argentina. Osgood (1947: 173) commented that Ptyssophorus and Tretomys, as well as Bothriomys and Necromys, the two latter also erected by Ameghino for Pleistocene specimens from Argentina,

resembled the living phyllotine Andinomys. Actually, Bothriomys is a synonym of Euneomys, and Necromys is a dubious genus, which Hershkovitz attempted to synonymize with Calomys (Hershkovitz, 1962: 480). As regards Ptyssophorus and Tretomys, they were found by Hershkovitz (1955: 646) to be congeneric with Reithrodon. Unfortunately, the original material on which Ameghino based these two genera was not found in the Ameghino's collection, when I looked for them several years ago. As happens with some other of Ameghino's original specimens (see Reig and Simpson, 1972, for the case of Hyperdidelphys acutidens), it is probable that they ought to be considered lost. The illustrations provided by Ameghino (1889, Table VI, fig. 1, 16) and reproduced by Merriam (op. cit.), strongly support Hershkovitz synonymy, though they are not accurate enough as to their identity with Reithrodon to be considered as quite conclusive. For all practical purposes, however, it is convenient to treat Ptyssophorus and Tretomys as junior synonyms of Reithrodon.

Ameghino (1908: 424) created Proreithrodon with P. chapadmalensis and P. incipiens as different species, on the basis of material from the Chapadmalal Formation. The types of these species have been found by me in the collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", where they are catalogued with numbers 6016 and 6017. The type chapadmalensis was illustrated by Rovereto (1914: 186, fig. 72). Rovereto correctly realized that Proreithrodon was inseparable from Reithrodon, and he also synonymized P. incipiens with P. chapadmalensis, an attitude which I also find quite reasonable. These synonymies were endorsed by Hershkovitz (1962) and by Reig (1958).

Hershkovitz went a step further, and placed R. chapadmalensis under the synonymy of the living species of R. auritus (named by him R. physodes, as already discussed). In my listing of the Chapadmalal mammals (Reig, 1958), I maintained R. chapadmalensis as a distinct species on the grounds, not expressed in that paper, that it seemed unlikely that the living species would have had so a long biochron, from the Upper Pliocene to the Recent. As I shall discuss next, I am now quite inclined to accept Hershkovitz's lumping of chapadmalensis into the living auritus.

Two other forms referable to Reithrodon have been described by Rusconi (1932) for specimens coming from the typical Ensenadan beds of the banks of the Rio de La Plata at Olivos. They are ?Ptyssophorus rotundatus, based on a fragmentary lower jaw, and Reithrodon olivensis, based on an almost complete skull and mandible, both illustrated by Rusconi (op. cit., fig. 1 and fig. 2). These nominal species have been based on specimens belonging to Mr. Hennig's private collection, and they have not been available for later study. On the basis of Rusconi's drawings and descriptions, I do not find any reason to distinguish them from the living species. Therefore, I here also believe it is reasonable to endorse the Hershkovitz (1955: 646) issue by placing the two Ensenadan nominal forms under the synonymy of auritus. This conclusion is further supported by my own results in studying a large sample of Ensenadan remains of Reithrodon from the south east of the Buenos Aires Province, which I shall discuss next.

Reithrodon is well represented in the collect-

ion I have available, in all levels of the stratigraphic sequence of the Mar del Plata region. To my astonishment, I did not find any character which could neither allow the distinguishing of different taxa in this sizable collection of fossil Reithrodon, nor any basis to distinguish the fossil specimens from the single recognized living species. Therefore, I shall record all the studied specimens as Reithrodon auritus.

Genus Reithrodon, Waterhouse

- 1837, Reithrodon, Waterhouse: Proc. Zool. Soc. London 1837: 29.
- 1839, Hesperomys, Wagner: Scrhebers Saugeth. Suppl., 3: 510.
- 1889, Ptyssophorus, Ameghino: Actas Acad. Nac. Ciencias Córdoba, 6: 111.
- 1889, ?Tretomys, Ameghino: Actas Acad. Nac. Ciencias Córdoba, 6:120.
- 1893, Phyllotis, Trouessart: Catal. Mammal., 2:533.
- 1908, Proreithrodon, Ameghino: Anal. Mus. Nacional Hist. Nat. Buenos Aires 17: 424.

Type species:

Reithrodon typicus Waterhouse (= Reithrodon auritus Fischer)

Cranial and dental character states:

Skull strong, with an extremely arched dorsal contour. Rostrum large, deep and narrow. Zygomata narrow and very upturned anteriorly, moderately convergent forwards, and not markedly expanded. Brain case shortened and moderately broad. Zygomatic plate very high, with the anterior border deeply emarginated, and with a strong triangular spine projecting forwards. Nasals long and fairly broad, their posterior borders truncate and on a line with the fronto-premaxillary suture. Interparietal well developed.

Fronto-parietal suture forming an oblique angle at midline. Palate broad and notably long, with posterolateral portion deeply excavated and marked by lateral pits. A pair of small anterior palatal pits on the maxillo-palatine suture. Mesopterygoid fossa extremely narrow, deep and V-shaped. Parapterygoid fossae broad and strongly excavated. Bullae slightly inflated. Mandible strong and with a very deep ramus, a long coronoid process, and an anteriorly distinctly marked lower masseteric ridge reaching forward beyond the anterior plane of the  $M_1$ , but not forming a projecting tubercle. Capsular process of the base of the incisor vestigial. Molars with highly hypsodont crowns, prismatic, with truly plane grinding surface. Cusps not apparent, laminated, and enamel pattern defined by transversally alternating flexi and flexids. Procingulum of  $M^1$  short and wide, undivided; procingulum of the  $M_1$  narrow, trilobate in unworn or little worn teeth, triangular with advanced wear. Metaloph shorter than paraloph in  $M^2$ . Protoflexus obsolete in  $M^2$  and  $M^3$ . Protoflexid well marked in unworn or little worn  $M_2$ , absent with advanced wear.  $M^3$  large, with well developed paraflexus and metaflexus, the latter confluent with the posteroflexus.  $M_3$  relatively large, sigmoid-shaped and highly involuted.

Included species:

a single one: auritus.

Distribution:

From southern Patagonia, in Chile and Argentina, north to the Pampas of Argentina and Uruguay by the east, to arid plains and mountain valleys west of Los Andes in Mendoza, and Neuquén, continuing through western up to Tucumán by the west.

Reithrodon auritus, Fischer, 1814

1814. Mus auritus, Fischer: Synop. Mammal.,  
Stuttgart, : 215.
- 1818, Mus physodes, Olfers: in Eswege, Neue Bibl.  
Reisenbr., 15: 200..
- 1819, Mus auritus, Desmarest: Nouv. Diction. Hist.  
Naturelle (2nd. edit.), art. Rat, esp. 25.
- 1837, Reithrodon typicus, Waterhouse: Proc. Zool.  
Soc. London: 30.
- 1837, Reithrodon cuniculoides, Waterhouse, Proc.  
Zool. Soc. London: 30.
- 1889, Ptyssophorus elegans, Ameghino: Actas Acad.  
Nac. Cienc. Córdoba, 6: 111.
- 1889, ?Tretomys atavus, Ameghino: Actas Acad. Nac.  
Cienc. Córdoba, 6: 120.
- 1900, Mus pachycephalus, Philippi: Annal. Mus. Nac.  
Chile, Zool., 14: 42.
- 1903, Reithrodon hatcheri, Allen: Bull. Amer. Mus.  
Nat. Hist., 19: 191.
- 1908, Proreithrodon chapadmalensis, Ameghino:  
Anal. Mus. Nac. Hist. Nat. Bs.As. 17: 424.
- 1908, Proreithrodon incipiens, Ameghino: Anal.  
Mus. Nac. Hist. Nat. Bs. As., 17: 424.
- 1920, Reithrodon caurinus, Thomas: Ann. Mag. Nat.  
Hist. (9) 5: 473.
- 1932, ?Ptyssophorus rotundatus, Rusconi: Notas  
Prelim. Mus. La Plata, 1: 334.
- 1932, Reithrodon olivensis, Rusconi: Notas Prelim.  
Mus. La Plata, 1: 336.

Holotype:

Unknown, probably in the Musée d'Histoire Naturelle  
de Paris.

Distribution:

As for the genus.

Character-states:

As for the genus.

Referred specimens:

- MACN 17875: Right maxilla with  $M_1$ - $M_3$ , probably Barranca Lobos Formation, Chapadmalal region, Partido de General Pueyrredón, Prov. de Buenos Aires, Argentina.
- MMP S-219(a) Right lower jaw with  $M_1$ - $M_3$ . Found by Galileo J. Scaglia in Miramar Formation, at the base of the cliffs north of Mar del Plata city, in front of the exit of the road to Buenos Aires, Buenos Aires Province, Argentina.
- MMP S-219(b): Right fragmentary lower jaw with  $M_1$  and  $M_2$ . Found in association with the former.
- MMP M-383: Left premaxilla and maxilla with incisor, and  $M^1$ - $M^3$ . Found by G.J. Scaglia in the Vorohué Formation, stratum II, 550 m north of Arroyo Brusquitas, Partido de General Pueyrredón, Buenos Aires Province, Argentina.
- MMP M-566: Left almost complete lower jaw with incisor and  $M_1$ - $M_3$ . Found by G.J. Scaglia in the lower levels of the Chapadmalal Formation at Baliza Caniú, base of the Atlantic Cliff. Partido de General Pueyrredón, etc.
- MMP M-640(a): Left maxilla with  $M^1$ - $M^3$ . Found by G.J. Scaglia in the Miramar Formation, at the Atlantic slopes in Santa Elena, north of Camet, Partido de Mar Chiquita, Prov. de Buenos Aires.
- MMP M-640(b): Right incomplete lower jaw with incisor and  $M_1$  and  $M_2$ . Found in association with the former, but obviously belonging to another individual because of the different degree of



abrasion of the molars.

- MMP S-638: Right incomplete maxilla with  $M^1$  and  $M^2$ . Found by G. Albañir in the Miramar Formation, at the Atlantic cliffs in front of Asilo Unzué, Mar del Plata city, Buenos Aires Province.
- MMP M-642: Right incomplete lower jaw with the incisor and  $M_1$ - $M_2$ ; portion of left maxilla with  $M^1$ - $M^2$ ; femur and humerus. Found by G.J. Scaglia in the Miramar Formation, at Santa Elena, north of Camet, Partido de Mar Chiquita, Buenos Aires Province. Found in association with MMP M-1157 (Bolomys sp), and the next.
- MMP M-1156: Left incomplete lower jaw with incisor and  $M_1$ - $M_2$ . Found in association with the former, but obviously belonging to another individual.
- MMP M-643: Left premaxilla and maxilla with incisor,  $M_1$  and  $M_3$ . Found by G.J. Scaglia in the formation "Médano Invasor" (Holocene), at Baliza San Andrés, Partido de General Pueyrredón, etc.
- MMP M-870: Left fragmentary lower jaw with  $M_1$  and  $M_2$ . Found by G.J. Scaglia in strata probably of Miramar Formation, included in a coprolithe, at the base of the cliffs, 2 Km north of La Perla beach, Mar del Plata city.
- MMP M-1065: Left incomplete lower jaw with  $M_1$  and  $M_2$ . Found by G.J. Scaglia in the San Andrés Formation, at Punta San Andrés, Partido de General Pueyrredón, etc.

MMP M-1072: Right incomplete lower jaw with incisor and  $M_1$ - $M_3$ ; both maxillae with  $M^1$ - $M^3$ , associated with postcranial bones of other mammals. Found by Silvio Lorenzini in beds of the Miramar Formation, at the Atlantic slopes in Mar del Sur, Partido de General Alvarado, Buenos Aires Province.

