v a topachevskii

fauna of the USSR:

mammals

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The book reviews fossil and present-day mole rats of the family Spalacidae (Rodentia, Mammalia) from all over the world. The general characteristics of the family, the basic adaptive characteristics of its ancestors and the occurrence of basic adaptations in phylogeny and postembryonic ontogeny are given. Data are presented on the distribution of this group in the past and at present. The phylogeny of the family has been worked out. A reconstruction of the taxonomy of mole rats has been made. A separation of subfamilies and certain genera has been done for the first time. A description of new taxa of different ranks has been given. Illustrations—87. Tables—2. Bibliography—210 names.

FOREWORD

This book is the first Russian work on living mole rats and the first compendium on fossil mole rats (Spalacidae) of the world.

The family Spalacidae is one of the least studied groups among the rodents of the old world. Quite a number of works have been devoted to the taxonomy of living and fossil representatives of Spalacidae; however, the major portion of these publications are in the form of preliminary reports describing in detail new species and subspecies. In the majority of such cases, the descriptions are not based on detailed research and hence they constitute sporadic efforts. If to this is added the incompleteness of precise criteria in the identification of species, sub-genera, and genera not to mention subfamilies, then the abundant synonyms appearing in special literature becomes clear. The only major account by Mehely (1909) on present-day mole rats published in the beginning of the century, has become out-of-date. All this has led to a considerable complication and confusion in the classification of the family. The plan of Mehely, or its variation made by Ognev (1947) without additions and reconstructions, is mainly used in the work of foreign specialists and also by many zoologists at home. Though old, it is quite adequate and coordinates the subgeneric categories and the species composition of the group as a whole. But in practical textbooks, like guides on the rodents and the mammalian fauna of the USSR and, also, in individual works on the mammalian fauna of the USSR, greatly simplified variations of this scheme have been used and as a result, many species appear to have been demoted to the level of subspecies without proper justification.

Moreover, the mole rat family has a specific economic significance because all its present representatives are the destroyers of field and garden crops, forage crops, and garden and forest plantations. The destruction brought about by the Spalacidae is increasing in the southern region of the USSR under conditions of intensive field-protecting forest belts. In addition, the mole rats act as hosts to both endo- and ecto-parasites which, in their turn, are either pathogenic to man and farm animals, or are carriers of transmissible diseases.

Sufficient data have accumulated during the last decade on fossil Spalacidae found near the Black Sea and the Azov Sea of the USSR, and some countries of western Europe like southern Poland, Czechoslovakia, Hungary, and Rumania. A further study of this material showed that the remains of mole rats, if identified with highest accuracy, could be of great importance in the stratigraphical breakup of Neocenic and Anthropogenic continental deposits in the southern region of the European part of the USSR and adjacent territories. Taking into consideration also the Pontiac origin of the Mediterranean Sea and the present distribution of Spalacidae, it is self-evident that the evolution and geographical distribution of the family in the past, and at present, were dictated by a distinct influence—mainly by the contours (Sarmatian, Miocean, and Pontiac Seas) of these basins during their entire geological history. As a result, data on the past and present distribution of individual representatives of the group, based on the firm foundation of a natural system, can greatly aid in paleogeographical profiles so important in geological practice.

Finally, a detailed study of this group of rodents, absolutely specialized for an underground mode of life, has great theoretical interest because it is accompanied by an interpretation of the adaptive significance of most of the important systemic traits and, also, the main stages of their development and the direction of that development in phylogeny. A study of individual morphological structures associated with the specificity of a burrowing cycle in mole rats can also serve as the starting point for further work in the field of simulation of such systems into operative practice.

As such, a monographical study on mole rats at this stage is, in our opinion, justified. Naturally, maximum attention should be paid to the taxonomy and phylogeny of Spalacidae because they are the least studied members of the group as a whole.

Many serious difficulties arose during the writing of this book. In addition to the above-mentioned incompleteness of specific criteria for the separation of taxa, starting from the subfamily and ending with species identified by various synonyms at every possible taxonomical level, the formation of a general compendium for fossil and living forms also rests on the problems of taxonomy and parataxonomy. This contradiction between zoological and paleozoological classifications can only be resolved by bringing all the different taxonomical groups of fossil and living organisms under a uniform criterion. Considering this, the author has made an attempt in the present work to describe, wherever possible, subfamilies, genera, subgenera, and species at one level, and has also included the fossil forms.

Naturally, the development of a unified classification at this time should be based on a very clear understanding of the main trends of specialization in this group during evolution, because the taxonomic subgrouping within the group reflects, in fact, the varying degree of this specialization. In this regard, the specialization of mole rats for obtaining food exclusively in underground conditions accompanied by a greatly developed adaptability for burrowing, will be the dominant factor. The specificity of the burrowing cycle of Spalacidae consists of digging with incisors, and throwing the dug out earth from the burrows and food inlets with the help of specific movements of the head and the anterior girdle of the links. In this way the formation of the natural system of mole rats is firmly related to an intensive study of the comparative and evolutionary aspects of structural modifications in the skeletal and muscular system which helps in the burrowing cycle, with a maximum interpolation of data obtained on living and fossil forms. The first in this category of systems is the whole mechanism of the masticatory apparatus of the mole rat, which is the basic organ for burrowing, and also a number of structures which assist in the second stage of the burrowing cycle, i.e. the throwing out of earth combined with complex morphological features of the skull, the neck, the thoracic parts of the vertebral column, and the anterior girdle of the links which help in bringing about a specific coordination in the movements of the atlantal axial-cranial, shoulder, and elbow joints (in conjunction with movements and defensive functions). It is also very important in taxonomy to study the mechanisms associated exclusively with feeding, primarily the structural development of permanent cheek teeth during evolution. However, these developments depend mainly upon the formation of the burrowing structures of the masticatory apparatus as a whole and, in my opinion, should be studied together with the latter.

Along with other mechanisms forming the general complex of burrowing adaptations, the structure of the masticatory apparatus has been mainly considered as the basis of systematics for the Spalacidae. This has made easier the preparation of a single classification for fossil and living forms because these structures have been more fully studied in present forms, and better preserved than other organs in fossil individuals of the group.

It is expedient to point out that the original systematics of Spalacidae proposed in this manual are, naturally, far from perfect. However, at the present stage of research based on specific factual data on this group as a whole, it seems to us that it is quite up-to-date and reflects the coordination and correlation of taxonomical subdivisions of different taxonomical levels in the whole family.

The commonly used methods of morphometry have been used in this work. The explanation of different measurements, indices, and similarly some of the specific details in the structure of the skull, lower jaw, teeth, and bones of the skeleton, have been explained through figures wherever necessary in the course of description. The abstract numbers in the text indicate the indices in percents. The number of examples taken for measurements, in the majority of cases, coincides with similar material available to us.

The so-called geochronological scheme for the Neocene and Anthropogen of Europe has been used by the author as in all his previous works. Its correlation with other schemes presently in vogue in literature is depicted in Figure 38.

Data from research on living representatives of this family from all over the world, and almost all the fossil forms, have been used while writing this monograph. Data which could not be obtained, especially on fossil mole rats from a number of places under excavation in western Europe, have been taken from literature. The author has made collections of fossil and present-day Spalacidae which are preserved in the following institutions of the Soviet Union and abroad:

1. Institute of Zoology AN Ukraine SSR;
2. Institute of Zoology AN SSSR;
3. Zoological Museum of Moscow State University;
4. Zoological Museum of Kiev, Odessa, and Chernovits State Universities;
5. Institute of Zoology AN Moldavian SSR;
6. Zoological Museum in the University of Humboldt in Berlin (German Democratic Republic);
7. Storing places in the USSR, Great Britain, France, and the United Arab Republic.

The present work has been carried out on behalf of the Institute of Zoology AN Ukraine SSR. The author is grateful to I. M. Gromov, Head of the Department of Mammals of this Institute, for acting as a consultant and giving constant direction and assistance in obtaining scientific data from different zoological institutes in this country and abroad; and also, to all the co-workers of this laboratory who contributed to the successful publication of this work. We are greatly indebted to the Head of the Department of Paleozoology of the Institute of Zoology AN Ukraine SSR; to corresponding member of the AN Ukraine SSR, Professor I. G. Pidoplichko, for invaluable consultation and help in the work; and also to all the colleagues and co-workers of this department who have taken part in the collecting and processing of data. The author is likewise grateful to Professor V. G. Geptner, Professor A. P. Korneeva, and scientific workers E. I. Yangolenko and M. N. Lozan for granting access to data collected by them. Sincere appreciation is expressed to Professor A. A. Strelkov who examined the manuscript of this book.

The majority of the figures have been drawn by S. L. Shmuilovich, artist of the Department of Mammals of the Institute of Zoology AN SSSR, and part of the illustrations have been drawn by the author.

CONTENTS

TAXONOMICAL INDEX OF SPECIES

FAMILY SPALACIDAE

1. Subfamily Prospalacinae

1. Genus *Prospalax* Mehely

2. Subfamily Spalacinae

1. Genus *Microspalax*

1. Subgenus *Microspalax*

2. Subgenus *Mesospalax*

2. Genus *Spalax*

PART I

INTRODUCTION

MAIN STAGES IN THE HISTORY OF RESEARCH IN THE TAXONOMY OF MOLE RATS (SPALACIDAE GRAY, 1821) AND THE MOST IMPORTANT SCHEMES FOR THEIR CLASSIFICATION

Güldenstaedt (1770) who identified the genus *Spalax* and described the species of common mole rat (*S. microphthalmus* Güld.), initiated taxonomical investigations of mole rats.

The family Spalacidae was identified by Gray later (1821). Until then, Pallas (1778) included mole rats in the genus *Mus* as a subtype of "underground mice" (*Mures subterranei*), along with Myospalacinae and the African Bathyergidae. Illiger (1811), who first proposed dividing the families within the limits of the order Rodentia, considered Spalacidae as mice along with marmots, hamsters, and batiergids. Waterhouse (1839a, 1839b, 1842, 1848), without observing that his series of works appeared twenty years after the publication of Gray's (1821), described mole rats as close to Arvicolidae, and artificially attached beavers and Geomyidae to this family. However, he subsequently reconsidered this nomenclature and, as a result, in his later works mole rats were included in the family Muridae as an independent subtype, *Spalacina*. Thereafter, until the publication of a major monograph on rodents by Tullberg (1899), no common approach was used by different authors to trace out the taxonomical rank of the group of mole rats. Though the majority of researchers were inclined like Gray to consider Spalacidae as an independent family of the group Myoidea (Brandt, 1855; Lilljeborg, 1866; Alston, 1876; Thomas, 1896; and others), still some authors traced them as a subfamily of the family Muridae (Gill, 1872). Tullberg (1899) quite clearly determined the position of Spalacidae as rodents in the family group Myoidea. Afterwards, a similar classification was also given by Miller and Gidley (1918), Weber (1928), Ellerman (1940, 1941, 1949a, 1949), Simpson (1945), Wood (1947), and subsequently Schaub (1968), I. M. Gromov and A. A. Gureev (1962). An unsuccessful interpretation of the taxonomical position of this family is found in the work of Winge (1887, 1941) who joined Spalacidae with jerboa (Dipodidae) as a subfamily. As will be shown later (page 113), a little similarity in the structure of the permanent cheekteeth and some individual skull structures between jerboa (Dipodidae) and mole rats indicate the preservation of ancient traits of the branches which had been separated long ago, and the genetic proximity of their Eocene ancestors. Afterwards, the specialization of these trunks of Myoidea continued in different directions until no basis was left for the joining of the representatives of these groups under one family. An unsuccessful placement of the family has been done in the latest and major compendium on rodents fauna of the world by Grasse, Dekeyser and Viret (1959), who artificially relate Spalacidae and Rhizomyidae to the joint group of Palaeotrogomorpha incertae sedis along with Thrynomyidae, Eupetauridae, Petromyidae, and Bathyergidae.

Tullberg (1899), and the majority of his predecessors, examined the family Spalacidae in considerably greater detail than is done at present, by artificially inserting in this group Rhizomyidae and Myospalacinae—usually independent taxonomical subdivisions of the rank of subfamily. The separation of Rhizomyidae and Myospalacinae from the composition of the family Spalacidae, first as a separate family, and second, as a subfamily Cricetidae which is close to Microtinae, was kept by Miller and Gidley (1918) though the prerequisites for this were laid in the still earlier publications of Brandt (1855), Winge (1887), and Thomas (1896), who considered Rhizomyidae to be in the family Spalacidae in the form of independent taxonomical subdivisions (Rhizodontes, Brandt; Rhizomyini, Winge; Rhizomyinae, Thomas), and Lilljeborg (1866) in the same way, as done in the case of Myospalacinae. However, the old scheme of Tullberg has been used for quite some time by scientists both here (Russia) and abroad (Mehely, 1909; Weber, 1928; Reshetnik, 1941; Ognev, 1947; Afanasev *et al.*, 1953).

The basis for generic, subgeneric, and species taxonomy, in addition to the above-mentioned publication of Güldenstaedt (1770) for modern, subfossil, and partially fossil representatives of Spalacidae, was laid by the works of Nordmann (1840, 1858), Nehring (1897, 1898a, 1898b), K. A. Satunin (1898), and Mehely (1909); and for fossil forms by Mehely (1908), Simionescu (1930), and Kormos (1932) who, notwithstanding some synonyms, worked out the species and subspecies classification of the group as a whole and mainly determined its species composition. Of the works mentioned above, the work of Mehely (1909) deserves special mention for his synthesis of the uncoordinated knowledge of present mole rats of the world contained in the works of his predecessors. A basis for the subgeneric classification of the genus *Spalax* is laid in this monograph, though its prerequisites were laid down in the publications of Nehring (1897) who suggested the separation of small mole rats into a subgenus, *Microspalax*. If one adds to this the genus *Prospalax* described by Mehely a few years earlier (1908), then the coordination of generic and subgeneric groups, together with the species composition of the family, would appear as follows:

Family Spalacidae Gray, 1821

Genus *Prospalax* Mehely, 1908
  P. priscus (Nehring, 1897)

Genus *Spalax* Güldenstaedt, 1770

Subgenus *Microspalax* Nehring, 1897
  S. ehrenbergi Nehring, 1897
  S. fritschi Nehring, 1902

Subgenus *Mesospalax* Mehely, 1909
  S. monticola Nehring, 1898
  S. hungaricus Nehring, 1898

Subgenus *Macrospalax* Mehely, 1909 (= *Spalax* s. str.)
  S. graecus Nehring, 1898
  S. istricus Mehely, 1909
  S. polonicus Mehely, 1909
  S. microphthalmus Güldenstaedt, 1770
  S. giganteus Nehring, 1897

Afterwards, the fossil representative of the genus *Prospalax*—Mid-Pliocene *P. rumanus* Simionescu—described by Simionescu (1930), and the fossil Pliocenic European mole rats, close to the recent Afro-Asiatic *M. ehrenbergi*, separated into a distinct genus *Pliospalax* Kormos by Kormos (1932), were added to the above-mentioned list [though Simionescu (1930) previously considered his as a form of the species *P. macoveii* Simionescu in the genus *Prospalax*]. Zoologists at home—V. I. Radugin (1917), K. A. Satunin (1920), and E. G. Reshetnik (1939, 1941) scrupulously followed the same classification in their works devoted to the study of the taxonomical position of mole rats of the fauna of the USSR. The classification of S. I. Ognev (1947) is quite similar to that of Mehely, differing only in details. Ognev, not knowing about the recent collections of the Afro-Asiatic *M. ehrenbergi*, joined the subgenera *Microspalax* and *Mesospalax* without proper basis. In addition to this, the species composition of the genus *Spalax* was completed by the new species, *S. arenarius* Reshetnik, described earlier by Reshetnik (1939) in the form of a subspecies, *S. polonicus* Mehely. A simplified version of Mehely's classification has been used in recent reviews by Simpson (1945), Ellerman (1949a) and Schaub (1958), who add three genera in the composition of the family—*Prospalax* Mehely, *Pliospalax* Kormos, and *Spalax* Güldenstaedt. Afterwards, the species composition was filled in with fossil forms (Topachevskii, 1957a, 1959, 1965). In his last publication, this author attempted to revise the systemic position of Middle Pliocenic mole rats from northwest of the Black Sea, separated by Kormos, as has been indicated above, into an independent genus *Pliospalax*.

Mehely's classification, along with subsequent additions, reflects the level of our present knowledge of this group fairly well. However, it appears to be an old one today from many angles—primarily due to the addition of new data on living forms and fossil representatives of the family. A detailed morpho-taxonomical study of the vast material on fossil and living mole rats of the world available in the collections of different institutions of USSR as well as in foreign stores, on the characteristics of past and present distributions of representatives of individual taxonomic subdivisions, and the phylogenetic relationship between individual groups within a family, together with the newest paleontological data, has made it possible to determine that the classification put forth above has a number of shortcomings such as:

1. The depth of the differences between *Prospalax* and *Spalax* (in the dimensions accepted by Mehely and all subsequent researchers) many times exceeds the criterion of a genus. Because of this, it is proper to divide Spalacidae into two independent subfamilies—Prospalacinae (extinct ancient mole rats) and Spalacinae (living mole rats).

2. The representatives of the subgenera *Microspalax* and *Mesospalax* have some common primitive peculiarities in the structure of the skull and skeleton, which brings them closer between themselves, and separates them in principle from those large mole rats of the subgenus *Spalax*. Because these traits correspond to the criteria of the genus, two generic groups are separated further from the composition of the subfamily Spalacinae—*Microspalax* Nehring (with subgenera—Nominal and *Mesospalax* Mehely), and *Spalax* Güld.

3. The fossil *Pliospalax* Kormos, remains of which are found in deposits of the Middle and Upper Pliocene of the northeast region around the Black Sea are, in principle, similar to other living Afro-Asiatic representatives of the nominal subgenus of the genus *Microspalax*. Hence, its separation into an independent genus, as done by Kormos (1932), is hardly justifiable at the present level of study. In all probability, this group of mole rats will have to be placed under the above-mentioned subgenus of the genus *Microspalax*.

4. The number of present-day species (including the partly fossil) is unnecessarily overstated. Differences between the following pairs of species —*M. ehrenbergi* Nehr. and *M. fritschi* Nehr.; *M. monticola* Nehr. and *M. hungaricus* Nehr.; and finally, *S. graecus* Nehr. and *S. Istricus* Mehely—described by Nehring and Mehely from only single examples, as seen from investigations of the series, in the majority of cases do not show up in, for example, the appearance of individual or sharp geographical variability and, as a result, the second name in the pairs has to be taken as a synonym for the first. This list contains some other deliberate synonyms. As shown in the investigations of Reshetnik (1941), *M. monticola* Nehring has to

be named *M. leucodon* Nordmann, after Nordmann (1840).

Taking into consideration the facts enumerated above, a reconstituted classification of the family Spalacidae has been given in the concluding part of this Introduction, in accordance with the present level of knowledge (page 130).

A SHORT MORPHOLOGICAL DESCRIPTION OF THE FAMILY SPALACIDAE

Description: Rodents of average dimensions, having characteristics greatly adapted to underground life, comprise the family of mole rats, Spalacidae. The body length of representatives of this group varies from 130 to 350 mm. The body is cylindrical, the feet short, and the neck is not well defined. The head thickens toward the top and is shaped like a narrow wedge. On the sides of the head, two skinny borders covered with hard bristles appear (Figure 1). The rather large eyeballs are hidden under the skin; the external ear differs from that of other rodents in being a vestigial skin fold. The large incisors are separate from the oral cavity (Figure 2), and are not confined to this cavity during digging activity. The tail is vestigial and not externally visible. The limbs are penta-digital; all digits are well-developed and have rounded claws. The hair is dense and

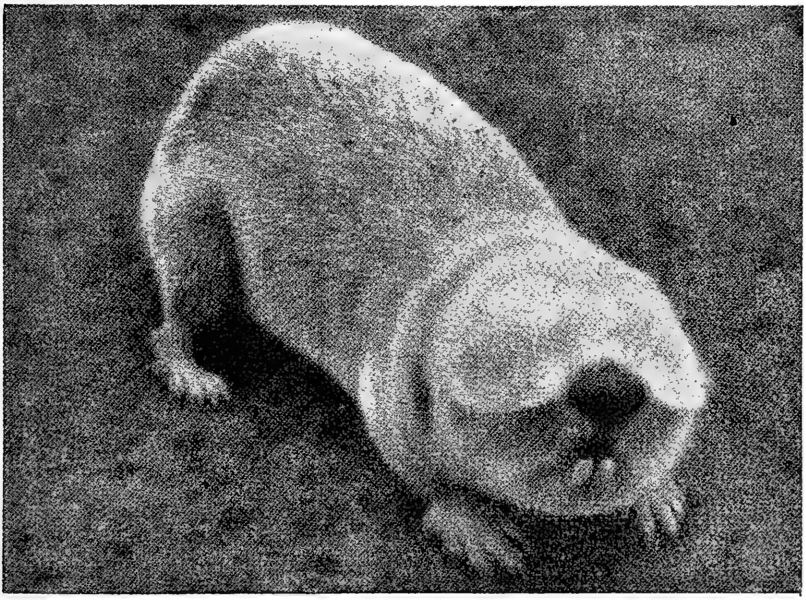

Figure 1. *Spalax arenarius* Resh. Photo by A. I. Gizenko.

weakly differentiated into coarse wool and under wool. The color is monotonous—from light-gray-straw to an appreciably darker brown. The majority of mole rats are similarly colored. A few differences are observed when large numbers of hides are examined. However, the overlapping in traits between separate species is so dominant that it is practically impossible to differentiate them by color. The giant mole rat is an exception; its fur color differs from that of other species.

The individuals of the genus *Microspalax* display the following kinds of coloring. The upper part of the head, the back, and the sides of mole rats Ehrenberg and Nehring, are a pale yellow-gray-buff with a light reddish tinge. The base of the hair is an intense gray. The area around the nose and eyes, and near the cheeks, is of a light mouse-gray color. The ventral part is lighter than the back and is generally mouse-gray. The short whiskers are pale yellow. There are some specimens with a predominance of reddish and buff coloring on the back and sides. The young are always colored a bit darker than the mature and old.

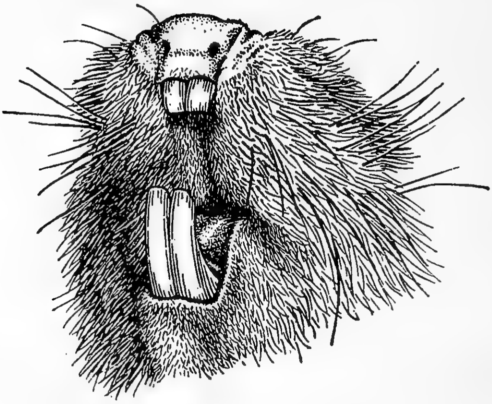

Figure 2. Construction of lips in mole rats. ×1.6.

The coloring of the white-toothed mole rat is very similar. However, the reddish tinges of the back are fainter than in the preceding species. On the whole, the representatives of the given type are characteristically buff-gray, sometimes even having a light yellow-buff fur. The front portion of the head, neck and body is grayer than the back.

Among representatives of the genus *Spalax*, the Podolsk and Bukovin mole rats have a similar coloration. There are quite a few similarities also between the coloration of the above-mentioned species and the white-toothed mole rat. For example, the posterior section of the head, back, and sides of a mature common mole rat is characterized by a pale yellow-gray-buff tinge. The base of the hair is mouse-gray, but as the ends of the hair wear away, the fur assumes a grayish tinge. The anterior portion of the head and neck is lighter than the back. Sometimes a white patch with a yellowish tinge is observed in the area of the forehead. The short whiskers are a pale-white-yellow, and the long ones are a whitish yellow. The ventral portion in the area of the throat, the chest, and the anterior portion of the stomach are mouse-gray; in the middle and posterior parts, it is pale-yellow-buff. The winter fur is up to 14 mm in length, and the summer fur, 10 to 11 mm. In the young, a gray tinge predominates along with a faint pale-yellow on the hair endings. The ventral part is intensively gray. According to S. I. Ognev (1947), the common mole rat found around the Saratov region differed from representatives of this species from the left bank of the steppes and forest steppes of the Ukrainian Soviet Socialist Republic, the central regions of the Russian Soviet Federal Socialist Republic, and the West Caucasus, by a total absence of buff-pale-yellow tinges in coloration, and by the presence in 80% individuals of a transverse white band in the occipital region, expressed in different degrees (starting from the base of the nose and proceeding along the forehead and occiput up to the neck). White fur appears around the mouth and partially on the cheeks. On the other hand, the ventral side of the body of the common mole rat from the Saratov region is darker than those from the region of Ukraine, the central black soils, and the West Caucasus. The throat and chest are of an intense gray color. The hair of the stomach and the surrounding areas is tinged pale-yellow-buff. Irregular white spots in the region of the chest and the posterior portion of the belly were observed in many cases. The phenomenon of albinism is rarely observed in the common mole rat.

In terms of coloration, the sandy mole rat takes a middle position between the common Podolsk and the Bukovin mole rat on the one hand, and the giant mole rat on the other. On the whole, this species is usually lighter in color than representatives of the group microphthalmus. Frequently, the posterior section of the head, back and sides of the body of mature animals is a pale-yellow-gray color. The base of the hair is gray. A whitish gray tinge with a pale-yellow tinge is predominant in the region of the forehead and cheeks. The fur of the ventral region is gray with a mixture of pale yellow-yellowish lines in the belly.

Finally, the lightest colored form is represented by the giant mole rat. The back and sides of the body are characteristically an extremely faint pale-gray, yellow-silver color. The head, in the region of the forehead, occiput, and cheeks, is of a faint, bright silvery-white tinge, with a slight yellow coloration. The lower portion of the body is grayer than that of the upper. The base of the hair is gray. Gray tinges are more predominant in the coloration of the young.

Data on the moulting of mole rats is extremely inadequate. It is only known that the thick winter fur of the common mole rat changes into a rather thin summer cover in May to June, and the autumn moulting takes place in September (Ognev, 1947). In my opinion the spring and autumn moulting in the Bukovin white-toothed mole rat is rather more prolonged. According to E. I. Yangolenko (1965) the spring moulting of the foregoing species takes place from March to May and the autumn one from August to November. The change of hair in males takes place quicker than in females. The young moult later than the older. The most intensive moulting occurs in March and the autumn moulting takes place in September. The sequence of moulting in mole rats of different species is almost similar. Initially the occipital region and the middle of the back begin to moult, then the shoulders and body, and finally the sides and belly. Moulting is accompanied by a darkening of the fleshy side of the hide and formation of black spots.

The skull is wedge-shaped from above and from the sides, with a very long facial section and a shortened brain area; the length of the facial section significantly exceeds the brain area. Differing from representatives of the majority of other families of rodents, except some Oligocenic Cylindrodontidae, the occipital surface is highly developed, widened, thickened, and considerably inclined in front, placing itself in relation to the prolonged line of teethrows at approximately a 45° angle. The width of the occipital surface significantly exceeds the length of the braincase and the apex of the lambdoid crest is situated approximately at the level of the winged bone processes (Figure 3). The rostrum is low and wide. Its least height is significantly less than its width. The nasal bones are long and narrow; their length is twice that of the upper row of permanent molars, and more than twice the greatest width of these bones (usually 2½ times). The edges of the nasal bones protrude significantly in front of the edge of the submaxillary bones (Figure 3). The orbit socket is large; its height is significantly greater than its width. In addition, the former, as a rule, is more than the combined length of the two front permanent molars, or approaches to it. The suborbital canal is present in representatives of the primitive subfamilies of the ancient mole rats (Prospalacinae) and is absent in the true mole rats (Spalacinae). Comparatively the zygomatic arches are poorly developed and are widely placed (Figure 3) with a slight downward bend. The base of the malar processes of the maxillary bone is slightly elevated in relation to the alveolar edge (Figure 3). The malar bone is very small and does not come in contact with the lacrimal. The supraorbital processes of the frontal bones are absent. In place of the infraorbital tubercle, there are vestigial short crests. The sagittal and longitudinal crests are well-developed; moreover, the latter is situated at the level of the posterior ends of the zygomatic arches and are comparable to them in width. The incisorial sockets are significantly shifted backward, and consequently the posterior length of the hard palate (measured from the posterior edge of the incisorial sockets or cavities) is less than half of the anterior length (measured from the anterior edge of the incisorial sockets). The masseter area is narrow (length is less than the similar area of the two anterior permanent molars), with

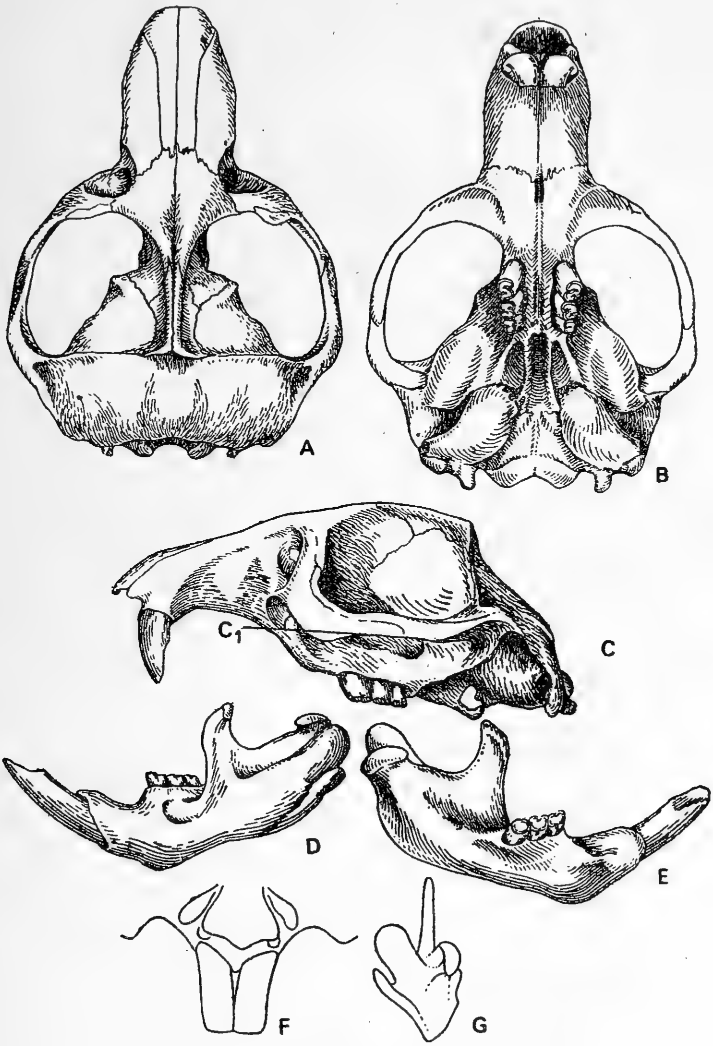

Figure 3. *Spalax giganteus* Nehr. ×1.2.

