TT70-53092

EVOLUTION OF THE ALIMENTARY SYSTEM IN MYOMORPH RODENTS

N.N. VORONTSOV

TRANSLATED FROM RUSSIAN

Published for the Smithsonian Institution and the National Science
Foundation, Washington, D.C. by the Indian National Scientific
Documentation Centre, New Delhi.

1979

EVOLUTION OF THE ALIMENTARY SYSTEM IN MYOMORPH RODENTS

TT70-53092

EVOLUTION OF THE ALIMENTARY SYSTEM IN MYOMORPH RODENTS

(Evolyutsiya Pishchevari tel'noi Sistemy Gryzunov Mysheobraznye).

N.N. VORONTSOV

Izdatel'stvo "Nauka", Sibirskoe Otdelenie, Novsibirsk, 1967

TRANSLATED FROM RUSSIAN

Published for the Smithsonian Institution and the National Science Foundation, Washington, D.C. by the Indian National Scientific Documentation Centre, New Delhi.

1979

Contract NSF-C466

Available from the
U.S. Department of Commerce
National Technical Information Service
Springfield, Va. 22161

Translated and Published for the Smithsonian Institution in Accordance with the Agreement with the National Science Foundation, Washington, D.C. by the Indian National Scientific Documentation Centre, Hillside Road, New Delhi - 110012, India.

Translated, Printed and Published by INSDOC, New Delhi 110 012

DEDICATION

In memory of dear
Yuri Alexandrovich Orlov

CONTENTS

SPECIAL PART

PREFACE

This work is intended for specialists in the field of mammalian taxonomy, ecology, comparative anatomy and paleontology. The extensive material drawn for study, also yielded the possibility of arriving at certain general laws of evolution. Special attention is paid to two problems: first to homology, parallelism and convergence in the structure of the rodent alimentary system, evaluation of the applicability of N.I. Vavilov's law of homologous series of inherited variability to supergeneric taxa and secondly, to the problem of biological coordinations, unequal rates of organic transformation in one functionally-bound system and substantiation of the principle of "compensation of functions" This second aspect of the general biological part of this book is ideologically connected with the studies of I.I. Schmalhauzen. It seems that certain general biological problems discussed in this book may be of specific interest not only to theriologists, but also to biologists with other specialized interests in the problems of evolution.

In the course of his work on morphology and phylogeny of rodents, the author has summed up the concepts on the conditions required for any ecological morphological, comparative anatomical and phylogenetic studies.

1. Phylogenetically allied groups of forms as a whole should be taken for the purpose of study. In this work the subfamily Cricetinae, the largest subfamily of mammals is studied taking the world fauna as a whole.

2. For explaining the degree of affinity, and the reasons for the development of one or other characters, and for the disparity in the instances of parallelism in development and convergence, it is advisable to study the trend of evolution in the strains allied to the group being studied. In this work repre-

sentatives of the groups of Madagascar rodents (Nesomyinae), gerbils, (Gerbillinae), voles (Microtinae), sokhors (Myospalacinae) and lophiomys (Lophiomyidae) are studied in full detail. The structures of the alimentary system in some members of mice (Muridae), dormice (Myoxidae), jerboas (Dipodidae), mole rats (Spalacidae), bamboo rats (Rhizomyidae) and representatives of other rodent orders (viz, gophers (Geomyidae) and African sand rats and mole rats (Bathyergidae) are studied as examples of parallel and convergent groups.

3. It is highly desirable to make use of the method of "ternary parallelism" for revealing the history of development of one or other characters: This method, recommended from the time of E. Heckel in all text books, is very rarely used owing to methodological difficulties and limited data.

The basic method employed in this work was comparative anatomy. Wherever possible, the paleontological method is also used and in controversial cases (proof for the secondary development of an insectivorous type in <u>Onychomys</u>, etc) even the embryological method of study is used for building a phylogenetic group system. The phylogenetic system cannot be formed on the basis of the study of the structure or the transformations of individual characters in ecological morphological, comparative anatomical or the phylogenetic series.

As this work is confined only to a review of the evolution of digestive organs, the data on the position of any group in the system of rodents contained in this book should be considered only as data for building the system of rodents.

The conditions necessary for the phylogenetic study mentioned above may be fulfilled to some extent, because the author had at his disposal more extensive material than the previous research workers.

Rodents from the collections of the Zoological Institute, Acad Sc., USSR at Leningrad and the Zoological Museum of the Moscow State University have provided specimens for morphological studies. The fossil materials are described from the collection of the Paleontology Institute, Acad. Sc. USSR, at Moscow and Geological Paleontological Museum in the names of A.P. Pavlov and M. V. Pavlov of the Moscow Institute of Geological Exploration.

South African specimens were furnished by Dr. D. Davis (Plague Research Laboratory, Johannesburg), Madagascar specimens by Prof. R. Mathey (Laboratorie de Zoologie et d' Anatomie comparie, Universite de Lausanne) South American specimens by Prof. Fr. Petter (Fr. Fetter, Museum National d'Histoire Naturelle, Laboratoire des mammiferes et oiseaux, Paris), U.S. and Mexican specimens by E. Hooper (E T. Hooper. Museum of Natural History, University of Michigan, Ann Arbor), Brazilian specimens by Dr. Carvalho (C.T. Carvalho, Departments de Zoologia, Sao Paulo), P. South and Central American specimens by Prof. P. Hershkovitz (Ph. Hershkovitz, Chicago Natural History Museum) and South European specimens by Prof. K. Zimmerman (Kl. Zimmermann, Institut fur spezielle Zoologie - und Zoologisches Museum der Humboldt-Universitat Zu Berlin). The list of species studied has lengthened considerably thanks to the assistance of these foreign zoologists. The author takes this opportunity to convey his deep gratitude to them.

Starting in this manner the author has tried to study the maximum number of species of closely allied groups, to get an idea of adaptive evolution of the entire group and not only the comparative morphology of a random group of species, limited by the size of such an extensive administrative territory as our country. The structure of the digestive system of more than 300 species of rodents belonging to 19 subfamilies was studied. In the study of most of the organs of the digestive system, the descriptions are not uniformly detailed, owing to the large number of objects of study. In the absence of data on the histology of the alimentary tract it is easy to criticize the author on the ground that the problems of homology of the dental system are dealt with largely on the basis of topographic and not embryological analyses. However, from the evolutionary point of view, the study of a wide collection of species has specific advantages over comparative, anatomical, histological and embryological analyses of some species. For that reason, the author is indebted to B.S. Vinogradov, V.G. Heptner and N.V. Shibanov, who have awakened his interest in the world fauna. So the study of groups is considered as an essential prerequisite for phylogenetic and systematic studies.

Some sections were discussed with N.K. Vereshchagin, B.S. Vinogradov, L.V. Ganeshina, V.G. Heptner, I.M. Gromov, A.N. Druzhinin, N.I. Kalabukov, V.V. Kucheruk, Yu.A. Labas, B.S. Matveev, P.P. Strelkov, V.B. Sukhanov, K.K. Flerov, V.I.

Tsalkin, I.I. Schmalhauzen, K.A. Yudin and A.V. Yablokov. Their advice and remarks, made at various stages of completion of this work, were very valuable.

Work on this monograph was begun in the Mammalian Laboratory of the Zoological Institute, Acad. Sci. USSR nearly completed in 1961, completed and revised at Novosibirsk in the Department of Evolution and Karyosystematics of the Institute of Cytology and Genetics affiliated with the Siberian Branch of the Acad. of Sciences, USSR.

INTRODUCTION

The type and composition of nutrition as well as the methods for assimilating food reserves define the role of a species within a community. Ecologists have already recognized the relationship between the type of nutrition and the basic ecological features of rodents: viz., the size of the individual portions, mobility, nocturnal activity, reproduction and numerical dynamics of population. They have also discovered the basic laws linking the type of nutrition of the species to its important ecological features (Elton, 1942 Voronov, 1947 and Naumov, 1948). Nutrition and evolution of food specialization is one of the most important problems of ecology. The considerable progress that ecologists have made in the study of nutritional specialization, has been hampered by the nonavailability of elementary information on the morphology of the digestive system.

The relationship between the type of nutrition and the structure of rodents has been studied, generally based on heterogeneous data at times related neither genetically nor ecologically (Luppa, 1956, 1958 b; Velichko, 1939a, 1939b; Velichko and Mokeeva, 1949, Kulaeva, 1956; Nazarova, 1958, etc.). Often, only the individual portions of the digestive system were studied. These limited studies have been of little value in determining the evolution of the entire system of relevant organs. As a break from ecology, as well as from the morphology of other organs of the digestive system, a monograph devoted to the comparative morphological description of the dental system of rodents was made by Stehlin and Schaub (1950).

Against this background Tullberg's (1899) classical monograph devoted to the problems of the system and phylogenesis of rodents, remains, the best and unsurpassed study to date on the structure of the digestive system of rodents. This monograph unique in all respects, is the only work, wherein all the organs of the digestive system are studied together. However, Tullberg was primarily interested in the problems of phylogenesis and the system of large taxa from family and above, in other words, in the problems of megaevolution. Hence the problems of adaptive evolution and adaptive radiation within the families, subfamilies and genera were not studied by Tullberg. It is doubtful that these problems could even have been raised at a time when very little was known of the ecology of rodents, physiology of digestion and even evolutionary morphology was not yet brought to a new level by the studies of A.N. Severtsov and P.P. Sushkin. The question of biological coordination was raised only in the thirties by I.I. Schmalhausen. N.I. Vavilov's Law of homologous series of inherited variability (mostly on plants) was adopted at the same time.

It was necessary to depend on ecological and physiological studies, for solving the problems of adaptive evolution of the digestive system, the problems in establishing the homology and parallelism in development, and the presence or absence of biological coordination. A series of ecological works by N.P. Naumov (1948), deserves the first mention, helping to establish a close relation between all aspects of the biology of rodents (including even such phenomenon as the variation in number which is important for man) and the exact type of nutrition.

A number of ecological studies on the nutrition of rodents, summarized by A.G. Voronov (1947) and N.P. Naumov (1948) saves the author from the unavoidable discussion of the traditional "ecological description" to the comparative anatomical part of this work. The required references on works devoted to the nutrition of one or more forms are given in the text in the appropriate portions of the book.

A special chapter in the recent report of A.D. Slonim (1962) is devoted to the physiology of digestion in mammals. Hence the physiological survey antecedent to the corresponding chapters of this work is also reduced to the minimum.

Thus, a study of the problems of adaptive evolution of the digestive system logically results, from the works of the comparative anatomical school of thinking of A.N. Severtsov, P.P. Sushkin, and I.I. Schmalhausen, and the evolutionary school of thinking of N.I. Vavilov mainly of the thirties and also from the works of ecologists and ecological physiologists of the forties and fifties. Finally, the recent achievements in the fields of genetics and molecular biology made in the early sixties, enable us to use a new approach to the interpretation of the problems of homological variability, polyphyly and reversibility of evolution.

SPECIAL PART

CHAPTER I

MECHANISM OF MASTICATORY MOVEMENTS AND EVOLUTION OF MAXILLARY APPARATUS

The structure of the skull, masticatory muscles, and teeth is determined by the general structural plan, depending upon the gene stock of the given group and by the adaptability to the processing of one or more food materials. The mechanism of masticatory movements and some rules of transformation of the maxillary apparatus and skull in rodents have been analyzed in earlier investigations (Vorontsov, 1961b, 1963d; Vorontsov and Labas, in litt).

I. Structure and Function of the Masticatory Muscles

The principal structural features of the masticatory muscles are common for the entire superfamily, Muroidea. A unified structural plan of the masticatory apparatus characterizes all members of this most extensive group of mammals. But, within the general structural plan, the adaptive characteristics of the different types of nutrition are so different that they may radically change the functional importance of some muscles.

The muscles of maxillary apparatus in Muroidea rodents perform the following functions:

1. M. digastricus abducts the lower jaw and opens the mouth.

2. M. transversus mandibulae to some extent pushes the halves of the jaws and sets the lower incisor. Perhaps, it acts simultaneously with m. pterygoideus externus and m. pterygoideus internus.

3. M. masseter lateralis (see Figs. 5 and 7), on the whole adducts and partly moves the lower jaw forward. The

functions of individual segments of this muscle change significantly depending on the adaptations to various types of nutrition.

a) The para anterior mainly moves the lower jaw forward. In the carnivorous and seed-eating forms and in those burrowing by incisor, it participates also in adducting the lower jaw. In the seed-eating forms, including all voles (Microtinae), it practically loses the function of adducting the jaw, and simply takes part in longitudinal frontal displacement of the lower jaw. On transition from a lipo-protein to a cellulose type of nutrition, this portion strengthens (and the point of attachment changes). The basic function is longitudinal grinding.

b) The para posterior adducts and partly moves the mandible. forward. With various types of nutrition it does not undergo significant transformation in the ecological morphological series of Muroidea. The main function is crushing of seeds and gnawing, i.e., adduction of the lower jaw.

c) In the wild, seed-eating forms, and forms burrowing with incisors, the pars profundus along with p. anterior of m. masseter medialis mainly participates in adducting the lower jaw and barely moves it forward. In the forms having cellulose type of nutrition, it not only adducts the lower jaw, but also moves it forward. The function is gripping and grawing.

4. M. masseter medialis depresses and partly moves the lower jaw forward.

a) The pars anterior adducts and barely moves the lower jaw forward. The main function is gnawing and crushing seeds. On transition from a protein-lipoid to a cellulose type of nutrition, its function does not change, but the size is greatly reduced (see Fig. 5).

b) The pars posterior adducts and pushes the lower jaw partly back. In function it resembles m. temporalis.

5. M temporalis adducts and pushes the lower jaw, partly back, bringing the articular head into the rear part of the articular surface.

6. M. pterygoideus consists of (see Fig. 4) two independent muscles with different functions Both the pterygoideus muscles push to a certain extent the rami of the lower jaw.

a) M. pterygoideus externus' main function is the contraction of the halves of the lower jaw, i.e., transverse grinding movements; pushing the lower series of molar teeth inside in relation to the upper one; along with m. transversus mandibulae it sets the lower incisors. In voles and zokhors (Myospalacinae), it removes the articular head from the articular pit participating in the preparation of gnawing movements, and partly moves the jaw forward.

b) M. pterygoideus internus pulls the corner part of the jaw inside and slightly forward and up; during this the upper portion of the mandible with the lower row of molar teeth is pushed externally with respect to the upper row of the molar, thereby participating in the transverse grinding movements. In the voles and zokhors this muscle takes part in moving the lower jaw forward, i.e. in a longitudinal grinding movement.

2. Mechanism and Types of Masticatory Movements in Rodents

The type of masticatory movements and the structure of grinding surfaces are vitally important for the structure of the cranium and teeth since these mainly determine the structure and shape of cranium.

During the processing of food the mandible performs complicated movements. The mandibular joint of rodents, possessing three degrees of freedom causes simultaneous movement in three interperpendicular directions. Composed of two interperpendicular harmonic oscillatory movements of various frequencies gives the trajectory of the movement in the shape of an ellipse, an eight, a double eight and more complicated figures. Very complicated trajectories corresponding to the movements of the lower jaw are formed by the three interperpendicularly directed harmonic oscillating movements. Any type of full movement can be conditionally broken into its components. It is quite permissible and very convenient to consider these components separately. The general scheme of the types of lower jaw movements during the processing of food could not be found in the literature, though references on the prevalence of one or the other type of masticatory movements are made very often (Tullberg, 1899, Hinton, 1926; Vinogradov, 1926; Ognev, 1940, 1947, 1948, 1950; Romer, 1938; Lebedkina, 1949).

Morphological analysis helps distinguish the following types of masticatory movements of the lower jaw :

1. Gnawing-adduction of lower jaw connected with the working of incisors on cracking nuts, seeds, holding and biting of food, primary processing of twigged feed and digging by incisors. Mainly m. pterygoideus externus, p. posterior and p. profundus m. masseter lateralis, and also (in seed-eating forms) p. anterior m. masseter lateralis (in voles this muscle mainly works during longitudinal grinding) take part in these movements. The oscillatory movements of the lower jaw in the vertical plane around the relatively fixed axis of the articulation of lower jaw with skull predominate in this type.

Vinogradov (1926) has described in detail some special adaptations of the maxillary apparatus of Rodentia relating to the gnawing movements of the jaw, abducted forward. Meanwhile, the gnawing movements of Rodentia take place in the front as well as in the rear position; few having a fixed axis of maxillary lever.

The fixation of the axis of the maxillary lever is important for the gnawing type of movements. This fixation is accomplished in Carnivora (gripping type, resembling the gnawing type at the rear portion of the jaw) by the hinge articulation of the jaw with the skull and in the majority of rodents, by the stress of the articulated head in fossa condyloidea. The processuss articularis, directed backward, takes a more horizontal position. Its articulated head assumes a vertical position and the articulated pit is displaced. This process of displacement of the articulated head is most prominent when comparing the structure of the lower jaws of piscivorous hamster (Ichthyomys), for which the process helping in prey catching is of much importance to the ordinary hamster (Cricetus) and herbivorous hamster (Neotoma) (Fig. 1).

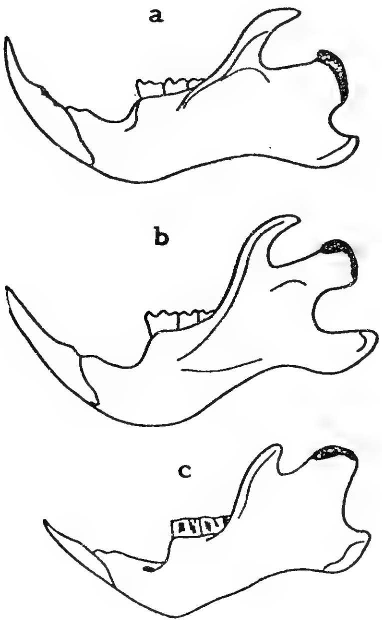


Fig. 1: *Position of the articular process and articular head. Left rami of the lower jaws, lateral view (Orig). (a) Ichthyomys soderstromi de Winton (gnawing-gripping type), (b) Cricetus cricetus L. (Intermediate type with nearly equal development of gnawing-crushing and grinding movements); (c) Neotoma cinerea Ord. (grinding type).*

Special adaptations for the axial attachment of the maxillary lever on gnawing are described earlier (Vorontsov 1963). The article states that the functions of gnawing and grinding are independent of each other in the various groups of rodents.

2. The crushing of seeds basically resembles gnawing by groups of operating muscles, since all the muscles adducting the jaw are in action during this. Besides, there are slightly circular, 8-shaped movements in the horizontal plane owing to the contraction of m. pterygoideus internus in transversus mandibulae, p. anterior, m. masseter lateralis and m. temporalis.

Crushing movements of the jaw are observed while bunodont rodents feed on seeds. Crushing movements combine with gnawing since during crushing (as during gnawing) the angle of deviation of the lower jaw from the position obtained when the molars are touching, is of importance; the magnitude of this angle is defined as the moment of force M_1 at the end of the lower incisor on gnawing and the moment of forces M_2, M_3 and M_n on every tubercle of the lower molar teeth. During crushing movements also, the axis - i.e., the articulation of the jaw with skull remains slightly mobile. The process of grain crushing combines with the adduction of the jaw and its insignificant displacement in the horizontal plane.

3. Grinding in transverse direction is effected by the alternate contraction of the pterygoid muscles and m. transversus mandibulae.

Grinding movements in transverse direction develop in the seed-eating and very rarely, in the herbivorous forms. According to Ognev (1940), the food of Duplicidentata, unlike other rodents, is ground only in the transverse direction, and in herbivorous forms including the crushing type grinding movements are mainly in transverse direction. Tullberg (1899) noticed circular movements of lower jaw in all members of Sciuromorpha.

Advantages of transverse movements of jaw for seed eating forms may be clearly explained thus: as it was shown (Vorontsov, 1963) that the gnawing-crushing movements of bunodonts are related to the fixation of the lever, where the axis is the articulation of jaw with skull; the axis remains undisturbed during transverse movements of the lower jaw, and grinding movements are accomplished in transverse direction simultaneously with gnawing and crushing movements. In herbivorous forms, grinding movements in transverse direction usually play an insignificant role while backward and forward grinding movements play an important role.

Exceptional types of rodents are those which burrow with incisors for which the axial fixation of maxillary lever is of special significance. They grind in transverse direction though they mainly feed on cellulose. Therefore the width of molar teeth increases so much that it may be equal to the length of each tooth (*Spalax*, *Rhizomys*, *Techyoryctes*, *Brachyuromys ramirohitra*). The enamel crests of molar change from transverse (Spalax) to an inclined position (*Rhizomys*) and, finally, to a position almost along the axis of the dental rows (Brachyuryetes, Brachyuromys ramirohitra). As the transverse movements of lower jaw are dominant the form of articulated head becomes spherical. This can be clearly traced among the Madagascan Cricetid Nesomyinae from Macrotarsomys to Brachyuromys ramirohitra (Vorontsov, 1963d).

Since the function of the third (rear) molars does not diminish while grinding in transverse direction, as observed in the forms having predominantly longitudinal movements of jaw, M^3 and M_3 are never reduced in such rodents, but are equal in size if not bigger than the two primary molars. This can very clearly be illustrated by comparing the teeth of two allied genera of Madagascan cricetid Nesomyinae. One of them (Brachytarsomys) is adapted to processing the cellulose food by longitudinal movements of the jaw (the first molars are elongated and the last ones are short, the teeth themselves are narrow and the enamel crests are transversely arranged) and the other (Brachyuromys ramirohitra) - mainly by transverse movements; thus the length of each tooth does not exceed its width, the width increases and the enamel crests are turned along the cranial axis. (See Figs 75 and 76).

The grinding movements in transverse direction are predominant and the width of the molars are more or less equal to their length not only in Myomorpha, but also in beaver, porcupines, coypu, in which the gnawing movements are much extended on processing the twig feed or digging of holes. In Hystricidae the enamel crests are arranged transversely as well as obliquely and almost longitudinally.

4. Grinding in the longitudinal direction is mainly accomplished by p. anterior, m. masseter lateralis (forward motion of the jaw) and m. temporalis (backward motion of the jaw). Grinding movements in the longitudinal direction is predominant in herbivorous forms. As shown by Tullberg, 1899, the processing of food in Murinae, takes place by longitudinal and lateral movements of the lower jaw and in Microtinae (Tullberg 1899; Hinton, 1926; Ognev, 1950) the mandible moves only longitudinally.

As shown by H.S. Lebedkina (1949), only the longitudinal forward movement can be considered as the operational movement of masticatory muscles during the working of molars in voles. Nevertheless, the grinding movements in longitudinal direction is always associated with similar movements in transverse direction. The less prevalence of the transverse-grinding movements in herbivorous animals can be explained as follows. In voles, food is processed directly by the enamel crests, dentinal areas do not actually take part in processing food. The grinding of food by molar teeth of voles in fact reduces to cutting and breaking of the plant parts by the enamel crests (Lebedkina, 1949). In this respect it is similar to the primary processing of food by incisors and can be compared with the working of a grater. That is why in forms whose food contains vegetative parts of plants (Andinomys, Neotoma, Microtus, Lemmus) the length of enamel crests increases because of the wide angle of the enamel prisms, the increase (transverse) of width and the decrease (longitudinal) of the length of the prisms.

The displacement should not be too large or too small during the forward movement of jaw. The greater the displacement, the greater the number of intersecting enamel crests involved in grinding of food (Lebedkina, 1949). But when the displacement of the lower jaw is considerable ;the number of intersecting enamel crests again decreases and a significant part of the displacement of lower jaw may become idle. Since there is a very small displacement, the frequency of longitudinal movements of the lower jaw should increase for compensating the slight grinding action resulting from the fewer number of intersecting enamel crests involved. Thus, it is clear that the transformation of the dental system in series from seed-eating hamsters to herbivorous hamsters and to voles, should bring about a general increase in the relative length of the dental row, and an increase in the number of the enamel crests and decrease in the longitudinal width of the enamel prisms. An increase in the angle of prisms, a general increase in the length of enamel crests and also transformation of teeth from tubercular to flat-crowned types and replacement of brachydont by hypsodont teeth would also result.

With the small width of the teeth, the transverse displacement already small in absolute value, may cause idle motion and an increase in the frequency of oscillatory movements of jaw becomes limited.

During the longitudinal movements of jaw, the significant (in absolute value) displacement will be, however, less than one half or two thirds of the length of the molars. Thus we will get the average amplitude and frequency of the oscillatory movements which will give the maximum work, in unit time with the minimum force.

Predominance of any type of movements leads to corresponding changes in the structure of the jaw. So, two types of motion of the lower jaw in processing food seem to be very important for voles, namely, longitudinal grinding and gnawing. The length of the cutting edge of molar teeth increases in the species having a predominantly longitudinal grinding movement by means of their elongation (*Clethrionomys rufocanus*), wide angle of the enamel prisms (*Midrotus*, *Lemmus*, *Myopus*), and an increase in the number of the loops of molars (*Microtus agrestis*, *M. socialis paradoxus*). Also the transition from the brachyodont to hypsodont teeth is observed (*Cl. rufocanus*-*Microt*) and diastema is short because of an increase in the length of the dental row (excluding highly specialized forms such as muskrats). In species having jaws where the grinding movement is predominant, the rows of molars are somewhat short, diastema increases in length, alveolar projection of the lower incisor approaches the articular head of the lower jaw (*Ellobius*) and the lower part itself is elongated.

The length of M^1 increases, along with the general increase in the length of the dental row in forms having a longitudinal - grinding movement where M^3 is generally many times shorter in them.

This is fully understood since, when the frontal advancement of the jaw is insignificant, the main food falls on M^1, while M^3 is cut off from the action.

Strictly speaking, the process of crushing seeds and any such hard matter occurs not only with the contraction of the lower and the upper dental rows, but also when the displacement is small with respect to one another by the rotary movements. It is appropriate to compare the process of crushing food with the pounding of grain in a mortar where the process is accomplished by the pressure of the pestle (similar to the tubercle of the tooth) as well as by the rotary movements in the mortar. However, grains can be broken, in a mortar but cannot be ground; a grater is necessary for grinding. While reducing the food substance into smaller bits on the grater, the pressure on the grinding object plays a subordinate role in comparison with its displacement with respect to the rubbing crests of the grater. The same is the case when the food is processed by longitudinal-grinding movements in Microtinae and some specialized Cricetinae (Andinomys, Neotoma).

The longitudinal (one row) or longitudinal transverse (two-three row) arrangement of the roots of the teeth correspond to the direction of the movements of the lower jaw. It is interesting that in Murinae, in which longitudinal and transverse movements are well developed the roots of the teeth are arranged in transverse as well as in a longitudinal direction. On cheek-toothed voles, the roots of the molars have been arranged longitudinally. Even when an additional third root appears in Clethrianomys, it is arranged on the longitudinal plane only.

The shape and the position of the articular head is of great significance for some movements of the lower jaw. Free displacement of the articular head of the lower jaw in the longitudinal direction along the fossa condyloidea is important for the grinding type of movement. This is achieved by the relatively vertical direction of the articular process and the horizontal position of the articular head on it. This is accomplished by a sufficient advancement of the mandibular row with respect to the maxillary row having a considerable length of the dental rows in the species where the grinding movements in the longitudinal direction are predominant. The process of displacement of the articular head is clearly seen by comparing the cheek-toothed and hypsodont voles (Vorontsov, 1961b).

5. A fifth type of jaw movement may also be observed namely, the type of separated scissors.

In seed-eaters the halves of the lower jaw, loosely connected between themselves, form the levers of the first order facilitating the cracking of nuts. The anterior ends of the mandibles are separated with the contraction of m. transversus mandibulae, m. ptergoideus externus, and m. pterygoideus internus. This type of movement is not discussed here since it does not play an important role in the evolution of the skull of rodents belonging to the family Muridae.

3. Functions of the Mastication organs of Rodents

It was shown in earlier investigations (Vorontsov, 1961b, 1962a, 1962b, 1973d) that in the seed-eating forms, the main type of movement is the movement of the jaw in the vertical plane (gnawing and crushing of seeds by the tubercles of molars); whereas, in the herbivorous forms the main movements are associated with grinding, i.e., the movements of the jaw in the horizontal plane in to-and fro directions. The process of the division of the functions of gnawing and grinding (Vorontsov, 1962a) goes on independently in different groups. The grinding movements in the transverse direction are developed mostly in the seed-eating and rarely in the herbivorous rodents. The grinding movements in the longitudinal direction prevail in the herbivorous form except in the species which burrow with incisors. The change in the points of attachment of P. anterior and M. masseter laterlis on the mandible results in a marked development of the grinding movements in the longitudinal direction from the seed-eating rodents to the herbivorous voles (Vorontsov, 1962a).

Even in 1899 Tullberg had assumed that the circular grinding movements was predominant in Murinae and longitudinal grinding, in Microtinae.

However, the functional consideration on the biomechanics of the maxillary apparatus of rodents was described on the basis of comparative anatomical study, unconfirmed by the data of the specific physiological experiment. Only recently, U.A. Labas developed a method of recording the masticatory movements (mastication graph) of rodents in the laboratory of A.D.Slonim, with the help of Holl's sensor device and magnet activated in the lower jaw (Slonim, 1962, Labas 1963a).

The mechanical processing of food in practically all the species under investigation, consists of consecutive stages of gnawing and grinding which continuously alternate while eating (Labas, 1963b; Vorontsov and Labas, in litt). While gnawing, the lower jaw moves in the longitudinally vertical plane, and while grinding, the main movements are on the horizontal plane including longitudinal as well as alternating transverse movements, combined with the slight movement of the jaw in the vertical plane.

The nature of the mastication graph was recorded while eating hard food matter (seed and vegetative portions of plants, dry bread, carrot, etc.) in all the species under study illustrates; first, the existence of two main types of the primary processing of food (gnawing and grinding) functionally different and divided by time and secondly, great differences in the relative duration and importance of these types in the various species of the rodents (Fig. 2; and Table 1.2).

The vole occupies the first place according to the frequency of grinding movements, while the mice occupy the first place according to the frequency of gnawing movements. The golden hamster is placed in an intermediate position between the voles and the bunodont family of mice (see Table 1).

The gnawing movements are reduced to the biting of food matter in the narrow skulled vole and gnawing of food is virtually absent. In this manner, grinding plays the main role in the processing of food in field-voles. In gerbils, the main burden of the processing of food matter rests on the incisors and in mice gnawing assumes the significant role whereas in bunodont hamsters belonging to Mesocricetus the role of gnawing and crushing movements is insignificant (see Table 2).

During gnawing and gripping of food, the oscillatory movements of the lower jaw in the vertical and longitudinal directions are frequent and uneven. The bunodont forms grind the food particles gnawed off by the molars performing eight-shaped movements in the three planes, including alternating transverse motions of the jaw sometimes to the left and sometimes to the right. These unequal lateral movements are evident in various species. They are easily observed by the alternation of high and low waves on the mastication graph recorded assymetrically by Holl's sensor device (Fig. 3).

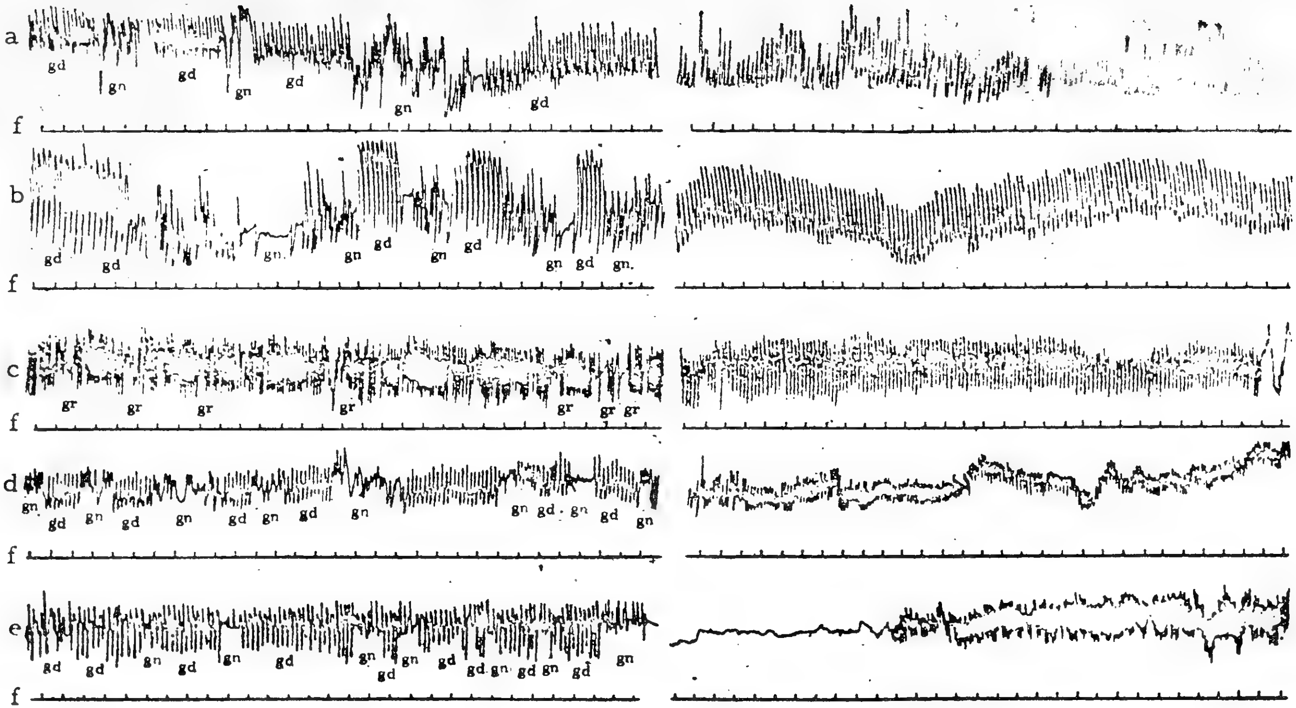


Fig. 2: *Recording of the movements of lower jaw in various species of rodents. Left - while eating hard food matter; right - while lapping water. (a) Mesocricetus auratus Watern.; (b) Rhombomys. opimus Licht.; (c) Stenocranius gregalis Pall; (d) Rattus norvegicus Berk.; (e) Mus musculus L.; (f) marking of time (1 sec); gn. = gnawing; (gd) grinding; (gr) = gripping food matter (in the case voles. After Labas.*

TABLE 1

Comparative frequency of the lower jaw movements in the rodents of the family Muroidea (after Labas from Vorontsov and Labas, in litt).

Species	Frequency of lower jaw movements per second while									
	gnawing			grinding			lapping.			
	min	m±m	max	min	M±m	max	min	M±m	max	Maximum frequency of the movements of jaw observed.
Golden hamster, (*Mesocricetus auratus*)	3.8	5.35± 0.23	8.0	4.35	5.15±0.15	6.00	4.20	4.54±0.15	4.62	12.0 grinding of incisors
Great gerbil.(*Rhombomys opimus*)	3.0	4.54±0.23	0.8	3.80	4.10±0.24	4.75	4.35	4.47±0.02	4.50	8.5 gnawing of hay
Narrow-skulled vole										9.0 grinding of hay
(*Stenocranius gregalis*)		-		4.50	7.09±0.37	8.20	5.90	6.28±0.09	6.60	11.0 gnawing of wood
Norway rat.(*Rattus norvegicus*)	5.0	6.55±0.20	8.3	4.67	5.56±0.31	7.40	6.52	6.98±0.16	7.50	
White rat,(*Rattus rattus* var. alb)	6.0	6.33±0.67	7.5	4.40	4.67±0.08	4.86	4.66	4.90±0.07	5.05	7.5 - grawing
White mouse(*Mus musculus*)	4.6	6.90±0.26	10.6	4.67	5.16±0.13	6.00	7.50	8.35±0.46	9.20	16.20 Cracking of seeds.

TABLE 2

Length of time of the gnawing and grinding in eating action in the rodents of the family Muroidea (after Labas from Vorontsov and Labas, in litt.)

Species	Duration of grinding					
	in seconds,			in % to the prolongation of subsequent period of grinding		
	min	m±m	max	min	m±m	max
Golden hamster (<u>Mesocricetus auratus</u>)	0.5	1.61±0.13	3.0	16.7	29.6±2.5	73.0
Great gerbil (<u>Rhombomys opimus</u>)	1.0	3.52±0.47	9.0	22.0	91.5±10.3	200.0
Norway rat (<u>Rattus norvegicus</u>)	0.5	1.31±0.11	3.5	22.0	65.9±7.9	186.0
White mouse. (<u>Mus musculus var. alb</u>)	0.5	2.40±0.23	6.2	5.0	78.2±5.4	150.0

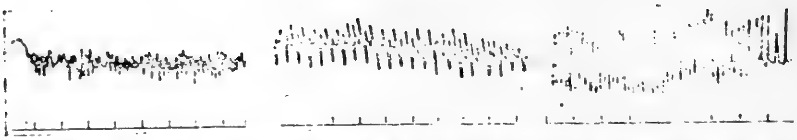


Fig. 3: Mastication graph of white mouse recorded assymetrically by Holl's sensor device placed on the skull. Left: recording during gnawing of hard food matter (dry bread); centre - during grinding, right; - while lapping water, below - registration time (1 sec.). After Labas.

The following main types of movements were observed on the basis of the experimental data: by Labas (Vorontsov and Labas, in litt.).

Abducting - while storing food in the cheek pouches in hamsters:

gnawing (also, possibly, crushing, which is difficult to distinguish from gnawing on the recorded waves).

grinding, associated with movements in longitudinal direction, particularly in voles it is strikingly expressed;

grinding - with a significant role of the transverse motion of the jaw to the right and the left (prevails while grinding in other species).

In this manner, the results of the comparative physiological experiment principally confirm the assumptions regarding the possible types of movements of the lower jaw made on the basis of comparative morphological studies (Tullberg, 1899; Vinogradov, 1926; Hinton, 1926; Lebedkina, 1949; Ognev, 1950; Vorontsov, 1962a, 1962b, 1963d).

The relationship of the exosomatic systems of the head and skull and with each other. The main line of Transformation of the skull and Maxillary Apparatus of the Cricetidae.

If the division of organs into exosomatic and endosomatic as proposed by A. N. Severtsov is applied, the skull is formed under the strong influence of exosomatic (masticatory apparatus, organs of small, hearing and to some extent, sight) as well as endosomatic organs (the formation of the skull is greatly influenced by the brain). The long standing doubt about the brain or the muscles affecting the structure of the cranium was solved in the past by the majority of anatomists assuming it to the musculature. The problem of the correlation of the structure of the sense organs with the shape of the cranium, and correlation between the structure of the capsular sections of the cranium and with the favourable solution of the biomechanical problems of gripping and processing of food has not been fully worked out.

Let us now consider certain tendencies in the transformation of the cranium of mice and voles, in the ecological series: *Ichthyomys*-*Oxymycterus*-*Orzyzomys*-*Peromyscus*-*Cricetus*-*Neotoma*-*Andinomys*-*Clethrionomys*-*Microtus*-*Lemmus*. This series is characterized by a tendency towards the transition from a purely protein diet, in *Ichthyomys* and *Oxymcterus*, through a mixed type of diet characteristic of the majority of mice and some primitive cheek-toothed voles to an exclusively cellulose diet, characteristic of the hypsodont voles and lemmings.

The relative size of the brain and the brain capsule of the animals of this series diminishes during the transition from those actively preying upon living objects to those feeding on plants. The transition from feeding on proteins obtained with difficulty to rich vegetative portions of plants leads to a reduction of the olfactory organ, that plays a distinct, though not a leading role in the life of seed-eating rodents (Ganeshina, Gurtavoi, 1953), Ganeshina, Vorontsov, Chabovskii, 1957).

The Development of simplification of the olfactory organ is associated not only with the complication or simplification of the ethmoturbinals which carry an olfactory epithelium, but also with the increase or decrease in the relative volume of the nasal cavity, as shown in insectivores (Ganeshina, Vorontsov and Chabovskii, 1957), and consequently with a slight inflation or elongation of the nasal part of the skull.

In view of the transition to low-calorie food, the activity in voles (Naumov, 1948) and in certain herbivorous mice (Hamilton, 1943) extends to nearly twenty four hours. [illegible] well developed in the nocturnal forms (Peromyscus), appreciably reduced in Andinomys, Sigmodon, and the entire Microtinae. The relative size of the eyeball also affects the structure of the cranium to a definite degree. Although the width of the zygomatic arch is related not only to the size of the eye, but also to the development of the masticatory muscles, it is sometimes possible to establish a specific relationship between the structure of the orbital region of the skull and the size of the eye. Thus in the line of the Dipodoidea from Sicista and Zapus to the present Dipodidae, no special reinforcement of the masticatory muscles is observed; but a sharp increase in the relative size of the eyeball and relative width of the zygomatic arch is noticed.

The development of the tympanic region (bulla tympani and bulla mastoidea) may result in a sharp change in the entire configuration of the skull, particularly the brain capsule (Dipodidae, Heteromyidae, Ctenodactylidae, Gerbillinae). In some cases hypertrophy of the tympanic region or the bony tube of the external auditory meatus, as it was shown by Vorontsov (1963), may facilitate the formation of unexpected connections between the lower jaw and the skull. However, the variability of the tympanic region is comparatively not very great within the group of Cricetidae studied.

Of all the exsosomatic organs in the Cricetidae, the structure of the masticatory organs has a decided influence on the development of the cranium. However, this "influence" is very closely associated with the evolution of the functions of other exsosomatic organs; the correlation between these systems is so profound and "expedient" that this influence should not at all be considered as a suppression of the functions of less important organs by the leading organs.

The volume of the cranium is extremely great in piscivorous Ichthyomys and Anatomys, Rheomys, Daptomys and other rodents of the tribe Ichthyomyini that are allied to it. Their food has a high-caloric value, procured with difficulty and easily processible. The quick and sharp adduction of the lower jaw in catching and gripping also plays a role in moving the lower jaw apart. The following changes take place in the cranium because of the strong development of the muscles adducting the lower jaw. The anterior part of the m. masseter medialis, which moves the jaw forward and upward while gripping the pray increases and the infraorbital foramen through which this muscle passes, widens the fossa pterygoideus lateralis is used for the attachment of M. pterygoideus and accounts for 17-18% of the length of the skull· m pterygoideus internus is fixed to a large area, is fleshy and does not have well marked tendinous layer by which it could be related to the dynamic type producing abrupt, intense and sharp movements.

Owing to the ease of processing and the small quantity of high-calorie food, the group of masticatory muscles, engaged in grinding movements is poorly developed. The zygomatic arches, to which are attached the posterior part of m. mass, lateralis, p. posterior m. mass, medialis and through which passes m. temporalis are very thin and poorly laid owing to the reduction of the masticatory muscles.

The size and thickness of the masseteric patch to which is attached p. profundus m. mass. lateralis is extremely small. The masseteric surface itself is placed at a slight angle to the plane of the dental rows, and is directed downward, to facilitate the gripping function of p. profundus m. mass. lateralis.

The anterior part of m. masseter lateralis is attached to a special, well-developed arm of the maxillary bone. The anterior part of the lateral masticatory muscle in Ichthyomys is attached along the lower edge of the mandible (see Fig.7 a). Such a construction leads to the fact that muscles like p. anterior m. lateralis, so adapted for the grinding of food in a to and fro direction takes a greater part in the gripping and crushing of food than in grinding it by the longitudinal movements of the lower jaw.

Of the sense organ [illegible] *Ichthyomys*, the organ of the sense of touch is expressed as in many other aquatic mammals; thus vibrissae are highly developed; the r innervating n. labialis superior, branching from the powerful n. infraorbitalis may obviously, result also in an increase in the size of the foramen infraorbitale. But this problem can be solved only after making a special study of the correlation between the development of vibrissae, the thickness of their innervating nerves and the size of the foramen infraorbitale.

The skull of Oxymycterus differs from that of Ichthyomys by a well developed nasal cavity. In Oxymycterus the foramen infraorbitale is enlarged, the fossa pterygoidea lateralis is longitudinally elongated and the zygomatic arch is extraordinarily slender and poorly branched. The masseteric surface of the maxillary bone is small (although greater than that in Ichthyomys), thin, but to some extent directed more upwards and forwards. Although the special process for the attachment of p. anterior m. mass. lateralis is absent, this muscle is attached from the lower side of the maxilla in Oxymycterus.

In Ichthyomys and Oxymycterus the masticatory surfaces are not strictly parallel to the plane of the base of the skull, but are directed slightly laterally in the upper and medially in the lower rows of teeth. This indicates the possibility of some lateral crushing type movement of the lower jaw while chewing food. Actually, in these forms the mandible is not inserted deeply in the skull; the articular depression is situated sufficiently low, and the difference between its level and the level of attachment of m. pterygoideus externus is not very great. With such cranial structure and the attachment of muscles the lower jaw moves insignificantly forward and downward and shifts appreciably medially with the contraction of this muscle.

The skull of Oxymycterus and that of a group of genera close to it (Lenoxus, Blarinomys and others) is characterized by the strong development of the nasal section of the cranium. This is associated with the intense development of the ethmoturbinal and correlates with an increase in the size (length and breadth) of the nasal cavity. The complication of the organs of smell in this group of insectivorous rodents results in an increase in the size of the olfactory lobes of the brain, which has a relation to the widening of the interorbital part of the skull The ethmoturbinals are situated in the fore part and the olfactory lobes of the brain in the posterior part of this section of the skull.

The skulls of Ichthyomys and particularly, of Oxymycterus are distinguished by the absence of the noticeable crest for the attachment of the masticatory muscle. This explains the relatively soft food (fish, insects, small invertebrates), taken by these rodents in small quantity because of the high caloric value.

The predominance of the cerebral section of the cranium ove the facial section is also characteristic of Ichthyomys and Oxymycterus.

Substantial transformation of the skull is observed in the series starting from the carnivorous rodents to the narrow specialized forms of field-voles. A change over to the continuous intake of food with plenty of cellulose matter, and a simplification of the nerve structure relative to the reduction of the sense organs sharply decreases the size of the cranium.

The function of gripping and the retention of food which is the main characteristic of Ichthyomys is replaced by the function of processing a large quantity of coarse, low-calorie, cellulose food matter which is the main characteristic of the field-voles and other herbivorous mice. In general, starting with the Neogene, this change of function is the most important moment in the evolution, of the entire Myomorpha. It should be emphasized that the transition from protein to a cellulose diet needed a sudden strengthening of the masticatory movements, resulting in the greater development of all masticatory muscles. The muscles adducting the lower jaw or producing gnawing motions also begin to be dominant in field-voles in comparison with the carnivorous or seed-eating mice. However, a general strengthening of the muscles such as m. temporalis and p. anterior, m. mass. medialis, is clearly noticeable, though insignificant in comparison with the strengthening of the grinding movement executed by the main group of masseteric muscles and especially by p. anterior m. mass. lateralis.

Since the role of gripping of prey is reduced, the ever decreasing part of the fibers of the p. anterior m. mass. medialis passing through the foramen infraorbitale causes this structure to become narrower. The point of attachment of part of the fibers shifts forward and upward, so that during contraction of the muscles the lower jaw moves not only upward, but to some extent forward.

The fossa pterygoidea lateralis becomes short and deep but in field-voles and zokors it even forms a pit oriented not along, but across the cranial axis. In this series its length in relation to that of the cranium decreases in the following manner:-

	%
Oxymycterus nasutus	18-19
Ichthyomys soderstromi	17-18
Oryzomys meridensis	15-16
Reithrodontomys soderstromi	14-15
Cricetus cricetus	11-12
Neotoma cincerea	"
Andinomys edax	9-10
Clethrionomys glareolus	7-8
Lemmus lemmus	5-6

M. pterygoideus internus, attached to the cranium of lemmus in a small area, is pierced by tendinous fibers and moves towards the static type of muscle, accomplishing long, slow masticatory movements (Fig. 4).

The area of masseteric attachment on the maxillary in this series sharply increases, moves forward and nearly takes a perpendicular position with respect to the plane of the dental series. This results in the change of motion of p. profundus m. mass. lateralis, which changes from a vertical direction in the primary members of the series to the inclined horizontal direction; that is, it takes part not only in the adduction of the lower jaw but also in forward movement (Fig. 5).

The change in the position and shape of the masseteric area is clearly observed in the series of Madagascan nesomyinae from Macrotarsomys to Brachyoromys (Fig. 6).

The point of attachment of p. anterior m. mass.lateralis shifts appreciably from the ventral side of the skull to the lateral side and displaces upwards to some extent. In Cricetidae we may observe a clearly marked tendency for the transfer of the point of attachment of the anterior part of the external masticatory muscles from the rear side of the lower margin of the angular outgrowth to the internal side of the posterior margin of the jaw, close to the notch between the angular and articular outgrowths (Fig. 7). This leads to the most intensive development of the grinding movements in the longitudinal direction and p. anterior m. mass. lateralis plays the most important role in these movements. In general, this muscle is adapted mainly for longitudi-

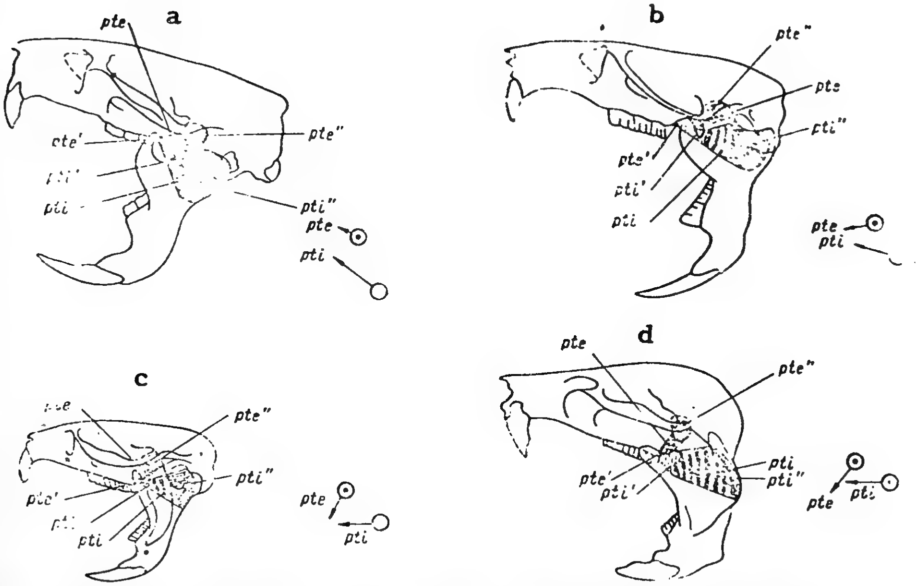


Fig. 4: Change in the points of attachment and functions of pterygoid muscles. (a) Cricetus cricetus L.; (b) Neotoma cinerea Ord.; (c) Microtus agrestis L.; (d) Myospalax fontanieri Milne-Edw. Dotted line is the point of attachment of the muscles on the lower jaw; vertical, broken shaded portion is the point of attachment of the muscles on the cranium; arrows show the direction of the action of the pterygoid muscles; pte, pte' and pte'' are pterygoideus externus, its attachment to the cranium and to the jaw; pti, pti' and pti'' are pterygoideus internus and its areas of attachment to the cranium and the jaw. The pterygoideus externus primarily takes part in the transverse displacement of the lower jaw. (a) and later adducts of the posterior part of the jaw (cd) The pterygoideus internus, primarily takes part in the abduction of the lower jaw, and the insignificant forward motion for gnawing in the posterior position (a), later takes part in the forward motion of the jaw (c,d). Vorontsov (1963).

nally grinding movements; but in all hamsters it plays a definite role while gnawing, crushing and gripping because of the attachment of a large part of fibers on the ventral side of the jaw.

The change in the point of attachment of this muscle on the posterior part of the lower jaw made it possible for the evolution of herbivorous forms among hamsters. The loss of the lower point of attachment of the anterior part of the lateral masticatory muscle and the increase in the area of its attachment on the internal side of the posterior margin of the lower jaw are the most

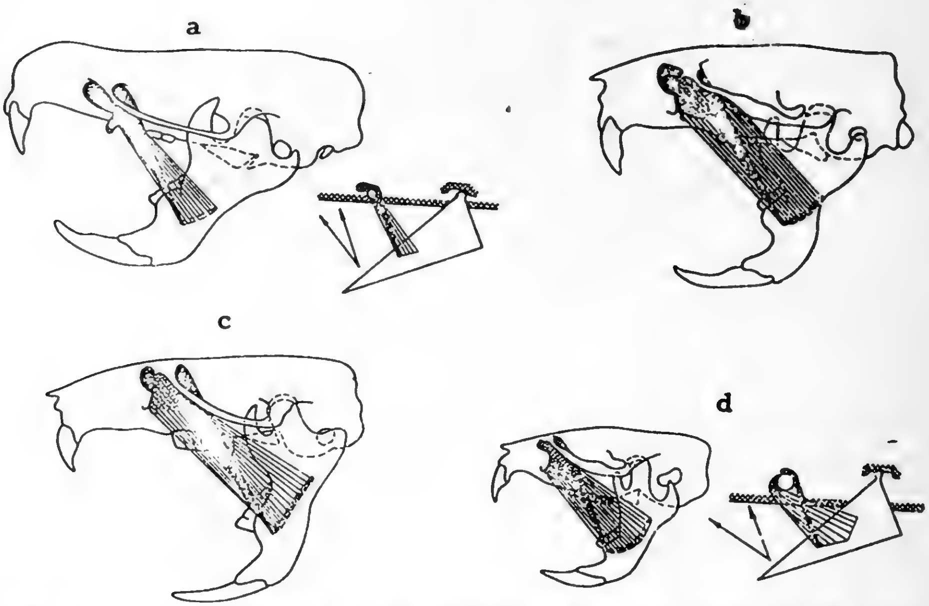


Fig. 5: *Transformation of the functions of muscles, adducting the lower jaw. (a) Ichthyomys soderstromi de Winton; (b) Cricetus cricetus L.; (c) Neotoma cinerea Ord.; (d) Microtus agrestris L The black portion shows the course of pars anterior m. mass. medialis; the shaded portion shows the course of pars profundus m. mass. lateralis; the dotted line shows the point of attachment of this muscle on the cranium. Right - diagrams showing the action of muscles in the later members of the series. We see a reduction in the relative size, and shifting of the point of attachment of p. anterior m. mass medialis upwards and backwards and that of the point of attachment of p. profundus m. mass. lateralis on the skull forwards and upwards but on the jaw backwards and perpendicularly upwards (After Vorontsov (1963)).*

important events in the evolution of Cricetidae which helped in the emergence of the large group of the present-day voles.

With the change of the points of attachment of the muscle, the field-voles lost their former functions of crushing food, and developed a dental system to adapt to new habits. This, as a matter of fact, is a unique feature that distinguishes hamsters (Cricetinae) from field-voles (Microtinae).

Powerful development of the posterior part of p. anterior m. mass. medialis, attached to the internal part of the zogymatic

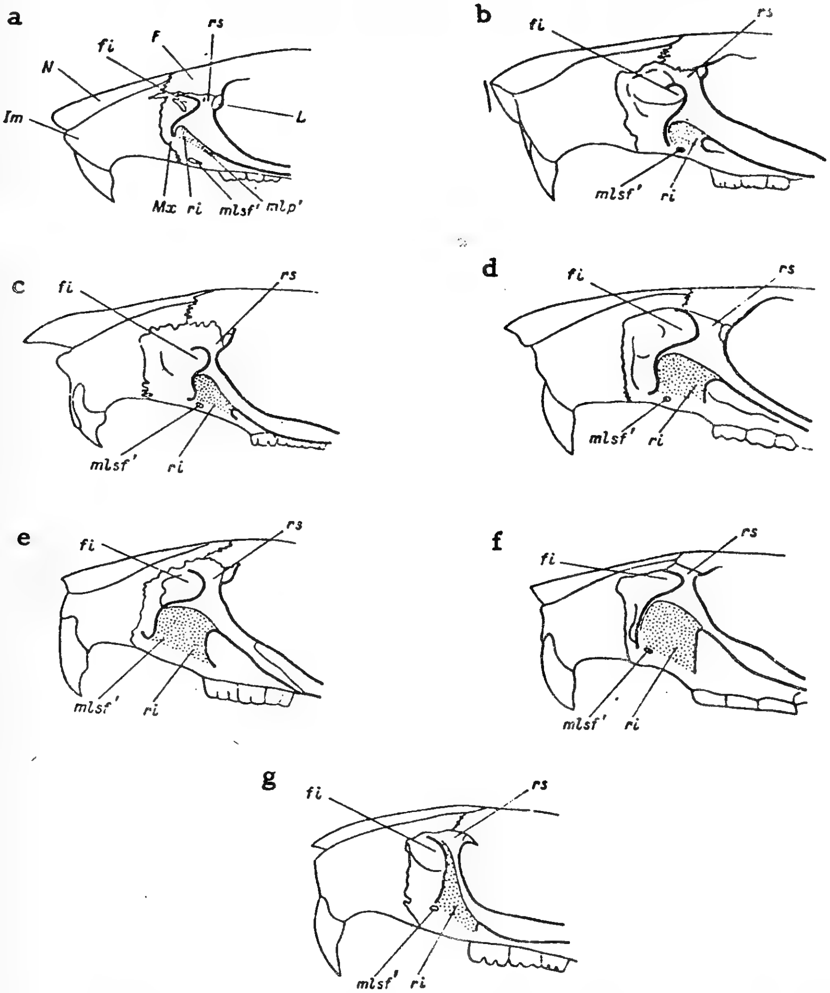


Fig. 6: *Anterior part of the cranium of Madagascan cricetids, Nesomyinae. Change in the position of masseteric area and suborbital orifice can be seen. (a) Macrotarsomys bastardi Milne-Edw. et Grandid; (b) Nesomys rufus Peters; (c) Gymnuromys roberti. F. Major; (d) Eliurus tanala F. Major; (e) Brachytarsomys albicauda Günth.; (f) Brachyuromys betsileoensis Bartl.; (g) Brachyuromys - ramirohitra. F. Major; (f) Frontale; Mx - maxillare; N - nasale; L - lacrymae; fi - foramen infraorbitale; Im - Intermaxillare; ri - ramus inferior; rs - ramus superior; mlsf' - point of attachment of m. mass lateralis p - anterior; mlp' - point of attachment of m. mass lateralis p - profundus. After Vorontsov (1963).*

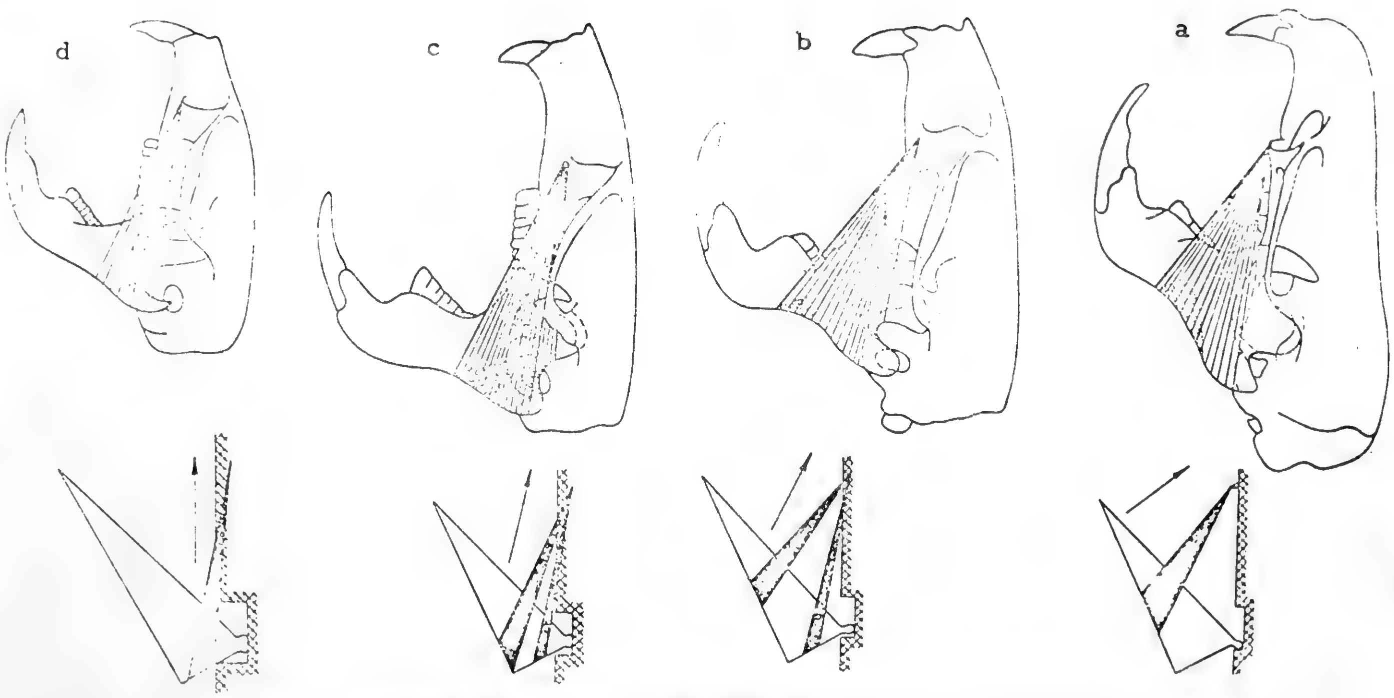


Fig. 7: *Change in the points of attachment and functions of pars anterior m. mass. lateralis. The attachment points of the muscle on the internal side of jaw are shown by dotted lines; cords of muscles, which are attached to the internal side of the jaw are delineated by bold lines. The diagrams on the right are of action of the external portion of the lateral masticatory muscle (in field-voles this muscle takes part only in the longitudinal - grinding movements).* ***(a) Ichthyomys soderstromi de Winton; (b) Cricetus cricetus L.; (c) Nectoma cinerea Ord.; (d) Nicotus agrestis L. From Vorontsov (1963).***

arch and filling a considerable part of the eye-socket, and the increase in the size of p. posterior m. mass. lateralis (see Fig. 7) lead to the strengthening and the widening of the zygomatic arches. A clear trend toward an increase in size and widening, and the attachment of zygomatic arches by the crests is observed in the series under consideration.

In the series from Oryzomys - Peromyscus (except the narrowly specialized Ichthyomys and Oxymeterus) to Microtinae, the organs of sense, associated with the search of food, smell and sight are greatly simplified. The ethmoturbinals are simplified (Ganeshina and Gurtovoi, 1953), and so the size of the olfactory parts of the brain, and the volume of the nasal cavity and the anterior section of the cranium decreases, and the interorbital section of the cranium contracts. With the relative decrease in the size of the eyeball in this series, the eye socket not only decreases, but, the width of the eye increases with its reduction because of the presence of the well developed, internal, masticatory muscles.

The structure of the interorbital space of the type found in Oxymycterus, Oryzomys, Peromyscus, and others, that does not meet all the new requirements, and rounded in the cross section, is replaced by the structure having a strong interorbital crest of the type found in Cricetus, Microtus and Lemmus, which successfully resist powerful forces developed by the masticatory muscles with the adduction of the lower jaw.

In this series the masticatory surfaces of the upper and lower molars become parallel to each other, which allows narrow and perfect adaptations to the grinding of food solely in the longitudinal direction. In the same series the level of the articular surface of the temporal bone rises above the level of the skull base, with the result that the lower jaw moves deeply into the cranium. On such cranial structure, m. pterygoideus externus works on the abduction of the posterior part of the jaw downwards and a little forward, which is significant during the gnawing movements of the lower jaw in the anterior position with unfixed axis of the maxillary lever. The possibilities of the lateral movements of jaws are limited (see Fig. 4).

The strengthening of the construction of the skull by additional crests for the attachment of the reinforced masticatory muscle, increases the relative thickness of the cranial bones and the appearance of new "costae of rigidity" in the shape of interorbital crests are observed in this series. The tendency for a decrease in the relative size of the cerebral part of the cranium and an increase in the size of the facial part is observed.

The evolution of these features although less visual, but sufficiently clear, is traced not only on slightly artificial ecological series from Ichthyomys to Lemmus taken for analysis, but also on more real comparative anatomical series. It is sufficient to take for example, such series of hamsters as : Phodopus-Cricetulus-Cricetus, Oryzomys-Nectomys, Phyllotis-Euneomys-Auliscomys-Chinchillula-Andinomys (Fig. 8), Holochilus-Sigmodon-Reithrodon or series of field-voles Dolomys-Clethrionomys-Ondatra-Microtus-Lemmus, to confirm the existence of the above described course of transformation of correlatively connected systems of the exosomatic organs of the head and the cranium itself.

Fig. 8: Silhouettes of the cranium of hamsters from the tribe of Phyllotiini. The relative expansion and thickening of the zygomatic arch and reduction of the interorbital space is observed in the series. (a) Phyllotis Watch.; (b) Euneomys. Coues.; (c) Auliscomys Osgood; (d) Chinchlillula Thom.; (e) Andinomys Thom. After Vorontsov (1963).

The line of development in the comparative anatomical series corresponding to the ecology of the forms under study have been established above; this series, however, can be read in the direction as described above, as well as the opposite way. To prove the initial state is very necessary since the reduction of the majority of sense organs is postulated as leading to the appearance of widely spread and prospering groups and simplification of brain. Let us take some paleontological and embryological data to prove that these series must be read in the same manner as they have been summarized above.

5. Paleontological and Embryological Proofs of the Main Direction of Evolution of the Cranium of Cricetidae.

The fragments of cranium of the paleogenic hamsters are very rarely found while restoring them. The thin zygomatic arch and the widely rounded and low-set foramen infraorbitale in the cranium in well preserved oligocence Cricetodon incertum Schlosser (from phosphorites of Kverci), is of interest.* The masseteric space is situated almost parallel to the plane of the cranial base (see Fig. 9, a 10, a) - such a low position of its masseteric space is not found in any of the latest members of Cricetidae. The attachment point of p. anterior m. mass. lateralis is situated on the ventral side of the maxillary bone. The dental surface has sharp tubercles and the exposure of dentinal fields is seen only on the crowns of molars.

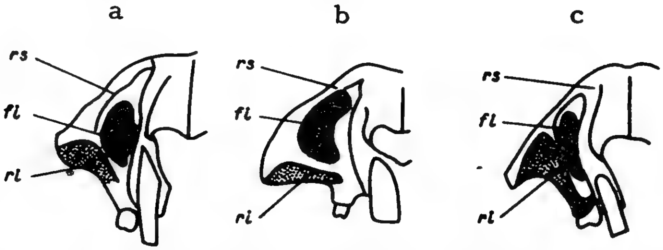


Fig. 9: The skull of some fossilized hamsters (front view). Contraction and displacement of preorbital orifice (shown in black) and displacement of masseteric space (attachment point of p. profundosm. mass. lateralis is indicated by dots). (a) Cricetodon incertum Schlosser (Oligocene), after Schaub (1925) with changes; (b) Cricetops (aff.) affinis Arg. (Oligocene), org.; (c) Cricetodon gregorium Schaub (Miocene), after Schaub (1925) with changes; ri - ramus inferior arches of preorbital orifice; fi-foramen infraorbitale; rs - romus superior, arches of preorbital orifice. After Vorontsov (1963).

The large sized Cricetops, classified by Simpson (1945) in a special tribe of Cricetopini stand apart from the paleogenic Cricetinae. In the well preserved skull of Cricetops (aff). affinis.

---

* *The description is given after the figures of Schaub (1925).*

Arg. (see Fig. 9, b 10, b) from the Oligocene formations of the Chelkar-Tenghiz lake (Kazhakstan), the features of the comparatively higher specializations are observed along with the primitive features.

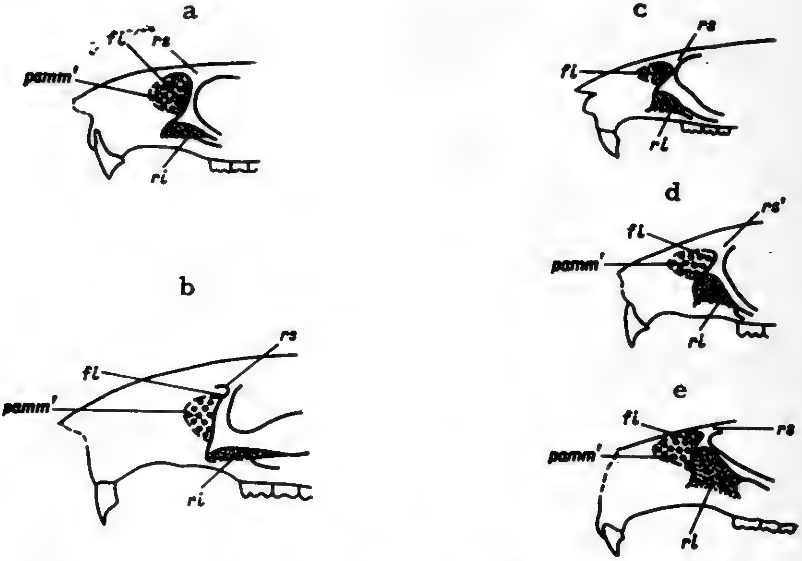


Fig. 10: Structure of the anterior part of the zygomatic arch and the attachment points of the masticatory muscle, in some fossilized hamsters, side view. (a) Cricetodon incertum Schlosser (Oligocene) after Schaub (1925) with changes; (b) Cricetops (aff.) affinis Arg. (Oligocene), orig.; (c) Cricetodon minus Lartet (Miocene), after Schaub (1925) with changes; (d) Criceton gregarium Schaub (Miocene), after Schaub (1925) with changes; (e) Cricetodon affine Schaub (Miocene), after Schaub (1926) with changes. Thick dots delineate the area of attachment of the anterior part of pars anterior m. mass. medialis (pamm); fine dots delineate masseteric space, the point of attachment of p. profundus m. mass. lateralis. Legends as shown in Fig. 9. After Vorontsov (1963).

The masseteric area, small in area and situated parallel to the plane of the skull base, and the very wide, lowly situated foramen infraorbitale (see Fig. 9b), are related to a number of primitive indications. The zygomatic arches are not widely arranged. Fossa pterygoidea lateralis is stretched longitudinally, accounting for nearly 14-15% of the length of the cranium. M. masseter lateralis, obviously, has not yet divided into three portions.

Meanwhile some features of Cricetops indicate further specialization in the structure of the cranium as compared to the Oligocene Cricetodon. In Cricetops (aff) affinis thick zygomatic arches are highly developed, greatly contracted interorbital space is fortified by paired crests and the facial section of cranium prevail over cerebral section. These characteristics indicate a substantial divergence of Cricetinae already in upper Oligocene, when the adaptations similar to the modern forms of Cricetus were evolved along with the type of modern forms of Muroidea of American hamsters, then represented by Cricetodon. However, these facts, in our opinion, cannot substantially change the above developed concept concerning the main direction of the evolution of the cranium of Cricetidae.

The excellent series of craniums of Cricetops collected by the Mongolian paleontological expedition (collection of the Institute of Paleontology, Middle or Upper Oligocene, Tatal - Hol, Mongolia), mainly confirms the results of the study of the Chelkar-Tenghiz specimen. Mongolian Cricetops from Tatal - Hol, belonging, evidently to a new species, which has not yet been described, differ by the position of the attachment of m. mass. lateralis in these hamsters; the masseteric space, serving as the attachment of p. profundus m. mass. lateralis so far does not exist.

The cranium of the Miocene Cricetodon minus Lartet (from Sansan), preserves the series of primitive characteristics.* The description is given on the basis of the figure of Schaub (1925). The zygomatic arches are tightly set and are thin, the masseteric space is situated at a relatively lower level (see Fig. 10c) and p. anterior m. mass. lateralis is attached to the ventral side of the cranium. The cerebral part of the cranium sharply prevails over the facial portion. Fossa pterygoidea lateralis stretched longitudinally accounts for 15-16% of the length of the skull (i.e., approaches to Oryzomys in dimensions). The nasal cavity is sufficiently well developed and resembles the nasal section of the cranium of Oryzomys in outline. The gnawing surface of the upper molars is slightly inclined outside (less than in Ichthyomys and Oxymycterus). The crests for the attachment of the masticatory muscle are not developed in the same way as in the fine forms of modern Oryzomys, Peromyscus, Hesperomys, etc.; but there is

---

** The description is given on the basis of the figures of Schaub (1925).*

a longitudinal crest on the basioccipitals for the attachment of muscles, which lowers the head. Special costae of rigidity on the interorbital part of the cranium are absent. The articulation of the mandible with the cranium is situated at a significantly lower level. The surface of the molars has sharp tubercles, but the exposure of dentinal fields on the worn out teeth is seen not only on the crowns of the tubercles but also in their bases and form a loop-shaped figure (Schaub, 1925, Taf. I, Fig. 5). On the whole, the craniums of *Cricetodon minus* and *Cricetodon incertum* stand nearest to the modern hamsters of "the generalized biological type" like *Oryzomys*. These oldest forms differ greatly from the narrowly specialized modern forms of *Ichthyomys* and *Oxymyceterus* and are far from the field-voles, like *Andinomys*, *Chinchillula* and even *Cricetus*.

In the Miocene *Cricetodon minus*, the following changes take place in comparison with oligocene *Cr. incertum*:foramen infraorbitale reduces to some extent and moves upward, raising the masseteric space. It is situated at a greater angle to the plane of the cranial base and becomes more powerful)(the position of the masseteric space resembles that of the modern forms of *Oryzomys* (*Melanomys phaeopus* Thom.). The molars have less pointed tubercles.

Further development of these tendencies in the evolution of the skull is found in the Miocene species, *Cricetodon gregarium* (Schaub.). Compared to the former species, the foramen infraorbitale is highly contracted in *Cr. gregarium*, and with the widest part of the preorbital orifice it moves upwards. The masseteric space is widened and the zygomatic arch becomes more powerful.

The masseteric space itself is turned upwards and forwards (see Fig. 9c, 10d).

Specializations of the skull in *Cricetodon affine* (Schaub) (see Fig. 10e) goes still further; the foramen infraorbitale connects from below, its widest portion is situated at the level of the lower boundary of nasale. The masseteric space moves sharply up and forward, thereby resembling many modern hamsters, but the upper arch of the preorbital orifice is thinner than in the latest forms having a similar structure of the masseteric space. The dental system is brachyodont, having a loop-shaped gnawing surface of molars in the adults slightly resembling the structure of molars of the modern forms of Nectomys. The tubercle, to which p. anterior m. mass. lateralis is attached, moves from the medial to the lateral side of the maxillary bone. The lower pleistocene Allocricetus* belong not to Cricetodontini fossils but to the latest Cricetini tribe, possess the characteristics of the cranium of the modern hamsters. The existence of the powerful, and obviously, widely set zygomatic arches, a strong and wide masseteric space directed forward and upward, and a greatly contracted foramen infraorbitale from below, should be noted.

This series cannot be treated as established since full remnants of the skull, the lower jaw and the teeth are not found in the fossils, But it may be said to be close to the primary structure of the skull of the ancient forms of Cricetidae and its evolution. It should be emphasized that the morphology of the skull of the oldest forms of Cricetidae resembles that of Oryzomys more, and hamsters closer to them, than those in the beginning of the ecological series of Ichthyomys and Oxymycterus as suggested above.

The above considerations on the evolution of the cranium of hamsters and Cricetidae can be confirmed by the data on the individual development of Cricetinae.

If we consider that the growth of the cerebral section of the cranium prevails over the growth of the facial section in the early stages of development then some characteristics of the cranium of young modern hamsters**are close to the fossils and the primitive forms of the modern Cricetinae.

Narrowly placed thin zygomatic arches, smaller deflection of the masseteric space forward and upward, central position of the point of attachment of p. anterior m. mass. lateralis, wide interorbital space not fortified by crests.Features which distinguish the craniums of the young ones of Cricetus cricetus from the craniums of adults confirm, the statements above on the primitive and specialized characteristics in the cranium of hamsters.

---

* *Description given according to the figures of Schaub (1930).*

***Materials of the postembryonal development of the skull of Cricetus cricetus and Phodopus sungorus served as the basis for studies.*

However, in the cranium of the young Cricetus cricetus (with a single cut M^1) the features related to the characteristics of specialization are observed. Foramen infraorbitale is almost as narrow as in the individual adults, and fossa pterygoidea lateralis is shorter than in the adult hamsters; the young Cr. cricetus resemble field-voles by their shape. It may be asked whether such a structure is not related to the herbivorous nature of the young rodents compared with adult ones - a phenomenon not yet understood.

On the whole, the fragments of data available on the Paleontology and the postembryonal development of Cricetinae confirm this system of transformation of the cranium of all forms of Cricetinae and enable us to establish the structure of the cranium close to the initial state in the modern forms of Cricetinae. The structure of the cranium of the hamsters of the Oryzomys group greatly resembles the "archetype" Cricetidae, suggested on the basis of the majority of features.

Ecological, morphological and functional anatomical analysis of the structure of the cranium and the masticatory muscles, supported by paleontological and embryological materials, enable us to understand not only the adaptive significance of the features widely used in classification but also to know the dynamics of the transformation of these features in phylo- and ontogenesis, and to trace their fate and to evaluate the significance of the appearance of some new formations in the history of development.

CHAPTER II

EVOLUTION OF THE DENTAL SYSTEM

I. General Notions: Terminology

The dental system of rodents Muroidea is differentiated only by two types of teeth, namely, incisors and real molars. Premolars are not present. The space between incisors and molars is occupied by intermaxillary and maxillary bones. The space is free of teeth and is known as diastema. The incisors, situated in the intermaxillary bones have a milk and permanent sets. In hamsters the incisors change in the embryonal age. The young ones of real hamsters are born with incisors; this is the systematic distinction of Cricetus, Cricetulus, Mesocricetus and Phodopus from all other Cricetidae. The molars are cut after a few days of growth: starting with the first, then, the second and the third molars. The dental formula of Cricetidae is constant: M_3 is absent in dwarf gerbil of the genus Desmodilliscus.* $i\frac{1}{1}\ \ m\frac{3}{3}$, whereas in Muridae the number of molars may be reduced to two (Hydromys, Neohydromys) and even to one in every jaw (Mayermys).

The masticatory part i.e., the crown and the root part resting in the bone, are distinguished in molar tooth. The teeth having a low crown which does not enter into the bone, are called brachyodont, the teeth having a crown of medium height, partially penetrating into the bone but with protective roots are called mesodont and the teeth having a high crown and reduced roots are called hypsodont. Hypsodont molars grow during the entire life of the animal. The chewing surface of molars may have sharp tubercles, or flat tubercles, or may be practically plane. In voles, the molar tooth not yet emerged has a tuberculate chewing surface completely covered with an enamel layer. As abrasion

---

* *M_3 is absent in dwarf gerbil of the genus Desmodilliscus.*

proceeds (first, on the tubercles) the dentinal fields bordering along the edges on the enamel crests are exposed. Since the thickness of the enamel is more than the thickness of dentine, the enamel layers always protrude over the dentinal fields, forming enamel crests. Attached to the so-called flat crowned tooth, dentinal fields are arranged in one level and over them rise enamel crests, forming a second level. The food matter is ground with the mutual intersection of enamel crests of the upper and the lower dental rows. Dentine serves as a matrix for the cutting enamel portions and does not take part in grinding food.

A very complicated figure formed by the alternation of enamel crests and dentinal fields, changing considerably with the age of the animal, preserves the features peculiar to a given taxonomical unit. Until now a unity does not exist in the nomenclature of basic and additional tubercles, protuberances, closed islets of enamel, and other important systematic characteristics.

The best terminology for the teeth of water hamsters, Nectomys was proposed by Hershkovitz (1944). However, like most of the other English authors he gives anglisized Latin terminology. Hershkovitz gives the meaning of the so-called inlet corners, but the enamel islets enclosed in the dentinal area is not named. Shotwell (1958) gave a successful system of terms for closed, enameled islets and flexus for the fossils of Mylagaullidae and Aplodontidae. In subsequent works on the structure of the fossils of hamsters carried out by American authors, the terminology proposed by Hershkovitz (Hopper, 1945, 1957), (Hershkovitz, 1955, 1962) was widely used.

Full use of the terminology of Hershkovitz on the large and varying materials somewhat impedes the conformation of tooth parts. Therefore, the system of Hershkovitz was slightly modified by using the nomenclature proposed by Shotwell for the meaning of flexus and closed enameled spaces adding to it some new meanings.

The structure of the masticatory surface of the second upper molar M^2 (see Fig. 11, a) is nearest to the original plan of the structure and it is constant.

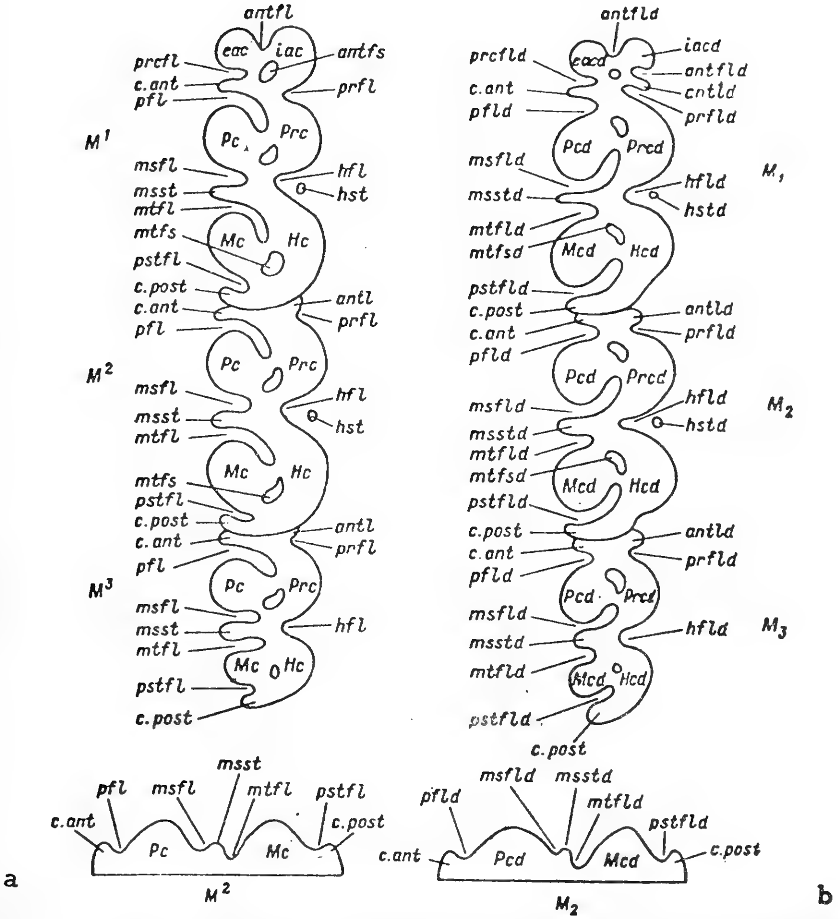


Fig. 11: *Scheme of the structure and the adopted nomenclature of molar teeth of Cricetidae. After Hershkovitz (1944) with changes and additions. (a) Upper molars (antfl - anteroflexus, antfs-anterofossa, antl-anteroloph; c. ant-anterior cingulum, c. post-posterior cingulum, eac-exteroanterocone, Hc-hypocone, hfl-hypoflexus, hfs-hypofossa, iae-interoanterocone, Mc-metacone, mtfl-metaflexus, mtfs-metafossa, msst-mesostyle, pfl-paraflexus, pafs-parafossa, Pc-paracone, Prc-protocone, prfl-protoflexus, pstl-posteroloph; (b) lower molars, antfld-anteroflexid, antfsal-anterofossetid, antld-anteroflexid, antfsd-anterofossetid, antld-anterolophid, c. anti-anterior cingulum, c. post-posterior cingulum, eacd-exteroanteroconid, Hcd-hypoconid, hfld-hypoflexid, hfsd-hypofossetid, iacd-interoanteroconid, Mcd-metaconid, mtfld-metaflexid, mtfsd-metafossetid, msstd-mesostylid, pfld-paraflexid, pafsd-parafossetid, Pcd-paraconid, Prcd-protoconid, prfld-protoflexid, pstfld-postflexid, pstld-posterolophid, antfld-anterolophiflexid, prcfld-procinguloflexid, hstd-hypostilid.*

The main tubercles of teeth are termed cusps, supplementary ones, cingula; these cingula join with the cusps by means of lophs. Flexuses, situated between tubercles are named according to the arrangement of the tubercles, i.e., hypoflexus when arranged in front of the hypocone, metaflexus when situated before metacone, and so on. A slight rise in the edge of the tooth between tubercles while grinding may lead to the isolation of the flexus in the closed, enamel islet. This fossa is named after the flexus from which it was tied off, e.g., when it is tied off from anteroflexus it is called anterofossa, when it is tied off from hypoflexus it is called hypofossa and so on.

Two main tubercles anterior (protocone) and posterior (hypocone) are distinctly seen from the lingual side of M^2. In front of protocone the anteroloph may be well developed with the formation of an outgrowth (sometimes called a heel) vallecula (or flexus) occurring between anteroloph and protocone is named protoflexus, and in case of snapping in the closed fossetus protofossa. Vallecula between protocone and hypocone is named hypoflexus, and in case of its closure into fossa, hypofossa.

The structure of the molars from the labial side is generally somewhat more complex than that from the lingual side. The two labial tubercles that are always present are called paracone (anterior) and metacone (posterior). In front of the paracone, usually there is an additional tubercle connecting, as detrition goes on, the crest with the axial elevated part of the tooth is termed the anterior cingulum. There may also be an additional tubercle between the paracone and metacone connecting the crest with the axial elevated part of tooth (it is named mesostylus). Finally behind metacone the posterior cingulum may be well developed. Flexus between the anterior cingulum and paracone is called paraflexus, and fossa situated at this place, parafossa. The depression between the paracone and the spur of mesostylus is named mesoflexus and fossa, mesofossa. The flexus between mesotyle and metacone is named metaflexus, and fossa, metafossa. Finally the cavity between the metacone and posterior cingulum is named postflexus and fossa, postfossa, M^3 is also characterized by the same plan of structure but generally slightly simplified.

M^1 in Cricetidae is complicated by the constant presence of anterocone in front of protocone. As a rule, anterocone is subdivided into internal (intero-anterocone) and external (extero-anterocone) in hamsters. The flexus dividing the internal and external protocones, is called anteroflexus and the fossa formed with the closure of this flexus is anterofossa.

The tubercles, flexuses and fossae of the lower molars (see Fig. 11,b) are named the same way as the upper ones, but with suffix 'id' added in the end, (protoconid, protoflexid, protofossetid, etc.).

(2) Types of masticatory movements and the structure of molars

The main types of masticatory movements of rodents have been discussed above (Chapter I) and some peculiarities of the structure of the masticatory apparatus in connection with some type of processing of the food have also been noted.

As already mentioned, gnawing movements of the incisors in the rear position may be very close by its trajectory to the crushing movements of the lower jaw. Processing of the seeds on the tubercular teeth may be compared with the cutting with pestle (tubercles) and mortar (corresponding flexus of the tooth). Movements on the horizontal plane carried out by the jaw of bunodont rodents are not great and, generally they have a somewhat circular pattern. The figure of the gnawing surface of the lower molars is represented as the reflection of the corresponding figure of the upper row of teeth, so that when the lower dental row moves, the tubercles moving against the corresponding tubercles of the upper row or vice versa form a flexus. A similar structure of teeth limits very much the possibility of the longitudinal displacement of dental rows with respect to each other, but then it provides an extremely close contact of the crushing surfaces of lower and upper dental rows. Since each tubercle and the flexus of its tooth play the role of mortar and pestle while processing the grains in the mouth, it can be fully understood why the tubercles are generally found in a good number on the molar teeth of the grain-eating rodents. This process can very well be traced in the structure of the teeth of the grain-eating hamsters such as Rhipidomys, Reithrodontomys and Peromyscus. Apparently, the three-row structure of tubercles in the forms of Muridae was also just a progressive feature enabling it to be excluded from the Old World grain-eating bunodont, the mouse-like hamsters now available only in the New World and Madagascar (if the Iranian form Calomyscus is not considered).