MMP M-1082: Left incomplete lower jaw with  $M_1$  and  $M_2$  and the incisor. Found by Sylvio Lorenzini in San Andrés Formation, in the Atlantic slopes known as "Barranca Parodi", north of the City of Miramar, Buenos Aires Province.

MMP M-1083: Both premaxillae with incisors and nasals; right complete maxilla with  $M^1$ - $M^3$ ; right almost complete lower jaw. Found by Silvio Lorenzini in association with the former.

MMP M-1150: Right incomplete lower jaw with  $M_3$ . Found by Mr. Prina in stratum VIII of the Chapadmalal Formation, at the Atlantic cliffs at Bajada Las Palomas, Partido de General Pueyrrefón, Buenos Aires Province.

MLP 62-VII-27-95 (e, and following): Sample of lower jaws, maxillae, premaxillae, isolated molar teeth and assorted post-cranial bones of at least 23 different individuals, found in association with remains of Akodon cf. cursor, Nectomys squamipes, and other rodents,

in strata of Miramar Formation. (see details of provenance and condition of the finding, under Nectomys squamipes).

MLP 63.VI-10-44 (g, and following): Sample of lower jaws, maxillae, isolated molar teeth and assorted postcranial bones of at least four individuals. Found by J. Pisano, E.J. Ortega and E. Tonni in a layer of green clay referred to the Lujanian stage, cropping out at the right bank of the Arroyo Indio Rico, Partido de Tres Arroyos, Buenos Aires Province. Found in association with remains of Eligmodontia typus, Ctenomys sp.

MLP 63.IX.25.17: Left maxilla with M<sup>1</sup>-M<sup>3</sup>. Found by E. Tonni and R. Parodi in the Miramar Formation, 100 m NE of Punta Hermengo, Miramar City, Partido de General Alvarado, Buenos Aires Province.

MLP 63-VII-31-4: Fragmentary left lower jaw with M<sub>2</sub>. Found by E. Tonni in beds of the Miramar Formation at Miramar, Partido de General Alvarado, etc.

MLP 63.IX.25-17: Left maxilla with M<sup>1</sup>-M<sup>3</sup>. Found by E. Tonni and R. Parodi in the Miramar Formation, 100 m NE of Punta Hermengo, Miramar City, etc.

MLP 63.VIII.31.2: Incomplete skull including the two maxillae and premaxillae, the right M<sup>1</sup>-M<sup>2</sup>. Found by E. Tonni in the Miramar Forma-

tion at the city of Miramar, Partido de General Alvarado, etc.

MLP 63-9-25-18: Portion of left maxilla including M<sup>2</sup> and M<sup>3</sup>, found by E. Tonni and R. Parodi in beds of the Miramar Formation, 100 m NE of Punta Hermengo, Miramar city, Partido de General Alvarado, etc.

MLP 63.VII.31-3: Portion of right maxilla with M<sup>1</sup> and M<sup>2</sup>, and portion of left maxilla with M<sup>1</sup>.

Found by E. Tonni in the Miramar Formation, at Miramar, Partido de General Alvarado, etc.

MLP 63.IX.25.15; MLP 63.Vii.31.1; MLP 52.X.3.31; MLP 63.IX.25.16; MLP 52.X.4.30 (a); MLP 52.X.1.98, and MLP 52.X.4.25 (a and b) also belong to R. auritus, but these specimens have not been included in this study because of their more dubious geological provenance, or their less significance.

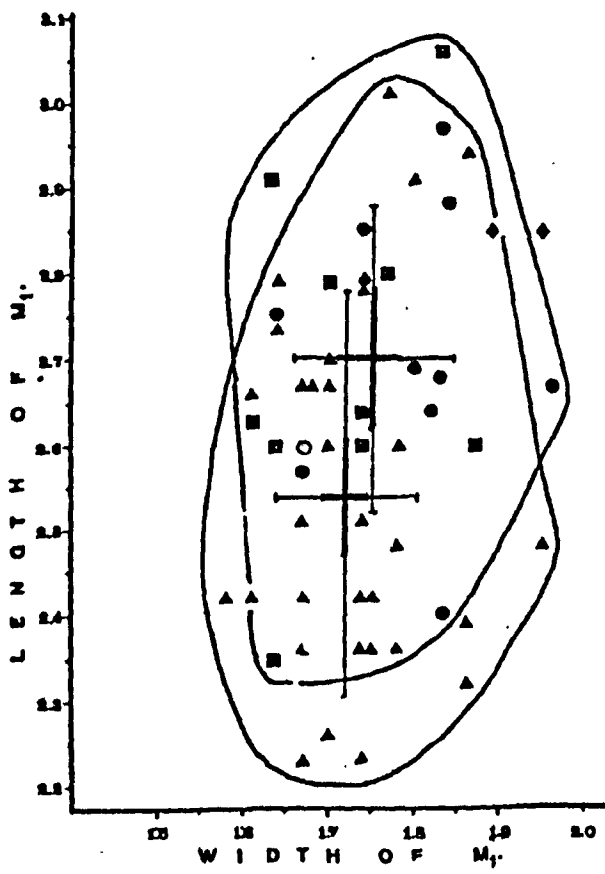
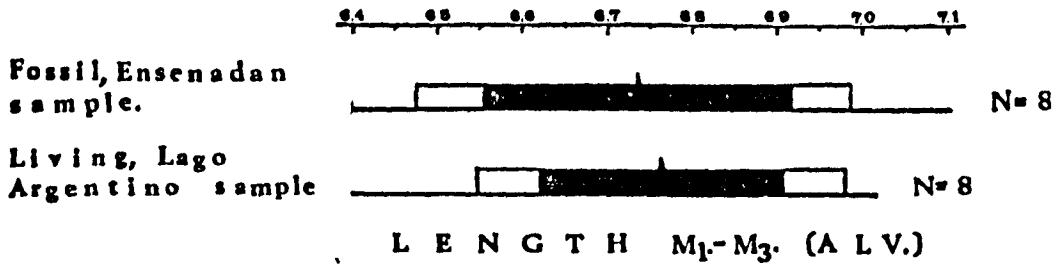
#### Discussion:

At first glance, it seems hard to admit that all the recorded specimens, belonging to about 58 individuals found in strata from the Upper Pliocene Chapadmalal Formation to the Holocene "Medano Invasor", belong to a single species, which is the same as that which lives at present in the same region where the fossils have been found and also in the vast area of Argentina and Uruguay. This invariance at the species level is not paralleled by other rodents of the same sequence and even by any other mammal, the biochron of most of the species of which is much more limited to particular sections of the same column. We must look at another Class, the Amphibia, to see the same species of horned

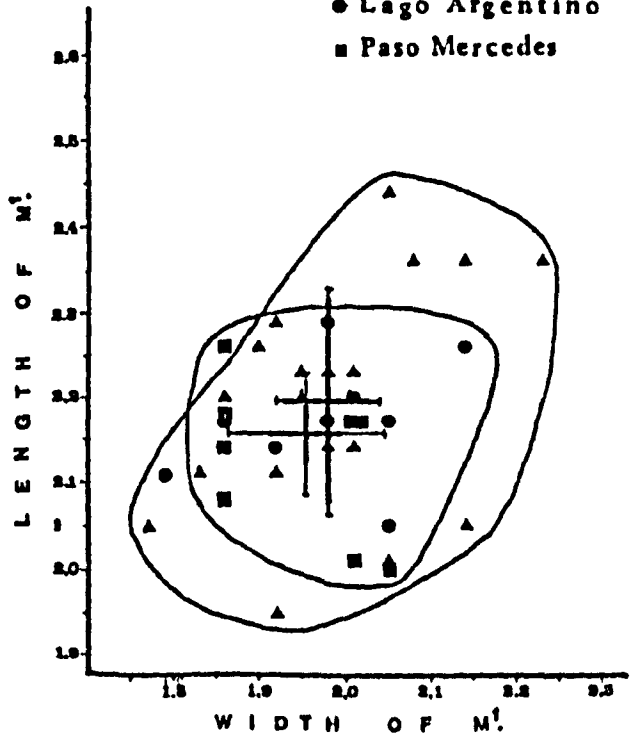
frog, Ceratophrys ornata, represented in the same sequence from the Chapadmalal up to the present (personal unpublished results). The same is probably true of the teyid lizard Tupinambis teguixin, which was found in the Chapadmalalan and the Vorohuean, and which lives at present in the same region. But for mammals, such a long biochron is unusual, and I have been sceptical for a long time in regarding all the fossil Reithrodon as belonging to one and the same living species. However, after examining the variation found in living populations of Reithrodon, and after studying the fossil sample now available to me, I have come to accept this view as the only one warranted by the present evidence.

It is true that the evidence refers only to size and details of morphology of parts of the skull, the lower jaw, and the molar teeth. But this kind of evidence, however, fragmentary, is allowed in the case of other taxa to indicate clear cut discontinuities or morphological differences which warrant inferences of species distinction. This is not the case in the available sample of remains of Reithrodon, which proved to be resistant to any taxonomical distinction. The series in the British Museum (Nat. Hist.) of the living species, allowed me to study the variability in metric and morphological characters in different populations from different regions of the distribution of auritus. I found that the living populations show a rather high degree of variation in size and morphology of the molar teeth. In particular, the variation of the latter is increased by considerable differences in the size and in the enamel pattern due to age. This age variation obviously hampers the study of variability, as the available

Fig. 44. Dice-gram and scattergram of measurements of the lower dentition in living and fossil Reithrodon auritus (Fischer).



Reithrodon auritus:  $\blacktriangle$  Miramar Ftion.  
 $\blacklozenge$  San Andrés Ftion.  
 $\circ$  Chapadmalal Ftion.  
 $\bullet$  Lago Argentino  
 $\blacksquare$  Paso Mercedes



samples represented different age-groups. The series were not large enough to permit a statistical treatment of samples of the same relative age. But this source of error was pooled in all the series, so that each of the samples could be considered as roughly equivalent. In any case, a definite statistical test of the variation of the different living populations as compared with the fossil sample, is not possible from the material available at present; except in the case of a few variates, and a thorough investigation must be postponed until more specimens are available.

My present preliminary exploration of the morphological and size variation in the living populations suggest that the range of variations in the samples of the living populations are not statistically significant for most of the examined variates ( $P > 0.2$ ), this confirming the view of Osgood that the main basis for subspecies recognition (if any, I would be inclined to add) is given by the characters of the fur.

In my fossil sample, most of the specimens come from the Miramar Formation and the particularly large sample catalogued in the Museum of La Plata under Nr. 66.VII. 27,95, allows a study of the variability of the  $M^1$  and  $M_1$  to an acceptable extent. It was found that the range of variation for the length of the  $M_1$ - $M_3$ , the length of the  $M_1$  and the length of the  $M^1$  of the Miramar sample falls within the range of variation found in samples of the living populations. In Fig. 44 and in Table 22 these data are given. It can be seen that the length of the  $M_1$  shows a slight difference in the mean values which the Student's test shows as statistically signifi-



cant at the 1% level. However, the Miramar sample is mostly

	Fossil, Miramar Formation	Living, Lago Argentino
Alveolar length $M_1-M_3$	t = 0.25	d.f.= 15 P > 0.2
Length of $M_1$	t = 3.00	d.f.= 51 P < 0.01
Length of $M^1$	t = 1.01	d.f.= 38 P > 0.2

TABLE 22. Student test of statistical significance of the means of three variates in a fossil and a living population of Reithrodon auritus.

composed of juvenile teeth, whereas the living population comprises only a few juvenile specimens, and therefore, the difference may merely be a reflection of an age difference between the two samples.