A—axial skull from above; *B*—the same from below; *C*—the same from the side; C_1—malar angle; *D*—lower jaw from outer side; *E*—the same from inner side; *F*—rostral section of skull, anterior view (diagrammatic); *G*—lower jaw, posterior view (diagrammatic).

a sharply outlined (in the form of a crest) anterior edge situated at almost a horizontal level. The crest of its anterior edge never reaches the sutures between the premaxillary and maxillary bones (Figure 3). In addition, the anterior edges of the masseter area show a considerable deviation in the posterior section of the diastemic palate (Figure 3). The planes of the processes of the winged bones are almost parallel. The winged processes of the wedge-shaped bones (Figure 4, ii) are narrow; the distance between the anterior boundary of the fossa pterygoidea and crista pterygoidea (posterior edge of the for. orbitorotundum) does not exceed half the anterior width of the nasal bones. The winged fossa coincides correspondingly with the foramen rotundum and the brain cavity. Differing from the majority of other families of the order, there are two areas on the skull for articulation with the lower jaw. The true articulating area (fossa glenoidea; Figure 4, i) is placed anteriorly to the false one (fossa pseudoglenoidea; Figure 4, iii) and sharply stretched in the same direction; its length exceeds that of the permanent molars. During digging and masticating, the lower jaw is fixed on it (anterior position). The malar process of the temporal bone is poorly developed and, consequently, the articulating surface does not extend to the zygomatic arch (Figure 4). The false articulating fossa is formed by the auditory bullae and the petromastoideum, and corresponds to the position of the jaw during mastication and inactivity (the posterior position of the lower jaw). The combined length of the true and false articulating surfaces is more than one and a half times the length of the line of permanent molars. The auditory bullae are small, compact, comparatively thick-walled, and lie in a horizontal position. Their external edges protrude; the external auditory meatus is situated approximately at the level of the occipital condyles and does not project laterally in relation to the occipital surface

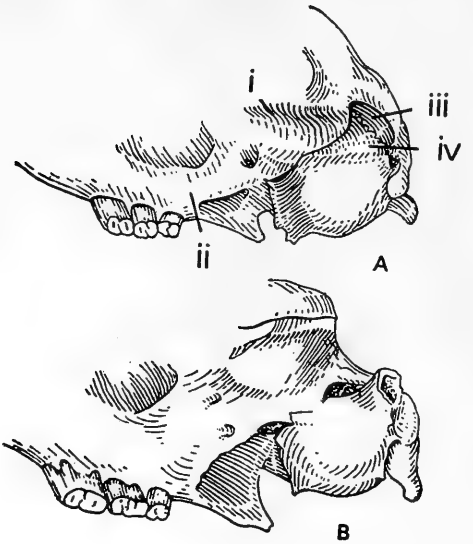

Figure 4. Structure of the articulating surfaces of the skull with lower jaw in (*A*) *Spalax* and (*B*) *Rhizomys*. ×1.8.

i—natural articulating surface; *ii*—wing-like process of wedge-shaped bone; *iii*—false articulating surface; *iv*—articulating plate of the auditory drum.

(Figure 4). The dorsal edge of the bulla is expanded into an articulating plate (Figure 4, iv), forming the ventral portion of the false articulating fossa. The mastoid bones are comparatively large, bulging, and placed low; the proc. mastoideus is external to the proc. paroccipitalis situated at the same level as the latter; the greatest height of the petromastoideum exceeds the length of the permanent molar line. The for. magnum is situated low; its height is approximately more than twice that of the occipital surface, measured from the upper boundary of the for. magnum to the apex of the lambdoid crest. The occipital condyles touch each other. The proc. paroccipitalis is weakly developed (Figure 4).

The lower jaw has an elongated articulating process turning sharply backward and inward, the longitudinal axis of which corresponds to the similar one of the horizontal branch (Figure 3). The length of the proc. condyloideus either exceeds the length of the lower line of permanent molars or approximates it. The coronary process is long, broad, and bent like a sickle; its anterior boundary is situated perpendicularly along the longitudinal axis of the jaw. The coronate articulating pattern is wide; its greatest width along the chord exceeds the length of the lower line of permanent molars, or is about equal to it. The alveolar process is always well-developed, and is less in height than its articulating one (subfamily Prospalacinae), or approximately equal to it or larger (subfamily Spalacinae). The structure and position of the coronary process vary. In representatives of a primitive subfamily of ancient mole rats, it is situated at the base of the corresponding process and has a common border with it; the posterior pattern of the jaw is well-developed (Figure 40). The length of the coronary process in this case may significantly exceed the combined length of the two anterior permanent molars; the sella externa is always absent (Figure 40). In true mole rats, the coronary process is shortened, displaced laterally and situated on the external wall of the alveoli; the posterior pattern is absent; the sella externa is always present (Figure 3).

In the works of the majority of the older authors (Tullberg, 1899; Mehely, 1909; and others), and also in some of the comparatively recent reviews on world fauna of rodents (Ellerman, 1940; Grasse, Dekeyser and Viret, 1955), the dental formula of Spalacidae has been interpreted as follows: $I\frac{1}{1}\ C\frac{0}{0}\ P\frac{0}{0}\ M\frac{3}{3}$ (total, 16 teeth). This formula has been used until now in Russian research also (Ognev, 1947; Gromov, 1962; Gromov *et al.*, 1963). However, Stehlin (1923) is inclined to consider the anterior molar tooth as $P\frac{1}{1}$ ($P\frac{4}{4}$ according to the scheme in general use, because the said author stuck to the order of nomenclature of premolar teeth in the reverse direction). On the whole, the dental formula looks like this: $I\frac{1}{1}\ C\frac{0}{0}\ P\frac{1}{1}\ M\frac{2}{2}$. This formula was used in subsequent works by Stehlin and Schaub (1941), and also in Schaub's most recent review (1958) on fossil rodents of world fauna. Such an interpretation of the dental formula of mole rats has quite a firm foundation because Stehlin (1923) very confidently proved the fact of the change of the anterior lower molars in Oligocenic rhizomys from the group of Rhizospalacidae which, in all probability, is the origin of mole rats. The presence of a vestigial additional tooth situated behind the proposed M^3 (Figure 5) in the upper toothrow of present-day mole rats of the genus *Spalax*, observed by us sometime back, may also serve as a partial proof for this. However, it is not ruled out that the aforesaid could be an accidental deviation from the normal because the presence of additional teeth has sometimes been observed in other families of rodents and also in hare-like animals. The said tooth has an appearance of a small pin with one root with a sharply reduced crown resembling P^4 of some Dipodidae in its general outline. Its alveolus is very small, almost a superficial fossa; as a result, this tooth is easily lost during the preparation of skulls.

Figure 5. Upper row of permanent molars in *Spalax arenarius* Resh. with additional tooth at the back M^3. ×3.7.

All the aforesaid confirms, as it were, Stehlin's idea. However, the dental formula proposed by him for Spalacidae warrants a review of the dental formula for all families forming the suborder Myoidea and foremost, for the fossilized Eocene Cricetidae among which one is likely to find common ancestors for Rhizosomidae and mole rats. The latter (Eocene Cricetidae) do not fall within the purview of the present research. Hence to avoid unnecessary complications, we will start from the generally used dental formula naming, for the time being, the fourth molarized premolar $M\frac{1}{1}$.

The upper and lower incisors are very strong and wide; their combined width, and individual width, respectively exceeds the combined length of the two permanent molars or, in the first instance, is equal to it, and in the second, is equal to $M\frac{1}{1}$.

The molar teeth have a pterydomidal[1] structure, and the crown is of average height. The roots have a tendency to fuse in highly specialized representatives. The dimension of the teeth increases in a forward direction. The masticating surface is folded; the original tuberculate type of its structure becomes evident only at the initial stage, before wearing starts. Originally, the upper permanent molars were characterized by the presence of one loop and two tubercles—protocone and hypocone—in the internal line; there are two to three loops of anterior and posterior

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[1] The fine tuberculated type of construction of the permanent molars is closer to the original one for rodents (Stehlin and Schaub, 1951; Gromov, 1962) (Figure 6).

openings, the paracone, mesocone, and metacone on the outer side (Figure 6). However in the majority of cases, the paracone has a tendency to fuse with the anterior inlet, the metacone with the posterior, and the mesocone gets reduced, having the greatest development only in the primitive representatives of the family. The loops, because of their wearing out, have a tendency to lock into marks as a result of tooth rubbing. The process of mark formation takes place more quickly in specialized than in primitive representatives of the family. In phylogenetic lines and with age, the contour of the surfaces of the permanent molars, in different successions, takes on a W–, Z– or S–, E– and C–type of outline. The lower permanent molars originally have one or, rarely, two (if the vestige of the anterior loop is to be considered, which happens when the second one is highly developed) loops, and two tubercles—protoconid and hypoconid—in the outer side, and one or two loops, anterior and posterior collars, and a metaconid, mesoconid, and entoconid in the inner side (Figure 6). As in the upper permanent molars, the structure of the teeth simplifies with age because of the fusion of the metaconid with the anterior collar, the entoconid with the posterior collar, reduction in the mesoconid and the anterior loop of the outer side, with a subsequent locking of the loops into marks with contours on the surface, principally in the same manner as in the upper permanent molars.

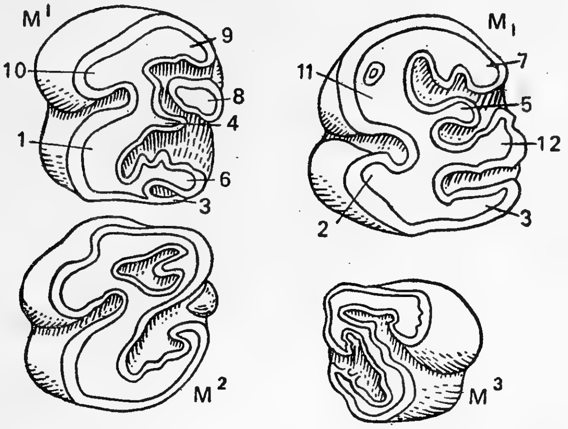

Figure 6. *Microspalax compositodontus* sp. nov., Late Miocene of South Ukraine.

Upper and lower permanent molars: *1*—hypocone; *2*—hypoconid; *3*—posterior collar; *4*—mesocone; *5*—mesoconid; *6*—metacone; *7*—metaconid; *8*—paracone; *9*—anterior collar; *10*—protocone; *11*—protoconid; *12*—entoconid.

The first cervical vertebra with an acute reduction of the thickened wings and a comparatively wide dorsal arch (width exceeds approximately two or more times the width of the ventral arch), has a faint impression of a neural spine (Figure 45). The articulating surfaces with the skull and the second cervical vertebra are spread up and significantly enter into the ventral part. The ends of the pair of articulating areas fuse together on it (Figure 45). The second cervical vertebra is drawn out slightly antero-posteriorly, with a highly developed neural spine the upper end of which is bifurcated (Figure 46); the largest antero-posterior diameter of this appendix is approximately equal to the length of the body of the vertebra and the greatest width (transversely) exceeds the width of the tooth-like appendix. The latter, in its lower border of the articulating surfaces, contacts the first cervical vertebra. The articulating surfaces for the atlas fuse together directly under the odontoid process of the axis. The transverse processes are almost completely reduced. The rest of the cervical vertebrae are spread up with thickened, unbent dorsal arches unfused but closely fitting to each other and firmly fixed (Figure 7). The neural spines are almost completely reduced and the transverse ones are hardly apparent. The sacral bone is formed by a complete fusion of four (genus *Spalax*), or five (genus *Microspalax*), vertebrae. The neural spines are completely

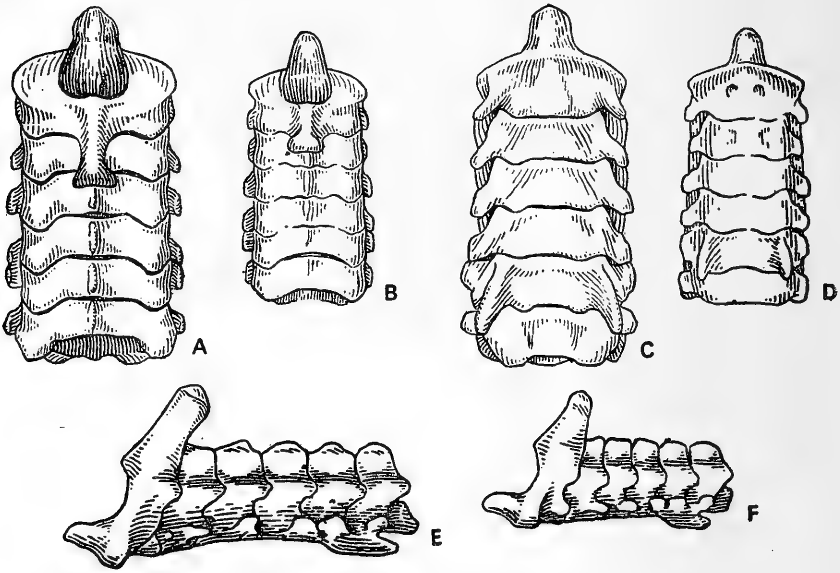

Figure 7. Cervical section of the vertebral column without atlas.

A, B, C—Spalax; *D, E, F—Microspalax*; *A, D*—from above; *B, E*—from below; *C, F*—from the side.

fused to form the dorsal crest (*Microspalax*) or exhibit a considerable tendency for fusion (*Spalax*) (Figure 49). The transverse processes (wings) of the sacral bone are not fused because the dorsal sacral openings are almost completely closed. The cranial and caudal articulating processes of the second to fourth vertebrae are completely reduced. The lateral boundaries of the wings (transverse processes) in the region of the third and fourth vertebrae have dorso-lateral crests.

The sternum is diamond-shaped with a well-developed handle that is narrow at its end and has a well-developed central crest (Figure 8). The thin clavicle, which is almost unbent throughout the width of its extremity, articulates with the scapula and is two and one-half times less than the width of the acromion process.

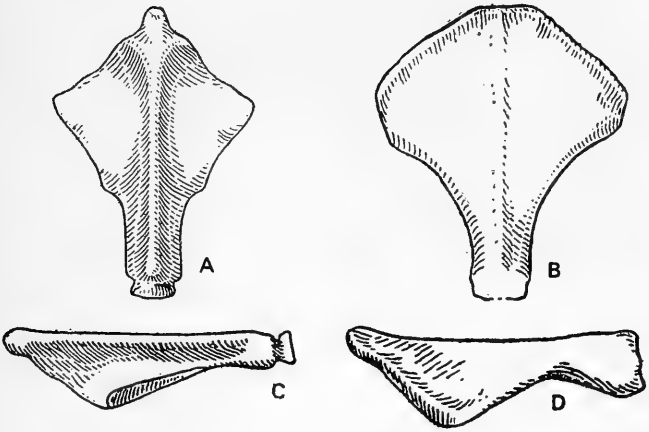

Figure 8. Sternum. ×3.6.

A, B—*Spalax*; *C, D*—*Rhizomys*; *A, C*—from below; *B, D*—from the side.

The scapula is relatively narrow with steadily approaching distalcranial and caudal borders; the distance between cranial and caudal angles (width of the proximal extremity) is twice narrower than the length of the bone measured from the farthest point of the beak-like process. The caudal border is widened because of the greatly developed caudal ridge (Figure 9). The acromion process is comparatively short; its length does not exceed one-third the length of the scapula; it ends a little short of the articulating fossa (a little less distance than the latero-medial cross section of the latter). The beak-like process is short and flat.

The humerus is strongly flattened in the antero-posterior direction; its width is more than the deltoid process (proc. deltoideus) by two and a half times and exceeds the antero-posterior cross section measured at the same place. The large tubercle is higher than the shoulder head. The deltoid ridge is strong, placed laterally, and bent sharply due to a backward protuberance. The medial epicondyl is sunken, its distal end is located below the similar trochlea (Figure 10). The epicondylar (supratrochlea) foramen is absent.

The ulna is particularly large in the arm, with a strongly developed

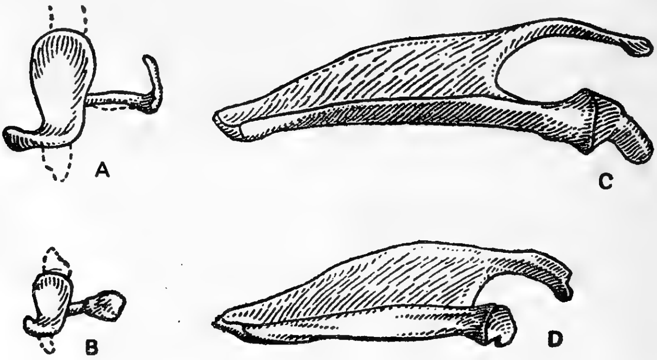

Figure 9. Scapula. ×1.6.

A, C—Rhizomys; *B, D—Spalax*; *A, B*—from the side of the articulating cavity; *C, D*—from the side of the caudal edge.

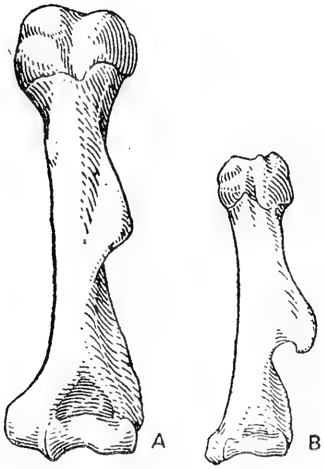

Figure 10. Humerus bone, anterior. ×1.6.

A—Rhizomys; *B—Spalax*.

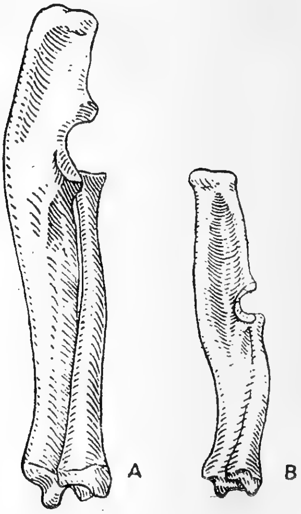

Figure 11. Radius and ulna bones from the outer side. ×1.6.

A—Rhizomys; *B—Spalax*.

massive elbow process (olecranon) whose length exceeds one-third of its entire length. The radius is a short bone, its length being one-third less than the ulna, with a strongly bent axis (bulging anteriorly) (Figure 11). The metapodia (metacarpals) and the phalanges of the fingers are short and broad (Figure 12).

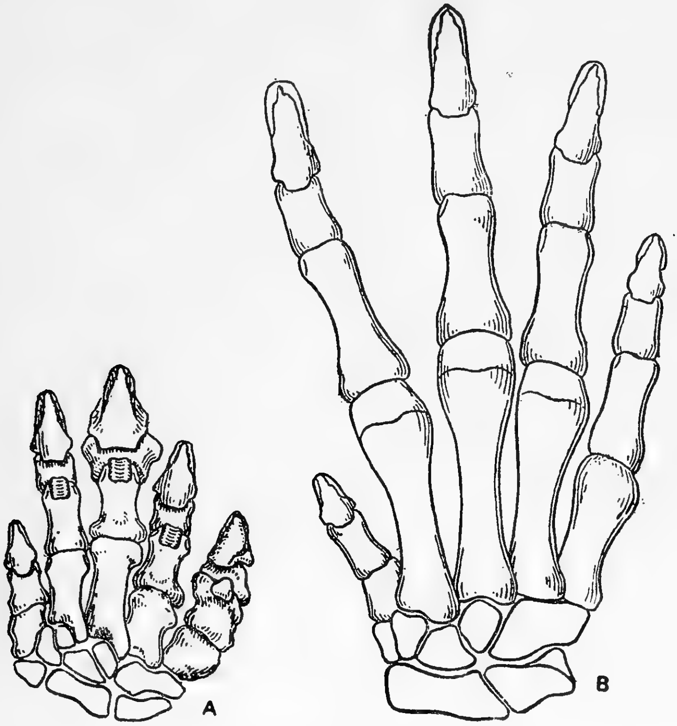

Figure 12. Paw. ×2.4.

A—Spalax; B—Rhizomys.

The pelvic bone has a well-developed sciatic ridge and bulge (Figure 49), with a reduced pubic bone, and a very small interlocking foramen; the height of the foramen is usually twice or more, less than the length of the articulating fossa; rarely, it is equal to the latter, or exceeds it a little. The pubic symphysis is delicate, sickle-shaped, and bent (Figure 49). The base of the seat is always protuberant (convex).

The femur is very strong in the antero-posterior axis, considerably large, and inclined proximally in relation to its head, with a large trochanter, and a strong, considerably bent lateral ridge (Figure 13). The lesser trochanter and head of the femur are close to each other. The block (pulley) for the knee cap (whirl bone) is thick.

The big tibia is thick, the proximal end is bent forward and within latero-medially, with a well-developed ridge—*crista tibiae* (enemial crest) which is medial. The fibula is completely fused with the tibia for almost half of its length. Its upper portion is in the shape of a flattened plate which, in turn, fuses with the epiphysis of the tibia. The borders of the fusion of the tibia and fibula are not visible in the first and second case (proximally or distally). The metapodia (metatarsals) and phalanges of the toes of the feet are characteristically short, as in the structure of the wrist.

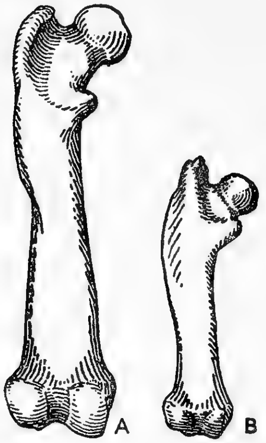

Figure 13. Femur, posterior view. ×1.5.

A—Rhizomys; *B—Spalax.*

Comparison. Mole rats represent an early differentiated group of specialized digging rodents, separating with *Rhizomys* of the branch of hamster-like animals from the general group somewhere in the Eocene period. Among the representatives of the present-day fauna of rodents, the nearest family appears to be that of the bamboo rat—Rhizomyidae—though the latter were differentiated from mole rats perhaps during sufficiently different times even in the Oligocene. The differences between mole rats and Myospalacinae are so great, notwithstanding some of the convergent similar traits in the structure of the skull and individual bones of the postcranial skeleton, related primarily to a similar adaptiveness in the excavation of earth during digging with the help of the head, that there is hardly any basis for a close relationship between these families. Their inclusion in one family (as done by Tullberg, 1899) is still less correct even if only at the level of independent subfamilies (Thomas, 1897), which found support in the works of some scientists in the USSR (Ognev, 1947; Afanas'ev *et al.*, 1953). Looking at the aforesaid, we are restricting ourselves to the comparison of mole rats, because at present there exists some confusion in the determination of their remains in the works of paleontologists (Bazhanov and Kozhamkulova, 1960).

Mole rats differ from representatives of the family Rhizomyidae as follows:

1. By eyes which are hidden under the skin, and by an almost eclipsed external ear and tail, neither of which are seen externally. In Rhizomyidae, the eyes are not hidden under the skin, the external ear is well-developed, and the tail length exceeds the length of the hind feet.

2. By long facial but shortened cranial sections of the skull. The length of the former considerably exceeds the length of the latter. In bamboo

rats, the facial portion of the skull is relatively short.

3. By a greatly developed, broadened, and considerably forward slanting occipital surface (situated in relation to the longitudinal axis of the toothrows at an angle of about 45°, while the apex of the lambdoidal crest is shifted anteriorly to the level of the processes of the winged bones; the width of the very surface is more than the length of the cranium). In Rhizomyidae, the occipital surface is moderately developed, is not broad, and is slightly inclined forward; it is situated almost perpendicularly in relation to the longitudinal axis of the toothrows; the apex of the lambdoid crest, behind the lateral pharyngeal tubercles, and the width of the very surface, is distinctly less than the length of the cranial portion (Figure 14).

4. By a lowered, wide rostrum, the width of which is considerably more than the least height. In the bamboo rat, it is narrow and high; its least height is considerably more than its width.

5. By elongated, narrow, and forward-protruding nasal bones; their length exceeds twice or more the length of the upper line of the permanent molars; the greatest width is more than twice the length (usually two and one-half times), and the anterior edges are drawn forward in relation to the anterior borders of the premaxillary bones. In Rhizomyidae, the length of the nasal bones exceeds less than twice the length of M^1 to M^3; their width is approximately twice less than the length, and the anterior extremities are shifted behind in relation to similar ones for the premaxillary bones.

6. By a large, relatively narrow, infraorbital foramen. Its height in Spalacidae is not less than the length of the two anterior permanent molars and always exceeds the width. In bamboo rats, this foramen is comparatively small, and wide; its height only slightly exceeds the length of M^1 or is even approximately equal to the latter, and the width is more than the height.

7. By zygomatic arch that is slender, a little bent down, and situated relatively low in relation to the toothrows. In bamboo rats, the arch is strong, wide, strongly bent down, and placed higher in relation to the toothrows.

8. By the disposition of the lambdoid ridge on the level of the posterior extremity of the zygomatic arch and a comparatively large prolongation of the latter; the length of this ridge is a little less than the largest jugal width, less than one and a half times. In bamboo rats, the posterior base of the zygomatic arch is considerably bent in front in relation to the lambdoid ridge and the total prolongation of the latter is more than twice less than the width of the skull in the jugal region.

9. By the incisorial openings which are considerably shifted posteriorly, as a result of which the length of the posterior hard palate exceeds much

less than twice the length of the former. In bamboo rats, the anterior palate is approximately twice shorter than the posterior one.

10. By the narrowed, horizontally situated masticating surface of the skull, with a sharply contoured (in the shape of a crest) anterior region, not reaching the suture between the premaxillary and maxillary bones;

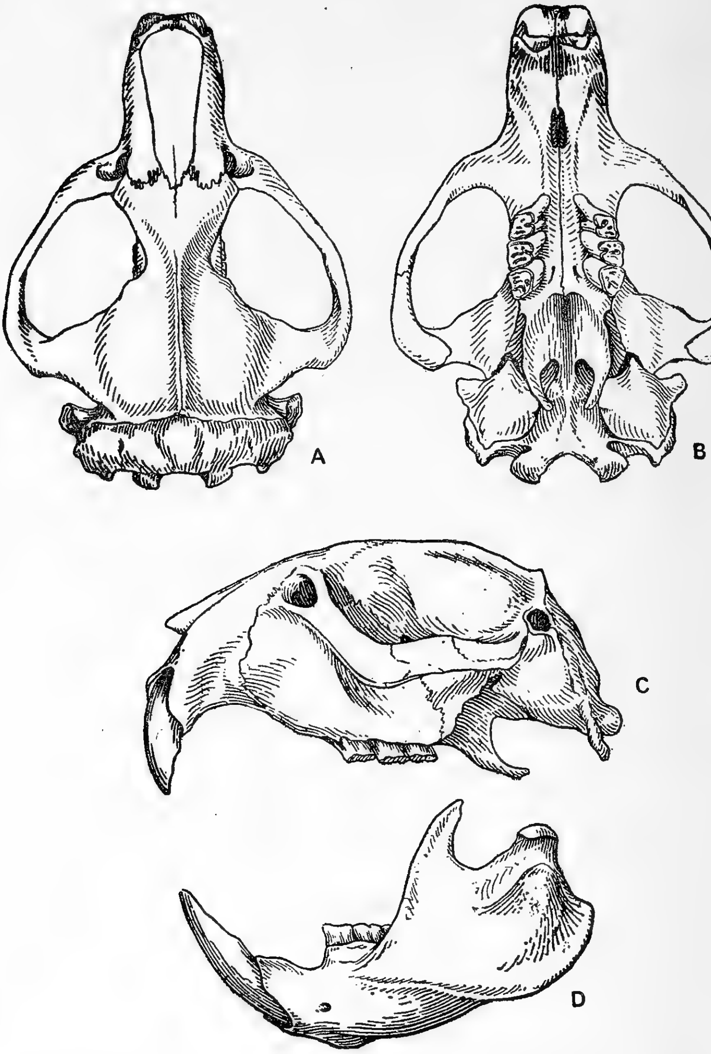

Figure 14. *Rhizomys* sp. Natural size.

A—skull from above (dorsal view); *B*—the same from below (ventral view); *C*—the same from the side (lateral view); *D*—lower jaw from the outer side.

the length of the masticating surface is less than the length of the two anterior permanent molars. In bamboo rats, this surface is relatively longer (its length is approximately equal to the length of a full line of M^1 to M^3), and situated in a vertical hollow; its anterior edge, without any contoured ridge, always encroaches on the premaxillary bone.

11. By a narrow, winged process of the cuniform (wedge-shaped) bone, the width of which does not exceed half of the anterior width of the nasal bones. It is wider in the bamboo rat; its width significantly exceeds half that of the anterior total width of the nasale, and in some cases exceeds even their full width.

12. By an unclosed winged depression; largely coinciding with the orbital foramen and the brain cavity. It is completely or almost completely closed in Rhizomyidae.

13. By a prolonged, true articulating surface whose length exceeds the length of the upper line of permanent molars, and additionally, the jugular process of the temporal bone in Spalacidae, as a result of which the articulating fossa is not present on the zygomatic arch. In bamboo rats, the true articulating fossa is shortened (length is less than that of the line of permanent molars), and the jugular process of the temporal bone is well-developed, as a result of which a considerable portion of the fossa glenoidea extends on the zygomatic arch.

14. By the construction of a false articulating fossa which is formed in Spalacidae by the petromastoideum and the dorsal edges of the auditory bullae forming an articulating plate. In bamboo rats, the lower jaw in the extreme posterior position rests exclusively in the thick tympano-turbinals of the auditory bullae, the articulating plates of the latter ones are absent, and the mastoid bones do not take part in the formation of the false articulating fossa.

15. By the protruding external edges of the auditory bullae, as a result of which the external auditory foramens are situated at about the same level as the occipital condyles and not laterally in relation to the occipital surface. In bamboo rats, the external edges of the auditory bullae are raised, the external foramens are situated at the level of the lambdoid ridge, and their edges are curled externally in relation to the same ones of the occipital surface.