The trajectory of motion of the mandible depends to a great extent on the mutual arrangement of tubercles with respect to each other. The opposite arrangement of tubercles with respect to each other is a characteristic (though varying in degree) of all the real palearctic hamsters (Crietini) and particularly of the Central Asian hamsters, Phodopus having a predominance of transverse movements of the mandible. For this the width of the molars increases a little in real hamsters. Since the role of M^3 during the processing of food matter is significant (it is less than the role of M^1, because of the smaller length of the arc of trajectory described by M^3 in comparison with M^1 with the angle of deflection of the lower jaw to the side remaining the same from the position of closed molars M^3 of such forms is not greatly reduced. But since a strong transverse displacement of the mandible in the case of a two-row arrangement can lead to 'idle motion' when the tubercles of the lower row do not meet the corresponding flexures of the upper row; the magnitude of lateral displacement of the lower jaw is limited and so such arrangement of tubercles of molars in the grain-eating forms of the family Crecitidae should be taken as "inadaptive" (in the sense proposed by V.O. Kovalevskii).

When the arrangement of tubercles of the external and internal rows is alternative with respect to each other (Reithrodontomys, Peromyscus, Calomyscus, etc.) the longitudinal movement of the lower row with respect to the upper one is dominant. In this case, when the mandible moves forward 1-2 tubercles in length, the particular tubercle is placed against the corresponding flexus, whereas a vigorous transverse movement of the jaw may lead to such a condition when tubercles will be placed opposite tubercles and flexus opposite flexus. In this longitudinally oriented type of crushing movements generally M^1 and M^2 are especially complicated whereas M^3 which ceases to touch the lower molars when the movement of the lower jaw is insignificant, may be reduced. The relative width of the dental row of the seed-eating forms with alternative arrangement of tubercles is a little less than those with compressed masticatory surface and with cellulose nutrition. The alternative type of arrangement of tubercles of seed-eating rodents must be taken as adaptive.

A few forms of hamsters, changing over to the carnivorous type of nutrition (piscivorous Ichthyomys, Rheomys, Daptomys, Anotomys etc., insectivorous Oxymycterus, Lenoxus, Blarinomys), undergo the following transformations of molars:

higher caloric value of the animal food than seeds leads to a decrease in the volume of the food consumed and its breaking up does not require a thorough biomechanical processing because of its reduced quantity and softness. Therefore, additional tubercles of teeth (mesostylus, anterior and posterior cingula, etc.) undergo reduction. The main biomechanical task, namely, gripping and grasping of the prey, falls on incisors but the molars possess sharper tubercles. A few tubercles of teeth (in comparison with seed-eating forms) are situated opposite, and the relative width of the dental row increases. The opposite and broad arrangement of tubercles facilitate grasping of the prey, sometimes much larger animals because the force exerted by the prey is directed longitudinally forward and the teeth holding the prey are transversely arranged. It is easy to understand that the alternative arrangement of tubercles and an increase in their number (always associated with the decrease in the relative height of tubercles) would appear to be biomechanically disadvantageous in this case. The reduction of the dental system on the whole is characteristic of the carnivorous forms of Cricetidae. This reduction always begins from the molars, but in the insectivorous forms the incisors may also be affected. Similar transformations are also experienced by the dental system of the carnivorous forms of Muridae. The opposite position of high tubercles of the molars is characteristic of the African carnivorous mice, Deomyinae. Apart from the carnivorous hamsters, reduction of molars begins in the pisciverous mice, Hydromyinae (number of molars decreases from three to two and even one), and also in insectivorous mice, Rhynchomyinae. In Rhynchomys incisors are also appreciably reduced.

Transition from the protein to the cellulose type of nutrition is connected with the transformation of the function of maxillary apparatus which tends, henceforth, to copy more and more the work of the grater in its evolution. The dental system, developing into the cellulose type of nutrition, loses the tubercular structure of molars, and manifests significant exposures of the dentinal fields fringed with the sharp enamel crests, which mutually intersect while processing cellulose food. The biomechanical advantage of longitudinal grinding movements of mandible compared with the transverse movement is shown in Chapter I. Depending on the prevalence of a particular type of movement, enamel crests which are always situated across the direction of the movement of dental rows are arranged accordingly: in the longitudinal type of masticatory movements the crests are arranged longitudinally. This is quite clear from the comparison of the structure of the teeth close to the family of the Madgascan Cricetids, Brachyuromys and Brachytarsomys (see Fig. 75, 76).

Muroidea, following the main course of development of grinding movements of mandible in the rodents proceeded through the development of the longitudinal grinding. Adaptation to longitudinal grinding in the structure of the molars as correctly noted by Hershkovitz (1955), proceeded in two directions namely, in the direction of the "terraced" and "plane" forms of the gnawing surface of teeth (Fig. 12). The terraced form of gnawing surface characteristic of many forms of Cricetidae (Holochilus, Nesomys, Gymnuromys, etc.), restricts the lateral movements of the mandible by its structure and biomechanically provides an advantageous longitudinal grinding. But, many hamsters (Chinchillula, Andinomys, Neotoma, etc.). specialized in the cellulose type of nutrition and all field voles (Microtinae) are characterized by having the "plane" form of gnawing surface. Transformations in the structure of the masticatory muscles in field voles have made the movements of the mandible impossible, and in hamsters specialized for the cellulose type of nutrition, they should be considerably limited (Vorontsov, 1963b). Prevalence of longitudinal grinding leads to an increase in the relative length of the dental row and the number of enamel loops. It is not difficult to note that the increase in the number of enamel loops, in the opposite arrangement of the tubercles, must cause a greater elongation of a tooth

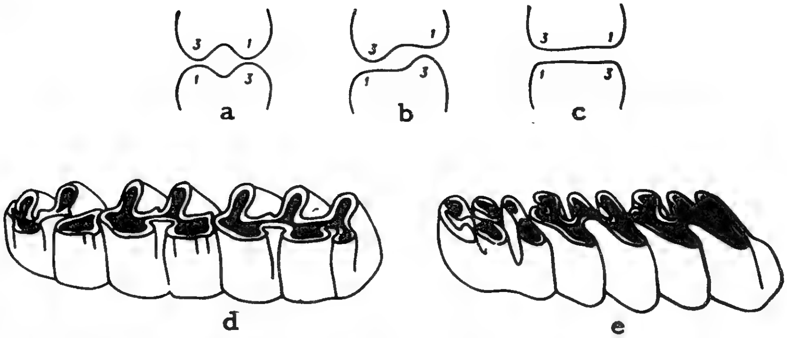


Fig. 12: Degree of thickening of molars in Cricetidae. After Hershkovitz, (1955). 1, protocone and protoconid; 3-paracone in the upper and metaconid in the lower row; (a) scheme of the tuberculate masticatory surface of hamsters; (b) scheme of terraced masticatory surface of hamsters; (c) scheme of thickened masticatory surface of Cricetidae; (d) terraced masticatory surface of the right, upper dental rows of a young hamster, Holochilus magnus Hershk; (e) thickened masticatory surface of the right, upper dental rows of the young hamster, Holochilus brasiliensis Desm.

than in the alternative arrangement; elongation of the dental row itself cannot have its own limit. In the opposite arrangement of tubercles that form enamel prisms, a greater part of the longitudinal course of the dental row, seems to have free motion, when the prism of the upper row is set against the flexus of the lower row (and vice versa). In this way, the opposite arrangement of the derivative tubercles, i.e., enamel prisms is not advantageous biomechanically. Actually, the opposite arrangement of the enamel prisms from the forms having a "plane" gnawing surface is found only in hamster, Irenomys and in field-voles less specialized in the cellulose ;type of nutrition. Alternate arrangement of enamel prisms is biochemically advantageous and from the point of view of evolution it is characteristic of the majority of herbivorous hamsters and field-voles.

Three-row arrangement of tubercles in Muridae leads to fusion of dentinal fields in most of the flat-crowned forms (Nesokia, Otomyinae) in opposite manner and not in alternative manner. In other words, absolute specialization to the seed-eating type of nutrition (three-row arrangement of tubercles) limits the possibility of transformations of molars, in the flat-crowned shape of tooth biomechanically advantageous to the cellulose type of nutrition. Maximum specialization in the direction of alternative arrangement of enamel fields is achieved in the mice, *Eropeplus* (see Fig. 83c), which is very far from those perfect adaptations of the cellulose type of nutrition, which are observed in Cricetidae.

Finally, the height of the crown increases with a sharp increase in the quantity of coarse feed used: from brachydont, (*Oryzomys*, *Rhipidomys*, *Cricetus*, *Mesocricetus*, *Hesperomys*, etc.) the molars are transformed into mesodont (*Neotomodon*: *Neotoma*, *Phyllotis*, *Andinomys*, *Fibrini*, etc.), and finally acquire constant growth and become hypsodont (*Lemmini*, *Microti*).

3. Change in the structure of the masticatory surface of molars with the age, within the groups and between the groups.

All forms of Cricetidae, at least in the early stages of growth, have a 2-rowed tuberculate structure of the masticatory surface of molars. Even the young forms of Microtinae retains the tubercles in the place of future prisms of molars (Ognev, 1948, 1950). But the fate of these tubercles is very different depending on the type of the masticatory movements. The data obtained by B.S. Matveev (1963), confirm, that the number of layers of the enamel organs of the rats correspond to the number of tubercles of the adult. This indicates that the tubercles of the tooth of the rodents, Muridae, are evidently not homologous to the tubercles of the molars of marsupial, insectivorous and carnivorous forms and thus the terms "protocone", "paracone", "metacone" and so on, derived from the tritubercular theory of Kopp-Osborn, may be used in relation to the teeth of the rodents only conditionally.

The thickness of the enamel layer at the top of the tubercles is extremely varied in bunodont and brachydont forms. The enamel layer on the top of tubercles is very thick in *Reithrodontomys*, *Peromyscus*, *Rhipidomys* and other seed-eating forms of Cricetidae. On the other hand, the thickness of the enamel layer on the top of the tubercles of voles and brachydont hamsters is not much while the thickness of the enamel layer in the main tubercles of these forms is quite considerable. Therefore, the juvenile tubercles of brachydont forms of Cricetidae wear out in the first days of independent nutrition of the animal whereas in the seed eating hamsters the tubercles are retained for the greater part of life. In forms with "terraced" masticatory surface (Holochilus, Gymnuromys), the thickness of the enamel layer is not uniform in the internal and external sides of the tooth. On one side the thickness of the enamel layers is at a higher level than on the other. As a result of uneven wearing of the juvenile tubercles from different sides, the masticatory surface may not have the terraced form.

The bunodont forms also do not have uniformly thick enamel layers. Tubercles of the upper molars usually have a thicker layer in the front than in the rear; tubercles of the lower molars are characterized by a reverse ratio. On the upper and the lower molars of the bunodont forms, tubercles are covered by a thicker layer of enamel from the outer side than from the inner. The differences in the thickness of the enamel covering of tubercles leads to their automatic sharpening as rubbing takes place against the tuberculous surfaces and the tooth is retained in the grown-up animals.

Young animals always possess relatively higher crown than the adults of the same species (this, of course, does not concern forms with real hypsodont tooth). According to the degree of transition from a protein to a cellulose type of nutrition, the tooth loses the tuberculous structure and attains a thick gnawing surface, i.e., attains the characteristic of the adult tooth even in early stages, or it changes from the brachydont to the hypsodont type, i.e., retains the characteristic of the young stage, even in adults as in the animals of original forms. This contradiction in the directions of development of the molars (adult feature while young and vice versa) takes place by a decrease in the thickness of the enamel layer on the tips of the tubercles and by the displacement of the juvenile stages of development of tooth in the more grown up stage.

As expressed by Hooper (1957), the concept about the strict constancy of the figure of the masticatory surface of the molars formed by the alternation of enamel and dentinal parts is not correct. The figure of the masticatory surface of the molar tooth of the grown up animal greatly varies depending on the height of the so-called primary and supplementary tubercles and their connecting crests (Fig. 13).

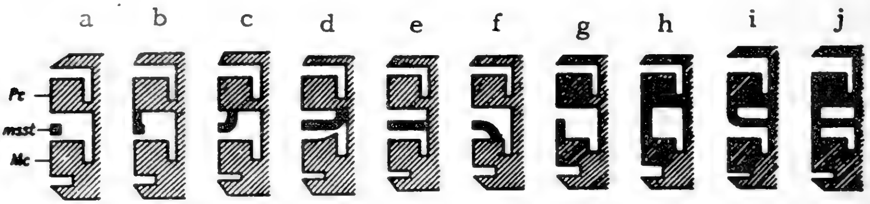


Fig. 13: Sketch of the possible ways of link of mesostylus with mesoloph paracone and metacone. After Hooper (1957), with changes and additions. (a) original state; (b - j) different types of link of mesostylus with the neighboring loph and cone.

Let us trace the fate of the mesostylus at different combinations of heights surrounding its cones and lophs:-

if the height of the mesoloph is a little less, equal or a little more than the height of the mesostylus and the labial loph extending from the mesostylus to paracone and metacone then the mesostylus joins the exposed portion of the axial dentinal area of tooth on grinding. (See Fig. 13, e; for example Reithrodontomys (Aprodon) tenuirostris, see Fig. 41, a);

if the height of the mesoloph is not only much more than that of the labial loph extending from mesostylus to paracone and metacone but also more than the height of the mesostylus itself, then the mesostylus may remain with the independent isolated tubercle (see Fig. 13, a for example Reithrodontomys (str.) fulvescens, see Fig. 41, b);

if the depth of the mesoflexus is much less than the depth of the paraflexus and the metaflexus then on grinding the mesostylus may merge with paracone (see Fig. 13, b, c; for example, Ichthyomys soderströmi, see Fig. 69 a; M^1 in Scotinomys teguina, see Fig. 48, a);

if the depth of the mesoflexus from the labial side is less than from the medial side, then the mesostylus fusing with paracone unlaces the fossetus covered by enamel i.e., mesofossetus (see Fig. 13, u, for example Neacomys spinosus, Nectomys (s. str.). squamipes, see Fig. 33, 36, c);

if the depth of the metaflexus and the mesoflexus from the labial side is less than from the medial side, then the mesostylus joins from the labial side with paracone and matacone unlacing mesofossa and metafossa (see Fig. 13, h, j; for example Nectomys (Sigmodontomys) alfari, Scotinomys tequina, see Fig. 36, c, 48).

In individual cases, the flexures of the lingual and the labial sides may join with each other. The figure of this type is characterized more by flat-crowned mice (Muridae) and sacculate rats (Geomyoidea) i.e., forms having a primarily three-row arrangement of tubercles can also be found in Cricetidae. So, in Nesomys rufus (see Fig. 71, a) paraflexus joins with hypoflexus and in Bachyuromys ramirohitra parafossa joins with hypoflexus (see Fig. 75a). The metaflexus in Brachytarsomys albicauda, which is like the molars of the Madagascan field vole may join with the hypoflexus. However, similar flexures extending across the entire tooth, are not typical for Cricetidae.

Transformation of the molars from tuberculate to flat-crowned is definitely associated with the relative thinning of the enamel layer on the rudiments of tubercles in the flat-crowned forms. In field-vole this process attains extreme development. Obviously the selection should have been in the direction of elimination of individuals with early developed roots. The entire variety of the structure of the molars of Cricetidae is connected with the selection to retain the juvenile surface even on the adult crown (in seed-eaters) or to acquire an effaced masticatory surface very early by the young animals while retaining the tall crown during the whole life. In this way age variability of the structure of the molars provides vast material for selection in different directions.

In spite of a large number of investigations carried out chiefly on field-voles (Ognev, 1948, 1950; Zimmermann, 1937, 1958, Stein, 1958, Kratochvil, 1959), on the significant range of variability of molars, the idea about a small intraspecific variability of the structure of molars still exists in systematics. Meanwhile the intraspecific variability of the structure of the molars in hamster is very much significant. In some forms, even characteristics such as the presence and absence of supplementary tubercles vary widely. Thus, in *Mesocricetus nowtani*, the mesostylid can exist on M_2, butit might be in a reduced form. The variations in the figure of masticatory surface of the molars formed by the differentiation of the enamel and dential fields are more noticeable. A little more or less height of loph connecting separate tubercles of molars in different species of *Peromyscus* gives different figures in different individuals while grinding (Hooper, 1957).

The figure of the masticatory surface of M^3 is particularly changed because of the fact that, as in field voles, this tooth takes the least part in the process of crushing food (Voronstsov 1961b, 1963d). Small individual distinctions in the manner of processing food, greater or smaller amplitude of displacement of mandible and participation of M^3 connected with it lead to different degrees of wearing to the various parts of the tooth while processing foodmatter causing different figures on the masticatory surface.

Hooper (1957) in his work, dedicated to the study of variability of the structure of molars of *Peromyscus* based on the detailed study of the structure of the masticatory surface of teeth in 1877 specimens of this genus, showed that the structure of the first and second molars of the lower and upper rows varies very greatly.

Thus in *Peromyscus eremicus*, the mesostylus is developed in 63% of the individuals on M^1, in 21% on M^2 and only in 19% on M^1 and M^2. In the same species the mesostylid is developed in 13% on M_1 in 6% on M_2 but in 5% of individuals on M_1 and M_2. The mesostylus and the mesostylid are present both on M^1 and M_1 in 7% and on M^2 and M_2 in less than 2% of the individuals. Finally, the mesostylus and the mesostylid are developed both on M_1 and M_2 and M^1 and M^2 in less than 2% animals. Similar data were received for mesoloph and mesolophid and hypostylus and hypostylid by Hooper for 17 species of the genus *Peromyscus*.

The data of Hooper convincingly speak about the exceptional range of the intraspecific variability of the structure of the masticatory surface in small hamsters. Wide intraspecific and increasing variability of the structure of molars in field-voles was convincingly shown by Ognev (1950) and Zejda (1960). These materials must be applied carefully to the systematic and Paleontologic descriptions made exceptionally (or mainly) on the basis of the morphological study of the dental system of single individuals. The materials of Hooper also show exceptional plasticity of the dental structure which cannot serve as a base for the selection of forms with biomechanically advantageous design of tooth.

Peculiarities of nutrition and the manner of processing food matter in different species are reflected to a great degree on the structure of the masticatory surface. Even small differences in the degree of density and in the composition of food matter lead to great changes in the form of the masticatory surface as a result of distinction in the degree and direction of grinding. On the contrary, similarity in the type of nutrition and in the manner of processing the food matter at the similar initial plan of the structure leads to surprising example of parallelisms in the structure of the dental system.

A comparison of the variability of the dental system both between different species and different groups with that of the organs of the digestive tube shows that the dental system is the most labile of the organs of the digestive system. This fully agrees with the principle of greater variability of the exosomatic than the endosomatic organs observed by A. N. Severtsov. Such a variability of the dental system, providing material for differentiation of forms must be applied with great care to the phylogenetic construction based chiefly on the morphological study of the molar teeth.

While studying regional materials, many taxonomists did not investigate the amplitude of the variability of the dental system in the whole group, and even introduced into the group diagnosis the features not at all characteristic of the whole group. This happened in the case of hamsters; the tuberculate structure of the molars of the palearctic genera was taken (unlike flat-crown structure in field-voles) as a distinctive feature of the this subfamily and introduced into the diagnosis (Vinogradov, Argiropulo, 1940; Ognev, 1948; Vinogradov, Gromov, 1952).

The structure of the dental system of the herbivorous hamsters, *Neotoma*, *Xenomys*, *Nelsonia*, *Chinchillus*, *Andinomys*, *Reithrodon*, *Sigmodon*, etc. closely resembles the structure of molars of the primitive cheek-toothed field-voles belonging to the Fibrini tribe. Adaptive radiation of the Madagascan Cricetidae, *Nesomyinae* led to a surprising convergence and parallelism in the structure of molars with other rodents. The structure of the molars of *Macrotarsomys* highly resembles that of *Calomyscus*; *Brachyuromys ramirohitra* is so similar to the African *Tachyoryctes* by the structure of molars that Ellerman (1941) and Hooper (1949) brought them to the closely allied group; molars of *Eliurus* highly resemble *Nesokia*, *Brachytarsomys* of the primitive Microtinae, and *Gymnuromys* convergently resembles *Muscardinus* by the structure of the molars. From all these facts we may conclude that while using the data on the structure of the dental system, for phylogenetic construction, greatest care and ability to distinguish the cases of adaptive radiation, parallelism and convergence are needed.

4. Structure of the molar teeth of Cricetidae in connection with their position in the system of Muroidea.

Disorderly arrangement of numerous tubercles of teeth in the primitive specimens of the family Dipodidae (*Sicista*, *Plesiosminthus*-Dipdoidea), mole-rats (Spalacidae) and bamboo-rats (Rhizomyidae) is replaced by an orderly two-row (Cricetidae) or three-row (Muridae) arrangement of tubercles in Muroidea. This process of oligomerization of homologous parts of the tooth (in a sense, introduced in the concept by V.A. Dogel) goes along with the reduction of premolars in the same row. It cannot lead to the reinforcement of masticatory movements of mandible and to the restriction of its directions that take a very definite trajectory (movements in the vertical plane while crushing seeds and, finally, movements in the horizontal plane while processing cellulose nutrition). This process of differentiation of masticatory movements in the same row leads to the division of the lateral masticatory muscle (M. mass. lateralis) into three parts.

Orderly arrangement of tubercles (or their rudiments) and the differentiation of lateral masticatory muscle are the distinctive characteristics of the group Muroidea. The only feature by which this largest super family of mammals is divided into two main families - Cricetidae and Muridae - is a two-row or a three-row arrangement of the tubercles on molars. A thorough study of the morphology of hamsters and murines undertaken by us did not indicate other features for the differentiation of these groups. It is necessary to establish, whether this characteristic is principally important, whether it offers a basis for the separation of these groups as it is done by Vinogradov (1933), Vinogradov and Arginopulo (1940), Vinogradov and Gromov (1952), Simpson (1945), Grasse and Dekeyser (1955) after Milier and Gidley (1918) or else the large super family of Muroidea should be considered as monotypic group of Muridae, following Ellerman (1940, 1941), Ognev (1948), Heptner (Heptner, Morozova, - Turova, Tsalkin, 1950) and many others.

The opposite arrangement of tubercles of molars in dwarf gerbils (Gerbillinae) closely resembles those of Murinae as correctly noticed by Stehlin and Schaub (1950), and in this way, it is apparently similar to the original structure of the tooth for the ancestors of murines. Some of the living specimens of Murinae (Acomys, Steatomys) possess only incomplete set of tubercles of the supplementary third row when according to Stehlin and Schaub, the minute state is primary and not associated with the secondary reduction ofthe supplementary row of the tubercles.

In Geomyoidea, the three-row arrangement of tubercles on the masticatory surface of the molars is found like in Murinae (see Fig. 84a). However, many specimens of that superfamily (Geomys, Heteromys) acquire flat-crown surface with the transition to the cellulose type of nutrition when the dentinal fields are formed by the fusion of three tubercles of one transverse row (see Fig. 84, b, c) i.e., in the same way as in flat-crowned Muridae (Nesokia, Malacomys, etc.).

Thus, the three-row arrangement of tubercles on the molars cannot be considered as a feature characteristic of Muridae only.

Peculiar difficulties for separating Muridae from Cricetidae are experienced while studying the structure of the molars of African Otomyinae. Molars of Otomyinae are extremely far from

Cricetinae and Murinae. Their masticatory surface may disappear from the teeth of not only Murinae but also Cricetidae having an opposite arrangement of tubercles which are characteristic of, say Gerbillinae. Until the study of embryonal development of Otomyinae teeth is made the problem of regularity or irregularity of the division of Muroidea into two large groups - Muridae and Cricetidae - may not be finally solved. The functional significance of a three-row structure of teeth in Muridae is extremely great. This form of the molars is better adapted to the processing of seed food. Evidently, the biomechanically advantageous structure of the teeth of Muridae was one of the important progressive characteristics of this group which resulted in liberating the muroid hamsters from the temperate and tropical zones of the Old World.

On the other hand, as it was already pointed out the three-row opposite arrangement of tubercles is less advantageous, in the transition from tuberculate to flat-crowned molars than the two-row, alternate arrangement from which the teeth of the progressive Microtinae are derived.

In this manner, specialization (progressive compared with Cricetidae) of Muridae teeth for the seed-eating type of nutrition was a factor which limited the possibility of adaptation of Muroidea to the herbivorous type of nutrition. On the contrary, the alternate two-row arrangement of tubercles on the teeth, specialized for the seed-eating type of nutrition of Cricetinae and more primitive than that of Murinae, was the base from where the teeth of advanced herbivorous hamsters and field-voles could develop.

Thus, the differences in the structure of the molar teeth between Cricetidae and Muridae should be considered as a characteristic of paramount functional significance and the division of Muroidea into Cricetidae and Muridae (this view is considered by the author in this work) is needed in further studies.

5. Transformation of Molar Teeth in the Phylogenesis of Cricetidae.

Oligocene Melissiodontinae, whose position in the system of Muroidea has not yet been explained, possess molars that have an extremely complex structure of masticatory surface. Tubercles are not arranged in rows and their number exceeds the known number for all real Cricetidae (Fig. 14). Numerous tubercles are not high and the cavities between them are not sufficiently marked which is biomechanically not advantageous. A.I. Argiropulo considers that Melissiodon possessed real quadritubercular tooth with highly complicated supplementary tubercles and crests. He thus described the structure of the molars of Malissiodon*.

Fig. 14: *Structure of the masticatory surface of the molars of Melissiodon quercyi Schaub. After Stehlin and Schaub (1950). Right rows: (a) upper; (b) lower. Note the irregular arrangement of tubercles.*

"The quandritubercular molars of the mandible have a nearly uniform length. The crown is divided by the enamel crests into hollow pits. The connections of the tubercles are designed in the plan, characteristic of hamsters, but greatly modified. The unnamed tubercle of the lower first molar (anteroconid-N.V.) is not long, unilobate or biolobate. The

---

** Here and hereafter, the description of Oligocene Cricetidae, given by A.I. Argiropulo, who was engaged in the study of Paleo tological Cricetidae, is cited. "Geological history and basic features of the evolution of Cricetidae in the tertiary period" - this text within quotation marks are taken from the incomplete description of Argiropulo, preserved in the Zoological Institute of Academy of Sciences, USSR.*

first upper molar is much elongated with a broad bilobate, unnamed tubercle (exterpocone and interpocone - N.V.)".

Traces of oligomerization of the number of tubercles and their arrangement in a proper order are found in the majority of the Oligocene Cricetidae.

According to Stehlin and Schaub (1950) Paracricetodon (Fig. 15) known from the Stampa stage of Europe is characterized by the most primitive structure of teeth. However, Paracricetodon, and all other members of the Oligocene Cricetidae possessed a clearly marked two-row arrangement of tubercles. Anterocone on M^1 is not divided into two tubercles and M^1 has thus, five tubercles. The tubercles have been arranged oppositely.

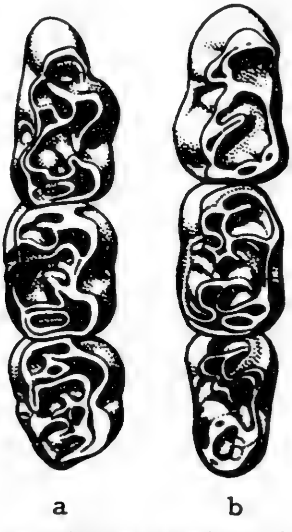


Fig. 15: Structure of the masticatory surface of the molars of Paracricetodon spectabilis Schlosser. After Stehlin and Schaub (1950). Right rows: (a) upper; (b) lower.

A. I. Argiropulo observed:

"The specimens of Paracricetodon are, in general, close to Cricetodon, but have a still more primitive structure of molars than the oligocene species of Cricetodon, while in the combination which does not repeat in other forms, the third lower molar is long at the independent posterior branch of hypoconid. Protocones on M^2 and M^3 are with the independent branch (this branch usually remains connected with protocone in Cricetodon).

The connecting crest is extremely short. The inner cavity (bay) is superficial. A clear connection is observed in between the posterior edgings of the internal tubercles, (metaconid and enteroconid). Thus Paracricetodon stands very far from Cricetodon by the structure of the upper molars than by the structural features of the lower".

Oligocene specimens of the European genus of Cricetodon - Cr. collatum Schaub, Cr. gerandianum Gervais and other species of this genus (Fig.16) are also characterized by the opposite arrangement of tubercles and five-tuberculate M^1.

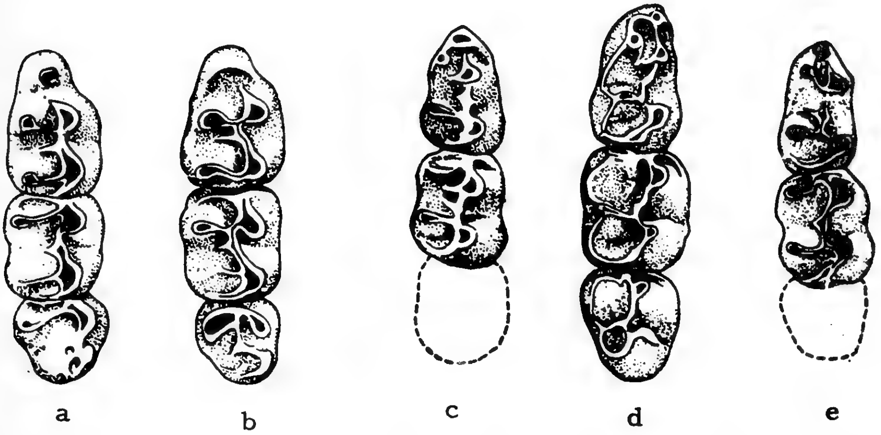


Fig. 16: *Structure of the masticatory surface of molars of Oligocene Cricetodon. After Schaub (1925). Right rows: a, (c) Cricetodon collatum. Schaub (a)-Upper, (c) lower; b, d - Cr. gerandianum Gervais (b - upper, d - lower); e - Cr. hauberi Schaub (lower row).*

A. I. Argiropulo gives some distinguishing features of all the forms of Oligocene Cricetodon:

(1) Tubercles of the lingual side (lower-row - N.V.) have an elongated form, and the middle crests are usually moved aside from the middle line of molars; (2) the spur of the meso-

stylid and the posterior branch of protoconid are well developed, the rear branch of hypoconid is also well developed, in some of the most ancient forms; (3) anterior supplementary tubercle on M_1 (anteroconid-according to terminology - N.V.) has a generally longitudinal loph; (4) metaconid often lies isolated.

As observed by Argiropulo, Cricetodon from the Stampa stage have the most primitive structure of molars. From the seven species of Cricetodon, known from the Stampa Stage "three have developed rear branches of protoconid, hypoconid and spur of mesostylid, in these the branch of hypoconid does not develop and only in Cricetodon huberi Schaub both these branches are not developed".

The structure of molars of Heterocricetodon, that is very distinct from Paracricetodon and especially Cricetodon indicates that the Oligocene hamsters of Europe were highly represented by various forms.

The masticatory surface of the molars of Heterocricetodon (Fig. 17) is compressed. The connection of tubercles of molars with enamel crests is highly complex and somewhat resembles Pseudotheridomys in its form; M^1 has five tubercles. The opposite arrangement of tubercles on the molars is retained in this genus.

Fig. 17: Structure of the masticatory surface of molars of Heterocricetodon helbingi Schaub. After Stehlin and Schaub (1950) Right rows: (a) upper; (b) lower.

The features of the structure of teeth of Heterocricetodon are characterized by A.I. Argiropulo in the following manner:

"Elements of labial side (maxillary series- N.V.) form elongated cross folds. Thus, on the front molar there are six cross folds formed by unnamed tubercles (anterocone-N.V.), anterior branch of protocone, tiny crest of protocone (anterior cigulum-N.V.), spur of mesostylus, crest of metacone and posterior labial cingulum.

Large sized Cricetops from the upper Oligocene of Kazakhstan and Mongolia possessed six-tuberculate M^1 and five-tuberculate M_1 (Fig. 18). The opposite arrangement of well developed tubercles is very characteristic of this genus.

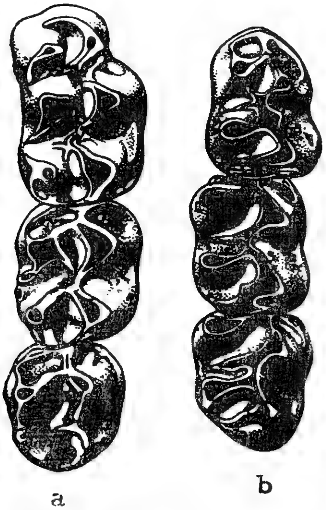


Fig. 18: Structure of the masticatory surface of molars of Cricetops dormitor Matth. at Gronger. After Stehlin and Schaub (1950).

The posterior branch of protoconid, writes Argiropulo, is in the form of a rear edging of trigonide and it has the shape of a false spure of mesostylid on M_2 and M_3. Hypoconid has a rudiment of the rear branch. The unnamed tubercles on M_1 (anteroconid-N.V.) have a very simplified structure, and those on M^1 are wide and bilobed (extero-and intero anterocones-N.V.). According to the details of the structure of molars, Cricetops stands totally by itself among other forms of Cricetidae, since a mixture of the sufficiently primitive and more advanced characteristics found in the forms of Neogene is discovered. For example, the formation of a bilobed, unnamed tubercles on M^1 (anterocone-N. V.) is never found in Oligocene Cricetidae and noticed only in a fraction of the forms of Miocene; this feature fully appears only in Pliocene and in recent forms. At the same time the unnamed tubercle on M_1 (anteroconid-N. V.) appears to be a highly primitive structure as seen in most of the earlier forms of Cricetodon or in Paracricetodon.

Oligocene forms of Cricetidae of North-America and Asia have many similarities in the structural plan (Argiropulo, 1940), Eumys, Leidymys and Scottimus preserve the five-tubercular structure of M^1 and M_1. However, Middle Oligocene Eumys is characterized by well marked tubercular structure of the masticatory surface having almost an opposite arrangement of tubercles on the molars, and in the Middle Oligocene Leidymys this tuberculation develops further, whereas the greatly compressed masticatory surface is characterized by Late-Oligocene Scottimus.

The molars of Eumys (Fig. 19) is characterized by the significant development of the supplementary tubercles and crests. Anterocone is not divided into two tubercles, but from it a short and high labial crest and a long sloping lingual crest branchs out aside. From the labial side, the crest, which can be connected with anteroloph and pinch a small enamel socket, branches out backwards from anterocone. The main tubercles of teeth are placed oppositely. Mesostylus is well developed. The marginal lingual crest connecting protocone and hypocone in such a way that while grinding vigorously hypoflexus is transformed into hypofossa, passing through the hypostylus. Posterior cingulum is very well developed, postflexus goes deep into the body of tooth. Posterior cingulum of M^1 and anterior cingulum of M^2, and posterior cingulum of M^2 and anterior cingulum M^2, and posterior cingulum of M^2 and anterior cingulum of M^3, as a matter of fact, form supplementary transverse rows of tubercles. Tubercles of labial side of the upper dental row are arranged notably opposite the lingual side of lower dental labial crest which passes through hypostylid are well developed. Tubercles of the lingual row of lower molars are slightly shifted forward with respect to the tubercles of the labial row.

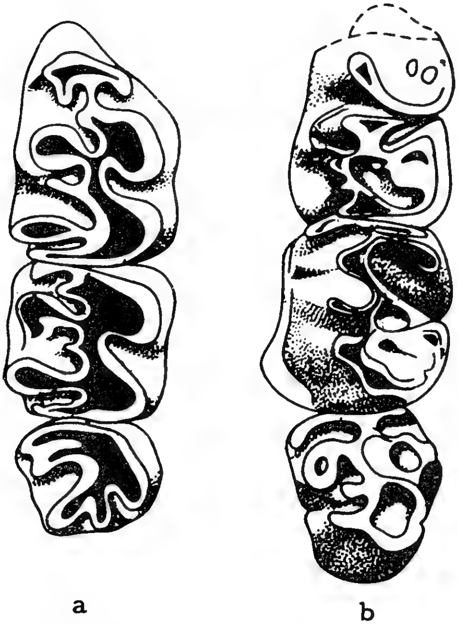


Fig. 19: Structure of the masticatory surface of molars of Eumys elegans Leidy (White River, USA, Oligocene, from the collection of V.O. Kovalevskii; Collection of Geological paleontological Museum named after A.P. and M.V. Pavlovs, at MGRI (Moscow Geological Prospecting Institute) Orig. Right rows: (a) upper adultus; (b) lower subadultus.

Upper molars of Scottimus (Fig. 20) retain the opposite arrangement of tubercles; dentinal fields fuse together on each side in pairs: the field of protocone with the field of hypocone, and the field of paracone with the field of metacone; on the other lower molars of Scottimus the tubercles of lingual and labial rows are slightly displaced about each other which when the dentinal fields fuse diagonally set the enamel crest right which passes from the tubercles of the lingual row to those of the labial row. Thus the fields of protoconid and enteroconid are connected.

The structure of the upper molars of Scottimus resembles the structure of those of the modern Central American hamsters, Scotinomys; it is analogous to the selendont teeth of hoofed animals. The shape of Scottinus molars indicates the significant role of grinding movements of the mandible in transverse direction which is not characteristic of the overwhelming majority of

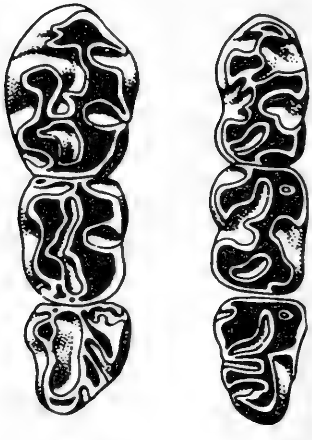


Fig. 20: Structure of the masticatory surface of the molars of ***Scottimus lophatus*** *Wood. After Wood (1937), from Stehlin and Schaub (1950) Right rows: (a) upper; (b) lower.*

modern Cricetidae. Similar "inadaptive" trend of specialization of the dental system in Scottimus seems to us as the "dead end" of evolution: actually we cannot derive the molars of subsequent Cricetidae of America including Scotinomys from the teeth of Scottinus.

Four genera in addition to Cricetops having highly specialized dental system are known in the Upper-Oligocene deposits of Asia. The most primitive of them by the structure of the dental system is Eumysodon described from Agispe* (Aral Sea).

The lower molars of Eumysodon have almost equal length (Fig. 21), M_1 is slightly longer than M_2 and M_3. The crown is brachyodont. The masticatory surface is tuberculate (Eum. - Crlovi Arg.) or compressed (Eum. spurius Arg.) Anteroconid is not divided into two tubercles. Anterior cingulum on M_1 is connected with the anteroconid along the lingual side of tooth.

**The question of the Oligocene Age of the idricoterie fauna of Agispe comes in for any further proof. The structure of molars of Eumysodon, and particularly Aralomys and Argyromys is extremely peculiar. According to the morphology of molars these forms are similar to the Miocene Cricetidae. According to the unpublished data of L. K. Glickmann, the deposits of Agispe may be related even to Middle Miocene. In "Principles of Paleontology" (1962) some authors relate the fauna of Agispe to the Late Oligocene, while others, to the Early Miocene.*

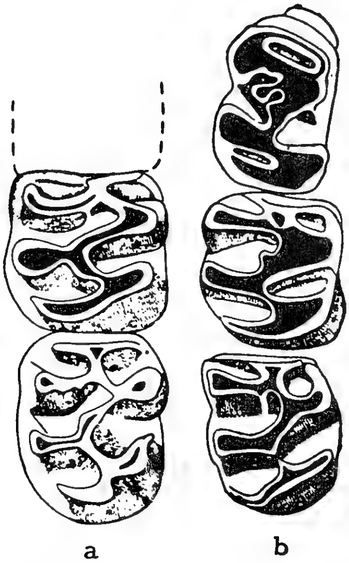
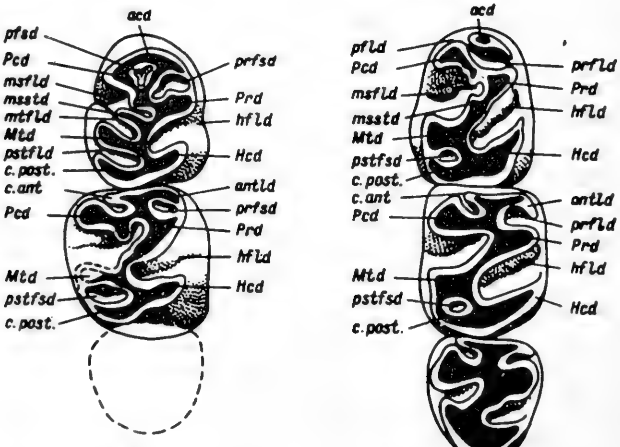


Fig. 21: Structure of the masticatory surface of molars of Eumysodon orlovi Arg. and Eumysodon spuris Arg. Orig. (a) Eumysodon orlovi Arg., type, M_2 - M_3 inf. sin., subad., mirror reflection (collection of the Institute of Paleontology, Acad. of Sciences, USSR, No. 210-261 or 210-262, Agispe, L. Miocene) orig.; (b) Eumysodon spurius Arg., type, M_1 - M_2 inf; sin. ad., mirror reflection (Collection of the Institute of Paleontology, Acad. of Sciences, USSR, No. 210-264, Agispe N. Miocene).

Protoflexid is separated by the elevated edge of enamel and transforms into shallow protofossetid. Postflexid is less deep than hypoflexid and metaflexid; on M_1 in Eum. spurius it is closed into postfossetid. The enamel socket the origin of which is not clear, may be left in the dentinal field of hypoconid. Protoconid grows a branch along the labial edge, and is directed backward, Mesostylid is developed but on grinding, it is fused with paraconid, pinching the mesoflexid. In the opinion of A. I. Argiropulo (in litt.) the presence of the branch of protoconid and the spur of mesostylid at the same time, a characteristic of the lower-Oligocene Cricetidae, should be considered as very primitive features whereas the compressed form of the masticatory surface of molars is the characteristic of the Neogene Cricetidae.

The features for adaptation to the cellulose type of nutrition are traced back to the structure of the molar teeth of huge forms of Cricetidae, Aralomys (Fig. 22), known in the Upper-Oligocene (?) deposits of the Aral Sea region. The crown is transitional between brachyodont and mesodont. Anteroconid is not divided into two tubercles and is poorly developed and lies apart. The paraconid is isolated from anteroconid as well as from protoconid fusing with each other by flexure formations of lingual and labial sides. Hypoconid is exceptionally stretched forward. On M_2, the anterior cingulum is turned down to the protoconid and has a well developed outgrowth from the lingual side. On M_3 this outgrowth is fused with the paraconid isolating the parafossetid. The posterior cingulum is marked on M_1 and M_2, its outgrowth directed forward pinches the postfossetid. The postfossetid is very shallow, wears off early and the dential field of the posterior cingulum merges with the dential exposure of metaconid. Diagonal direction of the enamel crest indicates the significant role of transverge grinding movements of mandible. As noticed by A. I. Argiropulo, "in the structure of the middle molar, Aralomys does not even reveal the traces of such elements of archaic complex structure, which are so common for the Oligocene forms and partially found in Miocene also.



a b

Fig. 22: Structure of the masticatory surface of lower molars of Aralomys gigas Arg. and Ar. glikmani Vorontz. After Vorontsov (1963 a). (a) mirror reflection of left M_1 - M_2 Ar. glikmani Vorontz? type (collection of the Institute of Paleontology, Acad. Sciences, USSR, No. 1978-1; (b) right M_1 - M_3 of Ar. gigas Arg., type (Collection of Institute of Paleontology, Acad. of Sciences, USSR, No. 210-263, Agispe; L. Miocene ?

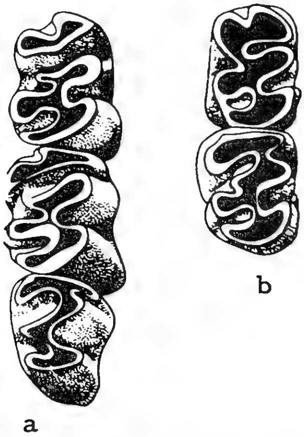


Fig. 23: Structure of the masticatory surface of the lower molars of Argyromys (= "Schaubeumys") aralensis Arg. and Arg. (= "Schaubeumys") woodi Arg. Orig. (a) Arg. aralensis Arg. M_1-M_2, dext., subad., type (collection of the Institute of Paleontology, Acad. of Sciences USSR, No. 210-261 Agispe, L. Miocene?); (b) Arg. woodi Arg. M_1-M_2, sin, mirror reflection ad., type (collection of Ins. of Pal., Acad. of Sci. USSR), No. 210-262, Agispe; L. Miocene?).

Argyromys Schaub ("Schaubeumys" Arg.) (Fig. 23) described from the same deposits as the previous genera was characterized by the highly specialized dental system. The masticatory surface of molars is compressed and the crown is mesodont. Tubercles on the lower molars are situated alternately, which leads to the diagonal fusing of dentinal fields. However, the front dentinal fields were merged oppositely and in Argyromys aralensis Arg. these were not joined with the tubercles occurring behind. Anteroconid is shifted nearer to the labial side of the tooth, and paraconid is greatly moved forward. As a result, a bi-tuberculate structure of the anterior margin of M_1, greatly resembling the latest hamsters having developed extero- and interoanteroconid. Paraflexid is moved much forward and is situated at the place of the late developing anteroflexid. The well developed mesostylid functionally plays the role of the paraconid; the paraconid carries out the function of the interoanteroconid, and the anteroconid, that of the extero-anteroconid. In this way, the structural plan of M_1 in Argyromys externally resembles the Neogone Cricetinae having six-tuberculate M_1. But this is similarly convergent, in as much as the similar structures of the teeth are formed from different rudiments. On M_2 the paraconid also is greatly displaced forward and the anterior cingulum is labially moved; dentinal fields of these tubercles are arranged oppositely and in Arg. aralensis they are not connected with the tubercles that lie behind. Arg. Woodi Arg. is characterized by a more and more compressed masticatory surface; the postflexid may be closed into the post-fossetid. Schaub (1958) observes that the structure of the molars of Argyromys resembles the structure of the masticatory surface of the Miocene Anomalomys but Anomalomys possesses a higher crown and a more compressed masticatory surface with highly developed fusion of dentinal fields.

The width of the divergence of Cricetidae in the Late Oligocene is particularly emphasized by the discovery of the striking Cricetid, Selenomys Matth. et Grand. (Fig. 24) from the formations of Tatal-Gol in Mongolia, like the North American Scottimus which lived at the same time and the latest Central American Scottinomys, the dentinal fields of the upper dental row,

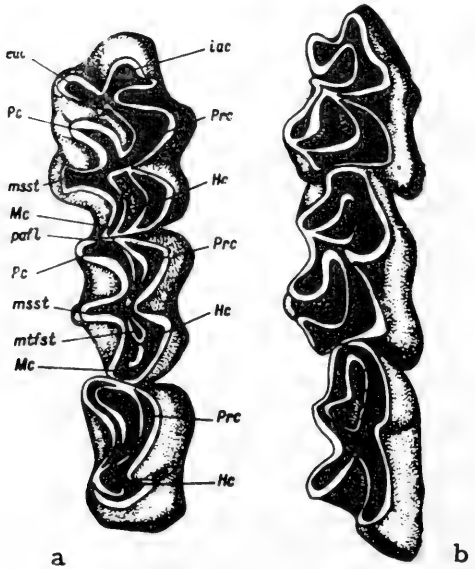


Fig. 24: Structure of the masticatory surface of Selenomys aff. mimicus Matth. et Grand. Orig. (a) upper right row (collection of Inst. of Paleont. Acad. of Sci. USSR No. 475-511/3548. Tatal-Gol, Mongolia; Oligocene); (b) lower left row, mirror reflection (collection of Inst. of Paleont., Acad. of Sci., USSR No. 475/3823. Tatal-Gol, Mongolia; Oligocene).

merge on the lingual side and separately on the labial side, after which along the middle line or the margin of tooth, the exposure of dentine of the lingual and labial sides can merge with each other. As a result, the structure of the upper molars of *Selenomys* imitates the selenodont teeth of the hoofed animals. Reduction of the initial tuberculate structural plan in *Selenomys* went even further than in *Scottimus*. As truly mentioned by Stehlin and Schaub, (1950), the lower molars of *Selenomys* are even more striking than the upper ones. M_1 has an undivided anteroconid; the tubercles are arranged alternatively and the dentinal fields merge diagonally. M_2 and M_3 resemble each other and are distinct by "selenodont form".

On completing the review of the structure of the dental system of Oligocene Cricetidae, let us mention that by the Late Oligocene, the Cricetidae of Asia and America have already achieved a great diversity in the structure of the dental system. The majority of the forms possesses the tuberculate structure of the tooth, whereas a number of forms of Cricetidae acquired clearly a compressed masticatory surface and mesodont crown, with the transition to a mixed nutrition.

Miocene Cricetidae, show an example of further complication of the tuberculate structure of tooth, associated with further specialization to the grain-eating type of nutrition, and the specimens losing the tuberculate structure of tooth and gaining the loop-shaped, field-vole like form of the masticatory surface of molars are found among the Miocene Cricetidae. The compressed masticatory surface of the molars is related to the transition from the grain-eating to the mixed type of nutrition and then to the exceptionally, grain-eating type of nutrition. This is caused by the significant process of their settling down to land which began in the Late Miocene.

Both the tendencies in the evolution of the Miocene Cricetidae, namely further complication of the tuberculate structure of the tooth and the compression of the masticatory surface of molars, are well traced among the Miocene specimens of the polytypic genus, *Cricetidon* (Fig. 25). Small forms of Cricetidae, *Cricetodon minus* Lartet possess a hexatubercular structure of the first upper molars, but their tubercles have a strictly opposite arrangement. Anteroconid is not divided into two tubercles (see Fig. 25, [illegible]

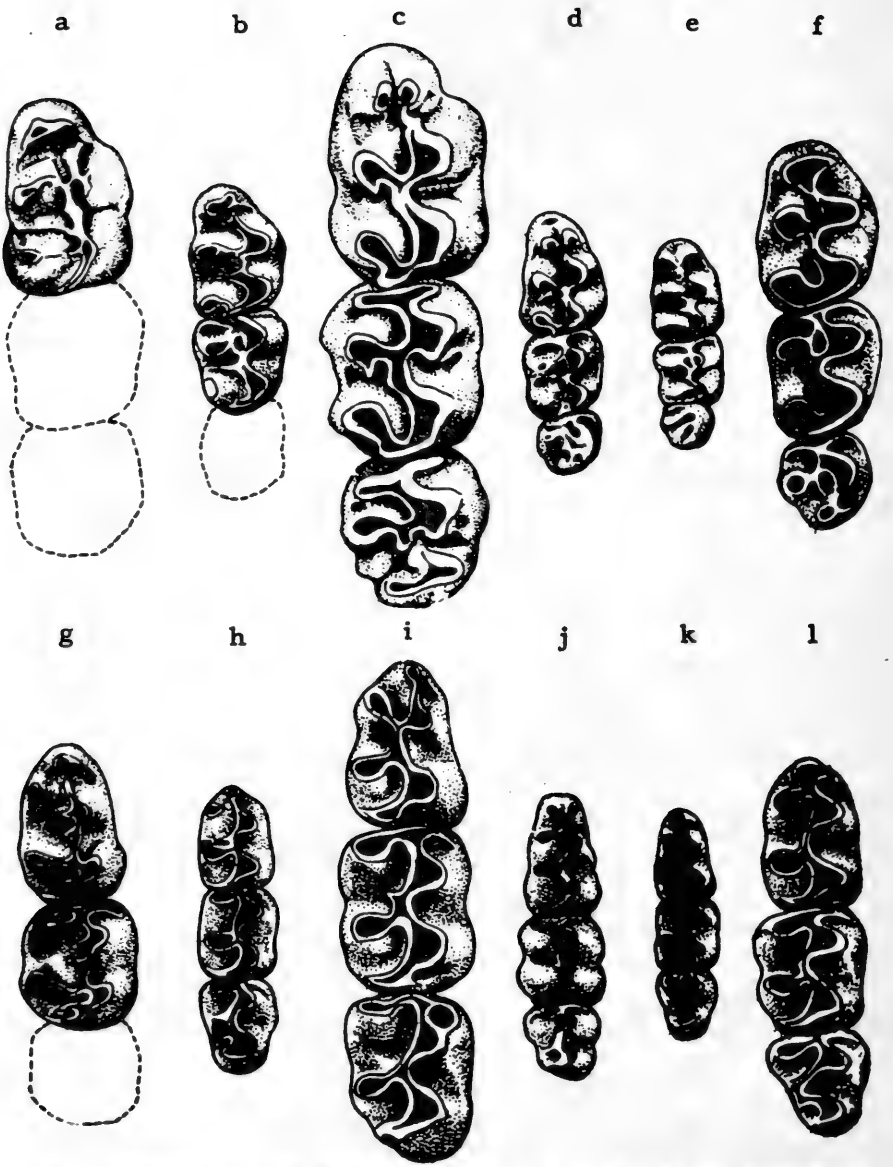


Fig. 25: Structure of the masticatory surface of molars of Cricetodon. After Schaub (1925). Right rows: a, g - Criceton haslachense Schaub (a, M^1, g - M_1-M_2); b, h - Cr. breve Schaub (b-$M^{1,2}$, h. M_{1-3}); c, i - Cr. sansaniese Lartet (c-M^{1-3}, j-M_{1-3}); d, j - Cr. gregarium Schaub (d - M^{1-3}, j-M_{1-3}); e, k - Cr. minus Lartet (e - M^{1-3}, k - M_{1-3}); f, 1 - Cr. larteti Schaub (f - M^{1-3}, 1 -M_{1-3}).

The initial stages of the division of anteroconid into two tubercles - exterocone and interocone - are observed in *Cricetodon sansaniense* Lartet (see Fig. 25, c.i.). In this respect *Cr. sansaniense* closely resembles the specimens of the modern subgenus *Aprodon* of North American *Reithrodontomys* hamsters. The tendency towards the alternate arrangement of tubercles of tooth is observed in *Cr. sansaniense,* as distinct from *Cr. minus.*

The hexatubercular structure of the upper as well as the lower molars has a well marked alternate arrangement of tubercles in *Cricetodon gregarium* (see Fig. 25, d, j).

The forms of *Cricetodon* preserved in Miocene have a pentatubercular first molar. (*Cr. breve* Schaub, *Cr. haslachiense* Schaub and others) acquire alternate arrangement of tubercles of molars (see Fig. 25, a, b, g, h).

Cricetodon larteti (see Fig. 25, f, 1) having an alternate arrangement of five tubercles on M^1 experiences a significant compression of the masticatory surface and a characteristic zig-zag-shaped structure is formed on merging of the dentinal fields.

Miocene Cricetidae of Europe, *Anomalomys* (Fig. 26) already possessed polyhypsodont (mesodont) crown and a compressed masticatory surface of molars. The figure of dentinal fields remotely resembles the modern Madagascan *Brachyuromys betsileoensis.* *Anomalomys,* apparently possessed an undivided anterocone and anteroconid and the tubercles of the lingual and labial sides are appreciably displaced about each other, though not alternately. Dentinal fields of upper molars get fused and fill the gap in between forming numerous closed enamel islets. Enamel crests are arranged slantingly indicating the significant development of circular movements of the mandible. Tubercles on the lower molars are slightly displaced about each other. Dentinal fields on M_1 and M_2 fuse transversally rather than diagonally, like the fusion of dentinal fields in *Meriones,* *Nesokia* and *Eliurus.* However, owing to the higher and thicker marginal layers of enamel, pinching of the flexures and flexids and formation of small enemeled fossettes and fossetids that get locked up within dentinal fields take place. These make the pattern of the masticatory surface look complicated.

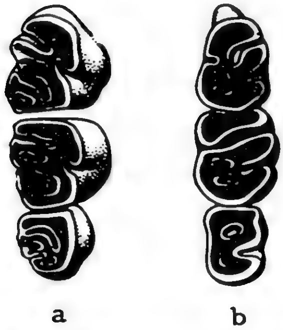


Fig. 26: Structure of the masticatory surface of Anomalomys gaudryi Gaillard. After Stehlin and Schaub (1950). Right rows: (a) upper; (b) lower.

Primitive zokors, Prosiphneus possessing mesodont prismatic molars, with a masticatory surface which is similar to that of the primitive field-voles are also found in the Late Miocene of Asia.

The fauna of hamsters of Pliocene, a period having a special significance in the evolution of Cricetidae and all Muroidea, contains specialized specimens of the ancient Oligocene branches as well as the young specimens of new, prospering group of Cricetidae.

The Lower Pliocene fauna (the fauna of the hipparion epoch) contained a large number of Cricetidae having progressive characteristics in the structure of molars, which indicate a further specialization of the cellulose type of nutrition.

The ancient Cricetodontini, which lived up to the Early Pliocene, include a number of forms in Asia with a compressed masticatory surface.

Paracricetulus Young retains the most primitive structure (Fig. 27, a). Anterocone is not divided into two tips and the displacement of tubercles of lingual and labial rows with respect to each other is not significant. Compression of the masticatory surface is expressed only on sufficiently worn out teeth. According to Schaub (1934) the primitive characteristics in the structure of molar teeth are also retained by Neocricetodon Schaub.

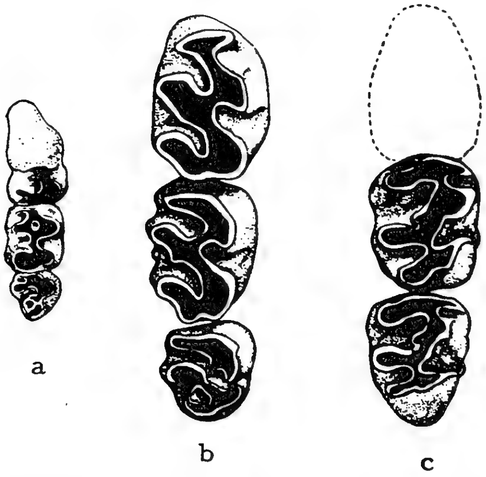


Fig. 27: *Structure of the masticatory surface of molars of the Pliocene Cricetodontini. After Schaub (1934). Right rows: (a) Paracricetulus schaubi Young (M^{1-3}); (b, c) Plesiodipus leci Young (b - M^{1-3}, c - M_{2-3}).*

Of all forms of Cricetodontini the Early Pliocene Plesiodipus Young (= Plesiocricetodon Shaub) (See fig. 27, b, c) possessed a dental system most specialized for cellulose nutrition. The fusion of dentinal fields of this form of Cricetidae with compressed masticatory surface takes place diagonally and the alternate arrangement of tubercles is particularly well expressed on the lower dental row. The crown is mesodont. Owing to the fusion of the dentinal fields it is difficult to establish whether anterocone has been divided into two tubercles; but, judging from the insignificant width of the front dentinal field on M^1, the extere-anterocone and the interoanterocone if present, would not be far from each other. The figure of the masticatory surface resembles that of the zokors and the primitive field-voles.

The Lower-Piocene specimen of the real hamsters of Sinocricetus Schaub (Fig. 28, a, c) is characterized like all other hamsters, 1) by paraflexus and metaflexus, which enter deeply inside the tooth, are directed backwards from the front and further deepen near the axial line of tooth, and 2) by meso- and post-flexids which enter deeply into the tooth and are directed forward from the back. As it gets worn out the elevated marginal part of these flexures fuse with the dentinal exposures of

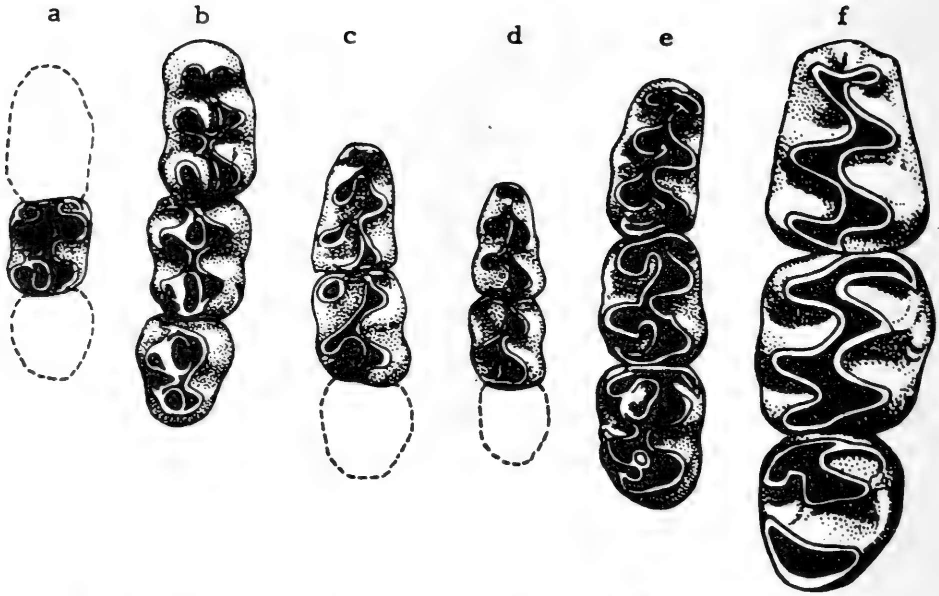


Fig. 28: Structure of the masticatory surface of the molars of Pliocene Cricetini. Right rows: a, c - Sinocricetus zdanskyi Schaub, after Schaub (1934) (a - M^2, c - M_{1-2}); d - Nannocricetus mongolicus Schaub (after Schaub, 1934) (M_{1-2}); b-e - Cricetus kormosi Schaub (after Schaub, 1939); b - M^{1-3}; e - M_{1-3}; f - Lophocricetus grubachi Schlosser (after Stehlin and Schaub, 1950) (M_{1-3}).

tubercles and pinch para- and metafossettes, and meso- and post-fossetids accordingly. These closed enamel islets are very typical of Cricetini from Lower Pliocene to this day. The tubercles on the upper molars of Sinocricetus are arranged alternately and the dentinal fields fused diagonally. The crown is brachyodont, and the tuberculate structure of the surface of the teeth is marked clearly in young mammals. Anterocone has the traces of breaking into exteroanterocone and interoanterocone.

Nannocricetus, according to the general structural plan of molars, closely resembles Sinocricetus. Anterocone is subdivided into extero- and interoanteroconid. Alternate arrangement of tubercle is clearly expressed. The fusion of dentinal fields has taken place diagonally (see Fig. 28, d).

The structure of the molar teeth of Cricetid, Pseudomeriones Schaub (Fig. 29, a, b) is peculiar. It is called so because

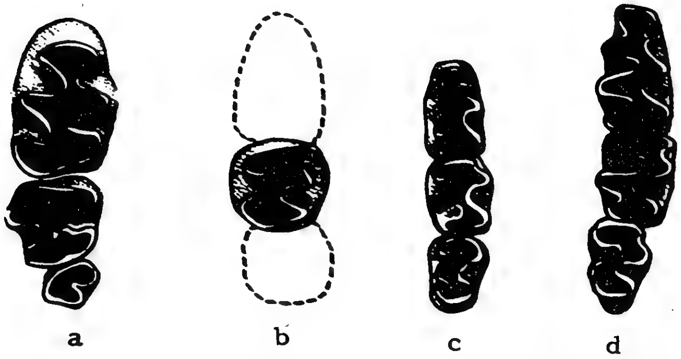


Fig. 29: The structure of the masticatory surface of molars of Pseudomeriones. Anatolomys and Microtodon. After Schaub (1934). Right rows: (a, b) Pseudomeriones abbreviatus Teilhard (a - M^{1-3}; b - M_2); (c) Anatolomys teilhardi Schaub (M_{1-3}); (d) Microtodon atovus Schlosser (M_{1-3}).

of the close similarity in shape of molars with gerbils. Judging from the width of the first dentinal field M^1 had intercone and exteroanterocone. The tubercles of the upper dental row had opposite arrangement. Flexures formed transversally but had no slopes, which are characteristic of the majority of the present day forms of Cricetini. Dentinal fields fused into pairs, connect with each other along the middle line of tooth when oppositely arranged juvenile tubercles begin to wear out. M^3 is poorly developed and the length of M^1 exceeds the length of M^2 and M3 taken together. The crown is intermediate between brachydont and mesodont. The masticatory surface is compressed.

Traces of the modern genus Cricetus are also well known from the Lower Pliocene of Europe. The early Pliocene form of Cricetus kormosi Schaub (see Fig. 28, b, e) already possessed molar teeth which closely resemble the modern specimens of this genus. Anterocone and anteroconid are distinctly divided into two tubercles. The tubercles are arranged almost oppositely but since the diagonal crests are situated higher than the transverse crests the fusion of dentinal fields in semiadults spread diagonally. The greater depth of the flexures near the axial part of the tooth in comparison with the marginal part results (as they get worn out) in the separation of enamel islets -fossette, surrounded by dentinal fields of oppositely placed tubercles. In the old individuals with worn out teeth, the enamel islets may disappear; dentinal fields of oppositely arranged tubercles fuse in pairs and they are connected with each other along the axial line.

The members of the Early Pliocene genus - Lophocricetus were distinguished by brachyodont crown, elongated M^1 and short M^3, which should be indicative of the prevalence of longitudinally oriented movements of the mandible. The tubercles of lower molars are placed alternately (see Fig. 28, f). The masticatory surface is compressed. Dentinal fields are fused diagonally. Flexures are not forming a bend characteristic of Cricetini. The external edge of the para and the metaflexids is higher than the internal part; protective islets of enamel i.e., parafossetid and metafossetid can be formed with detrition. These are arranged quite differently here than in Cricetus owing to the alternate arrangement of tubercles. The masticatory surface of Lophocricetus differ from Cricetus by some features of specialization to the cellulose type of nutrition.

Cricetidae of Anatolomys and Microtodon highly specialized in the structure of the dental system for the cellulose type of nutrition existed in the Early Pliocene of Mongolia.

Species of Anatolomys (see Fig. 29c) were characterized by brachyodont crown, compressed masticatory surface of the molar teeth. Tubercles of lingual and labial sides of the lower dental row are slightly displaced about each other and the dentinal fields merge horizontally. M_3 has quite a complex shape. The dental row is elongated and the width of the teeth is much less than their length.

Early - Miocene Microtodon (see Fig. 29d) attained further specialization for the cellulose type of nutrition by having a mesodont crown with a compressed masticatory surface on the molar teeth, similar to the structure of teeth of cheek-toothed field-voles of Fibrini. Flexures from the lingual side is appreciably deeper than those from the labial side. Dentinal fields, similar to the worn out tubercles are arranged alternately.

In the Early Pliocene layer of North America, along with the representatives of the ancient forms, .Eumyini-Copemys Macrognathomys Hall- and the ancient forms of the modern genus Peramyscus

Gloger. These forms though differ in their specializations for the seed-eating type of nutrition, do not substantially differ from the modern bunodont of the American Cricetinae.

The structure of the masticatory surface of teeth of Middle-Pliocene North American hamster of Pliotomodon Hoffmeister (Fig. 30) closely resembles that of the molars of the modern Central American Scotinomys. The division of anterocone into two tubercles is well expressed. Dentinal fields of the lingual side merge with each other and those of the labial side also merge with each other. On the lower molars the tubercles are arranged alternately and the dentinal field merges diagonally. The enamel crests of lower molars are arranged diagonally, and almost longitudinally on the upper molars. A similar structure indicates the significant role of transversely oriented masticatory movements while processing the food.

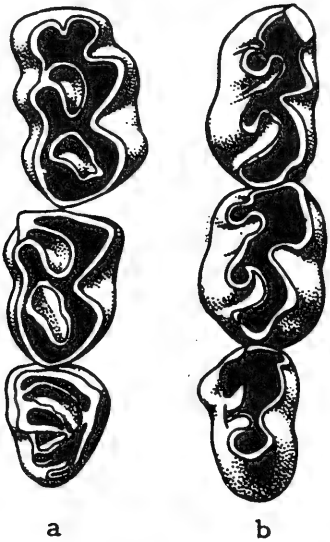


Fig. 30: *Structure of the masticatory surface of molar teeth of Pliotomodon primitivus Hoffmeister. After Hoffmeister, 1945, from Stehlin and Schaub (1950). Right rows: (a) M^{1-3}; (b) M_{1-3}.*

The first representatives of the advanced forms of the Muridae group distinguished by the three-row arrangement of tubercles on molars appear in the Early Pliocene of the Old World. These are Parapodemus Schaub., Anthracomys Schaub, Progonomys

Schaub and later Stephanomys Schaub and other genera. According to Vorontsov (1960 b), the appearance of mice in the Old World should have restricted these "radiation possibilities" of the seed-eating forms of Cricetidae of the Old World.

In Late Pliocene there appear numerous representatives of the present field-voles (Microtinae)-Synaptomys Baird, Poamys Matth., Microtoscoptes Schaub (from the Middle Pliocene), Pliopotamus Hibbart, Ondatra Link, Neofiber True, Phenacomys Merriam in North America, Mimomys Major in Palearctic and Allophajomys Kormos, Lagurus Gloger and Ungaromys Kormos in Europe. In this period there were a great number of representatives of the modern genera of hamsters: Baiomys True Onychomys Baird, Eligmodontia. Cuv. (Now only in South America), Sigmodon Say et Ord, Neotoma Say et Ord, and also the fossils of Parahodomys and Symmetrodontomys. A significant number of forms of Cricetidae from Late Pliocene already possessed, a compressed crown. The Cricetida Proreithrodon Ameghino, belonging to the modern genus Reithrodon according to the data of Hershkovitz (1955) existed in the Late Pliocene of South America. Obviously, in Late Pliocene the hamsters passed from North America to the South along the then established bridge between the Nearctic and Neogea Regions.

The Pleistocene fauna of Cricetidae almost did not have those genera which continued to live to this day. Transformation of the dental system of Cricetidae in Pleistocene is closely connected with the adaptive radiation of Cricetidae in South America and Madagascar. The dental system of Pleistocene hamsters of the New World is very different. The bunodont seed-eating forms, Peromyscus and Reithrodontomys having a highly complex structure of the masticatory surface and insectivorous forms, Oxymycterus and Blarinomys having primitive opposite arrangement of tubercles on molars, and forms having masticatory surface adapted to the cellulose type of nutrition (Phyllotis, Reithrodon and Holochilus) were represented here.

The Pleistocone Asian representatives of Cricetini namely Cricetinus (Fig. 31a, c) is almost characterized by the opposite arrangement of ;tubercles on the upper molars and by alternate arrangement on the lower molars. During detrition the closed

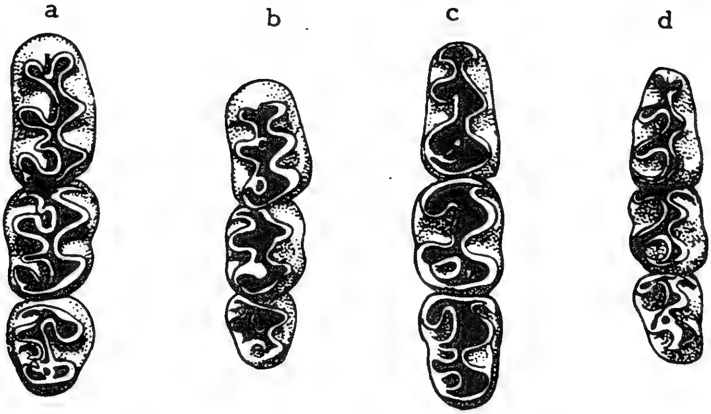


Fig. 31: Structure of the masticatory surface of the molar teeth of Pleistocene Cricetini - Cricetinus and Allocricetus. After Schaub (1930). Right rows: (a, c) Cricetinus varians Zdansky (a -M^{1-3}; c -M_{1-3}); (b, d) Allocricetus bursae Schaub (b -M^{1-3}, d -M_{1-3}).

enamel depressions characteristic of Cricetini are formed on the upper molars, whereas on the lower molars similar alveoli are not formed, while dentinal fields merge diagonally. Anterocone is not divided into two tubercles. Division of anterocoid into two tubercles so far as it is possible to judge from the figure of highly worn out tooth, was poorly marked.

The characteristic features of the present forms of Cricetini are expressed in the structure of the teeth of European Pleistocene hamsters of Allocricetus (see Fig. 31b, d). Anterocone and anteroconid are divided into two tubercles. The tubercles on the lower molars are arranged alternately, while the displacement of the tubercles of lingual and labial rows with respect to each other on the upper molars is sufficiently feebly expressed. Axial strip of dentine on lower molars is very much displaced labially in view of the fact that the lingual dentinal fields are greater than the labial.

The structure of the molar teeth of the Pleistocene representatives of modern genera will be described in the part, discussing the morphology of molars of modern hamsters.

The following principles are observed in the phylogenesis of the dental system of Cricetinae from Oligocene to Pleistocene. For the whole period of development of cricetids the dental system of

Cricetidae diverged sufficiently widely. From Oligocene to Pliocene the main trend of specialization of dental system of Cricetinae was the adaptation to the processing of grains and associated with this the complication of the tubercles, appearance of supplementary tubercles (mesostylus, hypostylus, etc.). However, the forms with compressed masticatory surface, adapted to the cellulose type of nutrition, are found among forms of Cricetidae now in the lower Oligocene.

The grand process of stepping down to land which started in Late Miocene led to the widening of areas, occupied by grassy-steppe associations (combinations) and to the increase in number of "niches" of herbivorous animals. Tropical forests of Paleogene were excluded from a greater part of the temperate zone of Holarctic. Similar change would appear to have directed the evolution of Cricetidae and of course the majority of other groups of herbivorous mammals, limiting the possibility of divergence of bunodont seminivorous forms and created favorable conditions for the emergence and wide radiation of herbivorous rodents having compressed masticatory surface.

It should be noted that seeds do not infrequently represent harder food than some vegetative parts of the plants. The first ones are usually processed by rodents having unreduced hard enamel coverings of the tooth, while the second ones are processed by enamel crests, lying on the soft dentinal base. However, in view of the fact that cellulose food has less caloric value than protein, rodents make use of the vegetative parts of the plants in an incomparably greater quantity than seeds. The cellulose for the subsequent masceration and fermentation in stomach and intestine needs more thorough mechanical processing than protein food. All this leads to strong abrasion of tooth and in forms where cellulose nutrition is predominant, the evolution is in the direction of selection of individuals having a higher crown.

Therefore, starting from the second half of Miocene, the dental system of Cricetidae evolves mainly in the direction of creation of forms having a compressed masticatory surface, and a mesodont and even hypsodont crown.

As it was shown above, longitudinal grinding and the corresponding form of molars characteristic of field-voles are biomechanically most advantageous for the cellulose type of nutrition. However, along with this adaptive trend of specialization of molars, along which the evolution of the majority forms of Cricetidae proceeds, some genera acquire a pseudo-selenodont form of tooth, in different periods independent of each other. Permitting the tuberculate structure of teeth of the seed-eating form to quickly transform into a compressed structure it does not seem to be evolutionally perspective, and is not concurrent with the forms, possessing the structure of tooth, which resembles that of the field-voles and, may be named as 'inadaptive' (in the view of V.O. Kovalevskii).

It should be noted that the only isolated forms of bunodont cricetids are left in pleistocene in the Palearctic but the number of bunodont forms is very great in the New World.

6. Structure of Molar Teeth of Recent Cricetidae.

In Oryzomys (Fig.32) the dental surfaces in adult individuals is tuberculate. The division of anterocone into two tubercles is noticed only in young individuals. The thickness of the enamel layer is not the same: it is more along the edges of the tooth and less on the internal side of the tubercle. The thickness of enamel is more on the labial side of the upper molars than on the lingual side; on the lower molars the thickness of enamel is more on the lingual than on the labial side. Such a structure leads to a durable preservation of the tuberculate and then the terraced structure of tooth in adults and even in old animals.

Internal sides of the tubercles are worn out most; the height of the middle part of the tooth, situated along the axial line, as well as the height of the tubercles are reduced with detrition. Owing to the unequal development of enamel on the lingual and labial sides, the exteroanterocone, the paracone and the metacone will be slightly taller than the protocone and the hypocone, but the paraconid and the metaconid will be taller than the protoconid and the hypoconid. Since the detrition of enamel is uneven the dentinal fields are arranged in different planes. The dentinal fields of the paracone and the metacone are oriented towards the lingual side and turned back, and rise much above their base while the dentinal fields of the protocone and the hypocone are oriented towards the labial slide and rise very slightly above the base of the tubercles. The dentinal fields of anterocone are oriented backwards. Accordingly, the dentinal fields of the para- and metaconids oriented towards the labial side, turned towards the front and rise much above the base of the tubercles, whereas the dentinal fields of protoconid and the hypoconid are oriented towards the lingual side and rise insignificantly above the level of the base of the tubercles. Dentinal exposure of the anteroconid rises much above the other dentinal fields and is oriented backwards.

From the labial side of the upper dental row passes the marginal crest, which connects the tips of the exteroanterocone, anterior cingulum, paracone, mesostylus, metacone and posterior cingulum with each other. As the detrition of tooth goes on, the flexures are pinched by this crest and enclosed in the dentinal fields of tooth in the form of closed enamel islets. Depending upon the greater or less height of tubercles and enamel crest, and the depth of flexure, the latter are pinched in different periods of time. First, the anteroflexus and the postflexus are pinched, forming anterofosette the postfossete. The depth of the postfossette is insignificant, and on further detrition of tooth, this enamel alveolus disappears and the dentinal fields of metacone and posterior cingulum merge together. Further, with detrition the mesoflexus is pinched to form mesofossette. Later highly deep paraflexus and metaflexus are closed to form parafossette and metafossette. Enamel elevations on the lingual side of protoflexus and hypoflexus have a very small height. The tubercle on hypoflexus is well marked on M^1 and M^2; it may be named as hypostylus*. In very old individuals protoflexus and hypoflexus can be pinched into protofossette and hypofossette.

Unequal depth of parafossette and metafossette formed by detrition may result in the division of these enamel alveoli into fine, rarely shallow secondary alveoli; their origin may be traced rarely on highly worn out tooth. On M^3, fossettes of lingual and labial sides may merge with each other.

The masticatory surface of M_1 is highly complicated by the existence of anterofossetid, prosingulofossetid and antero-

---

* *According to the terminology of Hooper (1957) hypostylus corresponds to ectostylus and hypostylid, ectostylid. Our hypolophus corresponds to endolophus, but hypolophid, to endolophid.*

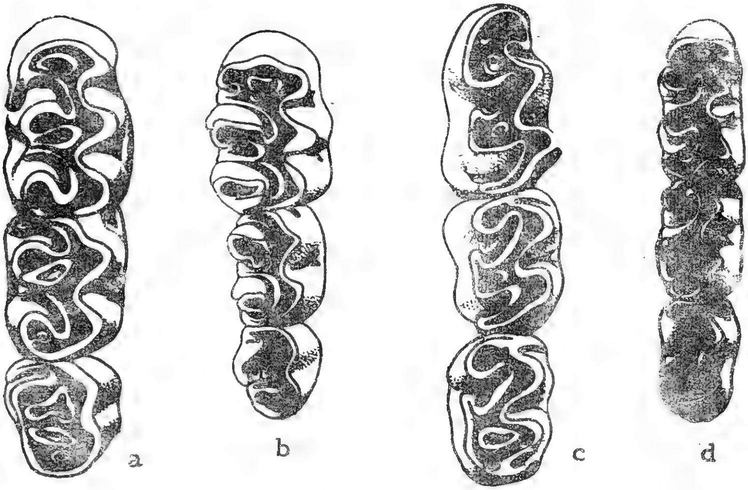


Fig. 32: Structure of the masticatory surface of molar teeth of Oryzomys. Right rows: (a, c) Orig. Oryzomys (s. str.) couei Alston according to specimens, from the collection of Institute of Zoology, Acad. Sc. USSR., No. 38387, Mexico., Chipas; (b, d) according to Hershkovitz (1960) Oryzomys (Oecomys) bicolor Tomes; (a, b) Upper rows; (b, d) lower rows.

lophoflexid. Postfossetid and sometimes mesofossetid break down into two alveoli formed by isolated enamel islets. Hypostylid is well marked both on M_1 and M_2. Proto- and metaflexids which form proto- and metafossetids are closed lastly. M_3 is not reduced and it is equal in length to M_2; M_3 is slightly smaller than M^2. The masticatory surface of upper molars is somewhat inclined outside and that of lower molars inside of tooth. Tubercles of upper and lower molars are arranged in an almost opposite manner, but dentinal fields merge diagonally. Harshkovitz (1960) described the structure of molars in the subgenus of Oecomys.

Small hamsters, Neacomys (Fig. 33) are characterized by the same structural plan as in Oryzomys. They differ from Oryzomys by a somewhat small size of M_3 in comparison with M_2.

The tubercular structure of molars is expressed more prominantly in specimens of Rhipidomys (Fig. 34) than in Oryzomys. Exteroanterocone and interoanterocone, and antero-

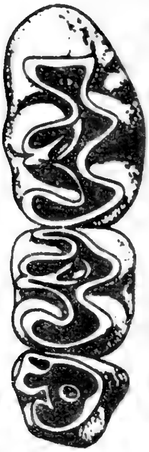


Fig. 33: Structure of the masticatory surface of molars of ***Neacomys spinosus*** *Thom., ad Institute of Zoology 39363.* ***Peru Juliaca.*** *Upper right row. Orig.*

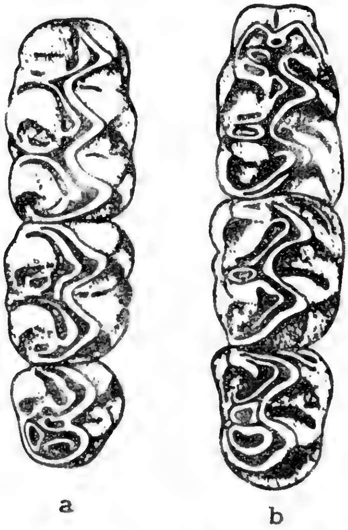


Fig. 34: Structure of the masticatory surface of molars of ***Rhipidomys*** *mastacalis Lunid subad., zool.* ***Museum, MGU No. S - 61073.*** *Brazil. Orig. Right rows: (a) M^{1-3}; (b) M_{1-3}.*

and interoanteroconids are well expressed. M^3 is appreciably smaller than M^2; M_3 is nearly equal to M_2. The general structural plan of Rhipidomys very much resembles Oryzomys, however flexures close into fossettes much later than in Oryzomys.

The general structural plan of tooth, characteristic of the group of genera close to Oryzomys, is well expressed in Thomosomys (Fig. 35). Exteroanterocone and interoanterocone are separated from each other for a long time. Anteroflexus is separated into anterofossette later than the appearance of parafossette and metafossette. Hypostylus is well developed. Exteroanterocone and interoanterocone come together but divided by a deep anteroflexid lately closing into anterofossetid. M^3 is appreciably smaller than M^2. M_3 is a bit shorter than M_2. Thomasomys is a form having clearly expressed tubercular structure of brachyodont crown, which is retained almost throughout the life.

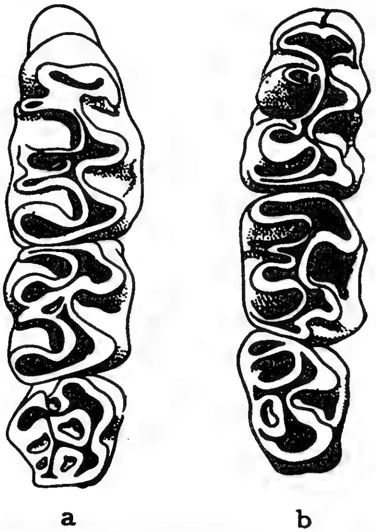


Fig. 35: Structure of the masticatory surface of molars of Thomasomys pyrrhonotus. Thoms. ad., Zool. Museum MGU., No. S Brazil. Orig. Right rows: (a) M^{1-3}; (b) M_{1-3}.

Judged by the photographs of teeth (Gyldenstolpe, 1932), Chilomys, Rhagomys, and Phaenomys are related to this group of genera. All the three genera are characterized by the tuberculate masticatory surface having strictly opposite (Phaeconomys) or almost opposite (Chilomys, Rhagomys) arrangement of tubercles and brachyodont crown. Exteroanterocone and interoanterocone are drawn nearer in Chilomys, the distance between exteroanterocone and interoanterocone increases in Phagomys and in Phaenomys they are so much apart from each other as paracone is from protocone. M^3 is smaller than M^2 in all the three genera. In *Rhagomys* and particularly in *Chilomys* M^3 is not very large.

The general structural plan of *Nectomys* molars may have been evolved from the bunodont *Rhipidomys*, *Thomasomys* and *Oryzomys*. The tuberculate structure of the teeth in *Nectomys* (Fig. 36) is not expressed or rather expressed only in very young animals, which have not started independent life. But even such young individuals have dentinal exposures, joined diagonally (Hershkovitz, 1944). The enamel on the labial side of the upper and lingual side of the lower dental rows is very thick and this leads to the formation of a compressed terraced dental surface. The crown is brachyodont. In the subgenus *Sigmodontomys*, even the traces of self-dependence of exteroanterocone and interoanterocone are seen whereas in the subgenus *Nectomys* s. str. the anteroflexus is closed and changed to anterofossette in the young individuals. Anteroflexid closing with detrition of the tooth into anterofossetid is seen in young individual of both the subgenera. The distinctive feature of *Nectomys* is the early constriction of flexures (flexures and flexids and formation of numerous closed enameled alveolate fossettes and fossetids). In this manner a significant increase is obtained in the length of transversely oriented enamel crests which intersect themselves during the longitudinal movements of the mandible and help in grinding cellulose food. Terraced surface of molars restrict most effectively transverse movements of mandible. M^3 is much smaller than M^2 and particularly the reduction of M^3 is clearly expressed in the subgenus *Sigmodontomys*. In our opinion (Vorontsov, 1963c), reduction of M^3 is related to the decrease in the rôle of this tooth during the development of longitudinally oriented grinding movements of mandible.

The development of the terraced masticatory surface in *Nectomys*, associated with a thicker layer of enamel on the lingual side of the lower molars and on the labial side of upper molars leads to the fact that unlike *Oryzomys* the protoflexus and hypoflexus, and protoflexid and hypoflexid are left open for a long time and only in very old individuals they

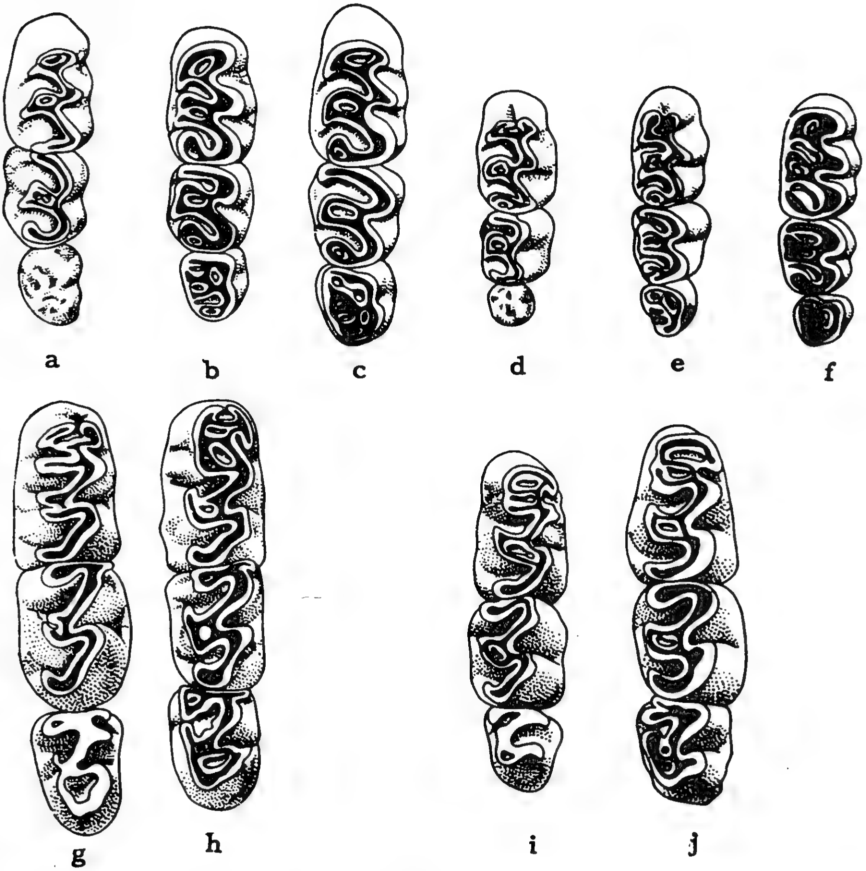


Fig. 36: Structure of the masticatory surface of Nectomys molars. After Hershkovitz (1944). Right rows: (a,b,c,g,h) N. (s. str. Squamipes Brants; (d,e,f,i,g) N (Sigmodontomys) alfari Allen; (a,b,c,d, e,f) Upper rows: g,h,i,j lower rows; a,g,h,d,j juvenis; b,h,e,j subadults; b,f, adults.

close in the form of fossette. In our opinion, the less prominent movements in comparison with the grinding movements, must lead to a simplification of the tuberculate structure of the tooth and this may be associated with the weak development of hypostylus and hypostylid in Nectomys as compared to Oryzomys. For the structure and development of the molars of Nectomys you may also see Hershkovitz (1944).