As regards the specimens of levels other than the Miramar Formation, unfortunately the samples here are too small as to be included in a statistical analysis. But they do not show any particular difference in size or morphology when compared with the Miramar sample and the living samples, and all seem to indicate they also belong to the same species. Therefore, I strongly believe that the available evidence is conclusive enough to demonstrate that one and the same species, Reithrodon auritus, occurs from the Chapadmalal Formation to the Present, and that the characters of the living species were already completely developed by Upper Pliocene times. Reithrodon is, however, a highly specialized member of the South American cricetid radiation, and the sudden appearance of the living species almost at the beginning of the fossil record of the Sigmodontinae, could hardly be compatible with the idea that this record indicates the time of arrival

of the Cricetidae into South America. The evolutionary conservatism of R. suritus is strongly suggestive of a long history of Reithrodon as a genus, and therefore, that its early differentiation from the common sigmodont stock may have occurred far back in Miocene times.

.7.7. NOTE ON A SMALL COLLECTION OF CRICETIDS  
FROM THE PLEISTOCENE OF BOLIVIA.

Fossil cricetids are not only known from Argentina. Apart from the Late Pleistocene and Holocene forms described by Winge (1888) from the cave deposits of Lagoa Santa, in south east Brazil, Hoffstetter (1963) mentioned the presence of Holochilus in the classical Tarija beds of southern Bolivia, and of Holochilus brasiliensis, and of Zygodontomys close to the living Zygodontomys lasiurus (= Bolomys lasiurus, according to my studies) in another Pleistocene deposit of the Chacoan region, also of southern Bolivia: the Nuapua fauna (Hoffstetter, 1968).

Thanks to the courtesy of Dr. Hoffstetter, I had opportunity to examine the material belonging to the family Cricetidae from these two deposits. I received these specimens too late to include a full description in this paper, but I was able to identify all the specimens, and I have included under the Scapteromyini section the description of one of the more significant elements in this collection: a mandible of Kunsia fronto.

The fossils from Tarija were found in three localities in the general area of Tarija: Tarija properly, Podcaya, and Palmar. Following Hoffstetter (1963) there is little doubt that all these three localities represent the typical Tarija beds, classically studied by Ameghino and Boule and Thevenin (see Hoffstetter, 1963, for a summary of the Tarija fauna and stratigraphy). This fauna was formerly considered as Pliocene or Early Pleistocene. It is now obvious that it cannot be considered as such but as Middle or Upper

Pleistocene. I believe that the cricetids I have identified suggest the second alternative. Below is a list of the identified taxa:

Kunsia fronto (Winge)

Oxymycterus cf. paramensis Thomas

Nectomys squamipes Brants

Phyllotis cf. darwini Waterhouse

Andinomys cf. edax Thomas

Calomys cf. lauchae (Fischer)<sup>1</sup>

Kunsia fronto is represented by a single lower jaw which I have already described and recorded. Nectomys squamipes is the more abundant fossil in this small collection, and it was undoubtedly on the basis of specimens of this species that Hoffstetter recorded the presence of Holochilus (as determined by F. Petter) in this faunule (Hoffstetter, 1963: 197). I include under squamipes the following specimens: MHNP TAR-3, left maxillae with M<sup>1</sup>-M<sup>3</sup>; MHNP TAR-4, left lower jaw with incisor and M<sub>1</sub>-M<sub>3</sub>, and MHNP TAR-5, left lower jaw with broken M<sub>1</sub> and complete M<sub>2</sub> and M<sub>3</sub>. I compared these specimens with the type and additional specimens of Nectomys garleppii Thomas (= N. squamipes garleppii fide Hershkovitz, 1944), which reaches in southern distribution to Cochabamba, Bolivia. I did not find any basis to separate the fossils from the living form, but as I did not undertake a careful examination of the limits of variation of the relevant characters of the several subspecies of squamipes, I believe that it is not advisable to identify the fossils straightforward as squamipes garleppii, and I prefer to assert their identification as Nectomys squamipes without subspecies

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(1) For revalidating Fischer's name for this species, see Langguth, 1966.

distinction. In any case, Nectomys squamipes is not found in the rather high and dry Andean valleys of the present Tarija region, and its occurrence there by the Pleistocene may be taken as an indication of a more humid environment at that time.

Oxymycterus cf. paramensis is represented by MHNP TAR-2, a fragmentary lower jaw with the incisor and the  $M_1$ . The species paramensis is living in the area now, and I find that this fragmentary remain is inseparable from a sample of the living forms. The material is too fragmentary, however, to ascertain a definite identification, and I prefer to identify it just as O. cf. paramensis. The same attitude is maintained as regards MHNP PAD-1, an incomplete left lower jaw with the  $M_1$ , which I refer to Andinomys cf. edax. The specimen is inseparable from the living species, which also occurs now in the same region, but here again the material only allows one to ascertain the generic identification with the probability that it belongs to the single known living species.

As regards Phyllotis cf. darwini, I identified as such specimen MHNP TAR-5, a left lower jaw of an old individual with a broken  $M_1$  and complete  $M_2$  and  $M_3$ . The specimen agrees in size and in morphology with the type of Ph. darwini and with other specimens of this species from the vicinity of the Tarija region I examined in the British Museum (Nat. Hist.). The molar teeth are too worn down to make the identification with darwini completely sure.

A small Calomys is represented by MHNP TAR-6, a complete left lower jaw with the whole dentition, and MHNP TAR-7, another left lower jaw in the same good condition and

and complete. These specimens obviously do not belong to Calomys lepidus or C. callosus, and they agree in size and morphology with specimens from the living fauna at Tarija, identified by Thomas (1926) as "Hesperomys" murillus cordovensis. This form was synonymized by Hershkovitz (1962) with Calomys laucha laucha. However, the status of the small forms of Calomys referred to bimaculatus, laucha, murillus, musculus and related forms, all of them lumped by Hershkovitz as Calomys laucha laucha, does not seem to me to be very clear. Massoia and Fornes (1965) argued that there were good reasons to distinguish two forms of Calomys, belonging to two different species, in the Pampean region: a short-tailed one, Calomys laucha laucha (Fischer) 1814, and a long-tailed one, Calomys musculus murillus Thomas 1916. More recently, in association with two other authors (Massoia, Fornes, Wainberg and Fronza, 1968), they tried to substantiate this view with some statistical data and chromosome information. Though the statistical treatment therein is not very accurate (tests of significance, for instance, are not provided), and the chromosome plates are very poor, the rough data afforded by these authors seem to indicate that they are probably right in their belief that there are two species of Calomys in the Pampean region. However, the possibility that the short-tailed form with high number of chromosomes, and the long-tailed form with a lower chromosome number, should actually be considered as polymorphic variants of one and the same species, ought also to be kept in mind. Moreover, the chromosome results so far reported must be corroborated by new and accurate karyological work, before they can be taken as a definite piece of evidence.

In any case, there is still the problem of the species name to be applied to these probably different forms. The short-tailed form should surely be named Calomys laucha, but I rather doubt that Calomys musculus would be the name to be applied to the other allegedly different entity. A revision now in progress of the types and original material of Thomas' concept of Calomys musculus strengthened my conviction that the typical musculus of northwestern Argentina is actually a third form to be distinguished in Hershkovitz's complexive concept of Calomys laucha laucha. If this distinction is at the species level, and if the Pampean long-tailed forms is also given species status, then this latter should probably be named Calomys murillus. But there is still not enough conclusive evidence to substantiate any of these issues, and until this evidence is available, I prefer to continue using the probably complexive concept of Calomys laucha to all of them, in agreement with the only seriously based, even when not completely convincing, modern revision of the group by Hershkovitz (1962). Therefore, the fossil specimens of Tarija are reported as C. cf. laucha, though it may eventually be demonstrated that they belong to one of the three, so far still obscurely visualized, forms which might be proved as included under Calomys laucha.

As regards the Nuapua faunule, it comprises remains of seven different individuals, which I identified as:

Holochilus cf. brasiliensis (Desmarest)

Calomys cf. callosus (Rengger)

Calomys cf. laucha (Fischer)

Phyllotis cf. griseoflavus Waterhouse

Holochilus is the more abundant fossil cricetid in the faunule, and its presence was already correctly reported by Hoffstetter (1968: 833). I refer to this genus MHNP NUA-1, the greater part of a skull with the dentition, damaged in brain case; MHNP NUA-2, left complete lower jaw and right femur; MHNP NUA-3, the two complete lower jaws, right premaxilla and maxilla with the teeth and some postcranial bones. These remains belong obviously to Holochilus, and they agree in size more with H. brasiliensis than with the other recognized living species by Hershkovitz (1955), H. magnus. However, a definite identification is hampered here by the fact that I am not quite sure that H. brasiliensis is actually a single species, and until a new revision of the forms of Holochilus is undertaken, I prefer to refer to this specimen as cf. brasiliensis.

MHNP NUA-4, a complete left lower jaw, and MHNP NUA-5, a right maxilla with the M<sup>1</sup> and the alveoli of M<sup>2</sup> and M<sup>3</sup> associated with assorted postcranial bones, are quite probably the specimens that Hoffstetter (1968: 833) referred to Zygodontomys (= Bolomys). They are, however, typically members of the genus Calomys in dental and mandible morphology, and by their size, they can only be compared with C. callosus, which now inhabits the Bolivian Chaco as part of its distribution. The mandible, however, is larger than any specimen of callosus examined by me, and it could even represent a distinct form. However, and until I study more carefully the limits of variation in callosus, I prefer to identify these two specimens as Calomys cf. callosus, which is indeed the more closely allied taxon, Calomys cf. laucha is



represented by MHNP NUA-5, a right lower jaw with  $M_1$ - $M_3$ , which obviously represents a small Calomys different than Calomys callosus or C. lepidus. It is quite probably conspecific with the specimens from the Tarija beds, and by the same reasons discussed when dealing with the latter, I identify this mandible provisionally as C. cf. laucha. MHNP NUA-7 is a right incomplete lower jaw with  $M_1$  and  $M_2$  obviously belonging to a Phyllotis of the subgenus Graomys. It is quite similar to the type specimen and other specimens of Ph. griseoflavus examined by me, and it does not seem to belong to Ph. domorum taterona, a larger form that now lives in the Andean region with Tarija as the type locality. The specimen is too fragmentary to allow an identification, more definite than the subgeneric one, and the probability that it belongs to the living griseoflavus.

These two faunules are closely related to the living faunas of each region, and this close resemblance could be considered as an indication of an Upper Pleistocene, Bon-aerian, age for the corresponding deposits.

8. BIOSTRATIGRAPHY.

In Table 23 I summarize the stratigraphic distribution of the fossil species of sigmodontine cricetids reported and discussed in the previous section.

In dealing with the biostratigraphic significance of these data, several cautions must be observed. It must be recognized that the available collections may only represent a part of the actual cricetid share of each of the succeeding faunules, and that further collecting may eventually enrich the lists. More complete specimens can also modify some of the taxonomic results arrived at here. These factors might alter in several details the biostratigraphic picture obtained so far. Moreover, we must keep in mind that we are dealing mostly with a succession of local faunules, and therefore, that our results apply only to a very restricted geographic area. Consequently, the first appearance of some taxa in the geological column of the Mar del Plata region, and their disappearance in succeeding strata, must reflect geographic changes in the distribution of the corresponding taxa, as well as of their effective phylogenetic emergence or extinction. Unfortunately, this latter caution is not given enough consideration in the current exercise of inferring biostratigraphic or phylogenetic conclusions from the obviously fragmentary evidence available to the palaeontologist. But with due regard to the accepted shortcomings of the evidence, we can set forth some worthwhile comments.

I have found that the Monte Hermoso formation has a poorer representation of the Sigmodontinae than the generally agreed later Chapadmalal formation. The Montcher-

TABLE No. 23. Stratigraphic distribution of the taxa of (fossil) Sigmodontine rodents reported in this paper.