16. By a large, low placed petromastoideum; the height of the mastoid bone exceeds the length of the row of permanent molars, and the lamellar processes are placed external to the jugular processes at about the same level as the latter. In bamboo rats, the mastoid bones are short (their height is considerably less than the length of M^1 to M^3), and raised (lamellar processes are situated directly under the large, wide proc. paroccipitalis).

17. By the lower occipital opening, the height of which is less than

twice or more times the height of the occipital surface measured from the upper edge of the foramen magnum. In bamboo rats, this opening is comparatively higher; its height is more, though less than twice the height of the occipital surface.

18. By occipital condyles which contact each other. These do not make contact in Rhizomyidae.

19. By a strongly slanted posteriorly articulating process of the lower jaw, the longitudinal axis of which approximately corresponds to the similar one of the horizontal branch. In bamboo rats, it is placed at a considerable angle or almost perpendicular in relation to the longitudinal axis of the horizontal branch.

20. By the almost perpendicular position of the anterior edge of the coronary process. In Rhizomyidae, it is considerably inclined back.

21. By a wide furrow on the coronary articulating surface; its width exceeds the length of the lower line of the permanent molars, or is about equal to it. It is narrow in bamboo rats. Its width is less than the length of M_1 to M_3.

22. By a more pronounced tubercular structure of the upper and lower permanent molars.

23. By the structure of the first cervical vertebra. The atlas has greatly reduced wings in Spalacidae, is thick with a comparatively wider dorsal arch (width exceeds twice or more the width of the ventral arch), and very faint traces of a bony process show. Additionally, the corresponding pair of surfaces for the condyles of the skull and the articulation with the second cervical vertebra largely cross the ventral arch, and are in contact with each other. In bamboo rats, the wings of the atlas are well-developed, the dorsal arch is bulging and narrow (its width is approximately equal to the ventral arch) with well-developed traces of a bony process. The right and left surfaces for articulation with the skull, and the second cervical vertebra, are almost not set in the ventral arch and are not in contact with each other.

24. By the structure of the second cervical vertebra. The bony process (neural spine) of this vertebra in mole rats is a little elongated in the antero-posterior direction, widely spread up, and bifurcated at the end. The greatest antero-posterior transverse section of this process is approximately equal to the body of the vertebra but the greatest width exceeds the width of the odentoid process. The latter is characterized by a thick dorsal surface and is situated above the lower edge of the articulating surface for articulation with the first cervical vertebra; the surfaces themselves fuse together directly under the odentoid process; the transverse processes are almost completely reduced. In bamboo rats, the bony process of the second cervical vertebra is strongly elongated in the antero-posterior direction (the largest antero-posterior transverse section exceeds the length

of the body of the vertebra), flattened transversely with an unbifurcated upper end; its width is less than the width of the dens epistrophei (odentoid process). There are round contours in the transverse section shifted ventrally in relation to the lower edge of the surfaces, not contacting each other for articulation with the atlas; the transverse processes are well-developed.

25. By wide, thick, dorsal arches of rest of the cervical vertebrae. The centra of these vertebrae and their dorsal arches fit closely forming an immovable part. The bony processes (neural spines) are almost reduced; the longitudinal ones are hardly marked. In bamboo rats, the dorsal arches of the cervical vertebrae are thin, bulge very much and are not fitted closely to each other (the cervical vertebrae are mobile), and the bony and transverse processes are well-developed.

26. By the bony process (neural spines) of the vertebrae of the sacral bone being fused or having a tendency to fuse to form the dorsal ridge; by its unfused wings having almost complete sacral openings, and a complete reduction of cranial and caudal processes of the second to the fourth vertebrae. In addition, the lateral edges of the wings of the sacral bone in the region of the third and fourth vertebrae have latero-dorsal ridges. In bamboo rats, the bony processes (neural spines) of the vertebrae of the sacral bone are not fused to form a dorsal ridge; the wings are more separated; since the sacral openings are oblique, the cranial and caudal processes of the second to the fourth vertebrae are well-developed, but the latero-dorsal ridges are absent.

27. By the diamond-shaped (rhomboid) contour of the sternum with a pointed handle at the end and a well-developed central crest (keel). In bamboo rats, the sternum is flask-shaped, its handle rounded, and the central ridge is absent.

28. By a thin, almost straight, clavicle, the width of which is one and a half times less than the width of the acromion process in the region of articulation with the scapula. In bamboo rats, this bone is relatively wider and bent when compared with the same in mole rats; its width is approximately equal to the width of the acromion process at the place of articulation with the scapula.

29. By a relatively narrow scapula, elongated longitudinally, with subsequently approaching cranial and caudal edges that are wide because of the well-developed caudal ridge at the caudal edge; by a comparatively short acromion process ending at a small distance from the articulating depression (less than the latero-medial transverse section of the latter); and by a short, widened, beak-like process. The distance between the cranial and caudal angle of the shoulder blade is more than twice shorter than its length, and the length of the acromion process does not exceed one-third the length of the latter. In Rhizomyidae this bone is short and

wedge-shaped because its cranial and caudal edges sharply approach in the direction of the articulating fossa, without the caudal ridge, with a relatively long acromion process (more than one-third the length of the scapula), terminating long before the articulating fossa (which exceeds the latero-medial cross section of the latter), by a long and narrow beak-like process; the distance between the cranial and caudal angles of the scapula significantly exceeds half the length of the latter.

30. By the humerus with a greatly compressed diaphysis in an antero-posterior direction (its width above the deltoid process exceeds one and a half times or more than its antero-posterior diameter); by a protuberance under the head of the humerus; by a strong laterally placed and acutely bent deltoid process with a distally lowered epicondyle, the lower end of which is placed under the trochlea. In Rhizomyidae, the diaphysis of the humerus is compressed very little in an antero-posterior direction (its width exceeds less than one and a half times the antero-posterior diameter); the proximal section of the large protuberance is placed under the head of the humerus; the deltoid process is weakly developed, directed anteriorly, and unbent; and the distal end of the epicondylus medialis is situated above a similar trochlea.

31. By a long, massive olecranon process of the ulna which considerably exceeds one-third the length of the ulna. In bamboo rats, the height of the olecranon process easily exceeds one-fourth the length of the ulna, or is approximately equal to a similar one.

32. By a shortened, strongly anteriorly bent radius; its length is shorter than the length of the ulna by more than one-third. In Rhizomyidae, the radius is elongated (shorter than the ulna by less than one-third) and is almost straight.

33. By the structure of the pelvic bone in which the ischial tubercle is well-developed; by a reduced pubic bone and a very small acetabulum (its height is usually twice or more, less than the articulating fossa, rarely equal to it, or a little exceeds the latter), by long, slender, sabre-shaped symphoidal branches of the pubic bone, and a bulging base of the seat. In bamboo rats, the ischial tubercle is vestigial, the pubic bone is well-developed, the blocked up foramen is large (its height considerably exceeds the length of the acetabulum), the symphoidal branches of the pubic bone are short and wide, but the base of the seat is thick.

34. By the structure of the femur bone with an antero-posteriorly strongly compressed diaphysis; by a large trochanter placed proximally to the head of the femur; by a strong and considerably externally curved lateral ridge; by a considerably closer femur head, and a lesser trochanter; by a compressed block (pulley) for the knee cap. In bamboo rats, the femur bone is less compressed in the antero-posterior direction, the proximal edge of the large trochanter is situated at the same level as the head

of the femur, with a comparatively weak lateral ridge, widely separated lesser trochanter, and caput humeri, and a strongly concave block (pulley) for the patella.

35. By the proximal portion of the large tibia, bent in a latero-medial direction and by the presence of a well-developed ridge—the large and medial-tibial ridge (cnemial crest). In bamboo rats, the diaphysis of the tibia is widened in its upper half and the ridges are hardly marked.

36. By the structure of the fibula. In Spalacidae, it is completely fused with the tibia almost up to half of its length; its upper portion is in the form of a wide plate, completely articulating with the tibial epiphysis; the line of the joining of both bones is not visible. In bamboo rats, the fibula is fused with the tibia for less than half of the length of the former, does not form a lamellar widening, and the sutures of the articulation are always well-defined.

37. By the shortened and widened metapodia and phalanges of the digits of the paw and foot. These are slender and long in Rhizomyidae.

Family composition. Two subfamilies are included: the ancient mole rats, Prospalacinae subfam. nov., and the present-day mole rats, Spalacinae Gray.

GENERAL NATURE OF THE MAJOR ADAPTATIONS OF MOLE RATS

Mole rats are highly specialized shrews whose life activities are related almost entirely to a subterranean way of life. Differing from other burrowing animals which obtain their food on the surface, and for whom underground tunnels act only as hideouts and storehouses for food, Spalacidae feed mainly on underground parts of vegetation, obtaining them in the process of constructing a feeding hole and rarely coming out on the surface. A constant life in underground conditions of absolute darkness, an atmosphere lacking in oxygen and saturated with carbon dioxide, specific conditions for obtaining food with limited possibilities for movement because each movement is accompanied by considerable effort, followed by considerable excavating activity—these have considerably influenced the external appearance of the animal, the structure of its cover (fur), its sense organs, respiratory and cardiovascular systems, and have led to a considerable modification of the skeleton and muscular system of the head and the rest of the body. While studying this, the typical mode of excavation by mole rats has to be taken into consideration; they loosen the soil with their strong and wide incisors, and transport and throw away the soil on the surface mainly with the help of the head. Along with this, if the geological age of the group which has differentiated itself from the general branch of Rhizomyidae, perhaps in the beginning of the Oligocene period, is taken into consideration, all the adaptations of its representatives to subterranean living, brought about through so long a period in the process of stabilizing the selection, are understood. We will consider below a few important aspects.

ADAPTIVE CHARACTERISTICS OF THE EXTERNAL FEATURES, HAIR AND SENSE ORGANS

External features. The external features of mole rats are an outstanding example of the coordination between the form of an animal and its living conditions. The representatives of this family have a characteristically cylindrical body because the wide head continues into the body without a distinct neck. This peculiarity of the external character is reflected in the structure of the skeleton and can be seen in the shortened and immovably articulated cervical part of the vertebral column with the sternal section, details of which will be given below (Figure 49). The constant life in comparatively narrow and low underground tunnels, accompanied by intensive excavating activity, is the main reason for an almost complete reduction of the external ears, preserved in representatives of mole rats only in the shape of a small skin flap, completely hidden by hair. The limited activity of the animal leads, similarly, to a considerable shortening of the tail (a process accompanied by a considerable reduction in the number of caudal vertebrae), because under these conditions it absolutely loses its function as an organ of equilibrium. The general tendency in representatives of mole rats to the aspects mentioned above, as compared with other burrowing animals, and a tendency toward a reduction in the length of the anterior and posterior limbs, well adapted for movement inside horizontal, slanting, and even vertical holes, and for lifting and fixing loads more than the weight of the animal, can be understood. The throwing out of the soil from the burrow with the help of the head leads to its becoming considerably broad and strong, giving it a shovel-shaped contour.

Hair. The structure and color of the hair of mammals is undoubtedly very important from the viewpoint of general adaptations which can be seen from the differences existing in various taxonomical, ecological and geographical groups of animals in the evolutionary process, expressed in various forms in ontogeny. The hair is not an exception from this point of view. It is characterized by the absence of differences in guard hair and undergrowth, differs in fineness (texture), and easily changes direction at the slightest touch. The adaptive character of such hair structure in these specialized shrews can be fully understood by realizing that restriction in movement of the animal in different directions underground is reduced to a minimum. Hard and long hair, specifically directed in one direction, would have been a considerable obstacle for movements of this animal in a direction opposite to its hair; moreover, under the comparatively constant humidity of the burrows and feeding holes, the role of the hair is restricted to thermal regulation, and its defensive function against direct effects of humidity is lost. Recently it was proved that the predominant color of rodents is for camouflaging. This is very true for mole rats also in which the predominant color is gray, yellowish, grayish-brown (fallow), yellowish-brown, brown, and other colors, i.e., colors which almost completely tally with the substrata on which these animals live. The significance of the camouflaging coloration of mole rats, inexplicable at first on looking at their way of life, becomes clear if it is noted that these animals have to leave their burrows at times. Considering the limited activity of these animals on the surface, a complete absence of eyesight, and a not very acute sense of hearing, it takes little imagination to realize what easy prey to different predators they would be, without their camouflaging coloration. Olfactory and communicating receptors adapted mainly to underground food finding, though well-developed, naturally cannot replace the effectiveness of other analyzing agents, nor guarantee the safety of the animals on the surface. As in all specialized earth-digging animals (shrews), and in the majority of burrowing animals, the color of mole rats has completely lost its property to change sharply according to the seasons of the year.

Sense organs. As mentioned above, mole rats have well-developed olfactory and communicating receptors. Sight is completely diminished, and the hearing capacity is considerably lower than in representatives of the majority of other families of Myoidea. These peculiarities of sensory perception come from the way of life these animals lead.

Vibrissae of different types, in addition to a sensitive epithelium on lips and nose, function as organs of perception in mole rats. Perhaps the lowering of the distal points of the front and hind limbs also plays a considerable role in perceiving the surrounding situation.

There are two types of vibrissae in Spalacidae. Orientation when in the burrow and food holes is most probably achieved with the help of long bristles distributed diffusely over most of the head. The lateral part is studded with them, although individual bristles can be observed from above and below (Figure 15). A similar function is possibly carried out by the short hairs on the paws and feet (Figure 16). The perception of objects during burrowing when the head is in the soil is probably achieved by, in addition to the sensitive epithelium on the nose, the anterior parts of the lips with the help of the sensitive skin funiculus (cord) extending from the nose at the side of the head to about two-thirds its length, which is densely covered with short bristles (Figure 15). Such structures are absent in other burrowing animals, and this serves as one more example of the narrow specialization of organs of perception toward specific conditions of underground food collection accompanied by burrowing activity. They are absent even in highly specialized burrowing animals such as Rhizomyidae zukor (*myospalax* spp.) and the mole vole (*Ellobius* spp.) among field voles. Most probably these adaptations are inherent in representatives of the given family of rodents. The innervation of

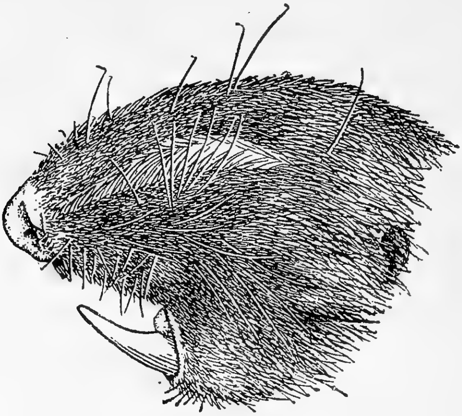

Figure 15. Head of *Microspalax nehringi* (Sat.) from the side. ×1.6.

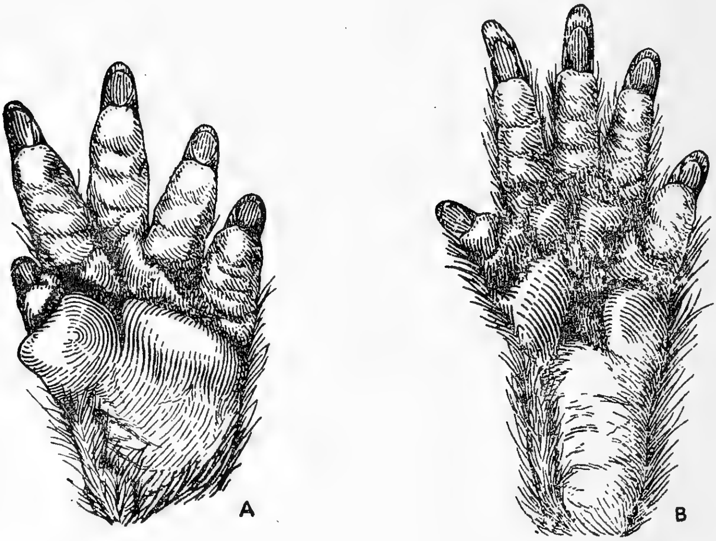

Figure 16. *A*—Hand, and *B*—Foot of *Microspalax nehringi* (Sat.). ×3.6.

whiskers of all types occurs through the superior labialis nerve, originating from the big infraorbitalis nerve (branches of the maxillaries). In ancient mole rats, there is a special closed canal through which this nerve passes.

The olfactory sense is well-developed in mole rats. This is quite evident from the structure of the nasal cavity; it is constructed for an acute sense of smell (classification of nasal cavity proposed by Sakharova, 1953); the nasal cavity is relatively short, the turbinals (nasoturbinal, maxilloturbinal and ethmoturbinal) are dense, and close to one another; the olfactory drums are situated in the posterior part of the cavity and are highly developed (Figure 17). This structure of the nasal cavity is inherent in rodents which lead a burrowing and underground life, and is the most "proper" adaptation of the olfactory organs to such living conditions. The presence of an acute olfactory sense in mole rats is proven by the highly developed olfactory lobes in the main brain in these animals which can be clearly seen in a section of the skull (Figure 17). Further, the ductus nasopharyngeum is relatively broad and straight, and its structure resembles that of rodents who have a "respiratory" type of nasal cavity. However, this peculiar construction of the nasal cavity in moles has its own functional explanation. The nasal cavity indicates, perhaps, a greater adaptation of the respiratory organs of the mole rat toward an increased CO_2 content in the burrows, in comparison with simple burrowing animals. This is expressed, perhaps, in terms of a lowered respiratory rhythm which, according to Tumanov, is a peculiarity of the venous circulation because Spalacidae do not have the venous sinuses characteristically present in other burrowing animals of the group Myoidea.

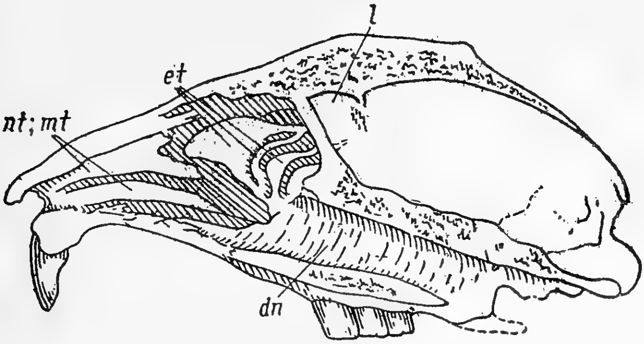

Figure 17. Longitudinal section of skull of *Spalax arenarius* Resh. ×1.75.

dn—ductus nasopharyngeum; *et*—ethmoturbinalia; *nt*, *mt*—naso- and maxillo-turbinalia; *l*—cerebellum.

An underground way of life caused the lessening of sight in mole rats, and because of this the optic receptors underwent significant adaptive changes. Among the rodents of the old world the living representatives of this family represent the only group whose eyeballs are completely hidden under a skin cover. Such a construction has mainly a defensive function. With this, the optical receptors themselves have changed comparatively little. The presence of well-developed eyeballs and well-developed optic nerves in living mole rats, and similarly the corresponding structures in the skull—large eye sockets, lacrimal fossa, and orbital apertures (Figure 3)—prove this. All this apparently points to a comparatively recent (in terms of geologic age) loss of sight in Spalacidae, if ultimately through special histological studies of the eye, its function of subcutaneous vision (at least differentiation of light and darkness) is not proven. Such a phenomenon of differentiation exists in some vertebrates adapted to conditions of absolute darkness in caves and sea depths.

Hearing is not as well-developed in mole rats as in mice and hamsters; this can be seen by the presence of comparatively smaller auditory bullae (length does not exceed one-fourth the condylobasal length of the skull) with a very small opening to the external ear. Furthermore, as seen above, the auditory bullae of Spalacidae participate in the formation of false articulating fossae.

MORPHO-FUNCTIONAL CHARACTERISTICS OF THE DENTITION OF MOLE RATS WITH REFERENCE TO ADAPTATION TOWARD BURROWING AND FEEDING

Of all the skull structures of mammals, the teeth are the most important from a taxonomical point of view. In the majority of cases the characteristics of structure could be the most important taxonomical traits, allowing not only a separation of different species and greater taxonomical categories, but even explaining their genetic relationships, evolutionary peculiarities, and the nature of specialization in individual groups of mammals. It has to be noted that the jaw apparatus, principally the teeth, is preserved better than other parts in fossil conditions, and is almost the only source for objective judgement about the phylogenetic relations of fossil and present-day forms.

In view of the foregoing facts, we consider it proper to describe in great detail the adaptive aspects of the dentition of mole rats; moreover, the taxonomy of the whole family is based on the peculiarities of this structure.

In the majority of Myoidea with a burrowing or underground mode of life, the teeth, in addition to their useful trophic functions associated with nibbling and grinding food, take upon themselves other functions originating from adaptation to digging with incisors. The adaptability of the teeth for digging becomes important in mole rats; the incisors serve as basic burrowing structures. The aforementioned peculiarities are themselves the leading trends in which a basic change of the bone and muscles associated with the jaw movement of Spalacidae took place in the process of adaptive evolution which is primarily directed toward the greatest "economic" comfort, and the restriction of masticating and digging movements. Some defensive adaptations also took place to protect the teeth from too much wear during direct ground breaking while, similarly, increasing the effective strength of friction on permanent molars, concerned with earth falling into the mouth cavity and false movements of the lower jaw which always accompany digging. However, the significance of trophic and digging specialization in the evolutionary process of mole rats is absolutely not the same. If it is assumed that the peculiarities of the masticatory movements in Spalacidae do not differ principally from similar ones in Myoidea, the entire typical structure of their masticatory apparatus, as a result of natural selection acting in the direction of an increased digging adaptability, would have to be accepted.

The functional adaptations of the masticatory apparatus of mole rats have been poorly investigated in literature. At present, we actually bank upon seven sources in which the authors refer to aspects of our subject in one way or another. Yet, the anatomical characteristics of the bone-muscle structure forming the masticatory complex of Spalacidae have been studied in detail. Very superficial information on the general plan of the structure of teeth, corresponding sections of the skull, of the lower jaw, and also of the masticatory muscles, can be found in Tullberg's review (1899). A sufficiently complete description of the dental system of mole rats and the structural characteristics of the masticatory parts of the skull and lower jaw is found in Mehely's monograph (1909). Mehely has also studied in detail the anatomy of the muscles attached to the masticatory complex. However, neither of the authors mentioned has given the peculiarities of the structures in the masticatory apparatus of mole rats an adequate functional explanation. B. S. Vinogradov (1926) has given a short analysis of the adaptive features of the construction of the bony structure of the masticatory part of the skull and lower jaw of mole rats as compared to specialized shrews and burrowing animals from other families. Further, the facts mentioned in this work were elaborated in a joint paper by B. S. Vinogradov and P. P. Gambaryan (1952) and, finally, were further developed in a comparatively recent monograph by P. P. Gambaryan (1960). In this work, P. P. Gambaryan studied the adaptation of the bony structures of the masticatory apparatus along with the masticatory muscles. An unsuccessful attempt to give a functional explanation to the nature of movements and the static position of the lower jaw in Spalacidae during the grinding of food and digging was done comparatively recently by N. N. Vorontsov (1963) who assumed that the lower jaw in Spalacidae is placed at the extreme posterior position during digging.

The masticatory apparatus of Spalacidae consists of the following structures: toothrows including the diastemata, the lower jaw and its articulating surfaces in the skull, the complex of masticatory muscles and special structural formations on the skull and lower jaw, the places of attachment of the masticatory muscles, and finally, the defensive devices protecting the lines of the permanent molars from too much wear and also devices for constant restoration or growth of the incisors.

In the complex adaptation of the masticatory apparatus of mole rats to digging, the differential movements of the lower jaw—concerned with chewing and grinding foodstuff on the one hand, and digging on the other—attain a special importance. Digging is achieved by the peculiar articulation of the lower jaw with the skull and, similarly, by the arrangement of the articulating process, particularly its condyle.

The investigations of B. S. Vinogradov (1926) on the skull of mole rats showed that in addition to the usual fossa glenoidea, there is one additional articulating fossa—fossa pseudoglenoidea or fossa posterior—which is situated behind the actual articulating surface (Figure 4). The false articulating fossa corresponds to the extreme posterior position of the lower jaw, when it is not working or during the grinding (crushing) movements, or during completely, or almost completely, closed upper and lower rows of permanent molars when the gap between the upper and lower rows of teeth (Δl) is less than M_1, or approximately equal to it, and in this position the tips of the posteriorly pushed lower incisors are situated behind the tips of the upper incisors (Figure 18A and B). During this, the condyle of the articulating process of the lower jaw is almost completely situated in the fossa pseudoglenoidea, only slightly touching by its anterior end the posterior edge of the fossa glenoidea (standstill position), or during lengthwise masticatory movements it periodically shifts to the posterior fourth of the latter. In both cases, the tips of the upper and lower incisors do not touch and do not hinder the masticatory movement. The apparent form of the false articulating fossa completely corresponds to the form of the masticatory movements of the lower jaw, encompassing the shift of the condyle of the articulating process of the latter, mainly in the horizontal plane, with a little more predominance of the lengthwise movement than of the transverse one. Thus, the main load during the masticatory process in mole rats falls on the false articulating surface and only partially on the posterior portion of the fossa glenoidea. In fact, the latter determined the adaptive characteristics of the construction of the fossa pseudoglenoidea which, as has been shown above (page 12), is bound up laterally and from behind by a comparatively thin petromastoideum, and medially by a special thick-walled articulating plate of the auditory bulla. This plate, together with the posterior edge of the true articulating surface, serves as the main support of the lever of the lower jaw during masticatory movements. The above-mentioned specification of the masticatory movements and the related construction of the false articulating fossa are characteristic peculiarities of Spalacidae, separating this group from the majority of Myoidea which lead an underground

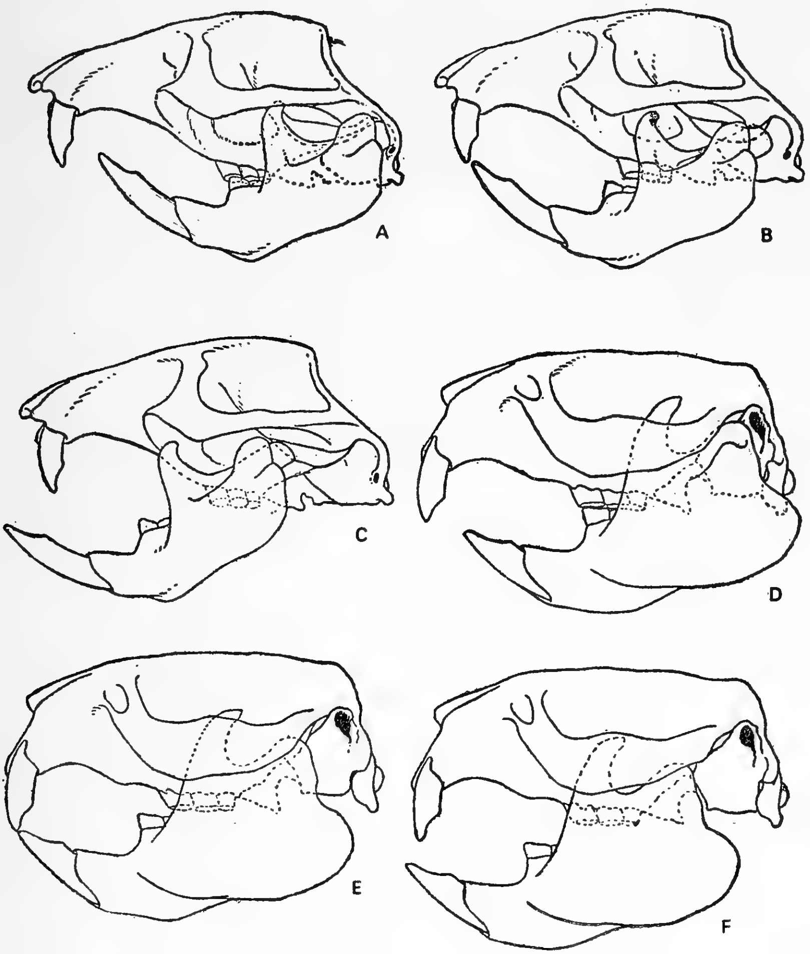

Figure 18. Position of the lower jaw. 4/5 of natural dimensions.

A to *C*—*Spalax*; *D* to *F*—*Rhizomys*; *A*, *D*—during rest and yawning; *B*, *E*—during crushing; *C*, *F*—during digging.

or burrowing way of life and dig with the help of incisors. The false articulating surface, though developed to a very small extent, is also found in the phylogenetically close Rhizomyidae and in convergently identical mole voles. However in the former, it is formed by a concave surface of the tube of the auditory bulla, thus differing from Spalacidae, and in the latter, it is represented by a small fossa on the temporal bone placed behind the fossa glenoidea. In both cases, the petromastoideum does not take part in its formation and the articulating plate of the auditory bulla is not present. Furthermore, the condyles of the lower jaw in Rhizomyidae extend into the fossa glenoidea in an extreme posterior position, in a manner which is more pronounced than in mole rats.

The grinding of foodstuff, the chewing of roots, stems, and big leaves of vegetation, is carried out when the incisors of the lower jaw are in the medium position and the grinding surfaces of the lower and upper rows of permanent molars are considerably separated in the lengthwise direction [$\Delta l > 1M_1$, but less than $1\ (M_1-M_3)$], and when the cutting surfaces of the upper and lower incisors are almost touching; the tips of the upper incisors are all the same, protruding a little in front in relation to the tips of the lower incisors (Figure 18B). In such a position of the lower jaw, the grinding movements are predominant in the sagittal level along the smaller arches, and also, some lengthwise movements take place in the horizontal plane. There is practically no longitudinal (up and down) grinding movements. This position of the lower jaw in mole rats was taken as anteriormost by B. S. Vinogradov (1926) and P. P. Gambaryan (1960). Because of this, the authors mixed the movements of the grinding and digging cycles, differentiating the digging movements only by the size of the arch in which they are carried out (small arches during grinding; larger ones during digging; Gambaryan, 1960). However, in this position the functional importance of the anterior half of the fossa glenoidea is not understandable because the condyle of the lower jaw, irrespective of the dimension of the arches on which the movements take place, is not shifted to this part of the natural articulating surface during such movement. So, an assumption comes up, naturally, that mole rats differ from Rhizomyidae in that the grinding and digging movements are carried out by the jaw approximately in one and the same position, and differ from each other only by the size of the arches; in addition to the two positions described above, there is a third for the lower jaw—the anteriormost—or the digging position. In this position, the condyle of the lower jaw shifts to the anterior half of the fossa glenoidea, the grinding surfaces of the upper and lower teeth are not in contact because $\Delta l \geqslant 1(M_1-M_3)$, and the cutting edges of the lower incisors move considerably forward in relation to the cutting edges of the incisors of the upper jaw. In this position, the lower jaw carries out chewing movements of great magnitude (through greater arches), accompanied by considerable displacement in a lengthwise direction. This type of movement in the mandibular joint is confirmed by the whole structure of the articulating surface which, in Spalacidae, has an appearance of a long groove (its length exceeds the length of the row of permanent molars, or is approximately equal to it) with well-developed fixtures restricting the lateral displacements, and also by the formation of the condyle and the whole articulating process of the lower jaw. The condyle of the articulating process is narrow, strongly elongated in a lengthwise direction (the width is less than half the length along the cord, and approximately equal to it or a little exceeds it), with an arched, bent up articulating surface, but the process itself is relatively long and strongly inclined posteriorly (situated almost parallel to the lengthwise axis of the surfaces of the permanent molars). Such a structure of the proc. condyloideus allows great movement of the jaw in the sagittal plane and also its lengthwise displacement while considerably restricting the grinding movements in a transverse direction.