According to the general structural plan of the molar-teeth, the genera discussed above, form a real group, and can be arranged in the following series according to the degree of adaptation to the cellulose type of nutrition: Rhipidomys → Thomasosmys → Oryzomys → Nectomys.

Bunodont and brachyodont Central American hamsters, Nyctomys (Fig. 37) have a structural plane of molar teeth that is close to Oryzomys. As in Oryzomys the tubercles of lingual and labial rows have unequal height. Orientation of dentinal fields of individual tubercles resembles that in Oryzomys. Unlike the last genus Nyctomys exteroanterocene and interoanterocene have been brought together so much that not only the anteroflexus but even the anterofossette is not well expressed. Hypsostylid is expressed very well.

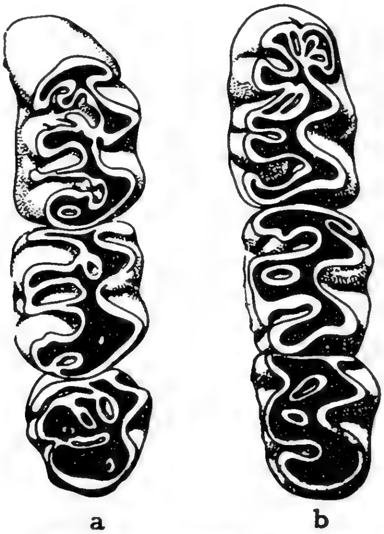


Fig. 37: Structure of the masticatory surface of molars of Nyctomys sumichrasti decolorus True Orig. Right rows: (a) upper row; (b) lower row. According to the specimen from the collection of Zool Institut. Acad. of Sc. USSR, No. 39371, Central America, Gonduras, Las Flores.

Considerable height of lingual margin on the upper molars and labial margin on lower molars leads to the early isolation of flexures of these sides and to the formation of protofossette and hypofossette, proto-fossetid and hypo-fessetid. Tubercles are arranged almost oppositely, and paracone is somewhat shifted back with respect to protocone. Unequal depth of flexures and flexids leads to the formation of plural fossettes and fossetids.

Thus, para- and metaflexures give two para- and metafossettes each on M^1 and M^2. The interior space of these closed areas is oriented in longitudinally stretched islets of enamel. Orientation of the enamel crests in transverse as well as longitudinal direction indicates that grinding movements in this form, obviously, take place in both transverse and longitudinal direction.

M^3 is smaller than M^2, but it cannot be considered as reduced; M_3 is almost equal to M_2 in length. On M_1 there is an anterofossetid, indicating the fact that anteroconid was formed by two tubercles.

The tuberculate structure of tooth in large-sized brachyodont of the Central American hamster, Tylomys* (Fig. 38). M^3 is,

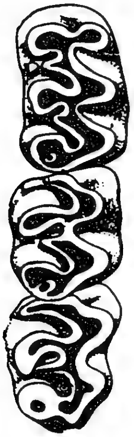


Fig. 38: Structure of the masticatory surface of Tylomys nudicaudus Peters. Orig. Right upper row. According to the specimen from the collection of Zool. Institute, Acad. of Sc., USSR, No. 1545 Central America, Guatemala, Vera Paz.

even slightly bigger than M^2. Exteroanterocone and interoanterocone are divided by a deep fissure-anteroflexus-and widely set apart; the distance between these tubercles is not less than the distance between paracone and protocone. Tubercles of M^1, have a strictly opposite arrangement. On M^2 and M^3, the tubercle of the lingual row is slightly bent forward compared to that of the labial row. Merging of dentinal fields takes place diagonally. Flexures are very deep as a result of which the enameled alveoli

---

** Only the upper Central row of Tylomys was studied.*

(fossettes) get pinched very late. Hypostylus is well developed. More thickness of enamel along the edges of tooth and less along the middle line leads to the situation that while grinding the central part of tooth grinds quicker than the lateral parts, and thus the two-row tuberculate structure of tooth is preserved for a long time even in old forms.

Peromyscus, Baiomys and Reithrodontomys form an independent group well separated from the previous genera by the structure of the molars. The following are the characteristics in the structure of the molars of this group:

alternate arrangement of well expressed tubercles;

five-tubercular structure of the first upper and lower molars (in subgenus Aprodon of the genus Reithrodontomys the anterocone is divided into two tubercles).

If the above developed conception on the biomechanical significance of the tuberculate structure of tooth is considered in the processing of seeds and food substances similar to them, then the alternate arrangement of tubercles on molars of this group should be regarded as an advanced feature, whereas the undivided anterocone and anteroconid should be considered as an ancient feature thus giving evidence of the connections of the specimens of this group with Paleogene Cricetidae. Molars are highly complicated by the formation of supplementary tubercles (mesostylus and mesostylid, hypostylus and hypostylid, etc.) in some representatives of this group of genera, paraflexus and paraflexid, and metaflexus and metaflexid, are generally not close' on the first two molars during the whole life.

The structure of molars is very simple in brachyodont Mexican hamster, Baiomys (Fig. 39). Here the anterocone is wider than in Calomyscus and along its front margin appears a shallow groove which may be taken as anteroflexus. Dentinal exposures of anterocone in young animals are 8-shaped which gives evidence of the starting division of anterocone into interoanterocone and exteroanterocone. The posterior cingulum is absent on the upper molars but mesostylus may be developed. M^3 is reduced to a less degree than in Calomyseus. Alternate arrangement of tubercles is well expressed. Anterocone is not divided into two tubercles.

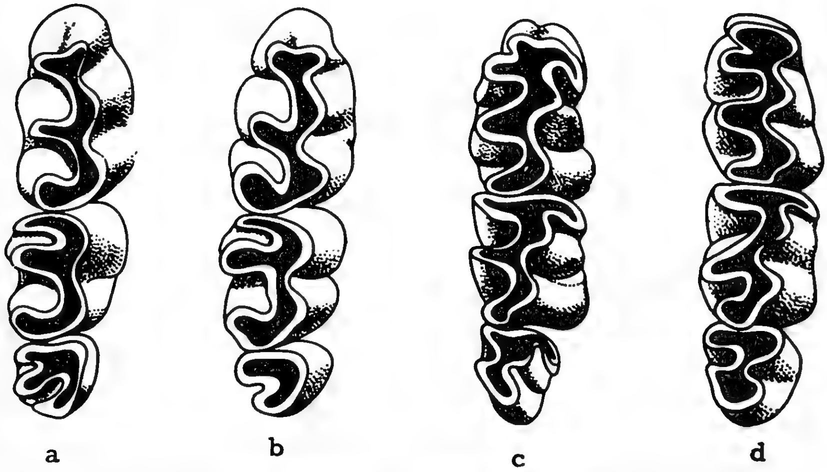


Fig. 39: *Structure of the masticatory surface of molars of Baiomys, After Packard (1960). Right rows: (a, c) B. taylor, Thom; (b, d) B. musculus Merriam; (a, b) upper rows; c, d lower rows.*

Hypostylid may be developed. During detrition, protoflexid, hypoflexid and later postflexid may be closed, but because of the greater height of the tubercles this is only observed in old animals. For the structure of molars of Baiomys see Packard (1960) also.

In the specimens of polytypic genus Peromyscus (Fig. 40), the tuberculate structure of tooth becomes further developed. Anterocone is relatively wide; sometimes along its front surface there appears a groove, which may be homologized with an outgrowth of anteroflexus. The latter, however, is never closed to form anterofossete. The closed enamel islets found in some forms (Peromyscus oaxacensis) in between the dentinal field of anterocone are derivatives of flexure between anterocone and cingulum anterior (Prosinguloflexus), prosingulofossette. The supplementary tubercles and crests connecting them with the main tubercles of tooth are highly developed. The anterior cingulum is present not only on M^2 but also on M1. Mesostylus and hypostylus are often developed. The posterior cingulum is situated close to metacone and frequently merges with it. At least, either mesostylus or hypostylus is positively developed on one of the teeth of the upper row. Anteroconid is evidently divided into interoanteroconid and exteroanteroconid. The posterior cingulum is always well developed on the first two lower molars. The supplementary tubercles – mesostylid and hypostylid – and the crests connecting them

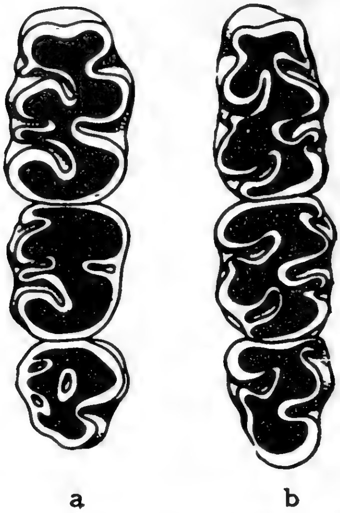


Fig. 40: Structure of the masticatory surface of molar teeth of Peromyscus zarhynchus Merriam. Orig. Right rows. According to the specimens from the collection of Zoology. Inst., Acad., Sc. USSR No. 39363, Mexico State Chiapas Pueblo Nuevo; a - upper row. b - lower row.

with the axial part of the tooth are often developed. The number and the degree of development of the supplementary tubercles and crests on the upper and lower teeth are extremely changeable (Hooper, 1957). The thick development of the enamel layer along the regional zones of the teeth also enables the preservation of the tuberculate structure of teeth in old individuals. Tubercles of the upper row of molars are oriented backward and those of the lower row forward. At the same time the dentinal exposures on the tubercles of the upper row on labial side are oriented backward and on lingual side outward and backward. The dentinal fields of the lower dental row on the labial side are oriented inward and forward, and those on the lingual side, backward. M^3 is much smaller than M^2, but it is not so reduced as in the previous genus. The rudiments of paracone, protocone, metacone and hypocone and anterior cingulum are traced in M^3. Alternate arrangement of the tubercles is well expressed. See the paper of Hooper (1957) for intraspecific and intrageneric variability of molars in Peromyscus.

The tuberculate structure of the tooth among the genera discussed attains the highest development in Reithrodontomys es-

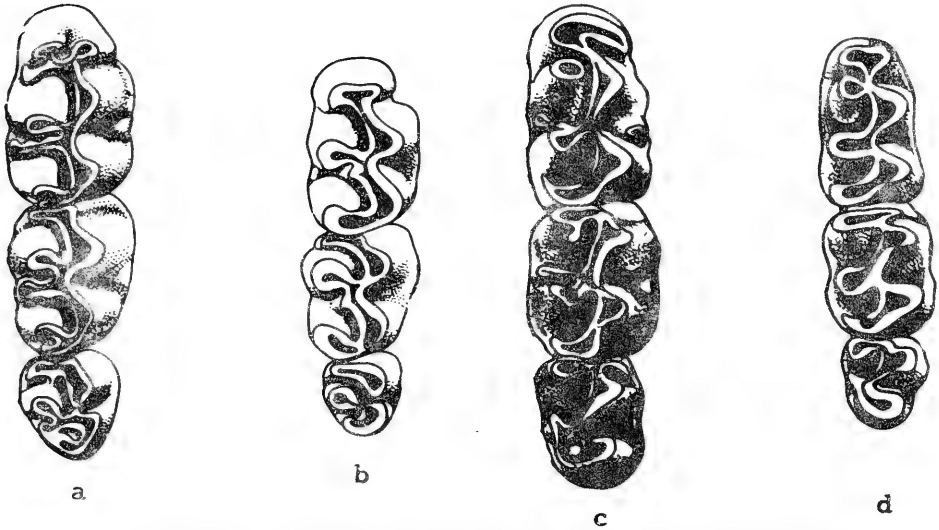


Fig. 41: Structure of the masticatory surface of Reithrodontomys molars. After Hooper (1952). Right rows: (a) R (Aprodon) tenuirostris, Merriam b, d R. (s. str.) fulvescens. J. Allen; a, b - upper rows; c, d - lower rows.

pecially in the subgenus Aprodon. Molars of Reithrodontomys (Fig. 41) very much resembles the molars of Peromyscus in structure, but M^3 and M_3 are more complex than in Peromyscus. Sometimes on M^3, the paraflexus joins the hypoflexus and grows in the opposite direction to enable the anterior cingulum merge with the protocone. The posterior cingulum on the upper molars is not generally separated from metacone. Supplementary tubercles - mesostylus and mesostylid, and hypostylus and hypostylid - are generally well developed, but the crests (mesolophus, hypolophus, etc.) connecting them with the axial part of tooth develop only in old individuals.

The teeth of the specimens of the subgenus Aprodon are highly specialized for the seed-eating type of nutrition. Extero-anterocone and interoanterocone are well developed. Supplementary tubercles are excellently developed on upper and lower molars. The posterior cingulum on the upper molars is developed and merges with the metacone only on considerable detrition of tooth. Alternate arrangement of tubercles is well expressed in both the subgenera. For the structure of the molars of Reithrodontomys see the paper of Hooper (1952).

Depending on the degree of decrease in adaptability of the dental system to the seed eating type of nutrition the above described forms can be placed in the following series: Aprodon → Reithrodontomys s. str. → Peromyscus → Baiomys.

According to the structure of the molar teeth, Onychomys (Fig. 42) relates to the described group of genera. Anterocone is not divided into two tubercles. The posterior cingulum on the upper molars is developed and it preserves its independence for a long time. Alternate arrangement of the tubercles is poorly expressed, hypocone and metacone have almost an opposite arrangement. The arrangement (almost opposite) of tubercles on molars facilitates the retention of the prey (Onychomys has almost exceptionally insectivorous forms, Hall, 1946). Evidently, Onychomys acquired the opposite arrangement of the tubercles for the second time with the secondary transition to the insectivorous nutrition (it will be discussed in detail). M^3 is extremely reduced. Tubercles of the lower molars are situated somewhat more alternately than the upper. The tubercles of the upper and the lower molars are extraordinarily high. Supplementary tubercles are not developed generally.

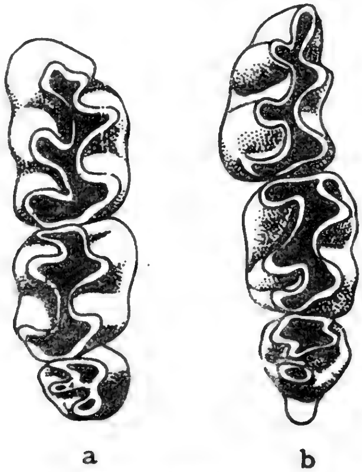


Fig. 42: Structure of the masticatory surface of molars of Onychomys leucogaster Wied. Orig. Right rows: Based on the specimens from the collection of Zool Museum, MSU, No. S-645480, Canada, Saskatchewan (a) upper row; (b) lower row.

The structure of the molars of the forms of the genus Calomyscus of muroid hamsters (Fig. 43), standing unique in the system of Cricetinae greatly resembles Onychomys.

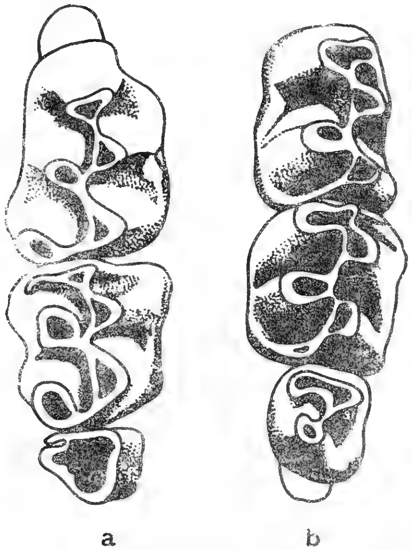


Fig. 43: Structure of the masticatory surface of molars of Calomyscus baluchi. Orig. Right rows: According to specimen from the collection of Zool. Museum, Mos. St. University Na S-44255, Baluchistan, Harboi (a) upper row; (b) lower row.

The teeth of Calomyscus are bunodont, and the crown is brachyodnot. Anterocone is not divided into two tubercles and is sufficiently narrow; mesostylus, posterior cingulum and anterior cingulum are not expressed on M^1. (Absence of posterior cingulum as it will be shown below, may be related to the primary absence of this element as well as to its inclusion in the composition of metacone). M^3 is highly reduced. Anteroconid is slightly wider than anterocone, but there is no basis to look for traces of exteroconid and anteroconid just because it is slightly broader. The posterior cingulum on the lower molars is developed and mesostylid is not present. Hypostylus and hypostylid are not marked. M3 is bigger than M^3. Alternate arrangement of the tubercles is clearly observed on the upper and the lower molars. The teeth of Calomyscus has a more compressed structure on bearing out than those of Peromyscus and Reithrodontomys owing to nearly equal thickness of the enamel on all the sides of the tubercles. The compressed nature of the tuberculate structure of molars alternate the arrangement of tubercles and the earlier formation of compressed masticatory surface enable us to consider the dental system of Calomyscus as less adaptive to the protein type of nutrition than the other genera of the group Peromyscus.

The hamsters of the genus Akodon (Fig. 44) are characterized by tuberculate, brachyodont, dental system. Tubercles are arranged almost oppositely (tubercles of the lingual row are displaced slightly forward with respect to the tubercles of the labial row). The posterior cingulum on the upper molars is not expressed (merged with metacone?). Little thickness of the enamel layer on the tips of the tubercles leads to a rather early exposure of dentine. The anterior cingulum, mesostylus and hypostylus are usually developed but merge very early with the main elements situated in front of them. Exteroanterocone and interoanterocone are well expressed in young individuals. Exteroanteroconid and interoanteroconid are brought together to each other. The posterior cingulum is clearly visible on the lower molars. Postflexid is pinched very early

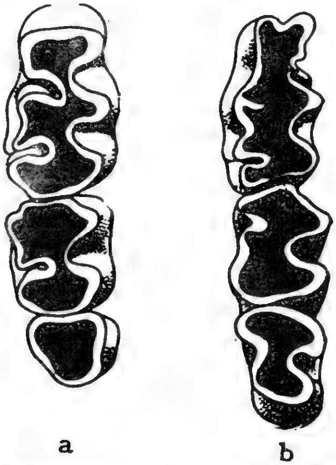


Fig. 44: Structure of the masticatory surface of molars of Akodon arvicoloides Wagn. Orig. Right rows: According to specimen from the collection of Zool Mus., Moscow St. University No. S-61072, Brazil (a) supper row; (b) lower row.

and forms postfossetid M^3 is reduced, but M_3 is not reduced, and it is not smaller than M_2 in length.

The group of genera (Oxymycterus, Lenoxus) related to Akodon is characterized by a much simplified structure of the masticatory surface of molars. This simplification is related to the adaptations to the insectivorous type of nutrition. Adaptations to the gripping movements of mandible lead to the loss of the multi-tuberculate structure of the tooth, calculated on the prevalence of the crushing movements during processing of seeds. A comparatively small number of main tubercles have an opposite arrangement. A very simple structure of the masticatory surface (Fig. 45) is formed in old individuals during detrition.

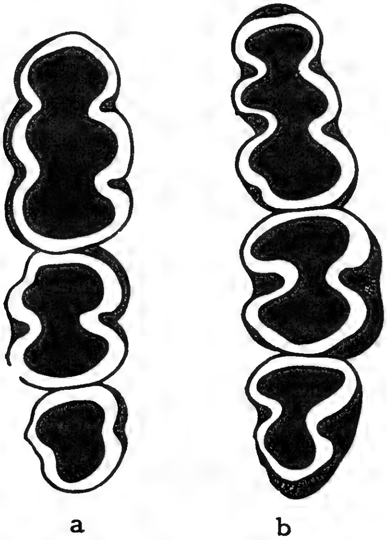


Fig. 45: *Structure of the masticatory surface of molars of Notimys negalonyx Waterh. Orig. Right rows of old individual. According to the specimen for the collection of the Museum of Natural History in Paris No. 1882, 2632, Chili (a) upper row; (b) lower row.*

The masticatory surface of molars of Lenoxus (Fig. 46) is sharply tuberculate, and crown brachyodont. The arrangement of tubercles of the upper dental row is almost opposite, tubercles of lingual row are slightly displaced forward with respect to the tubercles of the labial row. Exteranterocone and intero-

Fig. 46: *Structure of the masticatory surface of molars of Lenoxus apicalis boliviae. Orig.*

anterocone are separated from each other. The posterior cingulum on the upper molars is not prominent. Mesostylus and mesolophus are developed. The anterior cingulum on M^1 is approximated with paracone. Paraflexus and metaflexus are very deep in their interior part whereas the exterior part of these flexures are not deep. Therefore parafosette and metafossette, directed longitudinally and arranged along the axial line of tooth are formed early. M_3 is very small. Tubercles of the lingual row of the upper molars are projected outside, and of the labial row, inside and backward. Exteroanteroconid and interoanteroconid are approximated to each other. Hypostylid and hypolophid, mesostylid and mesolophid are generally well developed. The posterior cingulum on lower molars is well developed. Tubercles of the lingual row is exceptionally high and their dentinal exposures are directed forward and outside. Tubercles of the labial row of the lower molars are appreciably below and their dentinal exposures are turned inside. M_3 is shorter than M_2 but not reduced.

The tuberculate structure of the teeth of Lenoxus almost excludes the possibility of free mixing of the upper and the lower dental rows with respect to each other in the horizontal plane. When the dental rows are interlocked the closely situated exteroanteroconid and interoanteroconid are arranged in front of exteroanterocone and interoanterocone. Dentinal fields of the anteroconid rest against anteroflexus, tall exterocone enters into protoflexid and short interoanterocone into paraflexid, and so on. Mesoflexid is transformed early into postfossetid at a very late stage

The structure of the molar teeth of the insectivorous hamsters of Oxymycterus (Fig. 47) greatly resembles Lenoxus. Unlike Lenoxus the closed, enamel alveoli of the upper molars (fossettes) are arranged not along the middle line of the tooth but somewhat labially. M_3 is reduced still more than in the previous genus. Anteroflexid and anteroflexus are not prominent.

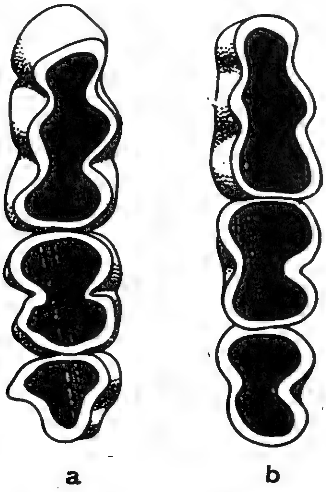


Fig. 47: Structure of masticatory surface of molars of Oxymycterus rosettellatus Wagn. Orig. Right rows of old individual: According to the specimen from the collection of Zool. Inst., Acad. of Sc., USSR. No. 6936, South America, Bahia (a) upper row; (b) lower row.

The extremely original structure of the molar teeth of Scotinomys (Fig. 48) may be deduced from the structure of the molars of Lenoxus. The tuberculate structure of tooth in Scotinomys is marked less strikingly than in the previous two genera. The crown in mesodont and the area of the dentinal exposures are significant. Tubercles of the upper molars are arranged almost oppositely. Interoanterocone is displaced forward with respect to exteroanterocone. Tubercles of the lingual

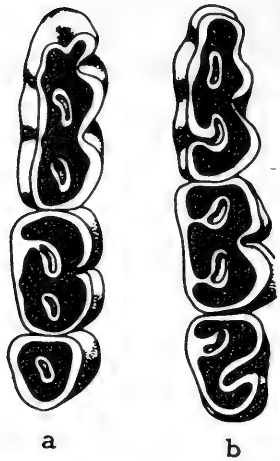


Fig. 48: Structure of the masticatory surface of molars of Scotinomys teguina irazu J. Allen. Orig. Right rows: According to the specimen from the collection of Zool. Inst. Acad. of Sc., USSR No. 39365, Central America, Costa Rica, Irazu (a) upper row; (b) lower row.

and the labial rows are approximated with each other. Anterior cingulum and mesostylus well developed, hypostylus not present. Posterior cingulum not developed. Interlocking of enamel crests and dentinal exposures that pinch the extremely deep paraflexus and metaflexus into parafossette and metafossette take place along the labial side of the upper molars. These enamel alveoli are arranged along the axial line of the dental row and parafossette acquires the form of a crescent, projecting like little 'horns'. As a result a tooth very similar to the selenodont tooth of the hoofed animals is formed. In the lower molars tubercles of the lingual row are appreciably displaced forward with respect to the tubercles of the labial row. Mesofossetid and postfossetid are formed later than the formation of similar alveoli on the upper molars, and acquire the shape of a crescent appearing as horns inside. Anterior cingulum, mesostylid and posterior cingulum are developed, hypostylid is not present. Merging of dentinal fields and enamel crests on lower molars takes place along the lingual side of the dental row.

The selenodont structure of the dental row often appeared in the phylogeny of Cricetidae: Scottimus, in the Oligocene of North America.

Salenomys in Oligocene of Mongolia,

Pliotomodon, in Pliocene of North America, which was perhaps related to Scottinomys.

The structure of the molar teeth of the selenodont hamsters indicates the significant role of the transverse grinding movements, biomechanically not as much advantageous, as the longitudinal grinding movement. Evidently, a small percentage of the selenodont hamsters is related to this in all the periods of their geological history. These are dead ends of development and adaptations to the masticatory systems.

As noticed by Stehlin and Schaub (1950) the structure of the molars of Mystromys (Fig. 49) resembles that of Cricetulus (Tscherskia) trition; but (Vorontsov, 1966), this similarity may not be considered as parallelism in the development of molars. Exteroanterocone and interoanterocone are drawn very close to each other. Tubercles of the lingual row of upper molars, including the interoanterocone are slightly shifted forward with respect to the tubercles of the labial row. Anterior cingulum mesostylus, mesolophus,

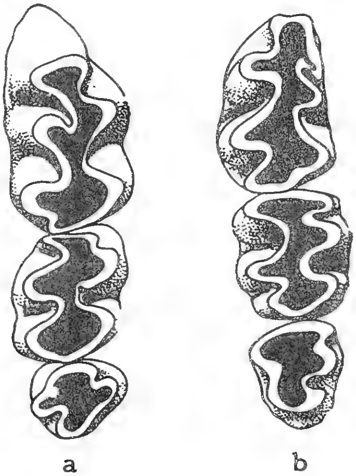


Fig. 49: Structure of the masticatory surface of molars of Mystromys albicoudatus Wagn. Orig. Right rows: According to the specimen from the collection of Zool. Inst. of Acad. of Sc., USSR, No. 39965, Union of South Africa, near Johannesburg (a) upper row; (b) lower row.

hypostylus, and hypolophus drawn apart from protocone are fairly developed. The transverse length of anterolophus, mesolophus and hypolophus is not much. Posterior cingulum is almost completely merged with metacone and postflexus is not expressed. Flexures do not close themselves. The characteristic peculiarity of the lower molars of Mystromys is the strong development of the anterior cingulum which is directed longitudinally on M_1; M^3 and M_3 are fairly well developed. The crown is brachyodont and the masticatory surface, tuberculate. Dentinal fields merge diagonally on detrition. For the structure of molars and family connections of Mystromys see the other paper by the author (Vorontsov, 1966).

The structure of molars in the present Palearctic hamsters (Cricetulus, Cricetus, Mesocricetus and Phodopus) can be deduced from the morphology of molars of Neogene Cricetini-Sinocricetus, Naunocricetus, and the Miocene specimen of the genus Cricetus. In all forms of this group anterocone and anteroconid are divided into two tubercles.

The mutual arrangement of tubercles of molars is very clear in various species of the genus Cricetulus (Fig. 50). In the subgenus Tscherskia the tubercles of the lingual row of the upper molars molars is slightly shifted forward with respect to the tubercles of the labial row. The tip of the anterior cingulum joins the paracone and mesostylus with metacone; these enamel crests pinch the inner part of paraflexus and metaflexus deep into parafossette and metafossette whereas the external parts of paraflexus and metaflexus remain open. The origin of metafossette is complex; it is formed only from the deeper inner part of metaflexus but also from postflexus pinched by enamel labial crests connecting posterior cingulum with metacone. Dential fields of the lingual row of upper molars have the form of (in the initial stages of detrition) little 'horns' turned outwards while dentinal fields of labial row are loop-shaped.

The structure of the lower molars resembles the mirror image of the structure of the upper molars, but closing of para-meso- and postflexids takes place later than the closing of flexures in view of their greater depth. Postflexid is deep and wide and widely separates metaconid from posterior cingulum. The crecent form of dentinal exposures having its 'horns' directed

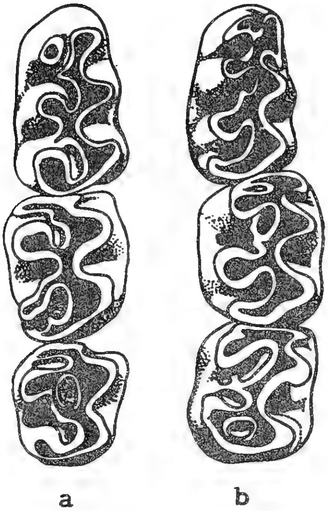


Fig. 50: *Structure of the masticatory surface of molar teeth of Cricetulus (Tscherskia) trition de Wint. Orig. Right rows: According to the specimen from Primorye District, Kazan Region, Kraskino (a) upper row; (b) lower row.*

inside is characteristic of the labial row, shifted much forward with respect to tubercles of the lingual row.

Forms of the subgenus, Cricetulus s. str. acquire a crecent form of the dentinal fields on the outer and the inner rows of tubercles. The arrangement of the features of the tubercles is not strictly opposite. However, because of the peculiarities of detrition (tubercles of lingual row of upper and labial row of lower molars are worn out more from the back, and the tubercles of the labial row of upper and lingual row of lower molars are worn out from the front) dentinal fields of adults are arranged opposite each other. Para- and metafossettes are arranged along the middle line of the row, enamel crests of these alveoli and also anteroflexus are stretched along the middle line of molars. A similar orientation of enamel crests indicates the significant role of transverse movements of mandible. Posterior cingulum is not well marked on upper molars. The teeth are wide.

The structure of molars of Cricetus (Fig. 51) greatly resembles the structure described above. Anterior cingulum on M^1

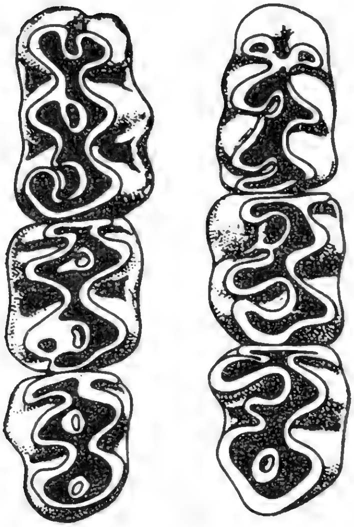


Fig. 51: Structure of the masticatory surface of molar teeth of Cricetus Cricetus L. Orig. Right rows: (a) upper; (b) lower.

stands very far from exteroanterocone. Para- and metafossettes are stretched longitudinally less than in Cricetus migratorius. Mesostylus and mesolophus are well developed and separate metafossette from metaflexus earlier than parafossette. Posterior cingulum is fairly well developed on wide upper molars. M^3 is a little shorter than M^2, M_3 and M_2 are equal in length. Arrangement of tubercles is almost opposite. Anterior cingulum on M_2 has a heel from the lingual side, which is much shorter than Cricetulus.

Mesocricetus (Fig. 52) can be considered as the last number of this series. Unlike the previous two genera anteroflexus closes into anterofossetus, posterior cingulum on the upper molars is clearly marked and anterior cingulum on M^2 does not have outgrowths from the lingual side. There may be a small additional rise to the front from the exteroanterocone. Mesostylid may be developed on M_2 and M_3. The marginal crest, connecting the exteroanteroconid with the protoconid and the protoconid with the hypostylid and the hypoconid may attain considerable height. However, fossetids are observed only in old individuals. Arrangement of tubercles of the upper molars is opposite and that of the lower molars alternate. The rows of molars are relatively narrow.

Fig. 52: Structure of the masticatory surface of molars of Mesocricetus newtoni Nehr. Right upper row. After Stehlin and Schaub (1950).

Molar teeth of Phodopus (Fig. 53), having almost the opposite arrangement of tubercles on the upper rows of Mesocricetus, sharply differ from the teeth of Cricetulus, Cricetus and Mesocricetus by the absence of parafossette and meta-fossette, which is related to the shallow internal parts of paraflexures and metaflexures. Posterior cingulum on upper molars is hardly developed. Anterior cingulum on M^2 gives lingual sprout unlike in Mesocricetus. Opposite fusion of dentinal fields and absence of closed enamel alveoli of Phodopus are convergently similar to Meriones. By the structure of the molars members of Phodopus are more adaptive to the processing of cellulose food, than Cricetulus, Cricetus and Mesocricetus and stand by themselves in this group of genera. By the degree of adaptability of the structure of teeth to the cellulose type of nutrition, the modern forms of Cricetini can be arranged in the following series: Cricetulus → Cricetus → Mesocricetus → Phodopus.

The structure of molars in Calomys, Eligomodontia, Zygodontomys, Graomys, Phyllotis, Punomys, Irenomys, Chinchillula and Andinomys is to a great extent, and sometimes, extremely adapted to the cellulose type of nutrition. Original members of this series (Colomys) still preserve bunodont teeth having a brachyodont crown. The general characteristics of the specimens of the entire group are as follow:

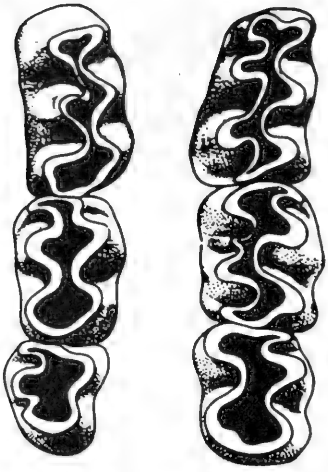


Fig. 53: Structure of the masticatory surface of molars of Phodopus sungorus sungorus Pall. Orig. Right rows: According to the specimen from the neighborhood of Novenskoe village of the Altai Region. (a) upper row; (b) lower row.

The presence of exteroanterocone and interoanterocone at least in newly-born animals;

the significant reduction of supplementary tubercles and crests: mesostylus, mesostylid, hypostylus, hypostylid, mesolophus and mesolophid, hypolophus and hypolophid;

the flexures M^1, M^2, M_1 and M_2 (flexures and flexids) do not usually close into fossettes and fossetids; compressed nature of the masticatory surface is well expressed;

and the enamel crests are arranged transversally.

The presence of additional tubercles on M_1, situated in between exteroanteroconid and protoconid is characteristic of the structure of the molars in the described group of genera. According to the nomenclature of Hershkovitz (1962) this tubercle is called the anterolabial stylid. In the young individuals of Phyllotis micropus, Ph. sublimis and Euneomys chinchilloides this tubercle is situated in an isolated manner. Frequently it is fused with exteroanteroconid, to form a long spur. It runs backwards from the latter after developing specially in Andinomys, Chinchillula, Eligmodontia and some forms of Phyllotis (Ph. griseoflavus, Ph. micropus);

The structure of molar teeth of Phyllotiini is described by Hershkovitz (1962).

Molars of Colomys have brachyodont crown with tuberculate masticatory surface (Fig. 54). Dentinal exposures in adults are more poorly developed than in Phyllotis. Because of the unequal thickness of the enamel layer on the external and internal sides of the tubercles of lingual and labial rows the tuberculate structure of tooth is retained not only in young and adult forms but also in old individuals. Arrangement of tubercles and dentinal fields on lower molars is strictly alternate, and on the upper molars it is in between opposite and alternate. The first molars are longer than the second molars and the second molars are longer than the third. The highly characteristic additional tubercle situated on M_1 in between protoconid and exteroanteroconid usually merges with the latter. Traces of the division of exteroanterocone, interoanterocone, exteroanteroconid and interoanteroconid are seen in young individuals.

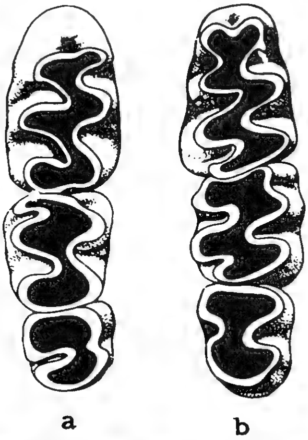


Fig. 54: Structure of the masticatory surface of molars of Calomys sorrella Thomas Orig. Right rows. According to the specimen from the collection of Zool. Institute, Acad.; of Sc., USSR No. 45385, '5, Peru, Lircay (a) upper row; (b) lower row.

Molars of Eligmodontia (Fig. 55) principally resemble Calomys, although the dentinal exposures are slightly better developed. The spur, which connects the exteroanteroconid with supplementary tubercles and almost closes up with protoconid is very well developed.

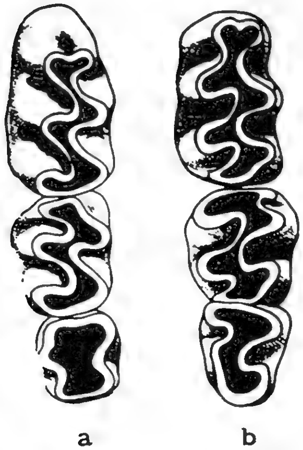


Fig. 55: Structure of the masticatory surface of the molars of Eligmodontia typus. F. Cuvier. Orig. Right rows. According to the specimen from the collection of Zool. Inst., Acad. of Sc., USSR No. 45375, Argentina; Neuquen Chosmalal (a) upper row; (b) lower row.

The genus Pseudoryzomys described in 1959 by Hershkovitz (1962) relates to these genera. Judging from the photographs and descriptions (Hershkovitz, 1962) the molars of Pseudoryzomys have clearly expressed tuberculate structure of the masticatory surface. Tubercles on the upper molars are arranged oppositely and on the lower molars tubercles of the lingual row is slightly displaced forward with respect to the tubercles of the labial row. The spur highly characteristic of Phyllotini and connecting the exteroanteroconid with the supplementary tubercles of the lingual side is developed.

The masticatory surface of the molars is compressed in Zygodontomys (Fig. 56). The crown is brachyodont. Dentinal fields which are derivative of the corresponding tubercles, are arranged on the upper molars almost oppositely and on the lower molars the dentinal fields of the lingual row are moved forward with respect to the dentinal fields of the labial row. Dentinal fields of exteroanterocone and interoanterocone are merged with each other and only shallow anteroflexus and considerable width of the first dentinal field of M^1 indicate the differentiation of anterocone into two tubercles. Mesostylus on M^1 and M^2 and anterior cingulum on M1 are embryonic or in general they are not developed at all. Posterior cingulum is not prominent (what the last dentinal field of the labial row - a derivative of only a single metacone or result of the merging of metacone with posterior cingulum -- represents cannot be taken for granted without the study of the tooth development); M^3 has two dentinal fields and is shorter than M^2. Mesostylid is poorly marked. Protoflexid on M_1 may be closed into protofossetid during detrition. Anteroflexid is not marked and the presence of extero-and intero-anteroconids can be judged only by the considerable width of the anteroconid. M_3 has two dentinal fields and is a bit shorter than M_2.

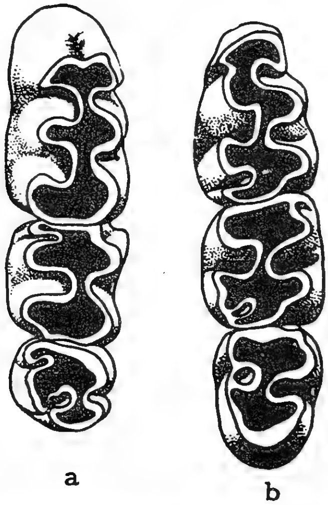


Fig. 56: Structure of the masticatory surface of molars of Zygodontomys breicanda thomosi J. Allen. Orig. Right rows. According to Specimens from the collection of Zoological Institute, Acad. of Sci , USSR, No. 45380, Venezuela, Rio Aurare (a) upper row; (b) lower row.

The crown is brachyodont and masticatory surface is compressed in Phyllotis (Fig. 57). Embryonal tubercles have a very thin layer of enamel on their own tips and so they are quickly worn out and become compressed. Thickness of the enamel layer on the external and internal sides of the tubercles of the lingual and labial rows is nearly the same. Therefore, wearing-out conditions are the same for all parts of the tooth, that retain the same height for a greater part of life. Arrange-

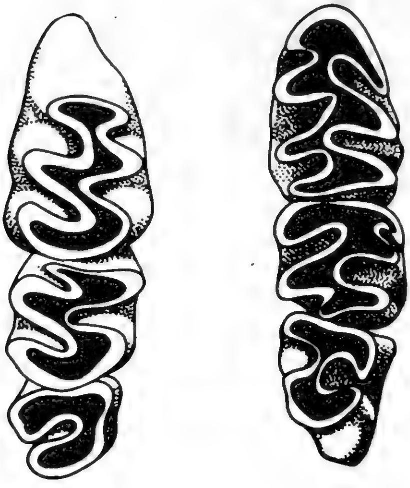


Fig. 57: Structure of the masticatory surface of molars of Phyllotis griseoflavus Waterh. Orig. Right rows: According to the specimens from the collection of Zool. Inst., Acad. of Sc., USSR, No. 45376. Paraguay, Gran Chaco (a) upper row; (b) lower row.

ment of dentinal fields (tubercles) is almost opposite; on the upper molars, the tubercles of the labial row, (but on the lower ones, those of the lingual row) are shifted forward. Posterior cingulum on the upper molars is not well expressed. Anterior cingulum which often merges with the dentinal field of paracone may be poorly developed on M^2.

From the lower molars posterior cingulum may be developed on M_1. However, owing to the slight depth of postflexid it may quite closely fuse with metaconid. Molar teeth of Phyllotis resemble the structure of the masticatory surface of the less specialized specimens of the cheek-toothed field-voles (Fibrini Hint.) Prometheomys, etc. Paraflexus and protoflexus, metaflexus and hypoflexus standing against each other are so close to each other that the portion of the crown enclosed between them almost fully consists of two enamel layers, divided by a small strip of dentine. These crosspieces subdivide dentinal fields which highly resemble the structucture of molars of the brachyodont field-voles.

The structure of molars in Galenomys (Fig. 58) resembles the structure described for Phyllotis.

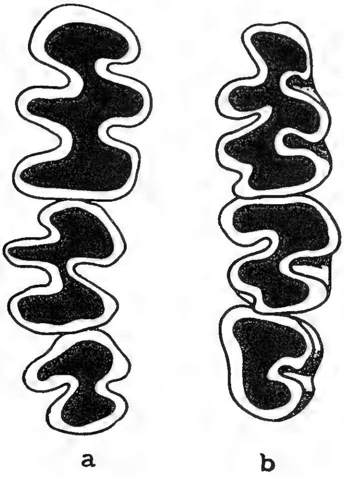


Fig. 58: *Structure of the masticatory surface of molars of* *Galenomys garleppi* *Thomas. Right rows. According to the photo of Hershkovitz (1962) (a) upper row; (b) lower row.*

Irenomys (Fig. 59) stands by itself amidst this group of genera in the structure of molars. Dentinal fields of the lingual and labial sides are arranged strictly oppositely on the upper molars and almost oppositely on the lower ones. Flexures of the external and the internal sides almost adjoin with each other - only a narrow enamel partition separates them. Dentinal spaces of any subsequent tubercle do practically not join with those of the previous tubercle. Anterior cingulum and posterior cing. are not well expressed. Each of the first molars have three dentinal fields, and each of the second and the third have two dentinal fields. The masticatory pattern is compressed and the crown mesodont. The lateral edges of the dentinal field are sharp. In our opinion the peculiar structure of Irenomys molars, mostly resembling that of some Gerbillinae molars, does not, however, give a basis for separation of Irenomys from other forms of Phyllotini, (Hershkovitz, 1962). The spur on M1 connecting exteroanteroconid with the arranged supplementary tubercles in front of protoconid is highly developed in Irenomys. Reduction of anterior cingulum and posterior cing. is marked in Chincillula though feebly. In such a manner, the peculiarity of adaptive evolution of the dental system of Irenomys originating by imitation of the tooth of gerbils does not give a basis for the separation of the genus Irenomys from the Phyllotini tribe.

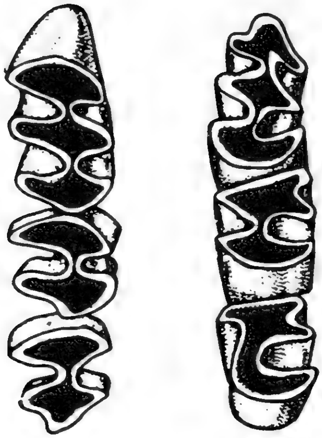
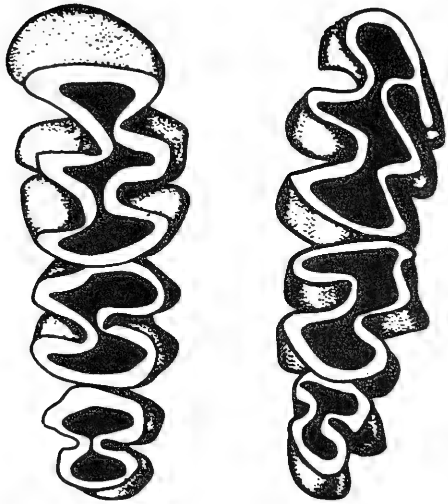


Fig. 59: Structure of the masticatory surface of molars of Irenomys tarsalis philippi. Orig. Right rows: According to the specimens from the collection of Zool Inst. of Acad. of Sc., USSR, No. 45374, Chile. Blanquihue, Peulla (a) upper row; (b) lower row.

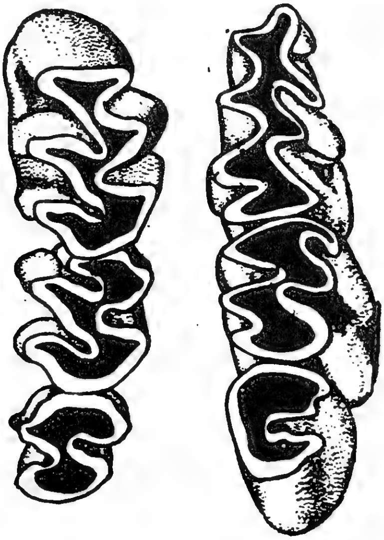
By the structure of molars Chinchillula occupies an intermediate position between Irenomys and Andinomys. Anterior cingulum and posterior cingulum are reduced similar to the genus described above and Chinchillula; but the tubercles of the lingual and the labial rows are out of line with respect to each other (Fig. 60). The spur moving to M_1 from exteroanteroconid backward is very much developed and the crown is mesodont.

Andinomys (Fig. 61) achieves extreme degrees of adaptation to the cellulose type of nutrition according to the structure of molars among all Cricetinae (along with Neotoma). The masticatory surface closely resembles Microtinae. The crown is mesodont. Dentinal fields that are homologs of tubercles are arranged alternately, and the dentinal fields merge diagonally. Flexures are very deep and are so close to each other, that the part of the crown enclosed between them, consists almost entirely of two enamel layers divided by anarrow strip of dentine. Enamel crests are directed transversally, which gives evidence of the unusual development of the longitudinal grinding movements of the mandible. The 'spur' moving to M_1 from the exteroanteroconid backwards is very clearly marked. Anterior cingulum and posterior cing. are developed on M^2, M_1 and



a b

Fig. 60: *Structure of the masticatory surface of molars of Chinchillula sahamae Thomas. Orig. Right rows: According to the specimen from the collection of Zool. Inst:, Acad. of Sc., USSR No. 45372, Peru, Arequipa, Cailloma (a) upper row; (b) lower row.*



a b

Fig. 61: *Structure of the masticatory surface of molars of Andinomys edax. Thomas. Orig. Right rows. According to the specimen from the collection of Zool. Inst, Acad. of Sc., USSR, No. 453681 Argentina, Huhui Province. (a) upper row; (b) lower row.*

M2. Additional tubercles (ectostylid according to the terminology of Hershkovitz, 1962) may be outlined on M_1 and M2 in front of hypoconid. On M_2 anteroconid also merges with the additional tubercle situated in front of protoconid and also forms a "spur" directed backwards. The tendency for the formation of additional tubercles and their merging with main tubercles very strikingly expressed in Andonomys leads to an increase in the length of the sectorial enameled crests.

Euneomys (Fig. 62) rather stands by itself from the group of the genera under consideration. According to the structure of the masticatory surface of the upper molars and of M_2 and M3, this genus having the same base can be approximated to Phyllotini and Sigmodontini. The structure of M_1 is remarkable. An additional tubercle which is, however, not connected with exteroanteroconid by a "spur" but is connected with protoconid is developed in front of protoconid. Self-dependence of extero-and interoanteroconids is preserved for a long time. Their dentinal fields, merging with each other during the whole life remain isolated from dentinal fields behind which lie proto- and metaconids. A similar type of merging of dentinal fields is highly characteristic of the primitive specimens of gerbils but is not absolutely found among hamsters having a compressed masticatory surface.

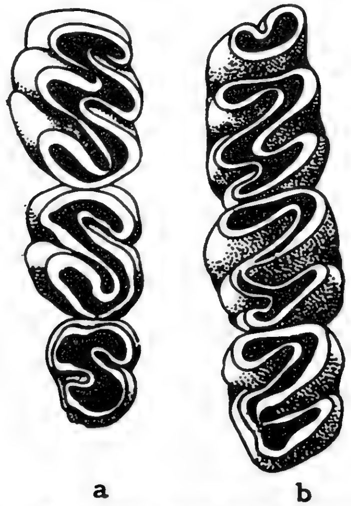


Fig. 62: Structure of the masticatory surface of molars of Euneomys chinchilloides Petersoni J. Allen, Orig. Right rows. According to the specimen from the collection of Zool. Inst., Acad. of Sc., USSR No. 45369, Chile, Laguna Lazo (a) upper row; (b) lower row.

On the whole, for the evolution of the dental system of the tribe Phyllotini, adaptibility to the processing of vegetative parts of plants is characteristic of the majority of its specimens. According to the degree of adaptation of molar teeth to the processing of cellulose food matter the specimens of the tribe can be arranged in a following series: *Calomys* → *Pseudoryzomys* → *Eligmodontia* → *Galenomys* → *Phyllotis* → *Chinchillula* → *Andinomys*. The genus *Irenomys* rather stands by itself, although it is close to *Chinchillula*. *Euneomys* possibly forms an independent group associating Phyllotini with *Sigmodontini*.

Sigmodon (including *Sigmomys*), *Holochilus*, *Neotomys* and *Reithrodon* (including *Proreithrodon*) form a common group by the structure of molars. The crown in all the specimens of this group is brachyodont and the masticatory surface does not have terraced (Holochilus) or compressed (*Sigmodon*, *Reithrodon* and other genera) tubercles. Exteroanterocone and interoanterocone are developed in the newly born, and in individual cases in the young animals also (*Holochilus magnus* Hershk). Supplementary tubercles and crests (mesostylus, mesostylid, hypostylus, hypostylid) are usually not developed. Unlike in *Phyllotini* flexures and flexids often close into fossettes and fossetids, at least in old individuals; it is associated with the rise of the marginal layer of enamel; during detrition of this the enamel flexures close into isolated alveoli. The molars are broad and enamel crests are frequently quite inclined (*Sigmodon*), and not directed strictly transversally as in the majority of *Phyllotiini*. Flexures are deeper (this is associated with considerable breadth of tooth as well as the bending capacity of flexures and flexids), than in the specimens of *Phyllotiini*. By the structure of molars this group of genera, being included by us in the tribe *Sigmodontini* is much more homogenous than *Phyllotiini*. No member of *Sigmodontini*, including *Reithrodon* does achieve such degrees of specialization to the cellulose type of nutrition as *Andinomys* of the group *Phyllotiini*. However, among *Sigmodontini*, forms having tuberculate masticatory surface are not found as among primitive forms of Phyllotiini (*Colomys*, *Eligmodontia*), and, so *Sigmodontini* is considered after *Phyllotiini*.

Forms of the genus *Holochilus* (Fig. 63) are characterized by the terraced form of the masticatory surface. This form

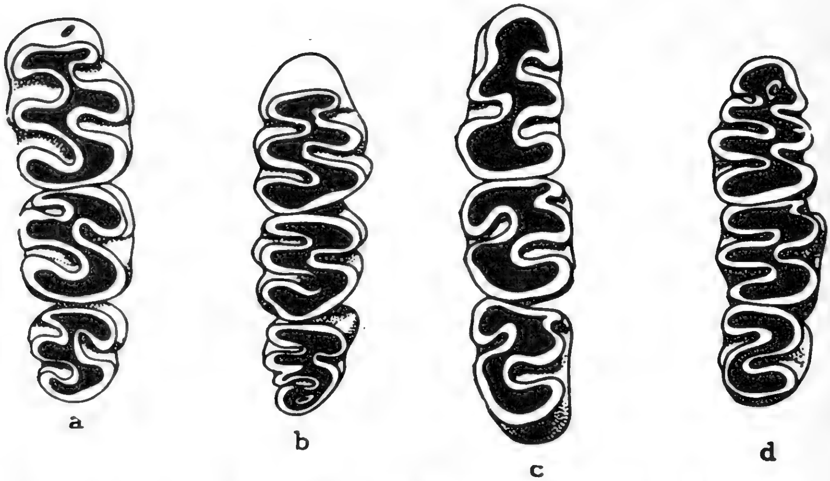


Fig. 63: Structure of the masticatory surface of molars of Holochilus. Right rows. According to the photo of Hershkovitz (1955), (a, c) H. magnus Thomas; (b, d) H. brasiliensis Hershk; (a, b) upper rows; (c, d) lower rows.

restricts transverse movements of mandible and permits lower dental rows to move only longitudinally. This adaptation indicates a clear specialization of the dental system of Holochilus to the cellulose type of nutrition. At the same time in Holochilus the tuberculate structure of molars is expressed not only in the newly born but also in those which have started independent life. Dentinal fields of the lingual and the labial sides - homologs of the corresponding tubercles - are situated considerably out of line with respect to each other in H. magnus and arranged alternately in H. brasiliensis. In H. brasiliensis the dentinal field of metacone has a protuberance from the labial side indicative of the development of posterior cingulum, merged with metacone during detrition. Mesostylus is developed in M^3. Frequently, paraflexus closes into parafossetes and metafossetes also exists on M^3 in H. brasiliensis. M^3 in Holochilus is slightly smaller or equal to M^2 but is narrowly noticeable.

Molars of Sigmodon (Fig. 64) are characterized by a compressed and not by a terraced form of masticatory surface. Enamel crests are arranged in an inclined position which indicates the great role of transverse movements of the mandible. Paraflexus on M^2 and M^3, meso- and postflexid on M_1-M_3 in adults and old individuals, are locked into enamel alveoli (fossetus and fossetid).

M^3 is slightly shorter and narrower than M^2. Arrangement of the tubercles is almost opposite but in view of the greater depth and bending capacity of flexus enamel crests have a significant length. In the structure of molars Sigmodon is much more primitive than Holochilus, but Sigmodon even when young, loses the tubercles and acquire a compressed masticatory surface unlike Holochilus.

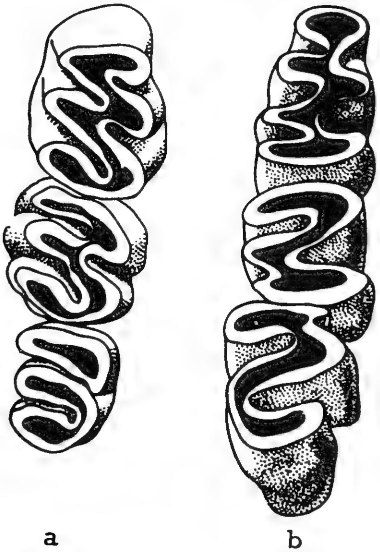


Fig. 64: *Structure of the masticatory surface of molars of Sigmodon hispidus texianus Aud. et Bachm. Orig. Right rows. According to the specimen from the collection of Zool. Mus. of Moscow St. University No. S-65644, USA, Kansas (a) upper row; (b) lower row.*

The structure of molars of Reithrodon (Fig. 65) closely resembles the structure of Sigmodon, but is distinct from it by the alternate arrangement of dentinal fields - homologs of corresponding tubercles - and nondiagonal arrangement of flexures. In R. cuniculoides the molars are very wide, flexures have an arched shape, and on M^3 and M^2 they close in (in the first instance from the labial side) the fossetids fairly early. In R. typicus Waterh., the molars are narrower, flexures and enamel crests are directed transversally, which indicates the increasing role of the longitudinally-oriented grinding movements of the mandible.

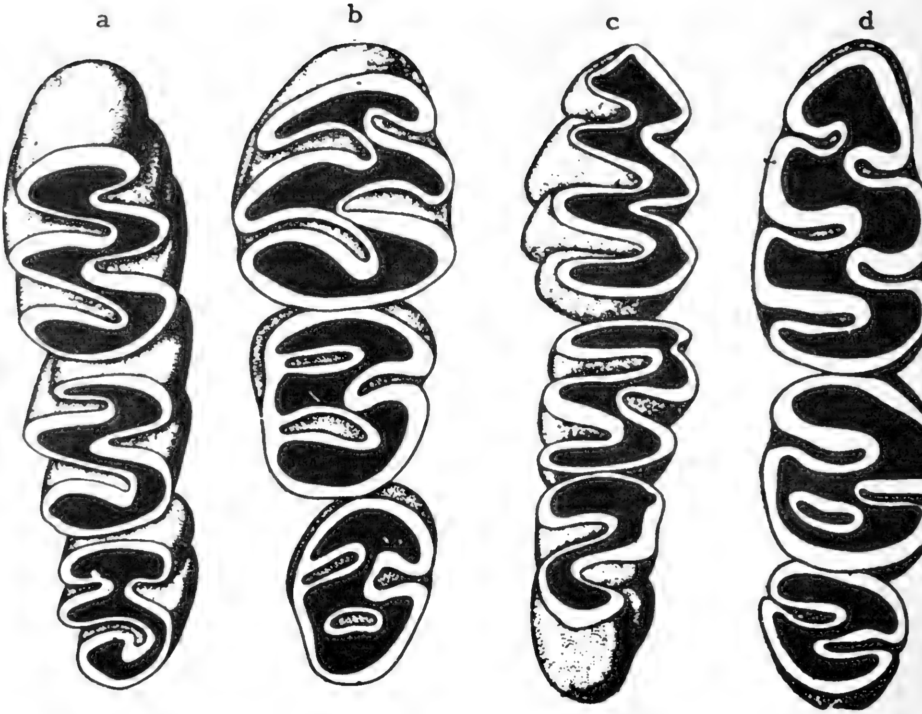


Fig. 65: Structure of the masticatory surface of molars of Reithrodon. Orig. Right rows: a, c: R. typicus Waterh., according to the specimen of Paris Museum of Natural History, No. 21-22, adult individual; b, d, R. cunicaloides Waterh, according to the specimen of the Paris Museum of Natural History, No. 1883-183. Older individuals (a, b) upper rows; (c, d) lower rows.

The alternate arrangement of tubercles in the members of the genus of Neotomys (Fig. 66) is clearly expressed. Like Holochilus magnus all species of this genus preserve poorly developed anteroflexus, hardly subdividing the dentinal fields of exteroanterocone and interoanterocone. The flexures and the corresponding enamel crests are directed transeversally and not slantingly as in Sigmodon and Holochilus, which gives evidence of the increasing role of the longitudinal grinding movements of the mandible. M^3 is longer than M^2 and has a complex shape. Posterior cingulum on M^3 is very well developed with an outgrowth on the lingual side, having an almost independent dentinal field.

According to the degree of adaptation of molars to the cellulose type of nutrition, Sigmodontini can be arranged in the follow-

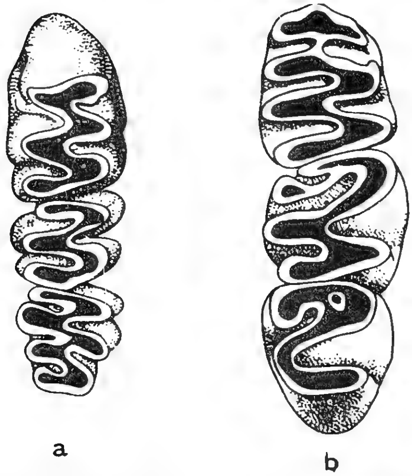


Fig. 66: Structure of the masticatory surface of molars of Neotomys ebriosus Thom. Right rows. According to the photo of Hershkovitz (1955) (a) upper row; (b) lower row.

ing order. Holochilus magnus → H. brasiliensis → Sigmodon → Reithrodon → Neotomys. The structure of the molars of Sigmodontini has been described in the paper of Hershkovitz (1955).

North American hamsters belonging to the tribe Neotomini (Neotomodon, Neotoma, Nelsonia and Xenomys) attain highly perfect specializations to the cellulose type of nutrition.

The molars of Neotomodon (Fig. 67) have a compressed masticatory surface. The crown is intermediate between brachyodont and mesodont. Dentinal fields - homologs of corresponding tubercles - are arranged alternately. The anterocone is, obviously, not divided into two tubercles. Additional tubercles and crests are not develooed. On M^1 and M^2 and on the lower molars flexures never close and form fossettes and fossetids. Flexures of internal and external sides do not have a uniform depth: on the upper molars the depth of flexures of the lingual side is more than that of the flexures of the labial side and on the lower molars it is just opposite. The dental system of Neotomodon is not fully specialized for the cellulose type of nutrition.

The molars of Neotoma, Nelsonia and Xenomys are highly adapted to the processing of cellulose food. The molars of Neotoma (Fig. 68) and the genera close to it with compressed masticatory

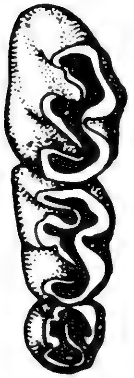


Fig. 67: *Structure of the masticatory surface of the upper molars of Neotomodon alstoni Merriam. Right rows. After Hoffmeister (1945)*

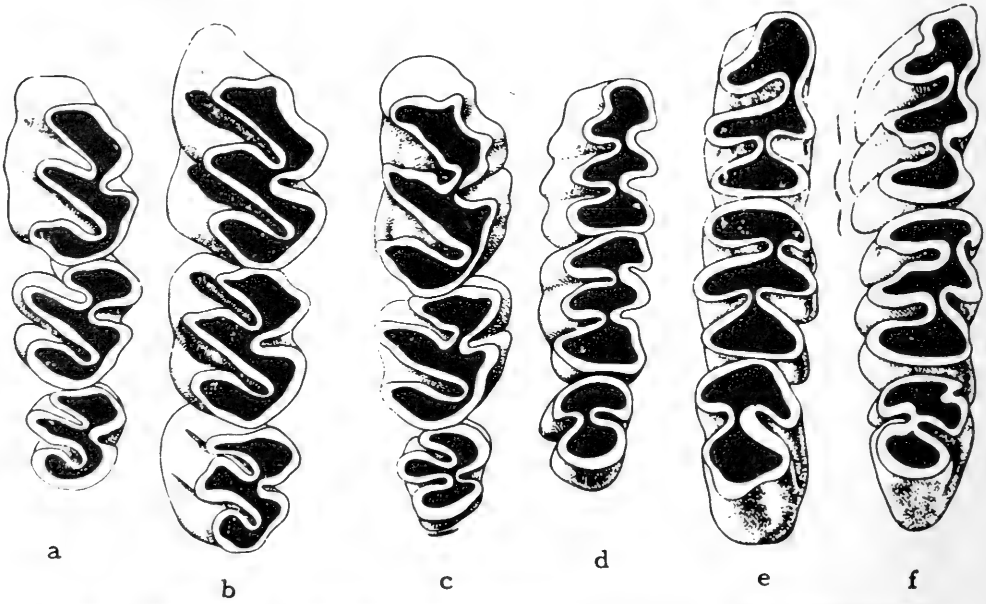


Fig. 68: *Structure of the masticatory surface of molar teeth of Neotoma. Orig. Right rows: a, d N. lepida Thomas, according to the specimen from the collection of Zool. Mus. Moscow St. University, No. S-60168, USA, Utah State, Tuele b, e N. fuscipes Baird. . according to the specimen from the collection of Zool. Mus., Moscow St. University No. S-35352, USA California, Gilroy, o, f N. albigula Hartley, according to the specimen from the collection of Zool. Mus., Moscow St. University, No. S-60169, USA, Arizona (a, b, c) upper rows; (d, e, f) lower rows.*

surface having a prismatic structure are very close to the field-voles and zokors. The crown is mesodont, but almost hypsodont when the rodents are young.

The young and the semi-adult forms of Neotoma do not have molars, but the bases of the prisms of molars are closed unlike the real hypsodont Microtini and in individuals growing old there appear roots without any special arrangement of maxillary bones. The development of roots in Neotoma highly resembles Clethrionomys, and considering the time the roots are laid and the degree of development of roots, Neotoma is close to the most hypsodont species of Clethrionomys to Cl. rufocanus. Evidently, Neotoma and other genera close to it possessed unbroken anterocone. Flexures of external and internal sides enter deeply towards each other. On the lower molars the dentinal fields of some forms of Neotoma do not even merge with each other and lie isolated by enamel constrictions remotely resembling thereby the structure of molars of Otomys. Unequal development of flexures and flexids leads to the fact that the structure of molars of Neotoma convergently resembles that of Myospalacinae. Dentinal fields of external and internal sides are arranged alternately. The dental row is stretched longitudinally and the majority of enamel crests is directed transversally indicating the prevalence of the longitudinally grinding movements of the mandible.

By specialization to the cellulose type of nutrition, Neotoma and the dloser genera resemble the South American hamster Andinomys and the most specialized forms of cheek-toothed field voles (Fibrini). According to the degree of specialization to the cellulose type of nutrition Neotomini can be arranged in the following order:

$$\text{Neotomodon}\left\{\begin{array}{l}\text{Neotoma}\\ \text{Xenomys}\\ \text{Nelsonia}\end{array}\right.$$

In all the above considered tribes of Cricetinae (except some of Akodontini - Oxymycterus, Lenoxus, Blarinomys) there was a tendency to the specialization of the dental system to the cellulose type of nutrition. The adaptation of the dental system in the piscivorous hamsters from the group Ichthyomyini (Ichthyomys, Rheomys, Anotomys, Daptomys, Neusticomys) started in a completely different direction.

Molars of Ichthyomys (Fig. 69) compared to bunodont Oryzomyini, undergo substantial changes: supplementary tubercles and crests are reduced and the main tubercles situated strictly in opposite direction achieve a significant height in return and are widely placed. Anterocone is divided into two tubercles. Molars have a significant width; M^3 is reduced. As it has been pointed above, the opposite arrangement of the widely placed tubercles facilitates retention of the prey for the force developed by the prey is directed longitudinally forward and the holding tubercles are oriented transversally.

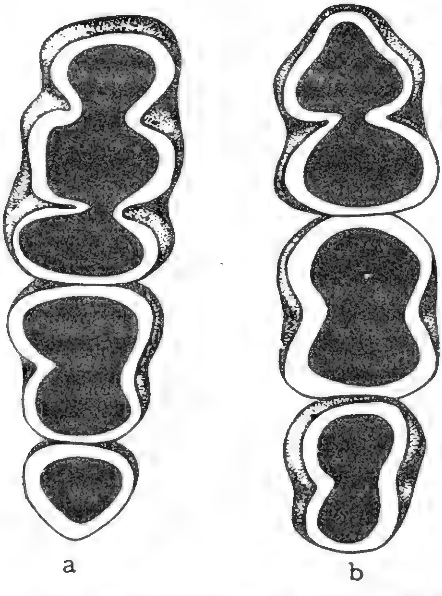


Fig. 69: Structure of the masticatory surface of molars of Ichthyomys soderstromi de Winton. Orig. Right rows of an old individual. According to the specimen from the Paris Museum of Natural History, No. 1932-2950. South America, Rio Blanco. Cacao Cocha (a) upper row; (b) lower row.

The adaptive radiation is very wide in the structure of the molars of Cricetinae. Within the subfamily almost a whole variety of dental system characteristic of the entire Cricetidae family is found: from the brachyodont sharp tuberculate tooth of seed-eating and predatory hamsters to the mesodont and almost hypsodont tooth having a compressed masticatory surface like that of the field vole in herbivorous hamsters. Depending on the type of nutrition the bunodont forms are characterized either by a masticatory surface complicated by pointed tuberculate teeth with crests having an alternate arrangement of tubercles (seed-eating Peromyscus, Reithrodontomys, etc.) or by one with compressed, pointed tubercles having an opposite arrangement of tips (insectivorous Oxymycterus, etc., piscivorous Ichthyomys, etc.). Finally, the forms having a false selenodont type of tooth (Scotinomys) appear as an exception among hamsters.

Practically not a single one of the above considered tribes (except Ichthomyini) possesses a similar structure of molars, or the same degree of specialization to any type of nutrition. The features for adaptation to the cellulose type of nutrition are observed in the structure of molar teeth of some forms existing in each of these groups.

Each of these tribes can be easily characterized by the tendency and range of variability in the structure of molars than by the common features of the structure of masticatory surface.

The variability series of the dental system within each of these tribes, are the homologous variability series according to N.I. Vavilov (1922).

Usually the members of a more progressive tribe attain greater degrees of specialization to the cellulose type of nutrition than the last forms of the previous tribes.

In many tribes individual genera occupy the same levels of specialization to the cellulose type of nutrition and may possess a very similar structure of molars. Parallelisms in the structure of molar teeth are characteristic of not only the members of different tribes of one subfamily but also in the forms of various subfamilies.

7. Structure of the Molar Teeth of Some Rodents, which belonged sometimes to Cricetinae (Nesomyinae, Tachyoryctinae, Myospalacinae, Lophiomidae, and Platacanthomyinae)

a. Nesomyinae

On the basis of the study of the structure of the dental system of the Madagascan rodents, Stehlin and Schaub (1950) already showed that Ellerman's idea (1940, 1941) of dividing Nesomyinae into five subfamilies had no base. The adaptive radiation of Nesomyinae went too far and the teeth turned out to be the most divergent of the organs in this group. However, a detailed study of the morphology of molars of Nesomyinae has helped to establish a single structural plan in all members of this striking group of animals.

The structure of molars of all modern forms of Nesomyinae can be deduced from Macrotarsomys (Fig. 70). Molars of M. bastardi are tuberculate and the crown is brachyodont. Anterocone is divided into exteroanterocone and interoanterocone (Stehlin and Schaub, 1950, Fig. 257, S. 174; see the figure of teeth of young animals). However, anteroflexure is not deep and the distance between these tubercles is not great, and with grinding, their dentinal fields merge early during detrition. Tubercles of the lingual side of upper molars and the labial side of lower molars are slightly disposed forward with respect to opposite sides. The supplementary tubercles and crests (mesostylus, mesolophus, etc.) are not developed. Cingulum posterior is seen on M^2 in young individuals. During detrition the dentinal field of the posterior cingulum quickly merges with the dentinal field of metacone. Alternate arrangement of tubercles is clearly expressed on the lower molars of M_1 and M_2, which generally have posterior cingulum; other supplementary formations on lower molars are undeveloped. M_3 and in particular, M^3 are reduced. The structure of the molars of Macrotarsomys greatly resembles the structure of those of Calomyscus Schaub (1934) even inclined to the idea of close relationship between these two series; later the same author (Stehlin and Schaub, 1950) considered resemblance in the structure of the molars of Macrotarsomys and Calomyscus

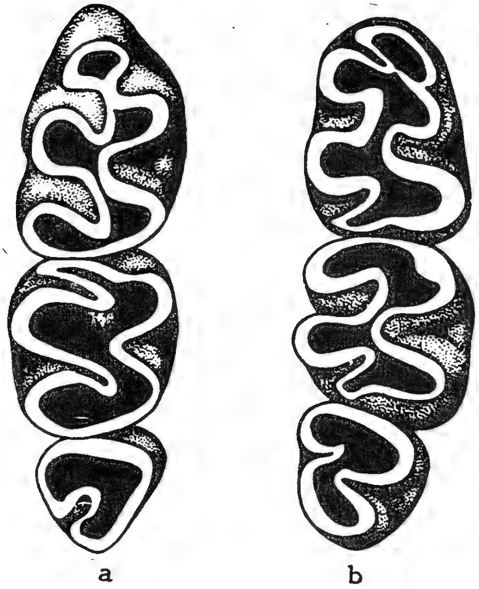


Fig. 70: Structure of the masticatory surface of molars of Macrotarosomys bastardi Milne-Edw. et. Grandidier. Orig. Right rows: According to the specimen from the collection of the Paris Museum of Natural History. No. 1912-134, Madagascar.

as an example of convergence. Schaub (Stehlin and Schaub, 1950) pays attention to the resemblance in the structure of molars between Macrotarsomys and the Miocene Cricetodon minus Lartet. However, the division of anterocone into two tubercles in Cr. minus was already expressed much more distinctly than in Macrotersomys. Similarity in the structure of molar teeth of Macrotarsomys with the Miocene Cricetodontini may be interpreted not as an example of convergence but as an evidence of spontaneous genetic link between these groups. It should not be forgotten that Madagascar was connected with the mass of land of the Old World only in Miocene (Termier H. et G., 1952; Strakhav, 1948) and, evidently, the migration of ancient Cricetidae to Madagascar (Vorontsov 1960b) took place in Pliocene when forms of Cricetodontini were existing in Europe and Africa.

From the structure of the molars of Macrotarsomys we find that the molars of Nesomys have a very complicated structure (Fig. 71). The molars are tuberculate and the crown is

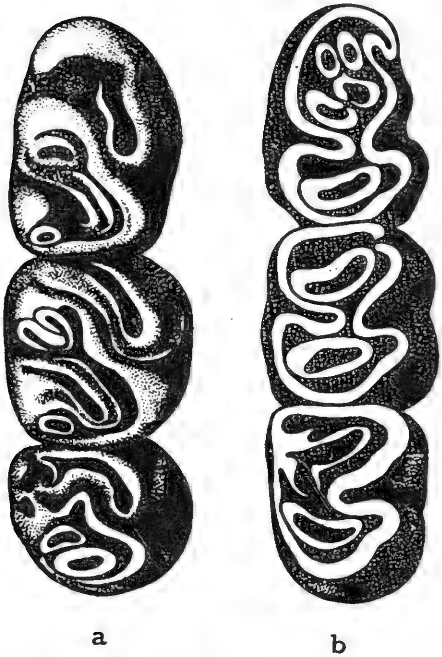


Fig. 71: Structure of the masticatory surface of the molars of Nesomys rufua Peters. Orig. Right rows. According to the specimen from the collection of Zool. Mus., Moscow State University, No. S-4293, Madagascar, Ampitambe forest, Betsileo (a) upper row; (b) lower row.

brachyodont. The tubercles of the labial side of the upper and the lingual side of the lower molars are much taller than the compressed tubercles of the lingual side of the upper and the labial side of the lower dental rows. Similar arrangement of tubercles is as if it is a transition to the "terraced" form of the masticatory surface characteristic of Gymnuromys. Anterocone and protocone on M^1, and anterior singulum and protocone on M^2 form a single dentinal field by fusion, paraflexure joins with hypoflexure which is a characteristic feature of the structure of the dental system of the majority of Nesomyinae, never found among the present Cricetinae. Mesostylus and posterior cingulum are developed on upper molars. Mesoflexure and postflexure are closed into shallow mesofossete and postfossete.

The structure of the masticatory surface of lower molars of Nesomys is very complex. Anterior cingulum merges with paraconid, protoflexid joins with mesoflexid very early and then during detrition they are pinched from the lingual and labial sides, and form a single closed alveolus, with the fusion of protofossetid with mesofossetid. Postfossetid is very big and, possibly, this alveolus appeared not only from postflexid but also by the constriction of the deepest part of hypoflexid merged with postflexid. Mesostylid and mesolophid are developed.

The structure of the front part of M_1 is exceptionally complex, where there are four closed enamel alveoli in between the dentinal field formed by anteroconid, protoconid, paraconid and mesostylid. The two posterior alveoli may be homologized as proto- and mesofossetids, one of the frontal as parafossetid, and the other, either as procingulofossetid or as anterofossetid. M^3 is not reduced, but its size is less than M^2; M_3 is nearly equal to M_2 and M_1. The molars of Nesomys are relatively broad. The structure of the upper molars of Nesomys is functionally almost the same as that of the molars of Rhipidomys, Reithrodontomys and other typically seed-eating American hamsters.

The structure of the masticatory surface is very complicated in Gymnuromys (Fig. 72) divided by Ellerman (1941) into a special subfamily of Gymnuromyinae. The masticatory surface is compressed, the crown is mesodont, and the teeth are made of a great number of frequently isolated plates of enamel having narrow dentinal exposures. The masticatory surface is of a terraced type. Anterocone and protocone on M^1, anterior cingulum and protocone on M^2 and M^3 join to form a single dentinal field, paraflexure is connected with hypoflexure, and protocone, as in Macrotarsomys and Nesomys, does not move forward and is opposite to paracone.

Mesostylus, mesolophus and posterior cingulum attain extraordinary development: the size of the mesostylus-mesolophus dentinal field is more than the dentinal field of metacone and are nearly equal to the field of paracone. It is remarkable that while additional tubercles are highly developed on labial side, the lingual side remains made up of only protocone and hypocone. On M^1, a labially oriented outgrowth moves away from the paracone; this outgrowth is a new formation not found in any other form of Cricetidae. On M^1 and M^2 the flexures are generally closed into fossettes. M^3 has an extremely complex form and homologization of its elements is very difficult.

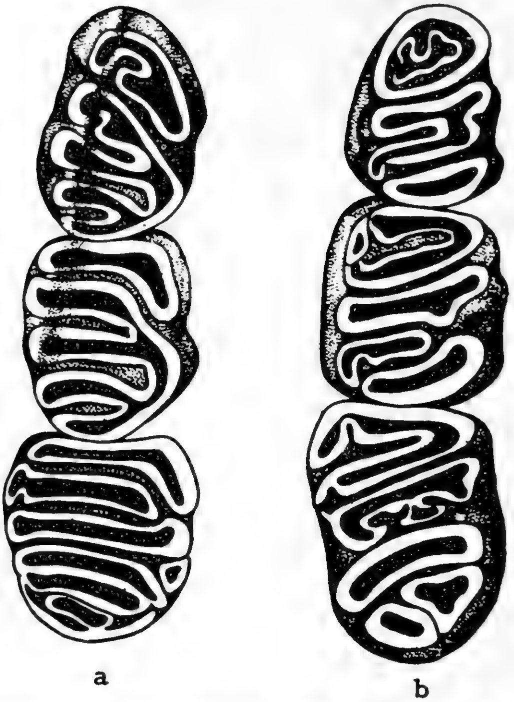
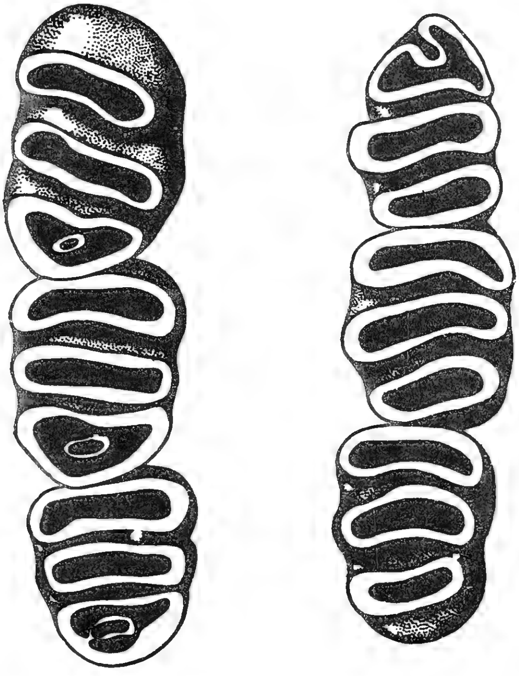


Fig. 72: *Structure of the masticatory surface of molars of Cymnuromys roberti F. Major Orig. Right rows. According to the specimen from the collection of Paris Museum of Natural History No. 1897-538. Madagascar (a) upper row; (b) lower row.*

The structure of the lower molars is more complex than the upper molars. Antero- and paraconids on M_1, and anterior cingulum and paraconid on M_2 and M_3 form a horse-shoe shaped dentinal field; paraflexid first closes on M_1, then on M_2 and later on M_3 to form parafossetid. Protoflexid is connected with mesoflexid and hypoflexid may be connected with postflexid (M_1, M_2 and M_3) and also with metaflexid (M_2). Similar depressions which cut the whole tooth transversally and have some inclination backward from the labial edge to the lingual isolate the separate plates of enamel and dentine. M^3 is not shorter and wider than M_2. M_3 is longer than M_2 and M_1. The structure of molars of Grymnuromys adapted to the cellulose type of nutrition retains the common structural plan of the molars of Nesomys. Functionally, the dentinal system of Gymnuromys is convergent to the molars of Muscardinus (Cliroidea) and Ctomys (Ctomyinae, Muridae).

The structure of the molars of Eliurus (Fig. 73) is peculiar. Flexures of external and internal sides are joined with each other, the deep transverse hollows intersect teeth, thus separating dentinal fields. Tubercles are arranged oppositely and the dentinal fields are fused in pairs. The figure of the masticatory surface highly resembles Nesokia (Murinae). The masticatory surface is compressed. Homologization of the parts is very difficult. Separate plates are formed of posterior cingulum and metacone (posterior), paracone (middle), exteroanterocone (M^1) or anterior cingulum (M^2 and M^3, anterior) from the labial side of the upper dental row. The origin of the lingual side of the upper row of plates is not clear; hypocone (rear plate), protocone (middle) and interoanterocone (front) could take part in its formation. However, some displacement of the lingual edge of the front plate and analogy with Nesomys, Gymnuromys and other Nesomyinae



a b

Fig. 73: *Structure of the masticatory surface of molars of Eliurus tanala F. Major. Orig. Right rows. According to the specimen from the collection of Paris Museum of Natural History No. 1932 - 3517, Madagascar (a) upper row; (b) lower row.*

enable us to assume that the hypocone in general was not taking any part in the formation of the posterior plate and its lingual edge was formed by the outgrowth of posterior cingulum; hypocone was taking part in the formation of the middle plate and protocone in the formation of the front plate. Thus, according to this hypothesis the front plate of M^1 in *Eliurus* is formed by three tubercles (exteroanterocone, interoanterocone and protocone).

Postflexure - the only flexure, not connected with flexures of the opposite side closes very easily into postfossette. The anterior lobe of M_1 is cut from the front by a flexid. Homologization of the parts of the lower molars is difficult. Each of the lower molars is formed by three transverse plates, enamel crests as on the upper molars are oriented transversally which indicates the prevalence of longitudinal movements of the mandible.

The change in the dental system in *Brachyuromys betsileoensis* and *Brachyuromys ramirohitra* united without special grounds in one genus, took place in another direction.

The features of the structural plan in *Nesomys* are still observed in the structure of the molar teeth of *Br. betsileoensis* (Fig. 74) while *Br. betsileoensis* represents a transitional form from *Nesomys* to *Brachyuromys remirohitra.* The masticatory surface of *Br. betsileoensis* molars is compressed and the crown is brachyodont. Flexures of external and internal sides are not merged with each other. Anterocone and protocone, and paracone and mesostylus form common dentinal fields. The labial side flexures are very much inclined to the back; the flexids of the lingual side are oriented forward. Paraflexure and metaflexure are closed into fossette with age; para- and metafossettes of M^3 may fuse with each other; during this the enamel crest of the newly formed alveolus are oriented longitudinally (Stehlin and Schaub, 1950, Fig. 260). The usual type of the opposite arrangement of flexures (paraflexid-protoflexid, metaflexid-hypoflexid) is changed in the lower molars on account of the drastic shifting of tubercles. The first dentinal field of M_1 is formed by the fusion of anteroconid with paraconid; protoflexid is fused with parafossetid and placed opposite to mesoflexid, and hypoflexid opposite to postflexid. On M_1 the anterior lobe is separated by

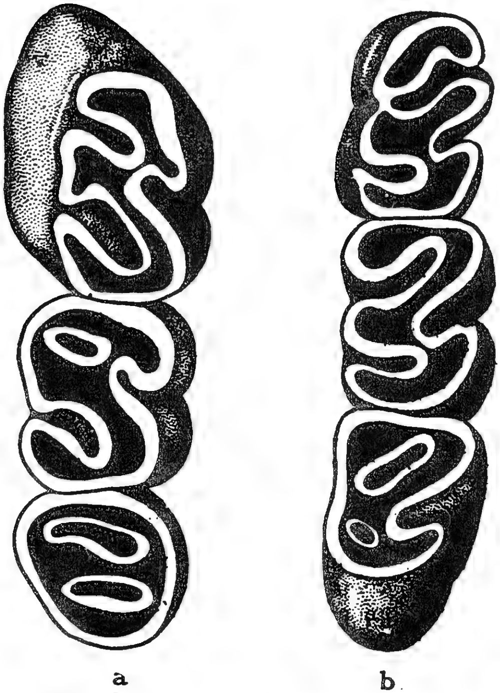


Fig. 74: *Structure of the masticatory surface of molars of Brachyuromys betsileoensis Bartl. Orig. Right rows. According to the specimen from the collection of Paris Museum of Natural History No. 45/ 1932. Madagascar (a) upper row; (b) lower row.*

a deep flexid of the labial side, whereas on M_2 the anterior lobe is separated by a deep flexure of the lingual side formed by the fusion of mesoflexid with protofossetid; on M_3 this flexure is closed into an alveolus having a mixed origin. Slanting arrangement of crests and the considerable width of molars of Br. betsileoensis indicate the great specific weight of circular (composed of longitudinal and transverse) movements of the mandible. M^1 is shorter than M^2, M_1 is as long as M_2.

Further development of the structural plan of the dental system of Nesomys into that of Br. betsileoensis is observed in Brachyuromys ramirohitra (Fig. 75). The masticatory surface is compressed, the crown is mesodont, the molars are exceptionally wide and the area of the dentinal fields is very large. Each molar tooth has more or less an oval shape and is cut by slanting deep flexures or closed alveoli. Deep flexures of the

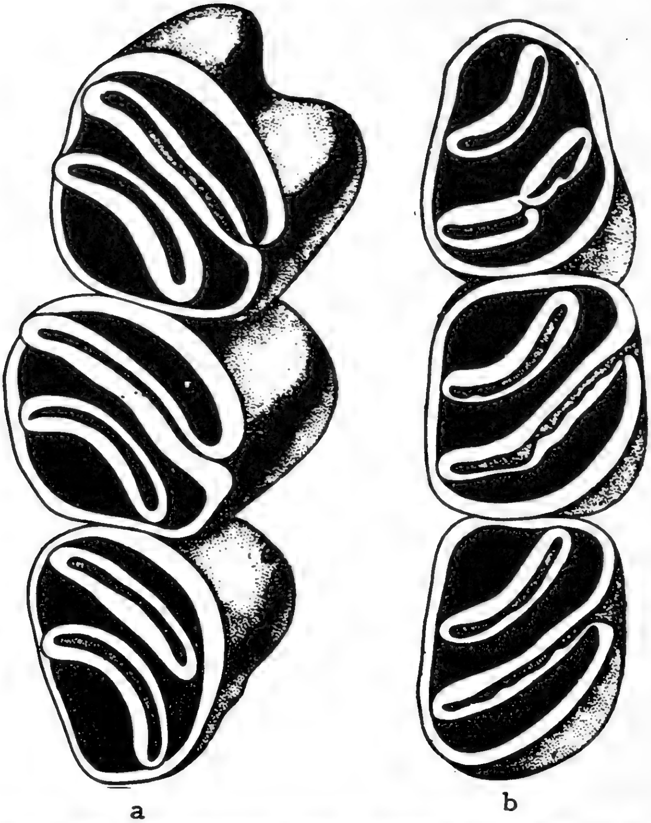


Fig. 75: Structure of the masticatory surface of molars of Perachyuromys ramirohitra. F. Major from Vorontosov (1963). Right rows. According to the specimen from the collection of Zool. Inst., Moscow St. University No. S-4299. Madagascar, Ampitambe, forest, Betsileo (a) upper row; (b) lower row.

lingual side of M^1 and M^2, across the entire tooth are formed as a result of the fusion of parafossette with hypoflexus: on M^3 this flexure is closed afresh also from the lingual side, forming a deep enamel alveolus which may be named as parahypofossette. Metafossette is very deep and intersects the whole tooth. The lower molars also are intersected by inclined flexures and closed alveoli. The first closed alveolus is formed by the fusion of mesofossetid with hypoflexid; on M^1 this depression is closed but the post- and hypofossetids contiguous to each other may remain independent and may not merge into a single alveolus. Each of the molars is nearly equal to the other in size and M_3

and M^3 are not reduced. Extreme width of the molars, and inclined (on M^3 even longitudinal) disposition of the enamel crests indicate the unusual development of the grinding movements of the mandible in transverse direction. The structure of the molars of Brachyuromys ramirohitra strikingly resembles the African burrowing form, Tashyoryctes. The problem on the interrelations of ;these forms will be discussed below.