Species	Geological formations and epochs.							
	RECENT	UPPER PLEISTOC.	Miramar Ftion.	San Andres Ftn.	Vorohué Ftion.	Bca. Lobos Ftn.	Chapadmalal Ftn.	Mte. Hermoso Ftn.
<u>Nectomys squamipes</u>	■	■	■					
<u>Bolomys bonapartei</u>								■
<u>Bolomys sp. A.</u>					■			
<u>Bolomys sp. B.</u>			■					
<u>Dankomys vorohuensis</u>					■	■		
<u>Dankomys simpsoni</u>							■	
<u>Akodon (Abrothrix) kermacki</u>						■	■	
<u>Akodon (Abrothrix) magnus</u>					■			
<u>Akodon (Akodon) cf. cursor</u>	■	■	■					
<u>Akodon (Akodon) lorenzinii</u>				■	■			
<u>Akodon (Akodon) johannis</u>			■					
<u>Akodon (Akodon) cf. iniscatus</u>	■	■	■					
<u>Scapteromys herskovitzi</u>				■	■			
<u>Kunsia fronto</u>	■	■						
<u>Phyllotis formosus</u>								■
<u>Phyllotis dorae<sup>id</sup></u>							■	
<u>Eligmodontia typus</u>	■	■						
<u>Reithrodon auritus</u>	■	■	■	■	■	■	■	■
<u>Cholomys pearsoni</u>					■			

mosian cricetids are only represented by two specimens belonging to two different taxa: a primitive species of the advanced akodontine Bolomys (B. bonapartei), and an advanced member of the genus Phyllotis (ph. Auliscomys formosus). The Chapadmalalan fauna shows four taxa of sigmodontines in the comparatively numerous collections so far obtained: a Reithrodon quite probably of the same species, R. auritus, which lives nowadays in the same area, an advanced Phyllotis (Ph. Graomys dorae) not closely related to the Montehermosian representative of the same genus, an extinct species of subgenus Abrothrix of the genus Akodon (A. A. kermacki), and an akodontine taxon probably related but more advanced than Bolomys.

The difference in the cricetid component of these two faunules might be a matter of different interpretations. Authors inclined to believe that the cricetids are rather modern invaders of South America, could conclude that the meagre Montehermosian representation, as compared with the Chapadmalalan one, is a clear indication that the Montehermosian times were very near to the early arrival of the Sigmodontinae to this continent, that the scarce number of taxa and specimens found in the Monte Hermoso beds demonstrate that these rodents were still very rare and probably no more than a first pioneering advance of a more massive eruption which took place from the Chapadmalalan onward. Actually, there are reasons to believe that the difference is merely a reflection of sampling bias. In fact, the Chapadmalal beds have been much more carefully worked in search of small mammals than the Monte Hermoso beds. It is significant that

the two specimens of Montehermosian cricetids so far discovered were found rather recently by the same person, José Bonaparte, in an attempt at modern and detailed thorough collecting in the Monte Hermoso beds. Against this, the fossil deposits of the Chapadmalal formation have been subjected to continuous and systematic collecting during the last thirty years.

But apart from that problem, there remains the question whether the Montehermosian and the Chapadmalalan cricetids give additional information on the problem of the distinction of the corresponding formations as regards geological age. The answer is not immediately obvious, as the sampling bias above mentioned might account for the differences found in the two faunules. Moreover, if the difference found in the available samples is an actual faunal difference, it can always be alleged that it represents an ecological or geographic distinction more than a distinction in evolutionary degree. It is true that the Montehermosian faunule includes a rather primitive species of Bolomys, and that the Chapadmalalan includes a more advanced and related akodontine: Dankomys simpsoni; but at the same time, an actual phylogenetic link between these two taxa cannot be assessed surely. Moreover, the Chapadmalalan yielded a form of Abrothrix, which can be thought of as a more primitive taxon than Bolomys, and a Phyllotis which is at least as advanced as the Montehermosian representative of the same genus. I think that the present evidence only indicates that the two faunules are different in their cricetid component, but that this difference, which can also be the outcome of sampling bias, does not provide positive

for the relative placing of the two corresponding formations in the geological time column.

Sampling bias used not be taken into account so seriously when dealing with the comparison of the cricetids found in the different strata of the sequence of the Chapadmalal region. Here, during the last thirty years, the various mammal-bearing rock-units have been worked in search of fossils almost to the same degree, mostly by the same people, who used the same techniques and were endowed by the same collecting skills. Therefore, the differences found in the cricetid samples of the succeeding strata must be here a more objective reflection of the true differences in the corresponding faunules.

As shown in the table, two of the four species of cricetids found in the Chapadmalal formation are also found in the overlying Barranca Lobos formation. The third species found in the latter is also found in the succeeding Vorohué formation. The cricetid fauna of the Vorohué comprises six species, one of which is also present in the Chapadmalal and another is common to Barranca Lobos. The species common to these three faunules is Reithrodon auritus, a form of an exceptionally long biochron, which still lives in the same area. This indicates that the Barranca Lobos faunule is intermediate between the Chapadmalal and the Vorohué ones, but somewhat more related to the former. In fact, the cricetid fauna of the Vorohué is more diverse and abundant than the preceding ones and it shows the first appearance in the area of Scapteromys, Akodon (Akodon), and the wiedomyines, as represented by Cholomys pearsoni. The other three elements can be considered as derivatives of taxa already present in

the Chapadmalal or the Barranca Lobos deposits: Akodon (Abrothrix), Dankomys and Reithrodon. Of the three, only Reithrodon will continue in the post-Vorohucan strata.

Turning our attention to the San Andrés faunule, the cricetids are represented in it by four species, three of which are common to the underlying Vorohué faunule. There is the chance, however, that the Scapteromys of the two deposits should belong to different species, as advanced when discussing the corresponding remains. The small Akodon (Akodon) lorenzinii is an undoubted common element of the two faunules, and so is the case of Reithrodon auritus, at least as far as the present evidence allows this conclusion. The clearly non-Vorohuen element of the San Andrés faunule is the species of Bolomys, which could be connected with the ancestry of the species living in the same area. We must conclude from these data that the cricetid rodents indicate a rather close faunal resemblance between the San Andrés and the Vorohué, but that the two faunules are different enough as to support the conclusion that we are dealing with two distinct substages.

As regards the cricetid fauna of the succeeding Miramar formation, there are here six different species, only one of which, the long living Reithrodon auritus, is also represented in the preceding strata. A major faunal break-up seems to have occurred by Ensenadan times, and the presence in the Miramar formation of such neotropical living species as Nectomys squamipes and Akodon cursor suggest that a climatic change was responsible for the faunal distinction. It is interesting to point out that of the six species of the Miramar faunule, only one, Akodon (Akodon) johannis is undoubtedly

extinct. This can be taken as an indication that by Ensenadan times (Middle Pleistocene) most of the living species were already in existence. The Upper Pleistocene is poorly represented in the collection of the southeast of the Buenos Aires Province, where only Reithrodon auritus and Eligmodontia typus, both living, are recorded. But the richer collection of Tarija and Nuapua, treated summarily in the previous section only yielded living species. This relative antiquity of the species of the living faunas would not be expected under the assumption that the impressive diversification of the living Sigmodontinae is the outcome of a very rapid evolutionary process which started in the Upper Pliocene.

The general picture is interesting in showing a gradual differentiation of the cricetid fauna in an almost continuous regional geological succession. Of the two main factors responsible for these changes: local phylogenetic succession and geographic displacements, the latter seems to have played the main role. In fact, evidence for direct ancestor-descendant sequences are scarce and dubious. We might include in this category the discussed case of probable phyletic speciation in the couple Akodon kermacki and Akodon magnus; the less probable of the pair of species Dankomys simpsoni and Dankomys vorohuensis, and the inconclusive suggestions of phyletic relations among the fossil and living Bolomys. All the remaining cases of faunal differences among the succeeding strata must be explained by irruptions and translations from and to other geographic areas. As is discussed further in the next section, the Pampean region was probably populated by expansive waves of cricetids coming from the



north and the west. These invaders belonged to stocks which experienced the main episodes of their differentiation in tropical and subtropical Andean homelands and which moved south and eastwards, probably in response to the changing conditions connected with the Andean orogeny and the Pleistocene climatic fluctuations. It is of interest to point out that the first cricetids to appear in the fossil record of the area are members of the phyllotine and akodontine groups, the two tribes which seem to have differentiated in more southern genocentres (see page 396). The total absence in the early record of this region of oryzomyines is also illustrative, as this group seems to have differentiated in north west South America. Oryzomys, which is represented in the living fauna of the same area by one species of the subgenus Oligoryzomys, was not found in any of the Pleistocene faunules, which suggest that the irruption into the Pampean region of this northern stock has been a rather recent event.

The first fossil cricetids of South America are the two species found in the Monte Hermoso beds, Upper Pliocene, of the south of the Province of Buenos Aires. It is of interest to emphasize that no mammal of nearctic origin other than these cricetids and Cyonasua, a procyonid also found in older, Huayquerian deposits, was found in the Monte Hermoso fauna. This is against the hypothesis that the cricetids are members of the same faunal stratum which brought to South America the massive irruption of nearctic mammals after the establishment of the Panamanian land bridge. As I shall demonstrate in the next section, the Sigmodontinae are probably members of the South American faunas since the earliest Miocene, and their sudden appearance in the Upper Pliocene of the Pampean region

could only be interpreted realistically as an indication that they had arrived at this area by those times, from areas in South America in which they have been evolving since much earlier times.

9. ORIGIN AND EVOLUTIONARY HISTORY OF THE SIGMODONTINAE

In the previous two sections, I have dealt with the fossil record of the Sigmodontinae, and with an exploration of the main outlines of their diversity. In Section 4, I discussed the problem of the placement of the Sigmodontinae in the system of the family Cricetidae, and I commented briefly on the question of the phylogenetic relationships among the various members of this family. Now the question of the bearing of the palaeontological and systematic evidence on three major problems of the study of the evolutionary history of the South American cricetids, namely, their phylogenetic and geographic origin, their antiquity as part of the South American fauna, and the evolutionary relationships among their subordinate taxa has to be considered in further detail. These three problems are tightly interwoven, but it is convenient to treat them separately.

9.1. Evolutionary relationships and main evolutionary pattern within the Sigmodontinae.

The problem of the geographical and phylogenetic origin of the Sigmodontinae, and the problem of their antiquity as part of the South American fauna can be discussed better after assessing the pattern of the relationships among the different tribes of the subfamily, and the main pathways of their evolutionary development. Some of my conclusions on these topics have been put forward in the preceding sections. They are part of an explanatory argument which can be stated as a set of hypotheses. Those connected with evolutionary relationships and evolutionary pattern within the subfamily are the following:

11.1.) The Sigmodontinae are a cohesive, monophyletic

group of the family Cricetidae.

H.2.) The tribal and generic diversification of the Sigmodontinae occurred in South America from an immigrant stock.

H.3.) The most primitive members of the subfamily belong to the tribe Oryzomyini, a stock of originally sylvan and omnivorous-insectivorous mice from which the other tribes arose, and which started its generic diversity in the Andes of north west South America.

H.4.) The Sigmodontini, Ichthyomyini, and probably also the Wiedomyini, represent early direct offshoots of the oryzomyine stem which radiated in north west South America to invade more specialized food niches and environments. They are likely to have been more flourishing and diverse in the past than they are now.

H.5.) The Akodontini are a primarily grass-land, insectivorous branch which departed from the oryzomyine stem later than the above and flourished in an extensive radiation, probably from a central Andean genocentre.

H.6.) The Phyllotini are pastoral, probably akodontine derivatives, which diversified as herbivorous in an extensive radiation, probably from a central Andean genocentre.

H.7.) The Scapteromyini are late direct derivatives from the oryzomyine stem which diverged as semiaquatic insectivorous and subterranean herbivorous forms, probably in low lands of central South America.