All the aforesaid is also confirmed by a functional analysis of the masticatory musculature of Spalacidae. However, before starting an analysis of the latter, it would be proper to give at least a short account of its construction because this has not been done by us in the preceding portion of this work.

The masticatory musculature is very schematically described and drawn in the major work of Tullberg (1899); more detailed descriptions are given by Mehely (1909) and Gambaryan (1960). The complex of the masticatory musculature includes the most complicated muscle M. masseter, the temporal muscle M. temporalis, the wing-like muscle M. pterygoideus, and the bilateral muscle M. digastricus.

The M. masseter is divided into two layers in Spalacidae, the external (M. masseter lateralis) and the internal (M. masseter medialis). The external layer consists of two portions, viz., the superficial one (M. m. lateralis superficialis) and a deeper one (M. m. lateralis profundus). Finally the superficial portion is represented by two parts, viz., the anterior (M. m. l. superficialis anterior) and the posterior (M. m. l. superficialis posterior). The former is attached to the anterior ridge of the masseter surface of the skull, and on the lower jaw it attaches itself on the external edge of the angular process all along its anterior half (Figure 19; mlsa). The second portion is attached laterally at one end along the entire zygomatic arch (starting from the jugal angle), and along the posterior half of the external edge of the angular process of the lower jaw (Figure 19; mlsp). The fibers of the superficial portion of the external layer of the masseter muscle are directed in some instances at an angle of less than 45° in relation to the longitudinal axis of the grinding surfaces of the permanent molars.

The deep portion of the external layer of the M. masseter is attached to the surface of the whole masseter area and along the whole edge of the zygomatic arch medially at the place of attachment of the superficial portion, and to the lower jaw along the edge of the angular process, including the sella externa above the place of attachment of the M. m. l. superficialis and along the whole masseter surface of the lower jaw (Figure 19; mlp). Its fibers are directed a little ahead during the posterior position of the lower jaw with relation to the longitudinal axis of the grinding surfaces of the toothrows, but at a greater angle than the similar ones for M. m. l. superficialis.

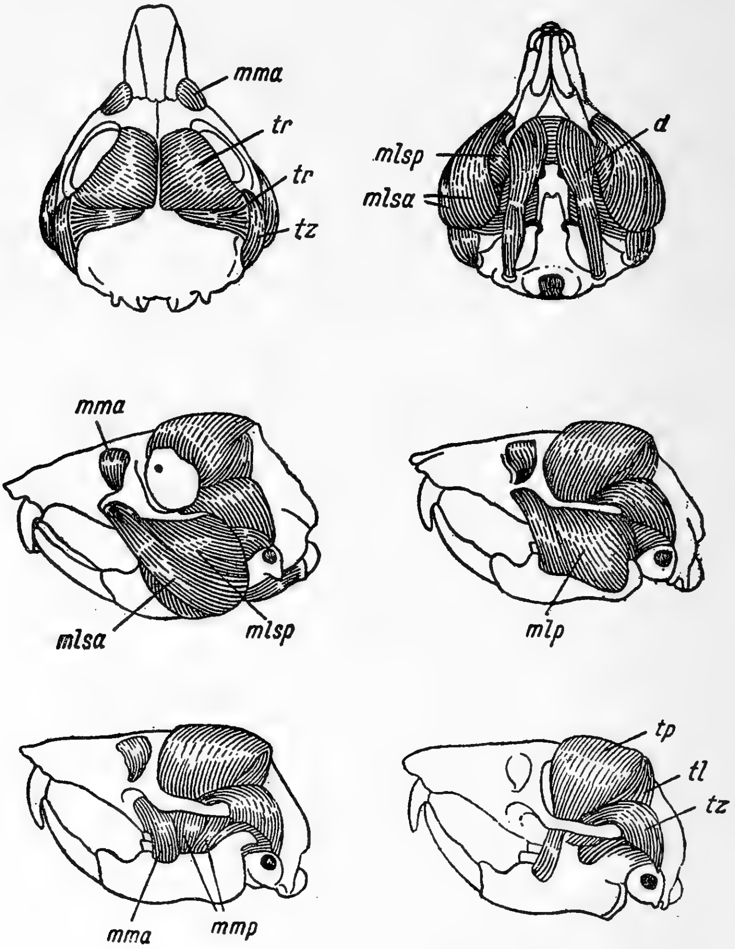

Figure 19. Structure of (*m*) masseter, (*t*) temporal and (*d*) digastricus muscles in the mole rat *Microspalax ehrenbergi* (Nehr.) (by Mehely, 1909).

See text for legend.

The inner layer of the masseter muscle (M. m. medialis) divides into two portions, the anterior (M. m. medialis anterior) and the posterior (M. m. medialis posterior). The first is attached to the skull on the upper and partially anterior edges of the suborbital foramen, passes through it, and becomes attached to the body of the lower jaw under the anterior permanent molars a little higher than the ridge on the masseter surface, anterior to the incoming branch (Figure 19; mma); the second originates from the medial edge of the central and posterior portions of the zygomatic arch and terminates partly on a special muscular depression on the external wall of the anterior portion of the incoming branch, and partly on the ridge on the corono-alveolar furrow (Figure 19; mmp). The fibers of the anterior portion are directed a little forward during the posterior position of the lower jaw, though at a greater angle than the similar deeper portions of the M. m. lateralis profundus, and the fibers of the posterior portion are arranged almost vertically.

The M. temporalis in mole rats is divided into three parts—parietal (pars parietalis), lambdoidal (pars lambdoidea) and temporal (pars suprazygomaticus). The parietal and lambdoidal parts are the most developed.

The parietal portion of the temporal muscle is attached to the skull all along the sagittal ridge including its bifurcated suborbital portion, and on the lower jaw it becomes attached above the anterior ridge of the masseter area directly under the permanent molars, including the space between the alveolar edge of the jaw, and by a special branch medially in relation to the areas of attachment of the anterior portion of the inner layer of the masseter muscle (Figure 19: tp).

The lambdoidal portion begins its attachment on the lambdoid ridge on the skull and ends on the coronate process of the lower jaw (Figure 19; tl).

Finally, the temporal portion of the M. temporalis begins its attachment on the lateral edge of the petromastoideum (above the external auditory meatus) and its direct prolongation, formed by the temporal bone, ends also on the coronate process of the lower jaw (Figure 19; tz).

The M. pterygoideus divides into two portions, the outer (M. p. lateralis) and the inner (M. p. medialis). Both portions originate on the skull from the fossa pterygoidea; moreover, the outer bifurcates into two strands which are attached to the lower jaw on the medial side of the articulating surface directly under the condyles (Figure 20; pl), and the inner one, on the medial side of the angular process below the sella externa (Figure 20; pm).

The M. digastricus is sufficiently well-developed in mole rats. It starts from the articulating ridge at the angle of the lower jaw and ends on the skull attaching to the proc. paroccipitalis (Figure 19; d).

Furthermore, the M. transversus mandibulae is well-developed in

Spalacidae, playing the role of an additional fixator (in addition to the immovable symphoidal junction) of the branches of the lower jaw. This muscle attaches itself all along between the angles of the jaw and the origin of the angular process on each of the horizontal branches of the lower jaw (Figure 20; mtm).

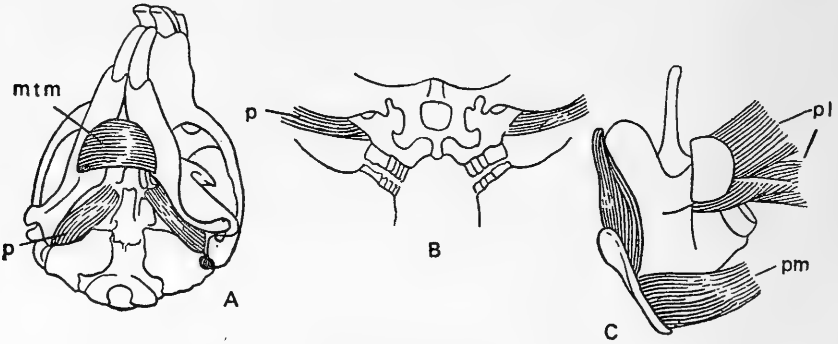

Figure 20. Structure of (*p*) pterygoideus and (*mtm*) longitudinal muscles of the mole rat *Microspalax ehrenbergi* (Nehr.) (by Mehely, 1909).

See text for legend.

Before beginning the functional analysis of the muscles of the masticatory complex of Spalacidae, the variability in the load taken by individual systems has to be pointed out first. This can be seen from a comparison of the relative weights of the individual muscles forming this complex. Thus, from data by P. P. Gambaryan (1960), the per cent relation of the weights of individual muscles to the general weight of the skeleton in *M. nehringi* (Satunin) is 9.85 for the masseter, 11.02 for the temporal, 1.55 for the pterygoideus, and finally, 1.01 for the digastricus muscle. Thus, it becomes clear from the given data that in Spalacidae, the masseter and temporal muscles attain the greatest development of all the muscles of the masticatory complex and so most of the load during burrowing is borne by them. The considerable development of the muscles of these groups is completely in order for the rodents which have specialized either fully or partly in burrowing with the help of teeth (Gambaryan, 1960). Hence, the great importance of the weights of these muscles in comparison with the majority of burrowing animals from the group Myoidea does not need further clarification. To some extent, as regards the degree of development of the masseter muscle, mole rats are analogous only to those specialized rodents that have a burrowing tendency of the same type such as mole voles (9.97), long-clawed field voles (*Promethea schapoechriteovi* Satunin) (9.12), and rats of the genus *Nesokia* (9.85) (in the rest of the Myoidea, the value of this index varies from four to eight); and in respect of the development of the temporal muscle, mole rats have had almost no parallel among representatives of the group (in mole voles and long-clawed field voles, the value of this index generally does not exceed five to seven; in other burrowing animals of the suborder Myoidea, it is considerably less). At the same time the weight of the muscles pterygoideus and digastricus does not differ significantly from the same muscles in the majority of other Myoidea. Considering the peculiarities of attachments for these muscles on the skull and lower jaw, it can be confidently said that they have the same function in Spalacidae as in other Myoidea, and they bear similar, comparatively smaller loads. The first muscle allows small horizontal movements of the lower jaw during yawning, and the second one allows its lowering down during pressing and biting movements.

As has been mentioned already, the development of the masseter and temporal muscles in Spalacidae is mainly concerned with the type of burrowing. Their structure and function can be understood only from this point of view. The morphological peculiarities of the masseter and temporal muscles have been discussed above in detail, and hence we will now consider only the functional analysis of these systems during different positions of the lower jaw at the time of mastication.

The structure and peculiarities of the attachments of the majority of the parts of the masseter muscle are such that they allow maximum movements of the lower jaw along with other important movements of different Myoidea. This can be seen by the slightly anteriorly placed basic parts of the masseter in the extreme posterior position of the lower jaw which is the case during the standstill position and masticating movements. Only the posterior portion of M. masseter medialis is an exception, fibers of which are directed vertically in that position of the lower jaw or directed even a little backward. It looks from this that its role is perhaps restricted by the movements carried out during the simultaneous contraction of the right and left muscle—the small transverse movements of the masticatory cycle. As regards all the remaining parts of the M. masseter, during chewing movements of the lower jaw, apart from the functions characteristic to the M. M. medialis posterior, it allows a little lengthwise movement of the latter and, moreover, the Δl in this case is less than the length of the lower front permanent molar, or is approximately equal to it. These movements of the lower jaw point to the comparatively lesser loads on the masseter muscle.

During the average position of the lower jaw, corresponding to the grinding of foodstuff, biting of roots, stems, and large leaves, the fibers of the anterior portion of the M. masseter medialis and also of the deeper portion of the external layer of the masseter muscle, take up a vertical or almost vertical position, as a result of which their function is almost exclusively restricted to the movements of the lower jaw. The further forward movements of the jaw are mainly carried out by the superficial layer of the M. masseter lateralis which, as yet, has maintained its position in relation to the longitudinal axis of the grinding surface of the permanent molars though the angle of its fiber direction is still acute. The posterior portion of the M. m. medialis is directed a little behind and perhaps plays a specific role during the movements of the jaw backward to the original position. If it is considered that the grinding movements in the above-described position of the lower jaw are carried out mainly along the small and medial arches, it becomes clear that the masseter muscle does not carry the maximum loads in the process of grinding food.

Finally, during the assumption of the extreme anterior position of the lower jaw, corresponding to burrowing action, all the component parts of the masseter muscle take up a vertical (or close to it) position, thus considerably enhancing the effort of the biting movements of the burrowing cycle directed mainly in the sagittal plane and taking place along the bigger arches. However, it has to be noted that the anterior position of the superficial layer of the external layer of the masseter muscle preserves the original tapering (bias). Hence the equivalent force which this part imparts to the lower jaw will never correspond to the reduced force. Besides, in the similar position of the lower jaw, the fibers of the deep portion of the M. m. lateralis and the anterior portion of the inner layer appear to be tapered; but in the backward direction, they perhaps play a specific role in its longitudinal movements in the opposite direction. As far as the function of the posterior portion of the internal layer is concerned, it remains similar as during the medium position of the jaw. It can also be assumed that the alternate contraction of the muscles of the right and left half allows certain transverse movements of the jaw during digging (burrowing). However, the scope (diapason) of such movements is very small. During this, the condyle of the jaw (mandible) fixes in the external ridge of the fossa glenoidea which, as was shown above, plays a role of fixator for specific types of movement in the mandibular joint. During this type of movement, the masseter muscle takes up the maximum load.

Of the muscles forming the masticatory complex, the temporal muscles attain the greatest development in mole rats. This is in complete accord from the viewpoint of adaptation to burrowing because the temporal muscle is a basic muscle which allows the forward movements of the lower jaw and, as a result, takes up the main load during digging along with the corresponding parts of the M. masseter medialis posterior which also allows the forward movements of the lower jaw from the anteriormost and medium positions to the original one.

As far as the unpaired transverse muscle of the lower jaw is concerned, its function is additional to the symphysis of the fixator of the rami of the lower jaw and has been discussed earlier.

Thus, the morpho-functional peculiarities of the structure of the muscles of the masticatory complex completely confirm the differentiation of the movements of the mandibular joint already described in the context of the articulation of the lower jaw with the skull during functionally different situations corresponding to the process of grinding food, biting (gnawing), and digging. There is no doubt about the adaptive nature of this process because along with direct specializations directed toward the perfection of the very process of digging, the defensive functions are also inherent which are primarily concerned with the protection of the teeth from premature erosion during "purposeless" (from a trophic point of view) forward movements of the lower jaw which accompany digging activity. The latter, as has been observed, is achieved by either partial or full non-coincidence of the grinding surfaces of the upper and lower molar rows.

It is known that the degree of development of the structures becoming attached to the bone is directly related to the degree of development and functional characteristics of the muscles to be attached; in other words, according to the direction and force of the muscular pressure which is experienced by them. In this regard, the research of N. S. Lebedkina (1957) is of much interest since it sufficiently shows that there is a close relationship of the corresponding structures of the skull to the force and peculiarities of distribution of masticulatory pressure on the masticatory apparatus of the Lagomorpha. Looking at these common regularities the functional importance of all the basic structural characteristics of the skull of Spalacidae, which are concerned in one way or another with the influence of the masticatory muscles, becomes understandable. A general character of the structure of the skull in all Spalacidae is the presence of a strong sagittal and a considerably long lambdoid ridge, besides a well-expressed zygomatic mastoidal edge. The adaptive nature of these structures becomes clear if it is considered that they are the sites of attachments of different parts of the temporal muscle, causing the forward movement of the lower jaw and thus taking up much of the load during biting movements of the excavation cycle. Of the three parts of the temporal muscle, the pars parietalis attains the greatest development because of which the sagittal ridge is considerably stronger and thicker than the lambdoidal ridge and the malar-mastoid ridge. Lastly, due to their being considerably weaker than the pars parietalis, the lambdoid and temporal portions of the temporal muscle are like comparatively thin-walled films. However, the lambdoid ridge is considerably inclined forward which, undoubtedly, increases its tenacity because it considerably substitutes the strength coupled with the contraction of the lambdoid portion of the temporal muscle directed in another position of the ridge.

In view of the morpho-functional peculiarities of external layer of the masseter muscle, the structural characteristics of the masseter surface of the skull, on which the masseter lateralis superficialis anterior and the masseter lateralis profundus muscle are attached, also become clear. This surface has a special structure for the attachment of the anterior part of the external layer of the masseter muscle—the anterior ridge and its other parts (site for attachment of the masseter lateralis profundus muscle) with a slight angle in relation to the longitudinal axis of the grinding surfaces of the rows of the permanent molars. Lastly, the research of N. N. Vorontsov (1963), carried out on skulls of Cricetidae of different types, serves as an example for the presence of biting movements in the sagittal plane. Perhaps the broadening of the jugal process of the mandible and of the external wall of the suborbital fossa has to be considered as a resistance to the forces directed toward the fissure and in some individual cases—also a considerable inclination of the anterior parts of the zygomatic arches from below—forming the malar angle. The large dimensions of the suborbital foramen are also most probably correlated with the degree of development in the masseter medialis anterior muscle passing through this foramen.

A specific complex of adaptations for digging with the help of incisors, directly related to the peculiarities of the working of the muscles of the masticatory apparatus, is observed in the lower jaw also. This is seen firstly by the presence of well-developed fossae and ridges. The places of attachment of the pars parietalis of the temporal muscle are on the horizontal branch in the intervening space between the alveolar edge and the ascending branch of the comparatively high and slightly backwardly inclined coronary process and the special corono-alveolar groove (notch), the upper edge of which has an appearance of a sharp ridge in highly specialized representatives. There is an attachment of the lambdoidal and temporal portions of the temporal muscle on the external side of the coronary process and in the region of the corono-alveolar groove. Significant differences in the structure and position of the angular process on the mandible, which serve as a site of attachment for all the superficial and partly deeper portions of external layers of the masseter muscle, are related to the development of mechanisms allowing maximum movement of the lower jaw in a lengthwise direction in the anteriormost position. The said process underwent considerable changes during evolution. In the primitive representatives of the family (subfamily Prospalacinae), it has a tendency only for shortening and bending outward, and in highly specialized ones (subfamily Spalacinae), it took the form of a prolonged, highly developed ridge completely sweeping laterally on the side walls of the alveolar process. Thus in the lower jaw, as in the skull, the most significant adaptive changes took place in the structures providing the most perfect and "economic" fixation of the musculature from the biomechanical point of view, which properly brought up the lower jaw in order to move it forward, i.e., the adaptive changes took place to enhance the movements of the burrowing cycle.

As far as the structure of the teeth is concerned, the incisors have been absolutely changed, particularly the lower ones. The latter is completely in order because, as has often been mentioned, the incisors take the main load while burrowing. However, the lower incisors being greatly movable, should play a larger role than the upper ones. Naturally, the incisors of mole rats have not lost the function of cutting (gnawing) foodstuff which is so characteristic of all other rodents. Yet, these adaptations cannot be taken as the most important ones because the nature of the grinding movements in Spalacidae does not differ principally from the same in the majority of representatives of other families of the order.

One of the main adaptive changes in the structure of the incisors of mole rats, related primarily to an increase in its working surface, can be seen in the trend of upper and lower teeth toward an increased width in comparison to the antero-posterior cross section. Because of this, the said peculiarity of the structure is better expressed in the lower incisors than in the upper. In addition, the lower incisors of mole rats are less curved as compared to forms in which the incisors are not adapted to burrowing which, perhaps, offers the most suitable direction to their working surfaces and happens to be common to specialized shrews and burrowing animals in which the process of burrowing in one or the other way is combined with the incisors.

As has been observed above, the upper incisors, because of their almost immovable fixation (the degree of mobility completely depends upon the range of movement of the skull), play mainly a passive role in burrowing. In fact, their function during burrowing is less than their function during gnawing and mainly consists of merely chewing lumps of soil cut by the lower incisors. Because of this, the structure of the upper incisors, with an exception of the already noted specific peculiarities, is on the whole similar to the same as in other Myoidea. The lower incisors carrying the main load, underwent considerably adaptive changes because of their great mobility, predetermined by the nature of the joint of the lower jaw with the skull. First of all, the tendency of these teeth for their general elongation during evolution has to be noted. Thus, the length of the lower incisors in some very specialized representatives of the family considerably exceeds the length of the jaw measured from the apex of the symphysis. This becomes possible because of the elongation of the free end of the incisor and also by a considerable development of the alveolar process. As in all rodents, the incisors of mole rats are without roots and are characterized by constant growth. The posterior portion of the tooth is the zone of reconstruction and, moreover, the incisor is pushed forward because of its growth. The significance of the highly developed alveolar process in mole rats is understood in the light of the aforesaid. The high development is primarily related to the maximum increase in the zone of development of the incisor which perfectly reconstructs the tooth during its constant wearing off at the time of burrowing. The alveolar process, as a site for an attachment of certain muscles of the masticatory complex, has to be given secondary importance.

The permanent molars of mole rats have been adapted mainly for feeding on comparatively soft and succulent vegetation (roots, bulbs, bulbiferous root crops, roots of different plants and, to a lesser extent, stems, leaves, seeds and tubers). The type of food completely explains the structure and the presence of permanent molars—only exhibiting a tendency for reduction in the lines from the primitive members to highly specialized representatives, average height of coronas, comparatively narrow grinding surfaces, and a predominance of folded structures above tubercular structures. The latter, along with the form of grinding surfaces for which little difference in the width and length of the corona is characteristic, and also the disposition of the molars in two rows, would seem to indicate a probably equal distribution of masticatory movement in longitudinal and horizontal directions. Most probably the masticatory movements in mole rats on the whole are ellipsoidal, the largest diameter of the ellipsis approximately corresponds to the direction of the longitudinal movement of the lower jaw. A reduction in the length of the toothrows is not only related to the type of food, but also at the same time represents a defensive device.

Among the other devices in mole rats whose function is to protect the rows of permanent molars from premature wearing, the presence of protuberant lips, specific for shrews (burrowing animals) which avoid earth entering the mouth during burrowing, is foremost, and in accordance with the latter, the elongated diastema provides a maximum carrying forward of the burrowing organ, incisors, beyond the masticatory section of the oral cavity.

Arrangement of the Skeletal and Muscular Systems of the Skull and the Postcranial Skeleton of Mole Rats for Transportation and Throwing out of Soil with the Help of the Head

One aspect of the burrowing cycle of mole rats is the transportation and throwing out of excavated earth from the entrance hole, mainly with the help of the head. The adaptive significance of ejection of soil is difficult to evaluate because Spalacidae are characterized by exclusively underground feeding habits and burrowed food tunnels, the length of which may exceed 300 meters. In burrowing, the soil is thrown out through special exit holes which are situated at a distance of 0.5 to 3.0 meters from one another all along the length of the feeding tunnel. This hole is connected to them by an almost vertical shaft of three to five cm or more in depth. The earth accumulates over them in so-called mounds (hills) so very representative of the burrowing activity of mole rats. The following data gives an idea of the intensity of soil ejection from burrows and feeding tunnels. As observed by P. P. Gambaryan (1960), *Microspalax nehringi* throws out 21.7 kg of earth in two hours of activity; according to N. M. Dukel'skaya (1932) who obtained data during a study of the burrowing activity of *Spalax microphthalmus* Güld, it was observed that the latter could eject five kg of soil on the surface within half an hour. In both cases, observations were made under natural conditions and hence the normal excavating activity of mole rats may be judged from them. It should be noted that *M. nehringi* burrowed tunnels in stony ground where almost half of the ejected soil contained chips of stones of small and average dimensions (up to 100 g) and some of them had weights of even more than 200 g.

The transportation of soil from food tunnels consists of two stages: (1) transportation of soil which has been dug out by the incisors and thrown by the front and hind feet in a horizontal or slightly inclined direction toward the outlet; and (2) pushing up the accumulated excavated soil along the vertical shaft on the outside. Both stages differ by different loads acting on the neck and head region and the pectoral and pelvic girdles.

In the first case, as has been observed by Gambaryan in *M. nehringi* under natural conditions, mole rats never transport portions of earth weighing more than 0.5 kg in the horizontal or slanting tunnels, and an accumulated mound of earth of more than five cm. The shafts of accumulated earth found in opening horizontal and vertical tunnels, weights and dimensions of which exceeded the aforementioned limits, were, in all cases without exception, proven to be the plugs which mole rats usually prepare at the end of their use. The earthen plug is usually denser than the surrounding earth and has some portions of earth excavated by mole rats. Its thickness may reach 20 cm. Thus, the transport of earth in horizontal and slanting food tunnels is accompanied by an ejection of a comparatively small quantity of earth of little weight. During this, the main load falls on the atlas-skull (occipital) joint and parts of the forelimbs, although some of it is shared by the hindlimbs. However, the role of the latter in the said process is very small. A proof of this is provided by the fact that the weight of the muscles of the pelvic girdle in Spalacidae is twice (2.2) less than the weight of the muscles of the shoulder girdle. Besides, compared to burrowing animals of the group Myoidea, the muscles of the hindlimbs of Spalacidae are least developed. Thus, according to Gambaryan (1960) the relative per cent of the weight of the muscles of the pelvic girdle to the general weight of the skeleton in Spalacidae is around 29.0 as against 55.3 in *Mesocricetus auratus* Waterhouse, 67.0 in *Microtus socialis* Pall. and 58.0 in *Rattus norvegicus* Berk. Perhaps the general weakening of the girdle of the hindlimbs is almost characteristic of shrews because the same phenomenon is also observed in zukors (34.0), mole voles (31.0), and also in those burrowing animals which are well adapted to burrowing like long-clawed field voles (36.0). Accordingly, in the process of transporting soil along the horizontal and slanting tunnels, most probably a complex movement comes into play related, firstly, to the lifting of the head and secondly, to the straightening of the elbow and shoulder joint. During this, slightly less energy is spent in transporting comparatively small portions of soil than for throwing out in a few attempts, larger portions through the vertical outlets, since the lesser weight of the thrown-out earth in this case is compensated by the considerably longer distance and, consequently, also by the time taken for the efforts necessary for carrying the soil to the outlet.

The ejection of soil to the surface through the narrow shaft leading to the surface is accompanied by short but vigorous efforts directed strictly upward. It is natural that the magnitude of these efforts is determined not only by the weight of the column of earth to be ejected but also by the extent of erosion of the wall of the outlet as well as the resistance of the already excavated earth partially adhering to the exit outlet through which the remaining portion of earth is thrown out. It should be remembered that while this takes place with one movement, the mole rat usually throws out quite a few transported portions of earth. Thus, as observed by P. P. Gambaryan (1960), columns of about 45 cm in height can be ejected onto the surface by the mole rat; according to A. F. Anisimova (1938), the giant mole rat can throw out an even larger quantity. As a result, the animal has to make a great effort when ejecting earth through the outlet though this process is of short duration. It was experimentally proven that *M. nehringi* can lift a load of 6.2 kg to a height of 7 cm. Generally, Spalacidae can easily lift comparatively large loads, i.e., loads which exceed by 30 to 40 times the weight of their own body, to a height of about 8 to 9 cm. Because the outlet shaft is strictly vertical, the complex movements performed during this should be similar to those accompanied by the lifting of loads during the experimental situation. Gambaryan (1953, 1960) with the help of X-ray determined that the individual elements of the skeleton of a mole rat take the positions shown in Figure 21 during the process of lifting a load. Thus, it is clear that during the process of ejecting earth, as well as transporting it, the basic movements are lifting the head, straightening the elbow and, to a lesser extent, the shoulder joints. However, it differs from the first stage—ejection of earth from the burrow accompanied by transportation under conditions of a horizontal or slanting feeding tunnel—in that the posterior extremities do not take an active part in this work, assuming only the role of body fixators in the space. During this, the center of gravity of the animal shifts into the region of the shoulder joints.

Hence, the nature of the movements in the process of transporting and ejecting earth is the same in principle, differing only by degree of partici-

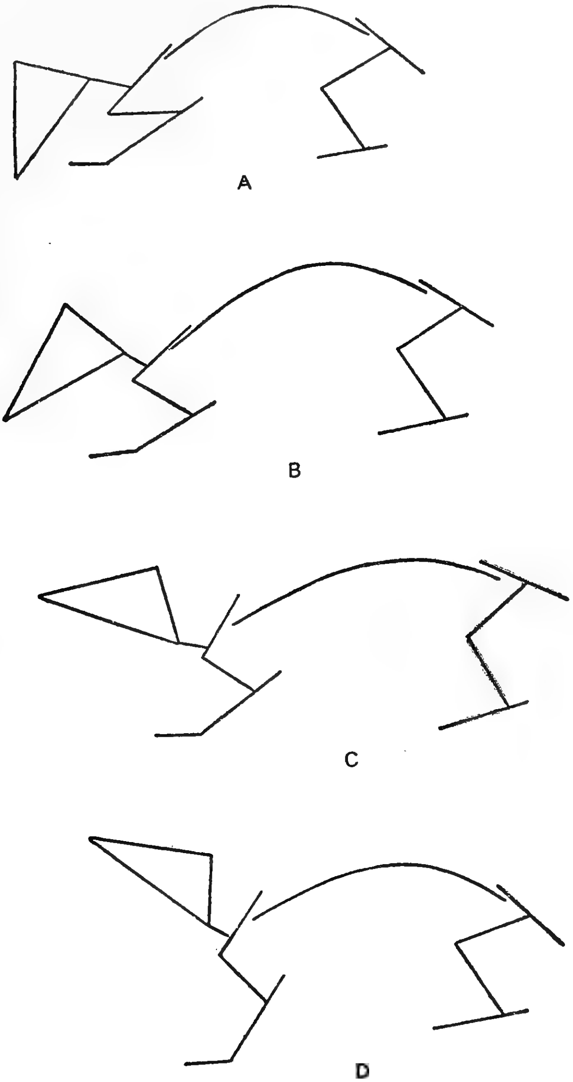

Figure 21. Skeleton contours of a mole rat lifting a load (by Gambaryan, 1960).

pation of the hind extremities and the magnitude of single loads. Consequently, the main adaptations corresponding to the above-mentioned specializations must be primarily related to a specific reconstruction of the skeleton and muscular systems of those sections of the anterior part, which take up the maximum load in this process. These are the atlal-axial-skull joint and the shoulder girdle. In addition, the springy and fixed adaptations of the body, which are related to the similar speciality of ejection of excavated earth, have to be taken into consideration. These systems have been very completely studied by P. P. Gambaryan (1960).