The development of molars of Brachytarsomys (Fig. 76) took place in an altogether different direction. Molar teeth in the members of this genus have a compressed masticatory surface and the crown is brachyodont. The figure of the masticatory surface closely resembles field-vole; on the basis of this resemblance, Ellerman (1941) related Brachytarsomys to Microtinae. Dentinal fields have an alternate arrangement and their fusion takes place diagonally. Some flexures of the external and the

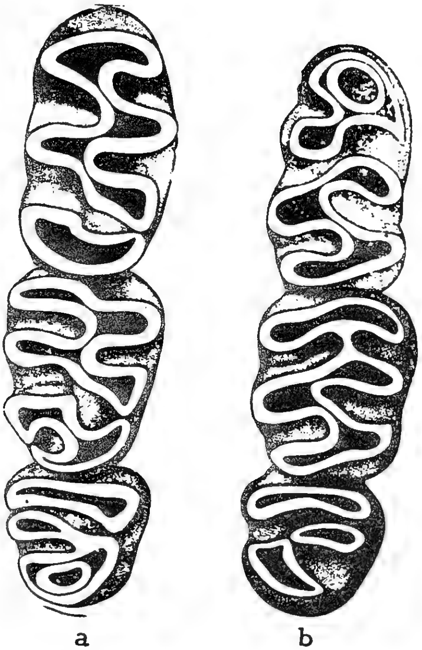
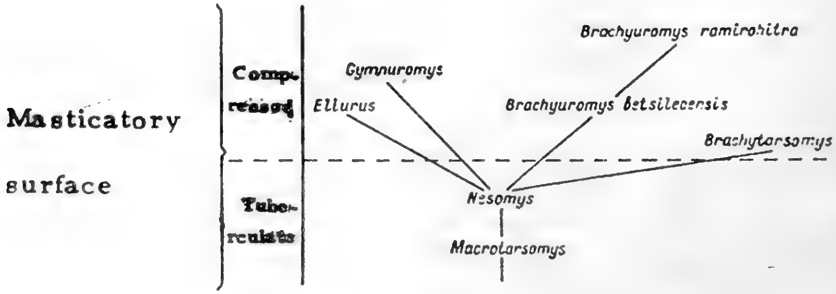


Fig. 76: Structure of the masticatory surface of molars of Brachytarsomys albicauda Gunth. from Vorontsov (1963) Right rows. According to the specimen from the collection of Zool. Mus., Moscow State University, No. S-4289, Madagascar, Vinanitelo, Betsileo (a) upper row; (b) lower row.

internal sides are closed, separating the dentinal fields from one another. Metaflexure on M^1 and M^2 goes up to the lingual side; on M^3 the paraflexure joins with protoflexus and on M_1 metaflexure joins with protoflexid. Similar fusion of flexures of the opposite sides (and these do not fuse each other as for example, on M_1) are characteristic of all forms of Nesomyinae and retained in Brachytarsomys also. Molars are drawn out in length; third molars are much shorter than second. Enamel crests are oriented transversely thus indicating the prevalence of the longitudinal movements of the mandible.

Out of the forms of Nesomyinae, only two (Macrotarsomys and Nesomys) retain the tuberculate structure of the tooth, while Gymnuromys, Eliurus, Brachyuromys and Brachytarsomys acquire compressed masticatory surface adapted to the processing of the cellulose food. However, among the present forms of Cricetinae adaptation to the cellulose type of nutrition in various tribes caused the appearance of forms highly similar to the form of molars of field-voles, whereas among the Madagascar forms of Nesomyinae only Brachytarsomys has a structure of the molars similar to that of Microtinae. This is perhaps because Nesomyinae represented the only rodents of Madagascar and their unlimited adaptive radiation, (in Central-America, members of Cricetinae were represented by a widespread and diverse group, Hystricomorpha), resulted in the creation of forms, diversely adapted to the cellulose type of nutrition.

The study of the structure of the dental system shows that this group is genetically homogeneous and the evolution of the dental system of the Madagascan Cricetidae can be schematically illustrated in this way:



Cricetinae may not have a different dental system than that of Nesomyinae. Madagascan Cricetidae are genetically connected with the ancient Cricetidae-Cricetodontini by the structure of the teeth.

The main trend of specialization of the dental system of Nesomyinae, like that of Cricetinae, was a transition from the bunodont structure of the molars adapted to the cellulose type of nutrition, to the compressed masticatory surface intersected by numerous enamel crests. Such form of molars is adapted to the cellulose type of nutrition. However, in isolated cases, such adaptation of teeth to the processing of cellulose food substance was brought about in a more diverse form than in Cricetinae.

b. Tachyoryctinae

The striking resemblance in the structure of the molars of Brachyuromys and Tachyoryctes was taken by some taxonomists for deciding the genetic relationship of these forms. Ellerman (1941) took Brachyuromys as the Brachyuromys group and related it to the subfamily of Tachyoryotinae under the family Muridae (Muroidea). Hooper (1949) related Tachyoryctes to Cricetinae along with Brachyuromys.

In fact the resemblance in the structure of Tachyoryctes (Fig. 77) and Brachyuromys is very close. Tachyoryctes are characterized by the compressed masticatory surface having a strong development of dentinal exposures, hypsodont crown, wide teeth and inclined (especially on upper molars) arrangement of enamel crests. Each molar is intersected by two pairs of enamel crests which surround the flexures or enamel alveoli. Marginal layers of enamel reduce very much in thickness and the main load falls on the enamel crests of flexures and fossettes during grinding of food.

However, as convincingly shown by Stehlin and Schaub, (1950), molars of Tachyoryctes are not homologous to those of Brachyuromys and represent the modification of the structural plan of Theridomys, while the molars of Brachyuromys can be traced out in the structural plan of the teeth of Cricetinae. In fact, the first dentinal field of Brachyuromys, arranged in front

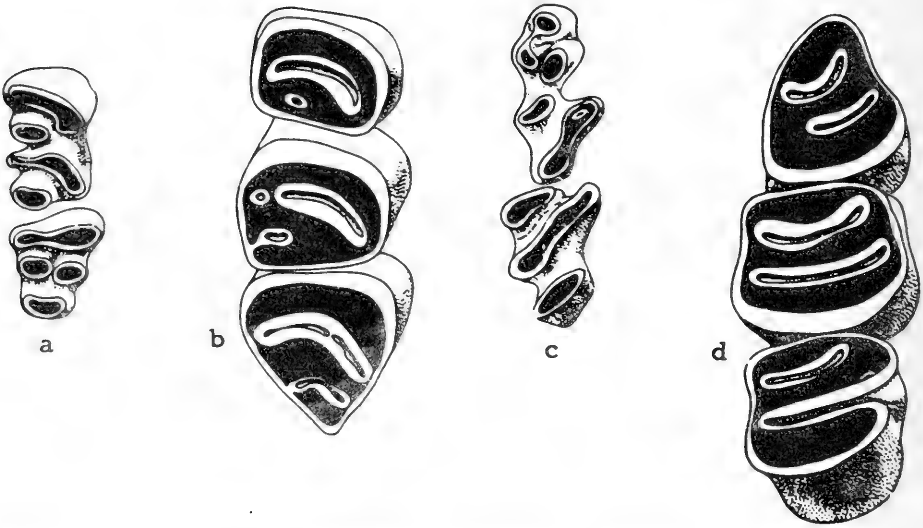


Fig. 77: Structure of the masticatory surface of molars of Techyoryctes splendens Rüpeel. Right rows: (a, b) according to Monmignaul, 1963; (b, d) Orig.; (a, c) M^{1-2} and M_{1-2} of a young specimen; (a, d) upper and lower rows of adult according to the specimen from the collection of Zool. Inst., Acad. of Sc., USSR, No. 70, -1922, (289). East Africa.

from a deep flexus is formed by anterocone and protocone, whereas paracone is arranged behind the flexus. In Tachyoryctes the first flexure is homologous to the second enamel alveolus of Brachyuromys, so that the paracone lies in front of this depression.

The data of Stehlin and Schaub (1950) on the homology of the teeth of Tachyoryctes itself are most interesting. These authors consider that in Tachyoryctes, like in rhizomys, Cannomys and Spalax, the first molar is premolar, while the second and the third molars are homologous to M_1 and M_2, the real M_3 (and M^3) being absent. Unfortunately, the authors do not substantiate this standpoint. If this point of view, is taken then Spalax, Rhizomys, Cannomys and Tachyoryctes cannot in general be related to Muroidea. However, the problem on the origin and homologization of Tachyoryctes cannot be solved without embryological studies. It is possible that the resemblance in the structure of molars of Tachyoryctes and Brachyuromys cannot be considered as an example of extreme degree of convergence in the structure of the dental system of specimens of distant groups. Judging from the figures of Major (1897), the teeth of young Tachyoryctes are characterized by a disorderly arrangement of the tubercles. The new data (Monmignaut, 1963) indicate the two-row arrangement of tubercles in young Tachyoryctes (Fig. 77). This indication bring them to other members of Cricetidae.

c. Myospalacinae

According to the structure of the molar teeth, zokers can not be considered very different from Cricetinae nor connected to them. The Miocene mesodont forms of Prosiphneus (Fig. 78a) and the modern hypsodont Myospalax (Fig. 78b) are characterized by the compressed and looped masticatory surface characteristic of the specialized Cricetidae and all Microtinae. The molars of Myospalacinae are undoubtedly of the cricetid type with two-rowed tubercles.

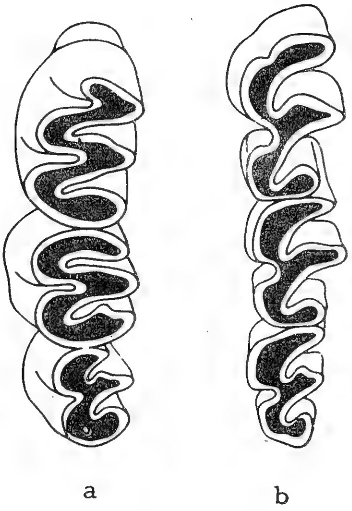


Fig. 78: Transformation of the dental system of zokors (Myospalacinae) in phylogenesis from brachyodont to hypsodont. The masticatory surface of upper molars. Left rows: (a) Prosiphneus T. de Chardin (miocene), according to Stehlin and Schaub (1950): (b) Myospalax psilurus Milne-Edw. (latest species). Orig.

1. Lophiomyidae

The resemblance in the structure of molars of *Lophiomys* with *Cricetus* and *Mesocricetus* was the only characteristic, on the basis of which Winge (1924) and following him Grasse and Dekeyser (1955) related *Lophiomys* (Fig. 79) to Cricetini, the tribe of the palearctic hamsters. Molars are tuberculate and the crown is brachyodont. Tubercles have an opposite arrangement. The remarkable feature of *Lophiomys* is the possession of supplementary tubercles in front of interoanterocone. Similar seven-tuberculate structure of the first upper molar is not found in any of the members of Muroidea. In other respects the molars of *Lophiomys* greatly resemble the teeth of the present palearctic hamsters especially *Mesocricetus*, but unlike the latter in *Lophiomys* anteroflexus is still not closed and the anterior cingulum on M^2 and M^3 has an outgrowth from the lingual side. Mesostylid is not developed. Fossettes and fossetids exist not only on the upper but also on the lower teeth. The semilunar form of dentinal exposures characteristic of Cricetinae is well expressed.

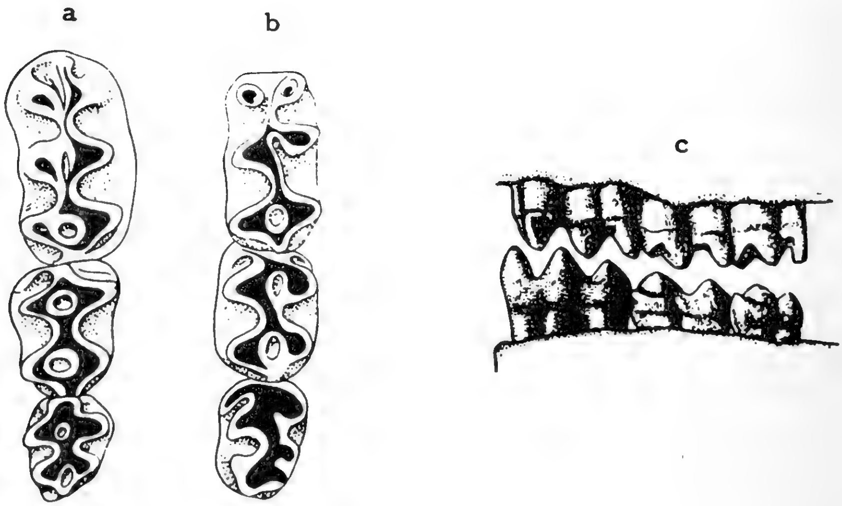


Fig. 79: Structure of molars of Lophiomys imhausi Milne Edw. Masticatory surface of right rows: (a) upper; (b) lower, according to Ellerman (1940), (c) profile of closed rows according to Milne-Edwards (1867).

Resemblance in the structure of the teeth of *Lophiomys* and present Cricetini is really very close. Stehlin and Schaub (1950) consider that the dental system of *Lophiomys*, related, to the tribe Lophiomyini of the subfamily of Cricetinae is genetically linked with the dental system of *Cricetini* and represent the final stage of specialization in the series *Tscherskia* → *Cricetus s. str.* → *Cricetus* → *Mesocricetus* → *Lophiomys*. Though the structure of the molar teeth of *Lophiomys* cannot contradict the relation of *Lophiomys* to Cricetinae, this singular characteristic cannot be taken as decisive for the final judgement on the state of *Lophiomys* towards hamsters. If the unusual plasticity of the dental system, its adaptiveness and wide-scale development of the phenomena of parallelism and convergence, are not taken into account then the forms such as *Andinomys*, *Neotoma*, *Brachytarsomys* can be related to field-voles, mice, *Eliurus* and so on. It is well known that such mistakes were committed by taxonomists just on the basis of the study of the structure of only one dental system.

Seven tubercules on the M1 of *Lophiomys* deserve special consideration. In *Mesocricetus* there appears a small additional elevation from the anterior end of M^1. However in *Mesocricetus*, it is arranged in front of the exteroanterocone, while the additional tubercles on M^1 of *Lophiomys* are associated with interoanterocone. These tips are evidently not homologous to each other and must have appeared independently.

Nothing is yet clear about the origin of the anterocone. According to some, the anterior tubercles of M^1 were formed from the fusion of the last pseudomolar with the first molar, and according to the others, the anterior tubercles of M^1 represent new formation. Though this problem can be finally solved only after detailed embryological studies, on the basis of the data available on the phylogeny of the dental system of hamsters we tend to support the second point of view.

Actually, the unpaired anterocone primarily appears in the form of a short protuberence on the anterior margin of tooth. Further it increases in height and then the division of protuberence into two paired tubercles and the divergence of exteroanterocone and interoanterocone towards the edges of tooth at the level of other tubercles are observed. In most of the latest forms of anterocone and extero- and interoanterocone the size is not smaller than that of the main tubercles, namely, paracone, protocone, metacone and hypocone. It is interesting that in some of the species, mesostylus undergoes the same fate as mesolophus: having appeared in the form of a small tubercle, mesostylus, in a few forms (*Gymnuromys*), exceeds the size of the main tubercles. Evidently it also happened with the anterior tubercles of M^1 (and M_1). Independent appearance of the seventh tubercle in *Lophiomys* and *Mesocricetus* shows that with the formation of the hexatuberculate M^1 the process of polymerization (according to the concept of V.A. Dogel, 1954) of the homologous rudiments of tooth is still not over. The anterior part of M^1 has been formed by the inclusion of pseudomolar tooth whereas the species having one, two or three additional tubercles have already been found among the various Oligocene forms. Actually the division of anterocone into two tubercles is met only among the Neogene, Cricetidae, and the forms having seven tubercles are generally unknown in fossilized state.

e. Platacanthomyinae

The structure and composition of the molars of *Platacanthomys* and *Typhlomys* undoubtedly, bring them closer to Cricetidae and clearly separate from Muridae. Unlike dormice (dental formula $i\ \frac{1}{1}$; pm $\frac{1}{1}$; m $\frac{3}{3}$) pseudomolars are absent in *Platacanthomys* and *Typhlomys*. It should be emphasized that in a number of dormice the tendency for the reduction of pm^4 is not observed. The origin and homologization of dental parts of Myoxidae are very difficult to study because of the extreme change of the masticatory surface by a thick, enamel layer having crests which do not wear off up to the dentine during the whole life of the animal. There is no doubt that the peculiar dental system of Platacanthomyinae cannot be deduced from the structural plan of the molars of Myoxidae.

As convincingly shown by Stehlin and Schaub (1950), the depressions intersecting the tooth of *Platacanthomys* teeth are not homologous to those of Myoxidae. Molars of Platacanthomyinae can be wholly deduced from the structural plan original to Cricetidae.

The molars of *Platacanthomys* (Fig. 80) have much in common in the structure with the teeth of *Gymnuromys*: from the lingual side only interoanterocone, protocone and hypocone are developed whereas on the labial side there are exteroanterocone, paracone, mesostylus with mesolophus, metacone and posterior cingulum. Hypoflexure is connected with mesoflexure (in *Gymnuromys* hypoflexure is joined with paraflexure). As detrition of primary and secondary tubercles go on, the flexures join with fossettes and fossetids, situated at some angle. The molars have a compressed masticatory surface and the crown is brachyodont. M^3 is only a little shorter than M^2 and well developed. The structure of the molars of *Platacanthomys* like those of *Gymnuromys* present an example for solving the biomechanical problem similar to Myoxidae in the same way, but on the basis of different rudiments.

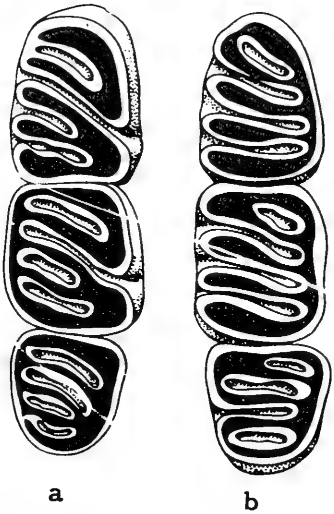


Fig. 80: Structure of the masticatory surface of molars of Platacanthomys Right rows. According to Ellerman (1940) (a) upper row; (b) lower row.

The molars of *Typhlomys* (Fig. 81) highly resemble *Platacanthomys* in the arrangement and origin of dentinal fields, flexures, fossettes, fossetids, etc., compressed nature of the masticatory surface and the brachyodont state of the crown. However unlike the previous genus the molars of *Typhlomys* are much narrower but the enamel crests, surrounding the flexures,

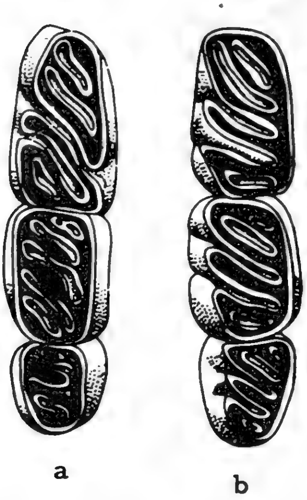


Fig. 81: Structure of the masticatory surface of molars of Typhlomys. Right rows. According to Ellerman (1940) (a) upper row; (b) lower row.

fossettes, flexids, and fossetids, are highly inclined. Narrowing of the molars and similar inclination of enamel crests are observed in the American forms of Napaeozapus (Zapadidae, Dipodoidea). The case of Brachyuromys, where the almost longitudinal inclined position of the enamel crests, is associated with the intensification of transversely oriented masticatory movements of the mandible, increase in the width of molars and in the size of M^3. In Typhlomys, judging from the structure of molars, the longitudinal movements of the mandible are prevalent, with the angle of intersection of enamel crests of the lower and the upper maxilla nearly equal to 90° and accordingly M^3 is much shorter than M^2.

The structure of the molars does not give a basis for the division of Platacanthomys and Typhlomys into two different subfamilies, as proposed by Ognev (1947) and followed by Grasse and Dekeyser (1955). The general structural plan of the molar teeth of Platacanthomyinae is sharply distinguished from Myoxidae and has a number of undisputable characteristics of relationship with Cricetidae.

8. Trends of Dental Specialization of some Primary Myomorph Rodents. Homologous and Parallel Variability series in the Dental System of Rodents

It was shown above that the main trend of dental specialization of Cricetinae (and Nesomyinae close to it) was the transformation of the bunodont masticatory surface into the compressed surface and the brachyodont crown into the mesodont.

A similar trend of the dental transformation is not characteristic of some hamsters, but widely spread among all rodents, particularly Muroidae.

A series of transformation of the tuberculate brachyodont tooth into hypsodont are established in the phylogenetic as well as in the comparative-anatomical series.

Among the modern forms of Gerbillinae (Fig. 82) the genera Gerbillus and Monodia, Taterillus, Taterina, and Desmodilliscus retain the tuberculate structure of the molars, Meriones are characterized by the compressed masticatory surface with a brachyodont crown, and finally, Rhombomys possess not only the compressed masticatory surface but also the hypsodont crown. However, the opposite arrangement of tubercles is retained in Meriones and Rhombomys and so the enamel crests are found to be not so long as in Neotoma or in Microtinae.

The old forms of Microtinae already possessed a compressed masticatory surface. Transformation of the dental system of Microtinae from Miocene till this day went on in the direction of acquisition of hypsodont crown and increase in the number of alternately arranged enamel prisms. The series of specialization of the dental system of Microtinae for the cellulose type of nutrition from the Miocene Mimomys to the modern Fibrini, from Fibrini to Microti, from Fibrini to Lemmini from Clethrionomys rutilus to Cl. rufocanus, from Microtus to Lagurus clearly illustrate this trend of dental specialization of field-voles.

Transformation of the dental system in the phylogenesis of Myospalocinae, from the Miocene Prosiphneus to the modern Myospalax took place in the same direction.


a
b
c
d
e
f
g
h
j
k
l

All these series of transformation are based on the two-row tuberculate structural plan of molars which is common for all forms of Cricetidae and can be considered as homologous variability series (from the standpoint of N. I. Vavilov, 1922). Since the main trend of variability and the original structural plan is found to be common for individual homologous series, the structure identical to minute details, of the given organ may appear to facilitate adaptation to similar functions of the members of different homologous series, which are situated at the same stages of specialization. Hence, the teeth of Andinomys and Neotoma may be very identical to the teeth of field-voles and hamsters, but the molars of Meriones are very much similar to Phodopus. Without taking into account the homologous variability and the principle of N. I. Vavilov, (this periodic system in biology) it is very easy to make gross phylogenetic mistakes during the structural study of an individual organ.

Similar biomechanical problems of adaptation to the cellulose type of nutrition in other rodents are solved on a different morphological basis.

The three-row arrangement of tubercles in Muridae is one of the progressive characteristics compared to those of Cricetidae by virtue of which Muridae displaced seed-eating bunodont hamsters from a greater part of the Old World. The main direction of specialization of the dental system of Muridae is a

Fig. 82: Transformation of the dental system of Gerbillinae from brachyodont to hypsodont, from sharp tuberculate to flat-crowned. The variability direction is homologous to hamsters, field-voles and zokors. Upper rows: a-i-structure of the masticatory surface; j-l-profile of molars (schematically); a, b - according to Grasse and Dekeyser (1965); c-f - according to Wettstein (1917); g - according to Patter (1959); h-l Orig.; a-Gerbillus pyramidum Geoffr.; b - Monodia mouritaniae Halm de Balsac; c - Taleirillus kaduglensis Wattst.; d - Tateina lorenzi Wettst.; e - Desmodilliscus brauneri Wattst.; f - Tatera rufa Wettst; g - Tatera sp. from Mesopotamia; h - Meriones meridianus Pall. According to the specimen from the collection of Zool. Mus. Moscow St. University No. S-28046 Turkmenia, Akhcha-Kaima, i - Rhombomys opinus Licht. According to the specimen from the collection of Zool. Mus., Moscow St. University No. S-52284, Turkmenia, North-western coast of Kapa Bogaz-Gol Bay, Bik-Tash; j - Gerbillus; k - Meriones; l - Rhombomys.

further complication of the tuberculate structure of the tooth. But individual terminal branches of the widely radiating tree of Muridae adapted to the cellulose type of nutrition for the second time. Generally opposite, three-row arrangement of tubercles led to the formation of a few forms of Muridae with flat-crowned dentinal fields by means of the fusion of transverse rows of tubercles (Nesokia, Olomys), whereas Cricetidae had usually alternately arranged enamel fields formed by the diagonal fusion. Even in Eropeplus, wherein the tubercles of the central row have greatly shifted forward in relation to lateral rows, the fusion of dentinal fields takes place in transverse rows and not diagonally (Fig. 83).

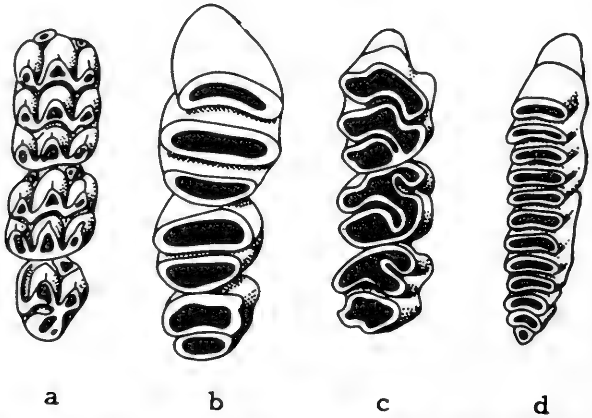


Fig. 83: Transformation of the dental system in Muridae. In connection with the transition from protein-lipoid to cellulose type of nutrition, the masticatory surface becomes complex and the small crust in elevated. Three-row arrangement of tubercles on upper molars which is not homologous to the two-row structure of Cricetidae leads to the fusion of all the three tubercles of transverse row and not to the formation of loopshaped tooth of field-voles. An example of convergence with field voles. Upper rows. From Vorontsov (1962): (a) Hapalomys longicaudatus; (b) Nesokia indica Gray et Hard; (c) Eropeplus canus; (d) Otomys tropicalis.

In the North-American Heteromyoidea, in which the three-row arrangement of tubercles appears regardless of Muridae, the compressed nature of the masticatory surface and the formation of hypsodont molars in the series from Perognathus to Heteromys and Geomys leads to the fusion of dentinal exposures of the tubercles (Fig. 84).

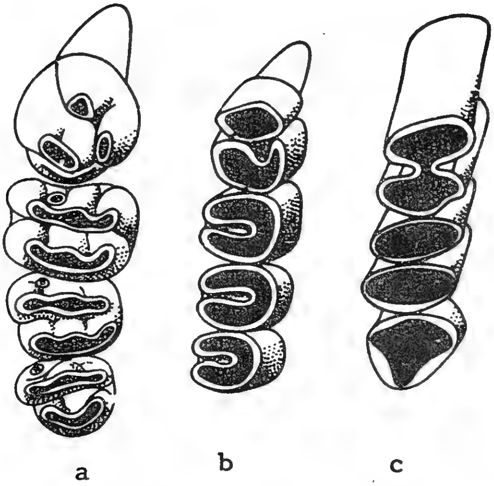


Fig. 84: Dental transformation in a number of forms of Geomyodea. Three-row arrangement of tubercles (convergence with mice) corresponds to the seed-eating type of nutrition; the masticatory surface is flattened the crown rises and enameled crests are oriented transversely during the transition to the cellulose type of nutrition. Upper rows. According to Grosse and Dekeyser (1955) from Vorontsov (1962 b). (a) Perognathus; (b) Heteromys; (c) Geomys.

The same tendency for flattening of the masticatory surface and elevation of the crown in view of the transition from the protein to the cellulose type of nutrition is observed in the series of Dipodoidea (Fig. 85) from Sicista to Zapus Napaeozapus, Allactaga and Alactagulus. Disorderly arrangement of tubercles in Dipodoidea would appear close to the two-row arrangement of tubercles of Cricetidae because of which the structure of molars of the mesodont jerboas closely resembles the structure of the molars of Cricetidae.

The teeth of Myoxidae (Fig. 86) are transformed on an altogether different basis. Even the least specialized forms of the modern Myoxidae possess a very thick layer of enamel on the surface of molars, complicated by transverse enamel "towers". The specialization of molar teeth of Myoxidae to the cellulose type of nutrition in the series from Myomimus, Eliomys and Dyromys to Glis and Muscardinus is marked by an increase in the number of transverse enamel columns from 4-5 to 7-8.

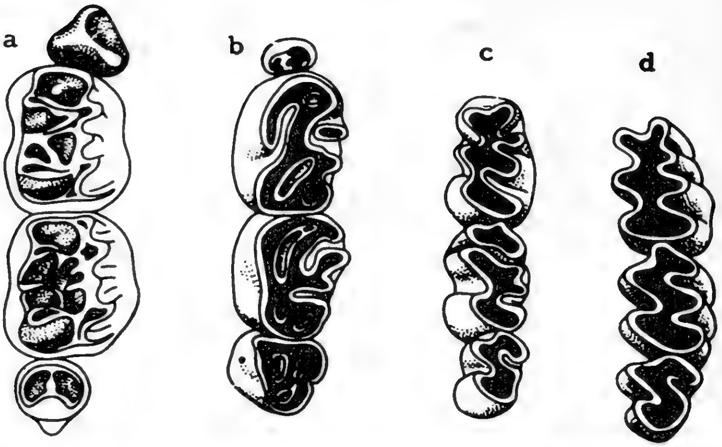


Fig. 85: Transformation of the dental system in a number of forms of Dipodoidea. An example of dental transformation, similar to Cricetidae. Upper rows: According to Grasse and Dekeyser (1955) from Vorontsov (1962 b) (a) Sicista betulina Pall; (b) Zapus hudsonicus Zimm; (c) Allactaga euphratica Thom; (d) Alactogulus acontion Pall.

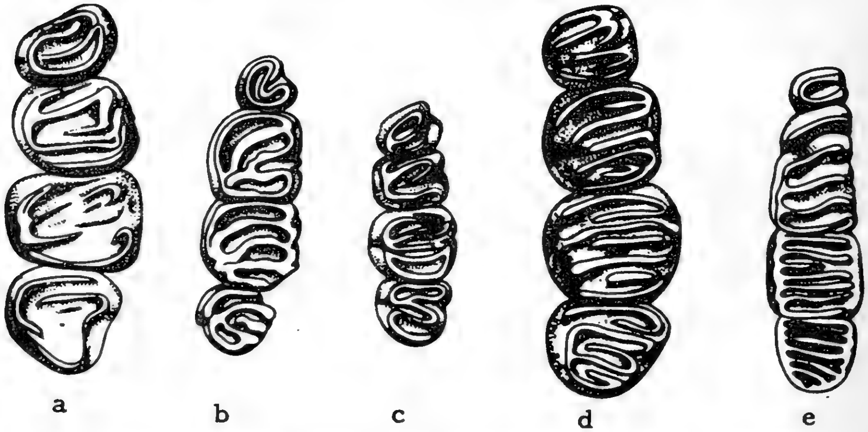


Fig. 86: Transformation of the dental system of Myoxidae: In view of the transition to the nutrition by a more coarse food substance the number of transversely oriented crests of molars increases. The direction of evolution resembles Cricetidae and Muroidea, but the same biomechanical problem is solved by a different method on the basis of outgrowths not homologous to each other. An example of convergence with field-voles. Upper rows (a - according to Ognev (1948); b-e - according to Grasse and Dekeyser (1955), from Vorontsov (1962). (a) Myomimus personatus Ogn.; (b) Eliomys quercinus L.; (c) Dyromys nitedula Pall.; (d) Glisglis L.; (e) Muscardinus avellanarius L.

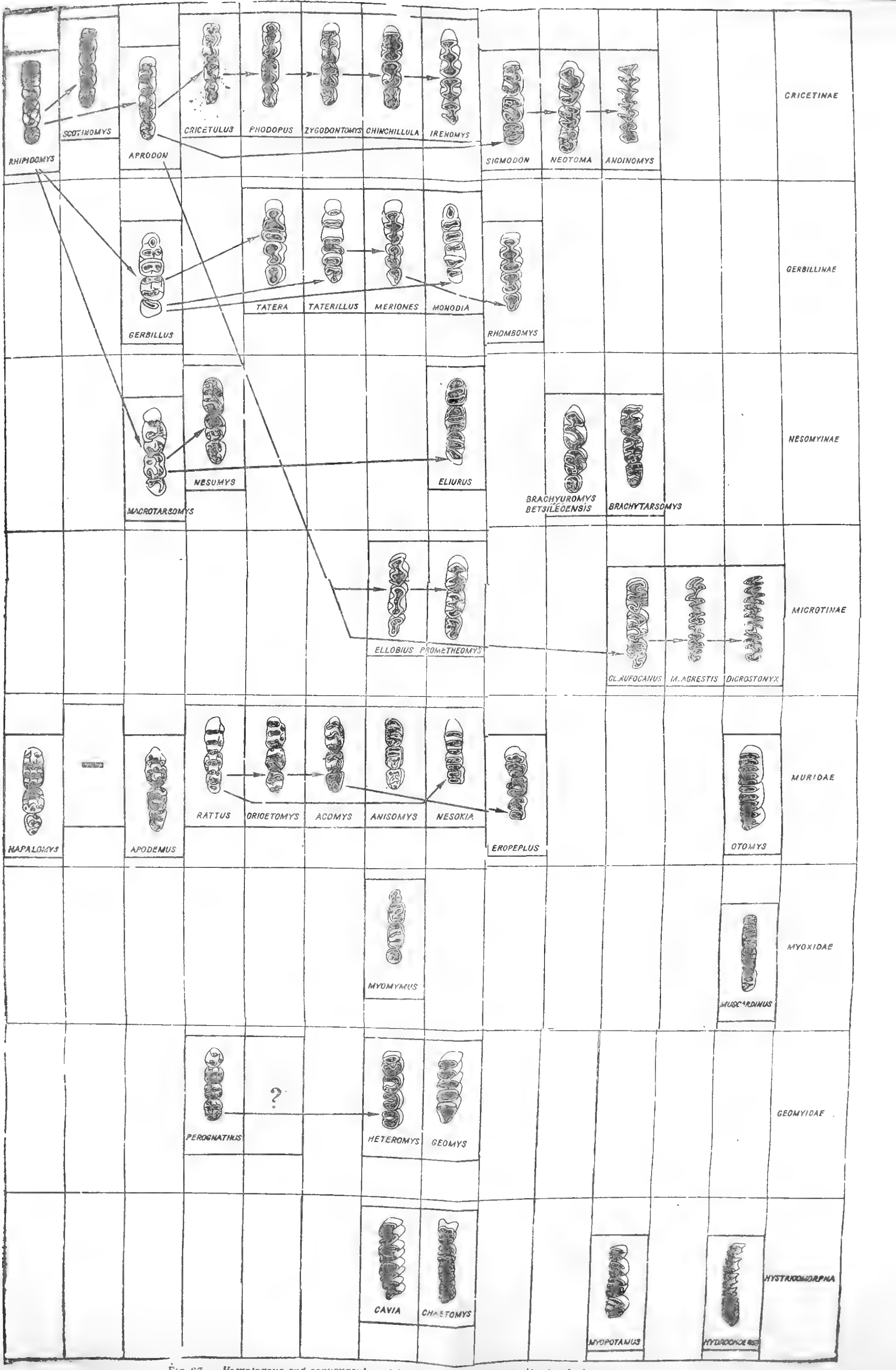


Fig. 87. Homologous and convergent variability series of molar teeth of rodents. Series Cricetinae, Gerbillinae, Nesomyinae and Microtinae are homologous to each other; series Cricetidae, Muridae, Myoxidae, Geomyidae and Hystricomorpha are convergent to each other.

The forms having a flat masticatory surface and an elevated crown are also found among a few forms of Sciuromorpha (Anomaluridae).

The tendency towards the formation of hypsodont teeth having a flat masticatory surface is highly characteristic of many forms of Hystricomorpha. In this regard Hystricomorpha - an elder group than Myomorpha advanced further and the initial stages of the tooth structure are found only in a few cases. Thus, the tuberculate structure of molars is retained in the genus Atherurus in Hystricidae while more highly organised Hystrix possess a flat masticatory surface of molars.

Among these forms of Hystricomorpha, the members of Hydrochoerus, that are most adaptive to the processing of coarse vegetative portion of plants, possess hypsodont molars, outwardly resembling the molars of field-voles, but sharply distinguishing by the structural features, like individual prisms are connected with each other by cement, while the prisms of teeth in all hypsodont forms of Cricetidae are connected with each other by enamel and dentine.

In this way, the process of transformation of brachyodont tooth to hypsodont and flattering of tuberculate masticatory surface (Fig. 87) are primarily observed in the structure of the dental system of the different groups independent of each other. These processes are associated with the independent transition of various groups of rodents varying from the mixed type of nutrition to the nutrition by vegetative portions of plants.

However in all these groups of rodents, similarly directed process of formation of the hypsodont forms and flattening of the masticatory surface undergoes starting from a different initial structural plan of tooth. As a result, similar stages of adaptation in different series bear characteristics only of superficial resemblance and they may be separated from each other without any difficulty. Similar variability series should be related in parallel.

Wide distribution of the phenomena of homologous varia bility among Cricetidae compels one to come very carefully to phylogenetic conclusions based only on the study of the dental system. All cases of parallelisms in the development of the dental system can be separated only on comparative-morphological study of the other systems of organs.

The maximum range of the individual and intragroup variability of the dental system is fully in agreement with A.N. Severtsov's point of view on the great variability of exosomatic organs (to which the dental system should be related) in comparison with the endosomatic organs.

CHAPTER III

EVOLUTION OF OTHER ORGANS OF THE MOUTH CAVITY (THE TONGUE AND THE CHEEK POUCHES)

1. Tongue

a. General outline of the tongue morphology in mammals.

The tongue (lingua) in mammals is the longitudinally stretched muscular body, covered with the connective tissue membrane.

The transversely striped muscle, concentrated in three fasciculi which pass in inter-perpendicular directions makes the thickness. Mucus of the tongue membrane of the mouth cavity (tunica mucosa s. tunica propria) passes onto the tongue from the back and the sides.

The upper surface or the back of the tongue (facies superior s. dorsum linguae) and the lower surface (facies inferior) are distinguished (Fig. 88). The lateral margins of the tongue are known as margines laterales and the anterior margin as margo anterior. The front portion of the tongue which is free is named apex linguae, and the middle portion of the tongue, associated only with the bottom of the mouth cavity, corpus linguae, while the hind, last one-third of the tongue, having a free dorsum is called the base or root (radix linguae). Corpus linguae on its facies superior may have an elevation-torus linguae. A crescent-shaped fissure called the sulcus semilunaris linguae may be found in front of the torus linguae-Papillae of the tongue on torus is not expressed papillae filiformes s. p. p. conicales on torus are large and, thus, the papillae of the corpus and apex linguae are sharply distinguished from each other; the boundary between papillae filiformes s. p. p. conicales of the apex and corpus linguae is called called linea semilunaris. The boundary of apex and corpus linguae is conditionally taken for crescent-fissure (or line).

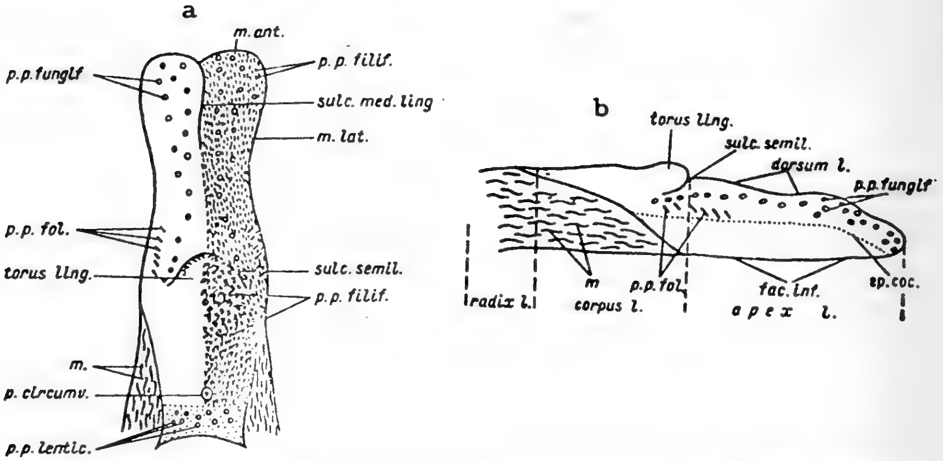


Fig. 88: *Tongue structure and the accepted nomenclature ~~after~~ Vorontsov (1958 b). (a) view from above; (b) side view (schematically); (c) boundary of the papillae layer m-muscles of the tongue. apex 1. - apex lingulae; corpus 1. - corpus linguale; corsum 1. - corsum linguale; fac. inf. - facies inferior linguale; m. ant. - margo anterior; m. lat. - margo lateralis; p. circumv. - papillus circumvallatus; p.p. filif. - pappillae filiformes; p.p. fol. - papillae foliatae; p.p. fungif. - papilae fungiformes; p.p. lentic - papillae lenticulares; radix 1. - radix linguae; sulc. med. ling. - sulcus medianus linguae; sulc. semil. - sulcus semilunaris; torus ling. - torus linguae.*

The longitudinal fissure (sulcus medianus linguae) can pass through the dorsum linguae in the apical part. The mucous membrane with its internal layer is fused with the perimysium of the tongue muscle. The muscular fibers of the tongue end spontaneously in tunica mucosa.

The mucous membrane of dorsal part of the tongue and sometimes of marginal zones (margins laterales et anterior) are very thick-papillae of five types.

Papillae filiformes s.p.p. conicales are almost spread along the whole dorsum of the tongue (only at the back pf pap. circumvallatae, they are displaced by lymphoid pap. lenticulares) and can move on fac. inferior, where, however, they generally occur in the marginal zone. Papillae filiformes of the apex are fine and have a conical shape whereas those of the corpus have the common form of leaflets or petals and are much bigger in size.

Papillae filiformes do not have taste buds. They accomplish definite functions while processing food; their direction is that of the flow of food particles.

The special role of papillae fungiformes in myrmecophaga and cheiroptera of the pollinizer of plants (for the tongue in the latter, see the work of Jaegar, 1954) is not considered here. The author does not stick to the division of papillae filiformes into pap. pectinees,, pap. tricuspides etc. as adopted in some special papers.

Papillae fungiformes are larger in size and spread only along the papillary part of the apex linguae. Their number varies very much in different species: in some it can reach up to 500, in others papillae fungiformes are absent (some field-voles, jerboae). The taste buds are located in papillae fungiformes. On this basis, some authors (Ganeshina, Herman, in litt.; Matveev, 1960) see a direct correlation between the number of papillae fungiformes and the degree of gustation. There is no unanimity in the literature even on the problem of distribution of taste buds in papillae fungiformes (Tonkov, 1933; Zavarzin, Schelkunov 1954, Shmalhauzen, 1947, and others).

1-15 papillae circumvallatae are present in the root part of the torus of mammals. There is only one* papilla circumvallatus in all Cricetinae. The taste buds are concentrated in papillae circumvallatae.

Papillae foliatae are concentrated along the edges of the tongue around the molar teeth. In many mammals including man, they are in reduced form. Papillae foliatae (called "lateral organs" by English authors) have taste buds.

Papillae lenticulares are located at the root of the tongue, behind the papillae filiformes and papillae circumvallatae. Many researchers do not even mention about the existence of pap. lenticulares, while describing the tongue morphology.

---

* *In the article devoted to the morphology of the tongue or palearctic hamsters (Vorontsov, 1958b), it is wrongly pointed out that all forms of Cricetidae have only one pap. circumvallatus. But Nesomyinae have three.*

b. Tongue structure in Cricetinae

The morphological study of the tongue of the palearctic hamsters (Vorontsov, 1958b) has shown, that even the representatives of such an ecologically uniform group as the present palearctic hamsters (Cricetini) can considerably differ from each other by the number and arrangement of the sensory papillae and by other features of the tongue structure (Fig. 89).

The study of the tongue structure in palearctic Cricetinae (Vorontsov, 1958b) and the comparison of the collected data with the material already recorded on the Nearctic Cricetinae, Microtinae, Gerbillinae and Muridae (Tuckerman, 1888; 1891 Tullberg, 1899; Sonntag, 1924) did not enable us to mark some peculiar features in the tongue structure of palearctic Cricetinae, characteristic of all the representatives of this group, and separate them from the rest of the cricetinae studied.

The most interesting fact is the discovery of papillae foliatae having a two-row arrangement, in Mesocricetus brandti and M. Raddei. This important characteristic separates Mesocricetus from the rest of the species of Muroidea studied.

Difference by this characteristic is one of the arguments against A. I. Argiropulo (1933) for combining Mesocricetus Nehr. and Cricetus (s. str.) Leske into one genus Cricetus.

Double number of papillae foliatae as against the usual number, their two-row arrangement and to some extent a relatively large number of papillae fungiformes separate Mesocricetus from the rest of the palearctic hamsters. Do these characteristics not give yet another proof of the polyploid origin of Mesocricetus (Sachs, 1952; Darlington, 1953) ?

The last assumption, of course, should not be taken to interpret the polyploid origin (after Sachs and Darlington) of Mesocricetus as a result of the hybridization of Cricetus and Cricetulus.

It should be emphasized that the absence of a deep sulcus semilunaris on the tongue of Mesocricetus raddei distinguishes

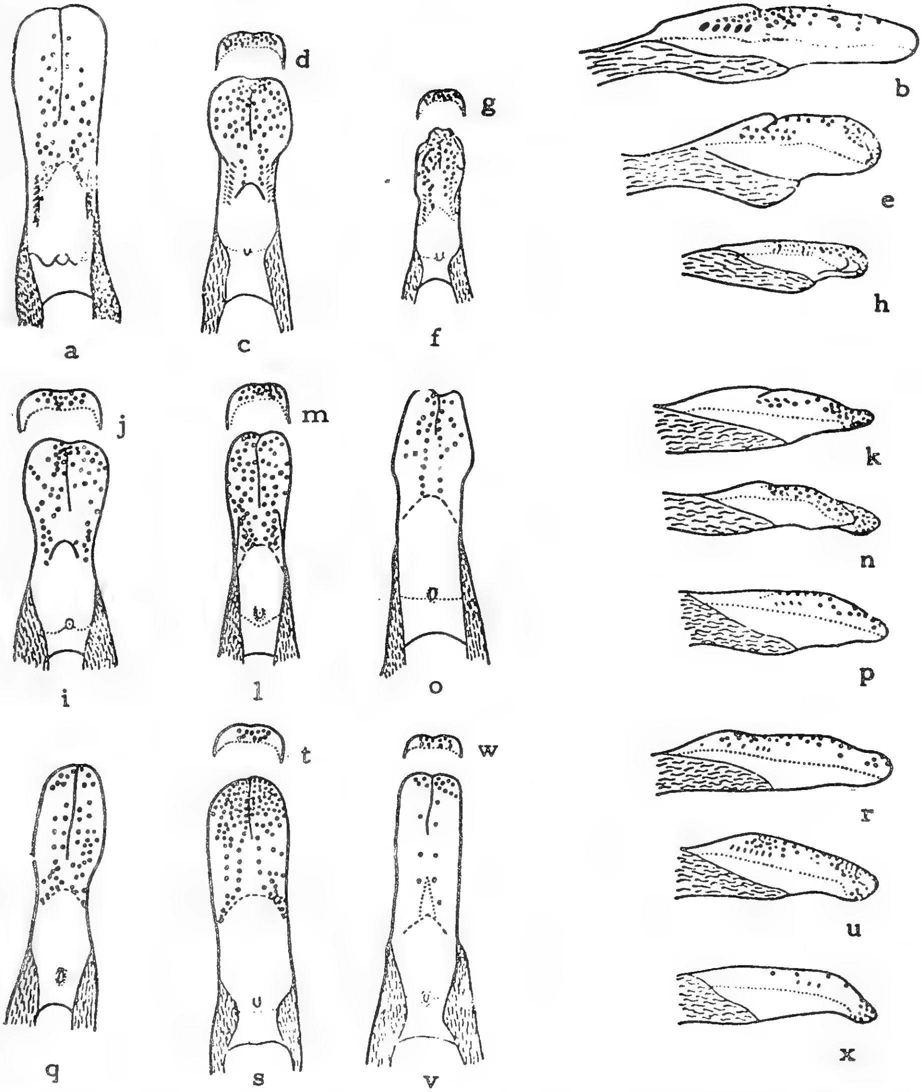


Fig. 89: *The structure of the tongue of the palearctic hamsters. Semi-schematic (After Vorontsov, 1958 b). (a, b) Cricetus cricetus L.; (c, d, e) Mesocricetus raddei Nehr.; (f, g, h) Mesocricetus brandti Nahr.; (i, j, k) Cricetulus (Allocricetulus) eversmanni Brandt.; (l, m, n) Cricetulus (Tscherskia) triton de Winton; (o, p) Cricetulus (s. str.) barabensis Pall.; (a, r) Gricetulus (s. str.) migratoruis Pall.; (s, t, u) Phodopus sungorus Pall.; (v, x, w) Calomyscus bailwardi Thom. (a, c, f, i, l, o, s, q, v - dorsal view, d, g, j, m, t, w - ventral view of the anterior part of tongue; b, e, h, k, n, p, r, u, x - side view.)*

it from *M. brandti* thus contradicting the opinion of Ellerman (1941) about the monotypical nature of the genus *Mesocricetus*.

The myomorph hamsters (*Calomyseus bailwardi*) are sharply distinguished from other palearctic hamsters by the absence of papillae linticulares.

A comparison of the features of the tongue structure leads to classify the following five groups among palearctic hamsters:

I. 1. *Calomyscus bailwardi* Thom.,

II. 2. *Cricetulus* (s. str.) *barabensis* Pall.
3. *Cricetulus* (s. str.) *longicaudatus* Milne-Edw.;
4. *Cricetulus* (s. str.) *migratorius* Pall.;
5. *Cricetulus* (*Tscherskia*) *triton* de Wint.;
6. *Cricetus cricetus* L.;

III. 7. *Cricetulus* (*Allocricetulus*) *eversmanni* Brandt.;
8. *Cricetulus* (*Allocricetulus*) *curtatus* Gl. All.;

IV. 9. *Phodopus sungorus* Pall.;

V. 10. *Mesocricetus brandti* Nehr.;
11. *Mesocricetus raddei* Nehr.

c. Tongue structure of some forms of Muroidea with reference to the interrelations of Cricetinae with allied subfamilies.

The tongue structure is closely associated with the features of the biomechanical processing of food, and the degree of development of the gustatory papillae depends on the type of nutrition. In the opinion of Ganeshina and German (in litt.) and Matveev (1960), there exists a direct correlation between the numbers of papillae fungiformes and the degree of development of gustatory perception of the species. Papillae fungiformes are numerous in view of the transition from protein food to the cellulose nutrition in the forms, characterized by a limited collection of high-calorie protein food. Papillae fungiformes can be reduced with a changeover to the consumption of the wide collection of vegetative parts of the plants. This conformity is traced by Ganeshina and German (in litt.) in some forms of Murinae and Microtinae.

The significant interspecific variability of the number and arrangement of papillae fungiformes, on the basis of their development, does not enable us to express particular phylogenetic formations. The number and the degree of development of papillae fungiformes are more constant.

How are the functions of the three types of gustatory papillae divided? Judging from their arrangement it can be assumed that the papillae fungiformes that are concentrated at the tip and the dorsum of the tongue take part in the gustatory perception of the food which is taken into the mouth. Papillae foliatae, situated along the molar teeth differentiate the taste of the food crushed by the teeth and papillae circumvallatae evaluate the taste of the food crushed and soaked by saliva.

The number of papillae circumvallatae in rodents usually ranges from one to three*.

All present forms of Sciuromorpha (representatives of the old, predominantly seed-eating group of rodents) usually have three papillae circumvallatae (Aplodontia Anomalurus, Sciurus, Eutamias). The number of p. circumvallatae among Hystricomorpha decreases from three (Hystrix, Castor) to two (Cavia, Erethizon, Chinchilla, Coelogenis, Myopotamus) when the middle papillae is reduced.

The rodents which burrow with incisors, have strongly developed torus linguae, which is evidently associated with the pushing off of soil that has entered the mouth with the tongue. Therefore, the main flow of the crushed food particles passes by the side of the torus or over the p. vallatae but not over central papilla. Evidently it is related to the fact that the majority of burrowing rodents, from different groups - Georychus (Batheygidae-Bathyergomorpha), Myospalax (Myospalacinae-Cricetidae-Myomorpha), Spalax (Spalacidae Myomorpha)

---

* *According to Tullberg (1899) Pedetes and Petaurista generally do not have papillae circumvallatae.*

Rhizomys (Rhizomyidae-Myomorpha) - possess two papillae circumvallatae, whereas the central papilla is reduced in them. Like all other non-burrowing members of the Geomyoidea group (Hoteomyinae, Dipodemyinae), only Geomys has one central circumvallate papilla.

The number of circumvallatae papillae in old Myomorph group - Myoxsidae and Dipididea - is equal to three. Among Muroidea, Nesomyinae (Gymnuromys Macrotarsomys, Brachyuromys) have three circumvallate papillae. In a number of Cricetidae in Myospalacinae the central papillae is reduced and two circumvallate papilae are left behind, and in Cricetinae (Cricetus Mesocricetus, Cricetulus, Phodopus, Mystromys, Peromyscus, Calomyscus, Sigmodon, Neotoma) Gerbillinae (Gerbillus Meriones, Rhombomys) and Microtinae (Clethrionomys, Prometheomys, Lemmus, Lagurus, Dicrostonyx and others), two lateral papillae are reduced and one central circumvallate papilla is left behind. Only forms of Cricetomyinae have three circumvallate papillae, among Muridae, whereas in the present Murinae (Rattus, Mus, Apodemus, Aryicanthis) Nesokia, Micromys, Pogonamys and others) there is only one circumvallate papilla.

In this manner, the oligomerization process of the number of circumvallate papilla takes place inside the various groups of rodents independent of each other. However the change in their number is noticed only in big groups (from subfamily and above), and within subfamilies and genera it is constant. That is why the number of circumvallate papillae is an important systematic characteristic, which gives evidence to the homogeneity of the group Nesomyinae and the separation of Nesomyinae from Cricetinae. The number of circumvallate papillae separates Myospalacinae both from Microtinae and Cricetinae to which they were related by different classifications. At the same time, we think that the agreement to the number of circumvallate papillae between Myospalacinae and Spalacidae, is caused by the convergence, associated with the burrowing life and cannot be considered as the evidence of kinship of these groups. Similar tongue morphology in such distant forms as Spalax and Georychus indicates definitely that the convergence in the tongue structure in the forms which burrows can go very far. Evidently, the resemblance in the tongue structure and number of circumvallate papillae in Spalax and Myospalax is caused by convergence.

In this connection, it is important to emphasize that the Madagascar forms of Nesomyinae, in spite of the extreme breadth of divergence, retain the same number of circumvallate papillae.

2. Cheek Pouches

Cheek pouches occur in various groups of rodents independent of each other.

In the family, Sciuridae, cheek pouches are characteristic of the representatives of the tribe Marrotini. They may not exist or may only be slightly developed in *Marmota* (Grasse and Dekeyser, 1955). They exist in the members of other genera of this tribe - *Citellus*, *Cynomys*, *Tamias* and *Eutamias*.

Cheek pouches are characteristic of the entire group of Geomyoidea (*Heteromys*, *Liomys*, *Perognathus*, *Microdipodops*, *Dipodomys*, *Thomomys*, *Geomys*, *Pappogeomys*, *Cratogeomys*, *Platygeomys*, *Orthogeomys*, *Heterogeomys*, *Macrogeomys*, *Zygogeomys*).

In the group Muroidea the cheek pouches appear, independent of each other, in some forms of Cricetidae (*Cricetus*, *Cricetulus*, *Mesocricetus*, *Phodopus*) and Muridae (*Beamys*, *Saccostomus*, *Cricetomys*).

Among *Hystricomorpha* the cheek pouches are developed in *Cuniculus*.

It is remarkable, that in all those groups the cheek pouches are not homologous to each other.

Cheek pouches are poorly developed in Marmotini. The cheek pouch is a growth of the lower part of the adoral cavity and moves downwards away from the dental row. The posterior part of the cheek pouches of Marmotini is drawn off by muscles of which one moves downward and back and is attached to the sternum, and the other moves back horizontally and is attached to the facies of muscles, which are attached to the front edge of the shoulder blade (Fig. 90).

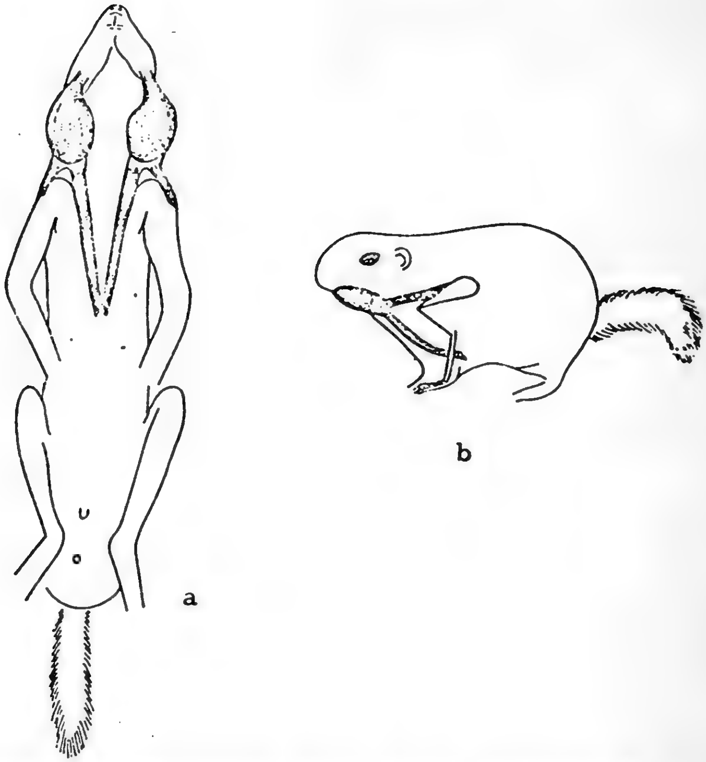


Fig. 90: Diagram showing attachment muscles of cheek pouches in squirrel family (Marmotini, Sciuridae, Sciuromorpha). Citellus undulatus, Original: According to the specimen from the Eastern Kazakhstan. Kalbin Altai. (a) ventral view; (b) side view.

The pouches for storing food are developed in Geomyoidea in the form of special folds on the lower surface of the face and in no way connected with the mouth cavity. These are blind pockets, covered with hair from inside and are used only for bringing food substance from the place, where food was found, to the nest (Fig. 91).

Cheek pouches of present hamsters (Cricetini) attain an unusual development. In inflated state they are stretched behind shoulder blade. Cheek pouches are used by hamsters not merely for storing the food substance. Cricetus cricetus takes the soil out of the deep burrows to the surface (Zverev, 1931) with the help of the cheek pouches. All forms of Cricetini use cheek

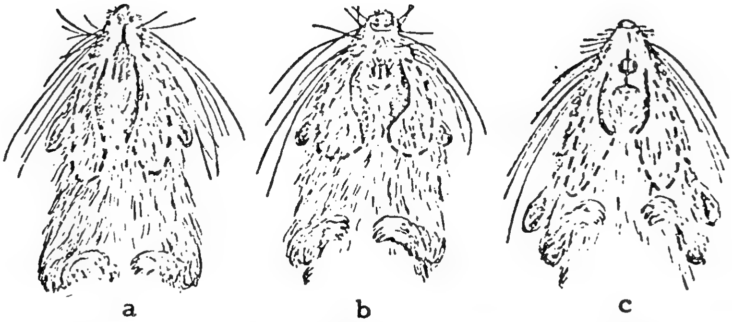


Fig. 91: *Topography of cheek pouches in Geomyoidea. View from the ventral side. Original (a) Liomys pictus Thomas, Mexico, Sinaloa; (b) Perognathus baileyi Merriam USA, Arizona; (c) Dipodomys marriami Mearni. USA New Mexico.*

pouches while swimming; in water the hamsters inflate the cheek pouches and swim, thus easily floating on the surface (we have observed it outselves).

The young forms of Phodopus sungorus and Mesocricetus auratus, still blind and hardly covered with wool, fill the cheek pouches with such large things as sunflower seeds. Evidently, in this manner, the animals, significantly increases the volume of cheek pouches while still young.

Usually the food is collected in one of the cheek pouches first and only when this is full it is collected in the other. It is remarkable that only after the cheek pouches are free of food, the hamsters start moving their shoulder and shoulder blade. For the role of cheek pouches in storing food in hamsters see A.G. Ponugaeva (1963).

In Cricetini cheek pouches are the growth of the posterior part of the adoral cavity (Fig. 92). The hole of the cheek pouches is situated in the diastema and blocked up by the sphincter formed by m. orbicularis oris. The cheek pouch is coriaceaus, easily stretchable organ, the internal surface of which is covered with horny epithelium. The empty cheek pouch is not very big, it comes together owing to the contraction of the fibers of the transversely striated muscle, longitudinally along its external surface; the internal surface of the cheek pouch is folded when it comes together. The folded growth of the internal surface fails into the posterior part of the cheek pouch from the internal side near the withdrawal point of the muscle inside the cheek pouch. In the lateral and the lower parts of the mouth opening there is a groove which leads to the cavity of the cheek pouch.

In Phodopus, unlike all other present forms of Cricetini, the initial part of the external side of the cheek pouch is covered from inside with small hair drawn inside.

The posterior part of the cheek pouch in Cricetini is drawn off by one muscle which moves backwards and upwards, and is attached near the lumbar vertebrae. This muscle, is evidently the derivative of m. trapezius (Priddy and Brodie, 1948). The muscle, which draws off the cheek pouch, envelops its posterior part from the ventral and the medial sides.

Absence of cheek pouches should be marked not only in all American* and Madgascan forms of Cricetidae, but also in Mystromys, Lophiomys and Calomyscus.

The strong development of the cheek pouches which could not be taken as the evidence of the prolonged and independent evolution of Cricetus, Cricetulus Mesocricetus and Phodopus is, as a matter of fact, one of the important characteristics, which compels us to separate Mystromys, Lophiomys and Calomyscus from the tribe, Cricetini.

In the family, Muridea the cheek pouches are developed in the genera Beamys and Saccostomys of the subfamily Murinae and in the monotypical subfamily Cricetomyinae. A representative of the last group of Cricetomys gambianus, named so owing to the cheek pouches, indicating its similarity with the hamster has been studied (Fig. 93).

---

* *The poorly developed cheek pouches, or more exactly, the significant increase in the size of the cavity situated between the cheek and molars occur in some forms of Peromyscus. However, the degree of development of the cheek pouch of Peromyscus is so insignificant in comparison with that of Cricetini, that there is no doubt about the independent origin of these formations in the Palearctic forms of Cricetini and the American forms of Peromyscus.*

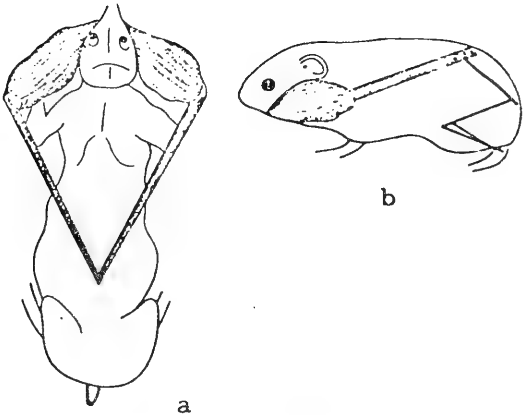


Fig. 92: *Diagram of muscle attachment of the cheek pouch in real hamsters (Cricetini, Cricetidae, Myomorpha). Phodopus sungorus sungorus Pall. Original. According to the specimen from Western Siberia. Novosibirsk region (a) view from above; (b) side view.*

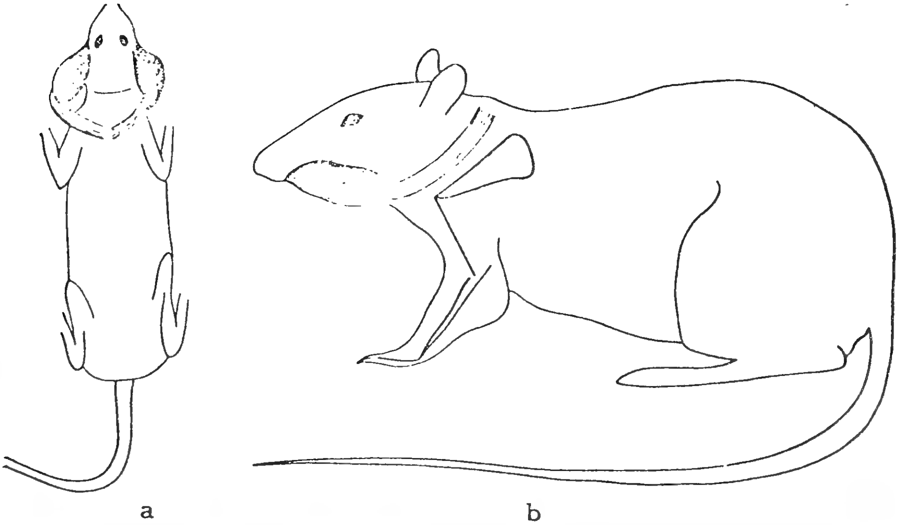


Fig. 93: *Diagram of the muscle attachment of cheek pouches in mice (Cricetomyinae, Muridae, Myomorpha). Cricetomys gambianis. According to the specimen from Central Africa (a) view from above; (b) side view.*

Cheek pouches are poorly developed in *Cricetomys.* They have a blunt growth near the mouth cavity. The posterior part of the cheek pouch is drawn off by one muscle, attached to the cervical vertebrae. The problem of the origin of this muscle, like that of the homologization of the muscle of the cheek pouches in Marmotini and Cricetini, needs special study, taking into account the innervation of this muscle.

Rodents having cheek pouches have a remarkable geographical distribution. The group Marmotini is undoubtedly, associated with open spaces; the majority of the representatives, except the Siberian Chipmonks, are found in steppes and semidesert regions.

The group Geomoidea is spread in steppes, semidesert, desert and hilly, desert landscapes of North America.

The present hamsters (Cricetini) inhabit the steppes and semi-desert regions of Palearctic.

The present mice (Murinae), possessing cheek pouches - *Saccostomus* and *Beamys* - are found in steppes desert and savanna of Africa. Only Cricetomyinae (a single species - *Cricetomys gambianis)* from steppes, deserts and savanna of Eastern and South-Eastern Africa penetrate into the humid and tropical forests of Western Africa.

Paca (*Cuniculus*) is distributed in open arid landscapes of central, and hilly parts of South America.

All these data on the geographical distribution of rodents which are far from each other and which independently acquire cheek pouches, indicate that the appearance of cheek pouches is associated with living conditions in the open arid zones of the globe having sharp variations of feeding conditions with seasons.

Cheek pouches help in storing food. It is not by coincidence that, in the capacity of the food stored, the hamsters occupy the first place among rodents and susliks the second place while the mice, mole-rats, and certain field-voles occupy generally much lower place. Storing of food, associated with the development of cheek pouches leads to a great extent, to the least dependence of the animals on unfavorable conditions of the medium.

Slight variations in the number (associated also with the storing of food for winter), which are characteristic of hamsters and resulting in the retardation of their evolution rate (Vorontsov, 1960b) may, to some extent, depend on the presence of extremely developed cheek pouches in Cricetini.

CHAPTER IV

THE EVOLUTION OF STOMACH

1. General Notions, Terminology

Food falls into the stomach from the gullet which is a deprivative of the ectoderm and is covered with horny epithelium. It has endodermic origin and is lined with glandular epithelium in most of the forms of Marsupialia and Eutheria.

The stomach (Venter), in its initial shape is a pouch-shaped expansion which is connected to the esophagus above and duodenum on the right. On the boundary between the esophagus and stomach there is the "border-line fold (Grenzfalte, as called by German authors) representing the growth of the connective tissue layer of the stomach and is lined with horny epithelium (Brummer 1876; Luppa, 1956) from the side of the gullet as well as the stomach.

At the opening between the gullet and the stomach the thick muscular ring forms a cardiac sphincter (sphincter cardia) which blocks the entrance of anything into the stomach, on contraction of the muscle. There is a large thickening of muscles at the opening between the stomach and the duodenum which forms the phylorus sphincter (sphincter pylori).

The part of the stomach contiguous to the gullet is called the cardiac portion (pars cardiaca or simply cardium); the main part of the stomach arranged mainly posteriorly from the cardium is called the fundic portion (p. fundica, or simply fundus); the narrow outlet is called the pyloric portion (p. pylorica or pylorus). The types of main glands, correspond to the division of the stomach in the one-chambered glandular stomach.

Cardial glands producing mucous alkaline secretion occupy a small area in the cardium. These glands can be easily reduced or displaced together with the border-line fold.

Fundic glands, which play a main role in the digestion of protein food, are situated at the bottom of the stomach. They are formed by ramified glands. The gland cells produce gastric juice - pepsin, chymosin and lipase, but the lining cells produce hydrochloric acid. Fundic glands which may occupy a greater or smaller surface area of the stomach, never disappear.

Pyloric glands, which produce an alkaline secretion containing pepsin, are situated in the pyloric portion. These glands may be displaced by the horny epithelium or generally reduced.

The surfaceof the glandular area of the stomach has alveolate form; small elevations are called areas (aereae gastricae), and shallow depressions, on the bottom of which there are openings of glands, are named crypts (faveolae gastricae).

Primarily the stomach in mammals is, a pouch-like expansion of the middle intestine. The part (primarily situated between the gullet and the duodenum) adjacent to the liver is called the minor curvature (curvatura minor); the caudal edge of the stomach forms an arc of greater radius called the major curvature (curvature major). As the stomach becomes more and more complicated the gullet and the duodenum come close to each other, and the radius of the minor curvature of stomach decreases. The part of the stomach, situated on the left of the cardium, is elevated forming a fornix (fornix ventriculi); the pyloric part of the stomach also is elevated. As a result the opening between the gullet and the stomach is situated more caudally than many portions of the stomach.

The muscular membrane of the stomach consists of three layers; external (longitudinal), middle (annular) and internal (oblique). The volume of the stomach in the non-inflated state may significantly decrease on the contraction of the muscles. Depending on the portion having less food, its volume reduces to few times owing to the contraction of the gastric muscles.

All sections of the stomach increase or decrease proportionately only during uniform inflation of the whole stomach by food or contraction owing to its complete absence. The degree of inflation and the state of contracted muscles determine the shape of the stomach of the animal under study. That is why the size of the blind pouch formed at the elevation of the fornix and the pylorus changes completely. Attempts of some researchers to judge the morphology of the stomach on the basis of superficial morphology without studying its internal structure are supported mainly by the ratio of the volumes of separate parts of stomach and cannot be considered as convincing. Because of the significant height of the glandular layer of the fundic part of the stomach the bottom stretches the least and its volume varies less than the remaining portions of the stomach.

Near the pyloric sphincter the pylorus is surrounded by a powerfully developed muscular sphincter (constrictor antrium pylori) which when contracts pushes the food from the stomach to the duodenum. The powerful horny folds which play the role of horny "teeth" may be developed where the pyloric part of the stomach is lined with the horny epithelium. Similar formation, well known (Pernkopf, 1937) and most clearly expressed in pangolin (*Manis javanica*) is not found so well expressed in some rodents.

Non-chambered stomach may be subdivided by folds into sub-sections. Generally the angular fold (Plica angularis), situated on the minor curvature of the stomach below (from behind) the opening between the gullet and to its right*, is very clearly expressed. The division of the stomach into two portions, characterized by real hamsters (Cricetini), is achieved by the powerful development of plica angularis. To the left of the opening between the gullet and stomach might develop a *cardial fold* (plica cardialis) which separates the blind pouch, and this pouch, is converted into an independent section of the stomach in some sandworts (Arenaria). In front of the muscular pylorus sphincter might develop a prepyloric fold (plica praepyloris) which may separate the pyloric section and convert it into an independent chamber.

---

* *Here and later when there is a description of the stomach it is considered from the dorsal side.*

The powerful development of the angular fold is generally associated with the formation of an external deepening of the constriction (isthmus). Similar recesses generally correspond to other most important folds of the internal surface of the stomach.

Depending on the epithelium which lines the internal surface of the stomach, the following types of stomach are distinguished (Pernkopf, 1937, Jedenov, 1958);

horny (only in Monotremata among mammals it is obviously, not homologous to the stomach of superior mammals and represents the expansion of the gullet i. e., the derivative of the anterior and not the middle intestine);

glandular (it is the initial stage of the superior mammals and spread among Insectivora Chiroptera, Carnivora, Pinnipedia, Prosimia, majority of Primates, some forms of the Cretacea, Edentata, Sirenia, among rodents in all forms of Sciuromorpha and Hystricomporpha, and in the suborder of Myomorpha among all forms of Dipodiodea and Gliroidea);

combined, when a part of the stomach is lined with horny epithelium having the origin of the gullet and the other part is lined with glandular. This type appears in different groups of the phytophagous mammals (Perissodactyla, Artiodoctyla, Hyracidae, Macropodidae, Bradypodidae, and among rodents it is spread in all Muroidea).

The stomach can be classified as simple, one-chambered, or complex (two-, three-, four-, five-, and six-chambered) types depending on the number of the sections. Generally the process of isolation of the chambers proceeds along with the formation of eipthelium of the stomach mixed according to types, but in individual cases (Yablokov, 1958) the multi-chambered stomach can also appear in forms having exceptionally glandular covering of stomach (Ziphius-Odontoceti).

The notion about the fact that the two-chambered type of stomach in rodents is found as an exception only in hamster (Oppel, 1869, Pernkopf, 1937; Jedenov, 1958), is based on the study of the limited number of forms: multi-chambered stomach develops into various groups of Muscidea.

The isolated left portion of the complex stomach of the rodents, lined with horny epithelium, similar to the rumen of ruminants is named the prestomach. Bline growths, which may be lined with horny as well as glandular diverticula branch off from the corpus of the stomach. On the aperture of the diverticulum (oryphiceum diverticuli) may have special sphincter (sphincter diverticuli).

The surface of the horny portion of the stomach is covered with folds particularly well expressed on the collapsed stomach. Undoubtedly, these folds of horny epithelium, sometimes having the form of thick horny protuberances moved by the stomach muscles, have a definite significance in its motor system.

The surface of the horny portion of the stomach may in extreme cases be strewn with papillae, lined with horny epithelium, or powerfully developed villiferous layer. The muscle enters the papillae, which may be mobile like the horny papillae, of the rumen of some ruminants. An increase in the area covered by horny epithelium is achieved with the development of papillae and fibers.

Along the minor curvature of the stomach from gullet to pylorus there exists an esophageal canal (sulcus oesophageus), which is a narrow corridor on the surface of the minor curvature of the stomach, with two longitudinal folds, having a muscular base. In hoofed animals the edges of these folds may close, forming a tube along which the milk and other food substances which do not require special processing in the corneous portions of the stomach, pass directly from the gullet into the glandular portion of the stomach (Jedenov, 1958). Most likely, the sulcus aesophageus performs similar function in the stomach of the rodents.

2. On the Physiology of Digestion in the Stomach. Functional Peculiarities of Glandular and Combined Stomachs, of Nonchambered and Multichambered Stomachs in Rodents.

The physiological characteristics of digestion in the stomach have not been studied much (Davenport and Yensen, 1949; Davenport, Schnoebell and Chavre, 1960; Ambrus G. Ambrus M. and Harrison, 1953, Pravdina, 1958 a, 1958b). However special studies of digestion in the glandular nonchambered stomach in predatory animals in the combined one-chambered stomach of horses, transitional to the multichambered combined stomach of pigs, and in the multichambered stomach of ruminants of hoofed animals (Pavlov, 1946; Verigo, 1906; Azimov, Krinitsin and Popov, 1954 ; Koshtoyants 1950) show the present general regularities of the physiology of digestion closely associated with the structure of the stomach. These data give us an idea of the process of digestion in the stomach of the rodents.

The food lump from the mouth cavity moistened by saliva falls into the stomach through the gullet. The process of digestion can start in the mouth cavity itself where by the action of amylase carbohydrates break up into polysaccharides. Breaking up of carbohydrates stops in the stomach under the influence of acidic medium.

The glandular stomach of mammals is strictly one-chambered. The fornix of the glandular type of stomach is never expressed. It becomes quite clear if we recall the features of secretion of the main types of gastric glands. Cardial and pyloric glands which never achieve such a concentration on a unit area as fundic glands, separate pepsin besides mucoid secretion. However neither the cardial nor the pyloric arch is capable of producing hydrochloric acid.* Meanwhile pepsin breaks up the protein only in acidic medium (optimum at pH = 1.5 - 2.0). The food substance which came from the horny cavity and mixed with saliva, has a mild alkaline reaction. Thus pepsin separated (in small quantities) by the cardial

---

** Exceptions are the Castors, in which the cardial glands produce not only pepsin, but also HCl (Nasset 1953; Orlova, 1956). Possibly, the glands of cardium in Castor originate from fundic glands, shifted to the minor curvature of the stomach.*

glands acts only in acidic medium, which is formed by oxyntic cells of the fundic glands, that secrete hydrochloric acid. Whatever be the section separating the cardial part of the stomach (secreting the ferment) from the fundal part (secreting the activator of its action) it is not justified functionally. In an exactly similar way the region of pyloric glands in the grandular type of stomach has not been separated from fundic region. In the same way, the pyloric glands secrete pepsin and are similarly not capable of secreting acid. However the food, entering from the fundal part of the stomach to pylorus, has already a clearly marked acidic reaction, in which the pepsin of the pyloric glands can act. Therefore, there may be an insignificant degree of isolation of the pyloric region of the stomach from the fundal part in the glandular type of stomach but the separation of the cardial part of the stomach from the fundal part is never observed.

At the bottom of the stomach fundal glands play the main role in splitting proteins, as stated by the works of I. P. Pavlov and his students. The number of fundal glands in a unit area of the stomach is more than the number of cardial and pyloric glands. They secrete the maximum quantity of pepsin, and only they secrete hydrochloric acid - the medium necessary for the action of pepsin.

Studies on domestic animals showed that in all phytophagous mammals (rabits, horses, pigs and ruminants) the gastric secretion flows continuously, whereas the predatory animals the secretion starts only at the sight of the prey - while chasing the prey or even only after the first swallowing movements (the feline species which catch prey from the ambush). These features of gastric secretion in phytophagous and predatory mammals are associated not only with the fact that in the case of irregular nutrition, in the absence of food, the continuous gastric secretion might result in self-digestion of the walls of stomach but also with the fact that the frequency of consumption, composition and caloric value of food substances, with which the representatives of these main ecological groups of mammals feed on, are diverse.

Since protein food has a high caloric content only a small quantity of such a food is required to be taken, and the process of food intake becomes less frequent. However, on taking exceptionally or mainly protein food it is necessary to have simultaneous secretion of a good quantity of highly concentrated secretion having ferments that split proteins.

Low caloris value of the vegetative parts of the plants requires a larger consumption of food in volume which even the highly complex digestive system of phytophagous mammals can handle during one feeding. For attaining the necessary colorie, therefore, the animal should eat round the clock. An extremely low content of proteins in the vegetative parts of the plants does not require a large quantity of concentrated secretion for processing it. Utilization of an insignificant quantity of proteins contained in this food is very important in the case of the low-calorie cellulose food, and requires constant secretion of a small quantity of gastric juice. It is interesting that in the same forms (in horses) the protein products cause an increase in the secretion of gastric juice whereas on eating of mainly cellulose food (hay) the quantity of gastric juice secreted is minimum (Azimov, Krinitsin, Popov, 1954).

According to the data of L.I. Pravdina (1958b) the gastric juice containing maximum acidity in rodents is secreted depending on the type of food specific for the given form: in field-voles - cellulose, and in susliks and mice - protein food. However, it is necessary to relate the data, acquired by a highly perfect method with care.

L. I. Pravdina (1958a) studied the duration of the food remaining in the stomach of common voles, social voles and white mice. In all these species the grass (cellulose form) remains in the stomach for 2 - 3.5 hours, while the grains (protein form) remain up to 5.9 hours (Table 3). This phenomenon to which Pravdina does not find explanations, is obviously associated with the fact that the main breakdown of protein takes place in the stomach, whereas the cellulose is subjected to break down generally in caecum and colon.

The food, more specific for a given species stays longer in the stomach than that less specific. However, in house mice, and common filed-vole, also protein food (grain) remains

TABLE 3.

Duration of food substances remaining in the stomach in the rodents Muroidea (according to Pravdina, 1958a), hour-min.

Species	Grass	Carrot	Grain
Microtus socialis	3 - 00	4 - 20	-
Microtus arcalis	3 - 30	4 - 40	5 - 20
Mus musculus var. alb.	2 - 00	3 - 25	5 - 55

in the stomach longer than cellulose (grass) food inspite of the difference in the duration of remaining in the stomach.

Low calorie value of mainly the cellulose food brings about the need to feed on round the clock. The quick passage of food through the digestive canal in such herbivorous forms as field voles, and the considerably greater duration of the stay of food in the digestive canal of rodents having combined type of nutrition (Table 4) (are associated with this. The experimental data (Mokeeva, 1948) shows, that in the cellular form the food stays longer than all in the blind and large portion of intestine, combined type of nutrition stays in the stomach and small portion of intestine.

It should, however, be noted that the duration of food remaining in the digestive tract of the Asia Minor sandwort twice longer than that of the gray hamster may depend not only on the differences in the types of nutrition of these species but also on the differences in the size of the animals and the lower metabolic activity in larger forms of sandworts.

The insignificant role of the cardial and pyloric glands, in the secretion of pepsin (in comparison with fundic glands) explains, why exactly these glands are subjected to reduction in many forms of phytophagous mammals. The reason for the reduction of glandular lining of stomach is the decrease in the role of protein food; the cellulose food is very coarse, and may easily hurt the mucous membrane of the stomach.

TABLE 4.

Duration of stay of food in the portions of digestive canal of rodents Muroidea. (according to Mokeev, 1949)

Species	Total duration of stay of food in the digestive canal (hour)	Relative duration of stay of food in different portions, %		
		stomach	small portion	blind and large portions
Microtus socialis	37.0	6.8	12.2	81.0
Microtus arvalis	36.0	8.3	13.9	77.8
Cricetulus migratorius	50.5	16.8	19.8	60.4
Meriones blackleri	149.0	26.8	33.6	39.6

It is not clear why the reduction of the number of glands in the stomach dissociated with the transition to the cellulose type of nutrition results not in the formation of mucous membrane devoid of digestive glands, but in the replacement of the glandular lining of the stomach by the horny epithelium of esophageal type.

The process of transformation of the glandular into the combined stomach is closely associated with the transformation of the one-chambered into the multichambered stomach. However, the division of the stomach into different parts starts a little later than the formation of combined (according to the types of epithelium) stomach.

With the formation of the combined type of stomach the border line fold which primarily separates the horny epithelium of the gullet from cardial glands, and which is situated in the forms having glandular stomach, strictly at the opening between the gullet and the stomach, moves into the stomach. The horny epithelium of the esophageal type is spread into the cardial portion of the stomach. According to the data of Luppa (1956), the horny epithelium in rodents having combined type of stomach is identical to epithelial lining of esophagus. The initial stages of the process of spreading of the horny epithelium into the stomach can be identified in Nesokia indica (see **Fig. 116, a**). Nectomys squamipes (see Fig. 94, b) and Sigmodon hispidus (see Fig. 110). In the lamellident rat, Nesokia indica more cardial glands are preserved in the stomach side by side with the presence of horny epithelium in the left part.

The form of the combined type of stomach is prevalent in rodents, wherein the horny epithelium completely replaces the cardial glands from the left half of the stomach and the border line folds divides the stomach into nearly two parts, coming very close to the fundic glands. A similar shape of the stomach is characteristic of many hamsters (Reithrodontomys megalotis, Calomyscus bailwardi, etc. water-vole Arivicola terrestris and the majority of sandworts.

The horny lining of the stomach serves as the surface of that reservoir where infusaria and extensive specific bacterial flora develop. According to the data of Kopperi (1935), a symbiotic protistofauna appears in the multichambered stomach of Cricetidae, which is qualitatively close to the fauna of the stomach and the intestine of ruminants. With the help of symbionts (the presence of bacteria in the combined stomach of rodents is undoubtful), fermentation takes place for the ferments, breaking down the cellulose (cellubiase) are not directly produced by mammals (Koshtoyants, 1950).

However, the bacterial flora and symbiotic protistofauna of the digestive system can exist only in a weakly alkaline medium, whereas these organisms are digested by pepsin in acidic medium at the fundus of the stomach. Similarly a weakly alkaline medium is created when the food moistened with saliva enters the stomach. It is quite obvious that the isolation of the horny portion of the stomach, where the weak alkaline medium must be preserved from the glandular parts of the fundus ventricoli having strong acidic medium, is a condition which is necessary for the development of bacterial flora and symbiotic protistofauna, i.e., a condition of assimilation with the organism of cellulose food substances. That is why in various groups of mammals and rodents the process of separation of the left part begins in the independent portion (viz., the horny prestomach) in view of the transition to the cellulose type of nutrition following the penetration of the horny part into the stomach.

Besides fermentation of cellulose symbionts help in the intensive processes of grinding in the horny prestomach with the help of horny columns, peristaltic and antiperistaltic contractions of the stomach muscle and maceration of the coarse cellulose food. These processes precede their fermentation.

The next stage of distribution of the horny epithelium in the stomach is the displacement of the pyloric glands by it from the pyloric portion of the stomach. The border line fold would appear to be divided into two parts: the main part which separates the fundic glands from the horny epithelium, and a small fold near the opening between the stomach and the duodenum, where the pyloric glands (Tullberg, 1899; Luppa, 1956) obviously having no function may be retained in the narrow area between the borderline fold and duodenum.

The nature of distribution of the pyloric glands (unlike the cardial) plays a significant role in breaking down proteins. Therefore, the process of keratinization of the pyloric portion of the stomach is obviously associated primarily with a decrease in the role of protein food substances consumed by some rodents adapted to the cellulose type of nutrition. The process of keratinization of the final portion of the stomach is characteristic of rodents, pangolins and some edentates and is not found among hoofed mammals. The functional significance of the formation of the horny lining of the pyloric portion of the stomach may only be assumed.

The horny epithelium in the pyloric portion of the stomach seldom forms large bulges. These formations moved by the powerful muscles of the pyloric sphincter, may have definite role in the mechanical process of the coarse cellulose food.

The field voles having the pyloric portion not divided up to the fundus (Microtus), may have a concentration of protein particles in the fundic glands region when we find in the stomach both the green parts of plants and seeds. But the cellulose food substance remains both in the anterior portion of the stomach in pyloric portion. This observation, repeatedly checked in our studies on northern field voles (Vorontsov, 1961b), must be explained physiologically, since the mechanism of dividing the various food fractions is not clear according to their chemical composition.

The entry of the fundic gland acid into the pyloric portion considerably inhibits the cellulose fermentation in the horny pyloric portion. The pyloric zone lined with the horny epithelium is an independent zone in the hamster Peromyscus californicus and field vole Prometheomys schaposchnikovi. This, to some extent, limits the entry of hydrochloric acid of the gastric juice into this section and facilitates the development of the bacterial flora. Even the borderline fold which separates the horny portion to some extent from the glandular portion is well developed in these forms.