The evidence in support of H.1. was discussed in Section 4. I demonstrated there that the different groups of the Sigmodontinae are more closely related to each other than with other cricetids in morphology of the phallus and baculum, accessory male reproductive glands, musculature,

pattern of scalation of the hairs and ectoparasites. To these characters one can add molar pattern, as whatever the degree of modifications of the enamelled structure of the cheek teeth of the different genera, the basic molar structure of each tribe can be traced to an original generalized oryzomyine pattern. The hypsodont and involuted molars of the advanced sigmodonts are connected to the oryzomyine molars by the molar pattern of Holochilus; the modified molars of the advanced phyllotines can be traced back to the akodontine pattern, and this can be easily derived from the oryzomyine pattern. The same conclusion can be arrived from the study of skull and mandible morphology. Unfortunately, other kind of evidence on the phenetic affinity within the group is not still available. Chromosome data are still fragmentary and mostly cover the Akodontini (Bianchi et al., 1971) and the Phyllotini (Pearson, 1972). Biochemical tests of affinity have not been performed so far. But the supporting evidence for this hypothesis is compelling, and it may be taken as very well grounded.

The second hypothesis involves two statements: the endemic diversification of the Sigmodontinae and their immigrant origin. As regards the latter, there can be little doubt that the ultimate ancestors of this taxon were not part of the ancient inhabitants of South America. Neither any group of the Rodentia, nor any group which could be realistically postulated as a rodent ancestor occur in the pre-Deseadan faunas of this continent. The Caviomorpha appear suddenly in the Deseadan, and their ancestors came surely from outside South America. The possibility of an origin of the Sigmodontinae in the Caviomorphs must be readily discarded. The Sigmodontinae are cricetids and myomorphs, and therefore, they

have no direct relationships with the hystricognathous caviomorphs. Vandebroek's (1966) suggestion of a morphological link between the molars of some caviomorphs and the "sigmodont" molar pattern, is completely unrealistic and contrary to all the facts and conclusions of rodent phylogeny. As true cricetids, the Sigmodontinae should be derived from a muroid stock. As we have discussed, the data of comparative anatomy and evolution indicate that the most probable ancestors of the Sigmodontinae are the Cricetodontinae, a group which flourished by Oligocene and Miocene times in Eurasia, North America and, inferentially, also in Africa.

As for the statement that the Sigmodontinae diversified within South America, this conclusion is imposed by the taxonomic cohesiveness of the group; its pervasive endemic diversity; the pattern of interrelationships among its subordinate tribes; the parasitological characteristics of the South American, the Central American and the North American members of this subfamily; the pattern of distribution and the known palaeontological history of the group. Their broad diversification and high endemism is an obvious handicap to any hypothesis holding that the genera, or even the tribes of this subfamily might have originated outside South America. But, under the pressure of the idea that the subfamily is not older in South America than the Upper Pliocene, and the realization that the span of time since then to the present is too short for the extensive radiation of this taxon to have taken place within the continent, the idea that their genera evolved in Central or North America was proposed by various authors (see Hooper, 1949; Patterson and Pascual, 1968). But, as we shall discuss next, the time of arrival of the ancestors of the Sigmodontinae

in South America was surely much older than the partial available fossil record tells us, and the hypothesis of an exogenous differentiation of the genera is in so strong a contradiction with other sort of evidence, that it is untenable.

As regards our third hypothesis, all students of South American cricetids have agreed on the primitive and ancestral character of the Oryzomyini, as indicated by the anatomy of various organs and their ecological characteristics (see Hershkovitz, 1962, 1966b, 1969; Vorontzov, 1959, 1967; and Section 7.1 of this paper). As I have recently advanced (in Bianchi et al., 1971, Fig. 7 :734), the northern Andean belt of western Venezuela, Colombia Ecuador and northern Perú, can be postulated as the probable centre of diversification of the Oryzomyini. This is the area of the greater density of species of this group, and where most of the subgenera of Oryzomys (Oryzomys s.s., Oligoryzomys, Microryzomys, Melanomys, Oecomys) overlap with most of the species of Thomasomys, Rhipidomys, Neacomys.

The majority of the species of the Oryzomyini are dwellers of mountain tropical forests ("sylvan") or inhabitants of the high paramos of the northern Andes. Though detailed information on their food habits is not abundant, they are known to be mainly omnivorous and insectivorous, small, generalized predators. Most of the species are scansorial and terrestrial, but there are also mainly or partially arboreal genera (Rhipidomys, Oecomys). Surely the diversity of habitats of the tropical Andes, and a changing landscape affected by the Andean orogeny, triggered the extensive diversification of the Oryzomyini, which developed within the varied resource zone which can be exploited by omnivorous-insectivorous small mammals.

It is interesting to point out that even when no placental mammals was exploiting this resource zone and developing this way of life in South America prior to the arrival of the Cricetidae, the metatherians were long ago, from the early Cenozoic and probably from the late Cretaceous, well adapted to this niche, as represented by the small didelphids and the coenolestids. The resulting ecological confrontation does not appear to have been one of competition and displacement, but of mutual adjustment, as it is now demonstrated by the successful sharing of the same general niches by Coenolestes and Thomasomys in the paramos, Oecomys and Monodelphis in the perisylvan savannas, and Rhipidomys and Marmosa in the forests.

But besides their primary characterization as mountain forest dwellers, the oryzomyines appear also as a plastic group capable of invading other habitats and geographic areas. Some species of Oryzomys (particularly of the subgenera Oecomys and Oligoryzomys) successfully invaded the low lands, savannas and prairies, although occupying the same food niche. Nectomys also is adapted to live in the low lands, but as a semiaquatic form, inhabitant of the marshes and the banks of the streams of the tropical and subtropical forests. The species of the Oryzomys palustris groups are also dwellers of inundated low lands, and so is Oryzomys delticola. Low land forms of semiaquatic habits are candidates for accidentally crossing sea barriers and populating new areas overseas. That this actually occurred in the case of the oryzomyines, is demonstrated by the presence of Megalomys in the West Indies and of Nesoryzomys in the Galapagos. The Oryzomys palustris group can be inferred to have reached North America from South American ancestors by oversea transportation previous to the



establishment of a land connection between those continents. I believe that Nyctomys and Otonyctomys, two genera of oryzomyines endemic of Middle America are in the same category. Hershkovitz (1966b) considered them as possible relicts from an archaic North or Middle American stock connected with the ancestry of the Thomasomys-like oryzomyines, but he also stated the possibility that they were Middle American immigrants derived from South American ancestors. I found that these two genera are somewhat more advanced in molar structure than their relatives Thomasomys and Rhipidomys, and I believe that the second alternative is the true one.

The fourth hypothesis refers to three tribes far less diversified than the Oryzomyini and, at least two of them, of distinct and divergent food adaptations. The Ichthyomyini are very characteristic by their specialized skull and dentitions and their modified body shape, which are adaptations to fish eating and aquatic life. They are obscure in origin and relationships, but it is quite probable, as suggested by its present scattered distribution in northern South America and Middle America, and the distinctiveness and relictual character of their genera, that they are early derivatives of the oryzomyine stock which originated and split in northern South America to invade later Middle America (Rheomys), probably after the establishment of the Panamian land bridge. Equally obscure are the Wiedomyini, but by their skull and dentition they are obviously related to the oryzomyines, and here again, the relictual character of the single living genus and species and the inferred ecological distinction of its pleistocene relative Cholomys, suggest a much broader diversification in the past and an early origin from the oryzomyine

.stem.

The Sigmodontini illustrate a definite shift of the early Sigmodontinae towards the exploitation of the vegetarian resource zone. Sigmodon, Neotomys and Reithrodon are undoubted plant-eaters, inhabitants of grassy prairies, savannas and mountain grass valleys. Holochilus is also a predominantly vegetarian form, though less specialized than the former and an inhabitant of inundated low lands. Though the four living genera are evidently related, they are well differentiated, suggesting an old origin. Sigmodon and Reithrodon are known as fossils since the Upper Pliocene, and by that time they were so divergent and so far apart in distribution that they could hardly be supposed as sharing a common ancestor later than the Early Pliocene and the Late Miocene. The long biochron of the specialized Reithrodon auritus confirms this inference. Holochilus is the most primitive of the living sigmodonts, and it joins this tribe to the Oryzomyini in molar structure and in phallic characters. If Holochilus can be supposed as close to the common ancestry of the more advanced genera, the time of the divergence of the tribe from the oryzomyine stock cannot be younger than Middle Miocene. The biogeographic history of Sigmodon is difficult to understand. The present distribution of their various species, and particularly of Sigmodon hispidus, which occurs in north western South America, Middle America and south and south eastern North America, together with the occurrence of fossil representatives of the genus in Late Pliocene and Pleistocene deposits of North America, suggest that the cotton rats might have originated in Middle or North America from a South American pre-Sigmodon over water emigrant.

Origin of the genus in northern South America and further raft dispersal to North America is another alternative. But in any case, it is almost sure that the species S. hispidus was a late immigrant in South America, coming from populations differentiated at the species level in North America and which spread into the Colombian and Venezuelan low lands through the Panamian land connection. The distribution of Reithrodon is the opposite to that of Sigmodon, occurring as it does only in the southern tip of South America. Whether it originated in the area of its present distribution, or migrated there from a northern centre of origin, is a moot case. Its probable closer relationships with the Andean Neotomys than with the remaining genera point in favour of the second alternative. But it is quite probable that the sigmodonts were represented by several other genera, now extinct, in the past. The origin of the present distribution of the living genera can hardly be understood in our present lack of knowledge of the past diversity of the tribe.

As regards the Akodontini, they represent a well distinctive major radiation of the Sigmodontinae. They are more advanced in molar morphology and body form than the oryzomyines, but they did not evolve progressive hypsodont and laminated cheek teeth as did the Sigmodontini and the Phyllotini. Only a few of them (Bolomys and Dankomys) seem to be able to include partially vegetable matter in their diet, and the whole tribe can be characterized as a group of mainly insectivorous small predators. They are only occasionally dwellers of the fringes of the mountain forests, being mostly inhabitants of open land, high Andean valleys and paramos, and low land scrub

and grassy prairies and savannas. It must be pointed out that they cannot be characterized as "pastoral" in a resource zone sense, but only in an environmental sense. In the grass lands they play the role of small predators of arthropods and other small invertebrates (In south east Buenos Aires Province, I found that the stomach contents of Akodon azarae and Oxymycterus rufus included larvae and imagoes of insects of several kinds, myriapods and snails, and almost nothing of green matter). By the anatomy of its digestive organs and its known diet, Oxymycterus is a specialized insect and meat eater of a terrestrial, cursorial life. Notiomys, Chelemys and Blarinomys are fossorial insect-eaters, and they represent the invasion of a particular adaptive zone apparently not previously exploited by any group of South American placental mammals (the fossil Necrolestes, allegedly a metatherian, seem to have been a fossorial insectivorous mammal), but which in other continents is exploited by the moles (Talpidae) and the golden moles (Chrysochloridae). In the overall picture, the akodontine radiation seems to represent a further narrowing and specialization of the insectivorous characteristics of the Oryzomyini.

In general morphology, the Akodontini can be thought of as direct derivatives from the oryzomyine stem. Their extensive diversification, and the fact that at least two of the living genera and one fossil genus are present in the Upper Pliocene, would indicate at least an Early Pliocene differentiation. The scarcity of relictual monotypic forms, and the advanced polytypy of most of the living genera, subgenera and species, can be taken as an indication that the process of diversification of the tribe is still on a very active stage.

However, if the Phyllotini are akodontine derivatives, as it seems likely, and given the advanced stage of evolution of the two known Upper Pliocene forms of Phyllotis, the splitting of the phyllotines from the akodontine stock can be inferred as not being younger than the earliest Pliocene or late Upper Miocene. This obliges us to postulate an earlier date, probably in the Upper Miocene, for the differentiation of the akodontines. It is not impossible, however, that akodontines and phyllotines could both have been derived from a common ancestor by Early Pliocene or Late Miocene times.