The head is lifted by the M. rhomboideus capitis which is a part of the complex M. rhomboideus, and also by the complex of the dorsal muscles of the neck in which M. splenius, M. semispinalis capitis and the M. rectus capitis dorsalis are rather well-developed. The per cent ratio of the weight of these muscles to the general weight of the muscles of the extremities in *M. nehringi* is 35.8, whereas it is only 6.2 for the rest of the muscles in the neck region. In addition, the above-mentioned muscles of mole rats are considerably better developed than in all other shrews and burrowing animals of the group Myoidea. Thus, the relative total weight is 24.26 in zukors; 15.5 in long-clawed field voles; 12.88 in average hamsters; 10.58 in mole voles; 8.0 in rats of the genus *Rattus;* and finally, 9.47 in rats of the genus *Nesokia.* In this way, the greatest similarity in the development of magnitude for this parameter is observed between mole rats and zukors for which the ejection of earth from burrows and food tunnels by the head is characteristic. However, the characters of specialization in this direction are more strongly developed in Spalacidae than in Myospalacinae. It is better to look into the details of the structure of each of these muscles in order to know their roles.

Of the muscles concerned with lifting the head, the M. rhomboideus is the best developed. For example, it is 12.65% of the muscles of the extremities in *M. nehringi.* Its relative weight exceeds more than four to five times the weight of the same muscle in shrews and burrowing animals from the group Myoidea in which the process of throwing out earth from burrows is not accompanied by head movements. Thus, the magnitude of the corresponding index is equal to 3.02 in average hamsters, 4.0 in long-clawed field voles, 2.48 in mole voles, 1.60 in rats of the genus *Rattus,* and 1.52 in rats of the genus *Nesokia.* However, similarities to mole rats are, after all, found in zukors (11.21). This muscle in mole rats originates all along the lambdoid ridge of the skull and terminates on the scapula covering a major portion of the axis of the latter and about one-fourth of the nearby fossa, starting from the cranial angle of the scapula (Figure 22).

The M. semispinalis capitis, whose relative weight is 10.29, is less developed in mole rats. To the degree of its development, it exceeds the same muscle in all other shrews and burrowing animals from the group Myoidea including even zukors. The magnitude of the ratio of its weight to the total weight of the muscles of the extremities is 6.17 in zukors, 6.30 in long-clawed field voles, 5.89 in mole voles, 4.87 in average hamsters, and finally, 3.82 and 3.86 respectively for rats of genera *Rattus* and *Nesokia.* This muscle originates from the occipital surface of the skull medial to the M. rhomboideus capitis and M. splenius and terminates on the lamellar processes of the first five sternal and transverse processes of the last two to three (sometimes four) cervical vertebrae (Figure 22).

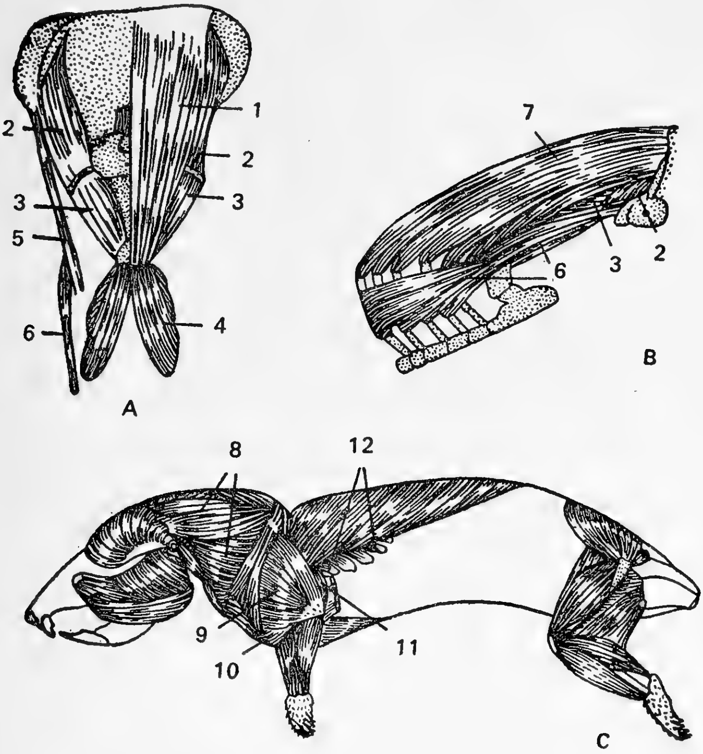

Figure 22. Muscles of the neck from (*A*) above and (*B*) the side, and (*C*) of the body in *Microspalax nehringi* (Sat.) (by Gambaryan, 1960).

1—M. rectus capitis dorsalis major; *2*—M. obliquus capitis cranialis; *3*—M. obliquus capitis caudalis; *4*—M. multifidus cervicalis; *5*—M. longissimus capitis; *6*—M. scalenus; *7*—M. semispinalis capitis; *8*—M. rhomboideus capitis; *9*—M. anconeus longus; *10*—M. anconeus lateralis; *11*—M. dorsoepitrochlearis; *12*—M. serratus ventralis.

The M. rectus capitis and M. splenius are almost equally developed in mole rats. The relative weight of the first is equal to 6.78, and the second, 6.08. Both muscles exceed twice or more the same in degree of development in other shrews and burrowing animals of the suborder Myoidea including zukors for example, as noted by Gambaryan (1960); the indices of relative weight for each of these muscles are equal respectively to 3.30 and 3.58 in zukors, 2.03 and 3.17 in long-clawed field voles; 1.96 and 3.03 in average hamsters, and 1.39 and 2.70 in *compositodontus* shrews. The splenius muscle represents the outer layer of the whole complex of dorsal muscles in the neck. It originates from the occipital bone, deeper than the rhomboid muscle, and terminates in the fascia stretched between the lamellar processes, neural ridge, and other bony process of the first three to six thoracic vertebrae, and the dorsal processes of the cervical vertebrae (Figure 22). The M. rectus capitis originates from the occipital surface of the skull, deeper and below to the site of the attachment on the M. semispinalis capitis, and terminates on the process of the axis and partially on the wings of the atlas (Figure 22).

The peculiarities of attachment for all the foregoing muscles show that they are the flexors of the atlanto-occipital joint; moreover, looking at the nature of the attachment, the most effective appears to be the rhomboid muscle of the head. Its considerable development in rodents and shrews can be explained on the basis of those which have adapted themselves to eject earth from the burrows and food tunnels with the help of the head, mainly mole voles and zukors, and can be proven from the above data about the relative weight of the rhomboideus capitis muscle in individuals of the above-mentioned families. However, in mole rats as distinct from Myospalacinae, the bending effort in the said joint increases many times in view of the additional efforts by similar muscles in the bending complex, first of all the muscles of the head and also the rectus capitis of the head, and scalemus muscle which is moderately developed in zukors. The latter fact indicates a better developed specialization in mole rats compared to Myospalacinae. The adaptive peculiarities of the construction of individual structures of the skull and the cervical region of the vertebral column, and also the peculiarity of articulation of the first with the last in mole rats, can be understood in the light of the aforesaid.

As already mentioned in previous sections of this work, the presence of a highly developed, broad, and considerably forward slanting occipital surface with a well-developed lambdoid ridge, is a specific character of the skull of Spalacidae. The greatest width of this surface considerably exceeds the length of the braincase of the skull and the angle of the slant in relation to the longitudinal axis of the grinding surfaces of the permanent molars is approximately equal to 45°. The adaptive significance of these systematic differences is quite clear because the occipital surface, including the lambdoid ridge, is a site of attachment for all muscles forming the complex of flexors of the atlanto-occipital joint, whose significance in conjunction with the adaptation for ejecting earth from burrows and feeding tunnels with the help of the head, was shown earlier. The anterior slant of the occipital surface also has a specific adaptive significance. It primarily plays a role in the fixation of different sections of the skull, and experiences considerable muscular tension. It is clear that such a position of the occipital surface facilitates a substitution of equivalent forces for the force of traction. It is interesting that such speciality of the skull among present-day families of the order Rodentia is characteristic only of Spalacidae and from fossil representatives, the specialized burrowing animals with possibly a mode of digging similar to mole rats, the Oligocene Cylindrodontidae. Differing from Spalacidae, the zukors have more or less well-defined structures on the occipital surface with a site for attachment of the rhomboid muscle of the head; however, because of the moderate development of all other muscles in the flexor complex of the atlal-axial-skull joints, the occipital surface is not so wide and has almost no forward inclination.

The structure of the cervical region of the vertebral column assumes a special function because of the above-mentioned peculiarities, experiencing the direct effect of the load lifted and of the muscular tensions accompanying the contraction of the dorsal muscles attached to the neck either fully or partially. A general shortening of the cervical section and the resultant reduction in the length of its individual components is an adaptive reaction to such influences during the process of evolution. The same is the case with individual vertebrae which are immovably fixed to each other and to the thoracic section, while retaining considerable mobility in the atlanto-occipital joint. The formation of an immovable cervical region in mole rats is accompanied by a development of the so-called interlocking joint of the 2nd to 7th cervical and the 1st thoracic vertebra. This is achieved by way of the cranium-like juxtaposition of comparatively large articulating surfaces of cranial and caudal articulating facets of adjoining vertebrae (Figure 7), and by the widening of their dorsal bows, as a result of which the edges of the latter closely attach to each other in adjoining vertebrae and also by the formation of special interlocking projections and concavities on the articulating surfaces of the body of the vertebrae. Perhaps there are some changes in the structure of the neural spines and the bony processes of the 2nd to 4th thoracic vertebrae, the site of attachment of M. rectus capitis of the head and M. splenius in the complex of the above-mentioned adaptations. Thus, the neural spine of the 2nd cervical vertebra in mole rats is considerably widened in a transverse direction with a bifurcated upper end, and the neural spines of the aforesaid thoracic vertebrae have a tendency toward a similar widening and sometimes even to a fork-like bifurcation of the upper ends.

The specificity of movement in the atlanto-occipital, accompanied mainly by the lifting and lowering of the head under considerable loads, brought about the peculiarities of the cranial joint with the 1st cervical vertebra, and of the latter in turn, with the axis. As has been shown in an earlier section of this work, a transgression of occipital condyles on the base of the occipital bone accompanied by a contact of the articulating surfaces of the right and left condyles in Spalacidae is characteristic. Corresponding to this, a considerable transgression on the ventral arch of the atlas of Spalacidae is observed for surfaces for the articulation of condyles of the skull with their reciprocal contacts. Hereafter the portions of the occipital condyles of the skull and their corresponding articulating surfaces on the 1st cervical vertebra, passing over the base of the occipital bone and ventral arch, differing from the basal ones, will be called ventral by us. When the head is lowered, the basal and ventral portions of the occipital condyles and their corresponding surfaces of the 1st cervical vertebra take equal part in the articulation. This type of articulation of the skull with the vertebral column is maintained also in the initial stages of the lifting of the head. However, the ventral portions of the articulating surfaces move apart and only their main portions take part in the articulation. Thus, the greatest contact of the articulating surfaces in the atlanto-occipital joint is made in the initial stages of its bending. The adaptive significance of the above-mentioned peculiarities of articulation of the skull with the atlas in Spalacidae becomes clear, if it is considered that the initial stage of the bending movement, accompanied by the lifting or hauling of a load with the help of the head, occurs with the greatest loads (Gambaryan, 1960). Similar functions are carried out, as a whole, also by the atlal-axial joint. The increase in the area of the contacting surfaces in Spalacidae is also accompanied by an increase in the ventral sections of the posterior articulating surface of the atlas, and also of the corresponding articulating surfaces of the 2nd cervical vertebra by way of its fusing under the odontoid process.

In the adaptation toward ejecting excavated soil from burrows and feeding tunnels with the help of the head, in addition to the above-mentioned characteristics of structure in the skeleto-muscular system of the atlanto-occipital joint, the specific structural formations of skeletal elements and muscles of the anterior limbs also play an important role in Spalacidae. The research of P. P. Gambaryan (1960) is sufficiently convincing that in addition to the aforementioned flexing movements of the atlanto-occipital joint, the load lifting is accompanied also by a maximum flexing of the elbow and shoulder joints (Figure 21). It is natural that such types of movements of the anterior limbs during the process of evolution are a result of stabilizing selection directed mainly toward the perfection of mechanisms allowing movement of the type described. This reformation in Spalacidae is mainly concerned with strengthening the extensor muscles of the elbow and shoulder joints, and also the places of their attachments, the corresponding point on the skeleton. P. P. Gambaryan (1960) observed equal muscular tension for the flexing and lifting of the elbow and shoulder joints (Figure 23). It becomes clear on the basis of the scheme drawn of the elbow joint extensors that the most appropriate, from a functional point of view, are the elongated head of the M. anconeus longus and the M. dorsoepitrochlearis, and to a lesser extent, the lateral and medial heads (M. anconeus lateralis and M. anconeus medialis); the least appropriate is the M. epitrochleoanconeus. One end of the M. anconeus longus of the shoulder is attached all along the caudal edge and caudal surface of the scapula including the caudal process, and the other end on the olecranon of the ultra—to be specific, on its apex—and the M. dorsoepitrochlearis originates on the broadest muscle of the back from its lateral side as a tendon, ending on the proximal end of the radial process of the radius. The M. anconeus lateralis and the M. anconeus medialis of the shoulder originate—the former on the distal part of the large tubercle and partially on the ridge, and the latter on the humerus—and terminate respectively on the lateral side of the olecranon right up to its base and its dorsal surface. Finally, the M. epitrochleoanconeus is attached on the medial condyle of the shoulder bone on one side and on the apex of the radial process of the radius from the other.

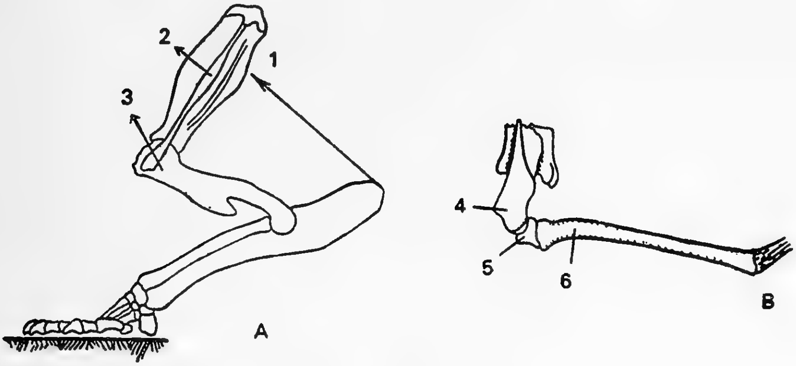

Figure 23. Resultant forces of elevation and extension of (*A*) the shoulder and elbow joints, and (*B*) structure of clavicle-shoulder joint of the mole rat *Microspalax nehringi* (Sat.) (by Gambaryan, 1960).

1—resultant extension of elbow joint; *2*—the same of shoulder joint; *3*—equally effective elevation of shoulder joint; *4*—acromion process of scapula; *5*—bony meniscus; *6*—clavicle.

The research of P. P. Gambaryan (1960) has shown that in Spalacidae the strengthening of some extensors of the elbow joint, having the most proper direction for equal force, takes place. Firstly, that of the M. dorsoepitrochlearis and the M. anconeus longus of Spalacidae exceeds twice or thrice the degree of development for similar muscles in the majority of highly specialized shrews and burrowing animals of the group Myoidea. For example, the per cent relation of the weight of the said muscles to the total weight of muscles in the limbs in Spalacidae is 1.8 against 0.6 in average hamsters, 0.3 in domestic voles, mole voles, and gray rats, 0.6 in long-clawed mole voles and finally 0.2 in *compositodontus* rats. Besides, the index of the relative weight of this muscle considerably increases in zukors (1.3), which is, however, related to the similar specialization of the anterior extremity of the representatives of this subfamily in ejecting excavated earth from underground burrows. An exactly similar tension is experienced by the M. anconeus longus in Spalacidae, the relative weight of which in mole rats is 8.6 against 4.3 in average hamsters, 4.5 in domestic voles, 6.2 in long-clawed mole voles, 5.8 in mole voles, 3.3 in gray rats, and 4.2 in rats of the genus *Nesokia.* In zukors the M. anconeus longus of the shoulder is better developed than in Spalacidae (9.5). In the opinion of P. P. Gambaryan (1960), the latter fact is explained, aside from the specialization for throwing out earth with the help of the head, by the additional functions of the anterior limbs concerned mainly with loosening the soil during the process of digging with the claws. As far as the M. lateral and medial anconeus of the shoulder and the M. epitrochleoanconeus are concerned, they are similar in degree of development in Spalacidae compared to the same in other shrews and burrowing animals of the group Myoidea. It has been stated above that maximum straightening of the head in mole rats is simultaneously accompanied by the straightening of the shoulder joint. Hence, it could be expected that in Spalacidae there is an opposite action on the effect of the M. anconeus longus which, though being an extensor of the elbow joint, acts as a flexor for the shoulder joint simultaneously. The latter is accomplished by the force of the M. rhomboideus of the head and also by the M. subclavius and M. supraspinatus, and the cervical part of the M. acromoitrapezius and the M. serratus ventralis, the role of which in the said process becomes clear only on the basis of the peculiarities of their attachments. In this connection, a short description of the above-mentioned muscles of the shoulder girdle is given below. The morpho-functional characteristics of the M. rhomboideus of the skull have been examined. The M. subclavius originates on the first rib and terminates in the clavicle and distal part of the acromion process of the scapula; moreover, this fixation on the scapula is seen exclusively among rodents in representatives of the families of mole rats and zukors. The M. supraspinatus starts from the supraspinatus fossa of the scapula and terminates on the large tubercle of the shoulder bone. The M. acromiotrapezius attaches itself by one end to the cervical and first two thoracic vertebrae (along the median line of the neck, starting from the lambdoid ridge of the skull) and by the other end on the axis of the scapula, starting from the axial tubercle up to the metacromion process. Finally, the M. serratus ventralis originates from the longitudinal processes of the last four cervical vertebrae and the first seven to nine ribs, terminating on the medial surface of the cranial edge of the scapula, distal to the site of fixation of the rhomboid muscle of the head.

Thus, all the muscles mentioned exert an influence on the scapula because of their disposition against the tension (force) of the M. anconeus longus of the shoulder equalizing or even enhancing the flexing effect (in the shoulder joint) and actually forcing the M. anconeus longus to exclusively flex the elbow joint. All these muscles in mole rats are considerably well-developed. However, of them the rhomboid muscle of the head and the subclavius muscle are better developed in comparison with other specialized shrews and burrowing animals of the group Myoidea. Data on the relative weight of the former have already been given above (page 51). As far as the latter is concerned, in Spalacidae it is five or more times better developed than the same muscles of other shrews and burrowing animals of this group of rodents, exception zukors again. Thus, the per cent relation of the weight of this muscle to the general weight of the musculature of the anterior and posterior limbs in Spalacidae is 3.41 against 2.30 in zukors, 0.35 in average hamsters, 0.28 in domestic moles, 0.42 in long-clawed mole voles, 0.70 in mole voles, 0.19 and 0.30 respectively in gray and *compositodontus* rats (Gambaryan, 1960).

All the aforesaid sufficiently explains the structure of individual elements of the skeleton of the anterior limbs of Spalacidae, directed mainly toward the perfection of mechanism that arranges the work of muscles most economical from a biomechanical point of view which, naturally, is first of all related to the formation of sites of attachments for the muscles. As has been shown, the sites of the attachment of basic muscle complexes taking part in the extension of the elbow and shoulder joints during soil ejection with the help of the head, are mainly the cranial and caudal edges of the scapula, its acromion process, and also the radial tubercle of the radius bone. Hence, it is in order that the above enumerated points of the skeleton of the anterior limbs underwent the greatest changes during the evolution of mole rats. It is known from previous sections of this work that the scapula in Spalacidae is elongated, naturally accompanied by a corresponding elongation of its cranial and caudal edges and also of the acromion process. The adaptive significance of such formations is quite clear if it is assumed that they are accompanied by a maximum development of the sites of attachments of the enumerated muscular complexes according to their functions. In addition, it is characteristic for the scapula of representatives of this family (Spalacidae) to have specific structures for the attachment of one of the main extensors of the elbow joint, the M. anconeus longus. The caudal process, absent in the same bones of all other Myoidea of the old world, even in zukors, is one of them. Moreover, a similar elongation of the scapula is characteristic only for Myospalacinae, of all the representatives of fossil and presently living families of the group Myoidea of the old world; this confirms the correctness of the functional evaluation of the trait discussed in mole rats as a specialization for throwing out earth from burrows and feeding tunnels with the help of the head.

During the lifting of loads with the head, accompanied in mole rats by an ejection of dug out earth from burrows and feeding tunnels, great strength is required, whereas the speed of movement plays a secondary role. An increase in the strength and function of muscles extending the elbow joint could be expected in this connection, especially because of a typical structure of the mechanism of this joint which, as is known, is a lever of the second type where the point of rest (fulcrum) is situated on the paw, the olecranon serving as a point of application of force, and the point of resistance is the site of the support of the shoulder bone in the forearm. It is natural that the greater the height of the radial process and the lesser the length of the rest of the part of the radius bone, the more powerful will be the straightening of the elbow joint though with less speed. Hence it could be expected in Spalacidae, looking at their specialization, that the olecranon should be considerably more developed in them than in shrews and burrowing animals of the group Myoidea in which the process of ejection of dug up soil is not accompanied by head movements. This fact has been convincingly shown by P. P. Gambaryan (1960). The per cent proportion of the length of the olecranon process to the length of the rest of the ulna in different representatives of Spalacidae is as follows: in *M. nehringi*, 53; in *Spalax giganteus* Nehr., 50; in *S. microphthalmus*, 60. In other Myoidea, the magnitude of this index is 21 in the common hamster, 18 in average hamsters, 23 in hoofed lemmings, 19 in true lemmings, 12 in gray field voles, 19 in water rats, 16 to 19 in rats of the genus *Microtus* and some other lemmings, 32 in long-clawed mole voles, 24 to 31 in mole voles, 12 in forest mice and, finally, 18 and 20 respectively in gray and *compositodontus* rats. At the same time, zukors again show a fine example of a convergent similarity to mole rats in the structure of the olecranon process which in Myospalacinae is considerably longer than in Spalacidae. The ratio of its length to the length of the rest of the ulna in representatives of this family is up to 75.

The straightening of the shoulder and elbow joints in mole rats during the process of lifting up loads is accompanied by a movement of the body forward and upward in relation to the limbs. The muscles allowing this movement also take part in the work of the extension of the shoulder joint. The forward movement of the body improves the working conditions of the rhomboid muscle of the head which is the main extensor of the atlanto-occipital joint. The subclavius muscle, the cervical part of the M. serratus ventralis (already described), and also the M. ectopectoralis considerably help in such a movement. The latter originates along the whole sternum and terminates on the ridge of the large tubercle of the shoulder bone. The considerable development of this muscle in mole rats is accompanied by a considerable reinforcement of the site of its attachment on the sternum, firstly by the formation of an elongated median ridge—the keel. Closely correlated to this process there is a considerable widening and shortening of the anterior ribs in Spalacidae because of which the fixation of the sternum is maximum. Besides, as has been mentioned before, the subclavius muscle originates from the anterior ribs. In the light of the aforesaid, the considerable reinforcement of the ridge of the large tubercle of the shoulder bone in Spalacidae (deltoid process) becomes understandable.

All the muscles mentioned above increase the power of extending or straightening of the shoulder joint. Their rather strong development in Spalacidae leads to a little weakening of the proper extensor of the shoulder joint, the M. supraspinatus (whose relative weight is 1.3 against 1.6 to 1.9 in other rodents). The predominance of the extension force in the shoulder joint above the flexion force is so considerable that in Spalacidae, the additional flexor of this joint—M. spinotrapezius—becomes well-developed as a compensation. It originates from the neural spines of the second last thoracic and the anterior lumbar vertebrae, terminating on the tubercle of the axis of the scapula. The indices of the relative weights of the latter allow one to examine its excellent development in Spalacidae as compared to other burrowing Myoidea. Thus, according to Gambaryan (1960), the value of this index in Spalacidae is 3.90 against 0.89 in average hamsters, 1.74 in long-clawed mole voles, 0.90 in domestic voles, 1.74 in zukors, 1.65 in mole voles, 1.15 in gray rats, and 1.27 in *compositodontus* rats.

Further, all the muscles mentioned above (M. serratus ventralis, subclavius, and ectopectoralis) play a role as fixators of the body at the time of lifting a load.

It becomes necessary to examine a number of adaptive structural formations in the distal points of the anterior limb which obstruct the compression (flattening) of the feet under the influence of the force of gravity, as compensatory reactions to the pressure of body weight which multiplies because of the load to be lifted from the earth. In such cases, the callus, bearing a specific structure, and also the arched structures formed by the elements of the carpus and metacarpus which are characteristic for representatives of this family, act as buffers. As has been shown in the research of P. P. Gambaryan (1960), the callus of mole rats considerably protrudes in relation to the free surface of the paw (Figure 16) and is very thick. The callus does not yield to pressure in a recently dead animal, whereas it does yield comparatively easily in other rodents. The density (thickness) increases because of the accumulation of fat cells in the layer of the porous connective tissue formation (Figure 24).

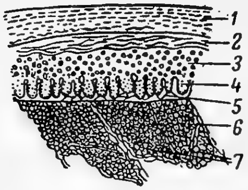

Figure 24. Structure of callus of *Microspalax nehringi* (Sat.) (by Gambaryan, 1960).

1—horny layer of epidermis; *2*—flat epithelium; *3*—cubicle epithelium; *4*—papillary layer; *5*—loose connective tissue; *6*—connective tissue septum; *7*—conglomeration of fat cells.

The compression of the paw and the disposition of individual elements of the carpus and metacarpus react in equal degree. The skeleton of the forefoot of a mole rat is characterized by the following peculiarities. The pisiform bone is placed laterally and prepolex medially (Figure 25). At the apex of these bones, the aponeurosis of the long, paw muscle joins with the fibrous tissue of the callus and the periosteum of these bones. Two of its strongly developed thickenings go to the prepolex and the pisiform bone, and approach the callus as very thin bundles fading into fibrous bundles of padding in the callus. The pisiform leans against the IV to V carpale and ulnare on one side and from the other, against the radius. The prepolex leans against the fused radiale and intermediate of the carpals and partly the fused radius (Figure 25). The distal portion of the callus spreads out up to the carpo-metacarpal joint of all the five metacarpals of the paw. Thus, an arch (arch cupola) is formed at the base of the forepaw of mole rats, the external boundary of which thrusts through the callus into the carpometacarpal joint, through the sesamoid bones into the carpal bones, and the posterior boundary passes through the prepolex and pisiform bone into the distal section of the forearm. The pressure passed on through the bones of the forearm tries to straighten this arch to which the dense callus offers an obstacle and the long paw muscle, thus enforced, approaches the boundary of the arch in Spalacidae (Gambaryan, 1960).

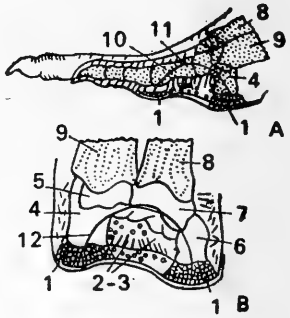

Figure 25. Scheme of structure of the wrist of the mole rat *Microspalax nehringi* (Sat.) (by Gambaryan, 1960).

A—longitudinal section; *B*—cross section. *1*—thickness of callus; *2, 3*—aspect of palm and long palm muscles; *4*—pisiform; *5*—ulnae bone of carpus; *6*—prepolex; *7*—radiale and intermediate bones of carpus; *8*—radius; *9*—ulna; *10*—metacarpus; *11*—longitudinal arch of joint; *12*—cross arch of joint.

In mole rats as far as the hind limbs are concerned, they carry out very insignificant lever-like functions during considerably complex process of ejecting earth from burrows and feeding tunnels, including the adjustment of the body in space, and during the first stages of burrowing accompanied directly by digging and transportation of earth in a horizontal or slanting tunnel, they have a very insignificant influence concerned mainly with forwarding the body and taking it back. Hence, it would be correct to explain, perhaps, the specific characteristics of their construction in repretatives of this family while explaining the manner of throwing out the dug up earth.

CERTAIN CHARACTERISTICS IN THE STRUCTURE OF THE LIMBS OF MOLE RATS RELATED TO ADAPTATIONS FOR EJECTING LOOSENED EARTH DURING THE PROCESS OF DIGGING

It is known that the limbs of mole rats do not play a direct part in loosening soil during the process of digging. However, they are totally involved in the next stage of the digging cycle, which directly precedes the stage of ejecting earth from burrows and feeding tunnels and is related to the throwing back of soil loosened by the incisors. In this complex of movements, the main load, as in other burrowing rodents, is taken up by the hind limbs which, in Spalacidae, underwent the greatest change. In addition, the specialization in this direction has influenced greatly the structure of the forelimbs, mainly the distal points which play a considerable role in the said process.