The separation of the fundic gland by the borderline fold on the one hand and the considerable development along the minor curvature of the esophageal groove, on the other, clearly demarcate the fundus portion from the pyloric. In some rodents the food passing through the fundic glands region may penetrate into the pyloric portion through the esophageal groove or the place through which it stretches along the minor curvature of the stomach. It is interesting to note that the penetration of the horny epithelium to the right half of the stomach, generally, begins only in the esophageal groove along the minor curvature of the stomach. It is well known that liquid food may pass through the esophageal groove while passing through the cardial portion and sometimes even through the other portions of the stomach. It is apparent that the slightly alkaline saliva which favours the development of the bacterial flora and fauna may penetrate through the minor curvature of the stomach into the pyloric portion where it creates conditions for the existence of symbionts. However, this hypothesis is yet to be proved experimentally. Even if the fermentation of cellulose takes place in the horny pyloric portion, the conditions here are not so favorable as in the "fore stomach". The main functions of the horny pyloric portion are maceration and grinding of the cellulose food.

Thus the basic tendency in the formation of the form and function of the stomach in rodents is not strictly analogous to those in ungulates. While the horny "fore stomach" of rodents is analogous to the rumen, reticulum and omasum of ruminants and the function of the fundal gland region is the same as that of abomasum in ruminants, the horny pyloric-portion of the stomach developing in some rodents does not have any analog among these organs of the ungulates.

3. Individual and age variation in the structure of the stomach

The stomachs of 231 specimens of Clothrionomys glareolus and 136 specimens of Clethrionomys nutilus have been studied. The structure of the stomach of not only palearctic rodents but also of 2-12 specimens were studied. As observed above, the ratio of the volumes of the blind sac of the first stomach and the pyloric portion depends on the amount of food contained in them and the state of the animal at the time of fixation. These cannot be considered as individual differences, but should be taken into consideration while studying the morphology of the stomach. Where-ever possible sketches of the stomach are made with approximately the same width of the stomach portions. However, the variation is so great that we did not always succeed in getting a homotypal material. These features of the change in the form of the stomach when it is full should be taken into consideration while making use of the figures prepared for this work. Meanwhile, the topography of the glands, the division of the stomach into portions and the development of the borderline fold strictly constant in all the individuals of this species - these were the characteristics studied by us.

Agewise variations in the structure of the stomach were studied by comparing the stomach of the new born, young and adult forms of true cricetinae and field voles. The stomachs of the new borns of true cricetinae and field voles have already been divided into two portions, but, the blind sac and the pyloric portion were relatively small compared to the fundal region. Young animals, changing to independent nutrition possess well developed fore stomach and pyloric portion. It is highly probable that the increase in the volume of these portions is connected not only with their late growth but also the strain caused by food contained in them.

The embryos of Mesocricetus auratus measuring 10-12 mm have a loopshaped curved stomach but it is not clearly divided into two portions. The embryo of common voles measuring 6-8 mm also have a loopshaped curved, one-chambered stomach where the fundal glands occupy most of the surface. These isolated observations show the origin of the two-chambered stomach in certain forms of Cricetidae from one-chambered stomach.

On the basis of the detailed embryological studies Pernkopf (1931 and 1937) and Gerke (1956) have established that the multichambered stomach of ruminants is formed by the division of an originally one-chambered stomach. That have, thereby proved that Aeby and Munk's view (see Gerke, 1956) that the horny portion of the stomach is homologous to the lower portion of the esophagus is erroneous. Our fragmental observations confirm that Pernkopf's (1931 and 1937) and Gerke's (1956) views hold good even for the rodents.

4. Stomach structure of Cricetinae

All members of Muroidea are characterized by the presence of a horny epithelium on the stomach whereas the subfamily Cricetinae, in this respect is similar to the remaining members of the Muridae family. However, the ratio of the areas lined with horny or glandular epithelia, one-chambered or multichambered stomach - all these are highly variable features. The characteristics of the stomach structure of the subfamily Cricetinae have none of the characteristics of the representatives of this large family.

The stomach of Oryzomys couesi (Fig.49a) is one-chambered and fornix ventriculi is raised above the opening between the gullet and the stomach. Thanks to the loopshaped bend of the lesser curvature of the stomach the opening between the gullet and the stomach and the opening between the duodenum and the stomach are close to each other. The borderline fold starts close to the right hand wall of the gullet and runs to the left. It divides the horny and the glandular portions of the stomach into two zones out of which the horny portion occupies a somewhat larger area owing to the prominence of the fornices. There is a prepyloric fold, well developed on the lesser curvature side of the stomach.

The stomach of Nectomys squamipes (see Fig. 94b) has a more primitive form than that of Oryzomis for it is sacculate, the fornix ventriculi is only slightly above the opening of the gullet; and the opening of the gullet and the outlet of the duodenum are not close to each other. The borderline fold is shifted more to the right than that in Oryzomys and passes along the right wall of the gullet. However, the caecum is clear and the areas lined with the horny and glandular epithelium are more or less equal owing to the poor development of fornices. Fundic glands line a large portion of fundus ventriculi, cardial glands remain only on the boundary of the glandular portion of the stomach and the well developed pyloric glands line the pylorus.

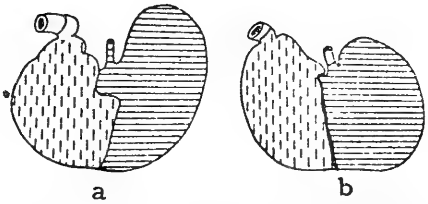


Fig. 94: Stomach structure of hamsters. (a) Oryzomys couesi Alston; (b) Nectomys squamipes Brants. Original. In Fig. 94-122 region of distribution of the glandular epithelium is shown by vertical discontinuous dashes and the region of distribution of horny epithelium with horizontal continuous lines. Ventral view of the stomach is shown. Esophagus is shown at the centre and duodenum on the left.

Further widening of the area occupied by the horny epithelium, eminence of the fornix and individuation of the stomach portions are observed in Calomyscus, Biomys, Reithrodontomys and Peromyscus (Fig. 95).

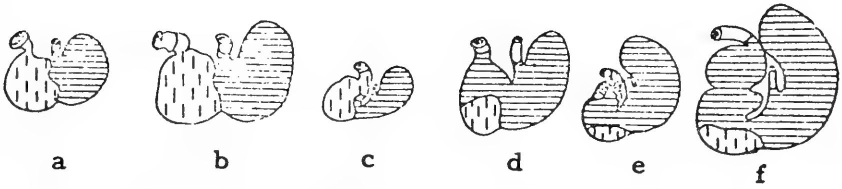


Fig. 95: Structure of the stomachs of hamsters of Reithrodontomyini and Calomyscus. Original. (a) Calomyscus bailwardi Thom.; (b) Baiomys musculus Merriam; (c) Reithrodontomys megalotis Baird; (d) Peromyscus (s. str.) leucopus Rafin; (e) Per. (s. str.) maniculatus Wagn; (f) Per (Haplomylomys) californicus Gambell.

In Calomyscus bailwardi (see Fig. 95, a) the fornix is clearly noticeable perhaps with a weakly developed fold, separating the upper portion of the caecum, on its lesser curvature. The esophagus and the duodenum are close to each other and there is a clear isthmus between the horny and the glandular portions. The borderline fold begins above the isthmus or on its right side, then turns to the left and divides the stomach approximately along the line on the right hand side of the esophagus. Owing to the development of the fornix, the area lined by the horny epithelium is slightly more than the glandular area, the fundic glands occupy a considerable area and are highly raised close to the borderline fold.

The structure of the stomach in Baiomys musculus (see Fig. 95b) is very much similar to this. In Reithrodontomys megalotis (see Fig. 95b and 96) the horny epithelium along the lesser curvature penetrates farther and farther into the pylorus portion, the plica angularis dividing the stomach into subdivisions is well developed, and there is the plica cardialis which to some extent separates the caecum of the fore stomach. In front of the fundic gland region, the borderline fold has well developed uniserial villi, which at the fundic ventriculi attain a length of 3 mm. These villi, demarcate the fundic region slightly from the side of the gullet and the horny zone of the stomach.

Species of the genus Peromyscus studied by us were characterized by the horny epithelium spreading along the pyloric portion. In Peromyscus (s. str.) leucopus and P. maniculatus (see Fig. 95d, c) the fornix is very eminent thanks to the high eminence of fornix ventriculi. A sharp increase in the size of the horny forestomach and a high development of the isthmus and plica angularis give the impression that the stomach is divided into separate portions similar to the present palearctic Cricetini; in the left half there is a sufficiently broad passage. Fundic glands are found only on a small portion of the fundal region.

The stomach of Peromyscus (Haplomylomys) californicus (see Fig. 95, f, and 97) is still more complex. If the distribution of the horny and the glandular epithelia is similar to those of the representatives of the subgenus Peromyscus (s. str.), the form

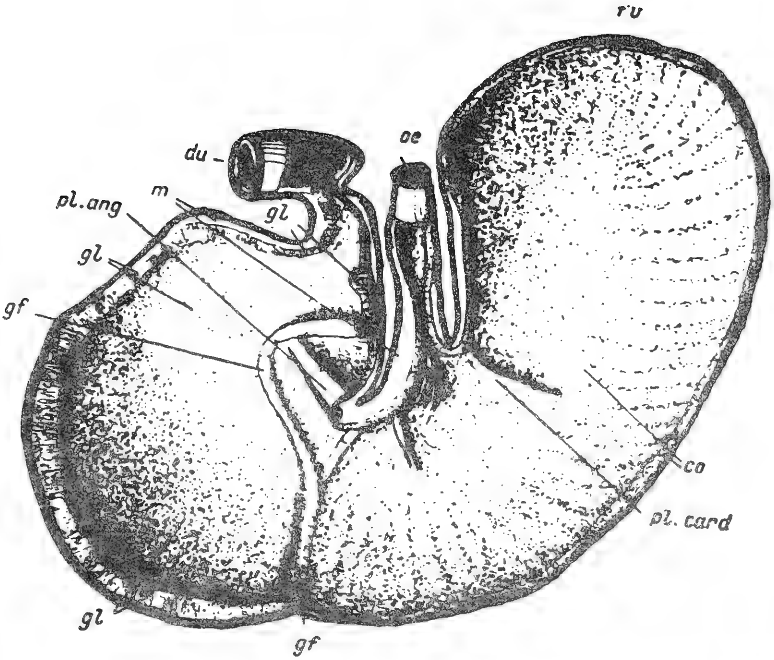


Fig. 96: Structure of the stomach of Reithrodontomys megalotis Baird. The stomach is demarcated into horny and glandular portions only slightly. From specimens from the collection of Zoological Institute, Acad. of Sciences, USSR, No. 18378.
C - cardium; co - horny epithelium; dv - glandular diverticulum; du - duodenum; fr - fornix ventriculi; gf - borderline fold between horny and glandular portions of stomach; gf - borderline fold between stomach and duodenum; gl - glandular epithelium; isth - isthmus between the left and the right portions of the stomach; m - section of the muscular layer; oe - esophagus; od - oryphicium diverticuli; P - pylorus; pl. ang. - plica angularis; pl. card. - plica cardialis; pl. praepyl. - plica praepyloricus and pp - pars pyloricus.

of the stomach is considerably complex. Plica angularis is well developed and the isthmus between the left and the right halves of the stomach is very noticeable; but, it is not so much as in Cricetini and Microtini. The pyloric portion which gets transformed into an independent portion of the stomach thanks to the well developed plica praepylorica and the corresponding ring shaped isthmus, is well developed in Cricetinae. Thus Peromyscus californicus has a stomach more or less three-chambered,

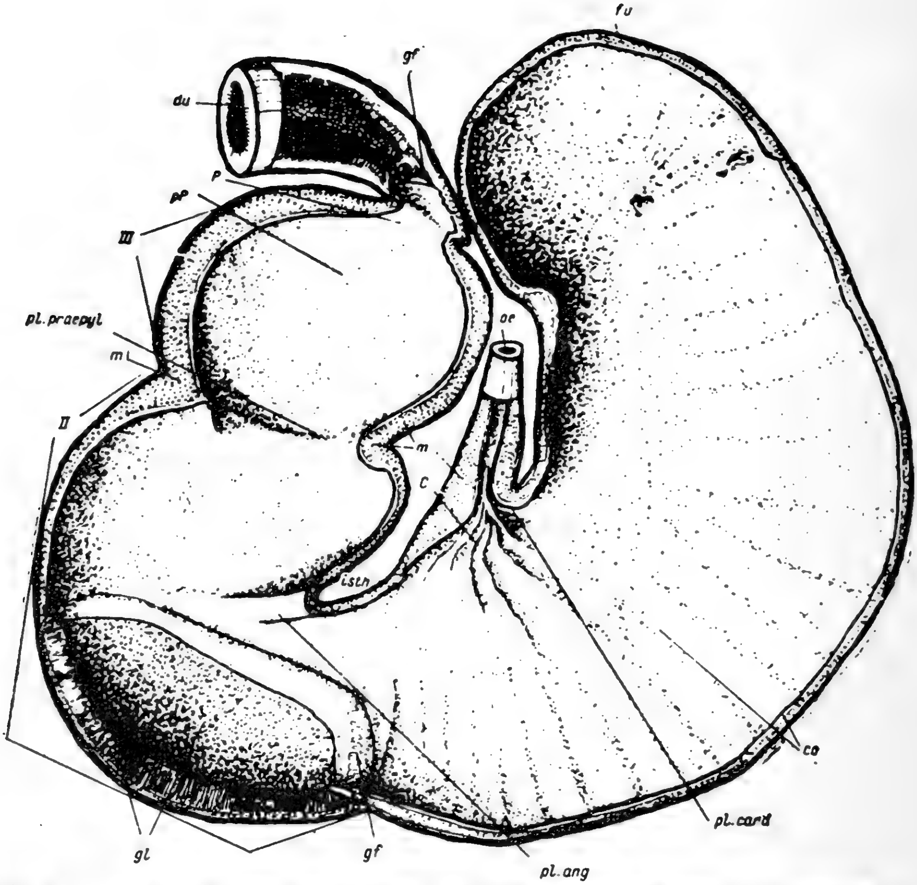


Fig. 97: *Stomach structure of* *<u>Peromyscus</u>* *(<u>Haplomylomys</u>)* *<u>californicus</u>* *Cambell. Original. Stomach more or less three-chambered, horny epithelium developed maximum and the glands concentrated only in a small area of the fundus ventriculi. From the collection of the Zool. Inst., Acad. of Sc., USSR, No. 18384. For legends see Fig. 96.*

where the first chamber is the horny fore stomach with a remarkable caecum, the second is the glandular, fundal region and the adjacent fundal region with corneous epithelium and the third is the horny pylorus chamber with very well developed muscles of the pyloric sphincter.

The stomach structure of the North American insectivorous hamsters, <u>Onychomys</u>, differs sharply from that of Reithrodontomyini. Both the species of this genus namely, <u>On.</u> <u>leucogaster</u>

(Fig. 98) and On. torridus have a true two-chambered stomach not at all homologous to the two-chambered stomach of palearctic Cricetini. The entire glandular portion is arranged in the special, isolated, caecal portion of the stomach - glandular diverticulum. The stomach of Onychomys is loop-shaped with caecum fornix of medium height and is lined from oesophagus to duodenum with horny epithelium forming folds, but in the pylorus region, there are thick, horny highly segmented rugae. At the fundus ventri-

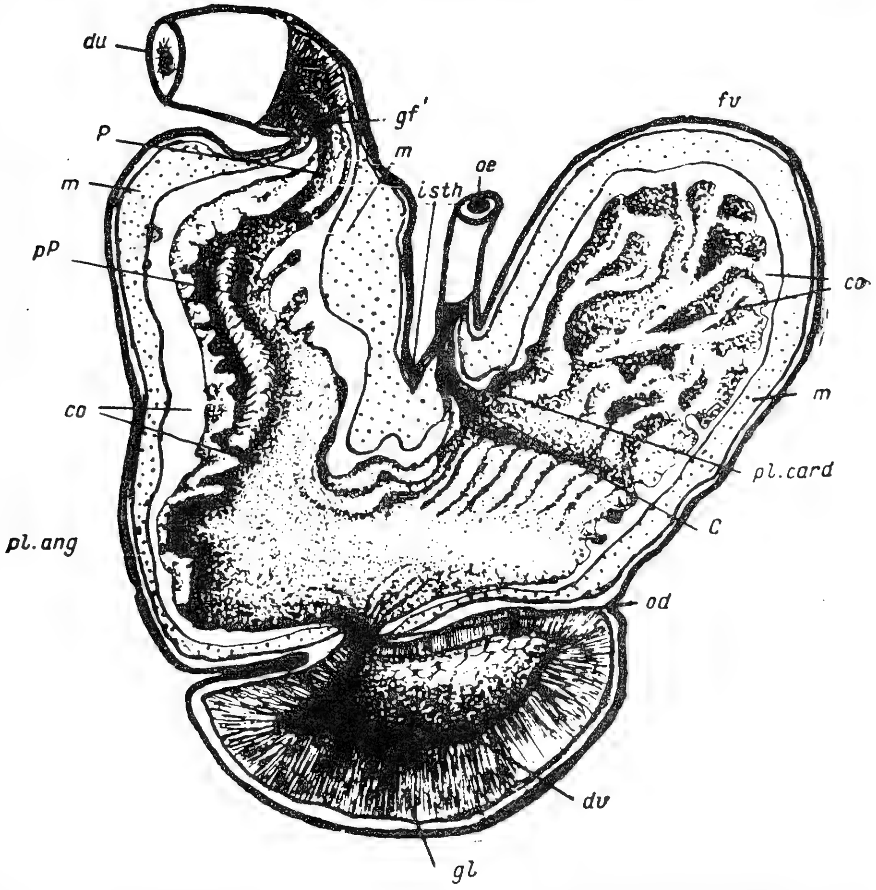


Fig. 98: *Stomach structure of insectivorous cricetins Onychomys leucogaster Wied. Original. Corneous epithelium extends from oesophagus to duodenum, the corneous portion of the stomach is divided into two portions by a fold and fundus glands are concentrated in the diverticulum. Convergence with the stomach of Pangolins, Manis javanica and parallelism with the stomach of the hamsters, Orymycterus. For legends see Fig. 96.*

culi there is a small aperture (ozyphiceum diverticuli) leading to the chamber lined completely with fundus type glandular epithelium. The aperture is more or less at the center of the spherical upper part of this cavity and has a musculature around it forming a special diverticular sphincter. The small size of the aperture, the special sphincter and the typical position show that food does not enter into the diverticulum. In fact, the diverticulum ventriculi of the stomach of Onychomys is a gigantic gland where gastric juice is produced. This juice enters the corneous portion through the diverticular aperture and breaks down the proteins primarily.

The form of the stomach in Manis javanica (Pholidota) is very similar. In the Javan forms of Pholidota, all the gastric glands are concentrated in the diverticulum on the fundus ventriculi, from where the gastric juice enters into the stomach lined with the corneous epithelium - (Pernkopf, 1937). The sphincter muscles are well developed in the pyloric portion and they put the corneous "radulae" made of corneous epithelium into action. The radulae (which are very well developed in Myrmecophaga) grind the solid chitinous parts of insects before they enter the thin mucous intestine.

It is well known that the role of insects (especially Orthoptera) in the food of Onychomys is very important. A continuous corneous stomach and the closing of the glandular portion into a special diverticulum are the prerequisites for the changeover to a predominantly (Onychomys) or exclusively (Manis) insectivorous nutrition.

A similar mode of nutrition, with the predominantly protein food substances causes a powerful development of the proventriculus. Proventriculus is a characteristic exclusively of Insectivora and Chiroptera. The glandular portion is well developed in hamsters like Oryzomys, Nectomys and Sigmodon.

However, the transition to feeding on adult insects (termites, ants and Orthoptera) does not present any new requirements from the chemism point of view of gastric secretion, but requires protection of the fine glandular lining of stomach from coarse chitinous parts which are difficult to digest. This has given rise independently to a process of cornification of the stomach and separation of the glandular region into a diverticulum. This is observed in ~~groups~~ groups very different from one another, such as pangolins and Cricetinae.

A remarkable feature of the stomach of Onychomys is the well developed corneous prominences, in the pyloric region surrounded by powerful pyloric sphincter muscles. These processes cannot even be called corneous "teeth" as in the case of Manis javanica and Myrmecophaga, but, it is undoubtful that these play a decisive role in the grinding of chitinous residues of insects before the chyme enters the stomach. Features of ontogenesis of Onychomys's stomach will be described in the special part.

The loop-shaped stomach of Onychomys and well developed fornix suggest that the hamsters can feed on insects as well as cellulose food. According to Sperry, (1929) and Hall, (1946) Onychomys fed on cellulose food in winter.

The stomach structure of Onychomys separates this species from other forms of North American Cricetinae, including Baiomys, Reithrodontomys, and Peromyscus. it is grouped with them because of certain similarities in the structure of the dental system. The stomach structure of Akodon arenicola (Fig. 99) is very primitive and comparable only to that of Oryzomys, Sigmodon and Neotomys. The stomach is one-chambered and sacciform. Fornix ventriculi is feebly marked. The borderline fold is shifted more to the right of oesophagus and the area lined with corneous epithelium is somewhat larger than the glandular portion. A major portion of this glandular zone is lined with fundic glands.

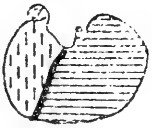


Fig. 99: Stomach structure of Akodon arenicola Waterh. After Vorontsov.

In their stomach structure the South American insectivorous hamsters, Oxymycterus, differ sharply from Akodon. Oxymycterus just as Onychomys have a glandular diverticulum whose existence was first mentioned by Tullberg (1899). He wrote :

"Internally the stomach of Oxymycterus is lined entirely with corneous epithelium, while the glands are restricted to a special thickening on the wall of the greater curvature of the stomach and open into the fundus ventriculi through a small aperture" (Tullberg 1899, s. 251).

Figures (Taf. XLI, 23, 24) drawn by Tullberg are very small and do not reveal the detailed structure of this noticeable formation in the stomach of the rodents. In his report on the digestive system of vertebrates Pernkopf (1937) redrew the sketch drawn by Tullberg erroneously and did not at all notice the diverticulum. He considered Oxymycterus rufus as a form with highly reduced glandular epithelium and even considered this species lower than the field voles. The author (Vorontsov, 1957) himself has committed this mistake by following Pernkopf.

The structure of the digestive system of a related species, Oxymycterus nasutus, was studied (Fig. 100) and found very similar, in as far as it can be judged from the schematic diagram and brief description given by Tullberg, to Ox. rufus in its stomach structure.

The stomach of Ox. nasutus is sacciform, fornix ventriculi is not marked and the main stomach-chamber is lined from esophagus to duodenum with corneous epithelium of esophageal origin. At the base, opposite to the opening between the esophagus and the stomach, there is a small aperture leading into an isolated blind chamber, the glandular diverticulum. The entire wall of the diverticulum is lined with considerably high fundic glands. The aperture of the diverticulum (as distinct from that of Onychomys) is on the left edge of its upper wall and is surrounded by a circular system of muscles forming a sphincter. As in Onychomys, the diverticulum of Oxymycterus presents a gigantic gland in which gastric juice is produced. This juice is periodically supplied to the corneous portion by opening the sphincter. Here the juice breaks down the proteins.

Unlike Onychomys, the pyloric portion in Oxymycterus does not have any special corneous prominence for grinding the chitinous residue of insects and is not separated from the remaining part of the stomach. The pyloric sphincter muscles are not so prominent as in Onychomys.

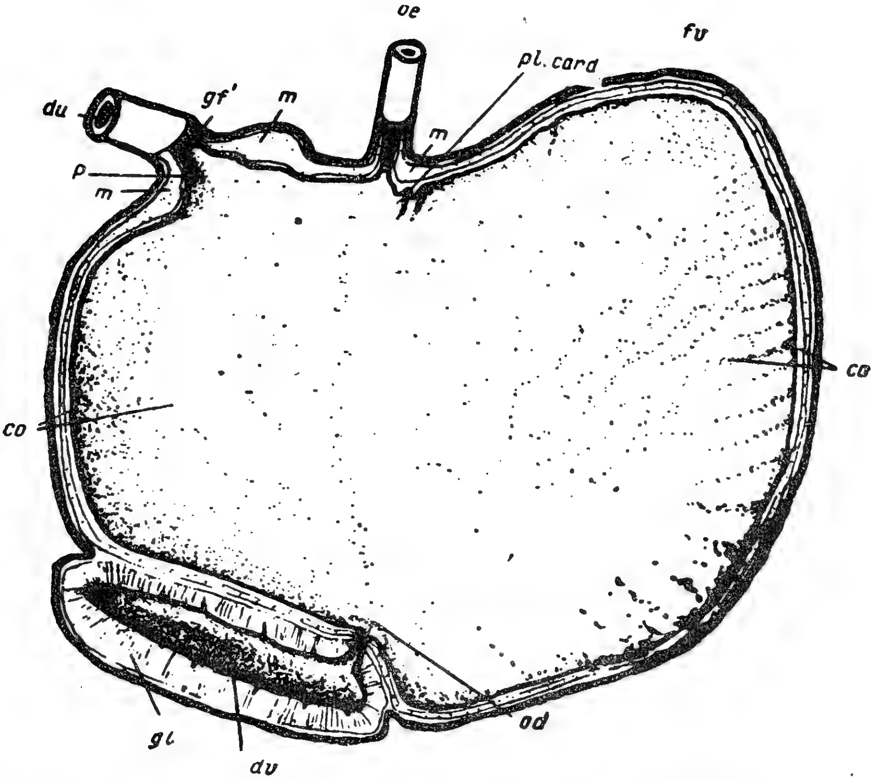


Fig. 100: Stomach structure of insectivorous hamster Oxymycterus rufus Desm. Original. Corneous epithelium developed from esophagus to duodenum, one-chambered corneous stomach and glands concentrated in the diverticulum. For legends see Fig. 96.

The absence of a blind sac of the first stomach suggests that cellulose food plays a minor role in the nutrition of Oxymycterus. This agrees with our views that Oxymycterus is found in the subtropic zone, where small invertebrates are active all the year round. Remnants of earth worms were found in the dissected stomach of Oxymycterus nasutus.

Palearctic hamsters (Cricetulus, Cricetus, Mesocricetus, Phodopus) and African Mystromys have a true two-chambered stomach.

The stomach of Mystromys (Fig. 101) is divided, into two well marked chambers, by the isthmus. The large corneous fore stomach is situated on the left of the oesophagus and the

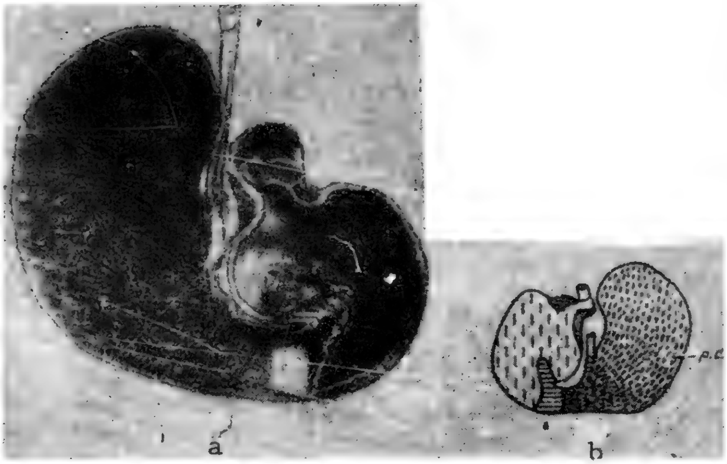


Fig. 101: Stomach structure of African hamsters Mystromys albicaudatus Wagn. The entire corneous portion of the stomach covered with villi. (a) Dorsal view, Original; (b) Stomach structure ventral view, after Vorontsov (1962 b). For legends see Fig. 96.

glandular portions of the stomach and by their development widely separates these chambers from one another. The corneous epithelium and the borderline fold separating it penetrate into the right hand side of the stomach only along the lesser curvature.

A remarkable feature which helps in distinguishing the stomach of Mystromys from that of all the remaining members of Cricetinae is the development of corneous columnar papillae covering almost the entire surface of the corneous fore stomach except a small portion in front of the borderline fold. The papillae are oriented along the direction of the food flow. The height of the papillae is 2-4 mm. They are especially abundant below the opening between the esophagus and the stomach, although their number in the blind sac of rumen is very high.

Development of papillae considerably increases the area of the corneous epithelium of the stomach. Besides, the complex surface of the rumen creates conditions favorable for the growth of the bacterial flora in the stomach. An increase in the surface of the forestomach is obtained in certain species by an increase in the volume of the forestomach itself, in certain others

(*Hypogeomys antimena*, *Nesomyinae*) - by the formation of additional folds in the forestomach, in a third group (Ruminantia) - by dividing the forestomach into separate chambers and in a fourth group (*Myospalax*, Myospalacinae) by the formation of a villose structure on the forestomach. Development of a papillary lining on the corneous portion of the stomach in *Mystromys* in an important new acquisition which particularly accelerates the fermentation of the cellulose food substance.

The special feature of the stomach structure in *Mystromys* is still one of the facts, showing that it is erroneous to group *Mystromys* and the present palearctic forms of Cricetini in one tribe.

The stomach structure of true palearctic Cricetini is of the same type. All the four genera of this group have an actually two-chambered stomach. The difference in the stomach structure of the individual species is, as a rule, insignificant (Fig. 102).

The two-chambered stomach of *Cricetus cricetus* (see Fig. 102, g) consists of a left corneous portion and a right glandular portion, more or less of the same size. A small portion of the corneous epithelium extends into the glandular portion along the minor curvature. Fundic glands occupy a considerable portion of the base of the right chamber. The well developed and distinct corneous forestomach and the large area lined with glandular epithelium show that the stomach is meant for processing both protein and cellulose food substances. This completely agrees with the data given by A. G. Voronov (1947) who has shown that *Cricetus cricetus* is omnivorous.

In its structure, the stomach of *Cricetulus (Tscherskia) triton* (see Fig. 102, b and 103) is similar to that of *Cricetus*. But it differs from that of *Cricetus* in certain minor features like the position of the borderline fold. Besides the corneous epithelium does not project into the right hand side chamber of the stomach along the lesser curvature.

The stomach of *Cricetulus (Allocricetulus) eversmanni* (see Fig. 102, a and 104) differs from that of the two previous

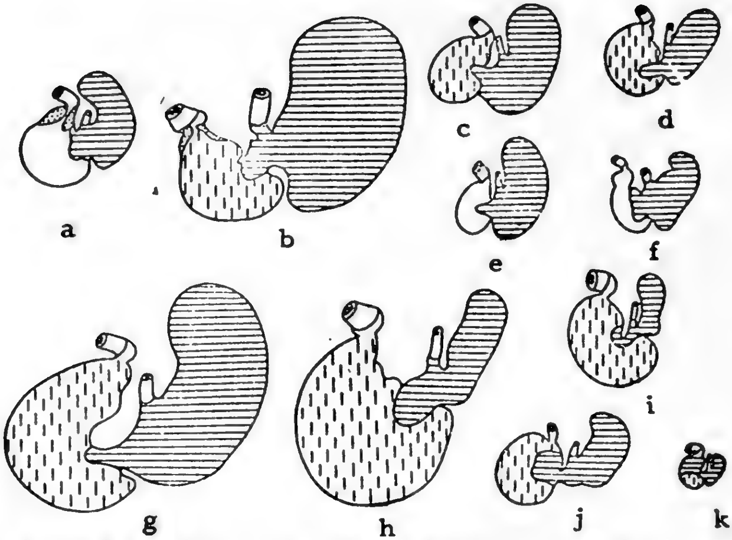


Fig. 102: Stomach structure of the present palearctic Cricetini. Two-chambered stomach: reduction in the area occupied by the glandular epithelium. From Vorontsov's work (1957, 1962 b). For legends see Fig. 96.
(a) Cricetulus (Allocricetulous) eversmanni Brandt; (b) Cricetulus (Tscherskia) triton der Winton; (c) Cricetulus (s. str.) migratorius Pall.; (d) Cricetulus (s. str.) barabensis Pall.; (e) Cricetulus (s. str.) longicaudatus Milne Edw.; (f) Cricetulus (s. str.) kamensis Satunin; (g) Cricetus cricetus L.; (h) Mesocricetus raddei Nehr.; (i) Mesocricetus brandti Nehr.; (j) Phodopus sungorus Pall.; (k) Phodopus roborovskii Sehunin.

forms by the high development of the borderline fold in addition to the peculiarities in the structure of the glandular chamber. Fundic glands are located at the bottom and further above along the greater curvature to the pylorus. The glandular surface in front of the pylorus forms a fold - a temporary form of separating the fundic gland region from the pyloric. The pyloric sphincter muscle is well developed. In the pyloric sphincter region the glands are very well developed along the lesser curvature. In its stomach structure *Cr. eversmanni* is more adapted among the palearctic Cricetinae for the protein type of nutrition. The stomach structure of *Cricetulus (Allocricetulus) curtatus* is similar to that of *Cricetulus (Allocricetulus) eversmanni.*

A tendency of the corneous epithelium to penetrate to the right hand side portion of the stomach is observed in members of

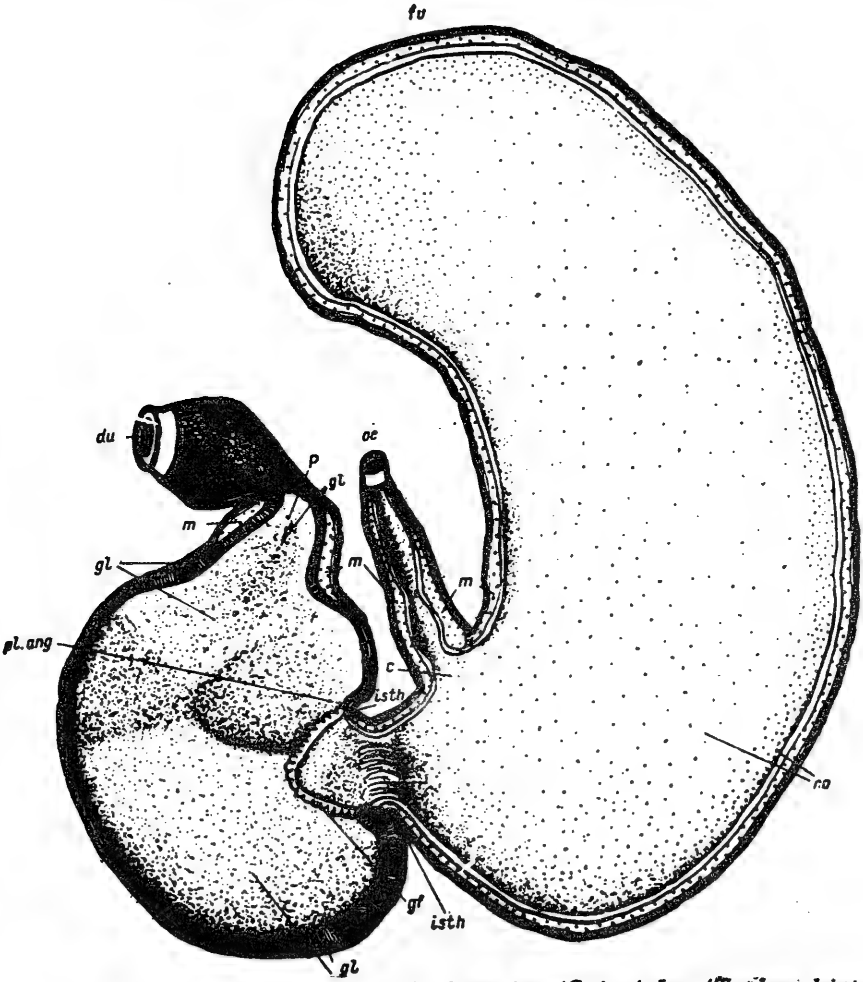


Fig. 103: Stomach structure of rat-like hamster (Cricetulus (Tscherskia) triton de. Winton); Stomach - actually two-chambered, the corneous forestomach is separated from the glandular portion by deep isthmuses. For legends see Fig. 96.

the subgenus Cricetulus (s. str.) among Cr. barabensis - Cr. longicaudatus - Cr. migratorius - Cr. kamensis (see Fig. 102, c, d, e and f). The corneous epithelium penetrates fairly well to the right hand portion of the stomach along the lesser curvature of the stomach in the last species (Fig. 105). A reduction in the area occupied by the fundic glands is also observed.

The stomach of the three species of the genus Mesocricetus viz., M. auratus, M. brandti (Fig. 106) and M. raddei (Fig.

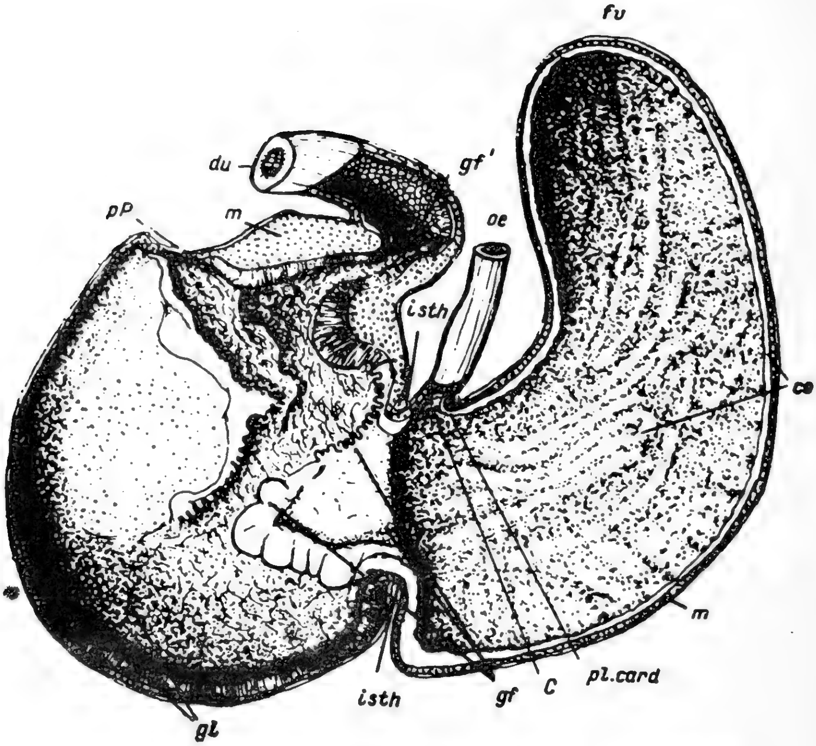


Fig. 104: Stomach structure of Eversmann's hamster, Cricetulus (Allocricetulus) eversmanni Brandt. From the specimen from Zavolshye. Division of the stomach into corneous and glandular portion is well expressed; well developed borderline fold is shifted to the glandular portion, which is divided into pyloric and fundus regions by pre-pyloric fold. For legends see Fig. 96.

107) - studied are identical. Minor details in the topography of the borderline fold which may shift slightly to the right glandular portion vary from individual to individual. A feature of the stomach of Mesocricetus is the considerable development of folds increasing the area of the corneous epithelium in the corneous forestomach. This shows that Mesocricetus is more adapted to the cellulose mode of nutrition than the palearctic cricetinae described above.

In Phodopus sungorus (Fig. 108) the corneous epithelium spreads less to the right hand portion of the stomach along the lesser curvature of the stomach than in Cr. kamensis.

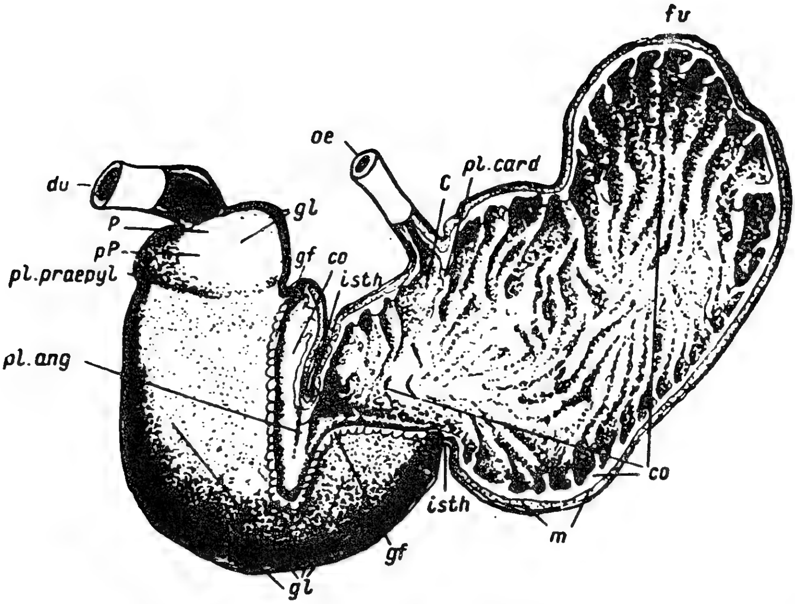


Fig. 105: Stomach structure of Kama hamsters Cricetulus (s. str.) kamensis Satunin. According to the typical specimen from Kama (Central China) Original. The borderline fold is shifted to the pyloric portion, the corneous epithelium begins to displace the glandular portion from the second half of the stomach. For legends see Fig. 96.

Stomach in Ph. roborovskii (Fig. 109) in which the corneous epithelium is distributed even along the pyloric portion, the pyloric glands are absent and the fundic glands limited by the borderline fold are concentrated only on a relatively small portion of the fundus ventriculi, differs from this type of stomach. On the basis of the stomach structure we stated (Vorontsov, 1957, 1960a) that the cellulose food substances should play an important role in the mode of nutrition of Ph. roborovskii than in the life of Ph. sungorus.

These hypotheses were confirmed by the results of the studies on the nutrition of Ph. roborovskii carried out Flint (1960), who convincingly proved the major role of cellulose in the food of Ph. roborovskii in comparison with Ph. sungorus. According to the stomach structure Ph. roborovskii is an extreme member of the order in the degree of adaptation to the

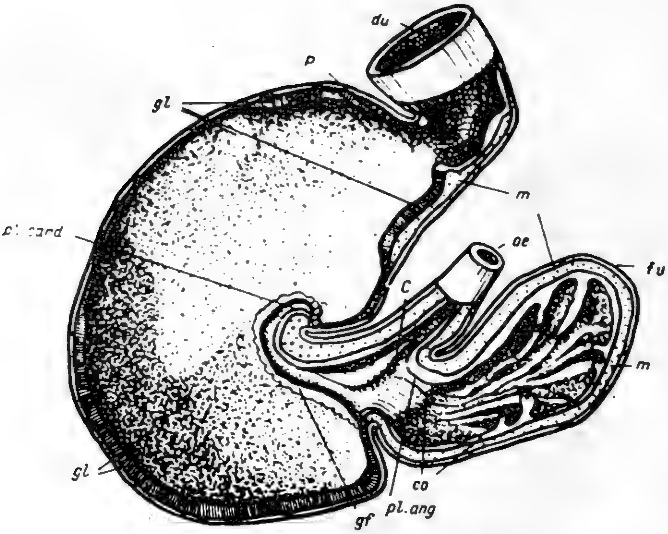


Fig. 106: Stomach structure of Transcaucasian hamster Mesocricetus brandti Nehr. Original. For legends see Fig. 96.

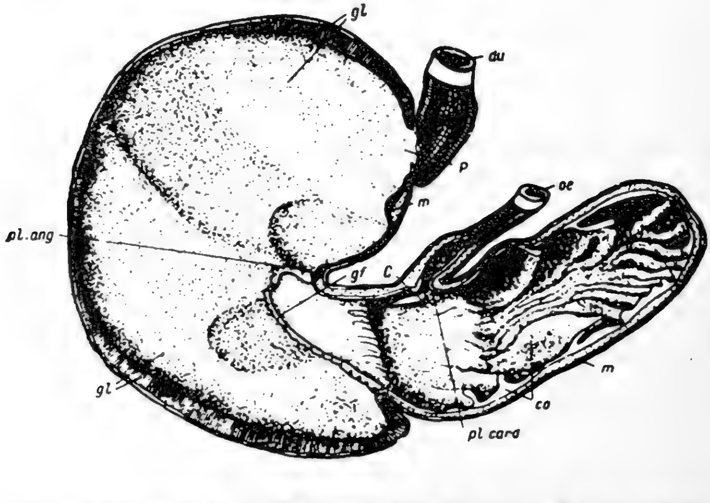


Fig. 107: Stomach structure of Precaucasian hamster Mesocricetus raddei Nehr. According to a specimen obtained from the vicinity of Khunsakh, Daghestan, Original. For legends see Fig. 96.

cellulose mode of nutrition among the palearctic hamsters just as Peromyscus californicus among the American hamsters.

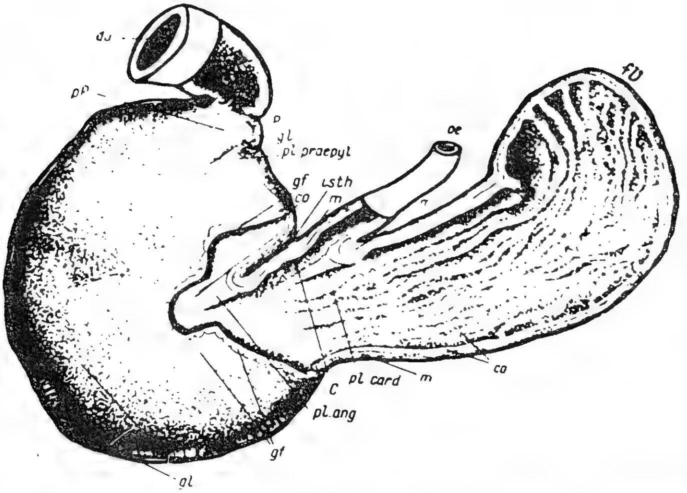


Fig. 108: *Stomach structure of striped hairy-footed hamster* *__Phodopus sungorus__* *Pall. According to a specimen from the vicinity of Kokchetav, North Kazakhstan. Original. For legends see Fig. 96.*

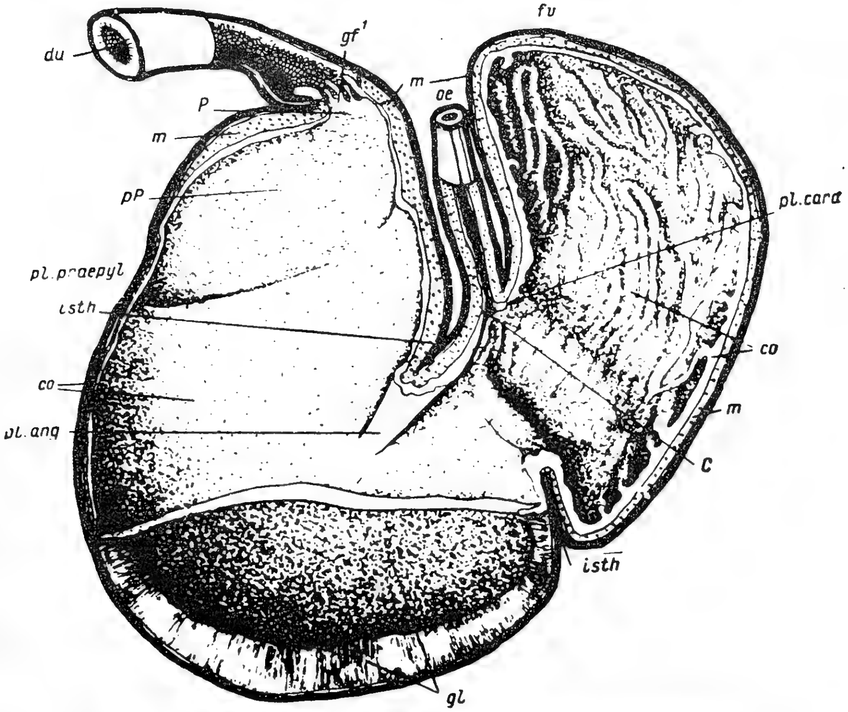


Fig. 109: *Stomach structure of the Roborovskii hamster* *__Phodopus roborovskii__* *Satunin. According to the specimen from Mongolia. Original.*

Based on their stomach structure, the palearctic Cricetini form a monolithic group, quite different not only from the American hamsters but also from Calomyscus and Mystromys.

The stomach structure of Sigmodon (Fig. 110) is very primitive. The stomach is one-chambered, the fornix ventriculi is above the oepning between the esophagus and the stomach. The borderline fold begins on the right wall of the esophagus and then turns to the left.* Of all the forms of Cricetinae studied Sigmodon has the lowest degree of development of the corneous epithelium in the stomach. But the stomach structure of Sigmodon is similar to that of Oryzomys, Nectomys and Akodon and differs greatly from the other members of the family Cricetidae.

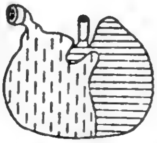


Fig. 110: Stomach structure of the hamsters, Sigmodon hispidus Say et Ord. From Vorontsov (1962b).

Neotomodon and Neotoma attain a considerable degree of specialization for the cellulose mode of nutrition. In Neotoma albigula (Fig. 111, a) and Neotomodon alstoni (see Fig. 111, c) the fornix is very eminent, the corneous epithelium spreads along the entire phloric portion of the stomach and the glands remain only on the bottom right half of the stomach. The left and right halves of the stomach are separated by a shallow isthmus marking the tendency for the formation of separate portions, the stomach, however, remaining one-chambered. The region where fundic glands are concentrated is a little less in Neotomodon than in Neotoma. Plica praephalorica is developed in Neotomodon and marks the tendency for the conversion of the pyloric portion of the stomach into an independent portion,

---

* *Earlier, the author has indicated erroneously that the glandular lining of the stomach in Sigmodon separates the corneous epithelium of esophagus from the corneous epithelium of the stomach. The description and figures (1 and 2) are based on the study of the badly fixed specimens preserved in spirit for more than 110 years. When new specimens were obtained, it was clear that the description made in the year 1957 was inaccurate. This mistake was rectified in the subsequent work (Vorontsov, 1962 b).*

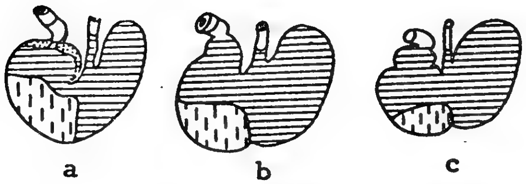


Fig. 111: Stomach structure of a few forms of Neotomini Original.
(a) Neotoma albigula Hartley; (b) Neotoma floridana Ord.;
(c) Neotomodon alstoni Merriam.

which, however, is less developed in this species than in Peromyseus. californicus.

The structure of the stomach in Cricetinae is quite diverse. Forms with primitive sacciform stomach with highly-developed glandular epithelium, adapted mostly for proetin nutrition (Oryzomys), species with two-chambered stomach of the type of Cricetus, adapted for the mixed type of nutrition and finally, certain hamsters (Phodopus roborovskii, Peromyscus californicus, Nestomodon and Neotoma), with their stomach structure highly adapted for the cellulose type of nutrition are found among the members of this subfamily. On the whole, the hamster tribes are clearly separated from one another in the plan of their stomach structure.

On the basis of the study on the stomach structure the following groups may be distinguished :

I. Oryzomys, Neotomys, Akodon, Sigmodon.

II. Calomyscus, Baiomys, Reithrodontomys, Peromyscus

III. Neotoma, Neotomodon;

IV. Oxymycterus;

V. Onychomys

VI. Cricetulus, Cricetus, Mesocricetus, Phodopus;

VII. Mystromys

Homologous sets of changes in the structure of the stomach associated with the process of adaptation to the cellulose type of nutrition taking place independently in the majority of these tribes, are observed within each of these groups, corresponding generally to the tribes classified by us. Members of the various tribes (Peromyscus maniculatus and Neotoma floridana) may be on the same levels of specialization and have similar stomach structure in the general basic plan of the structure. It should be noted that such a similarity is more frequently met with in the structure of the dental system than that of the stomach.

Along with the basic tendency for transformation of the stomach, associated with the transformation from the protein to the cellulose type of nutrition, there exists yet another tendency i.e., the tendency for transformation into insectivorous mode of nutrition, connected with the formation of the glandular diverticulum ventriculi of the stomach (Oxymycterus, Onychomys). The modes of transformation of stomach associated with the transition to the insectivorous type of nutrition will be dealt with in the next section.

5. Data on the Ontogenesis of the Stomach in Onychomys Modes of Food specialization and Secondary Development of Protein Nutrition in Insectivorous Hamsters.

How did the diverticulum ventriculus of the stomach develop in the insectivorous hamsters ? Studies of the embryonic development of the stomach of Onychomys (Fig. 112) give an answer to this question.

We had embryos of On. leucogaster representing three different stages of development as presented by Dr. Pfeifer of the USA. They were obtained one and a half month after catching and fixation; fixation of embryos was excellent.

First stage of embryos : body length* 17.4 - 17.6 mm, stomach length - 4.4 mm. Fornix ventriculi already expressed and stomach divided into two subsections. Corneous epithelium

---

* *Body length of embryos was measured by their projection in the natural position in the uterus. Thus, this is less than the actual body length.*

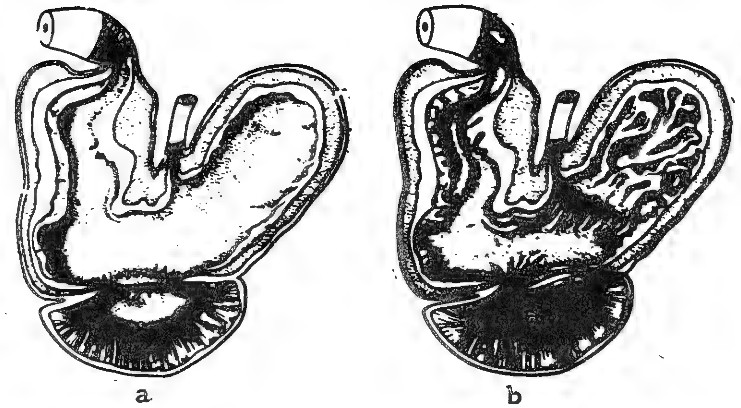


Fig. 112: Development of the glandular diverticulum ventriculus in insectivorous hamsters Onychomys leucogaster Wied. (a) stomach structure of the embryo. The glandular portion is only faintly separated from the corneous portions, the form of the stomach reminds us of the stomachs of Peromyscus and Microtus; (b) stomach structure of a fully grown individual. The glandular diverticulum ventriculus is a complex gland into which the food does not enter, the gastric juice is secreted into the corneous portion of the stomach. From Vorontsov (1962 b).

lines the entire left half of the stomach as well as its pyloric portion. Glands (of fundus only) are concentrated at the fundus ventriculi. The corneous epithelium forms many well expressed folds in the forestomach. Strong hornifications in the form of ridges and corneous "teeth" in the pyloric portion are still not observed. Glandular diverticulum absent. The fundic glands are separated from the corneous epithelium by the borderline fold which is only slightly bigger than that in rodents (adult individuals) like Microtus or Peromyscus. The form of the stomach of Onychomys embryo of this stage reminds us of the stomach of the adult Peromyscus leucopus.

The second stage of the development of embryos (body length 19.0 mm and stomach length 4.7 mm) does not differ much from the preceding one. The borderline fold is more developed than in the preceding stage, However, the fundic gland region is still not separated from the corneous portion.

In the third embryonic stage (body length 27.8 mm and stomach length 5.9 mm) the stomach has externally the same form as in the previous stage, differing only very little from the adult stomach. The borderline fold gets thickened and covers half the entrance into the region of glandular epithelium. The fundic glands which extend hither from the fundic gland region are located along the lower side of the thickened borderline fold. The upper side of the boundary fold is lined with corneous epithelium. The muscular layer which forms the sphincter of the diverticulum in adults penetrates into the boundary fold. The third stage studied by us correspond to the embryos 1-3 days before birth. Thus the final formation of the diverticulum ventriculus in the stomach of Onychomys takes place fairly late and it indicates the relatively insignificant growth of this adaptation.

Consequently, the glandular diverticulum of the stomach of Onychomys (and there are reasons to suggest that this is observed even in the ontogenesis of Oxymycetrus) develops by the growth of the boundary fold and spreading of fundic glands on its lower surface. Thus, the development of adaptation for protein nutrition in the insectivorous hamsters, Onychomys and Oxymycetrus has different basis than that in the seed-eating hamsters of the type of Oryzomys.

The stomach with the extreme distribution of the corneous equithelium and reduction of glands to a small area at the bottom i.e., stomach which has a form adapted to protein nutrition is the initial form which the stomach of insectivorous hamsters, Oxymycterus and Onychomys are formed. Hence, a very important conclusion may be drawn that the protein nutrition in insectivorous hamsters is a later acquisition and that these forms have changed over to protein nutrition secondarily.

Let us remind you that the original form of the stomach of Murodidea is a sacciform structure with preferential development of glandular epithelium. Then the process of displacement of the glandular epithelium by the corneous epithelium starts in the different groups of Muridae independent of one another. Besides this only a few extreme types of hamsters (Peromyscus, Neotoma, Phodopus robovskii) have attained that stage in which the glands are restricted only to a small portion of the fundus ventriculi. This is that form of the stomach which is more adapted to processing the cellulose food substance and is the base from which the stomach of insectivorous hamsters has developed as a result of a number of secondary transformations.

Development of the stomach in insectivorous hamsters is a clear example of the law of irreversibility of evolution established by L. Dollo more than half a century ago.

The question whether there is a secondary change over to protein nutrition in insectivorous hamsters and formation of glandular diverticulum as "a game of chance", i.e., peculiar secondary adaptation of two or three genera of hamsters or even the really insectivorous type* of nutrition cannot arise on the basis of the primary stomach (adapted to protein nutrition) or seed-eating hamsters. The last hypothesis, which is paradoxical at the first sight, is apparently true. Let us remember that the forms of stomach in hamsters feeding on mostly or exclusively on insects have a corneous lining for a major portion of the stomach and a separate glandular diverticulum whose glands produce gastric juice. The thick corneous lining protects the stomach wall from solid chitinous parts of insects. The stomach wall, as a rule, has powerful horny projections ("teeth"), that may additionally grind chitin. A similar stomach structure is found in Myrmecophaga jubata (Xenarthra) Manis javanica (Pholidota) and Onychomys and Oxymycterus (Rodentia) described here. It is interesting to note that the diverticulum ventriculus is not developed in all the pangolins; thus, Manis longicaudata (Pernkopf 1937) has a one-chambered stomach, where the glandular field separated by the boundary fold has not yet developed into a diverticulum.

Development of the glandular diverticulum in different groups of true insectivorous mammals suggests that the stomach of Manis javanica meets the specific functional requirements, i.e., maximum development of glands producing proteolytic enzymes with maximum protection of stomach from rough chitinous remains of insects.

It follows from the above that the stomach of the primitive seed-eating hamsters, in spite of the well developed glandular areas, cannot be taken as the morphological base from which the stomach of true insectivorous hamsters would have evolved, because of the poorly protected inner stomach wall. On the

---

** In ecology the term insectivorous type of nutrition means feeding not only on insects but also on molluses and worms.*

contrary the stomach of seed-eating rodents with well developed corneous lining (but with reduced glandular layer) was the base from where the stomach of Oxymycterus and Onychomys has developed. Thus, the true insectivorous type of nutrition could develop only (or mostly) in forms which are more or less adapted earlier to cellulose nutrition in its stomach structure.

Thus, in Cricetinae along with the basic trend of transformation of the digestive system from protein to cellulose type of nutrition individual forms may secondarily change over from cellulose to protein type of nutrition, thereby solving the old functional problem (of proteolysis) on a different morphological basis. The mode of development of insectivorous nutrition in Onychomys and Oxymycterus is one of the examples where the dialectical law of "negation of negation" and "spiral" development manifest themselves.

6. The Structure of Stomach in Certain Rodents belonging to Cricetinae (Nesomyinae, Myospalacinae and Lophiomyidae)

a. Nesomyinae

Adaptive radiation in the structure of the stomach of the Madagascar Nesomyinae is quite wide, although all members of this group retain the general plan of the stomach structure of Muroidea i.e., with two types of epithelium (Fig. 113).

By its structure* and degree of specialization for cellulose nutrition, the stomach of Gymnuromys roberti (see Fig. 113, a) highly resembles Oryzomys couesi. This one-chambered structure has a short fornix and a more or less equal distribution of corneous and glandular epithelia.

The stomach of Macrotarsomys bastardi and M. ingens (see Fig. 113b and c) do not differ structurally much from that of Gymnuromys, but the specialization for cellulose nutrition has advanced a little further in these species than in Gymnuromys, which is expressed by a slightly higher degree of penetration of the corneous epithelium to the left half of the stomach.

According to the figure and description given by Tullberg (1899).

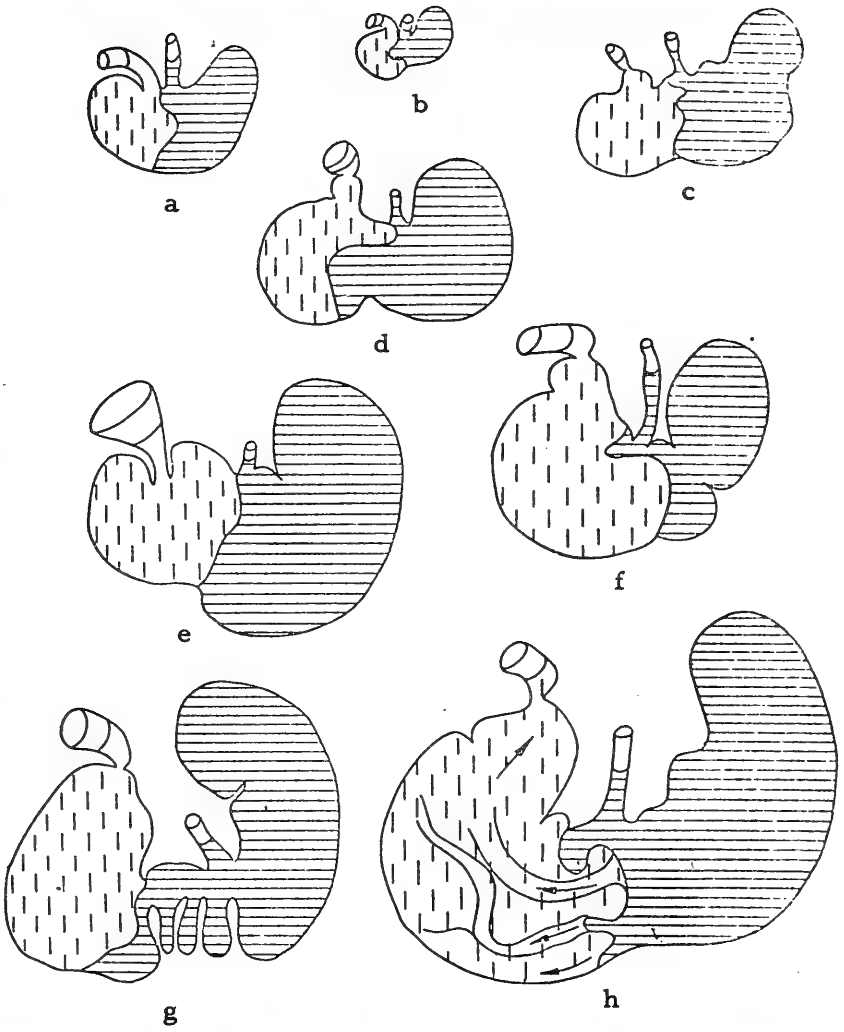


Fig. 113: Structure of the stomach in the Madgascar Nesomyinae. (a) according to Tullberg (1889); (b to h) Original (a - Gymnuromys roberti F. Major; (b) Macrotarsomys bastardi Milne - Edw. et Grandid; (c) Macrotarsomys ingens Petter; (d) Eliurus tanala F. Major; (e) Eliurus myoxinus; (f) Brachyuromys betsileonsis Bartl; (g) Brachytarsomys albicauda Gunth; and (h) Hypogeomys antimena.

The stomach structure of Eliurus tanala and El. myoxinus (see Fig. 113 d and e) is close to that of these species. However, fornix ventriculi is more prominent. In spite of the similarity in the position of their border-line fold with that of *Macrotarsomys*, the region of distribution of the corneous epithelium is relatively more than that of the glandular epithelium. In *El. myoxinus*, there is an isthmus separating the upper part of the left half of the stomach from the remaining corneous portion. In *E. tanala* the well-developed borderline fold has a fimbria of the lobes, reaching a height of 2 mm and increasing the degree of separation of the corneous subsection of the stomach from the glandular. It is not the fundus but the pyloric glands which attain the maximum development in the right half of the stomach. In both the species the stomach surface is lined with well expressed ridges in the pyloric region. This considerably increases the area lined with pyloric glands. It is as if the region of development of the pyloric sphincter musculature is drawn out into the stomach thereby forming an annular blind fornix of the stomach, where pyloric glands develop. The corneous epithelium extend a little to the right half of the stomach along the lesser curvature.

Basically, the morphology of the stomach of *Brachyuromys betsileoensis* (see Fig. 113, f) belongs to the group of species described above. High development of plica cardiaca considerably separates the blind sac of the left half of the stomach. Plica praepylorica is well marked and it separates the pyloric portion of the stoma from its remaining glandular portion. The ratio of the glandular and the corneous epithelia is similar to that in *Macrotarsomys* and *Eliurus*. Unfortunately, we did not study the internal organs of a close subgenus and species, *Brachyuromys ramirohitra*; but a comparison with *Br. betsileoensis* would have been particularly interesting.

Brachytarsomys albicaudata (see Fig. 113, g) which among the forms of Nesomyinae attains the maximum degree of specialization of stomach for the cellulose type of nutrition differs considerably from the above described species in its stomach structure. The fornix of the stomach has attained an unprecedented development not only among the forms of Nesomyinae but also among those of Cricetinae, Gerbillinae and even Microtinae. The left part of the stomach lined with the corneous epithelium is well developed. There is a deep notch separating the upper one-third of the corneous forestomach into a blind sac on its upper part, on the lesser curvature side. At the portion where esophagus opens into the stomach, the stomach is constricted f for a considerable distance and this leads to an almost complete separation of the right and left halves of the stomach.

Thus Brachytarsomys has a two-chambered stomach like the present Cricetini. There are four deep notches and folds having the form of the lobes of omasum of ruminants on the side of the greater curvature in the isthmus region. Corneous epithelium penetrates into the right half of the stomach along the lesser and particularly, along the greater curvature.

The structure of the glandular portion of the stomach is also equally complicated. The region where fundic glands are distributed is large, and stretches not only along the fundus but also along the lesser curvature of the stomach. The surface of the glandular portion of the stomach is complicated by folds increasing the area of distribution of glands, especially in the pyloric region. The deep fold at the beginning of the pyloric sphincter clearly separates the pylorus from the remaining glandular parts. In fact, the pylorus is separated into an independent chamber. However, the pyloric glands are distributed not only in the pylorus but also in the region of the lesser curvature in the penultimate chamber of the stomach. The stomach of Brachytarsomys may be considered four-chambered, where the first chamber forms an enormous corneous "rumen", second small chamber "omasum", also lined with corneous epithelium, third large chamber, the region of distribution of fundus and a portion of the pyloric glands and the fourth small chamber-pylorus, lined only with pyloric glands.

The stomach structure of the inadequately studied Madagascar forms of Cricetinae, Hypogeomys antimena (See Fig. 113, h and 114) is very peculiar. The stomach is two-chambered. The corneous portion of the stomach is separated from the glandular not so much by the development of a constriction more right of the esophagus and plica angularis as by the formation of powerful annular valve of the borderline fold. The corneous, forestomach is well developed, its inner lining has strong corneous folds and the upper part of the forestomach on the lesser curvature side is set apart by a notch separating the blind sac. The borderline

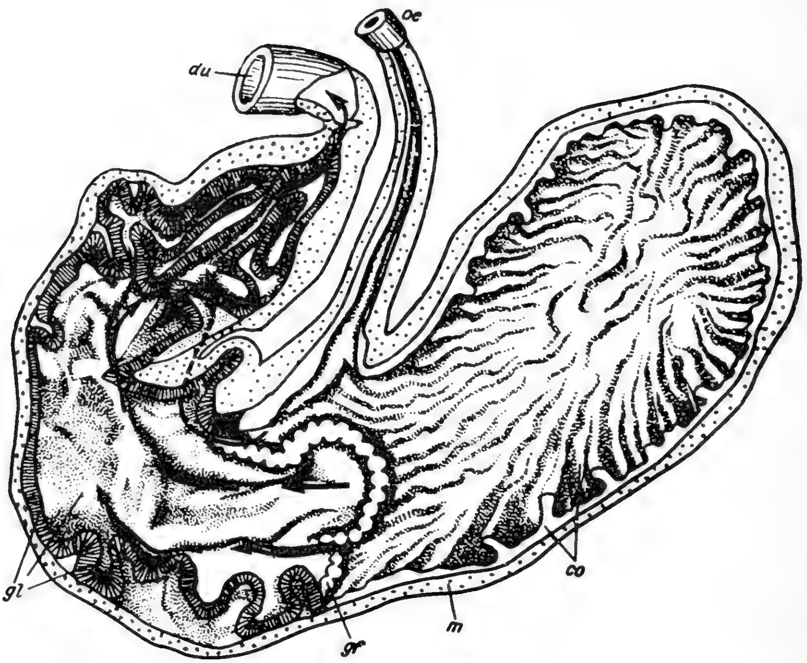


Fig. 114: Structure of the stomach in the Madagascar Hypogeomys antimena. For legends see Fig. 96.

fold runs along the lesser curvature upto plica angularis, whereas at the middle portion it runs on a level with the esophagus and at the bottom, in the greater curvature the region stretches a little into the right half of the stomach. The borderline fold along the lateral wall attains a height of up to 5-7 mm, while the entire width of the isthmus of the stomach is only 10-12 mm. It may be noted that the borderline fold in the isthmus region has three dilations formed at the place where the borderline fold is not so high. The first of these dilatations is near the lesser curvature at the place where the corneous epithelium penetrates into the right half of the stomach, the second, more or less in the glandular epithelium and the borderline penetrates deepest into the left glandular part of the stomach and the third one is near the fundus ventriculi in the greater curvature region where the second zone of penetration of the corneous epithelium to the right half of the stomach is located.

The grooves described above lead into the right glandular portion of the stomach whose structure is very remarkable. The entire right half of the stomach is formed by thick folds covered with well developed fundus and pyloric glands. These folds, almost connected with each other, sometimes interlocking together thereby separating the glandular portion of the stomach. In fact they divide the glandular portion of the stomach into several separate chambers, pockets and diverticula.

The lower groove of the borderline fold leads the food flow to the region of the fundus glands. The degree of their development is fully comparable with the glandular diverticulum of Onychomys and Oxymycterus. At the top, the region of distribution (more precisely the zone of exclusive development) of the fundic glands is limited by thick folds which hang down convergingly from the dorsal and the ventral sides of the stomach. These folds prevent the entry of food upwards, where the middle groove is extended. The food mass which has entered the fundic gland region through the lower groove is separated immediately after the borderline fold into two canals - ventrofundal (I) and dorsofundal (II) by an outgrowth of the fundic gland region of the stomach. This outgrowth has on its upper right hand side a small aperture, leading into a closed, separate cavity - the glandular diverticulum (III). It is not homologous with the glandular diverticuli of stomach of Onychomys and Oxymycterus, as it is formed not from the thick corneous borderline fold, but owing to the joining of the edges of the paired folds arising from the fundic gland region of the stomach and lined with the glandular epithelium. The aperture of the diverticulum from which gastric juice is secreted is situated at the point where the flow of food particles is divided into ventro and dorsofundal, where the food mass is acted upon by the first portions of, probably, the highly concentrated gastric juice. The food which has entered the lateral canals is also split up under the action of the gastric juice secreted by the fundic glands as well as the secretions from the diverticulum. The food as it comes out of these paired canals meets the fold on the ventral side. As a result of this the food particles coming out of the ventrofundal canal gets diverted to the dorsal wall of the stomach where it gets mixed with the mass coming out of the dorsofundal canal. This region (IV) situated along the greater curvature of the stomach above its fundic gland region, is also lined with fundic glands. There is a dilatation almost in closed folds limiting the region of fundic glands on the dorsal side of the stomach below the place where the stomach gets converted into duodenum. Through the dilatation the food enters the pylorus, also subdivided by folds and outgrowths, lined with pyloric glands, forming pouch-like cavities and grooves. Thanks to the thick outgrowth of the pylorus, the food entering the pylorus from the lower and middle grooves, moves mostly along the canal arranged along the greater curvature of the stomach (VII).

The middle groove of the borderline fold, entering into the glandular portion of the stomach, soon gets divided into paired dorsal (V) and ventral (VI) canals. The region of these canals is lined mostly with pyloric and at some places with cardial glands. There is a small funnel-shaped recess leading to the unpaired pocket (IV) lined with fundic glands beyond the region of diverticulum in the folds separating the middle digestive tract from the lower. However, a major part of the food flowing from the middle grooves enters directly into the pylorus, where it gets mixed with the food particles of the lower grooves coming out of the IV section and enters the pyloric canal (VII) running along the greater curvature of the stomach.

Finally, the food particles, falling into the right half of the stomach through the upper groove, after plica angularis, are directed by the thick fold hanging from the lesser curvature, into the paired ventral and dorsal grooves (VIII and IX). Passing smoothly through these grooves, the food particles fall into the paired canals, running along the lesser curvature of the pylorus (X and XI), from where the food enters the intestine. The last upper tract passes along those portions of the stomach, that are completely devoid of fundic glands. Here, the proteins may be subjected only to a weak splitting action by the enzymes of the pyloric glands.

Apparently the upper alimentary tract serves as a canal for protein-free food and the middle one - for mixed food, whereas the lower one serves as a canal for protein food. A similar hypothesis based on the undisputed "selectivity" of the separate sections of the stomach for biochemically different food masses has already been mentioned.

The extremely complex and peculiar structure of the stomach of *Hypogeomys* helps us consider it as a multifunctional formation adapted for a highly perfect treatment of protein as well as for cellulose food. It is highly probable that *Hypogeomys* feeds on small invertebrates for a considerable part of the year. The remarkable features of the stomach structure of this species should draw the attention of the ecologists for the study of nutrition of this relict form.

The special features of the stomach structure in Nesomyinae speak of the remarkable heterogeneity of this group. However, the remarkable features of the stomach structure in *Brochytarsomys*, makes this species of Nesomyinae somewhat closer to Microtinae. Similarity of *Macrotarsomys*, *Gymnuromys*, *Eliurus* and *Brachyuromys* with Cricetinae, Microtinae, Gerbillinae and Murinae in their stomach structure does not give any basis to group any one of these species with any of the above mentioned subfamilies.

According to the stomach structure Nesomyinae is divided into three groups, clearly distinguished from one another

I. *Gymnuromys roberti*; *Macrotarsomys bastardi*, *M. ingens*, *Eliurus tanala*, *El. myoxinus*, *Branchyuromys betsileoensis*.

II. *Brachytarsomys albicauda* and

III. *Hypogeomys antimena*.

b. Myospalacinae.

Stomach structure of zokors is very peculiar and it compels us to separate them from Microtinae, Cricetinae and Spalacidae to which they are related by many authors. The stomach is strictly one-chambered (unlike Cricetini and Microtinae) and fornix ventriculi is raised. The inner surface of the stomach is clearly divided, according to the tissues lining it, into three portions. Blind sac and fornix are lined with multiple petaloid villi reaching a height of 5-7 mm. The histological structure of the villi was not studied owing to the unsatisfactory fixing.

Macerated vegetative parts of plants and very frequently hair are found in the villose portion of the stomach.

The villose portion gets sharply torn in the left part of the esophagus and the entire cardial portion is lined with corneous epithelium common in the structure of Muroidea. The corneous epithelium has the form of a sector with its center at the place where the esophagus opens into the stomach and with an arch in the form of a greater curvature (Fig. 115).

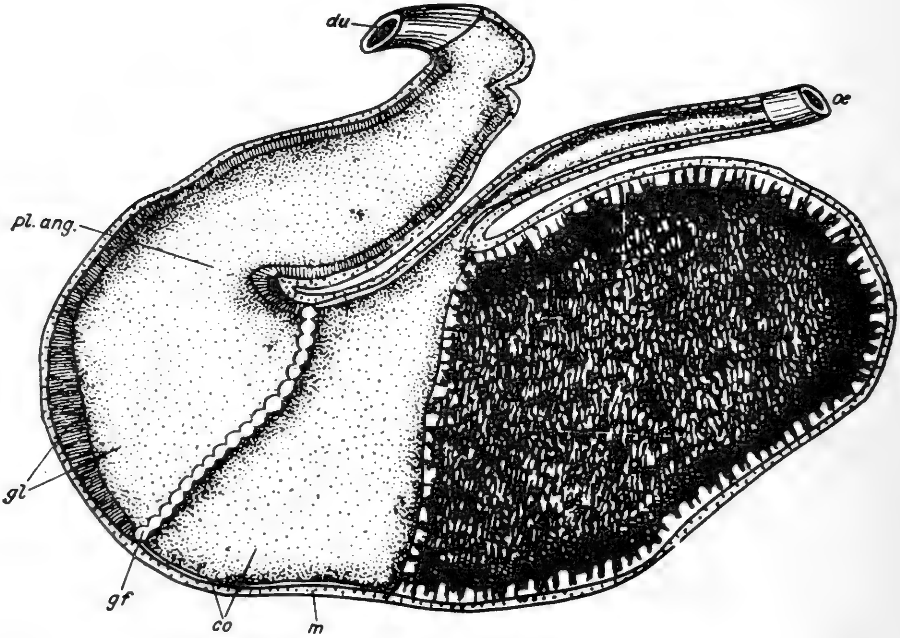


Fig. 115: Structure of the stomach of the zokor Myospalax myospalax Laxmann. Original.

The borderline fold extends on the right side of the esophagus. The usual glandular portion stretches behind this. The deep plica praepylorica on the lesser curvature side partially separates the pylorus from the fundus.

Presence of a villose portion in the stomach of Myospalax is a peculiar feature of this rodent. Well developed villi considerably increases the area of the fermenting-macerating cavity whose function is carried out by the blind sac of the corneous forestomach.

In its stomach structure Myospalax sharply differs from voles, hamsters and spalacids. However, the development of corneous epithelium in the stomach is a feature peculiar to Muroidea. This, undoubtedly, speaks of the affinity of zokors to Muroidea and suggests us to disagree with the opinion of P.P. Gambaryan (in litt.) that zokor does not even belong to Myomorpha.

The stomach structure of the zokor was first described by Milne-Edwards (1868-1874) in a monograph, in which a good figure of the stomach of Myospalax fontanieri was given. From this it is clear that the blind sac is lined with corneous epithelium. However, neither the morphologists specially describing the stomach structure of rodents (Oppel, 1896 and Pernkopf, 1937), nor the zoologists (Wings, 1924; Hinton, 1926; Ognev, 1947, 1948; Vinogradov and Gramov, 1952) who have made use of his work for describing the characteristics of zokors have paid attention to the indications of Milne-Edwards.

c. Lophiomyidae

The stomach of Lophiomys was described by Milne-Edwards (1867) who determined this species for the first time and grouped it in a separate family, Lophiomyidae. Figures of stomach not dissected from the dorsal side (Pl. VIII, 6), and the inner surface of the stomach (Pl. IX, 3, 4) are given in the work of Milne-Edwards. It is clear from the description and figures that forms of Lophiomys have a five-chambered stomach (an instance unprecedented in the rodents). It is surprising that such a feature in the stomach structure of Lophiomys had escaped the attention of taxonomists who included Lophiomys in different groups of rodents, and the morphologists, who studied the morphology of the stomach of mammals (Pernkopf, 1937).

The stomach of Lophiomys imhausi (Fig. 116, g) is extremely complicated. The esophagus opens into a U-shaped corneous forestomach which stretches not only to the left of the gullet where there is a short fornix ventriculi, but also to the

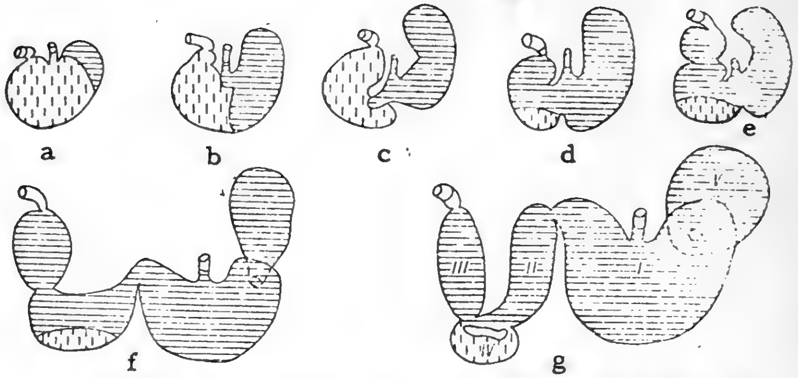


Fig. 116: Comparative-anatomical representation of some forms of Muroidea, that illustrates the possible stages towards the development of a five-chambered stomach in Lophiomys Original. (a) Nesokia indica Gray. One-chambered combined stomach with predominant development of the glandular epithelium; (b) Oryzomys couesi Alston. One-chambered stomach with more or less equal development of corneous and glandular eipthelia; (c) Cricetus cricetus L. Two-chambered stomach with more or less equal development of the corneous and glandular epithelia; (d) Phodopus robonovskii Satunin. Two-chambered stomach with predominant development of the corneous epithelium; (e) Peromyscus californicus Gamb. The stomach is almost three-chambered with the predominant development of the corneous epithelium; (f) Hypothetical ancestral form of Lophiomys; (g) Stomach structure of Lophiomys imhausi Milne-Edw. I - V portions of stomach (see text).

right of gullet where it gives rise to a secondary fornix ventriculi. Beyond the secondary fornix there is a sharp constriction which leads to the next descending portion of the stomach (II) also lined with corneous epithelium. A well developed alimentary canal along which food may enter directly into the descending portion passing through the forestomach stretches from the lesser curvature of the stomach down to the second portion of the stomach has a deep isthmus beyond which starts the ascending portion of the stomach (III) also lined with corneous epithelium. The duodenum begins from this ascending portion.

On the dorsal side of the corneous forestomach there is a dilatation leading to an isolated blind sac, i.e., corneous diverticulum ventriculus of the stomach (V), analogous to a similar formation in swine (Sus). Thus, the stomach of *Lophiomys* has four chambers lined with corneous epithelium.

The absolutely corneous forestomach (I chamber) is homologous to the corneous forestomach of the present hamsters and voles. However, unlike these forms Lophiomys has a part of its stomach, situated between the esophagus and plica angularis and isthmus, considerably drawn out and bent forward and upward.

The isthmus between the corneous forestomach (I) and the descending portion (II) of stomach is homologous to the common isthmus in the two-chambered stomach of the present hamsters and voles.

The descending portion (II) of the stomach in Lophiomys, is apparently homologous to the corneous part of the fundic gland region situated beyond the plica angularis and isthmus. and anterior to plica praephylorica in such forms as Peromyscus californicus and Prometheomys schaposchnikovi.

The isthmus between the descending (II) and the ascending (III) portions of the stomach is apparently homologous to plica praepylorica and the ascending part of the stomach of Lophiomys is homologous to the pyloric portion of the stomach in Peromyscus californicus and Prometheomys schaposchnikovi.

There is a formation similar to the corneous diverticulum ventriculus of the stomach (V) of Lophiomys in certain hamsters and gerbils thanks to the considerable development of plica postcardiaca, which constricts the blind sac of the forestomach. However, this blind sac is not arranged asymmetrically in gerbils, certain voles and hamsters, unlike in Lophiomys. The corneous diverticulum ventriculi and isthmus, separating this chamber from the forestomach in Lophiomys are not homologous to the blind sacs of the stomachs in hamsters, gerbils and voles, and isthmuses, separating these sacs from the forestomach.

There is a small orifice leading into a completely isolated glandular diverticulum ventriculi (IV) lined with fundic glands on the wall of the descending portion (II) close to its base on the greater curvature side. The opening of the glandular diverticulum ventriculi is quite close to the place of termination of the esophageal groove. The opening leading into the glandular diverticulum ventriculi of the stomach in Lophiomys is so small that food does not pass into this area and the protein foods are treated with the gastric juice secreted by the glandular diverticulum ventriculi, which in fact is a gigantic gland. in the fundic gland region of II and III chambers of the stomach (lined with corneous epithelium) into which it is secreted. However, the relative size of the glandular diverticulum ventriculi of Lophiomys is negligible in comparison with the analogous formations in the stomach of Onychomys and Oxymycterus.

The ecology of Lophiomys is not studied completely. We may assume, on the basis of the stomach structure, that cellulose food has an exclusive role in the nutrition of this species.

The five-chambered structure of the stomach in Lophiomys represents the extreme (among all the rodents hitherto studied) degree of adaptation to cellulose nutrition.

It is apparent that in their phylogeny Lophiomyidae should have passed through several complicated stages of stomach which may be illustrated by the comparative anatomical series from Nesokia indica to Oryzomys couesi, then to Cricetomys gambianus and Cricetus cricetus to Phodopus roborovskii, to Peromyscus californicus and Prometheomys schaposchnikovi (the last two forms already have a more or less three-chambered stomach). Displacement of portions II and III of the stomach with respect to one another and the beginning of the formation of the glandular diverticulum into the IV-chamber and blind sac into a corneous diverticulum i.e., the V chamber of the stomach the V chamber of the stomach probably marked the next stage in the transformation of the stomach in the predecessors of Lophiomyidae. This stage has not yet been discovered among the modern rodents. However it is undoubtful that Lophiomyidae should have passed through this stage (see Fig. 16f).

The truly five-chambered structure of the stomach and other features in the structure of the skeleton and respiratory organs clearly distinguish Lophiomys from Cricetidae. The classification of Lophiomys into a separate family Lophiomyidae as proposed early by Milne-Edwards, and later by Tullberg (1899) and Ellerman (1940 and 1941) is fully valid from this point of view. It should be noted that Milne-Edwards' comparative anatomical reasons for separating *Lophiomys* were incomparably more profound than those of Winge (1924) Stehlian and Schaub (1950), Grasse et Dekeyser (1955) and other authors who related *Lophiomys* to Cricetinae and even to the tribe Cricetini.

The combined type of stomach structure - presence of corneous as well as glandular linings of the stomach - along with various other characteristics enable us to include Lophimyidae in the subfamily Muroidae in which these extremely peculiar rodents of Abyssinian plateau occupy a special position.

7. The Structure and Trends of Stomach Specialization in Some mainly, Myomorph Rodents (Gerbillinae, Microtinae, Muridae, Spalacidae, Gliroidea, Dipodoidea and Bathyergoidea) - Homologous and Parallel Series of Variability in the Rodent Stomach Structure.

A basic trend in stomach specialization is the transformation of the one-chambered stomach into two- three- and even five-chambered one and distribution of corneous epithelium, displacing the cardial pyloric and, partially, fundic glands, characteristic not only of Cricetinae, Nesomyinae and Lophiomyidae but also the entire Muroidae. However, the range of variability of stomach is quite different for different groups.