The phyllotines are more typically pastoral than the akodontines, both in their environmental preferences and in having an increasingly vegetarian diet. Primitive phyllotines as Calomys and Zygodontomys (if the latter is truly a phyllotine), are close to Akodon and Bolomys in molar pattern and general adaptive type, and they can be considered at the stage of early akodontine descendants which started to include plant food in their diets. Phyllotis shows a more advanced trend in the same direction, but the species of Andinomys, Euncomys and Chinchillula have already attained a progressive adaptation as plant eaters. The whole phyllotine radiation can be conceived as an increasing invasion of the herbivorous resource zone in the subtropical and temperate, grassy or brushy and xerophytic mountain valleys and uplands, low land scrub and grassy prairies and rocklands. We have seen that the Sigmodontini are also plant eaters. Their genera can be compared to the more advanced phyllotines as vegetarian specialists. Therefore, a certain amount of competition would have occurred between members of the two tribes if they had evolved in the same areas. Actually, Sigmodon is now living in the same

savannas of Colombia and Venezuela where Zygodontomys occurs, and Reithrodon and Neotomys share areas with different phyllotine genera. However, the main centres of radiation of the two tribes are likely to have been quite separate, and probably the main events of their radiation occurred at different geological times. In fact, I believe that there is a strong suggestion that akodontines and phyllotines evolved much later than the sigmodonts in a central Andean region. I have suggested (in Bianchi et al., 1971: 733) that the geographical centre of differentiation of Akodon and most of the akodontine radiation occurred in the Andes of southern Perú, the Bolivian Plateau and the Andes of northern Argentina. The same area can be thought of as the centre of the radiation of the phyllotines, as they, as do the akodontines, show the higher number of taxa in this general area.

The Scapteromyini can be traced back directly to the oryzomyines by molar and cranial characters. Their two living genera, though they are taxonomically closely related, show very different adaptations: insectivorous water dwellers (Scapteromys) and herbivorous fossorial forms (Kunsia). The timing of separation of the Scapteromyini from the Oryzomyini is likely not to have been very old. Scapteromys is already represented in the Early Pleistocene, which indicates that the tribe must have originated not later than the Upper Pliocene. An earlier time is improbable, in view of its small taxonomic diversification.

To summarize, it must be pointed out that our argument led us to emphasize the role of the Andean range in the evolution of the South American cricetids, and to visualize at least two major episodes in their diversification: an

early radiation of the generalized sylvan omnivorous-insectivorous oryzomyines and their vegetarian (Sigmodontini), ichthyvorous (Ichthyomyini), and probably also insectivorous (Wiedomyini) descendants, and a later radiation of an insectivorous branch (Akodontini) and an increasingly herbivorous branch (Phyllotini). The first episode took probably place by Early Miocene times in the northern Andean region and the neighbouring low lands, and the second developed since the latest Miocene or earliest Pliocene from a central Andean genotype. A later and third minor radiation would be represented by the Scapteromyini.

#### 9.2. Ancestral group and its geographic origin.

It has been generally accepted that the South American cricetids took their origin from a North American cricetid stock (Simpson, 1950; Hooper, 1949; Hershkovitz, 1962, 1966b, 1969; Vorontzov, 1960, 1968; Patterson and Pacual, 1968). This hypothesis appears as imposed by geographical reasons and by its agreement with the overall pattern of faunal relationships of the South American mammals. It looked so obvious and sound that no other alternative was so far suggested. I shall describe it, but not without pointing out that an alternative is also plausible.

We must start by recognizing that whatever the likelihood of the hypothesis of ultimate origin in North America, it cannot be taken as a fully corroborated piece of scientific conclusion until an unequivocal ancestral taxon is identified in the North American fossil record. And we must agree that such a taxon has not until now been found, nor even carefully looked for.

As we have concluded in Section 4, the overwhelm-

ing majority of the South American Cricetidae, the Sigmodontinae, belong to a distinct group at the subfamily level as regards the majority of the living North American cricetids, the Peromyscinae. The latter are likely to have derived from a Copemys-like ancestor by Miocene times, and this ancestor is probably itself derived from early Miocene Eurasiatic cricetodontines. By the Oligocene and the early and middle Miocene, the North American cricetids belonged also to the subfamily Cricetodontinae (Eumys, Paracricetodon, Scottimys, Leidymys, Schaubeomys, Paciculus). Therefore, on the framework of the North American origin hypothesis, the Sigmodontinae should be derived either from the Oligo-Miocene cricetodontines or from the Miocene-Pliocene peromyscines.

The second alternative is unlikely. The peromyscines show derived character-states in the morphology of the glans penis, the baculum and the accessory male reproductive glands. The wide-spread occurrence in them of these progressive features suggests that they were already present in the genetic constitution of the original peromyscine stock. Moreover, many of the known fossil Mio-Pliocene peromyscine genera are closely connected to the ancestry of North American living genera of simple penis type, Copemys to Peromyscus and Baiomys, Miochomys to Onychomys, Pliotomodon to Neotoma, etc. (Clark, Dawson and Wook, 1964; Alker, 1967). The Sigmodontinae could not be descendants of any of these lineages. All sigmodontines are more primitive in male reproductive organs, and with the exception of the advanced pastoral forms, most of them, particularly the oryzomyines, are more primitive in molar morphology. The recently described Early Pliocene genera Tregomys and



Gnomomys (Wilson, 1968), and the Late Pliocene Simmetrodon-  
mys and Macrognomys are not so clearly connected with  
living North American genera, but they are also too advanced  
in evolution to be considered ancestors of the more primitive  
sigmodontines. In fact, this ancestor should be a genus poss-  
essing brachyodont molars with persistent mesolophs and meso-  
lophids, and should be pre-peromiscine in having a complex-  
type penis and a full battery of male reproductive glands. It  
is not excluded that some of the early forms of Copemys could  
fulfil these conditions, and they actually satisfied the re-  
quirements of cheek teeth morphology. It is reasonable to  
assume that if Copemys is an ancestral peromiscine, the charac-  
ters of this subfamily developed gradually from the early  
Copemys of the middle Miocene, and therefore, that at the  
starting point of this lineage, the ancestral Copemys could  
still retain a primitive type of penis and reproductive glands,  
being therefore compatible with the requirements of a sigmo-  
dontine ancestor. But such a Copemys would not be technically  
a peromiscine. Therefore, the Miocene and Pliocene pero-  
miscines must be dispensed of as plausible ancestors of the  
South American sigmodontine cricetids.

The other alternative is favoured by the fact  
that the Cricetodontinae are comparable in molar morphology  
to the ancestral oryzomyine sigmodontines, and by the infer-  
ence that they should have possessed a complex-type penis and  
a complete set of reproductive glands. Needless to say, the  
characteristics of the reproductive organs are not known in  
this fossil group, but it is reasonable to conclude that if  
the comparative anatomy tells us that the early muroids should

possess such characters (Hooper and Musser, 1964; Arata, 1964), and if the palaeontology tells us that the Cricetodontinae are the earliest and the more primitive muroids, they should possess complex penes and a complete number of male glands.

However, it is not easy to point to a North American cricetodontine which could be considered an undoubted sigmodontine ancestor. The most common Oligocene cricetid of North America, and at any rate, the most common North American Oligocene rodent, is obviously the cricetodontine Eumys (Wood, 1937; Alker, 1966, 1967). Although primitive in molar pattern, Eumys is rather specialized in cranial morphology, showing a heavily built skull and a deep and strong lower jaw. These characters are indicative of masticatory specializations that went well beyond the primitive masticatory apparatus of other cricetodontines (Vorontzov, 1967) and of the more generalized sigmodontines. Eumys is likely to represent a dead-line in cricetid evolution. Other Oligocene and Miocene North American cricetodontines (Leidymys, Scottimys, Schaubeomys, Paciculus) are still poorly known, and from their known features, they seem to have evolved divergently in molar structure from the generalized requirements of a sigmodontine ancestor. The Oligo-Miocene North American representatives of Paracricetodon (Alker, 1967, 1968), still poorly known, are unlikely to make better candidates for this ancestry. At least, this genus shows a primitive molar pattern compatible with oryzomyine ancestry, and it does not show any critical specialization which may preclude that possibility. Moreover, if Alker is right in placing Cotimus alikae (Black, 1961) in Paracricetodon, this genus would have had a long biochron in North America,

going from the Oligocene to the Late Miocene or Lower Pliocene. During this long span, it is not unlikely that some Paracricetodon-like derivative would have the chance to migrate to South America and to start there the sigmodontine radiation. As we have already discussed and shall discuss further later, the pattern of diversification of the Sigmodontinae suggests an old establishment of this subfamily in South America, and the starting time of their radiation could hardly be thought of as later than the early Miocene. On this ground, a Paracricetodon-like ancestry is more likely than a Copemys-like one, and the former has the advantage of not being directly connected with the peromiscine trend.

In any case, to assess that a Paracricetodon-like North American cricetodontine might be postulated as a sigmodontine ultimate ancestor, does not mean that we have unequivocally individualized this ancestor. We must be clear that at the present stage of the knowledge of the evolutionary history of the New World Cricetidae, well established ancestor-descendant sequence are not yet assessable. What is important here is that we have found that the hypothesis of an ultimate origin of the Sigmodontinae in North America is compatible with the presence in that continent at the right time of a potentially ancestral taxon.

A secondary problem which has been posed in the literature is whether the ancestral stock of the South American cricetids would be of direct North American origin, or of ultimate North American, but direct Middle American origin. Hershkovitz (1966b, 1969) has recently advocated the latter alternative. This is related to the idea of Middle America as an independent and rather isolated centre of faunal

differentiation, separated both from South and from North America by seaways during most of the Tertiary (see Hooper, 1949 : 72-73; Darlington, 1957 : 279-286). The palaeontological evidence is, however, in full contradiction with this idea, and there is no geological evidence of a northern seaway separating Middle America from North America in the Tertiary (see Patterson and Pascual, 1968 : 414). Contrariwise, all the evidence leads conclusively to demonstrate that Middle America was a tropical peninsula of North America, and a part of the Nearctic biogeographic region until the end of the Pliocene. Therefore, and at least as regards the possible distinction of North and Middle America as separate areas of potential origin of the sigmodontine ancestors, the posed problem is irrelevant. A more legitimate problem would be whether these ancestors evolved in temperate or in southern tropical areas of North America. Here again, the question only has a sense if the degree of ancestry is qualified. An ultimate North American sigmodontine ancestor was quite probably boreal, but an immediate ancestor is more likely to have been an inhabitant of the tropical Middle American North American peninsula, both by greater geographic proximity and by the tropical and sylvan character of the primitive oryzomyine sigmodontines.

But at this stage of still imprecise understanding, the speculative reasoning allows us to state another hypothesis, alternative to the North American origin. If the South American cricetids took their origin from an immigrant stock, whatever its geographical origin, it must be taken for granted that this stock should have reached the continent crossing an oceanic water barrier. The Palaeo-

geography and Palaeobiogeography of South America are conclusive in indicating that this continent was deprived of direct land connections, either with North America or with other continents, from the early Cenozoic to the Plio-Pleistocene boundary (Simpson, 1950, 1962; Harrington, 1962; Reig, 1968; Patterson and Pascual, 1968). Therefore, it may be considered if a continental area other than North America could also serve as a probable geographic source of the rafting ancestral stock of the Sigmodontinae. Cricetodontines potentially ancestors of the sigmodontines are known in the Oligo-Miocene of Europe and Asia. However, these continents are too far apart from South America, and a direct origin there must be considered as highly improbable. Australia must also be clearly ruled out for the same reason, but also by the stronger argument that it was not inhabited during the Cenozoic by any sort of rodent. There remains Africa, a continent which has been postulated by various authors as the probable place of origin of such typical South American groups of mammals as the caviomorph rodents and the ceboid monkeys (see discussion in Reig 1968).