As shown by the research of B. S. Vinogradov (1946) and P. P. Gambaryan (1960), rodents which loosen the soil during digging with the help of the claws of the forelimbs undergo considerable structural changes during evolution mainly related to an increase in their dimensions, predominantly in longitudinal elongation. During this, there is a thickening of the claw at the same time in a latero-medial direction, often accompanied by an almost complete closing of the borders of the claw plate on the volar surface of the latter with a maximum isolation of the sole plate. In mole rats which loosen soil with the help of incisors, the claws of the forelimbs are capable of only throwing it back; because of this, they appear to be shortened and flattened compared to the claws of rodents mentioned above. Thus, the height of the claw of the forelimbs in mole rats is usually less than its width or is approximately equal to it, whereas in zukors and long-clawed mole voles, the first measurement exceeds the second by more than one and a half times. The claw plate on the claws of the forelimbs of Spalacidae somewhat overhangs the volar edges, and the sole plate is strongly curved (Figure 26). The latter, in turn, considerably increases the expelling surface of the claw. It must also be noted that the claws of mole voles have exactly the same structure. These are rodents which, like mole rats, loosen the earth with the help of incisors. The validity of the functional evaluation of these structures in the construction of claws for the forelimbs is further confirmed by the fact that despite the differences in the type of digging, they have the same structure—almost similar to that of the hindlimbs of all of the above-mentioned burrowing animals of the group Myoidea. The latter fact is quite understandable because in mole rats, as in mole voles, zukors and long-clawed mole voles, the distal components of the hindlimbs, besides acting as a fulcrum, carry out no other function than that of throwing out dug up soil.

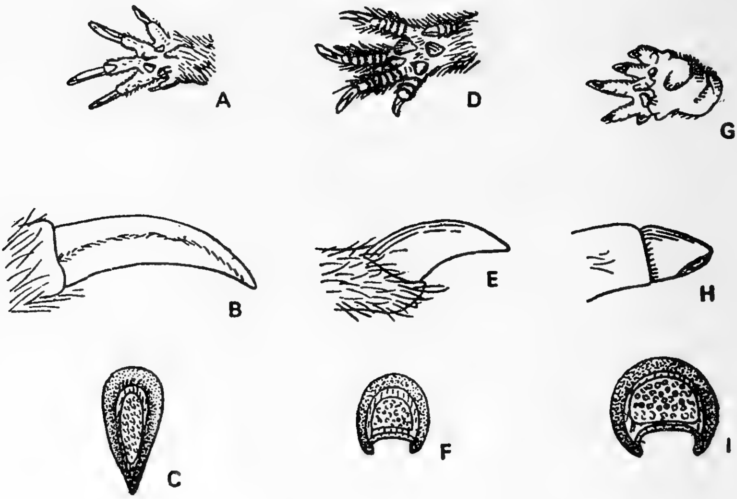

Figure 26. Structure of the claws of the wrist (by Gambaryan, 1960).

A to *C*—*Prometheomys schaposchnikovi* Sat.; *D* to *F*—*Microtus arvalis* Pall.; *G* to *I*—*Microspalax nehringi* (Sat.); *A*, *D*, *G*—wrist with free side; *B*, *E*, *H*—claw of third finger; *C*, *F*, *I*—same, transverse section.

The process of specialization toward loosening soil with the claws of the forelimbs is usually related to the reinforcement of the whole muscular complex in rodents—the flexors of the forefoot, mainly the M. flexor digitorum profundus. In Spalacidae, however, this muscle is not very well developed because the distal components of the forelimbs are adapted only for throwing back the already loosened soil. Thus, according to the data of P. P. Gambaryan (1960), the ratio of the weight of the M. flexor digitorum profundus to the total weight of the muscles of the anterior limbs in Spalacidae lies in the range of 1.40 against 5.87 in zukors, and 4.02 in long-clawed mole voles. Weak development of this muscle is characteristic of mole voles (1.82) as in Spalacidae. The lesser development of the flexors of the forefoot in mole rats is, perhaps, in close relation to the reduced surfaces of their attachment. The latter is mainly due to a general reduction in the distal components of the forelimbs in representatives of this family.

It should be noted that the specialization of digging with the help of the claws of the forefeet is accompanied by a reinforcement of the rotator of the foot, which again does not happen in Spalacidae; the degree of development of the round pronator and supinator is two to three times less than the same muscles in zukors and long-clawed mole voles.

As far as the proximal part of the anterior limb is concerned, rotation is characteristically absent here too. Thus, for example, in Spalacidae the shoulder joint underwent considerable changes related to its conversion from multiaxial to mainly monoaxial. The latter is possible because of the peculiarities of the structure of the clavicular-scapular joint, accompanied by the formation of a special bony menisculus (Figure 23), which is absent in similar joints in other burrowing rodents. The nature of such a joint restricts the range of movements in the said joint to strictly the sagittal plane (flexing-extending) which, as has been shown in a previous section, is mainly related to adaptations toward ejection of earth from burrows and feeding tunnels with the help of the head.

It has been said above that, in the process of throwing out loosened soil, the greatest load is taken up by the hindlimbs, which have undergone maximum changes in mole rats as compared to some other burrowing rodents. They are mainly related to the fixation of muscle complexes which take the body behind, while bending the knee joint, and at the same time pulling it upward. This process is related to a maximum lengthening and reinforcement of the caudal border of the ischium, and the formation of a very strong ischiatic tubercle in addition to the ischial ridge. The ischiatic tubercle and ridge are arranged on the pelvis of mole rats almost in a longitudinal direction which, perhaps, creates the best condition for working the aforementioned muscles. The general reinforcement of the ischiopubic portion of the pelvic girdle has to be seen as a compensatory reaction to the formation of a considerable muscular tension in this portion, accompanied by a reduction of the pubic bone due to fusion with the ischium, thus leading to a tendency toward an overgrown closed foramen characteristic of all representatives of Spalacidae without exception.

In Myoidea, some rearrangement of the mechanism of extension of the tarso-metatarsal joint, related to an increase in the relative length of the calcaneous tubercle and strengthening of the M. soleus, has to be viewed as an adaptation to throwing out soil loosened with the help of incisors. Thus, the per cent relation of the length of the calcaneous tubercle to the length of the third metatarsus bone in Spalacidae ranges from 51 to 53 against 43.3 in zukors, 36.0 to 37.0 in mole voles, 35.0 in long-clawed mole voles, 19.0 in average hamsters, 17.4 to 19.5 in voles of the genus *Microtus*. From the indices shown above, a general tendency toward elongation of the calcaneous tubercle is observed from burrowing animals to shrews of different degrees of specialization. The functional significance of this phenomenon becomes quite clear if it is considered that at the end of the calcaneous tubercle a number of muscles make their attachment (including the M. soleus), the contraction of which brings about the extension of the tarso-metatarsal joint. On the other hand, the proximal portion of the fibula is comparatively broader than in other Myoidea, and serves as a site for the attachment of the M. soleus. The above rearrangement of the sites of attachment for this muscle in Spalacidae and in mole voles is closely related to the degree of its development, because the relative weight of the M. soleus in representatives of the aforementioned families, about twice exceeds the same muscles in all other burrowing Myoidea (Gambaryan, 1960).

A SHORT ACCOUNT OF ADAPTIVE CHANGES OF CERTAIN STRUCTURES OF THE SKULL AND THE SKELETON IN THE EVOLUTION OF MOLE RATS

It has been seen in earlier sections that the main direction of specialization of mole rats in the process of evolution was an adaptation toward an underground way of life. Aspects of the digging cycle of representatives of this family, related to the loosening of soil with the help of incisors and its ejection from burrows and feeding tunnels with the help of the head, predetermined the greatest changes in the morphology of the muscular system of the skull and the skeleton performing the above process, mainly of the masticatory apparatus and the mechanisms related to an extension of the atlanto-occipital, the elbow, and partly, the shoulder joints. Unfortunately, the paleontological data available at present does not allow one to carry out a complete phylogenetic analysis of the changes in all the aforementioned structures. The remains of the mandibular rami isolated teeth and, to a lesser extent, broken portions of the masticatory sections of the skull of Spalacidae, are preserved in a fossil condition in a comparatively better manner and, as a result, offer a very promising basis for judging the character and trends of similar reconstructions of the masticatory apparatus, but the trend of changes during the process of evolution for other systems can be judged only on the basis of indirect data based primarily on observations of degrees of development for the various traits in living representatives of the family which have reached different degrees of specialization toward an underground way of life. Thus, the selection of the system during an analysis of its adaptive reformation during evolution is predetermined by the researcher, not so much by considering the importance of the system *per se* in the background of the whole adaptivity of the group, but by the peculiarities of preservation of the paleontological material.

In a previous section of this work it was shown that the masticatory apparatus of mole rats, together with normal feeding functions concerned with the chewing and grinding of foodstuff, also happens to provide the first stage of the digging cycle related to loosening the soil. In fact, the very speciality of the masticatory apparatus for burrowing in rodents of this family, happens to be the main trend in the evolutionary processes which determined, finally, all the adaptive characteristics of the skeleton and muscular systems of the skull. Comparatively minute adaptive changes of the structures functionally concerned with only normal feeding, mainly the permanent molars, existed in the phylogenetic morphology of the family, and existed perhaps in close dependence on the adaptation to burrowing, while possibly playing a specific selective role in the general process of specialization toward underground feeding habits.

A study of the characteristics of the structure of the masticatory apparatus in fossil and living representatives of the family, belonging to different stages of specialization for burrowing, permitted determining the main adaptive rearrangements of the said systems, and is the result of a stabilizing selection influencing mole rats mainly in the following basic directions:

1. A rearrangement of sites of attachment for the muscles of the masticatory complex related to providing the most suitable conditions for their working during the burrowing cycle from the viewpoint of "biomechanics";
2. A structural reconstruction of the very burrowing structures—incisors—directed mainly toward a perfection of their forms and their quickest replacement in the process of wearing;
3. A perfection of the defensive apparatus protecting the rows of permanent molars from premature wearing during meaningless movements of the lower jaw.

The changes in the structure of the sites of attachment for the masticatory muscles during the evolution of mole rats is achieved in the following way. In ancient mole rats the masseter surface of the skull, which serves as a site for the fixation of the M. masseter lateralis superficialis anterior and the M. m. lateralis profundus, though positioned in a horizontal plane, however, is not as markedly curved as in present-day mole rats because its anterior tubercle is almost absent (Figure 40). Further, during the process of evolution of the family, a tendency toward a relative enlargement of the suborbital foramen is observed, which is related to the degree of development of the anterior position of the M. masseter medialis, which passes through this foramen. Thus, in representatives of this subfamily of ancient mole rats, the greatest diameter of the suborbital foramen easily exceeded the combined length of the two anterior permanent molars, whereas in living mole rats it is approximately equal to the length of a full line of M^1 to M^3, or exceeds it. The dimensions of the suborbital foramen in representatives of the genus *Microspalax* are, on the average, less than in the more highly specialized *Spalax*.

Of the structures of the masticatory apparatus of mole rats, the greatest changes have occurred in the lower jaw during evolution. These rearrangements during evolution are as follows. In very primitive representatives of the subfamily of ancient mole rats, the lower jaw still maintained the plan of its construction as in rhyzomyides. This is observed mainly from the relative independence of the angular process placed on the articulating process and having a common edge with it (Figure 40), and also from the lateral position of the apex of the comparatively small alveolar process in relation to the similar proc. angularis. A certain compensation for that much of the unspecified structure of the angular process in ancient mole rats, differing very little in principle from the same structures in Myoidea, which are not specialized for underground feeding habits, is achieved by the profuse development of the lower tubercle of the masseter surface. The angular process loses its contact with the articulated in the highly specialized representatives of the subfamily of living mole rats because of the union of the alveolar process on the lateral wall. Additionally, it greatly loses its independence because it completely adheres to the proc. alveolaris and also strongly protrudes in front. As a result of such union with the proc. angularis, the apex is situated laterally to the similar one of the well-developed alveolar process (Figure 3). It should be noted here that in more primitive representatives of the genus *Microspalax*, especially in fossil Pliocene species, the angular process is characterized by a greater isolation than in more highly specialized fossil and present-day species of the genus *Spalax*. The functional significance of such a reconstruction of the angular section of the lower jaw during evolution is quite clear, because the most suitable conditions are produced in this way for strengthening the respective parts of the external layer of the masseter muscle, which becomes attached to this process, and finally, for allowing movements of the lower jaw in the anteriormost position, in addition to accompanying movements.

Along with the general development of the sites of attachment for the masticatory complex of muscles, a recent tendency toward increasing the extent of the natural and false articulating surfaces is observed in the evolution of mole rats. Thus, for example, the combined length of both surfaces of the skull serving for the articulation of the lower jaw in the relatively primitive *Microspalax* exceeds about two and a half times the length of the row of permanent molars, whereas in the majority of representatives of the highly specialized genus *Spalax*, the former measurement usually thrice exceeds the first. It has to be stressed, however, that there is no sharp difference in the degree of development of the given trait between the above-mentioned genera of mole rats. One of the most primitive representatives of the genus *Spalax*, the Bukovin mole rat, appears to be an intermediate stage in which the relative measurements of the lengths of the articulating surfaces approximately coincide with similar ones in the highly specialized species of the genus *Microspalax*. The importance of such reconstructions in the mandibular joint is very clear, viewed from the development of a rather greater differentiation of the movements of the digging and trophic cycles accompanied, in addition to the general development of the digging mechanism, by the development of defensive structures which protect the rows of permanent molars from premature wearing (see details on page 33).

It has been seen above that the structural reformations of the digging structures like incisors, during evolution, were mainly directed toward the development of a tooth form befitting the animal's mode of life, and also the development of special structures, causing the most rapid replacement of the incisors during the process of intensive wearing. It can be assumed theoretically that the development of a tooth form, whose basic function is related to digging in mole rats, is inevitably related to a maximum widening of its working surface, with an accompanying widening of the tooth crown. Investigations of the relative width of incisors in fossil and living representatives of the family which have attained different degrees of development during evolution in regard to an underground mode of life, allow one to determine a general trend toward a widening of the upper and lower incisors, increasing from ancient representatives of the group to highly specialized ones. This is quite clearly illustrated by the following data. The least wide incisors are carried by representatives of the Pliocene subfamily of ancient mole rats (Prospalacinae). Thus, the ratio of the width of lower incisors to an antero-posterior cross section is 68.6, in Mid-Pliocene *Prospalax rumanus* Simionescu 78.4, and in *P. priscus* (Nehring) 80.8. Among specialized subfamilies of present-day mole rats (Spalacinae), a species of the genus *Microspalax* has preserved comparatively narrow incisors. Hence, the values of corresponding ratios in *M. ehrenbergi* (Nehring) are 76.0 to 83.2 to 94.0 for the upper, and 64.0 to 74.5 to 86.2 for the lower teeth; 82.6 to 90.0 to 95.0 and 75.7, 80.6, 84.6, 87.5 in the Late Miocene-Early Pliocene *M. compositodontus* sp. nov.; 95.4, 100.0, 100.0 and 70.3 to 86.2 to 93.5 in the Mid-Pliocene *M. macoveii* (Simionescu); 72.2 to 87.2 to 95.8 and 71.4 to 81.2 to 90.0 in the Mid-Pliocene *M. odessanus* sp. nov.; 72.2 to 87.2 to 95.8 and 70.0 to 79.6 to 85.2 in the presently living *M. nehringi* (Satunin) and finally 86.4 to 101.5 to 119.0 and 80.0 to 92.1 to 115.0 in the modern *M. leucodon* (Nordmann). Representatives of the highly specialized genus *Spalax* have wider incisors. The values of the said indices are respectively: 100.0–104.2–108.6 and 90.0–97.7–104.1 in the Late Pliocene *S. minor* W. Topachevskii; 90.9–106.3–114.0 and 95.2–98.0–108.1 in present-day *S. giganteus*; 108.3–119.0–130.0 and 100.0–103.9–109.0 in the modern *S. arenarius* Reshetnik; 104.0–112.0–120.8 and 100.0–109.5–120.7 in Pleistocene (Glacial epoch) and present-day *S. microphthalmus*; 110.3–119.5–130.7 and 97.0–104.3–110.7 in present-day *S. polonicus* Mehely; and finally 110.3–115.8–133.0 and 100.0–101.2–103.0 in present-day and subfossil *S. graecus* Nehring. It has to be stressed, however, that this trait is influenced also by age variables; moreover, the changes in the above-mentioned types toward reducing the value of the said index in highly specialized representatives of the genus *Spalax* take place exclusively due to the young and a portion of semi-aged animals. This has been discussed in greater detail in the sections that follow.

As in all other rodents, the incisors of mole rats are characterized by a constant growth which, in itself, is a compensatory reaction to a rather intensive wearing out during the life of the animal in comparison to other teeth. As is known, the zone of development of the incisors is at its posterior portion. During growth, the tooth is progressively pushed out of the alveoli and during this process, the worn out working parts are restored. The evolution of the mechanism for restoring the wear and tear of the incisors is, first of all, related to the maximum growth of the general length of the tooth itself, and with an increase in the extent of its zone of growth. Thus in specialized shrews and burrowing animals, burrowing with the help of incisors, the incisors are subjected to a maximum wearing out during their lifetime and are characterized by the largest length in comparison to the incisors of rodents in which they have only a trophic function. In some cases of a high degree of specialization (Rhyzomyides, and especially mole rats, as well as some burrowing animals of the group Myoidea), the portion of the incisor within the jaw could exceed in length the portion out of the jaw. In view of this, the elongation of alveoli takes place due to the formation of alveolar tubercles and, in most specialized forms, even strong alveolar processes. During this, naturally, the formation of the latter is accompanied by a maximum increase in the general length of the zone of restoration of the tooth. Among all other Myoidea of the old world, the mole rats are forms whose alveolar processes have developed to the greatest extent. In primitive representatives of the group, it is usually less developed than in highly specialized ones; the development in the length of this process in the evolution of Spalacidae exemplifies this. In primitive fossil Prospalacinae, the alveolar processes are least developed. It is considerably lower in height and located laterally in relation to the angular articulated process. In fact, the proc. alveolaris still maintains its rhyzomyide plan of construction in representatives of this subfamily. An increased height of the alveolar process is observed in specialized Spalacinae compared to ancient mole rats; moreover, in the phylogenetical line in the forms of this subfamily depending upon the degree of specialization, there is a progressive growth of this trait. Thus, in representatives of the most primitive subgenus of the genus *Microspalax* (within the subfamily of true mole rats), in the European Pliocene *M. macoveii* and *M. odessanus*, and also in present-day North African and Asiatic *M. ehrenbergi*, the alveolar process is comparatively small (approximately equal in height to the articulated one), though the process of the blending of the angular process with the external wall of the alveoli is complete (Figure 50). In more specialized representatives of the genus *Microspalax* (subgenus *Mesospalax*), the alveolar process considerably exceeds in height the articulated one (Figure 61). Finally, in the majority of highly specialized representatives of the genus *Spalax* the height of this process considerably exceeds the same for proc. condyloideus. There is only one exception offered by one species of the genus *Spalax*—the present-day *S. giganteus*, whose degree of development of the alveolar process is about the same as that in *Mesospalax*. It has also to be noted that the general direction of formation for this trait in post-embryonic development in mole rats completely corresponds to the aforesaid tendency of its development in the evolutionary trend of the family.

Among the devices concerned with digging which also protect the rows of permanent molars from premature erosion during meaningless and trophic movements of the lower jaw, the mechanism of the mandibular joint comes first since, as was shown above, it allows full or partial non-contact of the rows of permanent molars during the movements of the digging cycle, and also the adaptation which allows maximum extension of the digging organs—the incisors—from the oral cavity, thus obstructing the entrance of soil into the mouth during digging. The latter is related to the lengthening of the diastema section of the skull and of the lower jaw, which is also noticed during evolution. Thus, of all the representatives of the family, the primitive fossil Prospalacinae has the shortest diastema. The value of the diastema tooth relationship is 151.0 for the upper jaw, and 66.0, 66.7 for the lower jaw. In the Mid-Pliocenic modern mole rats of the genus *Microspalax* (nominal subgenus) a tendency toward a lengthening of these sections is observed. For example, the value of the corresponding index of the lower jaw of the Mid-Pliocenic *M. macoveii* is equal to 62.5–70.8–75.0, and in the little later Mid-Pliocenic *M. odessanus*, 62.5–74.4–81.0. The values of the diastema-tooth relationship in the primitive but presently living *M. ehrenbergi* are within a very close range (141.4–179.4–213.5 for upper jaw, and 61.5–77.0–93.4 for the lower jaw). In more highly specialized modern representatives of the subgenus *Meso-*

spalax, the diastema is longer on an average (respectively 160.0–202.7–247.0, and 70.4–87.0–106.3 in *M. nehringi*; and 162.5–207.0–280.3 and 70.0–91.0–125.4 in *M. leucodon*). Finally, the lengthiest diastema is carried by representatives of the genus *Spalax*. Thus, the value of this index is 194.4–216.0–243.7 for the upper jaw, and 72.4–86.1–102.9 for the lower jaw in *S. giganteus*; and respectively, 178.3–224.6–266.7, and 84.3–111.9–126.6 in *S. arenarius*; 177.0–233.8–317.0, and 90.5–114.3–138.7 in *S. microphthalmus*; 198.8–230.4–263.6, and 100.0–109.3–122.0 in *S. polonicus*; and finally, 217.0–238.8–258.0, and 82.8–100.3–107.4 in *S. graecus*. The general trend of changes in this trait in evolution is confirmed also by the process of its restoration in post-embryonic development. The minimum values of the indices given above for each species belong exclusively to the young and partly semi-mature animals.

It was shown in previous sections of this work that the adaptations of the skull and the skeleton, which are functionally related to the ejection of dug up soil from burrows and feeding tunnels with the help of specific movements of the head and the factoral girdle of the limbs, play an important role in the life of mole rats. The structural modification regarding this specialization in the evolution of the family is concerned with, firstly, the reconstruction of the mechanisms for straightening the atlanto-occipital and elbow joints. Unfortunately, the paleontological material presently available is insufficient to arrive at firm conclusions about the basic direction in the evolution of these systems, though some additional information on contemporary forms which has come into the hands of research workers gives some starting point for arriving at such conclusions. As shown by researchers, a general tendency toward the reinforcement of the site of the muscular attachment is observed during the process of evolution for mole rats, viz., the flexors of the atlanto-occipital joint. This is particularly observed in evolutionary changes in the degree of development of the occipital process. Thus, for example, the least developed occipital process is observed in the most primitive representatives of the genus *Microspalax* (nominal subgenus), the Pliocene *M. odessanus*, and the contemporary *M. ehrenbergi*. Furthermore, a considerable reinforcement of these structures is seen in representatives of the subgenus *Mesospalax* within the said genus, which finally reaches maximum development in the most highly specialized representatives of the families—the fossil and present-day species of the genus *Spalax*. Along with the aforesaid processes in the evolution of the group, perhaps the changes in the structure of the whole occipital surface of the skull related to reformations directed fully to the stabilizing selection in the direction of widening it (occipital surface) and lessening the angle of its incline in relation to the base of the skull, were also included. It can also be assumed that during the evolutionary progress of the group the structures of the cervical and partly of the thoracic sections of the vertebral column underwent considerable changes. Most probably, these modifications are, as a whole, concerned with the perfection of the aforesaid (see page 46) attaching the protecting adaptations within a family, and in the highly specialized subfamily of present-day mole rats, are concerned with changes depending upon the differences in structure of these sections in *Microspalax* and *Spalax* (see page 125). It is highly probable that during the process of evolution of the group, considerable changes occurred in the individual structures of the proximal units of the anterior limbs concerned with the sites of attachment for the muscles; for example, the extensors of the elbow joint whose working attains a great importance as shown above (see page 54) in the whole complex of the specialization, and the throwing out of dug up soil from burrows and feeding tunnels, which is inherent in representatives of this family. The general tendency toward elongation of the elbow process of the ulna and for strengthening the caudal ridge of the scapula in very highly specialized representatives, would seem to point to a genetic development in mole rats.

Of the structures of the masticatory apparatus functionally concerned with a normal trophic activity and not with digging, first and foremost, are the permanent molars. During evolution a tendency toward simplification of their grinding surface is observed, which was caused by a full or partial reduction of their individual processes—at first the mesocone and paracone in the upper ones, and the mesoconid and entoconid in the lower teeth, and also caused by a reduction in the number of roots due to the fusion of the latter themselves. The evolution of the permanent molars in representatives of the subfamily of true mole rats can serve as an illustration of this. Thus, for example, in the most primitive species of the genus *Microspalax*, the Mid-Pliocenic *M. compositodontus*, the front upper and lower permanent molars have a free mesocone and paracone, the mesoconid and entoconid forming accordingly the external and internal forks. The corresponding process is widely placed. Sometimes the width of the neck of the internal fork of M_1 is approximately equal to one-third of the total length of the grinding surface of the tooth, or even exceeds it (Figure 6). In other species of this subgenus, the mesocone and the mesoconid exhibit all stages of reduction—even up to full reduction. Thus, the mesocone almost completely vanishes in the Mid-Pliocenic *M. macoveii* and *M. odessanus*, not to mention the recent *M. ehrenbergi*, and the mesoconid is comparatively highly developed in *M. macoveii* (preserved in the teeth of the young and partly in the semi-mature, though it is closer to the entoconid than in *M. compositodontus*, Figure 56), and is represented only by vestiges on similar molars (the initial stages of erosion) in *M. odessanus* and *M. ehrenbergi* (Figure 60). Furthermore, in representatives of another subgenus of the genus *Microspalax*, the present-day *Mesospalax*, the anterior permanent molars preserved a stage of development almost identical to the same of the Mid-Pliocenic *M. odessanus*, i.e., it is characterized by the presence of an unfused paracone during the initial and middle stages of erosion, and of a free entoconid only during the very beginning stage of tooth erosion. Finally in the highly specialized *Spalax*, the paracone is fused during all the stages of erosion with the anterior collar, occurring freely only in very young animals as an exception, and the entoconid is completely covered by the posterior collar, being preserved in the form of a small fold only in the initial stage of erosion in the permanent molars (Figures 75 and 76).

The general simplification in the structure of the grinding surfaces of permanent molars during evolutionary processes was, perhaps, accompanied by a reduction also in roots. This can be proven by the following data. Thus, for example, the number of roots in the anterior upper permanent molars in representatives of the genus *Microspalax* varies from two to four, and in the most highly developed *Spalax*, it varies from one to three.

The changes described above in the structure of permanent molars most probably reflect the general specialization of representatives of the group for eating underground portions of vegetation, during which process the decrease in the degree of folds of the teeth is compensated to a certain extent, by an increase in their hypsodont nature.

CHANGES IN CERTAIN STRUCTURE OF THE SKULL OF MOLE RATS DUE TO AGE. SEXUAL DIMORPHISM

The embryonic development of mole rats has not been studied recently. Hence in this section, we shall restrict ourselves only to the fixation of changes in some morphological structures in post-embryonic development.

The changes in the general structure of the body due to age and coloration of hair, except for their absolute measurements, are not very markedly expressed in mole rats. It can only be said that the young and semi-mature animals within a population are darker, as a rule, than the mature and aged. However, some individual structures of the skull and lower jaw demonstrate very clear changes due to age, which can be detected even visually, and also in the mean values of a number of indices. In some cases these changes correspond to the general trends in skull changes during the evolution of the group; thus in addition to important paleontological material, this data also serves as one more additional source for an objective examination of the basic trends of development in the evolution of the family.

Of the structures of the skull in mole rats which undergo the greatest change in post-embryonic development, the sagittal and lambdoid ridges are the main ones. These structures are absolutely not developed in the young, hardly formed in the semi-mature, and reach full development only in mature and aged animals (Figure 27). The form and dimensions of the parietal bone are closely related to the degree of development of these ridges, making it narrower because of the formation of the sagittal ridge (Table 1), and their combined forms change from being approximately perpendicular in the young and semi-mature to being mainly trapeze-shaped (genus *Microspalax*) or stellate (genus *Spalax*).

Data are given in Tables 1 and 2, which characterize the changes in individual parts of the skull and lower jaw of mole rats in post-embryonic development. They indicate that changes in the skull due to age are related

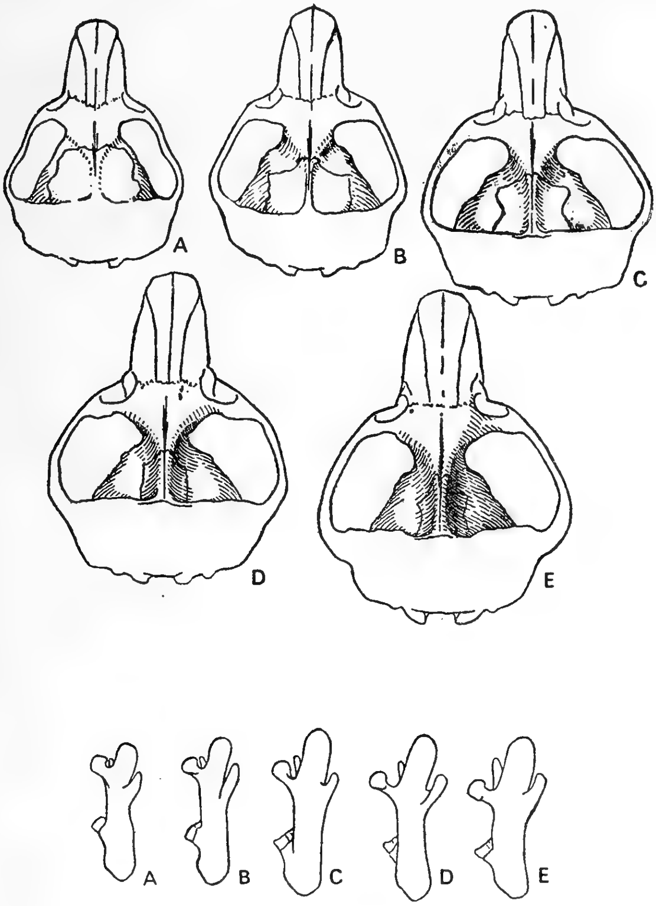

Figure 27. Changes in the axial skull and the lower jaw of mole rats according to age, *Spalax microphthalmus* Güld. ×1.6.

A—young; *B*—semi-mature; *C*, *D*—mature; *E*—old individuals.

Table 1. Changes according to age and sexual dimorphism in proportions of the skull of the common mole rat (*Spalax microphthalmus* Güld.)