In Gerbillinae (Fig. 117) mostly the single chambered stomach is prevalent. All members of Gerbillinae have a one-chambered stomach with more or less equal development of corneous and glandular portions. But even among the members of this extremely homogeneous subfamily of rodents, there may be forms with a stomach structure adapted in different degree to a mixed (with considerable fractions of cellulose food) type of nutrition. Fornix ventriculi and the isthmus separating the left corneous half of the stomach from the right glandular half are rather poorly marked in *Gerbillus pyramidum* and *Tatera indica* and in *Gerbillus dasyurus* the plica postcardiaca separates the blind sac of the corneous forestomach into an almost independent chamber. The isthmus between the corneous and the glandular portions of the stomach is clearly expressed in members of the genera *Meriones*, *Psammomys*, *Brachiones* and *Rhombomys*, but the process of extension of the corneous

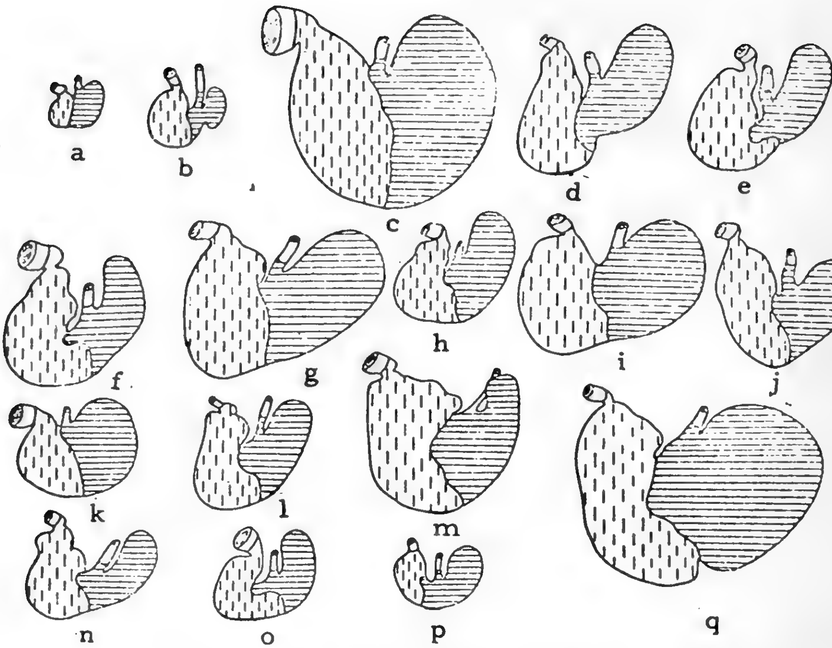


Fig. 117: Structure of stomach in Gerbillinae. Ventral view, schematic. Stomach structure varies less in this subfamily. A tendency to increase the area occupied by the corneous epithelium is observed and the stomach begins separated into two chambers. From Vorontsov (1962 b). (a) Gerbillus pyramidum Goeffr.; (b) Gerbillus dasyurus simoni Lataste; (c) Tatera indica Hardwicke; (d) Meriones (Paramerones) persicus Blanf; (e) Meriones (s. str.) vinogradovi Heptner.; (f) Meriones (s. str.) tamariscinus Pall.; (g) Meriones (Pallasiomys) unguiculaius Milne-Edw.; (h) Meriones (Pallasiomys) meridianus Pall.; (i) Meriones (Pallasiomys) shawi Duvernoy; (j) Meriones (Pallasiomys) tristrami Thom.; (k) Meriones (Pallasiomys) libycus Licht.; (l) Meriones (Pallasiomys) erythrourus Gray.; (m) Meriones (Pallasiomys) crassus charon Thom.; (n) Meriones (Pallasiomys) crassus swinhoei Scully; (o) Psammomys obesus Cretzsch.; (p) Brachiones przewalskii Büchner; (q) Rhombomys opimus Licht.

epithelium into the right half begins in Mer. vinogradovi, M. tristrami and M. crassus. In these species the fornix ventriculi attains a considerable height and the stomach is divided into separate portions -right and left halves of the stomach fairly clearly. Thus, a number of specializations in the stomach structure for mixed and cellulose type of nutrition are also observed among the members of Gerbillinae. The stomach in Gerbillinae represents by and large the stomach of seed-eating forms and those with mixed type of nutrition. Not even one of the species of *Gerbillinae* studied is adapted mostly or exclusively for cellulose nutrition. By their stomach structure (as well as by their basic ecological features) gerbils form a surprisingly homogeneous group of rodents. In the stomach structure of Gerbils there is not a single feature which separates them from Cricetinae, Microtinae and Muridae.

Diversity in the stomach structure is much more in Microtinae (Fig. 118). Certain forms of *Fibrini*: *Dolomys bogdanovi*, *Clethrionomys glareolus* and certain forms of *Microtini-Arvicola terrestria*, *Altiocola (Aschizomys) lemminus*, *Alt.* (s. str.) *argentatus*, *Lagurus luteus*, *Lag. lagurus*, have a stomach with more or less equally developed corneous and glandular epithelia; the stomach in all the voles are two-chambered: left chamber is always corneous while the right chamber may be both corneous and mixed (glandulo - corneous). In most of the voles the horny epithelium extends a little into the right half of the stomach. This process of extension of the corneous epithelium and its displacement by pyloric glands is observed not only in different tribes of voles, Fibrini, Microtini and Ellobiini but also among the different genera such as *Clethrionomys* and *Ellobius*.

Maximum diversity in the degree of development of the corneous and glandular epithelia is observed among the members of *Fibrini*. The stomach structure of *Dolomys bogdanovi* resembles that of the hamsters, like *Baiomys musculus*, *Calomyscus bailwardi* or *Reithrodontomys megalotis*; the isthmus is not so well expressed as in *Cricetini* and *Microtini* and the corneous epithelium extends only to a small part in the right half of the stomach. In *Clethrionomys glareolus* the stomach is clearly divided into two chambers, but the distribution of the corneous and the glandular epithelia remains the same as in *Dolomys*. In *Clethrionomys rutilus* the corneous epithelium extends into the right half of the stomach and lines the entire pyloric portion. Glands are restricted to a small area in the fundic gland region. It is paradoxical that the sharp differences in the stomach structure of *Cl. glareolus* and *Cl. rutilus* are just the opposite of the differences in their ecological species (For details see Vorontsov, 1961 b).

The stomach of Prometheomys schaposchinikovi is more specialized for cellulose nutrition not only among the members of Fibrini but also among the entire Microtinae. By its stomach structure it highly resembles Peromyscus (Haplomylomys) californicus. Plica postcardiaca (but not plica angularis as in P. californicus) separates the blind sac of the corneous forestomach to form an independent chamber, plica angularis divides the second chamber of the stomach, fundic glands are located at the bottom, the corneous epithelium runs along the lesser curvature of the chamber and the extensive pyloric portion lined with only corneous epithelium, forms a third chamber of the stomach.

The process of cornification of the pyloric portion is observed in the tribe Ellobiini. The stomach in all the species of the only genus of this tribe - Ellobius is strictly two-chambered. In Ell. lutescens the corneous epithelium extends into the pyloric portion along the lesser curvature before duodenum whereas there are pyloric glands up to the duodenum along the greater curvature. A similar stage of penetration of the corneous epithelium in to the right half of the stomach is observed very rarely as it is apparent that immediately after this stage the corneous epithelium spreads along the greater curvature and the borderline fold restricts the fundic glands to only a small portion in the fundic gland region.

Among all the species of rodents studied so far, this stage of penetration of the corneous epithelium into the pyloric portion, through which all species of Muroidea with stomach specialization for cellulose type of nutrition have passed, is found only in Ell. lutescens. In Ell. talpinus the corneous epithelium is already distributed along the entire pyloric portion. The pyloric glands separated from the corneous epithelium by a small portion of the borderline folds are restricted only to a small portion near duodenum around the pyloric sphincter. The main part of the borderline fold separates the fundic gland region from the corneous epithelium of the right half of the stomach. In Ell. talpinus the glands are distributed in a considerably larger portion on the fundic gland region (see Fig. 118 g and h).

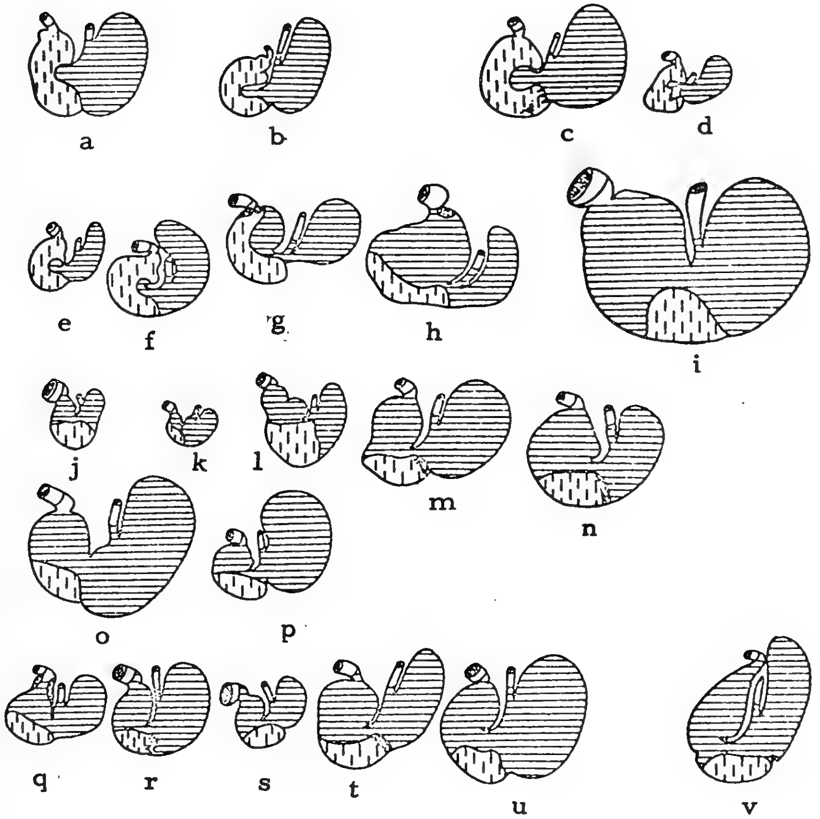


Fig. 118: Structure of the stomach in Microtinae. Ventral view, schematic. There is a tendency for the division of the stomach into two and three chambers and considerable extension of the corneous epithelium from the cardial to the pyloric portion of the stomach. The series is homologous to the series of hamsters and Gerbils. From Vorontsov (1962 b). (a) Arvicola terrestris L.; (b) Clethrionomys rufocanus Sund.; (c) Lagurus luteus Eversmann; (d) Lagurus lagurus Pall.; (e) Alticola (Aschizomys) lemminus Mill.; (f) Altiocola (s. str.) argentatus Severtzov; (g) Ellobius lutescens Thom.; (h) Ellobius talpinus Pall.; (i) Ondatra zibethica L.; (j) Myopus schisticolor Lill.; (k) Lemmus amurensis Vinogr.; (l) Lemmus obensis Brandt.; (m) Lemmus Chrysogaster J. Allen; (n) Lemmus lemmus L.; (o) Dicrostonyx torquatus Pall.; (p) Dicrostonyx hudsonicus Pall.; (q) Microtus (Chionomys) gud Satunin; (r) Microtus (Phaiomys) carruthersi Thom.; (s) Microtus (s. str.) hyperboreus Vinogr.; (t) Microtus (s. str.) ungurensis Kastschenko; (u) Microtus (s. str.) tortis Büchner; (v) Prometheomys schaposchnikovi Satunin.

Cornification of the stomach and its complete division into right and left halves takes place in the tribe Microtini also. Stomach of Arvicola terrestris is less specialized. Its division into two chambers is not so clear as in more specialized Microtini for almost the entire right half of the stomach is lined with glandular epithelium. Division of the stomach into two chambers is marked better in Lagurus luteus, Lag. lagurus, Alticola (Aschizomys)lemminus and Alticola (s. str.) argentatus than in Arv. terrestris, but here the corneous epithelium penetrates into the pyloric portion (true, into a small portion) along the lesser curvature of the stomach. The separation of the right half of the stomach from the left is more marked in the members of the genus Lagurus because of the development of crest-like, long villi, preventing the entry of food into the fundus portion, on the borderline fold in the region of the greater curvature. Members of the large genus Microtus, highly adapted to the requirements of the cellulose food are characterized by the reduction of glands to a small area on the fundus region and distribution of the corneous epithelium along the larger part of the right half of the stomach. (Microtus (s. str.) (arvalis, M. (s. str.) oeconomus, M. (s. str.) hyperboreus, M. (s. str.) agrestis, M. (s. str.) urgurensis, M. (s. str.) fortis, M. (Chionomys) gud, M. (Chionomys) nivalis and M. (Pyajomys) carruthersi have a similar stomach structure. The borderline fold in many of these species has villi similar to those developed in Lagurus in the isthmus region. The fundic glands occupy a somewhat larger portion in the stomach of Ondatra than in Microtus.

The stomach structure of Lemmini is more uniform. All the members of this tribe of voles highly adapted to cellulose nutrition are characterized by the distribution of the corneous epithelium even to the pyloric portion. A decrease in the area occupied by the fundic glands and the division of the stomach into left and right chambers are traced in Lemmini from Myopus schisticolor, Lemmus amurensis and L. obensis to Dicrostonyx husdonicus and D. torquatus through L. chrysogaster and L. lemmus.

Thus the trend in the transformation of stomach structure for better adaptability to digest cellulose food and the morphological basis for solving this problem is similar for Cricetinae, Gerbillinae and Microtinae. Hence a number of variations in the stomach structure of all the three subfamilies (and also Nesomyinae) seem to us as homologous series of hereditary variations. Let us recall that their dental system also shows a number of homologous variations.

It is remarkable that the adaptation of the stomach to cellulose nutrition in Muridae (unlike its dental system) is solved on the same hereditary basis as in Cricetidae. It is clear that veriations in the stomach structure not less than those observed among Cricetinae may be expected among the members of this largest group of rodents. Probably, examples of surprising parallelism in the stomach structure even with such abnormal forms as Mystromys and perhaps even with Onychomys as well as Oxymycterus may be found out. It is highly probable that the insectivorous rodents-African Deomys and Phillipine Rhynchomys - possess a stomach with glandular diverticulum of the type found in Onychomys. Even the simple material examined in Muridae, enables us to establish that a number of variations in the stomach structure connected with the transition to cellulose nutrition (Fig. 119) are homologous to those of Muridae.

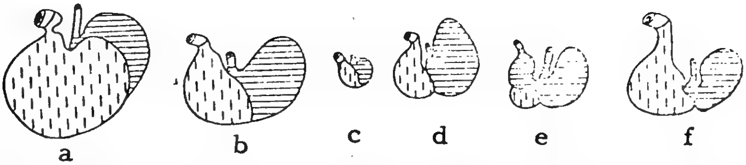


Fig. 119: Stomach structure of certain forms of Muridae. Ventral view, schematic. Tendency for transformation of the one-chambered stomach into a two-chambered one and penetration of the corneous epithelium from cardial to the pyloric portion. The series is homologous to the series of hamsters, nesomyins, gerbils and voles. b and e - after Luppa (1956) a, c, d and f - original from Vorontsov (1962 b). (a) Nesokia indica Gray; (b) Rattus norvegicus Berk.; (c) Micromys minutus Pall.; (d) Apodemus sylvaticus L.; (e) Apodemus agrarius Pall.; (f) Cricetomys gambianus.

The stomach of the bandicoot rat Nesokia indica is the least adapted to processing cellulose food. This is a one chambered scciform formation in which the corneous epithelium only starts penetrating along the greater curvature of the stomach. The stomach structure of Nesokia illustrates the very initial stages in the penetration of the corneous epithelium from esophagus to the left half of the stomach in all the members of Muroidae studied in this connection.

Further penetration of the corneous epithelium into the stomach and its distribution to the right portion of the stomach and the eminence of fornix are observed in the one-chambered stomachs of *Rattus norvegicus*, *R. rattus* and *Micromys minutus*. The structure of their stomach highly resembles the stomach structure of *Sigmodon hispidus* and *Oryzomys couesi.*

The stomach of *Apodemus sylvaticus* and *Ap. flaviocollis* divided into two considerably independent portions by the isthmus and plica angularis is the next stage in the adaptation to cellulose nutrition. The left chamber lined with the corneous epithelium is the forestomach, while the right one is lined entirely with the glandular epithelium. This stage in the transformation of the stomach of Muridae is homologous to *Reithrodontomys megalotis* and *Calomyscus bailwardi.*

In *Apodemus agrarius* the corneous epithelium lines the entire pyloric portion of the stomach, but the glands are concentrated only at the bottom of the right half of the stomach. The shallow plica praepylorica partly separates the corneous pyloric portion. Thus, the stomach of *Ap. agrarius* has three chambers partly separated from one another. But this division is not so clear as in Peromyscus (*Haplomyomys californicus*). According to the degree of reduction of the glandular epithelium and distribution of the corneous epithelium, *Ap. agrarius* is the form (among the forms of Muridae studied) most specialized for cellulose nutrition.

However, actual separation of the corneous epithelium from the glandular portion is achieved in the actually two-chambered stomach of *Cricetomys gambianus*, in which the entire right half of the stomach is lined with glandular epithelium. By its degree of specialization for cellulose nutrition the stomach structure of *Cricetomys gambianus* is homologous to the stomach of *Cricetus cricetus*.

By the stomach structure, Spalacidae also highly resembles the representatives of voles and hamsters highly adapted to cellulose nutrition. Spalax giganteus, Sp. microphthalmus and Sp. leucodon studied by us, have a similar stomach structure divided by a deep isthmus into two chambers (however, this division is not so clear as in Cricetini) and the corneous epithelium lines the entire left and a major portion of the right half of the stomach, whereas the glands are concentrated only in a small portion at the base. It is certain that Spalacidae in the process of adaptation to cellulose type of nutrition must have passed through all the stages through which the hamsters, voles and rodents have passed (or which now remain as little adapted forms).

The stomach structure of Spalax differs sharply from that of Myospalax and also other fossorial rodents (Geomys and Cryptomys). This enables us to confirm that the fossorial mode of life is not reflected on the structure of their digestive system and has not caused far reaching convergence. Consequently, the structure of the digestive system may give substantial hints at judging the genetic affinity of these forms.

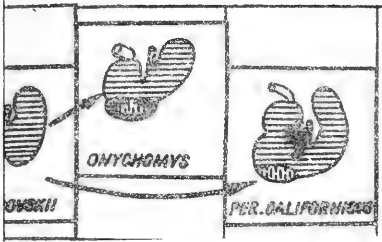
Thus, the glandular and the corneous epithelia in the stomach (which clearly distinguishes them from the remaining forms of Myomorpha), the tendency for the transformation of the one-chambered stomach into two-, three- or even five-chambered and more considerable distribution of the corneous epithelium and the replacement of the glandular epithelium by corneous epithelium, are characteristic features of Muroidea (Cricetinae, Lophiomyidae, Muridae and Spalacidae). The processes of transformation from protein to cellulose type of nutrition taking place independently in different subfamilies and tribes of this large group of mammals lead to analogous morphological variations in the stomach otherwise determined everywhere on an analogous genetic basis (on the basis of the general plan of the Muroidean stomach structure) with the development of glandular and corneous epithelia. Similar basic trend of specialization and the singular morphogenetic basis in the trend of the stomach structure of these forms lead to the fact that the homologous series of variation in the stomach structure are observed among the members of these groups. The similarity in the series of homological variability of the stomach structure of Muroidea is important and makes it possible to ascertain apriori that there existed a form with the Nesokia indica type of stomach earlier, if not at present. This suggests that there should be forms with the stomach similar to that of Oxymycterus and Onychomys among the insectivorous members of Myoidae of Austrialia, New Guinea and perhaps the South-East Asian Islands.

N. I. Vavilov's law of homologous hereditary variation series enables us not only to understand the trend of the process of adaptation but also to foretell about the morphological forms which will be created or are already created as a result of the evolution of this group by studying a relatively limited number of forms.

Homology of different organs of the same digestive system affects, at different phylogenetic levels : thus, the homological series of variability in the dental system are observed within the different families - Cricetidae (Cricetinae, Nesomyinae, Microtinae, Myospalacinae and Gerbillinae), Muridae (Murinae, Dendromyinae, Cricetomyinae, Otomyinae and Hydromyinae) and Spalacidae - but not among these families, whereas the homologous series of the variability in stomach structure is traced already within all the subfamilies of Muridae and Spalacidae (Fig. 120). Owing to the change-over from protein to cellulose type of nutrition this phenomenon of different levels of homology not only in the different organs but also in one system of organs shows that the systems based on a limited number of traits should be studied carefully. Besides the phenomenon of different levels of homology in the different organs highly facilitates the structuring of phylogenetic system, which will be dealt with in a separate chapter.

The same problem is solved in a different morphogenetic basis and therefore, differently in other rodent groups owing to the change-over from protein to cellulose type of nutrition. In a number of forms of Dipodoidea the stomach generally remains one-chambered and completely glandular.

The method of transformation of the stomach in Gliroidea (Fig. 121) is very remarkable. In Muscardinus avellanarius (an extreme member of Myoxidae) the one-chambered stomach gets converted into a two-chambered glandular-corneous stomach not by the penetration of the corneous epithelium from the esophagus into the stomach and the division of the latter into two portions


OVSKII
ONYCHOMYS
PER. CALIFORNICUS

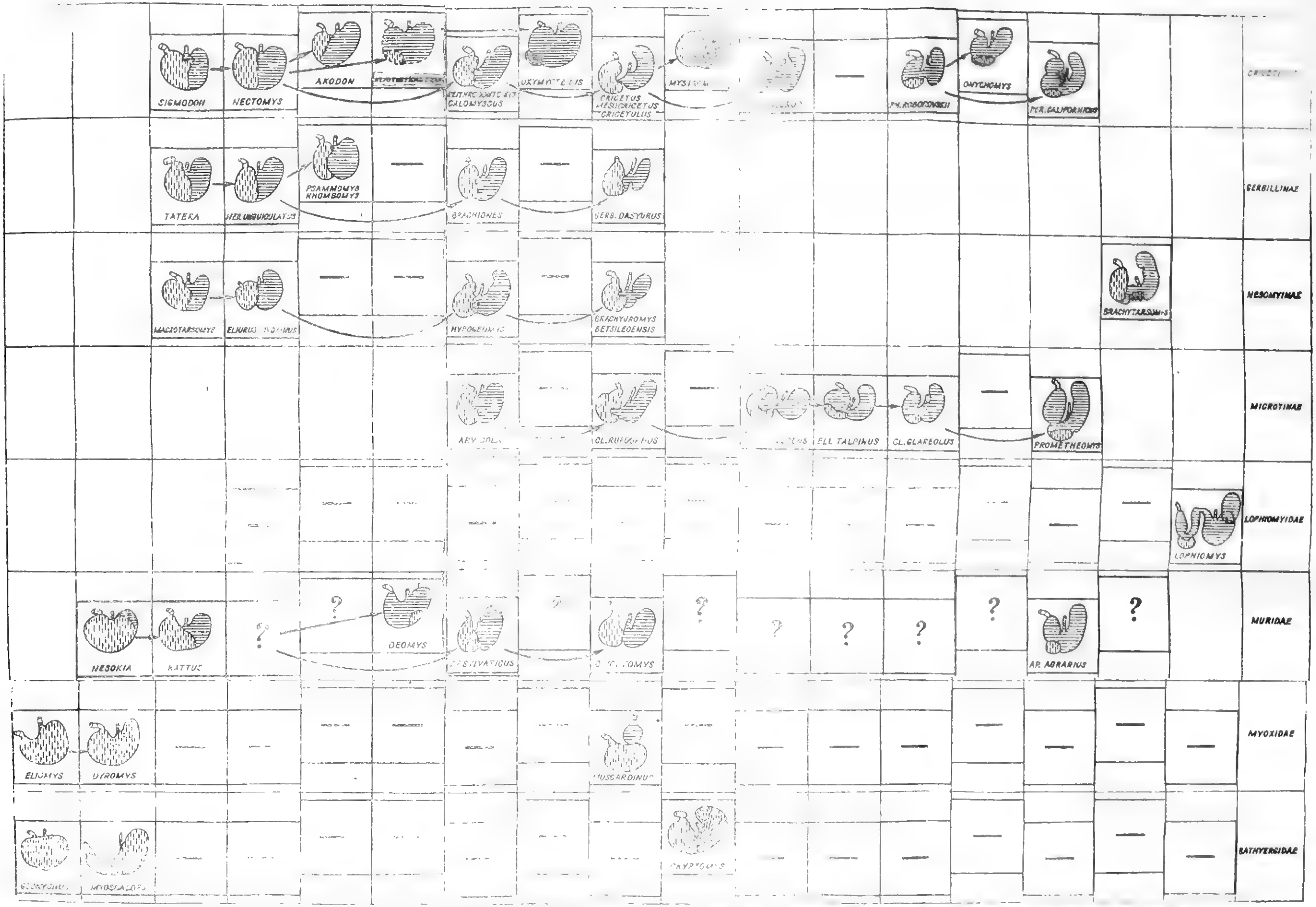


Fig. 120. Homologous and convergent series of [illegible] column, row corresponds to the variability of the systematic group. The side branches are placed in the upper sub-row, the basic line of development is shown in the lower sub-row. A row shows only the specialization stages, modern representatives having corresponding stomach structure are called phylogenetic. The series, Cricetinae, [illegible] Microtinae Lophiomyidae and Muridae are homologous to one another. The series Muroidae, Myoxidea and Bathyergoidea are convergent to [illegible] mean that the given plan of structure cannot be applied to the [illegible] of this group? It means that all forms of this group are not studied and the given plan of structure may be observed among species not yet studied.

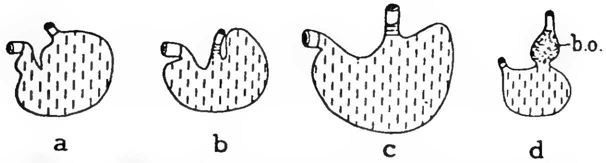


Fig. 121: Stomach structure of certain forms of Myoxidae. Ventral view, schematic. A two-chambered stomach is formed in Muscardinus avellanarius L. as a result of the bulging of oesophagus. An example of the convergence with Muridae. This series is not homologous to the series of Muridae -(a) according to Tullberg (1899); (b, c and d) original, from Vorontsov (1962, b)). (a) Glis glis L.; (b) Dyromys nitedula Pall.; (c) Eliomis guercinus L.; (d) Muscardinus avellanarius L.; (b-o) bulbus oesophagicus.

but by a special dilatation of the posterior end of esophagus named the bulbus esophagicus. This new formation is functionally analogous to the corneous forestomach of Muroidea. Special trabeculae grow in the corneous forestomach of *Muscardinus*. They get connected with each other and form a reticular globular structure embedded in the bulbus oesophagicus and remains as if it were the inner wall of bulbus oesophagicus.

A tendency for the transformation of the one-chambered sacciform stomach into a two-chambered one without the penetration of the corneous epithelium from the esophagus to the stomach (a series from *Georychus* to *Cryptomys* through Myoscalops; Fig. 122) is observed among Bathyergoidae (studied for learning the extent to which the fossorial mode of life affects the structure of the internal organs in the different groups of rodents).

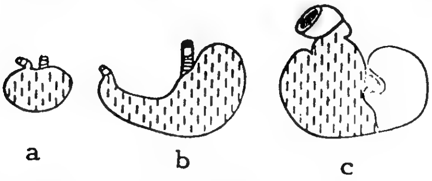


Fig. 122: Stomach structure of certain forms of Bathyergidae. View from the central side, schematic. Vertical broken dash line shows the region lined with glandular epithelium. The white portion shows region lined with villose epithelium. A tendency for the transformation of the saccular one-chambered stomach into a two-chambered one without the penetration of the conreous epithelium from oesophagus to the stomach is observed. An example of convergence with Muridae (a - according to Tullberg (1899) and b and c original, from Vorontsov (1962 b)). (a) Georychus capensis; (b) Myoscalops argentes and (c) Cryptomys damarensis Ogilby.

It is remarkable that a villose epithelium develops in the left half of the stomach in Cryptomys convergent with Myospalax and Tachyoryctes. Apparently the function of this portion consists of trapping the soil particles entering the stomach along with food, apart from maceration of cellulose.

The number of series of transformation of the stomach in connection with the transformation from protein to cellulose nutrition will undoubtedly increase after studying the digestive system of all the large groups of rodents.

However, in groups clearly separated from one another (in the studied examples, from subfamilies and above) the same degrees of adaptation in the different series have only surface similarity, caused as a result of convergence and may be called the parallel variability series.

When variability among the species of each group is very high, their stomach structure, unlike their dental system, is less variable and more stable (in their general features) for the representatives of a relatively larger group of rodents. This fact should draw the attention of taxonomists. It fully agrees with the law of least variability of endosomatic organs in comparison with exosomatic as proposed by A.N. Severtsov.

CHAPTER V

EVOLUTION OF INTESTINE

1. General concepts and terminology

The intestine is divided into a small and a large intestine.

The intestinal wall is formed of tunica mucosa (which varies greatly depending on the position i.e., the beginning, middle or end of the intestinal canal) tunica submucosa, tunica muscularis and tunica serova. The tunica muscularis is formed of inner circular and outer longitudinal layers of smooth muscles.

The surface of the small intestine may have been complicated by the presence of folds, (plica circulares) into which the tunica submucosa enters. The surface of the small intestine is lined with villi (villi intestinales) and the depressions between the villi are called crypts. In many cases the degree of development of villi determines the total area of the surface of the small intestine.

The so-called Lieberkuhn's glands are located deep in the crypts. These glands produce an alkaline secretion which contains a number of enzymes like, diastase, maltase, lactase, invertase, lipase, enterokinase, erepsin, etc. Lieberkuhn's glands in the large intestine do not secrete any enzymes (Zavarzin and Schchelkunov, 1954), but produce only mucus.

The histological change in the transition of stomach into intestine (the pyloric glands in the duodenum is replaced by Brünner's glands which secrete serous - mucoid secretion) is not very clear in those rodents in which the pylorus is lined with pyloric glands. The transition of the stomach into intestine is very clear in those forms where the pylorus is lined completely with the corneous epithelium. Here the corneous epithelium is replaced by the glandular and a part of the borderline fold, shifted from the oesophagus-stomach opening to the stomach-duodenum opening passes through the same spot.

The small intestine consists of duodenum (intestinum duodenum) and jejunum-ileum (intestinum jejunum-ileum). Duodenum is not suspended from the mesentary. Brünner's glands are located inside the duodenum. Hepatic duct and pancreas open into the duodenum. Immediately after its emergence from pylorus, the duodenum may have an enlargement - ampula duodeni - which is very clear in such forms as Peromyscus californicus and Eliurus myoxinus. The place of transition from duodenum to jejunum-ileum is detected by the presence of mesentary and absence of Brünner's glands. The number of villi and Lieberkühn's glands decreases from jejunum to ileum (the boundary between them is highly arbitrary).

There is a bush-shaped ileocaecal valve (valvula ileocoecalis) at the junction of the small and large intestines; to be more precise, at the junction of ileum and caecum (in the majority of the rodents). The large intestine begins after the valve.

The large intestine consists of a caecum (intestinum caecum) and the large intestine proper has a very long colon which leads into the rectum having transversely striated muscles on its wall.

The large intestine has an epithelium, similar in structure to that of the small intestine. However, its glands (here mostly goblet cells are present) secrete only a slightly alkaline mucous-serous secretion which does not contain any enzymes.

A minor section of the initial portion of the ileum may get considerably dilated to the diameter of caecum and forms the ampulla (ampula coli) here. The groove through which food from ileum may enter the colon through caecum stretches along the inner wall of the ampula coli. Functionally ampula coli is a part of the caecum and while measuring the length of the caecum we have taken into consideration the length of the caecum and ampula coli.

Ostium caeco-colicum may be isolated considerably from colon or it may not be developed at all. The degree of development of this valve is quite diverse in different species of rodents.

There is a well developed isthmus at the junction of the dilated ampula coli and the real colon in the large intenstine but in individual cases a special valve separating the caecum "functionally" from the large intestine may also develop here.

In the majority of rodents the colon, immediately after its emergence from ampula coli, forms spiral-shaped involution. The number of coils in this large intestine spiral is constant for each species. In Muroidea it varies from 0-1 to 11-12 coils. These coils form the so-called colic spiral (It is called by the name "Colonspirale" by German authors).

The ascending part of the colon, immediately after the colic spiral is highly complicated in a majority of the herbivorous rodents. Additional blind processes (ampulae coli accessori) analogous to the caecum develop in some forms. These additional blind projections may develop into additional caeca in certain mammals - Marsupialia (Hall and Rewell, 1954) and Hyracidae (Jacobshagen, 1937).

The inner surface of the ascending and transverse portions of the large intestine is complicated by right series of spiral folds (Plica obliquae). A narrow longitudinal foldless strip along which food mass that does not require further bacterial action may quickly run along one side of the intestine in the region where the spiral folds are located.

The additional blind processes and spiral folds considerably increase the absorptive surface area and give rise to a blind section where fermentation and splitting of cellulose take place under the action of bacteria.

Usually the caecum is more complicated. Its surface may be increased by the development of blind sacs (sacculi caecales) and appendix. In certain forms (Lagomorpha and Spalacidae) a high fold having the form of a "spiral valve" which surprisingly resembles the real spiral valve of Selyakhii and chondrostei.

This "spiral valve" divides the caecum into a number of portions isolated from one another.

The structure of the caecum and the ascending part of the colon do not vary within a species but varies from species to species and genera and is of interest to taxonomists. Much attention was paid to the structure of this portion and the relative development of the portions of stomach while studying the structure of the intestine and the length of the small intestine (without ampula coli) and the large intestine (without ampula coli and with the colic spiral uncoiled) was measured.

A comparison of the measurement of the relative length of intestine in freshly killed samples kept in formalin and spirit has shown that fixation and its degree do not have much effect on the relative dimensions of the intestine. However the absolute dimensions of the intestine depend greatly on fixation. Hence the data on the ratio of the length of intestines to that of the body given below should be taken only as preliminary data.

A study of the relative length variability of the vole intestine (Vorontsov 1961a) has shown that the measurement error and individual variations do not exceed ±1.5% while measuring small and large intestines and ± 0.6% while measuring caeca. However, the error in the determination of the relative length of the intestine may go up to ±7.5%. Myrcha (1964) has specially studied the individual, age and sexual variability in the size of the alimentary canal in *Clethrionomys glareolus*. By establishing the considerable age and sexual variability of the absolute size of the alimentary canals, Myrcha has proved that the ratio of the length of the portions of intestine to the total length of the intestine is constant. Thus, according to him, the relative length of the small intestine varies from 58.7 to 61.8% that of large intestine from 25.1 to 27.6% and that of the caecum from 12.0 to 14.2%. The ratio of intestine length to body length varies from 6.78 to 8.06 times (Myrcha 1964).

2. Physiology of Intestinal Digestion in Rodents.

The food enters the duodenum from the pylorus through the pyloric sphincter. The pancreatic and hepatic ducts open into the duodenum.

The pancreatic gland secrets enzymes of which trypsin and erepsin split up proteins and diastase and maltose hydrolyze carbohydrates. Pancreatic juice is alkaline in reaction owing to the large amount of sodium bicarbonate contained in it.

Trypsin hydrolyzes proteins not only into albumin and peptones but also into aminoacids at a pH = 8.87. The food matter passing out of the stomach has an acid reaction. Splitting up of proteins by pepsin ceases in the duodenum owing to the alkaline medium and bile inhibiting the action of pepsin on trypsin and trypsin and erepsin take the place of pepsin.

Bile acid salts are the coferments of amylase and lipase secreted by the pancreas.

Intestinal juice secreted by the glands of the small intestine wall is alkaline in reaction and contains enterokinase (as activator of trypsinogen), erepsin, lipase and some enzymes, that hydrolyze carbohydrates (Ginetsinskii and Lebedinskii 1956; Koshtoyants, 1950 and Lappa 1958b).

Although the alkaline medium of the small intestine is favorable for the development of bacteria, it is the protein, fat and carbohydrate splitting enzymes secreted by the organism itself that play the main part of digestion in this portion. Lactic acid bacteria develop only in the lower portions of the small intestine.

Digestive enzymes are generally absent in the secretion of the simple tubular glands in the caecum and the large intestine. It is well known that enzymes breaking down cellulose are completely absent in the secretions of the mammalian digestive glands (Koshtoyants, 1950). The slightly alkaline carbonate solution secreted by the mucous membrane glands of the large intestine and caecum creates conditions favorable for the development of bacterial flora and symbiotic protozoan fauna (Koshtoyants, 1950).

The enzymes secreted by symbionts break down cellulose first into cellobiose and then into dextrose.

According to the data of M.A. Velichko and T.M.Mokeeva (1949) anaerobic bacilli decomposing cellulose, yeasts that ferment glucose, coliform bacilli fermenting glucose and lactose and bacteria of lactic and butyric fermentation are observed among the microflora of caecum. Flora of the small intestine completely disappears in the caecum.

Although the chief digestive enzymes of the small intestine are secreted at the anterior part of the small intestine i.e., duodenum the splitting up of calorific food (proteins, fats and carbyohydrates) continues even in the lower portions of the small intestine. This decomposed food is absorbed here only.

Hence it is considered that the degree of the relative development of small intestine reflects the role of caloric food. chiefly proteins, in the nutrition of this species.

Decomposition of cellulose by symbionts requires the development of special "fermenting-macerating chambers" the function of which is carried out by the caecum and the blind processes of the large intestine.

The large intestine and caecum have developed not only on account of an increase in their absolute and relative lengths but also because of the considerable complexity in their structure. That is why the data on the relative length of the large intestine and particularly the caecum give somewhat low indexes of their real role in digestion.

3. The Structure of the Intestine in Cricetinae

In the relative development of the portions of intestine, Cricetinae, is the most diverse group. The range of variability of the relative dimensions of the intestine in Cricetinae is more or less equal to the range of variability of the entire Cricetinae family. Seed eating hamsters of the tribe Oryzomyini, protein-eating Akodon, insectivorous Oxymycterus and Onychomys and seed-eating Peromyscus are characterized by a considerable relative length of the small intestine. It is the small intestine that is reduced most in the members of the genus Mesocricetus. The degree of development of any portion of the intestine varies depending more on the mode of nutrition than on the systematic position of the species (Table 5).

TABLE 5.

Relative dimensions and relative development of the portions of the intestine in certain Cricetinae (according to Vorontsov, 1962 b, with certain additions).

Species	Relative length of a portion to the total length of the entire intestine, %			Ratio of the length of the intestine to the body length
	Small	Large	Caecum	
Akodon arenicola	85	12	3	8.0
Oxymycterus nasutus	85	10	5	5.0
Nectomys squamipes	80	14	6	8.4
Oryzomys couesi	80	15	4	-
Oxymycterus refus*	78	18	4	4.8
Peromyscus californicus	74	16	10	3.5
Onychomys leucogaster	74	20	6	5.0
Peromyscus leucopus	73	21	6	3.6
Sigmodon hispidus	70	20	10	6.7
Baiomys musculus	67	27	7	3.3
Calomyscus bailwardi	63	29	7	3.8
Mystromys albicaudatus	63	29	8	3.8
Cricetulus longicaudatus	63	28	9	3.5
Reithrodontomys megalotis	62	29	9	3.7
Cricetulus migratorius	62	28	11	4.1
Peromyscus maniculatus	61	29	11	3.1
Cricetulus eversmanni	60	28	14	3.5

Phodopus sungorus	60	27	13	3.6
Phodopus roborovskii	60	27	13	3.7
Neotoma albigula	59	21	20	3.7
Cricetus cricetus	58	32	10	6.4
Neotomodon alstoni	58	32	10	6.5
Cricetulus barabensis	56	31	13	3.4
Cricetulus triton	55	36	10	3.7
Cricetulus kamensis	54	34	13	4.0
Mesocricetus raddei	50	40	10	6.9
Mesocricetus brandti	48	42	10	5.8
Neotoma floridana*	42	47	11	5.7

---

* As per the data of Tullberg (1899)

The intestine of Oryzomys couesi (Fig. 124, a) is 3-4 times longer than its body. Its small intestine is 4 times longer than the large intestine and caecum. Caecum is small, simple in structure and has only one isthmus. Colic spiral has 1 - 1.5 coils. Large intestine is not complicated by additional digestive caeca and ampullae and does not have any spiral fold on its inner surface. Large intestine consists of an ascending, a very short transverse and descending columns. These columns do not form any complicated coils.

Intestine of herbivorous Nectomys squamipes (see Fig. 123 b) is 8.4 times longer than its body. Small intestine, as in the case of the previous species, is 4 times longer than the large intestine and caecum. Considerable elongation of the intestine as a whole increases the relative (in comparison with the size of the body) length of the large intestine and caecum. The caecum itself is very wide, has 2-3 isthmuses and 2-3 sacculi. However, its structure on the whole is very simple (see Fig. 131, b). Its functional volume increases owing to 10-16 ampullae coli at the beginning of the ascending column of the colon. Many ampullae coli extend along one side of the ascending column of the colon while plica obliquae run along its other side. A similar structure

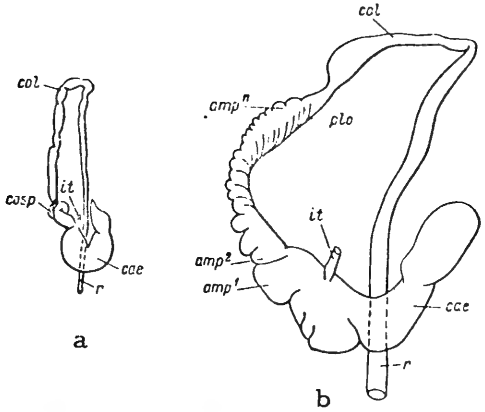


Fig. 123: *Structure of the large intestine and caecum of certain forms of Oryzomyini. Original. (a) Oryzomys couesi Alston; (b) Nectomys squamipes Brants. Legends for Fig. 123 - 141. amp - ampulla coli - blind process between the small intestine and isthmus of caecum; amp. acc. - additional ampullae coli after the colic spiral; app - appendix; cae - caecum; cae" - additional caecal process; col - colon; cosp - coli of the large intestinal spiral; it - intestinum tenue, plo - plica obliquae of the large intestine; r - rectum; sac - sacculus - caeca near the depression between the small intestine and additional caecal cavities; v c. - valvula coli - valve separating the real caecum from ampulla; and vsp - valcula spiralis of caecum.*

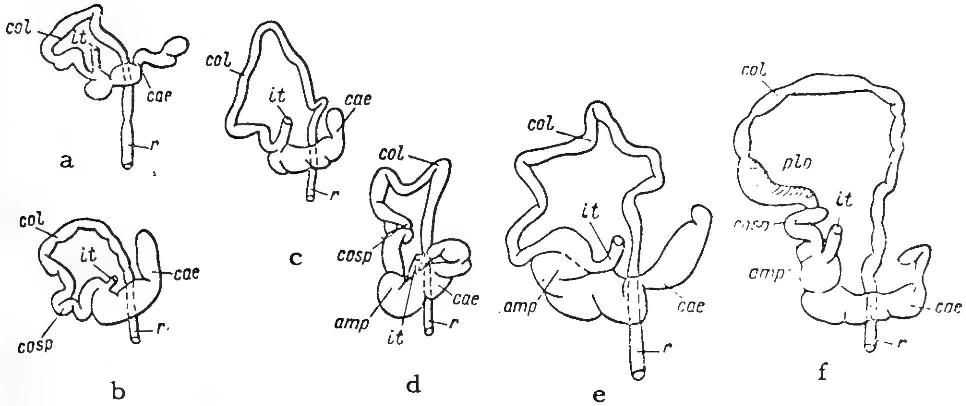


Fig. 124: *Structure of the large intestine and caecum of certain forms of Reithrodontomyini and Calomyscus. Original. (a) Reithrodontomys megalotis Baird; (b) Baiomys musculus Merriam; (c) Peromyscus (s. str.) leucopus Rafin; (d) Peromyscus (s. str.) maniculatus Wagn.; (e) Peromyscus (Haplomylomys) californicus Gambell; (f) Calomyscus bailwardi Thom. For legend see Fig. 123.*

of the initial portion of large intestine considerably compensates for the poorly developed caecum. The transverse column of the large intestine is short while the descending column runs more or less straight.

By their structure and relative development of the portions of intestine, the seed-eating Baiomys, Reithrodontomys, Peromyscus and Calomyscus (the intestine is 3.1 - 3.8 times longer than the body) form a unique group.

Intestine is Baiomys musculus (Fig. 124, b) is 3.3 times longer than its body. The small intestine is twice longer than the large intestine and caecum. The caecum is small, but fairly wide and has only one isthmus (see Fig. 131, g). The large intestine spiral has only a half turn. The large intestine is devoid of ampullae coli, ampullae, plicae obliquae and consists of an ascending column with numerous small bends, a short transverse column and a short but straight descending column.

The intestine of Reithrodontomys megalotis (see Fig. 124 a) is 3.7 times longer than its body. Small intestine is longer than large intestine and caecum less than double the caecum, developed more than that in the previous species and divided by three isthmuses into four portions though not completely separated from one another (See Fig. 131, e). The colon is not coiled at its beginning, but has asmall dilatation - the ampulla. The transverse column of the large intestine is short, while the descending column is long and straight.

The intestine of Peromyscus (Haplomylomys) californicus (see Fig. 124, b) is 3.5 times longer than its body. The small intestine is thrice longer than the large intestine and caecum. Caecum is wide, relatively long (10% of the length of the intestine) and has 3-4 isthmuses partially dividing it into chambers (see Fig. 131, j). The large intestine forms a large ampulla - a continuation of the caecum - after the caecum. Colic spiral and plicae obliquae are not developed in the ascending column of the large intestine. Ascending, transverse and descending columns have several bends.

Intestine length of Peromyscus (s. str.) leucopus (see Fig. 124, c) is 3.6 times more than its body length. Small intestine is twice longer than the large intestine and caecum. The caecum (see Fig. 131, h) is short, but has three deep isthmuses, separating it into sacculi, on its posterior side. Colic spiral, ampullae and plicae obliquae are not developed. The branches of the large intestine does not have any bends.

Peromyscus (s. str.) maniculatus (see Fig. 124 d) is an omnivorous species in comparison with P. leucopus, but the cellulose food plays an important role in its nutrition. Hence the caecum and the large intestine are well developed in this species, but the relative length of the intestine, longer than the body length only by 3. 1 times, decreases. The small intestine is only 1. 5 times longer than the large intestine and the caecum. The caecum (see Fig. 131, i) has four isthmuses dividing it into five chambers, incompletely separated from one another. The large blind ampulla formed at the pointwhere the large intestine emerges out from the caecum is a continuation of the large intestine. After the ampullae, the colon runs forward and only at a certain distance away from the caecum does not get spirally coiled forming 1. 5 coils. The ascending and transverse columns have knee-shaped bends while the descending column is straight.

The caecum and the large intestine are more complicated in Calomyscus bailwardi (See Fig. 124, e) than in Reithrodontomyini. Its small intestine is 2. 4 times longer than the large intestine and caecum, while the intestine itself is 3. 8 times longer than its body. The caecum (see Fig. 131, d) is divided into three portions by two isthmuses. The middle one is subdivided from the anterior side forming four sacculi in the middle portion. The hind-portion of the caecum forms an appendix having two bends. The anterior part of the caecum ends in an ampulla-dilatation at the initial part of the large intestine. Beyond the ampulla, the caecum is spirally coiled forming only an incomplete coil. Plicae obliquae develop on the inner surface of the ascending column situated beyond the colic spiral. The ascending, transverse and descending columns of the large intestine may be highly curved.

The characteristics of the intestine structure in Calomyscus bailwardi somewhat distinguishes this genus from Baiomys, Reithrodontomys and Peromyscus, but do not bring it closer to the forms of Cricetini. It should be noted that the variations in the intestine structure of Calomyscus and Peromyscus are much less than that between the undisputably allied genera, Nectomys and Oryzomys.

A reduction of the caecum and the large intestine and an increase in the size of the small intestine are observed in the insectivorous hamsters of the genus Onychomys - On. leucogaster (see Fig. 125, a) and On. torridus. The intestine is 5 times longer than its body and the small intestine thrice longer than the large intestine and caecum. The small caecum (Fig. 131, r) is incompletely divided into 3 subsections by 2 isthmuses. The colon has no colic spiral and plicae obliquae on its inner surface. Accessory sacculi are absent; but the ascending column may have 1-2 bends.

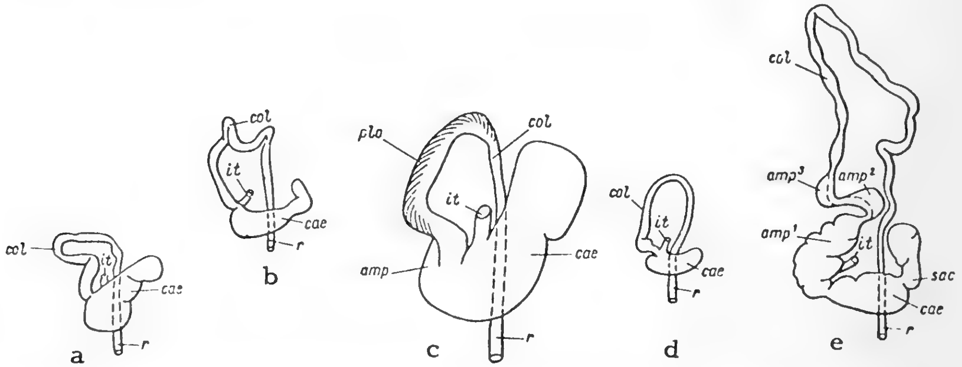


Fig. 125: Structure of the large intestine and caecum of Onychomys, Akodon Oxymycterus and Mystromys; d - according to Tullberg (1899); a, b, c, and e - original. (a) Onychomys leucogaster Wied; (b) Akodon arenicola Waterh.; (c) Oxymycterus nastus Waterh.; (d) Oxymycterus rufus Desm.; and (e) Mystromys albicaudatus Wagn. For legends see Fig. 123.

The intestine as such is large in Akodon arenicola, but its caecum and large intestine are reduced (see Fig. 125, b). Its intestine is 8 times longer than its body, while the small intestine is 5.7 times (maximum among the forms of Cricetidae) longer than the large intestine and caecum. The caecum is small in size (see Fig. 131, c) and very simple in form. There is a single isthmus separating the terminal portion of caecum from its body. Colic spiral, plicae obliquae of the large intestine and sacculi are absent in this portion. The transverse colon may have 1-2 bends.

Secondary* reduction of large intestine and caecum (is more marked in the insectivorous hamster - Oxymycterus nasutus (see Fig. 125 c). The intestine is 5 times longer than its body, while the small intestine, just as in the previous case, is 5. 7 times longer than the large intestine and caecum. However, in comparison with the body length, small intestine, large intestine and caecum are shorter than those in Akodon. In Ox. nasutus the caecum is a wide sac partially divided into 2 subsections by a small isthmus. A thick ampulla which becomes one with the caecum adjoins the caecum (see Fig. 131, d). Plicae obliquae are present on the ascending colon. The small intestine does not have any colic spiral and sacculi. The large intestine is very simple in form, the ascending colon is somewhat dilated in comparison with the transverse and descending colons.

According to the description and figures given by Tullberg (1899), a further reduction in caecum is observed in Ox. rufus (see Fig. 125, d). Caecum in this species is a small sacculus without any additional isthmuses, plicae and sections (see Fig. 131, e). The large intestine does not have any plicae obliquae and just as in the previous forms does not form colic spiral and sacculi.

The intestine structure of Mystromys albicaudatus (see Fig. 125, e) is very peculiar. It is 3. 8 times longer than the its body while its small intestine is 2. 3 times longer than the large intestine and the caecum. The caecum itself (see Fig. 131, r) is relatively small in size and has two sections more or less separated from one another, which in their turn are subdivided by isthmuses. A very large colic ampulla (ampulla coli) with size more or less equal to that of the actual caecum separated from it by an isthmus adjoins the caecum. This ampulla has a number of additional pocket-like outgrowths considerably increasing the functional volume of the caecum, along its greater curvature.

The colon has a noticeable bend - colic spiral primodium - after the ampulla. Both bends of this curvature has accessory

---

* *It is shown above (Chapter IV Section 5) that the stomach of Onychomys is secondarily adapted for protein nutrition.*

ampulla coli. Ascending and descending colons may have additional bends.

Thus in the *Mystromys* hardly half the volume of the blind part of the intestine is on the caecum, A similar development of additional sacculi in the large intestine portion, when the caecum itself has a relatively simple form (a characteristic not found in forms of Cricetini), clearly distinguishes *Mystromys* from all palearctic hamsters with which this genus was grouped by earlier investigators.

A progressive complexity in the caecum and its analogs and a decrease in the relative size of the large intestine are observed among the New World hamsters - *Cricetini* - from *Phodopus* and *Cricetulus* to *Cricetus* and *Mesocricetus*. While there is a general similarity in the structure of stomach (except *Ph. roborovskii)* and dental system, considerable radiation is observed in the structure and corresponding development of the parts of the intestine among the palearctic New World hamsters.

Intestine of *Phodopus sungorus* (Fig. 126, a) is 3.6 times longer than its body while that of *Ph. roborovskii* (see Fig. 126, b), 3.7 times. The relative sizes of the portions of the intestine are the same for both the species : their small intestines are 1.5 times longer than their large intestines and caecum. The structure of the caecum lying adjacent to the colon varies considerably among these species. In *Ph. sungorus* the caecum is divided into four portions not completely separated from one another by isthmuses. A large ampulla of the colon (see Fig. 131, m) joins the caecum. In *Ph. roborovskii* (see Fig. 131, a) the caecum is more distinctly divided into 3-4 chambers. Each of these chambers has small sacculi along the lesser and greater curvatures. In its turn the ampulla of the colon is subdivided into three portions by two isthmuses. As a result the total surface area of the caecum portion is much larger in *Ph. rogorovskii* than in *Ph. sungorus*. Colic spiral and plicae oblique of the ascending column are absent.

The large intestine and the caecum are considerably complex in the genus *Cricetulus*.

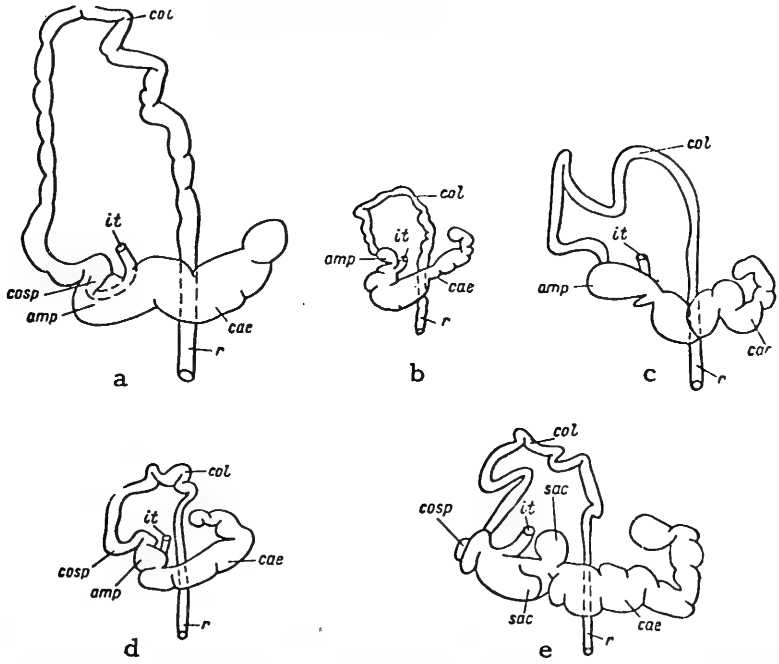


Fig. 126: Structure of the large intestine and caecum portions of hamsters Phodopus and Cricetulus (s. str.) Original. (a) Phodopus sungorus Pall.; (b) Phodopus roborovskii Satunin; (c) Cricetulus (s. str.) kamensis Satunin; (d) Cricetulus (s. str.) longicaudatus Milne-Edw.; (e) Cricetulus (s. str.) nigratorins Pall.; For legends see Fig. 123.

Intestine of Cr. (s. str.) longicaudatus is 3.5 times longer than its body, while its small intestine is 2.3 times longer than the large intestine and caecum. The intestine of Cr. (s. str.) kamensis is 4 times longer than its body, whereas the small intestine is 1.2 times longer than the large intestine and caecum. In Cr. (s. str.) migratorius the intestine is 4.1 times longer than its body; but the small intestine and caecum are 2.1 times longer. In Cr. longicaudatus the caecum is divided into several portions, forming two bends of the caecum by 5-7 isthmuses. Ampulla of the large intestine lies adjacent to it. Colic spiral and plicae obliquae are absent in the large intestine (see Fig. 126, c, d and e).

In Cr. kamensis (see Fig. 131, p) the caecum is complicated by the development of a sacculus close to the opening of the small intestine and greater separation of the portions of the intestine from one another. Colic spiral and plicae obliquae are absent in the large intestine of this species.

The caecum is still more complicated in Cr. migratorius (see Fig. 131, q). Here the caecum is divided into 10-12 chambers by isthmuses. There is a large sacculus, clearly distinct from the caecum close to the place where the small intestine opens into the large. There is a fold penetrating deep into the caecal cavity and separating a major portion of the caecum from its entrance on the anterior part of the caecum. The colon does not have ampulla and accessory ampullae, but on the other hand forms a colic spiral having two coils. The ascending and the transverse colons are bent and highly coiled.

The stomach structure of the representatives of the subgenus Allocricetulus is close to that of the species of the subgenus Cricetulus (s. str.) described above. Intestine of Cricetulus (Allocricetulus) eversmanni (Fig. 127, a) is 3.5 times longer than its body, while its small intestine is 1.5 times longer than its large intestine and caecum. The caecum (see Fig. 131, t) has a fairly complicated form and is divided into 9-10 chambers not completely separated from one another by isthmuses. Colic spiral forming one coil lies next to the caecum beyond which stretches the ampulla. Intestine, forming a part of the colic spiral and caecum has the same diameter as that of caecum and large intestine ampulla and is functionally the continuation of the caecum portion. Plica obliquae is not developed on the ascending colon. The transverse colon is highly coiled.

The intestinal structure of Cricetulus (Tscherskia) triton (see Fig. 127, b) differs considerably from those of the representatives of the genus Cricetulus described above. The length of intestine is 3.7 times more than the body length. Its small intestine attains a length 1.2 times more than that of the large intestine and the caecum (see Fig. 131, s) is complicated by the formation of outgrowths and isthmuses along the greater and lesser curvatures. The caecum is separated from the large ampulla of the large intestine by a deep isthmus near the point where the small intestine opens into the caecum. Along the inner surface of this ampulla, there are 4 plicae obliquae (homologous to the plicae obliquae of the large intestine) on the greater curvature side. The large intestine forms a colic spiral having

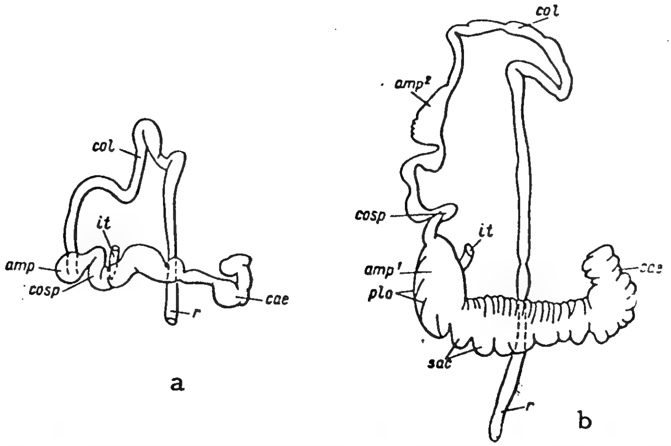


Fig. 127: Structure of large intestine and caecum portions of hamsters, genus Cricetulus and subgenera Allocricetulus and Tscherskia Original. (a) Cricetulus (Allocricetulus) eversmanni Brandt. and (b) Cr. (Tscherskia) triton de Winton. For legends see Fig. 123.

0.5 -1 coil beyond the ampulla and there are 4 ampullae coli in the ascending colon beyond the spiral. The latter attains considerable size and its external surface is complicated by short outgrowths. The transverse and descending colons may form 1-2 branches.

The intestine of Cricetus cricetus (Fig. 128, a) is 6.4 times longer than its body, while its small intestine is 1.4 times longer than its large intestine and caecum. The caecum is large in size and has 8 chambers clearly separated from one another by isthmuses. The ampulla, formed directly by colic spiral having only a single incomplete coil lies adjacent to the caecum. There are two more ampullae lying above this in the ascending colon. The ascending and especially the transverse colons are highly coiled and branched.

The small intestine is reduced to the maximum in the members of the genus Mesocricetus. The intestine in M. brandt is 5.8 times longer than its body whereas in M. raddei, it is 6.9 times. In M. raddei (see Fig. 128, b) the small intestine is equal to the length of the large intestine and caecum while in M. brandti (see Fig. 128, b) the small intestine constitute only 0.92 of the length of the large intestine and caecum. There are 12-14 blind projections increasing the caecal surface along

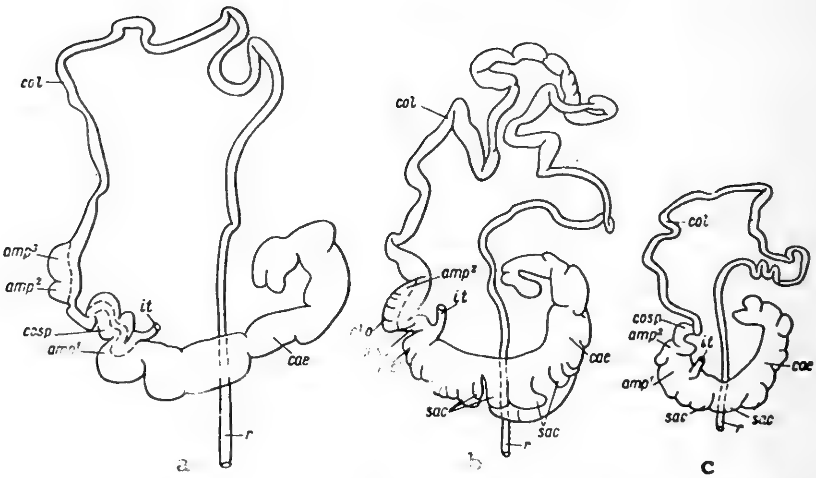


Fig. 128: Structure of the large intestine and caecum portions of the intestine in hamsters, Cricetus and Mesocricetus, Original. (a) Cricetus cricetus L.; (b) Mesocricetus brandti Nehr.; (c) Mesocricetus raddei Nahr For legends see Fig. 123.

its greater curvature in M. brandti. The caecum is followed by a large ampulla. The colic spiral which forms a single incomplete coil lies next to it. Two accessory ampullae coli develop at thebeginning of the ascending column.

The caecum is more complex in M. raddei (see Fig. 131, i). Large sacculi considerably increasing the volume of caecum develop along the greater curvature of the caecum on its dorsal and ventral sides. The ampulla is small in size and the colic spiral has hardly developed. Just as in the previous species there are two sacculi in the ascending colon.

The structure of the intestine especially that of caecum, naturally distinguishes Mesocricetus from Cricetus and enables one to determine the basic differences in the morphology of the intestine between M. raddei and M. brandti which Ellerman (1949) has grouped in a single species.

The structure of the intestine of Sigmodon hispidus (Fig. 129) is very peculiar. Here the intestine is 6.7 times longer than its body and the small intestine 2.3 times longer than the large intestine and caecum. The caecum is small in size and has two bends divided into 4 chambers by isthmuses and has a long

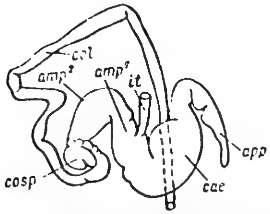


Fig. 129: Structure of large intestine and caecum of cotton hamster. Sigmodon hispidus Say et Ord. Original. For legends see Fig. 123.

appendix. There are two large ampullae increasing the volume of caecum by 1.5 times (see Fig. 131, y) lying adjacent to the caecum. The caecum has 4 bends including the ampallae. The colic spiral having 2-3 coils begins immediately after the ampullae. One of the coils of this spiral has a wavy outer surfaces which increases the area of the large intestine. The ascending colon has several bends.

The most complicated caecum among Cricetinae is found among the representatives of the genera Neotomodon and Neotoma

In Neotoma floridana (Tullberg 1899, Fig. 130, a) the intestine reaches a length 5.7 times more than its body. The small intestine forms only 0.7 of the length of the large intestine and the caecum. Among the entire Cricetinae, it is in this species

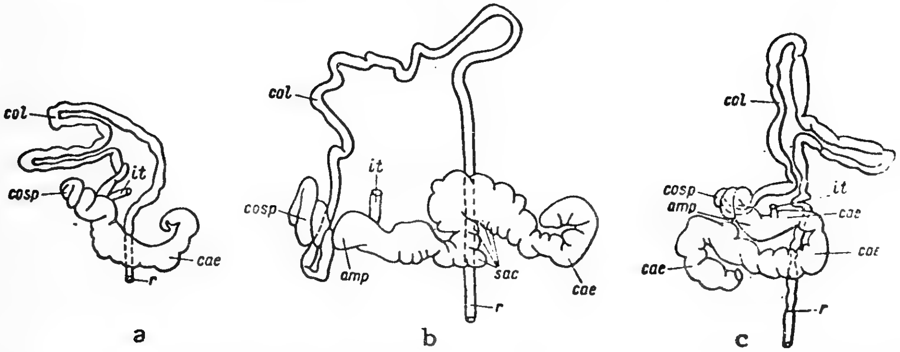


Fig. 130: Structure of the large intestine and the caecal portions of certain forms of Neotomini; (a) according Tullberg (1899), and (b and c) original. (a) Neotoma floridana Ord.; (b) Neotoma albigula Hartley and (c) Neotoma alstoni Merriam. For legends see Fig. 123.

that the large intestine attains the maximum development. The form of cacecum (Fig. 131, y) is not very complicated, and doubly bent. There are many shallow blind processes along the greater curvature. The colic spiral has several turns. Ampulla and plica obliquae are absent on the large intestine. The ascending colon is highly curled and has 6-8 bends, while the transverse and descending colons are of the ordinary structure.

Of all the members of the Cricetinae, it is Neotoma albigula (see Fig. 130, b) which has the most developed caecum but its large intestine is reduced. Its intestine is 3. 7 times longer than its body while its small intestine is longer than its large intestine and caecum by 1. 5 times. The caecum consists of 4 bends. Moreover the numerous sacculi and ampullae coli on the caecum are sometimes considerably separated from its body. The caecum has about eight portions clearly separated from one another. These chambers in their turn have accessory plicae, isthmuses and outgrowths (see Fig. 131, z). Colic spiral has four coils. The ampulla which considerably increases the size of caecum is in between the colic spiral and the caecum. The ascending and transverse colons have several flexures.

The intestine of Neotomodon alstoni is similar to that described above (see Fig. 130, b). Its intestine is 6. 5 times longer than its body - while its small intestine is 1. 4 times longer than the large intestine and the caecum has 3-4 bends (see Fig. 131, z), The chambers are fairly well separated from one another owing to the development of isthmuses. There is an ampulla of large intestine which continues as the colic spiral with 3 coils. The large intestine does not have plicae obliquae and necessary ampulla coli. The ascending, transverse and descending colons have several flexures.

The structure of the intestine of Ichthyomys is not described in detail. Thomas (1896) mentions that he caecum of Ichthyomys is not well developed. This suits to the protein nutrition of Ichthyomys. It is undoubtful that the reduction of caecum, in this form is connected with the secondary transition to exclusively protein nutrition.

The structure of the intestine is quite diverse in Cricetinae. Different degrees of intestinal adaptation for protein (Onchomys, *Oxymyceterus* and *Oryzomys*), combined (*Cricetini*) and cellulose (*Neotoma* and *Neotomodon*) types of nutrition are observed among the hamsters.

Cricetini is divided into several groups on the basis of the intestinal structure:

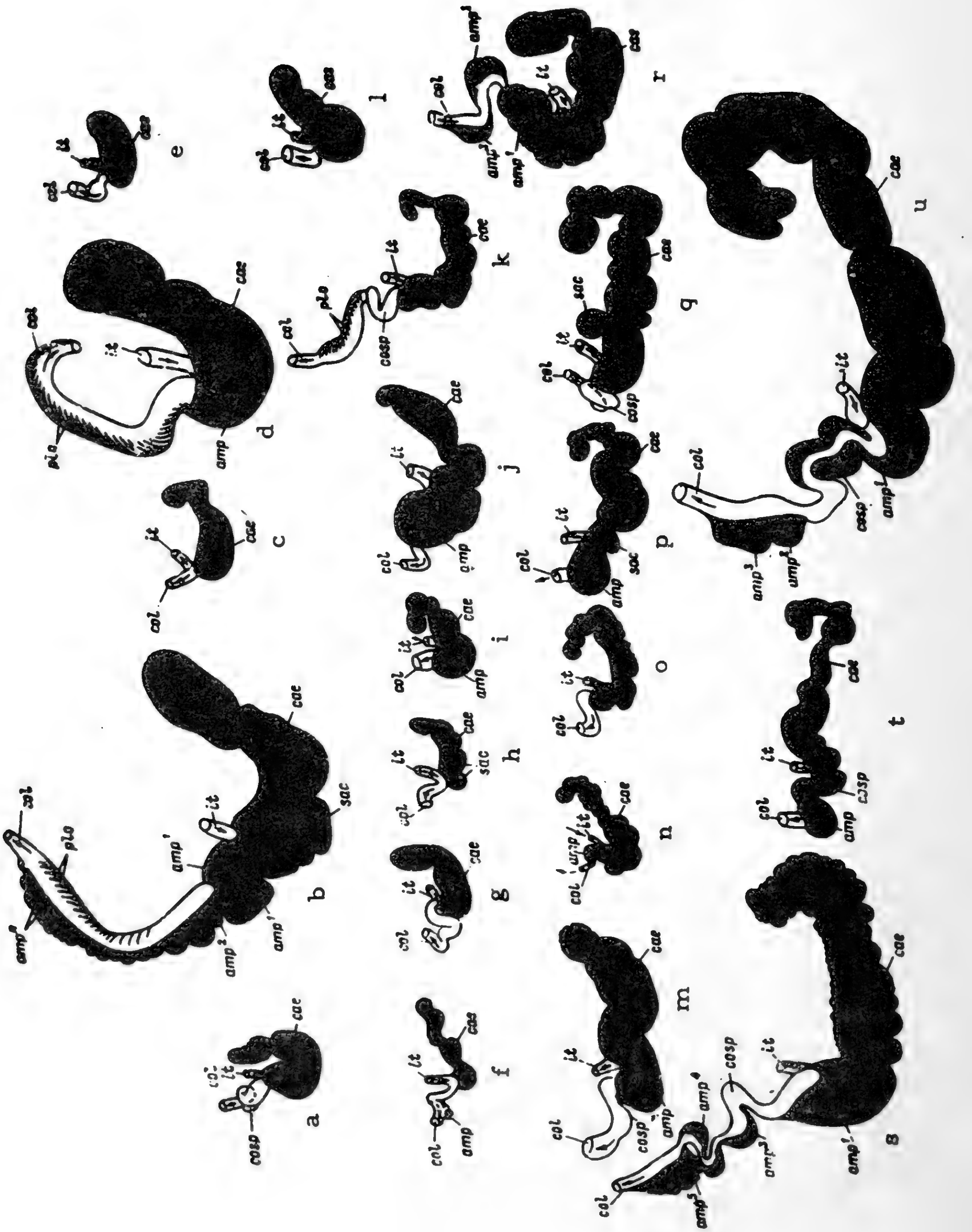
I. *Oryzomys*
II. *Nectomys*,
III. *Akodon*, *Oxymycterus*, *Onychomys**
IV. *Baiomys*, *Reithrodontomys*, *Peromyscus*, *Calomyscus*,
V. *Mystromys*,
VI. *Cricetulus* (s. str.), *Allocricetulus*, *Tscherskia*, *Cricetus*, *Mesocricetus*;
VII. *Sigmodon*; and
VIII. *Neotoma*, *Neotomodon*.

A tendency for the reduction of small intestine and enlargement and complexity of large intestine and caecum are observed. The large intestine and caecum are complicated as a result of their elongation, formation of isthmuses, plicae, sacculi increasing the volume of caecum, formation of colic spiral coils, ampullae, plicae obliquae and accessory ampullae coli in the large intestine (Fig. 131). However, an identical, uniform development of all these characteristics is not observed in any one of the above described species.

It is certain that the processes of transformation of intestine, owing to the adaptation to one particular type of nutrition, took place independent of one another not only in the different tribes but also in the different genera. In certain forms the homologous variability first changed certain features, while in some others certain other features changed. In certain forms adaptation to cellulose nutrition took place at equal levels. Judging from the structure of the intestine, the basic trend in the evolution of Cricetinae was a change over from protein nutrition to cellulose nutrition through combined nutrition. Forms secondarily adapted for protein nutrition have reduced the caecum and well developed small intestine.

---

* *According to the descriptions (Thomas 1896) the piscivorous hamsters Ichthyomys with hardly developed caecum also belongs to this group of genera.*


a
cosp
col
it
cae
b
amp²
col
plo
amp¹
it
sac
cae
amp²
amp¹
c
col
it
cae
d
plo
col
it
cae
amp
e
col
it
cae
f
col
amp
it
cae
g
col
it
cae
h
col
it
cae
sac
i
col
it
amp
cae
j
col
amp
it
cae
k
col
plo
cosp
it
cae
l
col
it
cae
m
col
cosp
amp
it
cae
n
col
amp
it
cae
o
col
it
p
col
amp
it
sac
cae
q
col
it
sac
cosp
cae
r
col
amp³
amp²
amp¹
it
cae
s
col
amp³
amp⁴
cosp
amp²
it
amp¹
cae
t
col
amp
it
cosp
cae
u
amp³
amp²
col
cosp
amp¹
it
cae

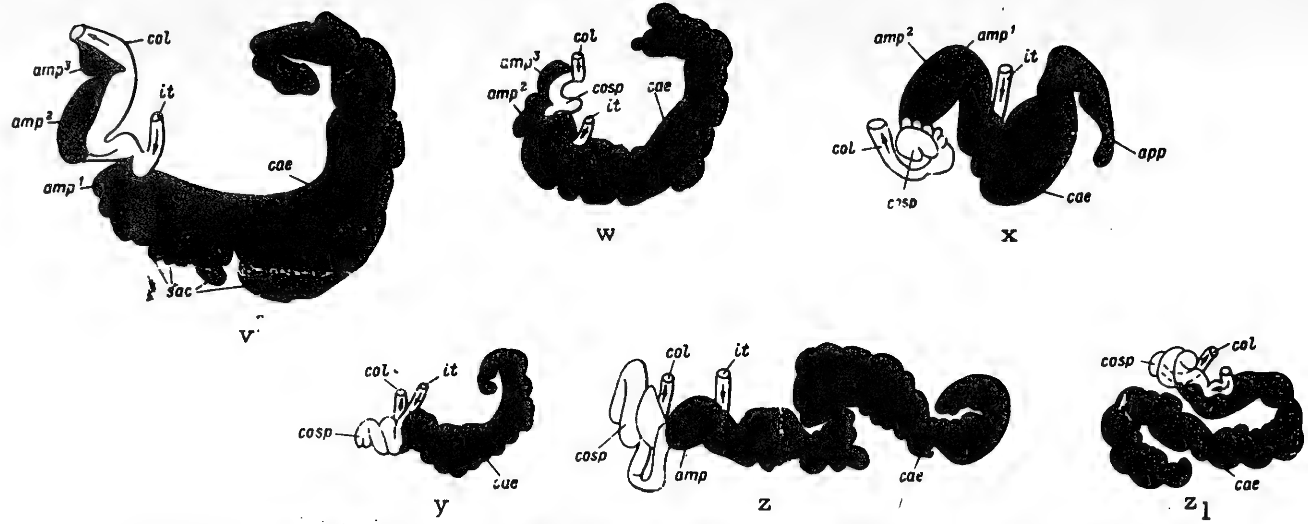


Fig. 131: Caecum and sacculi of the large intestine of Cricetinae; e, y - after Tullberg, the rest, original. From Vorontosov (1962). The caecum is complicated and divided into sections owing to the change-over to cellulose nutrition. (a) Oryzomys cousei Alston; (b) Nectomys sauamipes Brants; (c) Akodon arenicola Waterh.; (d) Oxymycterus nasutus Waterh.; (e) Oxymycterus rufus Desm.; (f) Reithrodontomys megalotis Baird.; (g) Baiomys muscullus Merriam; (h) Peromyscus (s. str.) leucopus Rafin.; (i) Peromyscus (s. str.) maniculatus Wagn.; (j) Peromyscus (Haplomylomys) californicus Gambell.; (k) Calomyscus bailwardi Thom. ; (l) Onychomys leucogaster Wield; (m) Phodopus sungorus Pall.; (n) Phodopus roborovskii Satunin; (o) Cricetulus (s. str.) longicaudatus Milne-Edw.; (p) Cricetulus (s. str.) kamensis Satunin; (q) Cricetulus (s. str.) migratorius Pall.; (r) Mystromys albicaucatus Wagn.; (s) Cricetulus (Tscherskia) triton de Winton; (t) Cricetulus (Allocricetulus) eversmanni Brandt.; (u) Cricetus cricetus L.; (v) Mesocricetus raddei Nahr.; (w) Mesocricetus brandti Nahr.; (x) Sigmodon hispidus Say et Ord.; (y) Neotoma floridana Ord.; (z) Neotoma albigula Hartley; (z_1) Neotomodon alstoni Merriam, See Fig. 123 for legends.

It is interesting that forms primarily adapted to predominantly protein (seed-eating) type of nutrition have relatively shorter intestine (*Peromyscus* 3. 4-4. 1 times longer than the body). The length of the intestine increases depending upon the extension of transition to mixed and predominantly cellulose type of nutrition (*Sigmodon hispidus* - 6. 7; *Cricetus cricetus* - 6. 4; *Mesocricetus raddei* - 6. 9; *Neotomodon alstoni* - 6. 5). But in forms secondarily changed over to the protein type of nutrition the relative length of the intestine becomes more than that in primarily seed-eating forms (*Onychomys* and *Oxymycterus* - 50; *Akodon arenicola* - 8. 0). In forms highly adapted to cellulose type of nutrition the length of the intestine may be reduced (*Neotoma floridana* - 3. 7; albigula - 3. 7).

4. Intestinal Structure of certain Rodents Relating to Cricetinae (Nesomycinae, Myospalacinae, Lophiomidae).

a. Nesomyinae

Nesomyinae is a group very much referred to interrelated development of sections and morphology of intestine. But the features of the structure of intestine do not facilitate the separation of Nesomyinae from Cricetinae.

The features for adaptation to the cellulose type of nutrition, reduction of small intestine and complication of caecum and large intestine can be very well traced in a number of forms of Nesomyinae (Fig. 132, 133; Table 6).

Macrotarsomys bastardi has an intestine which is only 2. 8 times longer than its body and is remarkably shorter than the intestine of most of the *Cricetinae* with protein nutrition. Caecum is small in size and has a very simple form and only one isthmus; its structure highly resembles that of *Oryzomys couesi*. The caecum is adjoining an ampulla, which is followed by the large intestine, that does not form any colic spiral ampullae and plicae obliquae (see Fig. 132, a; 133, a).

The intestine of *M. ingens* in its structure is close to the intestine of *M. bastardi*, but has peculiarities which justify the view of Petter (1959a) who had treated this form as an independent species. The intestine of *M. ingens* is 3. 6 times longer

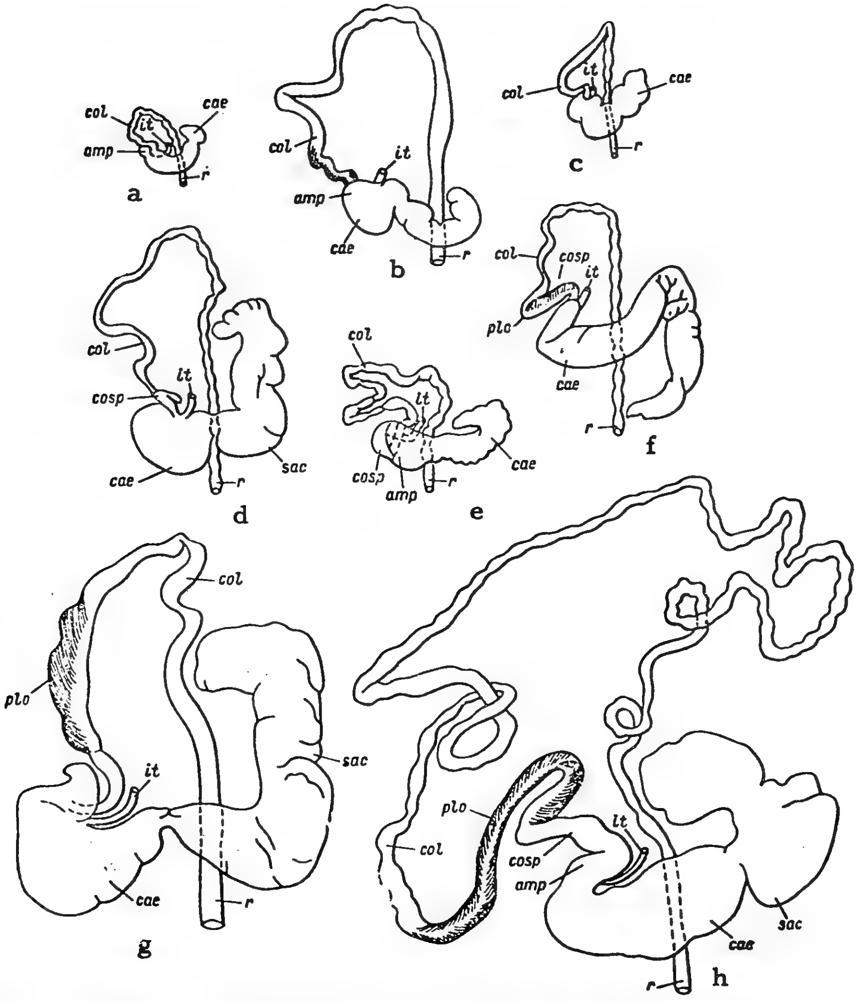


Fig. 132: Structure of large intestine and caecum of the Madagascar Nesomyinae; e - by Tullberg (1899) and the rest Orig. (a) Macrotarsomys bastardi Milne-Edw. et Grandidier; (b) Macaotarsomys ingens Petter; (c) Brachyuromys betsileoensis Bartl.; (d) Eliurus tanala F. Major; (e) Gymnuromys roberti; (f) Eliurus myoximus; (g) Brachytarsomys albicauda Günth; (h) Hypogoemys antimena. For legends see Fig. 123.

than its body while its small intestine is only 1.3 times longer than its large intestine and caecum. The relative size of the caecum is close to those of *M. bastardi*; the caecum is simple and resembles that of the previous species. However, the small

TABLE 6.

Relative dimensions and relative development of the sections of the intestine in Nesomyinae (Original)

Species	Relative length of the portion with respect to the total length of the entire intestine			Relative length of the intestine with respect to the body length
	Small	Large	Caecum	
Gymnuromys roberti[1]	75	19	6	8.8
Brachyuromys betsileoensis	68	26	6	7.2
Macrotarsomys bastardi	66	25	8	2.8
Eliurus tanala	58	26	16	4.6
Macrotarsomys ingens	57	33	10	3.6
Brachytarsomys albicauda	53	24	22	4.2
Hypogeomys antimena	48	43	9	-
Eliurus myoxinus	42	39	19	2.6

---

[1] According to the data given by Tullberg (1899).

intestine entering into the large intestine and outlet of the large intestine are close together. There is no ampulla. Additional sacculi of colic spiral also are absent. Spiral fold is developed on the ascending colon (see Fig. 132, b and 133b).

The length of the intestine of Brachyuromys betsileoensis exceeds its body length by 7. 2 times and its small intestine is 2. 1 times longer than its large intestine and caecum. The caecum is fairly wide for a short length and is divided into four separate chambers. The large intestine does not have any ampullae, accessory ampullae coli, colic spiral and plicae obliquae (see Fig. 132, c and Fig. 133, c).

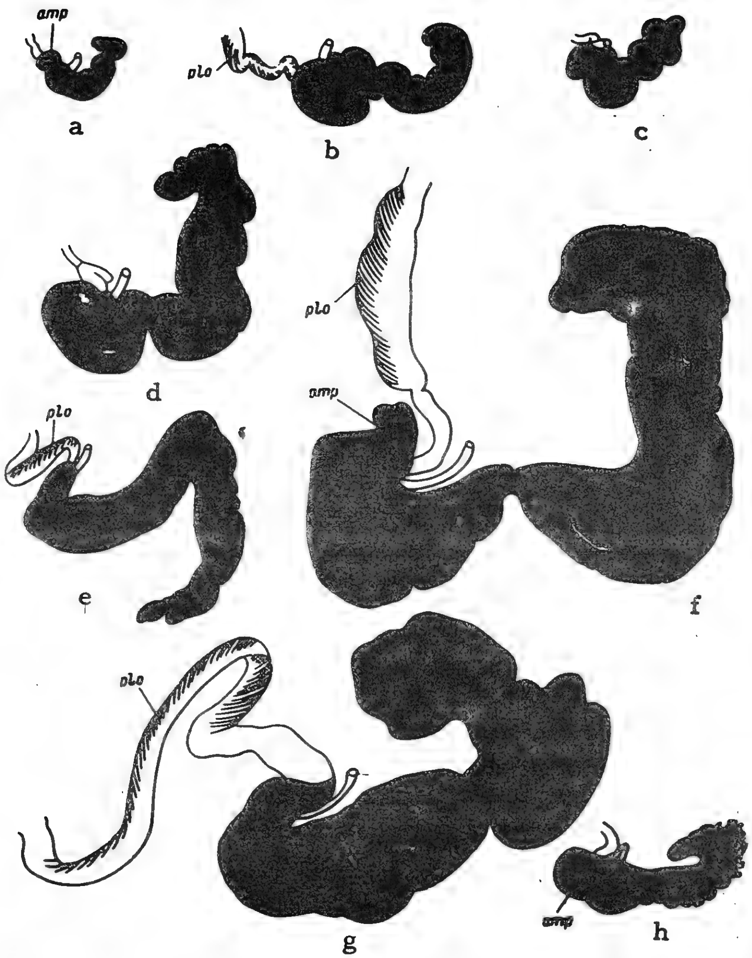


Fig. 133: Caecum and its analogs in the Madasgascar Nesomyinae; h - by Tullberg (1899); and the rest - Original. Complication of the caecum and its division into sections are traced. The series is homologous to the hamsters, voles and mice. (a) Macrotarsomys bastardi Milne-Edw. et Grandidier; (b) Macrotarsomys ingens Petter; (c) Brachyuromys betsi leoensis Bartl.; (d) Eliurus tanala F. Major; (e) Eliurus myoxinus; (f) Brachytarsomys albicauda Günth.; (g) Hypogeomys antimena; (h) Gymmuromys roberti. For legends see Fig. 123.

The intestine of Eliurus tanala is 4.6 times longer than its body while its small intestine is 1.4 times longer than the large intestine and caecum. The caecum is large in size but slightly segmented. Ampulla is absent. Colon does not form a spiral. Plicae obliquae are not developed on the large intestine (see Fig. 132, d and Fig. 133, d).

The intestine of El. myoximus differs sharply from that of El. tanala. Its intestine is 2.6 times longer than its body whereas its small intestine constitutes only 0.7 of the length of the large intestine and caecum. However, these figures cannot speak of the extreme reduction of small intestine. The duodenum is very well developed; its width is equal to or greater than the width of the stomach. The jejunum ileum portion is highly complicated owing to the formation of many plicae and spiral involutions of the intestine which greatly increases the area of the small intestine, even if it is short. The caecum is more complicated than in El. tanala and has three limbs separated from one another by isthmuses. The caecum has five chambers. Ampulla and colic spiral are absent. There is a spiral valve on the ascending colon (see Fig. 132, f and Fig. 133, e).

The differences in the intestinal structure of El. myoximus and El. tanala are so great that it is expedient to group these species in two different subgenera.

Further complication of the large intestine and caecum is observed in Brachytarsomys albicaudata. The length of the intestine exceeds its body length by 4.2 times whereas that of the small intestine, by 1.1 times. The caecum has three limbs. The middle one of these three limbs is divided into 2 clearly separated portions by an insthmus. There is a large caecum close to the place from where the large intestine begins. Ampulla and colic spiral are absent. There is a spiral valve on the ascending colon (see Fig. 132, g and Fig. 133, f).

Large intestine attains maximum development in Hypogeomys antimena. Here the small intestine is only 0.9 of the length of the large intestine and caecum. The form of the caecum highly resembles that of Brachytarsomys albicaudata, but the branching of caecum is still more pronounced - it consists of three chambers. Sacculus is absent near the beginning of the large intestine. Ampulla and colic spiral are absent. The large intestine is complicated in the ascending colon by considerable development of spiral valve; there is a dilation (ampulla coli accessorius) whose inner surface also is lined by spiral valve at the initial portion of the ascending colon. Ascending transverse and descending colons have bends increasing the length of this portion of the intestine (see Fig. 132, b and Fig. 133, g).

In Gymnuromys roberti (Tullberg 1899) the development of the caecum takes place by an increase in its surface owing to the formation of many blind pouch-like outgrowths along the greater curvature and not by a division of the caecum into chambers. The large intestine forms a colic spiral having one coil (see Fig. 132, e and Fig. 133 h).