As I have mentioned in Section 4, Africa was the theatre of an intensive cricetid radiation of its own. The pattern of diversification of the African cricetids suggests an early establishment of the family there, and derivation from a hypothetical cricetodontine stock which entered this continent by Oligocene times (Lavocat, 1959). If the cricetodontines were living in Africa in the Oligocene or early Miocene, as it seems probable, although not demonstrated by the fossil record (Cooke, 1968), they could have

reached South America by transatlantic over-sea transportation, in the same way that the caviomorphs and ceboids might have done. For such accidental arrivals, the present distance between the coasts of Africa and South America, even at their closest point, appears as a great handicap, turning extremely low the probability of a successful over-sea rafting colonization. However, it must be taken into account that the modern palaeogeographic theorizing based on plate tectonics (see Tarling and Tarling, 1971) takes for granted a Mesozoic connection between Africa and South America, a gradual separation of the two continents from the Cretaceous to the present (Myers, 1967), and a steady spreading of the intervening sea floor. Andez and Moore (1970) have recently calculated that the sea-floor spreading rate in the northern south Atlantic was of 1.6 to 2.0 cm per year. It is significant that Maxwell et al. (1970) arrived at a similar estimate, concluding that the spreading continued in the south Atlantic at essentially a constant rate of 2.0 cms per year in the past 67 million years. On the basis of these data, Keast (1972) estimated that the coast of Africa and South America at the place of their closest distance, may have been by Oligocene times only 400 Kms apart. This is not a great distance, and the probability of a successful accidental dispersal then is obviously much higher than under the present conditions. A similar argument is held by Lavocat (1969) to support the African origin of the caviomorphs.

Therefore, the hypothesis of an origin of the Sigmodontinae from an African cricetodontine ancestor emerges as a plausible one, though not necessarily as a better alternative to the North American origin hypothesis. The fate of

either of them will be dictated by new evidence to be obtained in the future, mainly from the fossil record. But at the present state of knowledge, origin from a North American ancestor is better supported by the actual occurrence in North America of a potential ancestral group, and by the broadly accepted pattern of biogeographic relations of the South American mammals. Additionally, the postulated place of the sigmodontine early radiation in northwestern South America, is in better agreement with the idea of a North American, rather than an African origin.

### 9.3. The anitquity of the South American cricetids.

The problem here to analyse is whether the South American cricetids are part of Simpson's third faunal stratum (an immigrant group of taxa of Neartic origin which invaded South America from the late Pliocene onwards, called by Reig, 1957, Plio-Pleistocene coenochron) of the history of the South American mammal faunas, or descendants of waif emigrant stock which entered this continent much earlier than the Upper Pliocene (Simpson's Stratum II). The question must be divided into two different ones, as the South American cricetids belong to two distinct taxonomic groups: the Sigmodontinae and the Peromiscineae. The latter are only represented by two or three species in South America, of a marginal distribution, and differentiated only at the subspecies level from their northern relatives. They are almost surely relatively fairly recent invaders, as advocated by Hershkovitz (1966b, 1969). The Sigmodontinae, with their outstanding endemic diversification reaching the tribal level, and their distribution over almost all the surface of the continent, make a quite different

case. It may be agreed that for most practical purposes, in the treatment of this topic by the various authors, the sigmodontines were under discussion.

As already noted, an old-established view recently restated by Vorontzov (1960, 1968) and Patterson and Pascual (1968), advocates the late Pliocene arrival of the sigmodontines into South America as part of the massive invasion of Neartic mammals which impinged southward after the establishment of the Central American land bridge. The main argument in support of this view is the absence of cricetids in the fossil mammalian faunas of South America earlier than the upper Pliocene. Recently, Hershkovitz (1966b, 1969) offered the alternative hypothesis of an earlier arrival, by Miocene times, of the ancestors of this group of rodents, which used rafting. The probable early separation of the sigmodontines and peromiscines, and the high degree of endemism and diversification of the former in South America, are the main arguments in support of this view.

The advocates of the Late Pliocene arrival hypothesis cope with the problem of the high degree of diversification of the sigmodontines by claiming either an acceleration of the rate of evolution in the rapid occupation of the abundant empty adaptive zones in the newly invaded areas, (Vorontzov, 1960; Hooper, 1949); or that much of the early diversification of the group, and the origin of their genera occurred in a postulated North American homeland, whereas the genera arriving at South America underwent not much more than an intensive process of speciation (Patterson and Pascual, 1968).



The acceleration of the evolutionary rate necessary to differentiate 41 genera and more than 180 species, not to mention the unknown number of extinct genera and species, must have been indeed exceptionally rapid. Exceptional to the extent that it could hardly be equated with the most rapid rates known in mammals. The only comparable case might be the evolution of the Arvicolidae (see Repening, 1968). But here the involved geological time span is longer, and the diversification was accomplished on a geographically much more extensive and diverse area (it occurred in the whole Holarctica). In any case, the supporters of a rapid evolutionary rate had in mind that the process was triggered by the occupation of empty niches and the wealth of opportunities in the invaded areas. The image of South America as a continent endowed with a plentiful of unexploited resources, and offering exceptional opportunities to the newcomers may be a fancy fiction herited from the times of the conquistadores, but it does not seem to match with biological facts and theoretical reasoning. Actually, most of the niches the sigmodontines occupied during their radiation in South America were not empty evolutionary spaced. The terrestrial and arboreal insectivorous niches were already occupied by small didelphids and coenolestids; the various available niches for small-sized herbivores were already occupied by octodontindas, echimids and other caviomorph rodents, small notoungulates and some metatherians. Apparently, the subterranean insectivorous niche was the only "empty" adaptive zone exploited by the cricetids in South America, and they did so only as a minor part of their whole radiation. Therefore, I do not believe that

the evolution of the sigmodontines has been favoured by special ecological opportunities. It is more likely that this process took place throughout a steady adjustment to new adaptive zones as it is the usual case in the expansion of invading groups.

Patterson and Pascual escape the difficulty of postulating an extremely rapid evolution by claiming that the Sigmodontinae only diversified in South America at the species level, and that the genera originated in Tropical North America (they admit, however, that a few genera may have originated in South America). They base this conclusion on a sweeping analysis of the distribution of the "simple penis" and "complex penis" cricetids which suggested that the former were predominantly tropical, "but with Andean elements" (1968: 444). Therefore, their genera should have diversified in tropical North America to expand into South America after the Panamanian land connection emerged, which provided to the arriving genera "with an escape hatch and well as a gateway to a great evolutionary opportunity" (op. cit.: 444). As noted above, the idea of special evolutionary opportunities is unable to stand a critical analysis. But more important, the whole argument of the tropical origin of the South American cricetid genera does not match with the known facts of their distribution. In fact, the Sigmodontinae are quite probably tropical in origin and there was the place of their first radiation, but this only holds for a part of the genera and the tribes. As discussed above, it holds for the Oryzomyini, and probably also for the Sigmodontini, the Ichthyomyini and the Wiedomyini. But the whole Akodontini and Phyllotini are quite probably

subtropical to temperate Andean in origin. For these two tribes the idea of a tropical North American origin of the genera is in full contradiction with their main pattern of distribution and adaptation. Therefore, even if we provisionally admit that origin for the first set of genera, we should have to admit an autochthonous origin of about half the number of the known living genera of complex-penis cricetids of South America, and geological time should have to be conceded for their local differentiation. Consequently, the hypothesis of the acceleration of the evolutionary rate should be re-established if an upper Pliocene time of entrance is still maintained. But the very origin of oryzomyines, ichthyomyines and sigmodonts in tropical North America is inconsistent with the known facts of diversity, distribution and fossil record. The north Andean belt is the area of major diversification of the ancestral oryzomyine group, and there is no reason to believe that the genera of this group originated elsewhere. Fossil oryzomyines are not known in the Pleistocene deposits of Mexico and Central America, which show peromyscine fossil forms. The occurrence of Sigmodon in the Late Pliocene and Pleistocene, and or Oryzomys in the Pleistocene of the United States is better explained by migration from South to North America than as a proof of the North American origin of these genera. This idea does not match the necessary timing and the pattern of relationships and diversity of the corresponding tribes. The idea of the tropical North American origin of the genera of the South American cricetids must be considered an ad hoc hypothesis unwarranted by the known facts and reasonable inference. This being the case,

.the only way to maintain the upper Pliocene arrival of the Sigmodontinae to South America, is to accept a particularly high rate of evolution.

There is a way to test the hypothesis of an upper Pliocene arrival and a speedy autochthonous diversification. If we accept this hypothesis we must predict that the fossil sigmodontines occurring in Upper Pliocene deposits of South America must be primitive and generalized forms, and that a steady progression and increasing taxonomic divergence would be observed in the successive Pleistocene faunules. In fact, the palaeontological evidence is in complete contradiction with this prediction. As we have already noted, the earliest South American cricetids found in the fossil record are the Montehermosian species Phyllotis (Auliscomys) formosus and Bolomys bonapartei. Each of them is comparable in degree of evolution to advanced living representatives of the phyllotines and akodontines, respectively. The more extensive faunule of the overlying late Pliocene Chapadmalal beds, yielded a living species of the sigmodonts (Reithrodon auritus), an advanced phyllotine (Phyllotis (Graomys) dorae) and two akodontines: one progressive fossil genus and species (Dankomys simpsoni) and a fossil species of the subgenus Abrothrix (A. kermacki) close to the living A. longipilis. Thus, the fossil record indicates that by the Upper Pliocene three progressive tribes of the Sigmodontinae, represented by living genera and subgenera, and even by a living species, were already in existence. Nothing like a primitive central stock has ever been found at what would on the hypothesis of an Upper Pliocene arrival be the very beginning of the di-

versification of this taxon. And later, in the early Pleistocene, the faunal changes observed in the succeeding strata point more to changes in the area of distribution of the intervening taxa than to a gradual development and progressive diversification of an ancestral stock. Most of the species of the middle Pleistocene, and all those of the upper Pleistocene, are inseparable from the living ones, which contradicts the idea of rapid rates of species formation.

I believe that the flat disagreement of the prediction discussed above with the facts dooms the hypothesis under scrutiny. On the contrary, in keeping with the unlikelihood of extremely rapid evolutionary rates and specially favourable evolutionary opportunities already discussed; we must conclude that the fossil record does not represent the actual antiquity of the Sigmodontinae in South America, and that their ancestral stock must have reached this continent in Early Miocene or Late Oligocene times. This dating is in rough agreement with Hershkovitz' Miocene proposal. Our arguments led us to arrive to a closer approximation.

In Section 9-1 we had concluded that the inferred evolutionary pattern of the diversity of the Sigmodontini suggested that this tribe separated from the Oryzomyini at least in the Middle Miocene, and that the separation of the Phyllotini and Akodontini probably occurred at the late Miocene or early Pliocene. Therefore, the early beginning of the diversification of the Oryzomyini, would have been an event that occurred from the latest Oligocene to the earliest Miocene. These datings provide enough time for the diversification of the subfamily to have occurred, avoiding the invocation to

the ad-hoc conjecture of an extreme acceleration of the evolutionary process.