Measurements and indices	♂♂ Mature and old males		♀♀ Mature and old females		♂♀ Young males and females	
	Absolute values (in mm)	Ratio of absolute values of individual parts of skull to length M^1–M^3 (in %)	Absolute values (in mm)	Ratio of absolute values of individual parts of skull to length M^1–M^3 (in %)	Absolute values (in mm)	Ratio of absolute values of individual parts of skull to length M^1–M^3 (in %)
Skull, condylobasal length	48.0–52.3–58.4		45.0–49.0–52.4		37.2–43.2–47.7	
Skull, basic length	45.4–49.3–54.2		42.4–45.6–49.2		34.3–39.8–43.9	
Nasal bones, length	19.7–22.3–25.9	241–270–306	19.2–20.0–22.8	231–249–300	15.8–17.7–19.2	205–220–231
Parietal and temporal bones, total length	18.8–20.9–24.0	218–228–302	18.4–19.6–22.0	220–239–264	15.9–17.0–18.5	209–218–227
Parietal bones, length	8.9–10.9–12.8	107–131–156	9.3–10.6–12.1	109–129–153	8.9–10.3–11.2	116–128–134
Diastema, length	18.6–20.9–24.7	218–254–317	17.2–18.7–21.0	204–228–276	13.4–15.5–17.6	177–192–214
Hard palate, length	29.6–32.5–37.1	350–393–463	27.9–29.8–32.0	334–363–421	23.0–25.9–28.5	302–322–347
M^1–M^3, length	7.3– 8.2– 9.0		7.6– 8.2– 8.7		7.0– 8.0– 8.5	
Nasal opening, width	6.5– 7.5– 8.5	80– 90–101	6.5– 7.0– 7.5	71– 86– 95	5.3– 6.1– 6.7	71– 77– 81
Incisors, width	8.2– 9.1–10.3	98–111–129	7.9– 8.6– 9.3	94–105–122	7.0– 7.5– 8.0	88– 94– 98

Nasal bones, width from front	7.6– 8.3– 9.6	91–101–121	7.1– 7.5– 8.1	85– 92–106	5.4– 6.5– 7.4	77– 82– 87
Rostral width	10.7–12.3–14.7	125–148–181	10.7–11.2–12.2	127–141–160	9.3–10.2–11.2	121–127–136
Suborbital width	6.7– 7.7– 9.0	78– 93–114	6.9– 7.8– 8.6	80– 95–102	8.7– 9.2– 9.9	102–115–124
Two parietale, width	8.7–10.8–13.8	80–130–167	11.2–12.4–13.7	126–150–179	13.8–14.4–15.4	166–176–195
Parietal bone, width	3.9– 5.3– 6.7	45– 65– 84	4.8– 5.8– 7.9	60– 72– 93	5.9– 6.0– 7.6	72– 86– 94
Malar width	36.7–41.1–45.9	443–498–575	35.9–38.2–39.0	438–466–539	31.1–32.7–34.4	398–406–415
Occiput, maximum width	32.5–35.3–38.8	333–422–521	30.9–33.4–34.9	383–408–459	26.3–28.7–31.4	333–360–378
Malar drums, length	12.3–13.3–14.5	141–160–186	11.6–12.4–13.1	140–151–169	10.7–11.6–13.0	136–144–158
Auditory bullae, width	7.8– 8.4– 9.1	93–102–116	7.8– 8.3– 8.8	93–101–106	7.4– 8.1– 8.9	98–101–108
Upper incisor, width	2.8– 3.1– 3.4	33– 39– 45	2.7– 2.9– 3.2	33– 36– 42	2.2– 2.4– 2.6	28– 30– 34
Antero-posterior cross section, upper incisor	2.5– 2.8– 3.8	29– 34– 41	2.4– 2.6– 3.0	29– 32– 39	2.0– 2.2– 2.4	25– 28– 30
Occipital bone, height from upper edge, for. magnum	16.8– 1.6–21.4	210–234–276	16.1–18.0–20.0	191–220–263	11.8–15.6–17.5	168–194–213
Nasal opening, height	2.8– 3.2– 4.0	33– 39– 52	2.4– 2.9– 3.5	29– 36– 45	2.4– 2.6– 3.2	31– 34– 46
$\frac{\text{Incisor, width}}{\text{Antero-posterior cross section of incisor}} \times 100$		106–112–119		107–114–121		104–108–114

to an elongation of the whole rostrum, the lower diastema and nasal openings, and to a reduced constriction behind the eyes. In addition, the width of spacing in the molar arches and the relative width and height of the occipital bone increase because of age. The height of the alveolar process on the lower jaw and of the horizontal branch considerably increases, as does the thickness of the latter. The upper and lower incisors show a tendency for widening. A simplification of the grinding surfaces of the permanent molars takes place with age due to full or partial disappearance of the individual processes due to erosion, and the fusion of other processes among themselves accompanied, as a rule, by a closure of the incoming loop into a mark. The nature of such changes can be seen at a glance in Figures 28 and 29. It has to be noted here that in highly specialized forms, the said process terminates at a rather earlier stage of teeth erosion than in the more primitive types. Detailed schemes of changes due to age in the structure of the rows of permanent molars in different representatives of the family have been given in the sections devoted to a description of individual species.

Thus, in the post-embryonic development of mole rats, as perhaps in all mammals in general, there is a restoration of the most important exosomatic structures from the viewpoint of taxonomy in the taxa of the lines of a family which mainly reflect the peculiarity of the specialization of the group as a whole, as well as of its individual representatives. The latter is proven by the fact that all the changes due to age mentioned above take place, after all, as a result of the activity of the main adaptations and structures related with them, functionally related to the peculiarity of the way of life of mole rats. Furthermore, some of the changes described above (elongation of diastemic portions, tendency toward a reinforcement of the ridges on the skull, an increase in the height of the alveolar process of the lower jaw, and a tendency toward a widening of the upper and lower incisors, etc.) in the post-embryonic development of the organism, considerably reflect the change during the evolution of the group.

Sexual dimorphism is not expressed in the external traits. Sexual differences can be determined only on serial data on the mean values for a number of traits in the structure of the skull and the lower jaw. Thus, the skulls of females differ from those of males, in addition to some smaller absolute measurements, on the average, by a rather shorter diastema and hard palate, narrowed rostrum, and elongated temporo-parietal sections. Furthermore, they are less in width in the area of the rostrum and incisors. The nasal bones anteriorly, and the parietal bones together and individually, are also relatively wider. The latter, perhaps, is correlated in females to a rather weakly developed sagittal ridge, as compared to males. It should also be noted that the occipital surface in females is placed far more low. The lower jaw of females differs from that of males, in addition

Table 2. Differences due to age and sexual dimorphism in proportions of the lower jaw of the common mole rat (*Spalax microphthalmus* Güld.)

Measurements and indices	♂♂ Mature and old males		♀♀ Mature and old females		♂ ♀ Young males and females	
	Absolute values (in mm)	Ratio of absolute values of individual parts of skull to length M^1–M^3 (in %)	Absolute values (in mm)	Ratio of absolute values of individual parts of skull to length M^1–M^3 (in %)	Absolute values (in mm)	Ratio of absolute values of individual parts of skull to length M^1–M^3 (in %)
Lower jaw, condyle length	31.0–34.8–40.1		29.6–32.2–35.6		24.2–28.4–30.7	
Lower jaw, angular length	31.3–34.1–39.8		29.8–31.3–34.7		23.3–27.5–30.7	
Diastema, length	7.8– 9.4–10.4	102.6–120.0–138.7	7.5– 8.5– 9.4	98.9–113.5–133.8	6.7– 7.5– 8.0	90.5– 96.9–104.0
M_1–M_3, length	7.0– 7.7– 8.4		6.8– 7.5– 8.1		7.3– 7.6– 8.0	
Horizontal branch, height at center level alveoli M_1	8.9–10.1–11.2	117.1–132.4–146.4	8.3– 9.4–10.5	109.0–125.4–139.7	6.8– 8.1– 9.5	92.0–106.0–125.0
Horizontal branch, thickness from level of M_2	4.4– 5.1– 6.5	54.5– 66.0– 74.3	4.3– 4.5– 5.2	53.1– 60.1– 67.5	3.5– 3.9– 4.7	46.7– 51.7– 61.0
Alveolar process, height from inside	7.6– 8.9–11.2	100.0–116.4–138.6	7.6– 8.3–10.1	95.0–111.0–136.1	3.5– 5.0– 6.3	47.3– 65.5– 82.0
Lower incisor, width	3.1– 3.4– 3.8		2.9– 3.0– 3.6		2.1– 2.5– 2.8	
Antero-posterior of lower incisor	2.7– 3.2– 3.7		2.5– 2.8– 3.4		1.8– 2.2– 2.7	
$\frac{\text{Lower incisor, width}}{\text{Antero-posterior cross section, lower incisor}} \times 100$		100.0–107.8–120.0		103.1–110.7–120.7		100– 105– 120

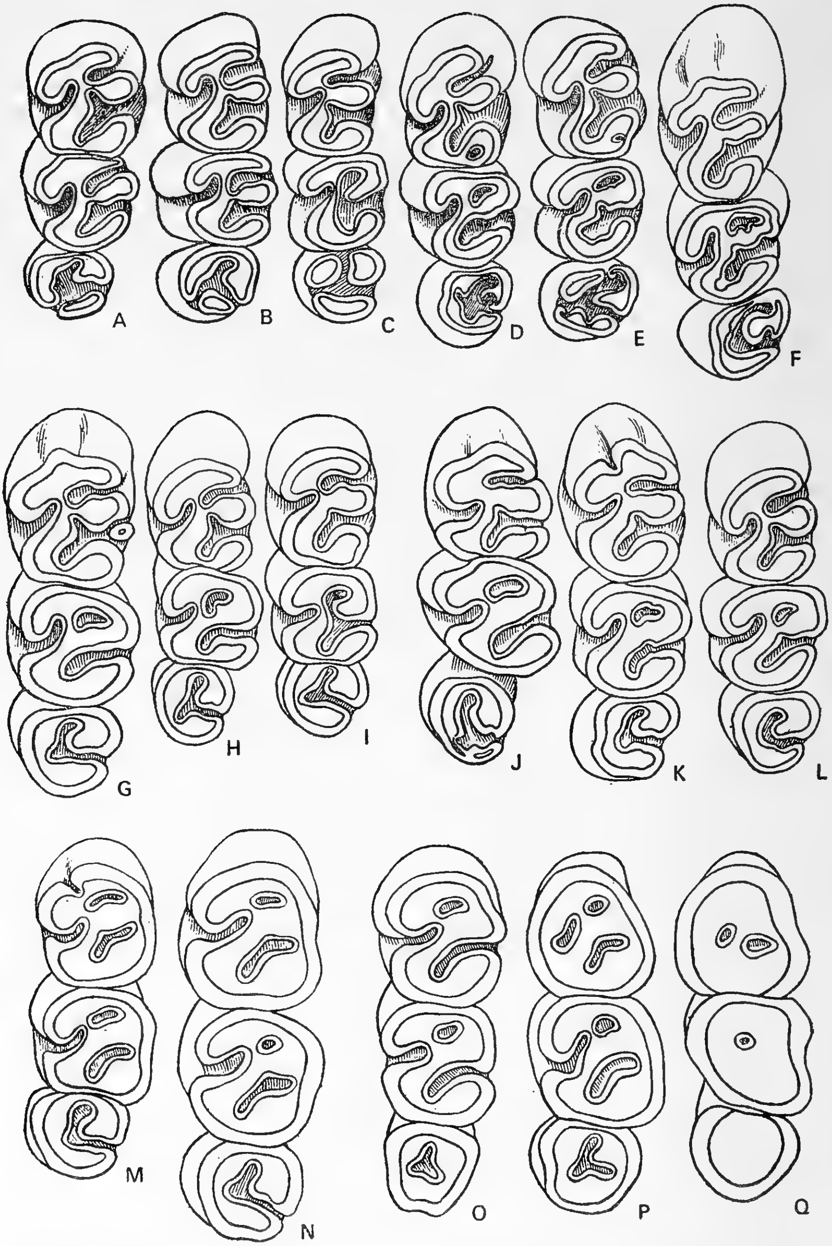

Figure 28. Changes in the upper row of permanent molars according to age in *Microspalax leucodon monticola* Nehr. ×5.

A to *E*—young; *F* to *I*—semi-mature; *J* to *N*—mature; *O* to *Q*—old individuals.

to smaller absolute measurements, by a shortened diastema and also by a relatively lesser height and thickness of the horizontal branch. The skulls and lower jaws of females occupy, so to speak, middle position regarding

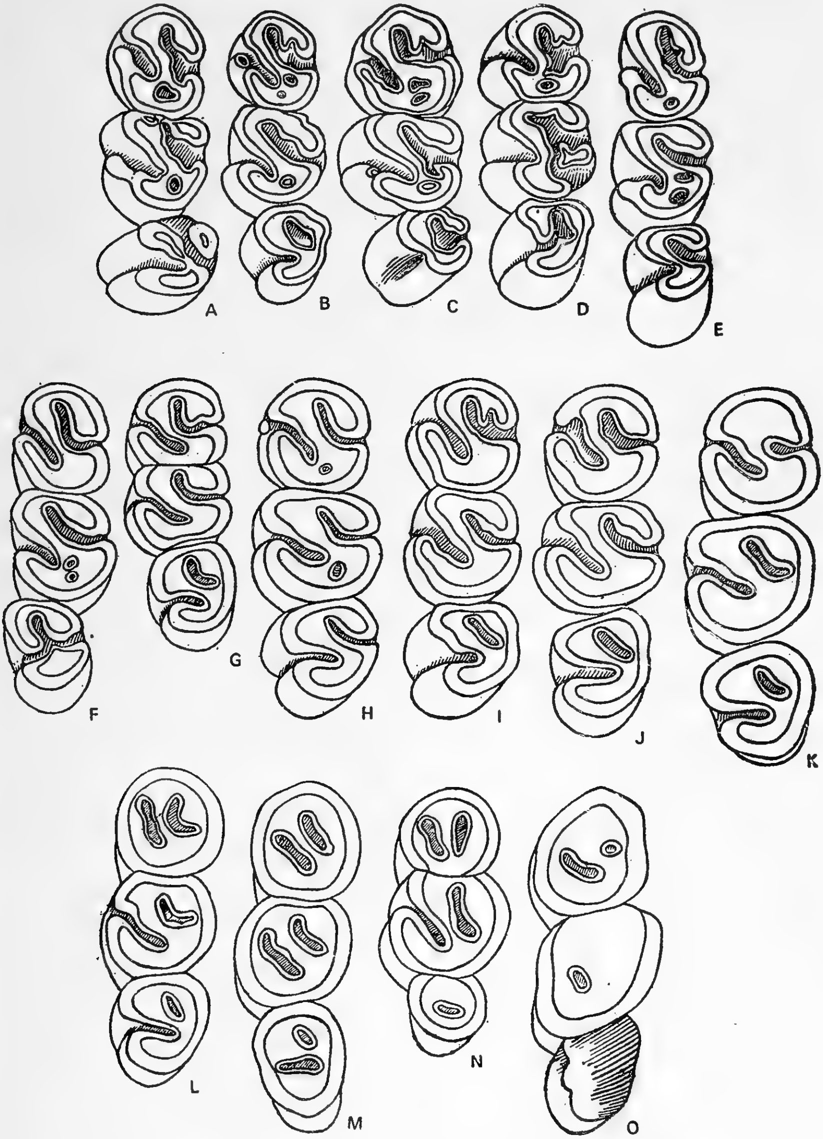

Figure 29. Age differences in the lower permanent molars of mole rats, *Microspalax leucodon monticola* Nehr. ×5.

A to *E*—young and semi-mature; *F* to *K*—mature; *L* to *O*—old individuals.

the degree of development for a number of traits mentioned above, between the same traits of mature and aged males on one hand and young animals on the other (Tables 1 and 2).

Of the skeletal bones, sexual dimorphism in mole rats is expressed only in the construction of the pelvis. In females of the genus *Microspalax*, the pelvic (ischial) axis of the said bones is only in contact with the wings of the sacrum, but in males it fuses completely with the latter. In addition, the pelvic bones in all representatives of the subfamily *Spalacinae*, without exception, are characterized by an absence of a symphysis of the pubic bones in females (open pelvis) as compared to the closed pelvis in males (Figure 49).

ECOLOGICAL FEATURES OF MOLE RATS, THEIR REPRODUCTION AND SIGNIFICANCE TO HUMAN BEINGS

Habitat and population numbers. Present-day mole rats are found mainly in the arid and semi-arid zones, steppes and forest steppes, and have even penetrated into the forests. It is very natural that within the foregoing agroclimatic zones, the habitat of individual species of this family is characterized by specific features. It was recently observed that the main factors limiting the spread and number of mole rats are adaptive and tropical. A common characteristic of the present-day Spalacidae, closely related to the complete underground way of life of all representatives of the family, is that they prefer soils of moderate density, avoiding quicksands as well as very dense hard soils. The saline content and humidity of soils play, in my opinion, an important role because it is known that mole rats are absent from highly humid, hard and saline soils (nonstructured white alkaline soil).

A large number of species are very dependent on the composition of the associated plant community, and further on the availability of abundant edible plants. Sometimes great numbers of mole rats live in places where there is an abundant grass stand.

The habitat and numbers of individual species of this family have not been studied regularly. The Afro-Asiatic mole rat of Ehrenberg has been the least studied. All that is known is that under the arid conditions of the African border of the Mediterranean Sea (Libya, United Arab Republic), the habitat of the species has a mosaic character. The habitat of *Microspalax ehrenbergi* is exclusively confined to more or less humic slopes; in the majority of cases they are greatly attracted to river basins. They are absent in clay and in sandy deserts. In Mediterranean Asia (Israel, Lebanon, Jordan, Syria, and Iraq), in my opinion, they live under conditions similar to those of *M. nehringi*. The extent and density of their vertical distribution in hilly areas is not clear.

The habitat of the Asia-Minor-trans-Caucasian mole rat Nehring (*M. nehringi*) has been studied in detail (Satunin, 1920; Pkhakadze, 1940; Pogosyan, 1946; Reed, 1958). In the trans-Caucasus this species lives in the belt of feather grass and beard grass steppes on chestnut soils, at heights of from 1,400 to 2,400 m above sea level (the population is thickest at the height of 1,500 to 1,600 m). Reed (1958) observed them living in northern Iraq in hilly areas at about 250 m above sea level, with an annual rainfall of 435 mm. According to K. A. Satunin (1920) mole rats Nehring live in humid valleys between hills covered with high grass stands and comparatively humid meadows in Caucasia and the mixed region of Turkey. A number of mole rat dugouts were observed where tulip plants abounded in plantations. According to the data of V. A. Pkhakadze (1940), in the Akhalkalak and Tsalkin regions in Georgia (USSR), they select their habitat in meadows, pastures, and grain fields, living in pairs; their preference is grain fields. Finally, as A. R. Pogosyan observes (1946) from the Spitak and Agin regions of Armenian USSR, the mole rat Nehring is often seen in grain fields and gardens; moreover, with reference to grain fields, they are usually found more in the cultivated areas than in uncultivated ones. According to Reed (1958), in northern Iraq, in addition to the open biotopes, they live on hilly slopes, in shrubs, forest fellings, and even penetrate into the thick of the forest. Data on the population density are very scanty. It is only known that in the fields of the Spitak and Agin regions in Armenian USSR, the population of mole rats Nehring is considerably high. In some years, the figure may go up to eight to nine beasts per hectare (Pogosyan, 1946).

The hilly European or white-toothed mole rat (*M. leucodon*), lives in the cultivated back steppes, on hill slopes, river banks, and ravines, including the roadside areas in the territory northwest of the Black Sea region in the Ukraine (SSR); Moldavian SSR; and the mixed region of Rumania. They are abundant in pastures, uncultivated gardens, vineyards, lucerne fields, and many other grasses, in potato fields, and in sugar cane, onion, and turnip plantations. Sometimes they are also found around a collective farm boundary and near residential zones. They also live near the forests and sometimes enter dense forest. They avoid highly humid marshy regions in river beds (Averin, Lozan and Rozinskii, 1962). According to E. I. Yangolenko (1965), within the Soviet territory they live under similar conditions (in preserved virgin soils, in valleys of rivers and ravines, and common pastures, as well as other soils which are not suitable for cultivation). They abound in hay-mowing grounds and cultivated lands under grass. Because of a reduction in virgin lands, they have shifted to cultivated lands. Seasonal vertical migrations have been observed in the hilly areas. The density of population is comparatively not high (from one on ten hectares, to six to eight on one hectare) in the territory of the Ukraine and Moldavia. It is considerably higher in the Soviet territory where on hay-mowing grounds or perennial grasses, it went up to 23 individuals per hectare.

Data on these aspects of giant mole rats (*Spalax giganteus*), are extremely scanty. They live in clay or sandy, semi-arid or arid zones, and are found in great numbers where humidity is limited—river valleys, hollow lakes, marshy steppes often with bushes, and islandic forests. Evidences of the digging activity of this species have been found in western Caucasus in uncultivated steppes, on black soils, and also on untouched sands (Ognev, 1947).

The sandy mole rat (*S. arenarius*) inhabits exclusively the area around the lower Dnieper (Aleskin) sands of the Kherson region (left bank of the Dnieper River and west of Kakhovka). According to E. G. Reshetnik (1941), it mainly lives on slightly moist, black sandy soils. It is absent on the quicksands, devoid of plants, in Kuchugurakh. Characteristic habitats of this species are abundantly found around the Golopristanskii region of Kherson. They are particularly abundant where eryngo (*Eryngium*), field wormwood, Ukrainian Salsify (*Tragapogon* sp.), pearly cornflower (*Centaurea* sp.), Bermuda grass bungloss (*Anchusa* sp.), couch grass, panicle, sedge (*Carex*), hilander, sheeps fescue, wheat grass (quitch grass), silky apre (*Festuca* sp.), and snakeweed (*Serozonera* sp.) are predominantly grown. In the majority of cases, the habitat of the sandy mole rat corresponds to that of *Scirtopoda telum* Licht. It is found around the forest in the Ivan-Rybalchanskii part of the Black Sea sanctuary and also in birch groves. It is completely absent from the shores of the Tendrov Gulf, Tendrov, and the surrounding islands. The number is considerably high (seven to ten individuals per hectare).

The common mole rat (*S. microphthalmus*) is a typical resident of flat steppes and the forest steppes west of the Dnieper River. It lives in the foothills of the Caucasus. It particularly lives on the slopes of ravines and in other lower areas, preferring fertile black soil with abundant grass. It is occasionally found on sandy soils and cultivated lands (stands of perennial grasses, millets, oats, maize, and other field crops, in gardens, melon fields, and crop-saving forest plantations). Individual burrows were found in the center of dense forests and populated areas. It avoids clay and very loose sandy soil subject to aridity and also, very rarely, portions of flood plains. N. M. Dukel'skaya (1932) gives the following characterization of a typical, common mole rat habitat around the Petrovskii district of the Saratov region. These mole rats live mainly in the grassy black soil steppes, intermittently between the cultivated lands and dense forests. They prefer those portions of steppes where dandelion, groundnut, and chicory are predominant. The tilling of steppes brings about a migration into the adjacent forest ranges, roadsides, and common pastures. After the harvest of perennial grasses, and after tilling, the migration of mole rats is reversed, but the main complex of burrows is concentrated in the common pastures. In fields of millets, oats, and other field grains, and similarly in gardens, there are lesser numbers. Usually, the habitats of mole rats correspond with that of the speckled suslik (gopher) and the common field vole. S. I. Ognev (1947) observed the common mole rat in great numbers in the steppes of the Voronezh region where numerous dugouts of these rats were concentrated on the slopes of ravines and gorges, the boundaries of forest, and rarely, in the thick of the forest. The habitats of mole rats have been observed on grit stone and sandy crests situated on the border of the forest of Khrenov in the Khrenov region where savory, wormwood, rabbit cabbage, and feather grass grow. The common mole rat lives in the left bank steppes and forest steppes in the Ukraine, under conditions similar to those described above (Reshetnik, 1941). According to L. B. Beme (1931), the most typical habitats of these mole rats in the Kuban steppes are portions of virgin lands and deposits on black soils which have abundant plantations of perennial herbs. Sometimes, it goes particularly to fields of perennial grasses. Evidence of digging activity, small mounds of earth, are also found on melon fields and in spring crops, and sometimes (rarely) in winter crops. Finally, according to K. N. Possikov (cited by Ognev, 1947) they live in open and hedge-covered slopes of limited humid ravines with black soil under conditions which exist in the hills of the West and Central Caucasus. It avoids clay and sandy soils which are subject to intense drying. On plateaus (tablelands), it is found in considerable numbers in valleys of the Malki and Baksana Rivers where it lives in flooded fields, glades (clearings), gardens, kitchen gardens, black thorn growths, plum orchards, areas with barberry, hawthorn, and in places where somehow black soil predominates over sandy or clay soils. Information on the density of population under different living conditions is extremely scanty. All that is known is that the approximate number of common mole rats per hectare in the Kharkov region may reach up to ten individuals in virgin land slopes in ravines, up to five to seven in hay fields, and two in cultivated fields (Reshetnik, 1941).

The Podolsk mole rat (*S. polonicus*) in the right bank steppes and forest steppes of the USSR lives in virgin land, roadsides, embankments of dirt roads and railroads, common pastures, slopes of ravines and slopes covered with bushes, afforestations, protected forest vegetations, forest creepers, thick forests, nurseries and stands of lucerne, clover, castor, and cotton. Sometimes it enters into grain fields and kitchen gardens. It prefers black soil; nevertheless, differing from the common mole rat, it is found quite often on sandy subsoils. According to K. F. Kessler (1851) and E. G. Reshetnik (1941), these rodents were found on horizontal terraces around the Kiev and Zhitomir regions. According to V. I. Abelentsev (1951), they were found in the right bank steppes of the Ukraine SSR where an intensive grain industry has developed [observations were carried out on the soil at the Vladimir Agro-silviculture (agricultural afforestation) Experimental Station in the Nikolai region and in the Apostol district of the Dneperpetrovsk region]. The Podolsk mole rat population is very thick in field protective planting (shelter belt) and the sowings of perennial grasses, though because of a deep ploughing of these grain fields (up to 27 cm), the majority of the burrows are destroyed and the animals die. The number of galleries and fresh piles of earth thrown out by mole rats, counted by Abelentsev in autumn and winter of 1949 and 1950, showed that the animals are particularly active in winter in forest plantations, but at the end of March and the beginning of April, digging is concentrated on plains and the area between the bands where seeds of perennial grasses are predominant. Mole rats are particularly abundant in field strips where shrubs have been cut (like shoots of oak, elm, maple, honeysuckle, and yellow acacia), and where a good stand of grass has come up. Here, the number of galleries in winter doubled. The number of animals in such types of bands fluctuates up to four individuals per hectare, in the autumn months, and up to eight in the summer months. In old shelter belts of forests where trees of 15 to 47 years have grown, the number per hectare varies in the range of 0.3 to 1.75 individuals in the spring, and 0.43 to 3.0 in the autumn. It prefers perennial grass stands of three years, or stands of old lucerne which, perhaps, is due to a greater number of roots and the density of the soil. The number of 1.3 individuals per hectare is reached under these conditions. The least density of population of this species is observed in summer and winter in one-year lucerne stands; moreover, in winter lucerne, the animals are seen only in pairs at sowing, and toward autumn reduce to 0.03 to 0.05 individuals per hectare. In fields and orchards where ploughing is not so deep, the number could increase up to two to three individuals, and finally, on virgin parts, it reaches about eight individuals per hectare (Reshetnik, 1941). The autumn migration of mole rats from between the belts into the afforested plantations is due, in the opinion of V. I. Abelentsev (1951), to the great degree of soil freezing in the fields. In the area between belts this happens up to a depth of 70 cm and only up to 10 cm in the belts themselves. It should be noted that mole rats inhabit field protecting forest belts from the moment of their planting, destroying the germinating seeds, shoots, and roots, especially at places where these belts are cultivated on a badly prepared hard soil. Where soil is ploughed deeply before cultivation, these animals vanish for two to three years. The habitation begins because of the hardening of the soil layer and is accompanied by an intensively damaged root system of trees and shrubs of many types.

In places very similar to those of the Podolsk mole rat, on the territory of Soviet Bukovina, the Bukovin mole rat—*S. graecus*—also lives (whose way of life has not been studied in the territory nearer to Rumania). According to E. I. Yangolenko (1959, 1965), it lives on virgin land portions, boundary strips, roadsides (dirt roads), pastures, orchards, sugar cane plantations, potato fields, stands of perennial grasses, and kitchen gardens. Seasonal variations are observed in the distribution of this species according to biotopes. The habitation of this mole rat in winter and early spring is in virgin land, low land, and in stands of perennial grasses. Where there is well-developed grass, habitation is denser. Because of the cultivation of virgin lands, and the accompanying difficulties in obtaining food, it migrates to fields and orchards. It is usually found in the field protective belts of forests and at the edge of forests. It rarely penetrates deep into forests. The numbers vary depending upon the character of the plantations, climatic conditions, abundance of food, and human cultivation operations. On the average, it comes to one to three individuals per hectare on cultivated lands, but on virgin lands and stands of perennial grasses, the number reaches up to twenty individuals per hectare.

Burrows. Differing from burrowing rodents whose burrows are either only hideouts or stores for food, mole rats, being very specialized earth diggers, are characterized by absolutely exclusive underground feeding. Because of this, the construction of their burrows is very complicated with prolonged feeding entrances built by the animals under the surface of the soil at a comparatively shallow depth. The construction of the burrows is very different. It depends upon many factors, the type (species) of animal, sex and age, duration of use, time of the year, plane of the site, soil character, level of subsoil water, and abundance of food.

The peculiarities of the construction of burrows are far from completely studied. At present, no data is available on the construction of the burrows of the Ehrenberg mole rat. Very scanty information on this subject is available on the mole rat of Nehring. According to V. A. Pkhakadze (1940), it is only known that on hilly meadows and pastures, the depth of burrows reaches up to 80 to 150 cm, and in fields of fallow soil, it is not more than 100 cm. In the hills of northern Iraq, Reed (1958) found burrows of mole rats of this type, 75 cm deep. The general length and features of the construction of food inlets have not been studied. The last mentioned are usually at a depth of 5 to 40 cm and have a diameter of 6 to 7 cm. In each burrow, there are one or two nest-like rooms, the dimensions of which vary somewhere between 20 by 20 or 25 by 12 cm. The nest-like rooms are abundantly filled with dry vegetation. Besides these nest-like rooms, the burrows of mole rats contain storerooms, the number and construction of which is not clear for the given species. As has been said already in the previous sections, mole rats throw dug up earth on the surface during the burrowing process, through comparatively narrow, slanting, or vertical burrows away from the food entries and their branches. The thrown-up earth accumulates near the outlets of the burrows in the form of small mounds—the dimensions and position of which, in my opinion, are important from a species specification point of view, and which, unfortunately, have not been satisfactorily studied for present-day mole rats. According to A. R. Pogosyan (1946), the density of the heap of earth thrown by the mole rat Nehring may reach 13 on 19 M^2, and their dimensions fall within the following ranges: height, 12 to 26 cm; width, 25 to 120 cm; and length, 26 to 158 cm. Usually the mounds of earth are of 12 to 20 cm in height, 26 to 64 cm in length, and 25 to 63 cm in width. The distance between them may range from 25 to 700 cm, but is most often 83 to 154 cm. No regularities were observed in the dispositions of these heaps. In some instances they were arranged in a line and sometimes were scattered all over (on three to four places and in different spaces). According to V. A. Pkhakadze (1940), the nest-like rooms in the majority of cases are under the largest mound.