A tendency for the adaptation of intestine for cellulose nutrition is traced in Nesomyinae. It is realized on the same morphological basis as in Cricetinae. The number of specializations of the intestine of Nesomyinae for cellulose nutrition are homologoust to that of hamster.

By its intestinal structure, the forms of Nesomyinae represent a widely radiated, but undoubtedly closely related group of forms of monophyletic origin.

b, Myospalacinae

The structure of the intestine in zokors is very peculiar (Fig. 134, b). In Myospalax myospalax the intestine is 7 times longer than its body. The small intestine forms 56% of the length of the entire intestine, large intestine -34 and caecum - 10%

The caecum has 2-3 bends and is subdivided into about 16 well separated chambers by numerous isthmuses and properly arranged plicae. However, in Myospalax these plicae on the inner wall of caecum do not have the form of "spiral valve" unlike in Spalax. A very large portion of the large intestine forming 5-6 ampullae, functionally one with the caecum lies adjoining the caecum. The large intestine immediately after the ampullae forms a colic spiral having 1.5-2 coils. Intestine in the colic spiral is 2-3 times wider than the large intestine and has up to 10-12 ampullae. The ascending, transverse and descending colons have numerous flexures and has many bends.

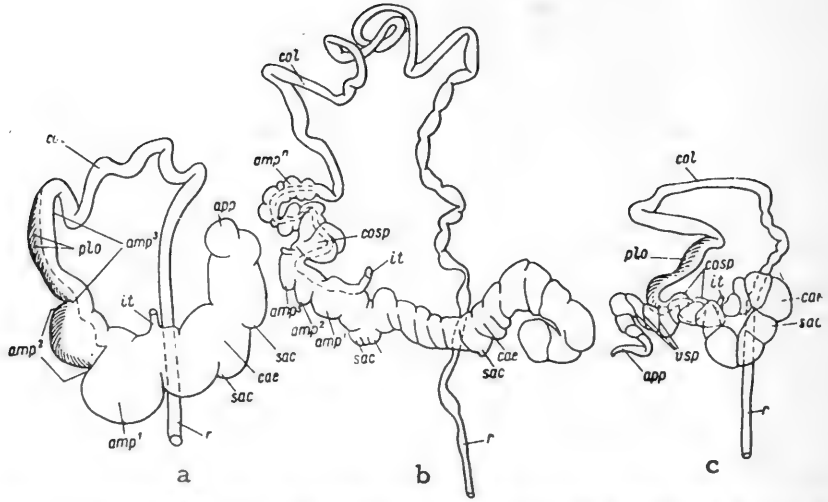


Fig. 134: Structure of the large intestine and caecum of certain fossorial rodents. Pay attention to the "spiral valve" in the caecum of Spalax, Original. (a) Geomys sp. (Geomyidae); (b) Myospalax myospalax Laxm. - (Myospalacinae, Cricetidae); (c) Spalax leucodon Güldenst (Spalacidae). For legends see Fig. 123.

Peculiarities in the structure of the caecum and the initial part of the large intestine distinguish Myospalax from Cricetinae, Microtinae and Spalacidae with which certain investigators have grouped the zokors. This throws light on the independent nature of this peculiar group of rodents.

c. Lophiomyidae

Milne-Edwards (1867) has described the caecum structure of Lophiomys imhausi and has given a figure of caecum in his work.

From the figure of the caecum given by Milne-Edwards it is seen that caecum has a fairly simple structure (Fig. 135). It is arch shaped and not differentiated into sections by isthmuses and folds. The volume of the caecum is half that of the stomach. A plica separating the caecum from the colon develops at the caecum - large intestine opening. Just after the isthmus the large intestine forms an ampulla which continues as the colic spiral with one coil. The spiral forming portions of the intestine are dilated before the ampulla formation.

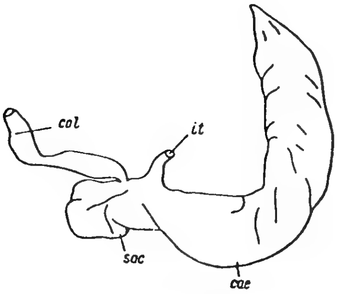


Fig. 135: Structure of caecum of Lophiomys imhausi Milne-Edw. (Lophiomyidae). After Milne-Edwards (1967). For legends see Fig. 123.

In the structure of the caecum and the initial portions of the large intestine Lophiomys does not at all differ from either Cricetinae or other members of Muroidea.

5. Structure and trends of the Specialization of the Intestine of some Rodents, mainly Myomorph rodents (Gerbillinae Microtinae, Muridae, Spalacidae, Bathyergoidea and Geomyoidea).

Homologous and parallel series of variability of the rodent intestine.

A number of changes in the structure of the intestine undergone on account of the change over from protein to cellulose nutrition are traced not only in Cricetinae and Nesomyinae, but also in other rodents allied to hamsters and far removed from them.

a. Gerbillinae

A tendency for reducing the small intestine and complicating the large intestine and caecum (Table 7) associated with the change over of certain members of Gerbillinae (Rhombomys opinus, etc.) to mostly cellulose nutrition is clearly traced in the series of Gerbillinae from Gerbillus and Meriones to Rhombomys and Psammomys.

Just as in Cricetinae, the transition of Gerbillinae to the cellulose nutrition leads not only to a change in the relative

TABLE 7

Relative dimensions and relative development of the divisions of the intestine in Gerbillinae (from Vorontsova, 1962 b).

Species	Relative length of the portion to the total length of the entire intestine %			Intestine length - body length ratio
	Small intestine	Large intestine	Caecum.	
Meriones shawi	73	17	11	5.0
Gerbillus pyramidum	72	22	6	1.9
Gerbillus dasyurus simoni	68	25	7	5.4
Meriones persicus	67	19	14	4.6
Meriones tamariscinus	65	25	10	5.6
Brachiones przewalskii	64	22	14	5.4
Meriones erythrourus	63	28	9	3.4
Meriones libycus libycus	61	26	12	4.6
Meriones vinogradovi	57	31	12	4.5
Meriones meridianus	57	31	12	4.1
Meriones unguiculatus	57	34	9	5.9
Meriones crassus swinhoei	56	31	13	4.1
Tatera indica	56	32	12	3.9
Meriones tristrami	55	30	12	3.5
Rhombomys opimus	54	35	11	5.2
Psammomys obesus	47	38	15	4.4

development of the intestine and complication of the large intestine and caecum, but also to the development of an ampulla and colic spiral. Increase in the volume of the caecum owing to the ampulla of the large intestine is faintly expressed in *Meriones persicus* and *M. tristrami* and well expressed in *M. vinogradovi*, *M. meridianus*, *Gerbillus pyramidum* and *Tatera indica.*

Colic spiral is developed in all members of Gerbillinae and has 1-3 coils. The colic spiral has only one coil in *Gerbillus pyramidum*, *Tatera indica*, *Psammomys obesus*, *Rhombomys opimus*, *Meriones erythrourus*, *M. unguiculatus*, *M. crassus* and *M. melanurus*. In *M. vinogradovi*, *M. meridianus*, *M. persicus*, *M. tamariscinus*, *M. tristrami* and *Brachiones przewalskii* the colic spiral has two coils whereas in *Gerbillus dasyurus* and *Meriones* shawi it has three coils.

While there is considerable similarity in the structure of the intestine and in the trend of its variability between Cricetinae and Gerbillinae, Gerbillinae are characterized by a considerably low range of variability in the intestinal structure.

b. Microtinae

The tendency for the reduction of small intestine and complication of large intestine and caecum is well expressed in Microtinae - a group adapted to cellulose food.

It is remarkable that while there is similarity between *Cricetinae* and *Gerbillinae* not only in the trend of variability of intestine but also in the methods of morphological resolution of the associated problems, Microtinae, which is even more primitive in these species, differs from *Cricetinae* and *Gerbillinae* by its considerable specialization for cellulose nutrition. *Dolomys* and *Prometheomys* of Microtinae more primitive from the point of view of specializations of the intestine may top the corresponding orders of *Cricetinae* and *Gerbillinae* in their degree of intestinal adaptation to cellulose nutrition.

The range of intergroup variability of the intestine is wider in Microtinae (Table 8 and Fig. 136) than in *Gerbillinae* and even *Cricetinae*.

TABLE 8

Relative sizes and correlative development of the sections of intestine of Microtinae (After Vorontsov, 1962 b, with supplementaries).

Species	Relative length of the portions with respect to the total length of the entire intestine, %			Intestine length-body length ratio.
	small intestine	large intestine	caecum	
Clethrionomys glareolus[1]	60	27	13	7.2
Dolomys bogdanovi	55	31	14	6.1
Prometheomys schaposchnikovi	55	28	17	6.3
Lemmus chrysogaster	55	31	14	7.4
Lemmus lemmus	54	29	17	6.9
Alticola argentatus	54	30	16	6.1
Dicrostonyx torquatus	51	37	11	7.8
Aschizomys lemminus	50	35	16	7.4
Microtus (Chionomys) gud.	50	32	18	6.3
Microtus (s.str.) oeconomus	50	37	14	5.7
Ondatra zibethica	50	35	16	7.2
Ellobius talpinus	49	32	19	4.7
Ellobius lutescens	48	33	19	4.2
Lemmus obensis	48	43	9	8.4
Lemmus amuirensis	48	45	7	-
Myopus schusticolor	48	45	8	9.2
Lagurus lagurus	47	33	19	5.9
Microtus (s.str.)ungurensis	47	35	19	4.1
Microtus (Phajomys) juldaschi	46	41	14	4.9
Arvicola terrestri	45	39	16	7.8
Microtus (s.str.) agrestis[2]	45	39	17	7.4

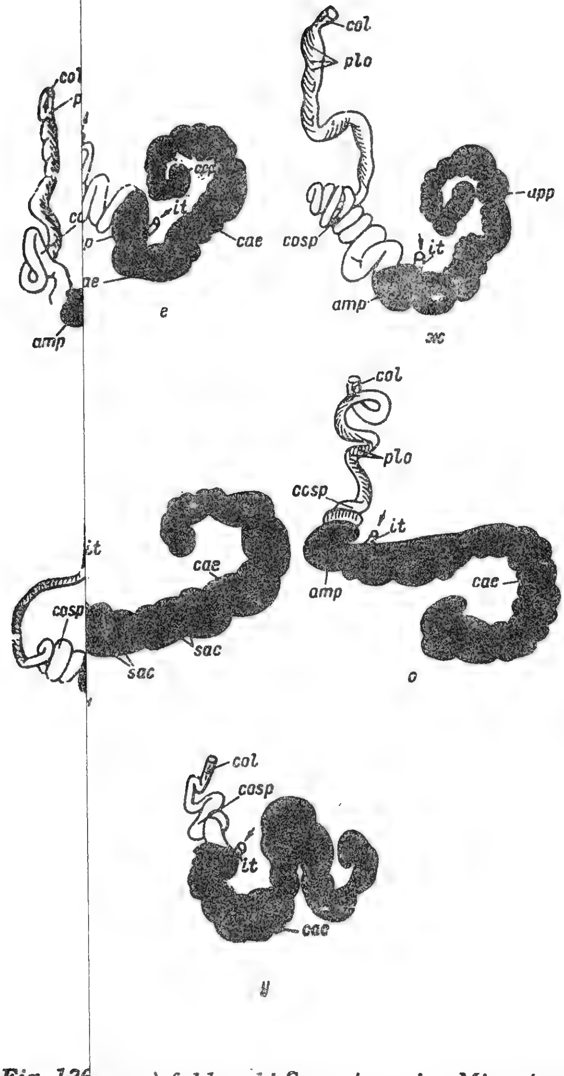


Fig. 136mys) fuldaschi Savertz. ; j - Microtus
The (s. str.) oeconomus Pall. ; l - Microtus
com(s.str.) fortis Buchner; n - Microtus
homa (s.str.) argentatus Severtz. ; p - Alticola
(196luteus Eversmann; r - Ellobius lutescens
Satusee Fig. 123.
amu

Fig. 136. ***Caecum and initial portion of the large intestine of Microtinae.*** *The series is arranged according to the degree of increase in dimensions and complexity of caecum; caecum and its analogs are shown in black. The series is homologous to the orders of Cricetinae, Nesomyinae and mice. After Vorontsov (1962, a). a - Dolomys bogdanovi Martino; b - Prometheomys schaposchnikovi Satunin; c - Dicrostonyx torquatus Pall; d - Myopus schisticolor Lill.; e - Lemmus amurensis Vinogr.; f- Lemmus lemmus L.; g - Lemmus obensis Brants; h - Microtus (ohionomys) gud Satunin; i - Micaotus (Phajomys) fuldaschi Savertz.; j - Microtus (Phajomys) carruthersi Thom; k - Microtus (s. str.) oeconomus Pall.; l - Microtus (s. str.) hyperboreus Vinogr.; m - Microtus (s. str.) fortis Buchner; n - Microtus (s. str.) ungurensis Kastschenko; o - Alticola (s. str.) argentatus Severtz.; p - Alticola (Aschizomys) lemminus Mill.; q - Lagurus luteus Eversmann; r - Ellobius lutescens Thom.; s - Ellobius talpinus. for legends see Fig. 123.*

Microtus (s.str.) *arvalis*[3]	44	38	18	6.3
Neofiber alleni	43	44	14	6.8
Microtus (s.str.) *michnoi*	41	37	22	5.8
Microtus (s.str.) *hyperboreus*	40	42	18	4.6
Lagurus luteus	39	47	14	7.5

---

1. According to the data given by Myrcha (1961)
2. According to the data given by T. Tullberg (1899)
3. According to the data given by N.P. Naumov (1948).

The volume of the large intestine and caecum of Microtinae increases as a result of their various adaptations: simple increase in the size of the caecum and the large intestine, development of large ampullae, very complicated colic spiral, spiral valves on the ascending colon, complication of the caecum by the formation of additional blind pouches, ampulla coli and isthmuses. It is interesting that a simultaneous development of all these characteristics and generally an equal level of adaptation to each one of these features is not observed in any species of Microtinae.

The structure of caecum and large intestine is simpler in the ancient and primitive forms of Microtinae, *Dolomys bogdanovi*. Here the caecum has only four chambers slightly separated from one another and adjoined by an ampulla and a three-coiled colic spiral. Spiral valves develop on the ascending colon (see Fig. 136, a).

In *Prometheomys schaposchnikovi* also belonging to the primitive tribe of rhizodental voles, *Fibrini* the size and the branching property of caecum into sacculations and outgrowths greatly increase. Ampulla consisting of two chambers also increases. However, the number of coils of the colic spiral is reduced to two. The degree of development of spiral valves remains unchanged (see Fig. 136, b).

Dicrostomyx torquatus - a member of the tribe Lemmini - has a very simple caecum consisting of three chambers. The size of the caecum increases 1.5 - 2 times owing to the development of two ampullae; colic spiral has four coils. Spiral valves are absent on the ascending colon (See Fig. 136, c).

The caecum is very much complicated in *Myopus schisticolor.* Here, it consists of 12-14 chambers and sacculations adjoined by 4 ampullae of the large intestine. The 7-8 coiled colic spiral stretches beyond the ampullae (see Fig. 136, d).

The structure of the caecum of the genus *Lemmus* (see Fig. 136, e, f, g) is much simpler than that in *Myopus.* This spirally twisted structure is divided into 10-14 chambers by shallow isthmuses. There is only one large ampulla in the intestine. However, if caecum and its analogs are considerably less developed in *Lemmus* than in *Myopus*, the colic spiral is very well developed and has 11-12 coils in *Lemmus obensis*. The spiral valve is not well developed on the ascending colons of *L. amurensis* and *L. lemmus* and is developed only in *L. obensis.*

According to the degree of development of the caecum, the forms of *Lemmini* examined are arranged in the following order :

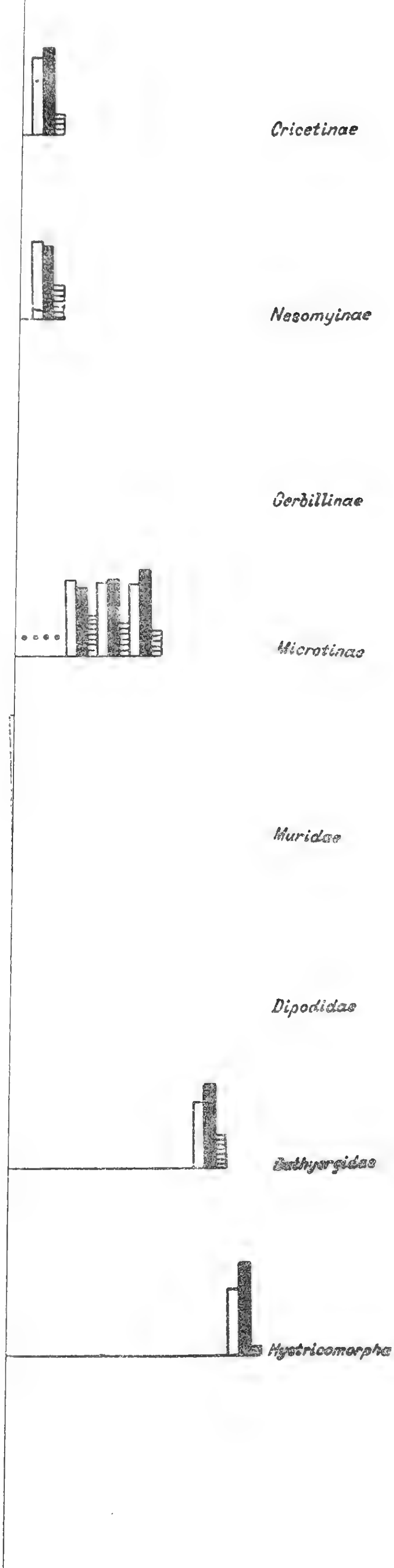
Dicrostonyx torquatus → *Lemmus amurensis* →

→ *L. Lemmus* → *L. obensis* → *Myopus schisticolor*

According to the degree of development of the spiral valve in the large intestine, the same species are arranged in another order.

$$\left.\begin{array}{l}\textit{Dicrost torquatus}\\ \textit{Myopus schisticolor}\\ \textit{L. amurensis}\\ \textit{L. Lemmus}\end{array}\right\} \quad \textit{L. obensis}$$

According to the complexity of colic spiral and increase in the number of its coils, the same species are arranged in yet another order.


Cricetinae
Nesomyinae
Gerbillinae
Microtinae
Muridae
Dipodidae
Bathyergidae
Hystricomorpha

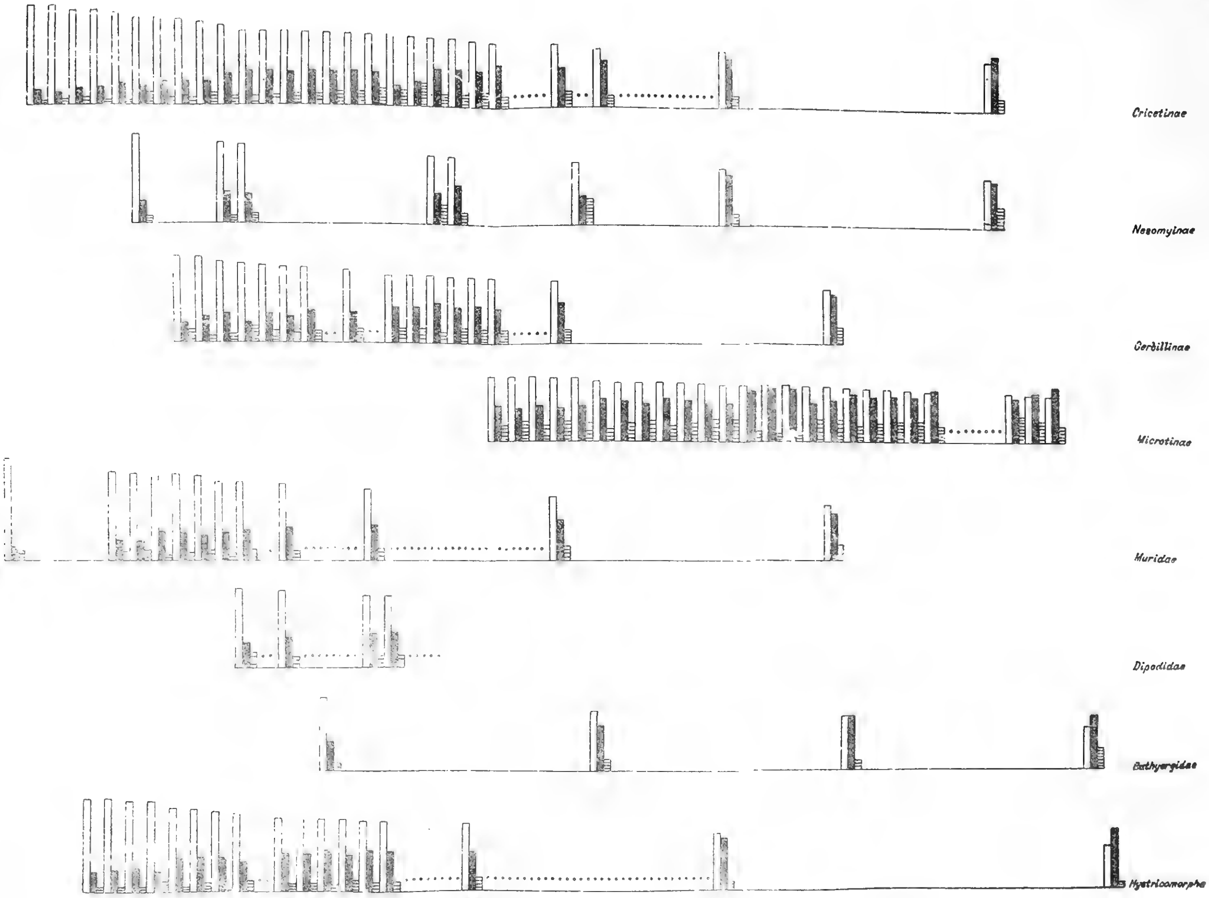


Fig. 133. Homologous and parallel series of variability in the correlative dimensions of intestine in certain groups of rodents.

The series are arranged (from left to right) according to the degree of the decrease in the relative dimensions of small intestine (white) and increase in the relative dimensions of large intestine (black) and caecum (horizontal hatching). Pay attention to the greater width of the range of variability of Cricetinae and Nesomyinae as compared with Gerbillinae and Microtinae.

Dicrost. torquatus → Myopus schisticolor →
→ L. Lemmus → L. amurensis → L. obensis

These facts show the non-uniformity in the rate of transformation of the individual parts of the digestive system (Vorontsov, 1961, a and 1963 e) within a closely related group of forms.

A progressive complication of caecum and large intestine is traced in the tribe Microtini in the central polytypic genus of this tribe, Microtus.

In Microtus (Chionomys) gud (see Fig. 136, h) and M. (Ch.) nivalis, the caecum has a wavy surface along the lesser curvature and is partially divided only into 3-4 chambers by shallow isthmuses. Ampullae are absent, colic spiral has three coils, whereas a spiral valve develops in the large intestine. Caecum is complicated in the subgenus Phajomys but here the spiral valve is poorly developed. In M. (Phajomys) carruthersi the caecum is complicated by the formation of many shallow ampulla coli along the greater curvature. The ampullae which also have small saccular outgrowths along the greater curvature increase the size of the caecum. Colic spiral is absent. There are two accessory ampullae coli at the initial portion of the ascending colon. The spiral-valve runs along the inner wall of these ampullae (see Fig. 136, j).

The saccular outgrowths along the greater curvature are better developed in M(Ph) juldaschi than in the previous species. Caecum has two bends. Ampulla is present. Colic spiral has 5-6 coils, but spiral valve is absent in the large intestine (see Fig. 136, i).

The caecum is complicated in the subgenus Microtus (s. str) as a result of its division into a number of chambers by isthmuses.

The caecum in M. (s. str.) oeconomus (see Fig. 136, k) is divided into 13-14 chambers. Ampullae absent, colic spiral with two coils. A slightly developed spiral valve is present in the ascending colon.

The division of caecum (into 10-12 chambers) is better expressed in M. (s.str.) hyperboreus than in the previous species. Ampulla is present. Colic spiral has 4-5 coils, but the spiral valve is poorly developed in the large intestine (see Fig. 136, l).

Caecum in M. (s.str.) ungurensis has two bends and is divided into about 14 chambers by isthmuses. Ampulla is developed, but the colic spiral has only 2-3 coils. In the large intestine the spiral valve is poorly developed (see Fig. 136, n)

In M. (s.str.) fortis also the caecum has two bends, but here it is complicated by lateral saccular outgrowths (in agreement with Mesocricetus raddei) which are considerably separated from the "body" of the caecum. Ampulla is small and colic spiral has only 4-5 coils. Spiral valve develops not only in the ascending colon but also on the transverse colon (see Fig. 136, m).

Intestinal adaptation of the genus Alticola to cellulose nutrition is reflected by the complication of the caecum and the increase in its absolute and relative dimensions. Meanwhile, the number of coils in the colic spiral does not exceed 3-4. Spiral valve is absent in the large intestine. Ampulla is poorly developed.

In Alt. (s.str.) argentatus the caecum is complicated by many annular isthmuses. Their position corresponds to the interior of caecum dividing it into 25-30 chambers. Ampulla is absent; colic spiral has coils. There is a fourth rudimentary coil also (see Fig. 136, o).

In Microtinae the division of caecum by isthumses and formation of sacculi reaches the maximum in Alt. (Aschizomys) lemminus. The number of chambers and appendices goes up to 30-35. Some of these chambers are considerably separated from the body of caecum. Here a small ampulla is present. Colic spiral has three coils (see Fig. 136, p).

Among Microtini and the entire Microtinae, large intestine and caecum achieve maximum development in Lagurus leuteus. Intestine is 7.5 times longer than its body, whereas the small intestine forms only 0.5 of the length of the large intestine and the caecum. Caecum is large in size and is divided into 2[illegible]-25 chambers separated from one another by isthmuses and well developed plicae of the inner surface of the intestine. There are many ampullae coli and sacculi along the greater and lesser curvatures of the stomach. Ampulla is present. Colic spiral has only 2 coils. A spiral valve develops in the ascending colon (see Fig. 136, q).

According to the degree of development of caecum the forms of Microtini studied are arranged in the following order.

M. (Chionomys) gud -> M. (Phajomys) carruthersi -> M (Ph). juldaschi -> M. (s. str.) oeconomus --> M. (s. str.) ungurensis --> M. (s. str.) hyperboreus --> M. (s. str.) fortis --> Alticola (s. str.) argentalus --> Alt. (Aschizomys) lemminus --> Lagurus luteus.

The same species are arranged in another order according to the degree of development of spiral valve in the large intestine.

M. (ph.) Juldaschi
Alt. (s. str.) argentatus
Alt. (Aschizomys) lamminus

M. (ph.) carruthersi
M. (s. str.) hyperboreus

M. (Ch.) gud
M. (s. str.) oeconomus
M. (s. str.) fortis
M. (s. str.) ungurensis
Lag. luteus

The same species form yet another order according to the degree of the increase in the number of colic spiral coils.

M. (ph.) carruthersi → { M. (s. str.) oeconomus
Lag. luteus } →

→ M. (s. str.) ungurensis { M. (Ch.) gud
Alt. (s. str.) argentatus
Alt. (Aschiz) lemminus } →

→ { M. (s. str.) hyperboreus
M. (s. str.) fortis } → M. (Ph.) juldaschi

All these facts show the high degree of non-uniformity in the rate of transformation of the organs of the digestive system, and may be considered as examples of the compensation of the functions of one organ by another (Vorontsov) 1961 a, 1963 e).

The same tendency of specialization of the intestine for cellulose nutrition is traced in the tribe Ellobiini also.

The intestine of *Ellobius lutescens* (see Fig. 136, r) is 4. 2 times longer than its body, while its small intestine constitutes only 0. 9 of the length of large intestine and caecum. The caecum is divided into 10 chambers by isthmuses and forms some projections and sacculi. Ampulla absent. Colic spiral has 4 coils. Spiral valve does not develop in the ascending colon. In *Ell. talpinus* (see Fig. 136, a) the caecum is complicated by bends: it has five bends; but sacculi are less developed than in *Ell. lutescens*. In *Ell. talpinus* the relative length of the intestine goes upto 4. 7 times. In other respects the intestine of *Ell. talpinus* is similar to that of *Ell. lutescens*.

The sharp differences in the intestinal structure of *Ellobius* and *Prometheomys* should be especially noted. According to the degree of intestinal adaptation for cellulose nutrition Ellobiini form the following order.

Ellobius lutescens → *Ell. talpinus*

c. *Muridae*

The family *Muridae* is more adapted to protein nutrition than *Cricetidae*. However, a tendency for the specialization of intestine for mixed nutrition with considerable amount of cellulose is traced in this group, consisting mainly of seed-eating rodents in spite of the fact that the number of species of this group studied is limited (Table 9 and Fig. 137).

Among the species of Muridae studied by us and described by Tullberg (1899) it is the Australian carnivorous rat *Hydromys chrysogaster* (see Fig. 137, a), our bandicoot rat *Nesokia indica* (see Fig. 137, b) and African mouse *Dendromys mesomelas* (see Fig. 137, c) which have a very simple structure of

TABLE 9

Relative dimensions and correlative development of the different portions of intestine in certain Muridae (orig.)

Species	Relative length of the portion with respect to the total length of the entire intestine			Intestine length-body length ratio.
	Small intestine	Large intestine	Caecum	
Hydromys chrysogaster[1]	86	11	3	6.8
Mus musculus[2]	74	19	7	6.0
Apodemus agrarius	73	19	8	4.6
Chiropodomys penicillatus[1]	72	24	4	4.7
Nesokia indica	72	23	6	4.8
Dendromys mesomelas[1]	71	21	8	4.7
Cricetomys gambianus	66	28	6	3.9
Apodemus flavicollis[2]	55	25	9	5.5
Conilurus penicillatus	64	28	8	-
Apodemys sylvaticus	60	29	10	3.8
Saccostomus lapidarius[2]	54	34	12	4.4
Otomys unisulcatus[1]	57	40	14	5.1

---

1) According to the data of T. Tullberg (1899).
2) According to N.P. Naumov (1948).

the caecum. The caecal structure of these species highly resembles that of the insectivorous hamsters, *Oxymycterus*. The large intestine is devoid of the colic spiral and spiral valves. The simplified structure of caecum and large intestine conforms to the mainly protein nutrition of *Hydromys* and *Dendromys*. However, the highly simplified caecum and large intestine of *Nesokia*, feeding mostly on the vegetative parts of the plants, may be explained only as a manifestation of the non-uniformity in the rates of transformation of the digestive organs. As a result

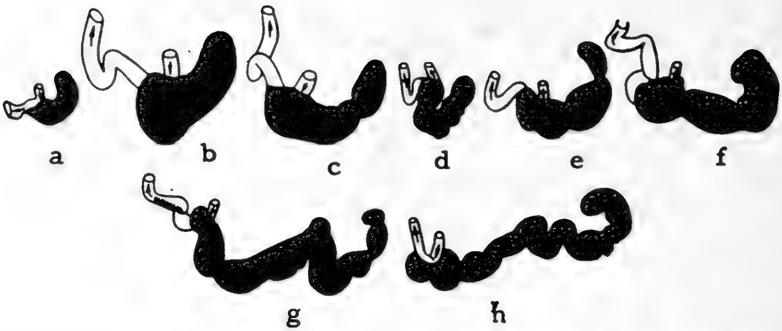


Fig. 137: Structure of caecum and its analogs in certain forms of Muridae; a, c, e - according to Tullberg (1899) and the rest-original. Complication of caecum and its differentiation into sections are traced. The series is homologous to that of Cricetinae, Nesomyinae and Microtinae. (a) Hydromys chrysogaster; (b) Nesokia indica Gray; (c) Dendromys mesomelas; (d) Rattus norvegicus Berk; (e) Conilurus penicillatus; (f) Saccostomus lapidarius; (g) Apodemys sylvaticus L.; (h) Crecetomys gambianus.

of this the caecum and the large intestine of Nesokia are balancing organs (Vorontsov, 1961 a and 1963 e).

The caecum is somewhat complicated in Rattus norvegicus. Here the caecum has two bends and is divided into three chambers. The large intestine is devoid of ampulla, colic spiral and spiral valves (see Fig. 137, e).

Large intestine and caecum are still more complicated in the African Savanna cricetid, Saccostomus lapidartus. Colic spiral forms one coil (see Fig. 137, f).

In the genus Apodemus, caecum and large intestine are more developed in Ap. sylvaticus (see Fig. 137, j). The caecum has four bends and is divided into 8 chambers by isthmuses. Large intestine has an ampulla and a spiral valve. Colic spiral is poorly developed.

The caecum is quite large in Cricetomys gambianus (see Fig. 137, h). It is divided into 8 chambers to which the ampulla of the large intestine is adjoined. The colic spiral and spiral valves are not present in the large intestine.

Judging from the data given by Tullberg, (1899) the caecum and the large intestine are better developed in Saccostomus and especially in Otomys.

In Hydromys (Tullberg, 1899), the sharp increase in the size of the small intestine and reduction of the caecum are, apparently, associated with the secondary transition to the predatory mode of nutrition (parallelism with Ichthyomys).

It is found that the range of variability in the structure of the intestine of Muridae is almost the same as that in Cricetidae.

In the structure of the intestine of Muridae there are no features that would permit us to contrast the members of Muridae from Cricetid.

d. Spalacidae and Rhizomyidae

Convergence of the structure of intestine in burrowing rodents.

Spalacidae and Rhizomyidae differ considerably from Cricetidae, Lophiomyidae and Muridae in the structure of their intestine.

A spiral fold dividing the caecum into 18-20 chambers, almost fully separated from one another, is developed in the caecum of Spalax. The structure of the caecum is Spalax (see Fig. 134, c) is similar to that of Leporidae and very convergently resembles the form of the spiral valve of the intestine of selyakhs and cartilaginous ganoid fishes. Large intestine has a three-coiled colic spiral and spiral folds.

"Spiral valve" develops in the caecum of Rhizomyidae also (Tullberg, 1899). Rhizomys also has a three coiled colic spiral. Differences in the structure of the intestine of Myospalax from that of Spalax and Rhizomys are as profound as the similarity between the latter two genera.

Attention should be paid to the fact that in Bathvergidae convergent with Spalacidae and Rhizomyidae, there appears (in Cryptomys) a "spiral valve" in its caecum.

Convergence caused by the burrowing way of life, is so profound in rodents that it affects not only the locomotion system, appearance and body proportion of the animal, but also the digestive system. Convergence in the relative development of the sections of the intestine in the distantly related and unrelated forms of burrowing rodents (Table 10) living under similar ecological conditions is of significance.

TABLE 10

Convergence in relative sizes and correlative development of the sections of the intestine in borrowing rodents of Holcartic steppe regions.

Species and their systematic position	Relative length of the portion with respect to the total length of the entire intestine, %			Intestine length-body length ratio
	Small intestine	Large intestine	Caecum	
Muroidea Cricetidae Myospalacinae				
Myospalax myospalax	56	34	10	7.0
Spalacidae				
Spalax microphtalmus	56	33	11	4.7
Spalax leucodon	55	34	11	4.5
Geomyoidea Geomyidae				
Geomys bulbivora	57		10	5.1

However, the convergence covers such superficial features as correlative development of the sections of the intestine, whereas the internal structure of the caecum and the large intestine in such forms as Myospalax, Spalax and Geomys differ considerably from one another.

Tullberg (1899) who has studied the intestine of Tachyoryctes does not mention anything about the "spiral valve" in the caecum of this genus.

e. Muroidea

It is observed that a process of adaptation of the structure of intestine for cellulose nutrition takes place independently of one another in the different subfamilies of the superfamily Muroidea within this large group of rodents. There are several series of homologous variability in the structure of the intestine on account of the adaptation for cellulose nutrition (Cricetinae, Nesomyinae, Myospalacinae, Gerbillinae, Microtinae and Muridae). In Spalacidae and Rhizomyidae the adaptation of intestine for cellulose nutrition is convergently different from that in Cricetidae, Muridae and Lophiomyidae.

The author cannot draw a demarcating line between the homologous series of each of the subfamilies of Muroidea. The intestine structure of the series may define the range of variability and the degree of the tendency for protein or cellulose nutrition (Fig. 138).

Along with the basic trend in intestine specialization - reduction of small intestine and enlargement of caecum and large intestine mastering of free niche of nutrition by certain forms (Ichthyomys, Oxymycterus, Onychomys, etc. of Cricetinae and Hydromys and allied genera of Muridae) leads them to a change over to protein nutrition. This results in the reduction of caecum and large intestine and an enlargement of small intestine. However, the basic trend in the intestine specialization of Muroidea is the adaptation for cellulose nutrition.

f. Other Myomorpha (Dipodoidea and Myoxoidea)

Muroidea, in its intestinal structure, does not differ from Dipodoidea. Complication and increase in the relative size of caecum and large intestine with change over from protein to combined nutrition with considerable amount of cellulose (Table 11) is traced in the latter group also.

Myoxoidea differs considerably from Muroidea and Dipodoidea in the absence of a caecum.

The genus Platacanthomys is allied to Myoxoidea in this respect, Typhlomys (Thomas, 1896) has a poorly developed caecum. It is justly observed by Ellerman (1940) that reduction of caecum may be so profound in certain Muroidea (Ichthyomys, Oxymyceterus, Hydromys, etc.) that it is not clear whether the reduction of caecum in Platacanthomys can be considered as a feature which distinguishes this genus from Typhlomys.

TABLE 11

Relative size and correlative development of the different sections of intestine in Dipodoidea. Calculated according to Tullberg's (1899) absolute data.

Species	Relative length of the portion with respect to the total length of the entire intestine			Intestine length-body length ratio
	Small intestine	Large intestine	Caecum	
Sicista subtilis	66	21	13	4.1
Dipus aegyptycus	64	25	9	7.1
Zapus hudsonicus	60	28	12	4.7
Allactaga faculus	60	30	10	7.9

g. Bathyergomorpha and Hystricomorpha

A tendency for the adaptation of intestine for cellulose nutrition is observed not only in the Myomorpha group but also in other rodent groups.

A progressive enlargement of the large intestine and caecum and complication of the caecum right up to the formation of a spiral valve is observed in Cryptomys (Figs. 139 and 140; and Table 12) of the ancient groups of rodents - fossorial Bathyergomorpha (unlike Spalacidae and Myospalacinae, Bathyergidae is not a monotypic group).

It is remarkable that in Cryptomys the complication of caecum is associated with the reduction in the relative length of the intestine as a whole.

It may be generalized that in the relatively more primitive and ancient groups adaptation for cellulose nutrition takes place mostly by an increase in the relative length of the entire intestine, especially the large intestine. In progressive groups of

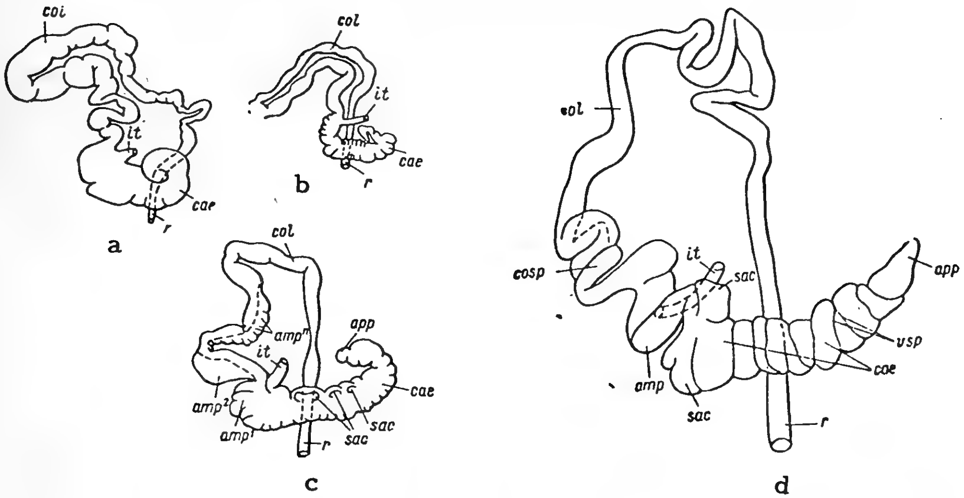


Fig. 139: Structure of large intestine and caecum of certain Bathyergidae: a and b after Tullberg (1899) c and d - original. (a) Bathyergus martimus; (b) Georychus capensis; (c) Myoscalpos argeutes; (d) Cryptomys damarensis Ogilby. For legend see Fig. 123.

TABLE 12

Relative length and correlative development of the sections of intestine of Bathyergidae.

Species	Relative length of a section to the total length of the intestine, %			Intestine length - body length ratio
	Small intestine	Large intestine	Caecum	
Myoscalops argentes	62	25	7	5.4
Georychus capensis[1]	51	38	10	5.7
Bathyergus martimus[1]	46	46	8	6.0
Cryptomys damarensis	36	46	18	4.2

1) According to T. Tullberg's (1899) data.

herbivorous rodents (in the tribe Microtini, Myospalacinae, Spalacidae, etc.) adaptation for cellulose nutrition is by a complication in the form of the caecum and large intestine with an intensification of their functions which leads to a secondary reduction in the intestinal length.

TABLE 13

Relative length and correlative development of the sections of the intestine of Hystricomorpha. Calculated on the basis of the absolute data of Tullberg (1899).

Species	Relative length of the section to the total length of the intestine, %			Intestine length-body length ratio
	Small intestine.	Large intestine	Caecum	
Dasyprocta aguti	78	19	4	12.3
Atherura africana	78	18	4	12.9
Hystrix cristata	76	19	4	11.6
Myopotamus coypus	76	17	8	16.9
Lagostomus trichodactylus	70	28	3	8.5
Hydrochoerus capibara	69	24	7	10.5
Coelogenys paca	67	29	3	31.0
Echinomys cayennensis	66	25	9	8.9
Nelomys antricola	62	32	6	7.7
Abrocoma bennetti	62	31	6	12.2
Erethizon dorsatus	61	34	5	9.4
Spalacopus poeppigi	61	30	9	5.5
Cavia porcellus	59	35	7	-
Octodon degus	59	34	8	7.3
Ctenomys magellanicus	57	32	11	7.5
Cannobatheomys amblyonyx	48	44	8	3.3
Chinchilla taniger	36	49	5	10.4

In the very old suborder of rodents, Hystricomorpha, the intestine is adapted for cellulose nutrition not only by a complication of caecum (Fig. 141) but also by an increase in the length of caecum and large intestine and an elongation of the entire intestinal tract (Table 13).

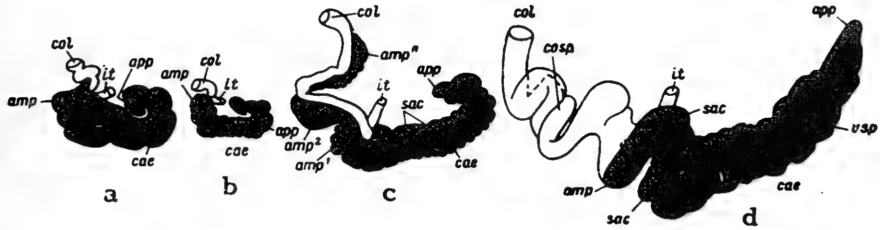


Fig. 140: *Caecum and its analogs in certain forms of Bathyergidae a and b, after Tullberg (1899) c and d original, after Vorontsov (1962). (a) Bathyergus martimus; (b) Georychus capensis; (c) Myoscalops argentes; (d) Cryptomys damaremsis Ogilby. For legend see Fig. 123.*

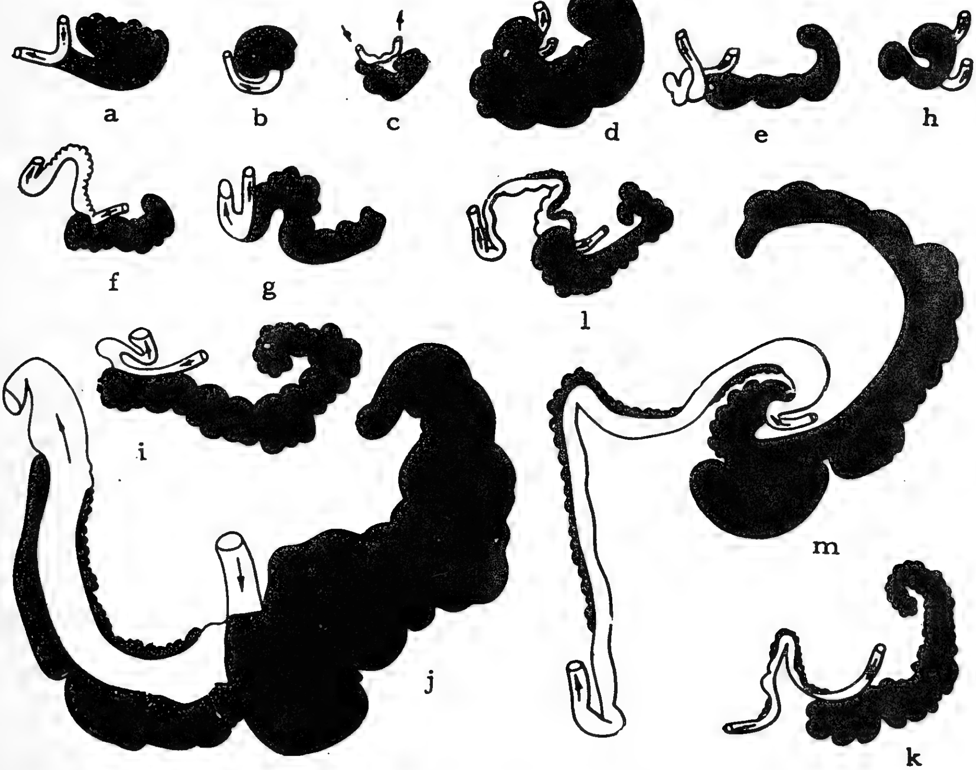


Fig. 141: *Caecum and its analogs in some members of the suborder Hystricomorpha. According to Tullberg (1899). (a) Chinchilla laniger; (b) Coelogenys paca; (c) Dasyprocta aguti; (d) Cavia porcellus; (e) Cannobatheomys ambiyonyx; (f) Spalacopus poeppigi; (g) Dolichotis patagonica; (h) Erethizon dorsatus; (i) Habracoma bennetti; (j) Hystrix cristata; (k) Ctenomys magellanicus; (l) Echinomys cayennensis; (m) Myocastor coypus. For legends see Fig. 123.*

Unlike the herbivorous Myomorpha the relative length of the caecum in Hystricomorpha almost never attains a two digit percent whereas, the relative length of intestine, as a rule, is 9-12 and in individual cases, 31 times more than the body length. Thus, the forms of Hystricomorpha, convergent with those of Myomorpha, solve the similar functional problem in a different manner. It seems to us that the means adopted by Myomorpha leading to the economy of construction material is progressive and more perspective from the evolution point of view.

Thus the intestine of Rodents belonging to different groups undergoes transformation independent of one another owing to the change over to cellulose nutrition. The series of intestinal transformations within the entire suborder Myomorpha should be considered homologous, whereas the orders Myomorpha and Hystricomorpha are parallel to one another.

CHAPTER VI

EVOLUTION OF LIVER

The nature of division of the liver into lobes and the presence or absence of the gall bladder are the specific features of mammals. However, the morphology of liver of a majority of wild mammalian species remains unstudied up to this day. Morphologists do not give any functional explanation for the type of the external structure of liver whereas the taxonomists overlook this organ although they are also aware of the fact that the structure of this gland in related forms (for example, Mus and Rattus) may differ considerably and thereby give data on specific phylogenetic structure.

The form and size of liver depend considerably on the complete development of the adjoining organs: stomach, kidneys, heart and even the lungs and also on the conditions of fixation of the material. Hence attention was paid mainly to the correlative development of the lobes and hepatic duct formation. It is also well known (Schwartz, 1959) that the relative weight of the liver is correlated with the absolute size of the animals.

The liver (hepar) of rodents is divided into inner and outer lobes (lobus sinister medialis, l. sinister lateralis, l. dexter medialis, l. dexter lateralis) that are always paired. The gall bladder (vesica fellea) usually lies between l. dexter medialis and l. sinister medialis. It usually unites the independent quadrate lobe (l. quadratus) and in this case it lies between l. quadratus and l. sinister medialis.

On the ventral side these lobes are superimposed by a three lobed caudate lobe (l. caudatus) which can be divided basically into independent lobes; the spigelian lobe (l. spigelli seu processus papillaris) lies over* l. sinister lateralis;

---

* *On examination of the liver from the caudal side.*

processus ventricularis enters the lesser curvature of the stomach along the sagittal line of the body and processus caudatus lies on l. dexter lateralis. From the ventral side of the form of liver resembles those of the adjacent organs - stomach and rodent kidney. There is a wide and shallow depression-impressio gastrica on l. sinister lateralis and impressio renalis on processus caudatus. Thus, the liver may consist of 8 (more or less equally developed) lobes and a gall bladder. However, a reduction of the gall bladder as well as the number of liver lobes is observed in many rodents.

The liver as a digestive gland secretes bile. Bile inhibits the action of pepsin on tripsin thereby accelerating protein digestion. Salts of bile acids serve as the coenzymes of amylase and lipase. The alkaline reaction of bile facilitates emulsification of fats, increases the surface of fatty droplets and facilitates their contact with lipase. Finally bile facilitates the dissolution of fatty acids.

In the entire carnivora and many rodents bile enters the intestine from the gall bladder where it is concentrated quantitatively and qualitatively (cystic bile contains only 80-86 percent water).

There is no gall bladder in certain rodents and ungulates with mainly cellulose nutrition.

What is the functional idea behind the presence or absence of the gall bladder? It seems to us that the presence of the gall bladder and the forms requiring the calorific proteo-lipoid food is linked with the irregular entry of this food (for example, in carnivores and seed-eating rodents). The irregular entry of large amounts of fats and proteins demand the supply of a considerably large amount of concentrated bile within a short period of time. Let us remember that the pH of cystic bile is 6.8 whereas that of hepatic bile is only 7.5 (Azimov et al. 1954).

Entry of low-calorie cellulose food is practically continuous but it contains only an insignificant amount of fats and proteins. In this case there could be a constant supply of less concentrated bile which is close in composition to hepatic bile. Thus in forms adapted mainly to cellulose nutrition, the gall bladder should lose its function of concentration and storing of bile. This leads to the total disappearance of the gall bladder in many rodents.

A majority of the American Cricetinae studied by us have a gall bladder and an eight-lobed liver.

In Oryzomys flavescens the square lobe is one of the largest liver lobes and gall bladder is present whereas in Or. couesi gall bladder and square lobe are absent. It is possible that these species are artificially grouped into one genus.

The size of the square lobe is relatively large in Nectomys squamipes but is less than that of Or. flavescens. A gradual reduction in the size of the square lobe is observed in Oxymycterus nasutus, Peromyscus californicus, Baiomys musculus and Onychomys leucogaster. Gall bladder is present in all these forms.

The square lobe attains the maximum development in Sigmodon hispidus in which it is subdivided by an isthmus into a large (outer) and a small (inner) lobes. Gall bladder is present.

In Thomasomys dorsalis and Reithrodontomys megalotis, gall bladder is present, but square lobe is absent whereas in Akodon arenicola the gall bladder also is absent.

Calomyscus bailwardi, just as Reithrodontomys megalotis, has a gall bladder but no square lobe.

New world palearctic Cricetini are characterized by the absence of square lobe. (Cricetulus longicaudatus has a small branching which may be a remnant of square lobe). Gall bladder is absent in the members of the entire Cricetini except Mesocricetus (M. raddei M. bandti and M. auratus).

Gall bladder is absent in Cricetulus (s. str.) longicaudatus, G. (s. str.) migratorius; G. (s. str.) barabensis, G. (Tscherskia) triton, Cricetus cricetus, Phodopus sungorus and Ph. roborovskii.

A considerable increase of l. dexter lateralis and a noticeable decrease in the size of l. caudatus, especially l.

spigelli and proc. ventricularis, take place within the order of Cricetini described above.

The gigantic l-Spigelli and presence of gall bladder (square lobe is absent) distinguish Mystromys albicaudatus clearly from palearctic Cricetini.

All species of Microtinae studied by us retain gall bladder. The square lobe was observed by us only in Prometheomys schaposchnikovi (having a large size). Dolomys bogdonovi and Alticola (Aschizomys) lemminus. It is present in Lemmus obensis, Myopus schisticolor, Microtus (Chiconomys) gud, M. (s. str.) michnoi, M. (s. str.) oeconomus, M. (s. str.) hyperboreus, M. (Phajomys) caruthersi, Alticola argentatus, Lagurus luteus and Ellobius talpinus. In its liver structure Microtinae is a considerably more homogenous group than Cricetinae.

Gall bladder is developed in all the 17 species of Gerbillinae studied by us. The square lobe of the liver is poorly developed in certain forms of Gerbillinae (Gerbillus pyramidum, Brachiones przewalskii, Meriones tamariscinus, M. persicus, M. crassus swinhoei, M. melanurus, M. shawi, Rhombomys opimus, Psammomys obesus) whereas it is completely absent in certain others (Meriones meridianus, M. erythrourus, M. tristrami, M. unguiculatus, M. crassus charon, Gerbillus dasyurus simoni and Tatera indica). By the liver structure Gerbillinae forms a highly homogenous group.

Myospalax myospalax has a gall bladder. The size of proc. ventricularis exceeds that of l. spigelli and proc. caudatus. The square lobe is absent.

Reduction of the gall bladder and disappearance of individual liver lobes are traced in the order of Muridae. Cricetomys gambianus has a gall bladder and a small square lobe. In Nesokia indica, Pogonomys lepida and Conilurus penicillatus, the gall bladder is absent, the square lobe is not developed and proc. venticularis and l. spigelli are highly reduced in size.

Reduction in the lobe structure is observed in other groups of rodents also. Thus, Myoscalops argentes has a gall bladder, small square lobe, small proc. ventricularis and reduced l.

spigelli. The gall bladder is retained in Cryptomys damarensis, but the square and spigelian lobes are absent.

Thus, a process of oligomerization* (Dogel, 1954) of homologous lobes and liver lobes takes place in the different groups of rodents independent of one another, but in certain forms the gall bladder may be reduced owing to the change over to cellulose nutrition.

---

* *The possibility for applying the phenomenon of oligomerization of homologous organs to the decrease in the lobulation of liver in mammals was first argued by N.S. Lebedkina. While presenting the paper at the Scientific Council of the Institute of Animal Morphology, Acad. of Sc., USSR. on 13th Feb. 1963, N.S. Lebedkina said, 'the author writes: "A process of oligomerization (Dogel, 1954) of homologous lobes and liver lobes takes place in the different groups of rodents independent of one another". But it is difficult to agree with his view as Dogel has assumed the principle of multiple laying of homologous organs as the essential prerequisite for the very process of oligomerization. The vertebrate liver by its origin is an unpaired intestinal outgrowth which gets branched secondarily. Dogel himself (page 41) writes "As far as the digestive system is concerned, we did not consider the branches and outgrowths of intestine as separate organs. Further (page 51) it is necessary to see whether we have before us branching or actual multiplicity of organs (short hand record of the conference of the Scientific Council of the Institute of Animal Morphology)". N.S. Lebedkina did not pay attention to the fact that this observation of V.A. Dogel relates to turbellaria. A wider explanation of the process of oligomerization as understood by Milne-Edwards, who paid attention to this phenomenon for the first time and by V.A. Dogel himself, appeals to us more than the narrow explanation put forward by N.S. Lebedkina. V.A. Dogel studies oligomerization in detail in such irregularly shaped animals, as Mollusca. In particular, Dogel examines, as instances of oligomerization, not only the reduction of liver lobes in the Mollusca, Placophora (Dogel, 1954) (page 119) but also decreases in the number of mammary glands in mammals. Meanwhile, it is well known that these glands are formed by the division of the portions of the "mammary line" laid out as a single formation. Hence we are inclined to consider it permissible to include such instances as the decrease in the number of lobes of liver and lungs under the phenomenon of oligomerization.*

GENERAL PART

CHAPTER VII

Ways of Food Specialization and Evolution of the Digestive System in Muroidea.

On the basis of the study of Muroidea intestinal structure, it may be concluded that the basic evolutionary trend in Muroidea and a majority of other phytophagous mammals, starting from the early miocene, was a change over from proteo-lipid to cellulose nutrition. This change in the type of nutrition was highly accelerated by the large settlement in the land taking place in pliocene (Vorontsov, 1959a, 1959b, 1960b, 1960c, 1961c, 1962a, 1962b and 1963b).

The change over from protein nutrition to cellulose nutrition signifies a transition from the high-calorie, food substances available with difficulty (seeds, small invertebrates) to low-calorie substances easily accessible (vegetative parts of plants). The change over from protein to cellulose nutrition leads to a decrease in the size of the individual portion and decrease in the mobility of the animals (Naumov, 1948), increase in the total volume of food required, transition from nocturnal activity (*Oryzomys* *Rhipidomys*, *Peromyscus*, *Calomyscus* and other members of *Cricetinae*, *Clethrionomys* *rutilus* of *Microtinae* and *Gerbillus* and many *Meriones* of *Gerbillinae*) to continuous or diurnal activity (*Sigmodon hispidus* of *Cricetinae*, *Microtus* and *Clethrionomys* *rutilus* of *Microtinae* and *Rhombomys* of *Gerbillinae*). This change over leads to the disappearance of the instinct to store food (Naumov, 1948 and Vorontsov 1956, 1961b) and to a change over from closed biotopes (characteristic of Cricetinae - *Oryzomys*, *Thomasomys*, *Rhipidomys*, *Peromyscus*, etc.; Microtinae - *Clethrionomys*; *Rodents* - *Apodemus*, *Rattus*, *Dendromys*, etc.; Dipodidae - *Sicista* *substidis* and *Zapus* *hudsonicus*) to open (typical Cricetinae - *Cricetus*, *Cricetulus*, *Mesocricetus*, *Rhodopus*, *Andinomys*, *Reithrodon*, etc.; Microtinae - *Microtus*, *Lemmus*, *Lagurus*, etc.; Rodents - *Nesokia*, *Otomys*, etc. and majority of Dipodidae.

With the reduction in the mobility the locomotor organs are reduced, relative length of the limbs, especially the hind limbs, is reduced and the tail gets shortened (series of Cricetinae from *Peromyscus*, *Thomasomys*, *Oryzomys* to *Sigmodon*, *Andinomys*, *Cricetus*, *Phodopus*; series of Microtinae from *Dolomys*, *Clethrionomys glareolus* to *Microtus*, *Lagurus* and *Lemmus*; and series of Rodents from *Apodemus* and Rattus to Nesokia).

With the simplification in the search for food, the sensitive organs beginning with the organs of smell, vision and taste (Matveev, 1960, and Ganeshina and Grutovoi, 1953; Ganeshina, Vorontsov and Chabovskii, 1957) and the size of the olfactory and the optic lobes of the brain and cerebellum get reduced (Matveev, 1960).

On the basis of the comparative ecological and morphological studies of the digestive system of different rodents it may be said that with the change over from protein to cellulose nutrition the digestive system undergoes the following changes :-

1. With the increase in the total amount of food required the entire set of muscles associated with chewing becomes stronger (series from Cricetinae to Microtinae; series, from *Oryzomys* to *Nectomys*, from *Phyllotis* to *Andinomys*, from *Peromyscus* and *Calomyscus* to *Cricetus*, from *Neotomodon* to *Neotoma*, etc. of *Cricetinae*, series from *Clethrioniomys* to *Microtus* and *Lemmus* of *Microtinae* and series from *Apodemus* to *Rattus* and *Nesokia*) (see Chapter I, 1-4).

2. Crushing of seeds (analogous with mortar) is suitable for crushing the seeds biomechanically whereas grinding (analogous with grinder) is suitable for grinding cellulose food. On the basis of this crushing and pressing movement, the jaw movements are divided into gnawing and grinding (Chapter I, 1, 2 and 3).

Division of the gnawing and grinding functions (Chapter I, 3) leads to differentiation of m. masseter lateralis into three portions of which pars anterior (Chapter I, 4) attains the maximum development. M. masster lateralis is still not differentiated in Gliroidea and Dipodoidea. Oligoene Cricetidae (Cricetops affinis) also, apparently, possessed a nondifferentiated m. masseter lateralis. Decrease in the role of catching the prey leads to a reduction of p. anterior m. masseter medialis and constriction of the foramen infraorbitale through which stretches this muscle. This regularity is traced in the evolution of Cricetodontini from Oligocene to Miocene (Chapter I, 5) and in the New World Cricetidae it is observed in the series Ichthyomys-Oxymycterus-Oryzomys-Cricetus-Clethrionomys-Microtus-Lemmus (Chapter I, 4).

Deepening and shortening of fossa pterygoidea lateralis are observed in this series; messeter area of maxilla highly increases and is moved forward and upward (series of fossil Cricetidae from Oligocene to Miocene and series of New World Muroidea from Ichthyomys to Microtus).

Thus, p. profundus m. masseter lateralis takes part not only in the adduction of mandible but also in pushing it forward (Vorontsov, 1963).

3. Molars of bunodontia are compressed and owing to the mastication of a large amount of coarse cellulose food substance they acquire the capacity for constant growth, loose their roots, and thus change (Chapter II, 2) into hypsodont dentition from brachyodont (series of fossil forms of Cricetodontini from bunodont Oligocene species to lophodont Upper Miocene species; series of fossil forms of Microtinae from Mimmomys to Lemmus (Chapter II, 5); series of New World Cricetinae from Oryzomys to Neotomys, from Akodon to Zygodontomys, from Holochilus magnus to H. brasiliensis, Sigmodon and Reithrodon, from Phyllotis to Irenomys and Andinomys from Neotomodon to Neotoma (Chapter II, 6); series of New World forms of Microtinae from Fibrini to Microtini and Lemmini, from Clethrionomys rutilus to Cl. rufocanus (Chapter II, 8); series of Gerbillinae from Gerbillus and Monodia to hypsodont Rhombomys through Meriones and Psammomys (Chapter II, 8); series of zokors, from Miocene Prosiphneus to New World forms of Myospalax

(Chapter II, 7c) and series of Muridae from *Hapalomys* to *Otomys* through *Nesokia* and *Eropeplus* (Chapter II, 8). Convergent with Muroidea, the series of variability in the dental system are known in Dipodoidea (from *Sicista* and *Zapus* to *Allactaga* and *Alactagulus*), in Gliroidea (from *Dyromys* and *Eliomys* to *Muscardinus*), in Geomyoidea (from *Perognathus* to *Heteromys* and *Geomys*), in Hystricidae (from *Atherurus* and *Hystrix*) and other groups of rodents (Chapter II, 8).

4. The masticatory surface of the molars is complicated by an increase in the number of enamel crown ridges which are always oriented across the direction of masticatory movements. Most forms of Myomorpha and Hystricomorpha, except certain forms which make burrows with their incisors have longitudinal grinding movements, for which (Chapter II, 2) the enamel crowns are oriented transversely (Microtinae, *Neotoma*, *Andinomys* *Reithrodon*, etc. of Cricetinae; *Rhombomys* of Gerbillinea; *Nesokia* and *Otomys* of Muridae, etc.). The relative length of the molars increases (series of Cricetinae from *Oryzomys* to *Neotoma* and series of Microtinae from *Clethrionomys* to *Microtus*, *Lagurus*, *Lemmus* and *Dicrostonyx*). If the grinding is in transverse direction the enamel crowns are oriented longitudinally, width of molars increases and M^3 attains the size of M^1.

(*Tachyoryctes* and *Brachyuromys* *ramirohitra*).

5. The articulated head of the mandible takes a horizontal position from the vertical one (series of Cricetinae from *Ichthyomys* to *Cricetus* and *Neotoma* and series of Microtinae and *Clethrionomys* *rutilus* to *Microtus*).

6. The sensitive papillae of the tongue (papillae fungiformes, papillae foliatae and papillae circumvallatae) are subjected to reduction. P. circumvallatae including three still present in the entire forms of Dipodoidea and Gliroidea, whereas in Muroidea, these three papillae are retained only in Nesomyinae and Cricetomyinae, Its number is reduced to two in Myospalacinae and one (Chapter III, 1) in the entire *Cricetinae*, *Microtinae*, *Gerbillinae* and *Murinae*.

7. The size of the entire alimentary canal (Chapter IV-V) increases owing to the considerable increase in the amount of food required.

8. In the stomach, the area lined by the corneous epithelium increases, the boundary fold between the corneous and the glandular portions is shifted to the pyloric portion and finally the glands are restricted to only a small portion of the fundus ventriculi. The one-chambered stomach is converted into a two-, three- or even five-chambered one. The first portion lined only with the corneous epithelium and analogous to the rumen of ruminants plays the role of a "fermenter" in the initial cellulose digestion. Similar series in the stomach structure are traced among cricetinae from *Neotomys* and *Sigmodon* to *Phodopus roborovskii*, *Neotoma cinerea* and *Peromyscus californicus* (Vorontsov, 1957); among Microtinae from *Arvicola, Lagurus, Alticola* to *Ondatra, Lemmus, Microtus* and *Promethe-omys* through *Ellobius lutescens* and *Ell. talpinus*; among *Muridae* from *Nesokia* to *Cricetomys* and *Ap. agrarius* through *Rattus* and *Apodemus sylvaticus* and among Muroidea from Cricetidae to Lophiomyidae. A tendency for the formation of a two-chambered stomach is observed among other groups of rodents also even at the expense of other rudiments. Thus the formation of an additional section of the stomach by the dilation of the rear part of the Oesophagus is observed in the series *Myoxidae*, from *Glis, Dyromys* and *Eliomys* to *Muscardinus*. A similar two-chambered stomach of the dormouse is not homologous to the two-chambered stomach of Muridae. We observe a series convergent with Muroidea by its stomach structure in Bathyergoidea (from *Georychus* and *Myoscalops* to *Cryptomys*) (see Chapter IV).

9. The relative length of the small intestine decreases, whereas the relative size of the large intestine and caecum increases.

10. The caecum not only increases in size, but also is complicated by the formation of small pockets and isthmuses and in extreme cases its surface increases owing to the folds which have the form of actual spiral valve (*Spalax* and *Cryptomys*). Such are the series of Cricetinae from *Oryzomys* to *Nectomys*, from *Phodopus* to *Mesocricetus*, from *Neotoma floridana* to *N. albigula* and *Neotomodon* (Chapter V, 3); series of Microtinae from *Dolomys* to *Alticola* and *Lagurus* (Chapter V, 5, b) series of Muridae from *Nesokia* and *Rattus* to *Apodemus* and *Cricetomys* (Chapter V, 5, c) and series of Bathyergidae from *Bathyergus* and *Georychus* to *Myoscalops* and *Cryptomys* (Chapter V, 5, g).

11. The surface of the large intestine increases by a simple elongation of the intestine and by the formation of accessory spiral folds on its inner surface and accessory ampullae coli (Chapter V, 3-5).

12. The number of coils in the spiral of the large intestine at its emergence from caecum increases. The size of the large intestine also increases. The number of coils in the spiral may attain 4 in Cricetinae (*Neotoma*), 2 in Gerbillinae (*Meriones*) 2 in Muridae (*Apodemus*) 6 in Bathyergidae (*Cryptomys*) and 10-12 in Microtinae (*Lemmus* and *Ondatra*) (Chapter V, 3-5).

13. The eight lobed liver (*Oryzomys*, *Nectomys*, *Peromyscus*, *Oxymycterus*, *Sigmodon*, *Akodon*, *Onychomys*, etc. of Cricetinae, *Promethemys*, *Dolomys*, etc. of Microtinae, *Brachiones* and many members of Gerbillinae and *Cricetomys* of Muridae) is transformed into a seven-lobed one (*Reithrodontomys*, *Calomyscus*, *Cricetulus*, *Mesocricetus*, etc., of *Cricetinae*, *Myopus*, *Lemmus*, etc. of *Microtinae*, certain forms of *Meriones* of *Gerbillinae*, *Apodemus* *Conilurus*, *Pogonomys* and *Nesokia* of Muridae).

The gall bladder is usually present in species with irregular nutrition of high-calorie proteo-lipoid food requiring concentrated supply of large amount of bile. With the change over to feeding on low-calorie food and consequently the frequent demand for mostly cellulose food, a continuous supply of bile is required, which may lead to the reduction of gall bladder (*Cricetus*, *Cricetulus*, *Phodopus* of Cricetinae and *Rattus* and *Nesokia* of Muridae) (see Chapter VI).

Morphological series of transition from proteo-lipoid nutrition to cellulose nutrition is determined for Cricetinae (from *Rhipidomys* to *Neotoma* and *Andinomys*), *Gerbillinae* (from *Gerbillus* to *Rhombomys*), Microtinae (from *Fibrini* to *Microtini* and *Lemmini*) Muridae (from *Micromys* to *Nesokia* and *Apodemus agrarius*), Dipodidae (from *Sicista* and *Allactaga*) and Myaxidae (from *Dyromys* to *Muscardimus*).

In addition to the basic trend in the evolution (transition to cellulose nutrition). Myroidea as well as other groups of rodents may occupy the niche of animals adapted exclusively to protein nutrition. This reverse trend in the specialization is especially clear under conditions of isolation and unsaturated biocoenosis. In South America in Pliocene Cricetinae occupied the niche of the insectivores which were absent there and gave rise to a series of insectivorous forms (Oxymycterus, Lenokus and Blarinomys) and also of the small piscivorous carnovores of the type Micropotamogale-Potamogale-Chrinonectes (Ichthyomys, Rheomys and Anotomys). Muridae of Indo-Malayan region which occupied the niche of fine piscivorous carnivores (Bayankamys, Hydromys, Parahydromys, Crossomys, Pseudohydromys, Neohydromys, Mayermys, Chrotomys and Celaenomys) had also undergone the same fate. The peculiarities in the structure and the development of the digestive system of the insectivorous Cricetinae show that the American Oxymycterus, Onychomys and others have secondarily changed from cellulose to protein nutrition (Chapter IV, 5).

Between the extreme trends of specialization basic with highly perfected adaptations for cellulose nutrition and just the opposite trends with adaptations for protein nutrition (here, there are primarily proteinic forms of the type Oryzomys and those secondarily adapted for this type of nutrition Ichthyomyini, Oxymycterus, etc.) there are many species and genera, adapted for cellulose nutrition. However, the basic trend in the evolution of Muroidea was transition from proteinic and proteocellulose to cellulose nutrition.

CHAPTER VIII

Unequal Rates of the Transformation of Organs and the Principle of Compensation of Functions

The problems of interrelationship of organs, development of this interrelationship and specialization and extinction associated with it, form the important parts in the study of evolution. Inspite of the fact that morphologists, paleontologists and evolutionists have paid attention to these problems, the problem of the transformation of the correlated systems of organisms still remains as one of the least studied problems in biology.

Solution to the most important biological problems at the cell level and the submicroscopic structure of the cell drew the attention of biologists from the problems of transformation of organs, their coadaptations and evolution and phylogenesis was treated somewhat like a "secondary science". Meanwhile the idea behind the understanding of the laws of molecular and cellular biology lie in the fact that by knowing the processes at some elementary level, we may pass on to the understanding and control of the processes of development of science at the level of tissues, organs, the organisms themselves and their society. The logic of the development of science is such that the present rapid progress in the field of molecular biology should inevitably deal with the solution of the problems of evolution studied by the phylogeneticists, zoologists, paleontologists and botanists. Unfortunately the intensity of research in the field of biology is at present little, but the 'rate of evolution' of these sciences is still not sufficiently high.

I. I. Schmalhausen's (1938) remark that the problem of integration has so far been an almost absolutely untouched problem is correct and it still remains to be so. As observed by I. I. Schmalhausen (1938), "it is necessary to study the factors that determine the coordination of parts in the phylogenetic transformations of the organism". He considered the method of development of the entire connecting mechanism and its role in further evolution as very important. This is an unbroken chain of problems of considerable theoretical and practical signficance not yet solved completely (pages 4, 5, I. I. Schmalhausen). The question of the so-called biological coordinations (Schmalhausen, 1938) belongs to the group of the least studied aspects of this problem.

1. Formation of Modern Views upon the Coordination of the Transformation of Organs in Phylogenesis, upon the Problems of Specialization and Extinction.

According to the classic notion, enunciated by Cuvier, when there is a change in the habitat, the organs of a system are transformed more or less in the same direction. I. I. Schmalhausen (1939b, page 84) has expressed this point of view thus:

"Biological coordination limits the possible changes in the organism by biologically agreeable changes of individual organs, i. e., by changes permissible by the given specific medium. If organ A directly related to a certain factor (for example, to herbaceous food) of a given medium (say, steppes) changes in a definite direction owing to a change in the climate or in the transition to any more specialized food (for example, a change over to feeding on succulent vegetation with constant increase in the arid nature and transformation of the steppe into a semi-desert), organ B, related to the same factor should change strictly in the same way.

According to this point of view, the biological coordinations restrict the possible independent change in an individual organ of the given system (Schmalhausen 1936b, page 85).

Adaptation of an organism to a restricted habitat permits only certain main trends of evolution of the organism, namely, only further specialization, i. e., adaptation for special conditions within a more restricted habitat. The more the network of biological coordination is complicated, the better the organism is adapted to the struggle for existence, but at the same time it looses its plasticity, i. e., the possibility for readjustment if there is any change in the habitat. During specialization, there develops a complex, and hence, the strong bond between the organism and the habitat. The organism becomes (in its evolution) completely dependent on the given habitat, and going out of this becomes a problem for it. Blind alleys of evolution are created thus.

The following important aspects of the modern theory of evolution and morphological and phylogenetic researches are based on these concepts of coordinated transformation of organs when there is a change in the habitat :-

possible reconstruction of the entire organism from its separate fragments,

loss of plasticity due to specialization,

specialization leading to the creation of blind alleys of evolution, and to extinction, and

the fact that these specialized forms cannot form the basis of new branches of development.

How did these concepts originate and develop?

It was G. Cuvier, who for the first time made a systematic study on the correlations which play an important positive role in the development of comparative anatomy especially in paleontology. The very idea of putting a question on the interrelationship and interdependence of the organs on one another was extremely progressive.

The organs of an animal form a unified system, whose parts depend on one another and act and react with respect to one another. Hence it is difficult to observe a change in one without corresponding changes in all the remaining parts (quotation from I. I. Schmalhausen, page 8, 1938).

In his "A discussion on the cataclysms on the surface of the globe" (page 130) Cuvier (1812) wrote :

"Any organized creature forms a single whole, closed system, whose parts correspond to one another and act with the same final aim by mutual influence. None of these parts can change without changing other parts and consequently each of these parts taken separately directs and determines all others."

Thus, as I have said elsewhere, if the intestine of an animal is so built that it can digest only meat, its jaws should be so designed as to shallow the prey, its claws to grasp and to tear, its teeth - to cut and split, its locomotor system - to chase and catch its prey, its sense organs - to detect the prey from a great distance and nature equips its brain with the necessary instinct so that it can hide and trap its victims.

Giving from his observations the form of a law, Cuvier (in the same book, page 132) wrote :

"In short the shape of a tooth entails the shape of an articulated head, shape of scapula and shape of claws just as the properties of a curve follows from the equation of a curve". Further (page 134) he wrote : "One such mark (of artiodactyls - N. V.) reveals to the observer the shape of teeth, jaw, vertebrae, all bones of legs, shoulder and pelvis of a recently extinct animal. This feature is more reliable than all the features of the Zodiac".

Cuvier (in the same book, page 135) observed that "there is some constant interrelationship between two organs which may seem quite alien and the gradation of their shapes inevitably corresponds to one another even when we cannot account for their relationship" (spacing out given by us - N. V.).

Later (1859, 1868 and 1875) Charles Darwin forwarded a new evolution concept in his study on the correlations, which was reviewed by him in connection with his study on the laws of variability. Thus Cuvier's basically static idea on the interrelationship of organs within an organism has turned out to be a theory, dynamic in spirit, on the interrelated and interdependent variations of organs in the process of evolution.

A. N. Severtsov (1931 and 1939) and I. I. Schmalhausen (1938, 1939a and 1939b) after L. Plate (1913) divided the phenomenon on correlative variability into two groups namely, actual correlations-interdependent, coordinated development of organs in ontogenesis and coordinations-variation according to the relation between the organs developing independent of one another and on a third organ in onto- and phylogenesis. As I. I. Schmalhausen (1939a) observes, Cuvier relates most of the examples of 'correlations' to coordinations.

Charles Darwin (1875) actually made a distinction between correlations and coordinations and while studying the difference between these groups of phenomena had especially studied the strictly correlative variation.

However, subsequent research workers extended Darwin's conclusions on the laws of correlative variations fully even to coordinative variability. The indistinct demarcations between correlation and coordination suggested by Darwin (1859) paved the way for criticisms of his teachings. Thus G. Spencer (1864) found in the coincidence of coordinated variations of organs one of his basic rejoinders to the natural selection theory and a decisive argument in favour of Lamarckism. In fact in his later statement (1875) on the theory of correlations, Darwin more frequently, than in 1859, had recourse to Lamarckian 'disuse of organs' in answering the criticism of Spencer.

E. Cope (1884) put forward his 'law of non-specialization' according to which new groups may develop only from non-specialized members of the parental groups. Developing the concepts of Cope, S. Dapiere formed the 'law of specialization of phylogenetic branches'. He emphasized (page 164 and 165) that 'specialization does not affect the entire organism as a whole. It covers one organ or a group of organs more or less closely related functionally. That is why frequently it seems as if specialization does not have any actual aim except gradual perfection of one specific function - swimming, flying, jumping, running, etc.'.

S. Dapiere (1915) relates specialization with extinction of group and considers (page 172) that 'under no circumstances is specialization a condition for the development and longevity of branches but, on the contrary, serves as a senile feature which precedes their imminent extinction.

S. Dapiere, just like many other paleontologists considered that Darwinism cannot solve the problems of extinction (page 186). 'The struggle for existence is decisively insufficient to explain the extinction of species'. Instead of Darwin's interpretation, Dapiere has put forward a theory, according to which each phylogenetic branch has to pass through the development stages, youth, which corresponds to a low level of specialization and ageing stage which corresponds to a high level of specialization. The latter stage, according to Dapiere, 'prepares' the extinction of group. The Cope-Dapiere theory on extinction, as a result of narrow specialization, was a logical development and continuation of the study on coordinated transformation of organs in phylogenesis.

L. Plate (1913), who has put forward the concept of 'phyletic correlations' corresponding to Severtsov's "coordinations", considered that during the transformation of "complex coadaptations" "a large number of elements change step by step in a definite direction and often simultaneously" (Plate 1908, page 350).

A similar concept on more or less uniform and unidirectional transformation of organs in the process of specialization, or on the close coordination of this transformation and on the fact that this coordination narrows down the potential adaptability of the organism and leads to extinction of the group is prevalent until now (Franz 1935; and Schmalhausen, 1938, 1939a, 1939b, 1946).

Even in olden days naturalists had paid attention to the occurrence of noncorrelation in the structure of organs of one biological trend and later, with the development of ideas of evolution and some irregularities in the rates of transformation of organs. First examples of the manifestation of incomplete correlations was given even by Aristotle.

S. Cuvier in 1812 observes that "the necessity for a more complex digestive system for species whose dental system is less perfect is fully understood" (Cuvier 1937, page 133). However, this observation just like a slightly abandoned observation gets lost among the large number of conclusions and facts, given by Cuvier in favour of the idea of direct coordination of organs.

The law of compensation was formed by N. V. Gete (1957) in 1795 and published in the "first sketch of the general introduction to comparative anatomy derived from osteology". He expressed it thus :

"Nothing can be added to one part without at the same time removing something from another and vice-versa".

I. I. Kanaev (1957) rightly observes that Gete's idea of compensation, is, in essence, close to the law of conservation of matter and energy. A little later the same idea was put forward under the name "compensation of growth" by Zhoffrua St. Hilaire (1830).

Considering the ideas of Gete and Z. St. Hilaire Charles Darwin (1859) has expressed the correct idea that,

"Certain instances of compensation given here as well as similar and certain other factors may be grouped under a wider principle, namely, a tendency for natural selection is to constantly observe an economy with respect to all parts of organization" (Charles Darwin, collected works, vol. III, 1939 page 377, 378).

However paradoxical it may be, neither the ideas of pre-Darwinian naturalists nor those of Darwin himself had the least influence on the formation of the ideas about coordinated transformation of the system of organs, in connection with the new requirements of the habitat put forward in the post-Darwinian period. It is possible that this disregard for Gete's ideas was a "relatiatory reaction" of qualified experts to the old naturalists and philosophers on naive formulations supported hardly by any actual data.

L. Dollo (1895) was the first to pay attention to the fact that the phylogenetic series of forms proposed by paleontologists and Darwinists were, in essence, not direct series. Studying the phylogenesis of dipnoi fishes, he emphasized that the series, formed on the basis of certain features, cannot correspond to the series, formed on the basis of the study of the structure of other features. Dollo showed that the phylogenetic series known to us are not direct series of the forms and are formed on the basis of the study of a limited number of features in the lateral branches of the original stock. He put forward the concept of "crisscrossing of specialization" for characterizing the phenomena of the non-coincidence of the series formed on the basis of the study of different features.

Dollo's concept of 'crisscrossing of specialization' was developed by O. Abel (1929) who wrote :

"Contrasts in the interpretations of different authors on the position in the series of different fossil forms of one stock is mainly due to the fact that during the formation and deepening of our knowledge of the morphology of individual forms it was proved that a number of series of specialization change with respect to different organs. So we take an entirely different genetic grouping, if we take organ A with its degree of specialization as the basis for the formation of series, than if we select another organ B for which the sequence of specialization is quite different".

Abel at first criticized Cuvier's correlation theory and indicated many mistakes, committed by the paleontologists, who reconstructed the whole organism on the basis of the study of its fragments, starting from Cuvier's correlation theory without considering the phenomena of "Crisscrossing of specialization".

However, many examples of the "crisscrossing of specialization" relate to different groups of phenomena not distinguished by Abel. These included the crisscrossings of specialization of different functionally unrelated systems of organs (series of adaptations in the groups of Cetacea of the families Balaenidae and Balenopteridae, built on the basis of the structure of cervical vertebrae which do not correspond to the series of specialization of the fore limbs) as well as crisscrossings of the specializations of individual traits in the phylogenesis of an organ (structure of molars of the fossil rhinoceros, Rhinocerotidae).

Abel paid attention also to the non-uniformity in the rates of transformation of individual traits in phylogenesis. However, he started from the false notion that a trait once developed in phylogenesis cannot return to the original state. Non-uniformity in so broad an interpretation of the law of irreversibility of evolution put forward by L. Dollo was shown even by P.P. Sushkin (1915) and subsequently by C.I. Ognev (1945). N.I. Vavilov (1922) foretold the possible emergence of homologous mutations in allied groups and based on the researches of geneticists, marked the reversibility of the process of emergence of new traits. Abel bypassed these works and proposed the application of the phenomenon of "crisscrossing of specialization" for establishing the geneological tree whether we are concerned with the direct phylogenetic series (when crisscrossing of specialization is absent) or the lateral branches of this geneological tree (when crisscrossing of specialization is present). These concepts of Abel on the application of crisscrossing of specialization is graphically represented in Fig. 142.

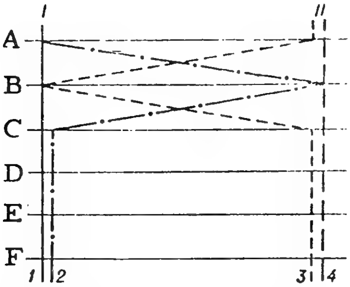


Fig. 142: Chart of Abel's concepts on possible application of "crisscrossing of specialization" for the formation of the phylogenetic tree. After Vorontsov (1963, e). A, B, C, D, E and F - individual traits: I. primitive state of these traits: II - specialized state of these traits; 1, 2, 3, and 4 - species with primitive or specialized traits. There is no crisscrossing of specialization among the species 1, 2 and 4 (direct phylogenetic series) species 2 and 3 with crisscrossing of specialization at least one of these species should be on the lateral branch of the phylogenetic tree.

A Remane (1956) has severely criticized the method of forming the phylogenetic charts on the basis of the presence or absence of "crisscrossing of specialization". Meanwhile, it is undisputable that the idea of non-uniformity of the rate of transformation of individual features and organs in phylogenesis laid down in Abel's concepts on crisscrossing of specialization, are undoubtedly reliable and progressive.

One can only be surprised at the fact that during 30 years after the publication of Abel's book, his ideas are rarely made use of and, have not yet been used essentially in phylogenetic researches.

A.N. Severtsov, apparently, could not consider Abels' concept on "crisscrossing of specialization" since the first addition of his "Morphological regularities of Evolution" (1931) came out soon after Abel's "Palaeobiology and History of Origin" (1929).

While studying the phylogenesis of the family, Equidae, A.N. Severtsov explains the simultaneous and parallel variations of the different systems of organs (skull, teeth and limbs) "as the condition that the animals referred to are simultaneously adapted for different types of changes taking place parallely in the surrounding medium." He emphasizes that there are instances of transformation of organs taking place not simultaneously but successively "in different, functionally unrelated systems of organs".

The problem on non-uniformity in the rates of transformation of organs was not studied by Severtsov's school. Teachings of I.I. Schmalhausen (1939a, 1939b, and 1946) on the adaptationmorphosis and its forms and biological coordinations were further developments of the views of Cope, Depiere, and Severtsov on the coordinated transformation of organs of single biological function.

According to Schamalhausen (1946, page 471) telomorphosis is a specialization of organism, associated with the transition from a more general to a specialized, more limited environment. Besides there is unilateral development of certain organs and partial reduction of others. Progressive differentiation is restricted by those parts of the organism, which are connected with peculiar conditions of the given environment. The organization as a whole is at a fairly low level or experiences some simplification. Here specialization covers mainly the organs of nutrition and food catching as well as means of locomotion.

As I.I. Schmalhausen (1946, page 473) observes "in particular, the biologically coordinated adaptations are characteristics of allomorphosis and even more for telomorphosis combination of the changes is explained by the relation of the organs with certain general factors of the environment".

Reviewing the relation between the specialization of the organism and the problem of extinction, I.I. Schmalhausen (1946, page 475) writes :

"Specialized organisms are strongly connected with the limited environment and hence lose their plasticity. Telomorphosis closes many possibilities of further evolution. Hence even the question of progressive specialization of organisms is close to the question of its extinction. Unilateral specialization is, in fact, related to a real danger of extinction. This does not mean that specialization leads to extinction owing to inevitable internal factors".

A way out from such a "blind alley" caused by specialization, according to I.I. Schmalhausen (1940, page 484), is a regression of the slightly specialized organs leading to relative despecialization. When there are quick changes in the environment it is apparent that only degeneration may, at times, save the organism from extinction".

Thus, unlike E, Cope, S. Depiere and others, I.I. Schmalhausen sees possible means for further evolution of forms with highly specialized organs.

B.C. Matveev (1940, page 391) emphasizes that rearrangement of ontogenesis is an important means for overspecialization of species adapted to limited environmental conditions.

"For such specializations, the means for further evolution during the rearrangement of all features of organization to others, frequently inversely proportional to the environment, is not closed. A complete rearrangement of organization <u>in another direction is quite possible in those stages of ontogenesis when the process of morphogenesis is not yet complete</u>" (underlined by B.S. Matveev).

Summing up our discussion of the views on the coordinated nature of transformation of organs in phylogenesis, it may be concluded that biology till today abounds in views which state that when there is a change in the conditions of the habitat, the organs of a system (in biological coordination with one another) get transformed more or less synchronizingly in the same direction).

These biological coordinations limit the possibility for independent variation in the individual organ of a given system (or systems, in biological coordination). A similar "total" specialization of all the biologically coordinated organs leads to loss in ecological plasticity, creation of blind alleys of evolution and extinction. That is why specialized forms cannot form the basis of new branches of development. Hence we may draw the practical conclusion whether it is possible to reconstruct the entire organism from its separate fragments on the basis of the presence of more or less strictly coordinated nature in the transformation of organs.

Is it so?

The author published a review of these concepts in 1961 and 1963 (Vorontsov, 1961a, 1961d and 1963e). Our interpretation of the non-uniformity in the rate of transformation of organs was supported by E.I. Lukin (1964), B.S. Matveev (1966) and A.V. Yablokov (1966).