The question arises, however, why the cricetines are not present in the rich faunas of the Miocene and early and middle Pliocene of Argentina. In opposition to Hershkovitz' claim of a Miocene antiquity, Patterson and Pascual reply that the fossil record contradicts this: "Had something like Oryzomys inhabited South America in the Miocene, cricetines (Sigmodontinae) would have appeared in deposits of that age and later.." (1968: 444). We add that this may be probable, but that it is not mandatory in view of the inherent incompleteness of the fossil record, and that fossils can only be expected to be found in the area where sigmodontines were living at the time, which was by no means the whole territory of South America. We have concluded that the main areas of evolution of the Sigmodontinae were first the northern, and later the central Andes. If this suggestion is right, the occupation of the low lands was a later event. It can be conjectured that there was at first spreading over the savannas of Colombia and Venezuela and the Amazonian basin in the early burst of the Oryzomyini and their suggested immediate pastoral descendants. This early stock could have spread to more southern lowlands later. From the central Andes, the akodontines and phyllotines spread mainly to the south following the Andean axis, to invade from there the Chacoan region, the Pampean plains and the Patagonian tablelands, probably in that order. Therefore, even when the cricetids were present in the Miocene and early to middle Pliocene at their main areas of differentiation in the northern and central Andes and their vicinity,

they would not have reached until later more southern latitudes through the Andes, and they would have invaded the lowlands of the southern cone of South America even later still. This explains why the cricetids are not present in the rich mammal bearing deposits of the Miocene of Patagonia, the Early and Middle Pliocene of the Pampean region, and also of the Lower Middle Pliocene of Catamarca, San Juan and Mendoza. Moreover, it must be stressed that knowledge of Miocene and Pliocene fossiliferous mammal deposits is almost nil in the critical areas of Bolivia, Perú, Ecuador and southern Colombia. There is a rich mammal bearing deposit in northern Colombia in La Venta, and cricetids have not been described from it. This is unexpected for our hypothesis, which would be nicely confirmed if mice occurred in La Venta fauna. But it is far from being affected by this lack of confirmation, as cricetids could be lacking in La Venta by absence of specialized collections, difficulty of preservation under particular taphonomic conditions, or sheer local absence at the time of the deposition of the sediments by ecological or microgeographic reasons.

Patterson and Pascual raised two other objections to Hershkovitz's hypothesis of a Miocene arrival. If the cricetids had inhabited South America in the Miocene and later, "the caviomorphs would not have had things all their own way during the later Tertiary, and cricetine radiation on the continent would surely have gone beyond the generic group stage" (1968: 444). The suggestion that the late Tertiary evolution of the caviomorphs could have been hampered if the cricetids would have been present in the same times in South America, involves the presupposition of competence and displacement be-

tween the two groups of rodents. This is not supported by the examination of the living fauna, which proves that caviomorphs of different families, and different kinds of sigmodontines coexist successfully under the most different environmental conditions. Moreover, the possibility of ecological incompatibility between the two groups was disregarded by Patterson and Pascual in a previous passage of the same paper, where they stressed the idea that the cricetids did not affect seriously the other families of rodents in South America, being predominantly "insinulators" that is to say, a kind of immigrant element able to move into the gap and chinks of the fauna of the penetrated area, rather than a better adapted competitor group able to displace the old-established ecologically related forms (op. cit. :442, 443). As regards the remaining objection, Patterson and Pascual had probably in mind the diversification of the Caviomorpha in different families and superfamilies from the late Oligocene ahead. But it is well known that the rates of morphological and taxonomical evolution differ from group to group of organisms. If compared to the diversification attained by the Didelphinae since the Late Cretaceous, the Sigmodontinae could be postulated as being even older than these marsupials, which is obviously absurd. Moreover, the degree of diversification attained by the Sigmodontinae in South America is in good keeping with the rates known in other members of the same group of rodents. The sigmodontine diversification, for instance, is greater than the one reached by the Peromyscinae, which are known to have started their splitting in the upper Miocene. In opposition to Patterson and Pascual, I would say that the degree of diversi-



fication attained by the South American cricetids, is not a handicap, but supports the idea of an early Miocene antiquity of these rodents in that continent.

Therefore, all the arguments led to support the hypothesis of an old establishment and of an autochthonous diversification of the Sigmodontinae, from a late Oligocene or early Miocene immigrant stock, probably of North American origin.

10. CONCLUSIONS.

In Sections 4, 7 and 8 we have dealt with an analysis of the systematic, palaeontological and biostratigraphic evidence bearing upon the problems of the evolutionary history of the South American cricetids as stated in Section 2. Sections 5 and 6 were necessary to elucidate matters of nomenclature, method and geochronological time-scale previous to this analysis. Finally, in Section 9 we have discussed the analyzed data and previous interpretations, to arrive to a general explanation of the major events of the evolutionary history of the Sigmodontinae. We included in this explanation a testing of the opposing views on the origin and antiquity of these rodents, but we also attempted a more detailed account of the main aspects of the process. It is time now to summarize our conclusions.

The discussion of the major classification of the muroids and of the place of the South American cricetids in the system of this superfamily, led us to a reassessment of the hierarchical ranking of the various groups of the Cricetidae. It was concluded that the typical South American cricetids belong to a subfamily of their own, the Sigmodontinae. This subfamily is clearly distinct as regards their North American relatives (the Peromyscinae), the Eurasiatic cricetids (the Cricetinae) and the Oligo-Miocene fossil Cricetodontinae. The Sigmodontinae are diversified in the living South American fauna in forty-one genera and about 186 species. The pattern of relationships among their genera leads to their grouping in seven different distinct and cohesive tribes, each of which is postulated as a monophyletic group which experienc-

ed a particular radiation in the exploitation of a given main resource zone.

The data of the comparative anatomy, the comparison with known phylogenies in other cricetids, and inferences from the ecological and evolutionary body of theory, suggest a main pattern of evolution within the Sigmodontinae. This is likely to have started from generalized, ecologically plastic, omnivorous-insectivorous forest dwellers with brachyodont and bunolophodont molars. The Oryzomyines are the group involved here. From the oryzomyines the evolution proceeded to more progressive forms which resulted of a more specialized exploitation of various resource zones: small terrestrial insectivorous predators and subterranean insectivorous inhabitants of pastoral habitats (Akodontini), aquatic, fish-eating forest dwellers (Ichthyomyini), small to medium sized pastoral herbivores (Sigmodontini), or omnivorous-herbivorous to fully herbivorous inhabitants of pastoral habitats (Phyllotini). The Scapteromyini represent both the semiaquatic insectivorous (Scapteromys) and the fossorial-herbivorous (Kunsia) adaptations. Members of the here proposed new tribe Wiedomyini are still poorly known in adaptive type, but they seem to represent an early insectivorous radiation.

The pattern of distribution and diversity of the various tribes suggests that the evolution of the subfamily was a stepwise process, both in time and in space. The generalized oryzomyines were the ancestral group of the whole radiation, and at the same time their evolution is still at a flourishing stage, as demonstrated by the high number of living species. The Sigmodontini, the Ichthyomyini, and probably also the

Wiedomyini, are likely to have been early offshoots of the oryzomyine stem. These four tribes represent an early and pervasive radiation, which the data of the present distribution suggest to have taken place from a north Andean genocentre. The Sigmodontini have been the first pastoral and fully herbivorous South American cricetids, and the advanced distinctiveness of their four known genera, together with the known antiquity of two of them, is taken as an indication that they were more flourishing and diverse in the past. The Akodontini and the Phyllotini show a present distribution suggestive of diversification from a central Andean genocentre. The former are quite likely direct oryzomyine derivatives, which evolved as more specialized insectivores. The latter quite probably took their origin from the Akodontini, or they might have shared with them a common oryzomyine ancestor, evolving as increasingly herbivorous forms. This two more advanced and greatly polytypic tribes are postulated to represent a second and more southern Andean radiation which is still on an ongoing stage. The Scapteromyini are likely to represent a later and minor radiation of their own, probably from a Chacoan or Pampean genocentre.

Although an undoubted ancestral stock has not yet been fully individualized, the still inconclusive available evidence bolsters the hypothesis that the ancestry of the Sigmodontinae is to be sought among the Oligocene Cricetodontinae of North America. An unspecialized cricetodontine as Paracricetodon, could have become a potential ancestral Sigmodontinae in the tropical forests of southern North America, and it might have reached the north western

coasts of South America by over water dispersal. The alternative hypothesis of an origin from an African cricetodontine stock is also plausible, specially when it is taken into account that by Oligocene times the coasts of Africa and South America were not so far apart as to make the success of an overwater dispersal quite unlikely. However, this hypothesis seems to be less probable than the hypothesis of a North American origin.

The time of arrival of the ancestral sigmodontine stock to South America could hardly be later than the lower-most Miocene. This dating is required by the necessary timing of the complexive and stepwise radiation of the subfamily in the continent, by the advanced character of the known upper Pliocene and early Pleistocene fossils, and also by the antiquity of the postulated ancestral group in North America.

The first arrivals experienced a fairly wide radiation during early and middle Miocene times in north western South America. This radiation was probably triggered by the high ecological diversity and the dynamic relief of the Andean chains. Most of the genera of the Oryzomyini could have evolved then, and the Sigmodontini and Ichthyomyine could have started then their differentiation as ecological specialists. During Miocene and Pliocene times, some of the taxa resulted from this first differentiation gained, by a reversed over water dispersal, the tropical southern peninsula of North America. Nyctomys, Otonyctomys, Sigmodon and the Oryzomys palustris group, are probably representatives of this migration. Other taxa reached the West Indies

(Megalomys) and Galapagos (Nesoryzomys). Members of an oryzomyine population which invaded open lands or paramos of the Andes, may have reached in their southward expansion, the central Andes by late Miocene or early Pliocene times, becoming the founder populations of the Akodontini and the Phyllotini. These taxa radiated as complementary ecological specialists in the Central Andes, and later expanded, mostly southward, throughout the Andean region to reach southern Chile and Argentina. The occupation of the eastern low lands (Chaco, Pampas and Patagonia) must have been a later event, which started probably in the middle Pliocene and was complemented by the expansive wave of a few oryzomyines (subgenus Oligoryzomys) and to a lesser extent, subgenus Oecomys and genus Nectomys and Thomasomys) and the sigmodont Reithrodon. As documented in the fossil record, the occupation of the south eastern Pampean region by akodontines, phyllotines and Reithrodon started in the upper Pliocene. Scapteromyines, Oryzomyines (Nectomys) and wiedomyines arrived there later, by the early and middle Pleistocene. The phyllotines did not expand in the Andean region northward beyond north of Perú and south of Ecuador, but one group of species of Akodon (the Akodon urichi group) reached far to the north and established in the Andes of Colombia and Venezuela, the coastal ranges of Venezuela and the table lands of the Orinoco region. Zygodontomys, if it is really a phyllotine and not a direct derivative of the oryzomyines, should be considered an early northern immigrant of the phyllotine stock, which invaded the savannas of northern South America.

Once the Panamian land bridge was established,

an exchange of cricetids took place between South and Middle America. The northern peromyscines Aporodon, Tylomys and perhaps also Peromyscus, occupied marginal areas in north western South America. Probably also Sigmodon reached the continent with them. At the same time, various oryzomyines (Oryzomys, Neacomys, Nectomys, Rhipidomys), Zygodontomys and the ichthyomyine Rheomys, reached Middle America. Most of the invaders did not evolve beyond the subspecies level.

Therefore, the diversification of the Sigmodontinae appears as a fully South American phenomenon, and their genera and tribes (with the dubious case of Sigmodon as a probable exception) are autochthonous on this continent. They must be considered as waif immigrants of South America, in the same category of the caviomorph rodents and the platyrrhine primates among the mammals, or the testudinid chelonians among reptiles. Therefore, they are a rather old component of the South American fauna, and their evolution can be explained without invoking any kind of special evolutionary processes or circumstances, as an unusual acceleration of the rate of evolution or an explosive burst in newly available empty niches. They evolved at horotelic rates and in the steady process of their adaptive diversification they invaded gradually new resource zones and new geographic areas from the north to the south and from the Andean range to the eastern plains. Their sudden appearance in the fossil record of the Pampean region in the Upper Pliocene, and their absence in the Miocene of Patagonia and Early and Middle Pliocene of the Pampean and sub Andine regions, is not only compatible with this explanation, but it is also supporting evidence for this hypothesis.

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