It should be noted that Lukin (1964) has put the question in a wider perspective. His articles (1961a and 1963e) deal with the non-uniformity of the rates of transformation of organs belonging to one biologically coordinated system. E.I. Lukin considers the phenomenon of non-uniformity in the rates of transformation applicable to the different systems of organs, often not directly coordinated with one another biologically. Such an approach is close to Abel's approach (see above).

According to E.I. Lukin (1964, page 1118) "retardation of any systems and adaptations may be liquidated in the process of further evolution, but is retained in a number of instances. The reasons for retaining them may be : a) compensation of the poorly developed lagging systems by other systems and adaptations, b) ensuring divergence with other groups as a result of retardation of certain systems and adaptations suitable for the given group of animals and c) development of new correlations of the lagging systems and adaptations with more quickly developing systems and adaptations if it is not visibly reflected on the general adaptability of organisms."

Since this book deals with organs of one biologically coordinated system, only the phenomena connected with the evolution of organs of this system shall be discussed further. Without denying the possibility for a wider interpretation of the phenomena of non-uniformity in the rate of transformation of organs proposed by E.I. Lukin (1964), we restrict ourselves to reviewing the regularities in the phylogenetic transformation of organs of one system.

2. Unequal Rates of Transformation of Biologically Coordinated Organs in the Process of Specialization.

Starting from the traditional point of view given above, it may be expected that equal degree of specialization of each portion of the digestive system in forms, most adapted to one or the other mode of nutrition (Fig. 143). Meanwhile, a study of the rodent digestive system shows that the individual organs of species may be at completely different levels of specialization (Vorontsov, 1957, 1961a, 1961b, 1962a and 1962b) and the series of specialization on the basis of the study of one organ do not correspond to the series on the basis of other organs of portions of the digestive system.

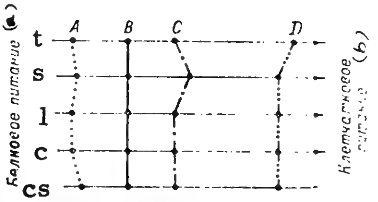


Fig. 143: ***Chart of equal rates of transformation of biologically coordinated system of digestive organs. Vorontsov (1961 a). t - teeth, s - stomach, l - liver, c - caecum and cs - colic spiral of large intestine. Left-extreme degree of adaptation for proteo-lipoid nutrition: brachyodont, one-chambered glandular stomach, eight-lobed liver with gall bladder, poorly developed caecum, large intestine colic spiral having 0-1 turn. Right-extreme degree of specialization for cellulose nutrition, hypsodont, prism-shaped molars, multichambered stomach with predominance of corneous epithelium, six-lobed liver without gall bladder, complex caecum with spiral valve, large intestinal colic spiral with 9-10 coils; center-intermediate types of structure, A, B, C, and D hypothetical forms with synchronized transformation of digestive organs. (a) Protein nutrition; (b) Cellulose nutrition.***

Absence of complete coordination between the stomach structure and the corresponding development of the sections of the intestine have already been observed (Vorontsov, 1957) in certain forms of Cricetinae. A large number of examples of the unequal rates of transformation of the digestive organs (Fig. 144, II) is observed in the widely divergent ancient group of Cricetinae.

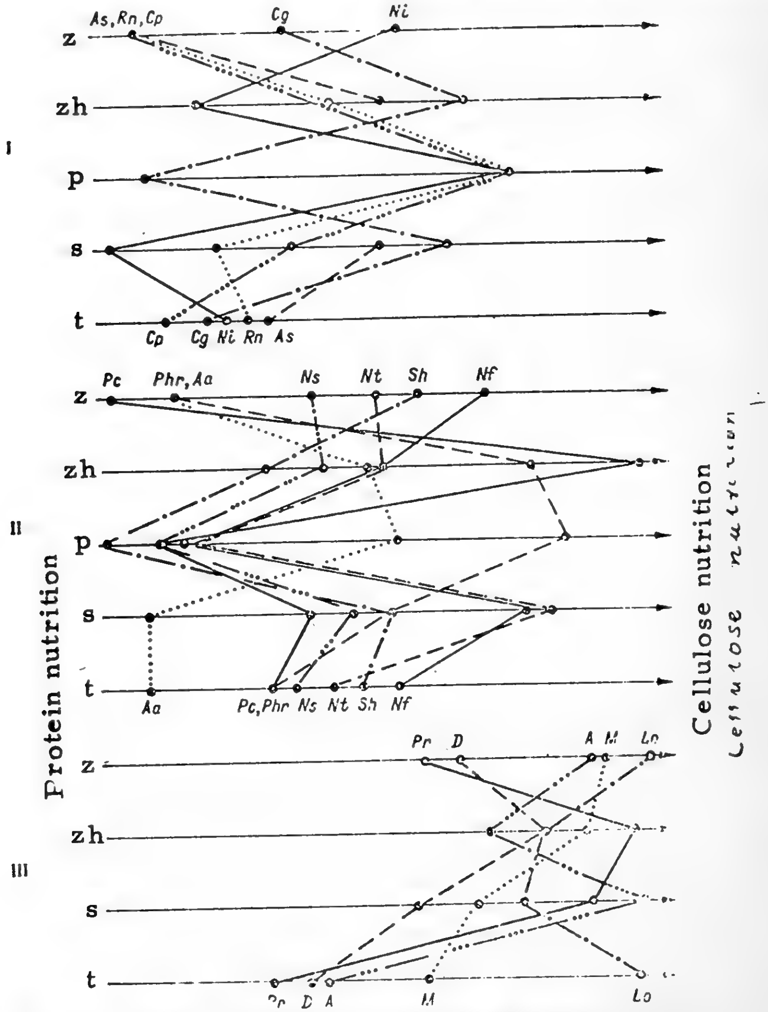


Fig. 144: *Scheme of the unequal rates of transformation of the digestive organs in different groups of rodents. After Vorontsov 1961 a). I-Murinae; II- Cricetinae; III- Microtinae; A- Alticola argentatus; Aa- Akodon arenicola; As- Apodemus sylvaticus; Cg- Cricetomys gabianus; Cp- Conilurus penicillatus; D- Dolomys bogdanovi; Lo- Lemmus obensis; M- Microtus oeconomus; Nf- Neotoma floridana; Ni- Nesokia indica; Nectomys squamipes; Nt- Neotomodon alstoni Pc- Peromyscus californicus; Phr- Phodopus roborovskii; Pr- Prometheomys schaposchnikov; Rn- Rattus norvegicus; Sh- sigmodon hispidus. (For the remaining legend see Fig. 143).*

Mostly herbivorous *Sigmodon hipidus* has highly specialized teeth, initiating the molar structure of Microtinae. *Sigmodon* has in its large intestine accessory ampullae coli-ampullae and complex spiral of large intestine but in its morphology of stomach and liver this is the most primitive species among all the forms of Cricetinae studied.

Among the entire Cricetinae it is the seed-eating brachyodont, *Peromyscus californicus* that is characterized by the most complex three-chambered stomach, homologous to the stomach of *Prometheomys*, which is adapted to digest the cellulose food.

In its structure of the dental system and caecum, *Nectomys squamipes* is the form that is most adapted among all the members of *Oryzomyini* to cellulose nutrition. However, by its stomach structure, N. squamipes is more adapted to proteolipoid nutrition than the seed-eating *Oryzomys* as such.

The structure of molars of *Neotomodon alstoni* is less adapted to cellulose nutrition than of *Neotoma*, but the stomach structure and development of caecum in *Neotomodon* is more suitable for cellulose nutrition than in *Neotoma floridana* and even in *N. albigula*. However, by the large intestinal structure, *Neotoma* is more adapted to cellulose nutrition than *Neotomodon*.

Teeth and liver structure as well as the correlative development of the sections of the intestine are quite identical in the hamsters *Phodopus sungorus* and *Ph. roborovskii*, whereas the stomach of the latter species is more adapted to taking the vegetative parts of the plants.

It would seem as if the bunodont teeth and the simple caecum of *Lophiomys imhausi* are mostly for proteolipoid nutrition, whereas its five-chambered stomach with well developed corneous portions shows that this species is perfectly adapted to cellulose nutrition.

Considerable variability of the dental system is observed in the forms of the subfamily (Gerbillinae from brachyodont, clearly bunodont (Monodia and Gerbillus) to brachyodont, but with simplified masticatory surfaces (*Meriones*) and finally to hypsodont with simplified masticatory surface and constant growth of the prismatic molars (Rhombomys). Meanwhile the stomach structure and correlative portions of the intestine of this series do not vary practically.

Highly specialized lemmings (Lemmus) have highly complicated prism shaped teeth constantly growing throughout their life, the number of coils in the large intestine spiral goes up to 10 but the stomach and caecum of lemmings, unlike many other forms of Microtinae, are not highly specialized for cellulose nutrition (Fig. 145 B).

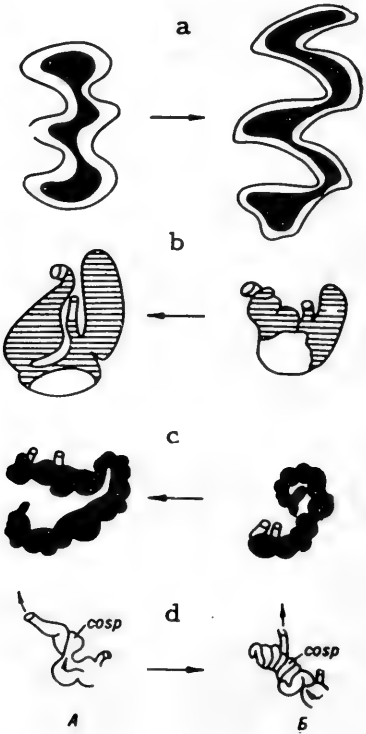


Fig. 145: Unequal rates of the transformation of digestive system and compensation of functions in Microtinae. After Vorontsov (1961, a). A - Prometheomys, B - Lemmus: (a) masticatory surface M1; (b) stomach (corneous epithelium is shown crosshatched); (c) caecum; (d) colic spiral of large intesine (cosp). Arrows indicate the direction from less specialized to more specialized structure.

The primitive Microtinae, *Prometheomys schaposchnikovi* have simple brachyodont teeth, its large intestine spiral has only 2 coils whereas the caecum is considerably large in size. By its stomach structure this is the most specialized species in the whole of Microtinae (see Fig. 145 A).

The simple structure of caecum in *Lemmini* is compensated by the elongation of the entire intestine. The complete structure of caecum compensates for the relatively short length of the intestine *as such*. The highly complicated colic spiral of *Ondatra zibethica* compensates the function of the relatively simple caecum of this species.

It is well known that *Apodemus aquarius* differs considerably from mostly seed-eating *Ap. sylvaticus* and *Ap. flavicollis* in its cellulose nutrition. However the caecum is less developed in *Ap. aquarius* than in *Ap. flavicollis* and *Ap. sylvaticus* (this was established even by N. P. Naumov 1948); meanwhile, by its stomach structure, which fully agrees with the ecology of these species, *Ap. aquarius* is more adapted for digesting cellulose food than *Ap. sylvaticus* (Fig. 146).

Highly unequal rates of transformation of the different organs of the digestive system may be observed in *Nesokia indica* (Fig. 144,1,146). By the structure of its dental system, this form feeding mostly on the underground parts of the plants, is more adapted to cellulose nutrition than the other members of *Murinae*. Stomach and caecum of *Nesokia indica* are more adapted to protein nutrition than in all other members of Muroidea (1), whereas reduction of all gall bladder and square lobe shows that the process of adaptation of liver to cellulose nutrition has advanced further.

In the groups Dipodoidea the structure of molars varies from bunodont with low crown (Sicista) to the type of teeth with simple masticatory surface and prism shaped molars, crown is raised from brachyodont to mesodont (Allactaga, Alactagulus, Pygerethmus). Meanwhile a highly similar stomach structure of the glandular type adapted to protein nutrition is a characteristic feature of Dipodoidea, when certain forms have changed over almost exclusively to cellulose nutrition (*Pygerethmus*).

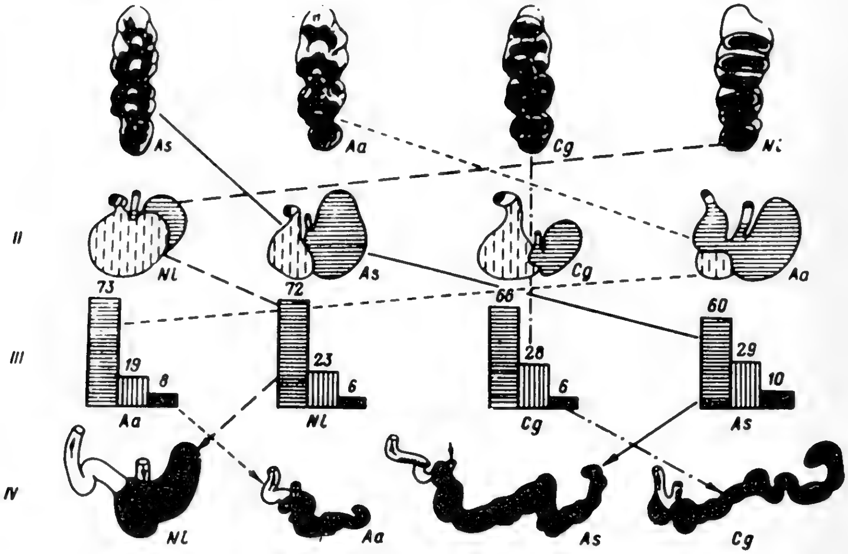


Fig. 146: Unequal rates of transformation of the organs of digestive system and compensation Of functions in Muridae. After Vorontsov (1963 e). I - Structure of the masticatory surface of molars; II - Stomach structure, horizontal crosshatched lines indicate corneous epithelium and vertical lines - glandular epithelium; III - Relative development of the sections of intestine, horizontal crosshatched lines - small intestine vertical crosshatched lines - small intestine vertical crosshatched lines - large intestine marked in black - caecum; the numbers show the relative length to the total length of the intestine (%); and IV - caecum structure. Left - structure of organs adapted for proteolipoid nutrition, right - for cellulose nutrition A_a - Apodemus agrarius, As - Apodemus sylvaticus, C_g - cricetomys gambianus and N_i - Nesokia indica.

N. V. Olkova (1960), studying the structure of intestinal tract in certain species of rodents, has arrived at similar conclusions :

"Insufficient development of one or the other component of the structure constituting the surface of mucosa of any portion is compensated by the development of other components of the structure leading to an increase in the surface. Thus, insufficient area of the surface of mucosa may be compensated by greater height of glands; short length of one or the other section by the large diameter of lumen, insufficient height of glands", by the development of outgrowths, folds etc." (page 234).

The number of examples of the unequal rates of transformation of organs of the digestive system may increase considerably when any group of rodents is analyzed in detail. A study of the digestive system of rodents and even other mammals shows the universal nature of the given phenomenon-different levels of specialization of the individual links of the single system of digestive organs. We may state that in the different groups of rodents, changes in the mode of nutrition reflect on the different organs of the digestive system. Unequal degree of specialization of the different organs of the digestive system is, apparently, related to the hereditarily caused stability of certain organs and liability of other organs.

In rodents, digestion of cellulose food includes basically the grinding and crushing of the vegetative parts of the plants by teeth, maceration and fermentation in the corneous "proventriculus", caecum and large intestine. A more thorough crushing of food simplifies its maceration and fermentation may make up for the cellulose food less thoroughly treated mechanically in the mouth cavity.

Examples of unequal rates of transformation of organs, in biological coordination, may be met with not only in the study of the digestive system. In burrowing rodents the fore-limbs as well as the incisors with which they stir up the soil are strengthened. In all fossorial rodents both incisors and fore limbs are strengthened in comparison with their closely related forms;however, the development of one part always leads to the development of another. In Spalacidae (Spalax) incisors are more powerfully developed than in zokors (Myospalax), whereas the paw of zokor is provided with well developed claws (Fig. 147). The same relation between the structure of incisors and front-limb claws is observed also in fossorial voles and lemmings. In mole-voles (Ellobius) the incisors are hypertrophized whereas the fore-claws are somewhat larger than in forms less specialized for burrowing (Microtus, Glethrinomys). In long-clawed mole-vole (Prometheomys) the reverse relation-front paw claws-well developed whereas the incisors are only insignificantly enlarged (Fig. 148).

Jaeckel (1957) observes that in cephalopoda there exists a relation between the development of siphon and velum - organs

Fig. 147: Compensation of the function of fossorial organs. After Vorontsov ([illegible]). A - in Spalacidae (Spalax), B - in zokor (Myospalax). A the animal burrows with its incisors, the claws are poorly developed, but B burrows with the claws, the incisors are poorly developed. Left-skull, right-fore paws. All figures are in the same scale.

of the jet propulsion locomotion of these forms. Species with strong siphon and well developed apparatus for closing the mouth slits possess poorly developed velum, whereas species with well developed membrane between the claws are characterized by small siphon and poorly developed apparatus for closing the mantle slit.

N. I. Kalabukhov turned the author's attention to the unequal rates of development of functional shifts in the intensity of metabolism and ensuring its maintenance of respiration and blood circulation. He writes :

"With hypoxia observed while climbing mountains the same result, namely facilitating the tissue respiration (in spite of the low pressure of oxygen in the atmosphere) is obtained by altogether different means in closely related forms, for example in the mountain and plain specimens of the same species or

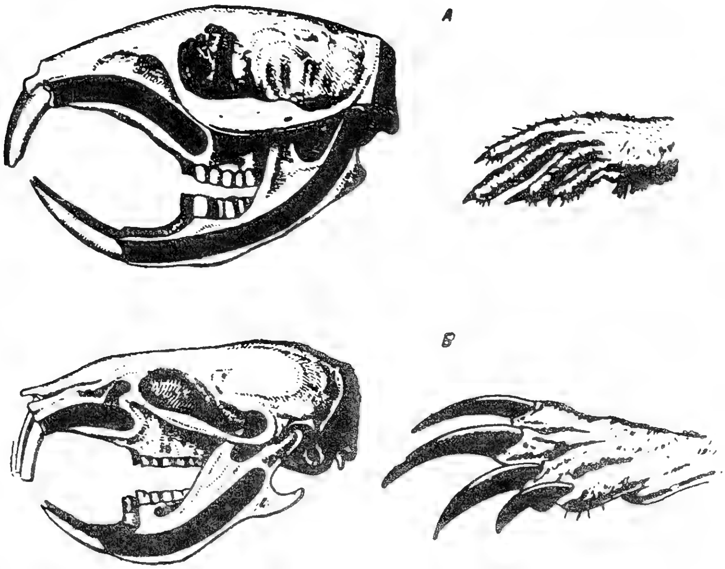


Fig. 148: Compensation of functions of burrowing organs. After Vorontsov (1963 e). A - in mole-voles (Ellobius), B - in long-clawed mole-voles (Prometheomys). If the animal burrows with its incisors, the claws are ill developed and if it burrows with its claws the incisors are ill developed. Left-skull, right-fore paws. All the figures are in the same scale.

closely related species. The forms living on high mountains are perfectly adapted to this hypoxia, (the level of its cellular metabolism is relatively low...) in those living at medium high mountains this compensation is provided by increased haemoglobin content in the blood and finally, animals living in plains in the first period of "acclimatization" to hypoxia react by increasing the rate of blood circulation then only by increasing the number of erythrocytes in blood."*

3. The Principle of Compensation of Functions. Importance of Unequal Rates of Transformation of Organs for Despecialization.

In all the instances described above we have encountered the phenomenon of compensation of functions of one organ of the given system by another of the same system. It seems to us that this phenomenon is one of the types of phylogenetic varia-

---

* *N.I. Kalabukhov, Verbal statement.*

tions of the organs and should find a place in Severtsov's classification system of the principles of similar variations (Severtsov, 1939).

By the principle of compensation of functions is meant the phenomena of phylogenetic variability of organs of one system, in which a quick and complete (in the sense of narrow specialization) variation of certain organs owing to environmental requirements compensates the long lag in the rates of the development of other organs of the same system. Besides, the organs subjected to this quick variation intensify their functions whereas intensification of the functions of another organ of the same system may not set in at all or alternatively the intensification of the functions of the latter organ will take place at slow speed. Unlike the principle of physiological substitution of organs, formulated by D. M. Fedotov (1927), the compensating organ does not acquire any new functions during this, but only intensifies its characteristic functions earlier.

Unequal rates of transformation of organs and the compensation phenomenon, as is evident from a literary review were widely known to zoologists. The concept of "reverse biological coordination put forward by I. I. Schmalhausen (1939b and 1946) is close to the group of phenomena being described.

It is important to note that, in nature, along with the close correlation of organs, to which the biologists first pay their attention, there exists a certain fraction of "freedom", relative independence and absence of complete correlation between organs; this enables the organism to adapt itself to any change in the environmental conditions quickly most economically and in shortest means.

It is remarkable that extreme degrees of specialization for cellulose nutrition is not observed in all the organs of the digestive system even in such forms as lemmings that are highly *specialized* and passing through a period of decline. This indicates that *even highly adapted stenobathic forms are not doomed to extinction when there is a change in the environmental conditions.* Thanks to the unequal rates of transformation of organs there remains in these species some less specialized features which when there is a change in the environmental conditions, may develop in a direction opposite to that in which the compensating organs have developed earlier. When there is such a change in the ecological condition, the compensated organ may become the compensating one and vice versa.

Protein nutrition (seeds and small invertebrates) is mostly a characteristic of the primitive forms of Cricetinae (*Oryzomys*, etc.). Sharp bunodont teeth and stomach predominantly covered with glandular epithelium match this type of nutrition. Many hamsters have passed on to mixed and then purely cellulose nutrition. In certain forms a similar change in nutrition has caused, in the first instance, a simplification of the surface of molars, with the retention of the initial form of the stomach (*Sigmodon hispidus*), in certain other forms - a corneous epithelium develops in the stomach and the glands are restricted only to a small portion of the fundus ventriculi, whereas the dental system remains without any corresponding changes (*Phodopus roborovskii*, etc.). When there is a change in the ecological conditions owing to the penetration of hamsters into a region where insectivorous mammals are absent, certain forms (*Oxymycterus*, *Blarinomys* and also the North American *Onychomis*) secondarily pass on to proteo-lipoid nutrition (Vorontsov, 1959a, 1962a and 1962b). Presence of corneous epithelium in stomach, inherited from herbivorous forms enabled these species to be specialized for insectivorous nutrition, as the corneous epithelium protects the stomach from coarse chitinous parts. In *Oxymycterus* and *Onychomys* the fundus glands are separated into special diverticulum ventriculi of the stomach, which is in fact a large gland producing gastric juice. In these forms the glandular diverticulum compensates the less distribution of the glandular fields along the stomach walls. The dental system of the herbivorous ancestors of the insectivorous hamsters had, in their times, almost remained unchanged and its lagging should be compensated by an intensification of maceration and fermentation functions of the horny stomach. When there is a change in the ecological conditions, this lag in the development of dental system enables the hamsters of the group *Oxymycterus*, *Blarinomys* and *Onychomys* to quickly adapt themselves to insectivorous nutrition, i.e., to secondarily pass over to proteo-lipoid nutrition.

The widespread unequal rates of organ-transformation, with a change in the habitat conditions and the compensation of functions enable us to consider these phenomena as regularities of general biological importance. We did not succeed in finding in general not even a single instance of synchronized transformation of all the organs of a system in the investigated material.

High specialization of all organs of a given system to the present day conditions, if such a specialization exists, generally would have created conditions for the flourishing of this group at present, but it would also have made this group nonprospective in evolution plan. It is well known that radically new forms originate from animals of the so-called "generalized" biological type and not from highly specialized forms. Meanwhile, universal biological forms are always adapted to particular ecological conditions and may, often, not only be eurybathic, but also stenobathic. This stenobenthic nature is achieved by high specialization of certain links of a system of organs, whereas the remaining organs of the same system remain slighly specialized. The principle of compensation established above is applicable here. Similar stenobenthic, but highly specialized forms where the functions of certain organs are compensated by other organs of the same system may subsequently, when there is a change in life condition,be perspective from the evolution point of view, while the organs of the given system specialized earlier will be subjected to specialization.

When there is a change in the direction of specialization, the organs of the given system that were conservative (for development in one direction) earlier, may turn out to be more tended to the development in another direction; they will be quickly and more narrowly specialized than the organs of the same system that are narrowly specialized (in another direction). These newly specialized organs may compensate the imperfections in the functions of other organs, which have played earlier the paramount role in the life of the organism and the activity of the given system, ensuring thereby conditions for the survival and flourishing of the group in the new ecological conditions. We should remember that the more vigorously the given organ functions, the lesser its variability, and the less the functioning organs are characterized by the maximum variability range. Starting from this long-known proposition, it may be considered that the variability of the organs to be compensated should be more than that of the compensating ones; considerable range of variability of the organs to be compensated facilitates their transformation when there is a change in the ecological conditions.

It does not follow from this that the unequal rates of organ-transformation prevent the onward course of evolution and specialization of organisms. Inspite of the unequal rates of transformation, the organs of the digestive system of herbivorous group of Microtinae derived from Cricetinae, are distinguished by the narrow specialization features. The most primitive forms of Microtinae (Fibrini) ~~is~~ more adapted to feeding on coarse food than the primitive forms of Cricetinae most specialized forms of Microtinae (Microtini and Gemmini) are more highly specialized than the most herbivorous Cricetinae (Andinomys and Neotoma). However, this specialization is seen only as a general tendency while comparing the entire digestive system as such and not while studying its individual organs, which, by virtue of the unequal rates of transformation, may be in quite different levels or degrees of specialization.

4. Importance of Unequal Rates of Organ-Transformation and Compensation of Functions in Ontogenesis.

Ecologists' concepts of the degree of eurybenthic and stenobenthic nature of the species are fairly schematic. They become still more schematic at the hands of ecological morphologists, sometimes reducing morphological series to ecological series, and wishing to see complete correlation of the former with the latter.

Meanwhile the life conditions of the species are quite diverse. These are not the same for young, adult and old individuals, but vary considerably with seasons, vary within the same season of different years and vary considerably in different parts of the area.

To what extent does the range of intraspecific variability of morphological structures in all its forms (depending on age, season, geography, etc.) correspond to the extremely wide range of variability of ecological conditions? To a very small extent, is the answer. Geographic, seasonal and even age intraspecific variability in the nutrition of rust-colored (Clethrionomys glareolus) and northern redbacked (Cl. rutilus) voles fully coincides with the interspecific variations in the nutrition of these forms when they have a common habitat (Vorontsov, 1961b). Besides, the geographic variability of the digestive system within these species has a negligible range. Even in the same zone, and the same season of different years, the nutrition of a species may vary in the way distantly related forms of different ecological groups as a whole vary. In the districts near Moscow, during September and December, seeds were found in 77.1% of stomachs and plants - only in 14.3% of stomachs Cl. glareolus, which according to the nutrition spectrum is close to the nutrition of such seed-eating species, as Apodemus sylvatious (seed in 94.3% of stomachs and plants in 14.6% of stomachs, N.P. Naumov 1948) and in the period November-December of the snowless winter of 1954, in the same districts, seeds were observed in only 15.0% of stomachs, whereas plants were observed in 77.5% of the individuals studied (Vorontsov, 1961b) which according to the nutrition spectrum is close to such herbivorous species as Microtus socialis (seeds in 19.1% of stomachs and plants in 97.6%, N.P. Naumov, 1948). In summer, the food of grasshopper mice (Onychomys leucogaster) consists of 79% of insects and animal food, 89% of the volume of food (Hall, 1946) whereas in winter they feed on vegetable materials.

In all these instances the digestive system should ensure the processing and digestion of these quite different food materials. Undoubtedly there should be some physiological mechanism for regulating the digestion of the biochemically different food materials. It is similarly undoubtful that the morphological structure of the digestive organsis adapted to a larger or lesser extent to thenatural changes in the life conditions, expressed clearly by a change in the type of nutrition.

That is why it is well assumed that the unequal rates of the transformation of organs of the digestive system serves not only as a reflection of the phylogenetic history of the species, but also as an adaptation for the seasonal variability of environmental factors. It is possible that, in the life of an organism, the organ 'A' may compensate the function of organ B in a season, whereas in another season organ B may compensate the function of the organ A.

If this assumption is right, the unequal rates of organ-transformation should be expressed less in forms living for a long time under the same environmental conditions, without seasonal fluctuations, than in forms living under conditions where the seasonal fluctuations are clearly expressed.

If the specialization of an organ of the digestive system is fairly high, the unequal rates of organ-transformation only creates conditions for the multifunctional action of the entire system.

In this sense it may be said that the phenomena of the unequal rates of organ transformation and compensation of functions serve as the morphological basis of the potential adaptability of the species, not only in phylogenesis, but also in ontogenesis.

From this it follows that the phenomena described here should be taken into consideration also for acclimatization. Actually, the niche similar to the native place should be selected for a species for acclimatization, without the consideration of the phenomena of compensation. This considerably decreases the number of species recommended for introduction. On the other hand it is necessary to consider the wide morphological basis of the potential adaptability of species as a result of which the species often considerably change their habits and become pests under the new conditions, after entering into the new niche.

The degree of unequal rates of organ-transformation is an index for determining the potential damage spectrum while studying the pests.

Thus, unequal rates of organ-transformation not only facilitate adaptation to a change in the habitat conditions in phylogenesis, but also enable to get used to the different possible groups of food in the life of an organism. The same unequal rates and compensation of functions lie at the root of such ecological phenomena, as seasonal and geographical change in the life conditions.

It should be emphasized that forms, similar or approximately similar in the structure of their digestive system may differ from one another in the type of their nutrition. The structure of the digestive system of the genera *Cricetulus*, *Allocricetulus*, *Cricetus* and *Mesocricetus* is very similar; but *Allocricetulus* and *Cricetulus barabensis* are carnivorous, whereas *Mesocricetus* is mostly herbivorous. As V.D. Spanovskaya (1961) observes, though all fishes of the genus *Gobio* are "morphologically similar" some of them are stenophagous in their mode of nutrition, others are euryphagous (page 1522). Examples of similar genus are fairly numerous and may be seen in any group of animals.

Thus, unequal rates of organ-transformation and compensation of functions provide quick and economical means of the adaptation of an organism to the changes in the habitat conditions both in phylogenesis and ontogenesis.

The unequal rates of organ-transformation and compensation of functions serve as the biological and morphological basis of the phenomena of eurybenthic and stenobenthic nature. The "generalized" forms prospective from the point of view of evolution are adapted to the concrete conditions of the present day by the compensation of functions.

The unequal rates of organ-transformation and the principle of the compensation of functions, in fact, lead to a more general law namely, the nature by selection creates "perfect adaptations" by more economical and brief means.

While judging the structure of the organism on the basis of the study of its parts and paleontological reconstructions, morphology and particularly paleontology should be taken into consideration along with the unequal rates of organ-transformation in the process of adaptation.

CHAPTER IX

Homologous variability

Many examples of homologous series of variability are given in Chapters II-VI of this work. It is expedient to discuss the considerable material on the homologous variability of the digestive organs not only from the point of view of comparative anatomy and evolution-morphology but also from that of genetics.

The law of homologous series of inherited variability put forward by N.I. Vavilov in 1922 is rightly considered bv many a biologist as an analog of D.I. Mendeleev's periodic system of chemical elements. N.I. Davilov's law enables us to foretell the presence and properties of not-yet-described forms of a second series, living under conditions similar to the homologous forms of the first series (Table 14) after studying a series of homologous variability of one species (or genus) and observing the homologous series of variability of another allied species or genus.

TABLE 14

N.I. Vavilov's system of homologous series of variability (original).

Systematic category	Niche.													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
I	A^1	B^1	C^1	D^1	E^1	F^1	G^1	H^1	I^1	J^1	K^1	L^1	M^1	N^1
II	A^2	B^2	C^2	D^2	?	F^2	G^2	?	I^2	J^2	?	?	M^2	N^2
III	?	?	C^3	D^3	E^3	F^3	G^3	H^3	I^3	?	?	L^3	M^3	?
IV	?	?	?	D^4	E^4	F^4	G^4	H^4	?	?	K^4	L^4	M^4	N^4

After establishing the complete series of variability within the group (genus and species) I from A^1 to N^1 and observing that a few forms inhabiting the niches 5, 8, 11 and 12 of the series from A^2 to N^2 of the allied group II are not yet studied, we may predict their basic morphological and ecological properties and confirm that if group II also occupies niches 5, 8, 11 and 12 as group I the similarity among the forms living in similar niches will be quite striking. Thus the very existence as well as the peculiarities of forms E^2, H^2, K^2 and L^2 not yet discovered may be predicted. The characteristics of the extreme members of the series not yet studied may be predicted less authentically. Thus characteristics and existence of forms I^3 and K^3 of group III may be predicted on the basis of the comparison between the series C^3-M^3 and C^1-M^1 as well as C^2-M^2. However, in spite of the presence of such niches forms A^3, B^3 and N^3 may be absent. This may be caused by a general decrease in the range of variability of group III, for example, as a result of the preceding inhabitance under more uniform conditions and loss of genes leading to extreme significant manifestation of certain traits, i.e., as a result of stabilizing selection

A quite similar interpretation follows from N.I. Vavilov's studies. In its original form N.I. Vavilov's laws of homologous series of inherited variability plays an exclusive role. Like the chemists of later XIX and early XX centuries, the biologists could predict the existence of undiscovered ecotypes, races, species and genera and to describe their characteristics.

Analogy of N.I. Vavilov's law with D.I. Mendeleev's system goes further. D.I. Mendeleev discovered the phenomenon of periodicity in the properties of elements, but did not explain the reason for this phenomenon. Only the discovery of atomic structure in the early XX century (E. Rutherford, J. Thompson and N. Bor) revealed that the periodicity in the characters of elements depends on the structure of the electronic shell of atoms. In 1922 N.I. Vavilov could not even explain the cause of the "periodicity" in the characters of the members of the homologous series.

Later N.I. Vavilov (1939, page 138, 139) wrote "According to us the nature of this homologous variability consists first of all in the affinity and unity in the genetic structure of the related species and genera. On the other hand it is the result of the environment, and selection in a particular direction, under specific conditions." He continues further "New profound genetic studies, have of course, helped us to deepen our understanding of the phenomena of variability and to differentiate them. In certain cases, they have among them a similarity of genes and in other cases their phylogenetic characters.

1. Cytogenetic and molecular bases of homologous and back mutations.

Progress in the field of evolutionary genetics in the late thirties enabled us to indicate that on the basis of similar phenotypic changes of allied species and genera there may be similarity in their genotypes. The homologous nature of genes in the allied species of Drosophila was established. It was also shown that considerable portions of the chromosomes in different species may have similar genes (Dobzhansky, 1937). At present it is known that allied species may differ from one another only by a small number of genes, and genetic isolation between these species may be maintained by another grouping of the genic material by intra- and interchromosomal translocations.

Homology of genes in allied forms results in the formation of different homologous species among the newly formed mutations. Living in similar niches (for example, in the different islands and continents and subjected to similar effect of selection, these species give homologous forms, belonging to one and the same "group" of Vavilov's system.

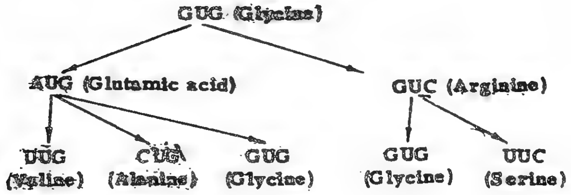
It is difficult to establish homology between mutations yielding similar phenotypic effect. It is well known, for example, that the formation of the brown pigment in the ommatidia of insects' eyes is determined by a chain of reactions: tryptophan formylkynurenine→kynurenine → oxykinurenine → pigment (Wagner and Mitchell, 1958). Mutations destroying any of this chain of reactions lead to similar phenotypic effect. However, these mutations act at different stages of pigment synthesis. Recessive mutation blocks formylkynurenine and kynurenine synthesis in the homozygote of vermilion (v/v) and oxykynurenine in the homozygote of cinnabar (cn/cn). Mutation in the individuals of scarlet with genotype st/st blocks kynurenine and oxykynurenine synthesis. Cardinal recessive mutation in the homozygote cd/cd leads to blocking of the extreme parts of the reaction-breaks formylknurenine and pigment from oxykynurenine. All these mutations were observed in Drosophila melanogaster (Wagner and Mitchell, 1958). It is remarkable that mutation of vermilion arises in other species of Drosophila also Dr. simulans. Dr. pseudoobscura, Dr. affinis and Dr. virilis. Mutation of cinnabar is known also for Dr. affinis and Dr. virilis and mutation of scarlet and cardinal are described for Dr. virilis.

A break in the synthesis of oxykynurenine from kynurenine is observed even in the mutants of other groups of insects - in Diptera (Phryne-fenestris,) Ghalcididae (Habrobracon), and even in Bombycidae (Bombyx mori), i. e., in most of the species of insects studied genetically. Whether the mechanism of suppression of oxykynurenine synthesis is homologous in very remote systematic species is not yet known.

Genetics at present does not give a definite answer to this question. On the one hand it is well known that biosynthesis of certain aminoacids (histidine, arginine) takes place in the same way in very remote organisms, as Escherichia coli and Neurospora, and on the other the biosynthesis of one and the same compounds (lysine, for example) may be realized by different methods (Wagner and Mitchell, 1958).

The process of development of back mutations (Timofeev-Resovskii, 1927, 1929, 1934) plays a major role in homologous variability. However till recently it was not sure that back mutation was manifested by previous phenocopy. Recent experimental studies have shown that back mutations, in fact completely repeat the course and is not a phenocopy but genocopy. Yanofsky (1960) obtained mutation of the gene governing the synthesis of the enzyme tryptophane synthetase in Escherichia coli - Mutation change of individual nucleotides of the triplet coding the synthesis of any aminoacid (G-Guanine, C-Cytocine, U-Uracil and A-Adenine) was observed in the subsequent generations.

These experimental data which caused a keen interest among molecular scientists failed to draw the attention of evolutionists. As it is well known, the difference in some amino-



acids serves as the basis for the specificity of proteins which is a phenomenon of great evolutionary significance.

Experiments on the mutability of gene, governing the synthesis of tryptophane synthetase have shown that reversibility of code is possible. Possibility for the development of identical triplets (triplet GUG, coding the synthesis of glycine may arise both from the triplet AUG coding the glutamic acid synthesis and triplet GUC coding arginine synthesis) also deserves special attention. Thus it is experimentally proved that organisms having a certain common characteristic may arise from two organisms different in this characteristic (and according to the code of these characteristics).

Let us remember that Ingram (1959) has shown, on anomalous haemoglobin of man, that one mutation causes a change in one aminoacid in the protein molecule. This change in aminoacids leads to considerable changes in the individual's character (for the selective significance of these changes, see- Efroimson, 1964).

Thus recent data show that homological mutations are possible in genotypically different forms (for example, in different species). Besides, they show the reversibility of mutations and that of back mutations are possible in genotypically different forms.

2. Homology of characters and genotypes. Reversibility of characters and irreversibility of evolution.

Just as there is a large discontinuity between the studies of research scientists of micro- and magaevolutionary processes in the evolution biology, so also is there an equally vast gap between the studies of molecular and evolutionary biologists.

It should be hoped that in the near future, all round attempts will be made to bridge the gap. However, much sacrifice has to be made before trying this. The author is aware of the fact that while trying to cross the bridge between the data of molecular genetics and those of the ancestors of evolution-comparative anatomy and paleontology, he finds himself not as a builder, but as an unwary traveler who has fallen into this abyss.

The concept of homology of organs and their parts developed in comparative anatomy, describes only the phenomenology of events. The data of comparative anatomy, throwing light only on the later stages of ontogenesis, do not give a causal analysis of the phenomenon of homology, although these may be decisive in judging the divergent or convergent origin of any formation.

It should be emphasized that the concepts of "homology" and "homologous elements" used in the special part of this work is based on the phenomenological approach to the same extent as other works on evolutionary morphology.

What do we mean by saying that an organ of a species is homologous to the organ of another species? We start only from the topographic aspects, usually supported by a comparative embryological analysis. At the moment there is no connection between the comparative anatomy concept of "homology" and the genetic concept of "homology". Apparently, it may be suggested that anatomical homology depends on genetic homology. The possibility of the existence of homologous groups of genes ~~govern~~ governing the development of homologous organs in allied species and genera may be considered.

What is to be done with the systematically remote groups? Is it possible to say that the development of notochord of an appendicularian, a lancelet, a shark and a rat is regulated by homologous genes retained even in terrestrial vertebrates? We cannot give a precise answer to this question. It is perfectly clearl, however, that the comparative anatomists should unconsciously stick to such a point of view.

A considerable number of mutations causing similar phenotypic effect on individuals of highly remote systematic groups are known. Higher primates are distinguished from majority of the mammals studied by the presence of uric acid in their urine, whereas in other mammals the urine mostly contains allantoin. These differences are connected with the corresponding differences in the structure and functioning of the kidney membrane. However, in one of the species of dogs - Dalmatian - the excretion of uric acid considerably increases and that of allantoin decreases (Wagner and Mitchell, 1958).

Mutations changing the basic structural plan, characteristic of the representatives of a high ranking taxonomic group should draw the special attention of evolution morphologists. A few examples are given below.

Mutation of tetraptera causes in flies (members of the order Diptera) the formation of four wings - a character of another order. The mutants in this gene are characterized also by an increase in the number of body segments, i. e., in this character it goes beyond the limits ot the class of insects. This mutation takes place in different species of the genera Drosophila (Hoddington, 1964).

Mutation of aristapedia changes not only the segmentation of limbs in diptera (five segmented claw to four segmented claw i. e., one of ;the characters of the order Diptera is lost), but also may lead to the conversion of antenna into a limb. This mutation is found in different species of Drosophila and Musca.

Metanephros (Wagner and Mitchell, 1958) does not develop in the homozygote of Denford, short-tailed mouse strains, i. e., one of the important characters distinguishing terrestrial vertebrates-amniotes from the aquatic vertebrates-Anamnia.

The number of similar examples of mutations dealing with the principles of the organisation of animals may increase greatly. Such mutations are known among ichneumon flies, diptera (Drosophila and Musca), silkworms, mice, rats, goldcolored hamsters i. e., for all animals well studied genetically. The fact that homologous mutations, changing the cardinal characters, develop in different species, genera and even families is more remarkable.

This enables us to propose that the homology of the genotype forms the basis for morphological homology and homologous genes may be found in the members of systematically remote groups of animals.

Existence of back mutations leads us to the conclusions about the possible reversibility of characters in phylogenesis, and repeatedly occurring characters may be homologous before they disappear. All these data confirm the correctness of the suggestion by P.P. Sushkin (1915) who assumed that there was a possible reversibility of characters in phylogenesis.

P.P. Sushkin (1915) correctly projected against the extraordinary interpretation of the law of nonreversibility of evolution put forward by Luis Dollo. Nonreversibility of evolution does not exclude the possibility of repeated return of characteristics disappeared earlier.

Does not the recognition of the possible reversibility of characters in phylogenesis signify the recognition of the reversibility of the evolutionary process? No; even the allied species do not differ from one another in a number of characters. Even a change in certain genes on account of correlations, pleiotropism and interrelation of genes leads to substantial changes in the individual's phenotypes, controlled by selection. Populations and not individuals evolve, selecting not individual characters but their complex, controlled not by a selection of genes but gene complexes. That is why back mutation by a given character may lead to repeated developmen of this gene, but not the genotype as a whole and repeated appearance of the given character, but not the phenotype as a whole.

Repeated development of mutation and even repeated appearance of conditions of selection, favoring its retention and accumulation are reliable statistically but repeated appearance of gene complexes once disappeared and phenotypes once lost are not reliable. Irreversibility of evolution is a statistical process.

3. Monophyly and the possibility of Parallel Occurrence of Superspecific Groups.

Strict monophyly presupposes that all members of a given taxon are derived from a common ancestral species. Such a concept was not reviewed even though a good number of data on the polyphyletic origin of groups, considered earlier as monophyletic have been collected in the last one and a half decade.

Institution of polyphyly became, perhaps, the order of the day. It is acknowledged that Glires is a collective group and has two orders, Lagomorpha and Rodentia. The question on the polyphyletic origin of Cetacea and its division into orders Mysticeti and Odontoceti is in the stage of discussion. Not only the collective nature of the group Edentata (which is classified with orders, Palaeanodonta, Pilosa and Cingulata) but also the polyphyly of Pinnipedia is being discussed. Notions on the polyphyletic origin of mammals and reptiles are wide spread.

If subsequently the concept of "strict monophyly" is applied to all taxa above the family, we will soon come to the conclusion that all the large systematic groups of the animal kingdom have originated polyphyletically.

It is believed that there is no actual basis at the moment for applying the concept of "strict monophyly". It is clear that the general homologous genes are retained in the allied species, genera and families. These homologous genes may mutate homologically.

Under similar conditions of existence (not necessarily in homologous niche only) the selection trend will be similar and leads to retention of homologous mutations developed in forms which have differed earlier in other characters.

The change in the conditions of existence at the end of Paleozoic era and general "drying of earth" facilitated the elimination of semiacquatic forms associated with water (reproduction, cutaneous and pulmonary respiration, acquatic stage in development) led to reproduction independent of the acquatic medium (emergence of amniotes), protection of skin from drying (appearance of scales, reduction of glands, reduction of cutaneous respiration with compensating complex structure of lungs), perfection of loçomotion, etc. The entire, closely allied system of characters distinguishing the reptiles from amphibians is the result of the selection of innumerable combinations of repeated occurrence of mutations. Naturally the transition from amphibian "level of organization" to the reptile one was not simultaneous in all its characters. Seymouria in its many characters, formed an odd combination of the features of both the classes (Schmalhausen, 1964b), some amphibian characters and some of colylosauria were retained. Schmalhausen (1964b) considers the origin of ichthyosaurs from embolomeri as independent. Thus the gap at the reptelian level of organization is filled at least by two different amphibian groups. However, it is significant that both these groups are derived only from one of the branches of development of amphibia, namely anthracosaurs. It is certain that the members of one line of amphibia possessed a considerable number of homologous genes. Homologous mutation of these genes and free directions of selection led to a parallel "gap" in the different descendants of anthrocosaurs at the reptilian level. Cooling off towards the end of Mesozoic era and increase of moisture led to similar selection to different groups of vertebrates. In the descendents of the much diverged branches of reptiles-aves and mammals - a heat protecting coat developed convergently. They acquired a constant body temperature and a four-chambered heart; one of their aortic arches was reduced and the respiratory organs became highly complicated.

Reptiles belonging to one of the branches (Theromorpha), apparently made several attempts to attain the level of warm-bloodedness. But, owing to the generality in the genetic composition, all the descendants of this group with beastly characters are considered mammals. It is undoubtful that the mammalian level was achieved in certain places. When there is divergence of species in special characters (adaptation in the narrow sense) the generality in the gene composition of the diverged forms may, apparently, be retained for long. Transition to another "adaptive zone" (Simpson, 1948) - aromorphosis - may affect not one, but many species, possibly, belonging to different families of the class. As a result of aromorphosis selection of homologous mutations leads to the emergence of forms so well distinguished in the cardinal features of organization that we may take them to be a new order or even class. However in this case, it will be hardly right to speak of the polyphyletic origin of groups. The very possibility of homologous mutation and parallel development of descendents of the groups divergent sometime was due to similarity in their genotypes, i. e., in the final analysis on the commonness of origin.

I. I. Schmalhausen (1947, page 191, 192) cautioned about the extraordinary increase of "strict monophyly".

"Monophyly should not be understood in a very narrow sense. Concrete organisms evolve into a great number of individuals, among which there takes place constant differentiation. This entire mass as a rule, continues to develop under similar (in general) biological conditions, and consequently, parallely. Hence all these individual stocks, branches, allied strains, etc. which were discussed ...... are not branches and individual strains, but a group of branches of innumerable number of parallel (in general) strains, which we present only as branches for simplicity and clarity. Underlying such branches, let there be always a group (and not individual) of freely interbreeding individuals even at the depth of stock".

It is believed that one is competent to speak of the polyphyletic origin of forms of any taxon only if these are derived from two different taxa of the same systematic rank, for example, a branch of mammals evolved from reptiles and the other, directly from amphibia. Polyphyly cannot be taken under the same conditions when it is established that the forms of a high ranking taxon are derived from two forms of a low ranking taxon (associated with one another in a high ranking taxon). For example, in our view, one should not speak of polyphyletic origin of the order Pinnipedia on the basis of the fact that the different families of Pinnipedia were perhaps derived, from the different families of the order Carnivora. In the latter case we can talk of only parallelism and not polyphyly. It is believed that a clear demarcation of these concepts and final denial of "strict monophyly" will help in bringing clarity to phylogenetic researches.

4. Different levels of homology in different organs of a united system

A substantial conclusion that can be drawn on the basis of the study of the series of variability of different organs in the rodent digestive system consists in establishing different levels of homology in the different organs of a svstem.

Thus the homologous series of variability in the dental system were observed only within the families (Cricetidae - Cricetinae, Gerbillinae, Nesomyinae, Microtinae, Myospalacinae; Muridae - Murinae, Hydromyinae, Dendromyinae, Cricetomyinae) and orders of allied families (Cricetidae and Muridae) are parallel, but not homologous. In other words, the structure of molar teeth of the forms of Muridae not yet described should not be predicted on the basis of the study of the order of Cricetidae.

As far as the stomach structure is concerned, the homologous series of variability are observed within the subfamilies (Muroidea - Cricetidae, Muridae, Spalacidae and Lophiomyidae).

In this case, after studying the series of variability of stomachs of Cricetidae, the stomach structure of the forms of Muridae that have not been studied in this connection, but the stomach structure of Dipoideae, cannot be predicted.

Thus it may be expected that if Phillipinian Rhynchomys and African Deomys actually feed on insects (like Oxymcterus and Onychomys of Cricetinae), a major portion of their stomach should be lined with corneous epithelium and the fundus glands are locked within the glandular diverticulum.

The different levels of homology are, of course, connected with the change in the control of genes over the characters in evolution does not take place simultaneously. A portion of the homologous genes remains; the homologous mutations also remain. Besides, a portion of the genes, governing other organs may be replaced, the mutations again occurring in them will not be homologous to those in the ancestral group.

The establishment of different levels of homology while studying homologous, parallel, and convergent variability may substantially facilitate classification.

LITERATURE

1. Azimov, G. I., D. Ya. Krinitsyn and N. F. Popov, Fiziologiya selskokhozyaisatsvennykh zhivotnykh (Physiology of Farm Animals). Moscow "Sovetskaya nauka", 1954.

2. Argiropulo, A. I. 1933. Rody i vidy khomyakov (Cricetinae) Palearktiki (Genera and species of Palearctic Cricetinae) Tr. Zool. in-ta ANSSSR, vol. 1, No. 3, 4 1933.

3. Argiropulo, A. I., Obzor nakhodok tretichnykh gryzunov na territorii SSSR i smezhnykh oblastei Azii (Review on the Discovery of Tertiary rodents in the USSR and the Adjoining Regions of Asia. Priroda, No. 12, 1940.

4. Argiropulo, A. I. O proiskhozhdenii myshei (sem. Muridae) (Origin of mice-family Muridae) Priroda, No. 2, 1941.

5. Vavilov, N. I. Zakon gomologicheskikh ryadov v nasledstvennoi izmenchivosti (Law of homological series in the hereditary variability). Moscow, Leningrad, OGIS, (1922) 1935.

6. Vavilov, N. I. Vystuplenie na soveshchanii po genetike i selektsii (Proceedings of the Conference on Genetics and Selection). Pod znamenem marksizma No. 11, 1939.

7. Wagner, R., and G. Mitchell. Genetike i obmen veshchestv (Genetics and Metabolism M.,) IL Moscow, (1955), 1958.

8. Velichko, M. A., O nekotorykh osobennostyakh stroeniya pishchevoda i zheludka dikikh gryzunov (Certain Peculiarities in the Esophagus and Stomach structure of Wild

Rodents). Arkheol. anat., gistol i embriol., vol. 20, No. 2, seriya anat, kn. 2, 1939a.

9. Velichko, M.A. Kishechnikh Gryzynov (Rodentia) (Intestine of Rodentia) Uch. zap. fak. estestv. Leningr. ped. in-ta in Pokrovskogo, No. 2, 1939b.

10. Velichko, M.A. and T.M. Mokeeva. O nekotorykh kharakternykh osobennostyakh stroeniya i funktsii kishechnika gryzunov (Certain characteristic Features of the Structure and Function of Intestine in Rodents). Tr. Vses. in-ta zashchity rast. 2, 1949.

11. Verigo, B.B. Osnovy fiziologii cheloveka i vysshikh zhivotnykh (Basis of Human and Higher animals Physiology). vol. 2, St. Petersburg (Leningrad), 1909.

12. Vinogradov,. B.S. On the Mechanism of the Gnawing and Mastication in some Fossorial Rodents Ezhegodn. Zool. muzeya An SSSR, vol. 27, 1926.

13. Vinogradov, B.S. Opredelitelnye tablitsy po faune SSSR (Specific Tables on the Fauna of the USSR) Gryzuny SSSR. Moscow-Leningrad, Izd-vo, AN SSSR, 1933.

14. Vinogradov, B.S. and A.I. Argiropulo Opredelitel gryzunov (Classification of Rodents) Fauna SSSR. nov. seriya, No. 29, Moscow, Leningrad, Izd-vo, AN SSR, 1940.

15. Vinogradov, B.S. and I.M. Gromov. Gryzuny fauny SSSR (Rodents of the fauna of the USSR) Opredeliteli po faune SSSR Izd. Zool in-ta AN SSR, No. 48, Moscow-Leningrad, Izd-vo AN SSR.

16. Voronov, A.G. Pitanie nekotorykh myshevidnykh gryzunov i ego vliyanie na ikh razmnozhenie (Nutrition of some members of Muridae and its Influence on Reproduction) Diss. na soisk uch. step. d-ra biol. nauk. Zool. in-ta, AN SSSR.

17. Vorontsov N.N. O zapasanii korma krasnoi polevkoi (Cleithrionomys rutilus Pall. Hoarding by Northern Redbacked Vole) (Clethrionomys rutilus Pall.), Byull. MOIP, otd. biol., vol. LXI, No. 4, 1956.

18. Vorontsov, N.N. Stroenie zheludka i soothnoisitelnoe razvitie otdelov kishechnika khomyakov (Cricetinae, Rodentia and Mammalia) Palearktiki i Novogo Sveta, (Stomach structure and correlative Development of the sections of intestine in Cricetidae (Cricetinae, Rodentia and Mammalia) of Palearctic and New World). Dokl. AN SSSR, vol. 117, No. 3, 1957.

19. Vorontsov, N.N. Novyi vid tolstokhvostogo tushkanchika (Pygerethmus vinogradovi sp. n.) iz Zaisanskoi kotloviny i zametki o tushkanchikakh roda Pygerethmus Gloger (Dipodidae, Rodentia Mammalia) (New Species of thick-tailed Jerboa (Pygerethmus vinogradovi sp. n) from Zaisan Crater and Notes on Jerboa of the genus Pygerethmus Gloger (Dipodidae, Rodentia, Mammalia). Zool. Zh., vol. XXVII, No. 1, 1958a.

20. Vorontsov, N.N. Stroenie yazyka palearkticheskikh khomyakov (Cricetinae) (Tongue structure of Palearctic hamsters (Cricetinae)). Tr. Zool. in-ta AN SSSR, vol. XXV, 1958b.

21. Vorontsov, N.N. Sistema khomyakov (Cricetinae) mirovoi fauny i ikh filogeneticheskie svyazi - (System of Hamsters) (Cricetinae of world Fauna and their Phylogenetic Connections). Byull. MOIP, otd. biol. vol. LXIV, No. 5, 1959a.

22. Vorontsov, N.N. Geograficheskoe rasprostranenie khomyakov (Cricetinae) i Nekotorye vorprosy Zoogeografii Novogo Sveta (Geographic Distribution of Hamsters (Cricetinae) and some questions of Zoogeography of the New World). Byull. MOIP, otd. biol., vol. XIV, No. 5, 1959b.

23. Vorontsov, N.N. Vidy khomyakov Palearktiki (Cricetinae-Rodentia) in statu nascendi (Palearctic Hamsters species (Cricetinae-Rodentia) in statu nascendi) Dokl. AN SSSR, vol. 132, No. 6, 1960a.

24. Vorontsov, N.N. Tempy evolyutsii khomyakov (Cricetinae) i nekotorye faktory, oppredelyavshie ee skorost (Rates of Evolution of hamsters (Cricetinae) and some factors determining its speed) Dokl. AN SSSR, vol. 133, No. 4, 1960b.

25. Vorontsov, N.N. The ways of Food Specialization and Evolution of the Alimentary system in Muroidea. Intern. Symposium on Methods of Theriological Investigation. Brno, 26 Aug. - 5 Sept. 1960 b.

26. Vorontsov, N.N. Nervnomernost tempov preobrazovaniya organov pishchevaritelnoi sistemy gryzunov i printsip kompensatsii funktsii. (Unequal Rates of Organ Transformation of the Digestive system of Rodents and the Principle of Compensation of Functions). Dokl. AN SSSR, vol. 136, No. 6, 1961a.

27. Vorontsov, N.N. Ekologicheskie i nekotorye morfologicheskie osobennosti ryzhikh polevok (Ecological and Certain Morphological Features of Blank Voles (Clethrionomys tilesius) of North East Europe) Tr. Zool. in-ta, AN SSSR, vol. XXIX, 1961b.

28. Vorontsov, N.N. Die Evolutionsgeschwindigkeit der Hamsters (Cricetinae) und einige sie beeinflussende Faktoren - Sowjetwissenschaft, Naturwissenschaftiliche Beitrage, H.Z. 1961c.

29. Vorontsov N.N. Die asynchrone Unwandlung des Verdaunungsystems bei Nagetieren wahred der Evolution und das. Prinzip der Kompensation von Funktionen. Ibid., H. 6, 1961d.

30. Vorontsov, N.N. Puti pishchevoi spetsializatsii i evolyutsiya pishchevarietelinoi sistemy i nekotorykh, preimushchenno mysheobraznykh (Muroidea), gryzunov (Means of food specialization and evolution of Digestive system in certain, mostly Muridae, rodents) Avtoref. Kand. diss. Moscow, 1962a.

31. Vorontsov, N.N. The ways of Food specialization and Evolution of the alimentary system in Muroidea Proc. Intern. Symposium on Methods of Mammalogical Invest. Praha, 1962b.

32. Vorontsov, N.N. Aralomys glikmani - novyi vid khomyakoobraznykh (Aralomys glikmani - A new Species of Cricetidae). Paleont. zh. No. 2, 1963a.

33. Vorontsov, N.N. Istoriya stanovleniya sovremennogo areala mysheobraznykh (Muroidea) gryzunov (History of Establishment of Modern Area of Muroidea Rodents) Soveshch po vopr. zool. kartografii (Tezisy dokl.) Moscow, 1963b.

34. Vorontsov, N.N. Morfologicheskaya konvergentsiya i konvergentsiya tipov arealov (Morphological Convergence and Convergence of the Types of the Area). Soveshch. po vopr. zool. kartografii (tezizy dokl.) Moscow, 1963c.

35. Vorontsov, N.N.O mekhanizme zhevatelnykh dvizhenii i gryzunov i evolyutsii chelyustnogo apparata i cherepa i khomyakoobraznykh (Cricetidae).(On the Mechanism of Masticatory Movements in Rodents and Evolution of Maxillary Apparatus and Skull in Cricetidae). Tr. Mosk. ob-va ispytat. prirodv, vol. X (Biologiva, biogeografiya i sistematika mlekopitayushchikh SSSR), Moscow, Izd-vo AN SSSR, 1963d.

36. Vorontsov, N.N. Neravnomernost tempov preobrzovaniya organov i printsip kompensatsii funktsii (Unequal Rates of Organ Transformation and Principle of Compensation of Functions). zool. zh. vol. XLII, No. 9, 1963e.

37. Vorontsov, N.N. Sistematicheskoe polozhenie i obzor khomyakov roda Mystromys Wagn. (Systematic Position and Review of hamsters of the genus Mystromys Wagn.) Zool. a, vol. XLV, No. 3, 1966.

38. Vorontsov, N.N. and N.N. Gurtovoi. Stroenie Srednebryushnoi zhelezy nastoyashchikh khomyakov (Cricetini - Cricetinae-Rodentia - Mammalia) (Structure of midpere-

tonial glands of New World. Hamsters (Cricetini - Cricetinae-Rodentia-Mammalia)) Dokl. AN SSSR, vol. 125, No. 3, 1959.

39. Vorontsov, N.N. and Yu. A. Labas (in litt.) K sravnitelnoi biomekhanika chelyusnogo apparata nekotorykh mysheobraznykh (Muroidea) gryzunov.(Comparative Biomechanism of the maxillary Apparatus of certain Muroidea Rodents). Byull. MOIP, Otd. biol.

40. Ganeshina, L.V. and N.N. Gurtovoi. Stroenie organov obonyaniya myshei i polevok (Structure of the olfactory organs of Mice and Voles). Zool. zh. vol. XXXII, No. 4, 1953.

41. Ganeshina, L.V. and A.D. German. Sravnitelnomorfologicheskie izuchenie stroeniya yazhyka u myshevidnykh gryzunov v zavisiomosti ot osobennostei ikh pitaniya (rukopis) (Comparative-morphological study of the structure of Tongue in Muroidea Rodents depending on their nutritional peculiarities (manuscript)), 1955.

42. Ganesihna, L.V,, N.N. Vorontsov and V.I. Chabovskii. Sravnitelno-morfologicheskoe izuchenie stroeniya nosovoi polosti u nekotorykh predstavitelei otryada nasekomoyadnykh (Comparative Morphological study on the Nasal Cavity structure in Certain Representatives of the Order Insectivora) Zool. z., vol. XXXV, No. 1, 1957.

43. Geptner, V.G.L.G. Morosova-Turova and V.I. Tsalkin. Vrednye i polznye zveri raionov polezashchitnykh nasazhdenii (Animal Pests and Useful Animals of the shelterbelt plantations) Moscow, Izd-vo Mosk. gos. un-ta, 1950.

44. Geptner, V.G. Fauna pozvonochnykh zhivotnykh Badkhyza (Yushnyi Turkmenistan Vertebrate Fauna of Badkhyz (South Turkmenistan). Ashkhabad, Izd-vo, AN Turkm. SSR, 1956.

45. Gerke, P. Ya. Razvitie zheludka mlekopitayushchikh (Development of stomach in Mammals). Tr. in-ta eksperim. med. AN Latv. SSR, vol. XI, 1956.

46. Gete, I.V. Izbrannye sochineniya po estest-voznaniyu (Collected Works on Natural Science). Izd-vo AN SSSR, series "Klassiki nauki", 1957.

47. Ginetsinskii, A.G. and A.V. Lebedinskii. Kurs normalnoi fiziologii (A Course on Normal Physiology). Moscow, Medgiz, 1956.

48. Darwin, C. Proiskhozdenie vidov putem estestvennogo otbora (Origin of Species by Natural Selection). Soch., vol. 3, Izd-vo AN SSSR, 1939.

49. Darwin, C. Izmenenie zhivotnykh i rastenii v domashnem sostoyanii (Change of Plants and Animals under the Domestic Condition). Moscow-Leningrad, Selkhozgiz, 1941.

50. Deipere, S. Prevrashcheniya zhivotnogo mira (Transformation of the Animal World), Pg. 1915.

51. Dogel, V.A. Oligomerizatsiya gomologichnykh organov kak odin iz glavnykh putei evolyutsii zhivotnykh (Oligomerization of Homologous Organs as one of the Important Means of Animal Evolution). Izd-vo Leningr. gos. un-ta 1954.

52. Zedenov, V.N. Obshchaya anatomiya domashnikh zhivotnykh (General Anatomy of Domesticated Animals). Moscow "Sovetskaya nauka", 1958.

53. Zavarzin, A.A. and C.C. Shchelkunov. Rudovodstvo po gistologii (A Hand Book of Histology), Leningrad Medgiz, 1954.

54. Zverev, M.D. Biologicheskie nabludeniya nad khomyakom i metod otravlennykh primanok v borbe s nim (Biological Observations on Hamster and Method of Poisoned Bait in Combating it). Tr. po. zashchite rast. Sibiri, vol. (8). Novosibirsk, 1931.

55. Kanaev, I.I. Gete-Naturalist. Kommentarii v kn. Gete, I.V. "Izbrannye sochineniya po estestvovaniya" Gete, the Naturalist. Commentary. - in Book Gete I.V. "Collected Works on Natural Science".

56. Koshtovants, Kh. S. Osnovy sravnitelnoi fiziologii (Fundamentals of comparative physiology). Vol. 1, Moscow, Izd-vo AN SSSR, 1950.

57. Kulaeva, T.M. Sravnitelnaya ekologiya ryzhikh polevok Tatarskoi ASSR (Comparative Ecology of Bank Voles of Tartar ASSR (Avtoref. Kand. diss Zool. in the AN SSSR.

58. Cuvier. J. Rassuzhdeniya o perevorotakh na poverkhnosti zemnogo shara (Discussion on the cataclysms on Earth's surface) Moscow, Biomedgiz, 1937.

59. Labas, Yu. A., K metodike izucheniya dvigatelnogo Komponenta akta edy u melkikh tryumov (The method of Studying the functional parts in the Act of Eating small Rodents). v. sb. "opyt izucheniya regulyatsii fiziol. funktsii vol. VI, Moscow-Leningrad, Izd-vo AN SSSR, 1963a.

60. Labas, Yu. A. Issledovaniya dvigatelnogo komponenta akta edy u myshevidnykh gryzunov (A study of the Operating Part of Muroidea Rodents in Act of Eating). V. sb. "opyt izucheniya regulyatsii fiziol. funktsii vol. VI, Moscow-Leningrad, Izd-vo AN SSSR, 1963b.

61. Lebedkina, N.S. Morfo-funktsionalnyi analiz cherepa zaitsev i polevok (Morph ofunctional Analysis of the skull of Leponidae and Microtinae) (Avtoref. kand. diss) 1949.

62. Lebedkina, N.S. Morfo-funktsionalnyi analiz chelyustnogo apparata zaitsev (Morpho-functional Analysis of the Masticatory Apparatus in Leoporidae). Zool. zh., vol. XXXVI, No. 10, 1957.

63. Lukin, E.I. Razlichiya v skorosti evolyutsii raznykh sistem organov i prisposobleniya k razmnozheniyu i razvitiyu zhivotnykh (Difference in the Rate of Evolution of Different systems of Organs and adaptation to Reproduction and Development of Animals). Zool. zh. vol. XIII, No. 8, 1964.

LITERATURE

64. Matveev, B.S. O smene funktsii i drugikh tipakh preobrazovaniya formy i funktsii organov v ontogeneze (on the Change of functions and other Types of Transformation of Form and Function of Organs in Ontogenesis). Zh. obshch. biol. vol. 1, No. 3, 1940.

65. Matveev, B.S. Ekologo-morfologicheskii osobennosti v stroenii organov chuvstv blizkikh vidov, rodov i semeistv mlekopitayushchikh (Ecologic morphological Peculiarities in the Structure of the sense Organs in Allied Species, Genera and Families of Mammals). Byull. MOIP, Otd. Biol., vol, 65, No. 1, 1960.

66. Matveev, B.S. O proiskhozhdenii geterodontnoi zubnoi sistemy mlekopitayushchikh po dannym ontogeneza (On the Origin of Heterodont Dentition in Mammals according to the Data on Ontogenesis). Tr. Mosk. ob-va ispytat. prirody, vol. X (Biology, biogegraphy and taxonomy of the mammals of USSR) Moscow, Izd-vo AN SSSR.

67. Mokeeva, T.M. Kormovaya spetsializatsiya u nekotorykh vidov myshevidnykh gryzunov v svyazi osobennostyami ikh termoregulyatsii (Avtoref. Kand. diss) (Food specialization in certain species of Muroidea Rodents due to the Peculiarities in their Heat Insulation) Leningrad, 1949.

68. Nazarova, I.V., Ekologo-morfologicheskii ocherk serykh polevok Volzhsko-Kamskogo Kraya (Ecologic-morphological Sketch of common voles of Volga-Kama region). Izv. Kazanskogo fil. AN SSSR, seriya biol. nauk, zool., No. 6, 1958.

69. Naumov, N.P. Ocherki sravnitelnoi ekologii myshevidnykh gryzunov (Outlines of Comparative Ecology of Muroidea Rodents) Moscow-Leningrad 1948.

70. Ognev, S.I. Zveri SSSR i prilezhashchikh stran (Animals of the USSR and Adjoining Countries) Moscow-Leningrad, Izd-vo AN SSSR, vol. IV, 1940.

71. Ognev, S.I. Obratim li protsess evolyutsii? (Is the process of Evolution Reversible) Byull. Mosk. ob-va ispyt. prirody, otd. biol, vol. 50, No. 1, 1945.

72. Ognev, S.I. Zveri SSSR i prilezhashchikh stran, (Animals of the USSR and Adjoining Countries) Moscow-Leningrad, Izd-vo AN SSSR, vol. VI, 1948.

73. Ognev, S.I. Zveri SSSR i prilezhashchikh stran. (Animals of the USSR and Adjoining Countries) Moscow-Leningrad, Izd-vo AN SSSR, vol. VIII, 1950.

74. Olkova, N.V. Stravnitelinye dannye o stroenii kishechnika nekotorykh vidov zabaikalskikh gryzunov (Competitive Data on Intestine structure of some species of Baikal Rodents) Izv. irkutskogo nauch. - issled protivochumn in-ta Sibiri i dalnego Vostoka, vol. 23, 1960.

75. Orlova, I.I. Mikroskopicheskaya anatomiya bolshoi zheludochnoi zhelezy bobra (Predvaritelnoe soobshchenie). (Microscopic Anatomy of Large Gastric glands of Beaver (Preliminary Report)), Tr. Voronezhskogo gos. zapovedn. vyp. 6.

76. Osnovy paleontologii Mlekopitayushchie (Fundamentals of Paleontology Mammals) Editor V.I. Gromova 1962.

77. Pavlov, I.P. Poln. sobr. trudov (Complete collection of Works), vol. II Lektsii, stati, vystupleniya po fiziologii pishchevareniya Moscow-Leningrad, Izd-vo AN SSSR, 1946.

78 Ponugaeva, A.G. Rol Zashchechnykh meshkov pri zapasanii korma u zolotistogo khomyaka (Role of cheek pouches in Food Storage of Golden Hamster) V. Sb. "Opyt izycheniya regulyatsii fiziol. funktsii" vol. VI. Moscow-Leningrad. Izd-vo AN SSSR, 1963.

79. Pravdina, Z.I. O. dlitelnosti prebyvaniya korma v pishchevaritelnom trakte obyknovennoi i obshchestvennoi polevok (On the Duration of Food remaining in the Digestive Tract of common and social Voles) Tr. VIZR, No. 12, 1958a.

80. Pravdina, L.I. O kislotnosti soderzhimogo zheludkov nekotorykh vidov gryzunov (On the acidity of the contents of the stomach in some species of rodents) Tr. VIZR, No. 12, 1958b.

81. Romer, A.S. Paleontologiya pozvonochnykh (Paleontology of Vertebrates), 1938.

82. Severtsov, A.N. Etyudy po teorii evolyutsii. Individualnoe razvitie i evolyutsiya (Studies on the Theory of Evolution. Individual Development and Evolution). Gosizdat RSFSR, 1922 (1921).

83. Severtsov, A.N. Morfologicheskie zakonomernosti evolyutsii (Morphological Regularities of Evolution). Moscow-Leningrad. Izd-vo AN SSSR, 1931 (1939).

84. Simpson, J.G. Tempy i formy evolyutsii (Rate's and Forms of Evolution) Translation Moscow (1944) 1948.

85. Slonim, A.D. Chastnaya ekologicheskaya fiziologiya mlekopitayushchikh (Special Ecological Physiology of Mammals) Moscow-Leningrad, Izd-vo AN SSSR, 1962.

86. Spanovskaya, V.D. Stenofagiya i evrifagiya u ryb podsemeistva Gobiinae (Stenophagy and Euryphagy in Fishes of the subfamily Gobiinae). Zool. zh., vol. 40, No. 10, 1961.

87. Spenser, G. Nedostatochnost estestvennogo podbora (Insufficiency of Natural Selection) Petersburg, 1894.

88. Sushkin, P.P. Obratim li protsess evolyutsii? Novye idei v biologii (Is the Process of Evolution Reversible? New Ideas in Biology). No. 8, 1915.

89 Sedzher, R. and F. Rain. Tsitologicheskie i khimicheskie osnovy nasledstvennosti (Cytological and Chemical Basis of Heredity). Moscow, "Mir", 1964.

90. Takhtadzhyan, A.L. O printsipakh i metodakh filogeneticheskikh postroenii (Principles and Methods of Phylogenetic Reconstructions) (Tezisy dokl. nauch. sessii posvyashchennoi 10-letiyu so dnya smerti akad. A.N. Severtsov) Moscow, 1946.

91. Timofeef-Ressovsky N.W. A Reverse Genovariation in <u>Drosophila funebris</u> - Genetics, XII, 1927.

92. Timofeef-Ressovsky N.W. Ruckgenovariationen und Genovariabilitat in verschiedenen Richtungen Archiv f. Entwicklungsmechanik, CXV, 1929.

93. Timofeef-Ressovsky N.W. The Experimental Production of Mutations -Biol. Reviews, 9, 1934.

94. Tonkov, V.P. Uchebnik normalnoi anatomii cheloveka (A text Book of Normal Human Anatomy). Part II, Moscow-Leningrad, Medgiz, 1933.

95. Tupikova, N.V. and L.V. Kaleda. Opredelenii vozrasta gryzunov (Determination of the Growth of Rodents) Izd-vo Mosk gos. un-ta, 1933.

96. Woddington, K. Morfogenez i genetika (Morphogenesis and Genetics). Moscow, "Mir", 1964.

97. Fedotov, D.M. O nekotorykh sluchayakh morfologicheskoi i fiziologicheskoi substitutsii (Certain Instances of Morphological and Physiological substitution). Tr. II, Sezda zool. anat. i gistol.

98. Flint, V.E. K. biologii khomyachka Roborovskogo (Biology of Roborovskii Hamster) Byull. MOIP, otd. biol, vol. LXV, No. 5, 1960.

99. Schwartz, S.S. Nekotorye voprosy problemy vida u nazemnykh pozvonochnykh zhivotnykh (Some aspects of the problem of species in Terrestrial Vertebrates). Tr. In-ta. biol. Uralskogo fil. AN SSSR, No. 1, Sverdlovsk., 1959.

100. Schmalhausen, I.I. Organizm kak Tseloe v individualnom i istoricheskom razvitii (Organism as an Entity in Individual and Historic Development) Moscow-Leningrad, Izd-vo AN SSSR, 1938.

101. Schmalhausen I.I. Znachenie Korrelyatsii v evolyutsii zhivotnykh (Significance of correlations in Animal Evolution) v. sb. "Pamyati akad. A.N. Severtsova" vol. 1, Moscow-Leningrad, Izd-vo AN SSSR, 1939a.

102. Schmalhausen, I.I. Puti i zakonomernosti evolyutsionnogo protsessa (Means and Regularities of the Process of Evolution) Moscow-Leningrad, Izd-vo AN SSSR, 1939b.

103. Schmalhausen I.I. Problemy Darwinism (Problems of Darwinism). Moscow, Svetskaya Nauka", 1946.

104. Schmalhausen, I.I. Osnovy sravnitelnoi anatomii pozvonochnykh (Fundamentals of comparative Anatomy of Vertebrates). Moscow, "Sovetskaya Nauka", 1947.

105. Schmalhausen, I.I. Regulyatsya Formoobrazovaniya v individualnom razvitii (Regulation of Form Development in Individual Development). Moscow, "Nauka", 1964a.

106. Schmalhausen, I.I. Proiskhozhdenie nazemnykh pozvonochnykh (Origin of Terrestrial Vertebrates). Moscow, "Nauka".

107. Efroimson, V.P. Vvedenie v meditsinskuyu genetiku (Introduction to Medical Genetics). Moscow, Medgiz, 1964.

108. Yablokov, A.V. Morfologii pishchevaritelinogo trakta zubatykh kitoobraznykh (Morphology of the Digestive Tract in toothed Cetaceans). Zool. zh. vol. XXXVII, No. 4, 1958.

109. Abel O., 1929. Paläobiologie und Stammesgeschichte - Gustav Fischer Verl. Jena.

110. Ambrus, G.L., Ambrus N.A. and Harrison G., 1953. Gastric acid secretion and gastric ulcer formation of Rats and guinea Pigs - Amer. Journ. Phisiol., 175, No. 1,

111. Brümmer, J., 1876. Anatomische und histologische Untersuchungen über den zusam-mengesetzter Magen verschiedenen Säugethiere - Deutsch. Zeitschr. f. Thiermed, und vergl. Pathol., Bd. 2.

112. Cope E., 1884. The origin of fittest. Essays on evolution. Lond; - 1896. The Primary factors of organic evolution. Chicago.

113. Davenport H.W. and Yensen, V., 1949. Observations on the secretion of acid by the mouse stomach in vitro. Gastroenterology, 12 N. 4.

114. Davenport H.W. Schneeble G.Z. and Chavre V.Y., 1950. Factors affecting acid secretion and citological structure of mouse stomachs incubated in vitro - Federation Proc., v. 9, No. 1, Part 1.

115. Darlington, C.D., 1953. Polyploidy in Animals Origins of Polyploidy - Nature, 173, N. 4344.

116. Dobzhansky Th., 1937. Genetics and origin of species N.Y.

117. Dollo, L., 1895. Sur la Phylogenie des Dipneustes - Bull. Soc. Belge de Geol., de Paleontologie et d'Hydrologie, v.9.

118. Ellerman J., 1940, 1941, 1947. The familia and genera of living rodents. v. 1, II, III.

119. Elton C., 1942. Voles, Mice and Lemmings: problems in population dynamics. Oxford Univ. Pess.

120. Franz V., 1935. Der biologische Fortschritt - Gustav Fischer verl. Jena.

121. Gyldenstolpe N., 1932. A Manual of Neotropical Sigmodont Rodents. Kungl. Svenska vetensk. Akad. Handl. 3, fasc. 11, No. 3.

122. Grasse P.P. et P.L. Dekeyser. 1955. Orde des Rongeurs - Traite de Zoologie., T. XVII. Mammiferes. Second fascicule.

123. Hall, F.E., 1946. Mammals of Nevada. Berkeley and Los Angeles, Univ. of California press.

124. Hamilton, W.J., 1943. The mammals of eastern United States. An account of recent land mammals occurring east of the Missisippi. Ithaca - N.Y.

125. Hershkovitz Ph., 1944. A systematic review of the Neotropical Water Rats of the Genus Nectomys (Cricetinae). - Misc. Publ. Mus Zool. Univ. Michigan, Ann. Arbor, N. 58, I-IV.

126. Hershkovitz Ph., 1955. South American Marsh Rats, genus Holochilus with a summary of Sigmodont Rodents. Fieldiana - Zoology, v. 37, Chicago.

127. Hershkovitz, Ph. 1960. Mammals of Northern Colombia, Preliminary Report, No. 8: Arboreal rice Rats, as systematic revision of the subgenus Oecomys, genus Oryzomys - Proc. U.S. Nat., v. 110, No. 3420.

128. Hershkovitz Ph., 1962. Evolution of Neotopical Cricetinae Rodents (Muridae) with special reference to the Phyllotine group. Fieldiana: Zoology, v. 46. (Chicago).

129. Hinton, M.A.G., 1926. Monograph of the voles and lemmings. I. London.

130. Hoffstetter R., 1954. Les mammiferes fossiles de l' Amerique du Sud et la biogeographie - Rev. gen. Sci. pur appl., 61.

131. Hooper E.T., 1949. Faunal relationships of recent North American Rodents -Misc. Publ. Mus. of Zool. Univ. of Michigan, No. 72.

132. Hooper E.T., 1952. A systematic review of the Harvest Mice (Genus Reithrodontomys) of Latin America - Misc. Publ. Mus. of Zool. Univ. of Michigan., No. 77, Pl. I-IX.

133. Hooper, E.T., 1957. Dental patterns in Mice of the genus Peromyscus - Misc. Publ. Mus. of Zool. Univ. of Michigan No. 99.

134. Ingram, V., 1959. Biochem, and biophys., acta, 36.

135. Jaeckel, 1957. Kopffüsser (Tintenfische). Ziemsen Verl. Wittenberg.

136. Jaeger, P., 1954. Les aspects actuels du probleme de la Chieroptorogami - Bull de l'Inst. Franc. d'Afrique Noire, ser. A, XVI, 3 Dakar.

137. Kopperi A.J., 1935. Über die nicht - pathogene Protozoenfauna des Blinddarmes einiger Nagetiere - Ann. Soc. Zool. - Bot. Fennicae, 3, No. 2.

138. Kratochvil, J. 1959. Hrabos polni *Microtus arvalis*. Praha NCA Véd.

139. Luppa, H.W. 1956. Morphologie und Histologie des Magens der Bismratte (*Ondatra zibethica*). Eine vergleichende Betrachtung. Wiss. Ztschr. Martin - Luther Univers. Halle - Wittenberg, Math - Nat. Jahrg. B.V. H. 4.

140. Luppa H.W., 1957. Über die Colonspirale der Bisamratte (*Ondatra zibethica*). Ibid. B. VI, H. 4.

141. Luppa H.W., 1958a. Ein Beitrag zur Kenntnis Vorderdarmes der Bisamratte (*Ondatra zibethica*) und elniger muriden Nager (*Microtus arvalis* Pall; *Arvicola terrestris* L., *Clethrionomys glareolus* Schreb., *Apodemus flavicollis* Melch.). Ibid. B. VII, H. 2.

142. Luppa H.W., 1958b. Zur Histologie und Kohlenhydrathistochemie des Dünndarmes der Bisamratte (*Ondatra zibethica*) im Vergleich zu einiger muriden Nager. Ibid. B. VIII, H. 1.

143. Nasset E.S., 1953. Gastric secretion in the beaver (*Castor canadensis*) - J. Mammal, v. 34.

144. Major F.M., 1897. On the Malgashy Rodent genus *Brachyuromys* and on the natural relations of some groups of the Muridae (Hesperomyinae, Microtinae, Murinae and Spalacidae) with each other and with the Malgashy Nesomyinae - Proc. Zool. Soc. London.

145. Miller G.S. and Gidley, J.W., 1918. Synopsis of the supergeneric groups of rodents. Washingt. D.C. J. Acad. Sic. 8.

146. Milne-Edwards M. A., 1867. Memoire sur le type d'une nouvelli Famille de l'ords des Rongeurs Nouvelles Archives du Museums d'Hist. Natur. Paris. Memories c. III.

147. Milne-Edwards H., 1868-1874. Recherches pour survir a l'histoire naturelle des mammiferes comprenant des considerations sur la classification de ces animaux. Paris. Gr. Masson.

148. Monmignaut Cl,, 1963. Elude d'une animalie de l'email des dents jugales chez des Rongeurs nouveau-nes - Mammalia T. 27, N 2.

149. Myrcha A., 1964. Variations in thelength and weight of the alimentary tract of Clethrionomys glareolus (Schreber, 1780). - Acta theriologica. Bialowieza. v. IX, 10.

150. Oppel, 1896. Anat. Anz., 11.

151. Osborn H.F., 1896. From the Grecks to Darwin, London,

152. Packard, R.L., 1960. Speciation and evolution of the Pygmy Mice genus Baiomys. Univ. Kansas Publ. Mus. Nat. Host. V. 9, N. 23.

153. Pernkopf E., 1931. Die Entwicklung des Vorderdarmes, insbesondere des Magens der Wiederkäufer. Z. Anat. Entw - Gesch. Berl., 94.

154. Pernkopf E., 1937. Vorderdarmkanal - Handb. der vergleichenden Anatomie der Wirbeltiere, 3, Berlin.

155. Pernkopf E., und Lerner J., 1937. Mitteldarmkanal. Handb. der Vergleichenden Anatomie der Wirbelterie 3, Berlin.

156. Petter Fr., 1959a. Un nouveau rongeur de Madagascar (Nesomyinae) Macrotarsomys ingens nov. sp. - Mammalia, T. 22, N. 2.

157. Petter Fr., 1959b. Evolution du dessin de la surface d'usure des molaires des Gerbillides - Mammalia, T. 23, N. 3.

158. Petter Fr., 1961. Affinites des genres *Spalax et Brachyuromys* (Rongeurs, Cricetidae). - Mammalia, T. 25, N.4.

159. Plate L., 1908. Selectionsprinzip und Probleme der Artbildung. Ein Handbuch des Darwinismus. Leipzig.

160. Plate L., 1913. Verebungslehre. Leipzig.

161. Remane A., 1956. Die Grundlagen des naturlichen Systems, der vergleichenden Anatomie und der Phylogenetik. Akad. Verl. Leipzig.

162. Sachs, L., 1952. Polyploid evolution and Mammalian chromosomes. - Heredity, vol. 6,

163. Schaub S.. 1925. Die Hamsterartigen Nagetiere des Tertiärs und ihre lebenden Verwandten. Eine systematischodontologisch Studie. Abhandl. Schweiz. Paleont. Gesel'sch B. XLV.

164. Schaub S.. 1930. Quartäre und jungtertiare Hamster. Ibid. B. IL.

165. Schaub S., 1934. Über einige fossile Simplicidentaten aus China und der Mongolei - Ibid. B. LIV.

166. Schaub S., 1958. Simplicidentata. B. Traite de Paleontologie T. VI. Mammiferes evolution, v. 2, Ed., Masson.

167. Shotwell J.A., 1958. Evolution and biogeography of the Aplodontid and Mylagauild Rodents - Evolution, v. XII, N. 4.

168. Simpson G.G., 1945. The Principles of Classification and a Classification of Mammals - Bull. Amer. Mus. Nat. Hist., v. 85, N. Y.

169. Sonntag C.F., 1924. The Comparative anatomy of the tongues of the Mammalia. X. Rodentia - Proc. Zool. Soc. London.

170. Sperry C.C., 1929. Laboratory Studies of the food of Onychomys - U.S. Dep. Agric. Tech. Bul., 145 (pt. 2).

171. Stehlin H.G. und Schaub S.S., 1950. Die Trigonodontie der simplicidentaten Nager. Schweiz. Paleont. Abhandl. B. 67.

172. Stein G., 1958. Uber simplex - Zahnform bei der Feldmaus - Zool. Jahrb. Abt. 3, 86. N. 1-2.

173. St. Hilaire. Geoffrey., 1830. Principles de Phisolophie Zoologique. Paris.

174. Termier H. et G., 1952. Histoire geologique de la Biosphere, Paris. Ed. Masson.

175. Thomas O., 1896. Proc. Zool. Soc. Lond., 1896.

176. Tuckerman F., 1888. The tongue and gustatory organs of the Fiber zibeticus. - Journ. Anat. a Physiol., N.S., II.

177. Tuckerman F., 1891. Further observations on the gustatory organs of the Mammalia. Journ. of Morphol.

178. Tullberg, T., 1899. Über das system der Nagethiere. Eine phylogenetische Studie - Upsala.

179. Wettstein O. von., 1917. Bearbeitung der auf der Expedition gesammelten Vögel und Säugetiere. Wissensch. Ergebnisse der mit Unterstützung der Kaiserlichen Akad. der Wissensch. in Wien aus der Erbschaft Treitl von F. Werner unternommenen zoologischen Expedition nach dem anglo-egyptischen Sudan (Kordofan).

180. Winge D., 1924. Pattedyr-Slaegter, 2. Rodentia, Carnivora, Primates. Coperhagen. H. Hagerups Forlag.

181. Yanofsky C., 1960. The tryptophan synthetase system - Bact. Rev., v. 24.

182. Yapes J., 1936. Considerationes sobre el genero Andinomys (Cricetinae) y description de una forma nueva - Ann. Mus nac. B. Ayres, 38.

183. Zejda J.. 1960. The influence of age on the formation of third upper molar in Bank vole Clethrionomys glareolus (Schreber, 1780) - Folia Zoologica, Rocnik IX (XXIII).

184. Zimmerman Kl., 1937. Die markscheRotelmaus - Analyse einer Population. Markische Tierwelt Bd. 3. H 1/2.

185. Zimmerman Kl., 1958. Selektionswert der Simplex - Zahnform bei der Feldmaus? (Eine Entgegnung). - Zool. Jahrb., 1958, Abt. 3, 86, N. 1-2.