Information on the construction of burrows by white-toothed mole rats is very scanty. According to Yu. V. Averin *et al.* (1962), the burrows of this species consist of slanting entrances (the burrow itself) and horizontal feeding galleries. The galleries are situated at a depth of 5 to 30 cm and have a diameter of 6 to 9 cm. Their total length may exceed 65 to 100 m. At about each 45th m from the feeding entrance, there are three to four stores. The depth of the burrows is about 17 by 20 cm. The height is approximately 20 cm (Reshetnik, 1941). It throws the earth in heaps having a diameter of 20 to 25 cm and a height of 25 to 30 cm. In the opinion of Averin *et al.* (1962), the position of the heap approximately corresponds to the common direction of the feeding entrance. As new feeding entrances are constructed, the older ones become obstructed by earth. After some time, the animals leave even their nest-like rooms and dig new ones. The presence of old, grown grass on the thrown up earth is perhaps an indication that the burrow has been abandoned.

The construction of burrows of the common mole rat has been studied in detail (Figure 30, Dukel'skaya, 1932; Reshetnik, 1941). The system of entrances for each burrow of a grown mole rat consists of superficial horizontal feeding alleys and deeper entrances joining the living spaces, storing spaces, and "latrine" (not more than 10 to 15 cm of the burrowed branch, closed with an earthen stopper and filled with excretion). The diameter of the entrance depends upon the age of the animal (5 to 7 cm for young, and 8 to 12 for old). The horizontal feeding alleys are zigzag and at a depth of 10 to 25 cm. Their total length usually varies from 170 to 250 m. In some instances there are burrows with a total length of feeding alleys exceeding 350 m. There are vertical entrances from the feeding galleries to the nest-like rooms, storerooms, and such deeper parts of the burrow, which reach a depth of 120 to 320 cm. Each burrow has at least two vertical entrances; sometimes this number reaches four. From the vertical entrances start, in turn, a number of deep galleries joining the nest-like room and storehouse. There are one or two nest-like rooms. Their dimensions fall within the following ranges: length, 25 to 30 cm; width, 18 to 20 cm; and height, 15 to 18 cm. In one room the remains of food and fresh bedding are usually found, and in the other, the decaying remains of the latter. In the opinion of N. M. Dukel'skaya (1932), mole rats use only one nest room and when it becomes dirty and infested by parasites, they dig a new one. The bedding in the nest room consists mainly of cereal plants. It is made of mainly meadow grass with interspersed Koelaria, brome grass (*Bromus* sp.), wheat, sheeps fescue (*Festuca* sp.), and hair-like bentgrass (*Agrostis* sp.). The number of storerooms varies from four to nine. They are situated at a depth of 17 to 160 cm (Ognev, 1947). The shape and dimensions of the mounds of earth thrown out by the common mole rat

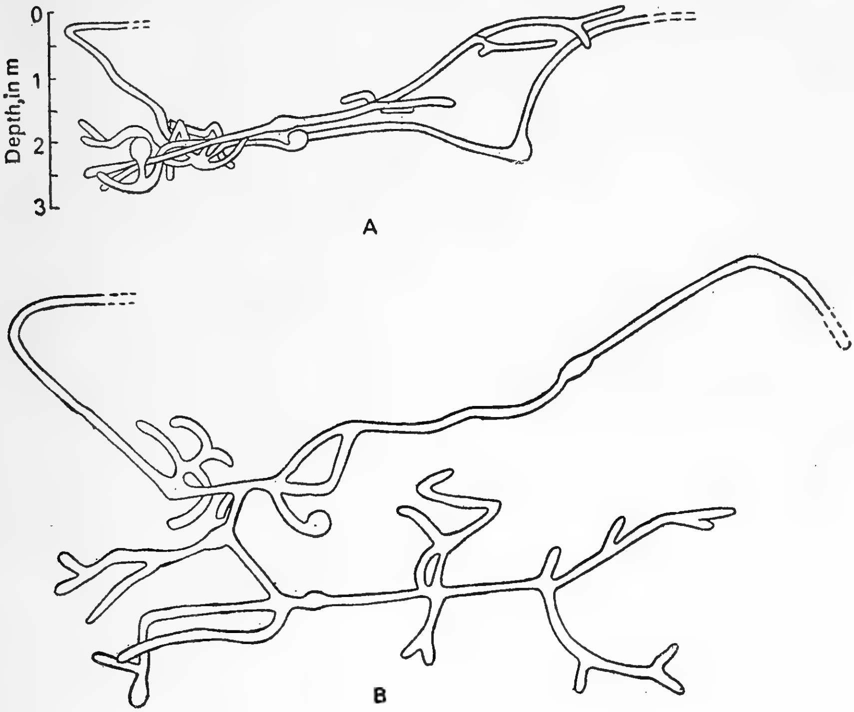

Figure 30. Scheme of a burrow of the common mole rat (by Ognev, 1947).

A—cross section; *B*—plan.

vary. The base of the freshly thrown out hillock is round. The mounds are formed of separate layers of earth and, moreover, some of them even preserve a cyclindrical form, the diameter of which corresponds to that of the entrance leading to the exit hold out of which the earth is thrown. Through drying and atmospheric showers, the mounds become flattened hillocks. The size of individual mounds varies from 20 by 20 cm to 230 by 240 cm. Mounds of 50 to 60 cm in diameter are most frequent. Small mounds are thrown out in one stroke; larger ones undergo many changes during their formation and are the result of fusion of many small mounds; to fill the intervening space, earth is thrown out for quite a long period. Thus, as observed by N. M. Dukel'skaya, a complex mound was formed in 39 days. The distance between the mounds was 20 to 1,175 cm (more frequently 100 to 200 cm). The majority of the mounds are concentrated in the area of food entrances. The deeper entrances usually have no external peculiarities; however, in some cases, large mounds of earth have been noticed near the nest-like rooms indicating the disposition of vertical entrances. The thrown-out earth is not situated near the main food entrance. The dug out earth is transported through branches of the burrows, the length of which could reach up to 75 cm and which end by an exit hole. The main portion of the pushed-out soil comes out through this. Hence, the direction of the disposition of mounds does not correspond to the same for the food entrance. N. M. Dukel'skaya (1932) divides the burrows of common mole rats into the following four groups depending upon the locations of the thrown-out mounds.

1. The mounds are placed straight along with one or two short branches. The general prolongation of the area of thrown-out earth is varied. In individual cases the distance between the two extreme points of thrown-out earth may be up to 169 m and the number of mounds, 114.
2. The mounds are situated radially in relation to one or two centers. In this case, some individual large burrows may account for 90 mounds and the maximum distance between the two extreme points of thrown-out earth may be about 250 m.
3. The mounds are positioned irregularly. In such a situation, one burrow may account for more than 100 throw-outs in an area of 100 square meters.
4. A portion of the mounds is placed straight and there are groups of irregularly placed points of thrown earth. Burrows of this type occupy a maximum area. For example, a mole rat released on an experimental area dug out 284 mounds of earth on an area of about 61 hectares during a period of four months (May 9 to September 12).

In Dukel'skaya's opinion (1932), burrows of young mole rats differ considerably at first sight from those of aged ones. Thus, mole rats which have only just started their independent life, throw out small mounds of earth (diameter, 10 to 30 cm), situated on a close but haphazard path. Only in the region of the nest-like room are there one to two large mounds (40 to 50 cm in diameter). The feeding entrance of the burrow is located at a depth of 10 to 16 cm and gradually passes into deeper parts, ending in a depth of 50 to 75 cm. The nest-like place is situate at a depth of 20 to 30 cm and by it the burrow-branch communicates with the food entrance. However, burrows of such types have also been observed for aged animals which have recently transferred themselves. The difference lies only in the dimensions of the thrown-out mounds and in the diameter of the entrance. As a result, both the young and aged build burrows of the same type. The burrowing activity of the animal is not always accompanied by an excavation of earth from the burrows because a portion of the soil is used for closing old entrances with earth stoppers. During the excavation of burrows made by the common mole rat, a considerable number of old surface entrances filled with various roots, very rarely occurring in external excavations, were observed. The appearance of abandoned food entrances begins from the end of spring. Thus, according to Dukel'skaya (1932) all food entrances are still joined with each other in the spring. Starting from the latter half of May, the earth stoppers begin to appear isolating individual portions of the entrances. The number of abandoned food entrances increases in the summer months.

The temperature of burrows varies at small intervals depending upon the depth of the burrow and the temperature on the soil surface. According to L. B. Beme (cited by Ognev, 1947) the temperature of the food entrance of the mole rat in June and July varied within 5°C (23.5 to 28.7°), whereas on the soil surface, the difference of temperature was 14°C (23 to 37°).

The construction of burrows by the Podolsk mole rat is similar in principle to that of the common mole rat. However, V. I. Abelentsev (1951) indicates that the length of the burrow-branches of food entrances leading to the hole through which earth is thrown out, does not exceed 25 cm in this species, under conditions of the right bank steppes of the Ukraine SSR. Hence, the earth mounds thrown out by the Podolsk mole rat are usually situated at a distance of 10 to 25 cm from the main food entrance. The form of the food entrances is quite varied, as in the case of the common mole rat. Straight or slanting galleries are found often, but rarely in the form of radial lines and least of all, circular. The general length of food entrances is in the range of 10 to 275 m, the depth is 13 to 21 cm, and the diameter is 6 to 7 cm for the young, but 8 to 12 cm for the mature. The depth of the vertical entrances leading to the nest-like rooms, storerooms, and the "latrine" is 90 to 275 cm. The number of vertical entrances varies from two to six; the nest-like rooms are one to two; and storerooms, three to five. The nest-like rooms are situated at a depth of 90 to 275 cm and have a diameter of 25 to 30 cm. The storerooms have the same measurements. Sometimes, the nest-like rooms and the storerooms are joined by burrow branches with a circular, deep gallery which, in turn, communicates with the vertical entrances. The number of excavated mounds of soil from one burrow varies from 6 to 217. The distance between them is from 20 to 1,175 cm. The diameter of the external excavations is 30 to 67 cm, and the height is 10 to 23 cm.

No detailed description of the burrows of the Bukovin mole rat has been given in literature. On the basis of available data (Yangolenko, 1959, 1965), it can be assumed that their burrows are similar to those of the Podolsk mole rat.

The burrows of giant and sandy mole rats also have much in common in their construction with the burrows of the Podolsk mole rat. However, in living places related to sandy soils, the food entrances are usually situated at a greater depth of 40 to 50 cm in the lower Dnieper sandy arena, due to the humidity and the resultant texture of the soil as well as the temperature threshold which, for the given species, should not exceed 27°C. The giant mole rat also constructs similar feeding entrances on similar depth (Anisimov, 1938). Furthermore, the depth of the vertical entrances built by the sandy mole rat usually slightly exceeds 100 cm which, most probably, is due to an excess of humidity at great depths, related to a considerably high level of subsoil water. In the giant mole rat, the depth of the burrow could reach three meters, and more. The position of the excavated mounds of earth, in relation to the main food entry for sandy mole rats, is similar to that of the Podolsk mole rat as the length of burrow-branches, through which the transportation of earth to the exit hole takes place, usually does not exceed 25 cm. This branch of the burrow is inclined in relation to the food entrance at an angle of about 45° in the majority of cases. The dimensions of the externally excavated earth by sandy mole rats, for example, corresponds to that of the Podolsk mole rat; the giant mole rat's exceeds that of the sandy mole rat (diameter of excavated mounds, 40 to 275 cm; height, 25 to 75 cm).

Food. The basic food of mole rats consists of roots, tubers, and rhizomes of varied vegetation. While constructing the feeding channels, the animals chew the underground portion of vegetation, preferring them to succulent foods. The superficial green parts of vegetation—stems and leaves—are significant in the food of mole rats. They obtain the leaves without coming out of the feeding tunnels, reaching through their upper walls. The animals chew the filaments of the roots and by loosening the soil near the roots, pull the whole plant into the entrance. The vegetation for bedding in the nest-like rooms is obtained in the same way.

The food for different species of mole rats has been irregularly studied. Information on this point is extremely scanty for the Ehrenberg mole rat. The diet of the Nehring mole rat in Caucasia has been completely studied.

The main food for this species in hilly meadows consists of onions, tulips, star of Bethlehem (*Ornithogalum umbellatum*) and fritillary (*Fritillaria* sp.) (Satunin, 1920). In the storeroom of the Nehring mole rat (experiments were conducted on the territory at Akhalikalakskii and Stalkinskii regions in Georgia, USSR), the following vegetations were found; geranium (Cranesbill), turnip-rooted chervil (*Chaerophyllum bulbosum*), carrot, gladiolus, star of Bethlehem, grass peavine (*L. sativus*), rampion (*Campanulla rapunculus*), sedge (*Carex gracilis*), wheat grass, salsify (*Tragopogon* sp.) sheep fescue, creeping clover, cummin (*Trachyspermum corticum*), and onion. The storing of food for winter goes on in the summer months. The quantity of store considerably increases toward spring. If in August the quantity of edible vegetation in the store was 130 g, then toward November it increases up to 600 g.

The food of the western forms of the European white-toothed mole rat has not been studied. In the Moldavian and Odessa regions, 25 types of vegetation were found as the food of this species, of which the majority were grains (Averin *et al.*, 1962). The stores consisted mainly of root and, in less quantity, the parts of vegetation above ground. However acorn, maize, grains, and pulses were also found. Of grasses, the following are particularly popular: dandelion, forget-me-not (*Myosotis* sp.), chicory (*Cichorium* sp.), clover, lucerne, different types of melilot (*Melitotus* sp.), garden burnet (*Salod burnet*), sedge (*Carex gracilis*), bindweed (*Glorybond*), different types of sow thistle (*Sonchus* sp.), wormwood, vetch (*Vicia* sp.) wild garlic, and feather grass (*Stipa* sp.). On cultivated sands and field-protecting forest plantations, the white-toothed mole rat's activity destroyed orchard crops and forest plantations. Thus, in the store of these animals, considerable quantities (sometimes more than ten kilograms) of potatoes, sugarcane, carrots, onions, garlic, and even the roots of oak seedlings were found. Sometimes, insects can be found in burrows in the fields.

In the region of Chernovitskii in the Ukraine SSR, the basic components of food for white-toothed mole rats are as follows, according to data presented by Yangolenko (1965): dropwort (*Filipendule hexapetala*), groundnut, peavine (*L. cicera*), comfrey, cow parsnip (*Heracleum* sp.), field snow thistle (*S. arvensis*), gray thistle, clover, lucerne, chicory, dandelion, and salsify. In the autumn-winter period, they feed on crops like sugar cane, carrot and melons in addition to wild vegetation. It has also been observed that vegetation like the families of thistle and pulses predominate in the food of mole rats of Soviet Bukovina in spring, and in the autumn, bulbous vegetation (gladiolus, onion, garlic) predominates. The daily food requirement of this animal usually exceeds that of its body weight. The weight of the stomach with contents is 18 g, on an average. Information on the duration of storage of food and its quantity in general is scanty. The total weight of stores may reach up to 14 kg (Yangolenko, 1965).

Very scanty information is available on the diet of the giant and sandy mole rats. It can only be assumed that in the food of the sandy mole rat the vegetation generally available in abundance in the habitat of this species would predominate. The list of this vegetation has been given above (page 82); salsify (*Tragopogon* sp.) is liked best,* the roots of which are abundantly found in the store of this animal (Reshetnik, 1941).

The most complete information on feeding habits is given for common mole rats. Thus, Dukel'skaya (1932) obtained, as a result of digging up burrows of this species in the Saratov region, abundant tubers of dropwort, gladiolus, onions, roots, leaves and stems of gladiolus and sedge (*Carex gracilis*), leaves and stems of alpine clover, buttercup (crowfoot, *Ranunclus* sp.) and wild forget-me-nots, and leaves of Autumn milk gowan (*Leontogon* sp.). Of the foregoing, the dropwort predominates. Full grown acorns sometimes in great quantities have been found in burrows closely situated to forests. Thus, from one burrow dug up in May, out of 916 g of total stores of the common mole rat, 613 g were acorns of oak. E. G. Reshetnik (1941) puts forward the following list of edible vegetation, found during the digging of burrows of the common mole rat of the left bank steppes and the forest steppes of the Ukraine SSR: lilac sage (*Salvia verticilata*), salsify (*Tragopogon* sp.), goats beard, common chicory, gladiolus, groundnut peavine, dropwort, knapweed (*Centaurea*), carrot eryngo (*Eryngium* sp.), turnip-rooted chervil (*Chaerophyllum bulbosum*), annual everlasting (*Xeranthemum annum*), sneakweed (*Scorzonera* sp.), yarrow (*Archilles* sp.), locorice (*Glycyrrihiza* sp.), wheat grass, Jerusalem sage (*Phlomis* sp.), birthwort (*Corydalis* sp.), tulip, saffron (*Crocus sativus*), sedge (*Carex gracites*), and clover. In the afforested zones and in the zones of field-protecting forest belts and orchard forest plantations, the roots of trees from the pine family and also germinating acorns were likewise found. Thus, according to Silant'ev (cited by Ognev, 1947) in the stores of the common mole rat, living in the territory of the Veliko-Anadolskii forestations of the Donets region, the roots of seedlings and to a lesser extent, acorns were found. In the ark plantations around the city of Kharkov, roots of young mulberry trees (*Morus* sp.), seedlings of the oaks and white acacia were found during the digging up of burrows (Reshetnik, 1941). Of orchard crops, the most frequently found are potatoes, carrots, and sugarcane. Maize, onion, beans, and cucumbers were found rather rarely. The total weight of the stored vegetable mass varied from 8 to 14 kg. The distribution of these stores in storerooms was irregular. The general quan-

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*Giant mole rats in captivity readily eat clover, lucerne, various cereals, radish, onion, and potato (Anisimov, 1938). According to S. I. Ognev (1947), lucerne is preferred by them and this is confirmed by his field observations.

tity of food increased with the depth at which the storeroom was situated. The storing of food took place mainly in the summer months and in early autumn. In addition to vegetable remains, some insects were also found when the stomach contents were studied. Finally, though rarely, some bones and wool of mouse-like rodents and the wool of their own bodies were likewise found (Barbash-Nikiforov, 1928; Reshetnik, 1941).

The food of the Podolsk mole rat has been least studied. All that is known is that in the right bank steppes of the Ukraine SSR (Nikolaev and potentially the Dnieper-Petrov regions) in the burrows roots of lucerne in abundance, and to a lesser extent the roots of wild chicory, bindweed (glorybind) and mallow (*Malva* sp.) were found close to the protecting belts, roots of trees of the pine family, oak, honey locust (*Gleditschia* sp.), white and yellow acacia, and elm (*Elmus* sp.) were found. According to V. I. Abelentsev (1951), the mole rat loves to eat roots of young creepers and stems of trees and shrubs in winter. In the field-protecting belts where burrows have been located, dried seedlings were usually found along with roots chewed up by the animals.

The species composition of the vegetation eaten by the Bukovin mole rat is quite similar to that of the white-toothed mole rat living in the region of Chernovitskii, Ukraine SSR. These first of all are the different species of the family Leguminosae, Compositae, Umbelliferae, Labiatae, and Rosaceae. Some seasonal changes in composition of food are observed in this species as in the white-toothed mole rat of the Soviet Bukovina. The quantity of stored food varies considerably. According to E. I. Yangolenko (1965), 0.5 to 6 kg of different vegetation was found in the stores of the Bukovin mole rat on haying fields; on the best fields, from 1 to 12 kg of tubers, and on stands of perennial grass, up to 4 kg of wild vegetation. The daily food consumption of the animal exceeded its own weight, and the weight of acorns in it was, on an average, 25 g.

Reproduction. Information on the reproduction of mole rats is very scanty and questionable. The mole rats of Ehrenberg and Nehring have been least studied in this aspect. It is only known at present that under conditions of the Soviet Caucasus, the mole rat Nehring perhaps reproduces once in a year and moreover, the litter consists of not more than two offspring (Pkhakadze, 1940). No data on the time of mating, sex ratio, ovulation and spermato-genesis, sexual maturity, nutrition, and colonization of the young is available.

Rather complete information on reproduction is available on the white-toothed mole rat. Moreover, the Bukovin populations have been studied better than the Moldavian and Black Sea region ones in the Ukraine. There is no data on the reproduction of the Balkanski subtype. According to E. I. Yangolenko (1965), the weight of the testis and, correspondingly, the diameter of the seminiferous tubules, is largest in February and March in white-toothed mole rats. At the same time, the weight, length, and the width of the ovaries increased, but the maximum length and breadth of the uterine horns were observed in March and April. All this indicates one ovulation in a year. The females mature when they are two years old. One female has, on an average, 3.15 embryos. There are only immature follicles in the first year of life in the ovarian stroma. Copulation takes place in the burrows, from the tenth day of January, perhaps, to March. The young are born till first half of April. The migration and colonization of young animals begins in May. The lactation period does not exceed three weeks. Animals of 85 g of weight and a length of 10 cm can feed independently on grassy vegetation. The sex ratio is about 1 : 1.

The Bukovin white-toothed mole rat populations and populations of the Moldavian and Black Sea regions of the Ukraine of the same species differ; literature gives information about two litters in one year—in the spring (March to April) and in the autumn (November). This was first observed by Nordmann (1840) and has been confirmed subsequently by many authors. Moreover Yu. V. Averin *et al.* (1962) has reconfirmed the presence of a spring generation of this species lately. It is quite possible that some of the spring births correspond to the warmest season and a prolonged vegetation cover. The number of offspring in a litter is two to four, usually three. In some instances, this number has reached to six to eight (Reshetnik, 1941). The lactation period, colonization, and maturity of the young are similar, perhaps, to the same traits seen in the Bukovin white-toothed mole rat. The young leaves the maternal burrow when they are two months old and dig their own burrows.

There is no information on the reproduction of the giant, sandy, and Podolsk mole rats. There is information only on the colonization by the young of the sandy mole rat in March (Reshetnik, 1941).

Information on the reproduction of the common mole rat is extremely scanty. According to Dukel'skaya (1932), of eleven females of this species obtained in April from the Petrovski region of Stavropol district not one was found to be pregnant. In only four of them were the teats and milk glands developed. This, perhaps, denotes the end of lactation. Of fifteen females caught by E. G. Reshetnik (1941) in the Barvinkov region of the Kharkov district in the first half of April, seven were lactating. Four of them were caught along with their young ones. All this apparently points to the appearance of the young in March and to the end of lactation by the end of May. In May and in the beginning of the year, they colonize intensively (Dukel'skaya, 1932; Reshetnik, 1941). Very similar periods of reproduction for the common mole rat living in a valley portion of the Western Cis-Caucasus have been observed by K. G. Rossikov (1887). However, in the foothills, Rossikov caught a pregnant female in the beginning of June. According to Ognev (1947) this fact possibly confirms the delay in periods of reproduction in the foothills of the Western Cis-Caucasus. The majority of researchers are inclined to say that the common mole rat reproduces once a year and has two to six offspring in a litter.

The characteristics of reproduction have been studied in great detail in Bukovin mole rats. They are in many respects similar to those of the white-toothed Soviet Bukovin mole rat. However, unlike the latter, the mating time in the Bukovin mole rat is prolonged into the second week of January and, as a result, the whole cycle of development of the offspring occurs later correspondingly. Furthermore, compared to the white-toothed mole rat of Soviet Bukovin this species is less fertile. One female has, on an average, 2.75 embryos. The number of offspring in a brood varies from two to five (Yangolenko, 1965).

Mode of life. Mole rats are characterized by year-round activity. They do not hibernate during the winter. However, because the ground freezes during winter, they move into the deeper parts of the burrow. A marked decrease in digging activity is observed during the winter months. Thus E. G. Reshetnik (1941) saw in January only rare fresh mounds of earth thrown out during the period of freezing temperatures and thawing (experiments were conducted on the territory of Lozovskii, Bliznyukovskii and Barvinskii regions of the Kharkov district of Ukraine SSR). Besides, some individuals of the same species were obtained on the surface in February. Under greatly frozen temperatures, the digging activity is, perhaps, completely stopped. A winter migration is usual for some species of mole rats. Thus, in the autumn-winter period, the Podolsk mole rat concentrates itself in the forest belts where the earth freezes to a lesser depth than in open fields. The migration of animals to open spaces takes place in the spring (Abelentsev, 1951).

Excavating activity sharply increases in the spring months, reaching its maximum in the second half of March, April, and the first half of May. For example, the number of excavations by common mole rats varies from two to three to fifteen to eighteen per day in this period. A decline in digging is observed during the summer months which, on one hand, is due to an increase in food as a result of increased roots in vegetation, and, on the other hand, to the warming up of the ground (Reshetnik, 1941).

Because of its underground way of life, the daily activity of the mole rat has not been studied sufficiently. Data available in literature are almost exclusively obtained as a result of observations on hourly throw-outs of earth per day, and do not give a complete picture of the digging activity, or all the intelligent actions of the animals in the burrow and food entrance; this is not always accompanied by an outpushing of earth on to the surface. The existing controversy about this question can be explained to some extent. Thus, for example, according to data by Vasarhelyi (cited by

Hamar, Suteu and Sutova, 1964), mole rats are active only during the day; according to S. I. Ognev (1947) they are active in the evening hours, night, and morning hours; and finally, according to N. M. Dukel'skaya (1932) and E. G. Reshetnik (1941) they are active around the clock. The most significant data on the daily activity of mole rats were obtained by Hamar *et al.* (1964), for the white-toothed mole rat by labeling them with ^{60}Co. It has been proven that the white-toothed mole rat of Rumania is characterized by a round-the-clock multiphased and arhythmic daily activity. The number of phases of activity during twenty-four hours varied from two to ten depending upon the season. In the autumn months the activity of the animals is perhaps less than in the spring-summer period. Thus the number of phases of activity for the marked experimental animals extended from two to five in September, whereas for marked animals in the spring-summer months, it reached seven to ten. The duration of each phase of activity may vary from fifteen minutes to 3.5 hours. The maximum duration of activity varied from 23.8 to 47.9% of the time of the day. The interval of time between phases was not the same. The number of movements in the burrow may reach 554 during the day, and the total distance traveled, say, about 1.5 km. The food entrances are not used regularly during this. There are regions liked by them in the burrows, and their number varies from one to four. The rate of construction of feeding alleys under conditions of firm soil is about one meter per 24 hours. Mole rats maintain their feeding entrances and burrows in a typically standard pattern, and when the slightest destruction occurs, they immediately repair it.

Each mole rat has his individual territory which, unless a great necessity compels it to abandon it, he attempts to hold. Usually one animal lives in a burrow. Females feeding the young are the only exception. A transgression of the burrow by any animal other than the owner is a rare phenomenon because the mole rat jealously guards its burrow and food entrances from unwanted intruders, and depending upon the circumstances, even chases them out. The time of mating, when males find the burrows of females and enter, is an exception. The young live with the mother only during the period of lactation, and at its end they leave the maternal burrow and move to some free territory where they dig their own burrows. The time of migration of the young has been given above. In addition to seasonal migrations and migrations of the young, the mole rat may sometimes leave its burrow. This happens when the burrows are affected by intensive field operations and particularly when deep ploughing destroys the feeding entrances of the animal.

Foes, parasites and epidemiological significance. Due to their underground way of life, the enemies of mole rats among vertebrates are not many. Sometimes the animals fall prey to wild birds when they go out of their burrows. The young ones migrating from the maternal burrows usually die like this. The owl, hen carrier (*Cirus cyaneus*), desert eagle, and black kite (*Milvus migrans*) are some of their avian enemies. The deadliest predators are the desert and black polecats (*Putorius eversmannii*). Mole rats are sometimes sought by other carnivorous animals like foxes, weasels (Mustelidae) and cats. According to Abelentsev (1951) the above-mentioned species and species of marten (*Mustela*) particularly hunt in the autumn and winter months for mole rats, entering their underground abode. Thus, as observed by the above-mentioned author, of the 157 burrows of Podolsk mole rat investigated in the autumn period, on the right bank steppes of the Ukraine SSR (Nikolaev and part of the Dneperpetrovsk region), 68 had been opened by polecats. Of the 276 winter burrows of mole rats investigated, 102 had footprints of these carnivores around the mounds.

Of the ecto-parasites on mole rats, fleas of the genus *Ctenophthalmus* —*C. caucasica* Tasch. and *C. spalacis* Jord. and Roth.—are found abundantly on white-toothed mole rats, *C. spalacis* and *C. gigantospalacis* Ioff on common mole rats, *C. gigantospalacis* and *C. uralospalacis* Tiflov and Usov on giant mole rats, and finally *C. Jeanneli* Jord. on Bukovin mole rats. In addition to these, in the nests and on the bodies of white-toothed mole rats of the territory of Moldavia are found fleas *Ceratophyllum consimilis* Wag. and *Oropsylla ilovaiskii* Wag., lice of the genus *Hoplopleura* and ticks *Euryparasitus emarginatus* Koch, *Northolespis decoloratus* Koch, *Eulaelaps stabularis* Koch, *Haemogamasus nidi* Misch., *H. hirsutosimilis* Will., *Hirstionyssus macedonicus* Hirst, *Ixodes ricinus* Latr., *I. laguri* Ol. and *Dermacentor marginatus* Sulz. In Moldavian SSR the per cent ectoparasitism may be as high as 94.3% (Andreiko, 1963).

Information on the species composition of endo-parasites is very scanty. It is only known that in some individuals of the common mole rat, considerable numbers of nematodes in general and, to a lesser degree, Trichiurodia are found (Reshetnik, 1941). The endo-parasitic species of the Bukovin mole rat have been studied in somewhat greater detail. Yangolenko (1965) has observed *Hidatigera taeniceformis* Batsch, *Taenia polyacantha* Jeuck., *Trichocephalus spalacis* Petr. and Potech. *Ganguleterakis spalacis* Kozl. and Jang. and *Heligmosomum spalacis* Kirsch. The Bukovin mole rat is 100% infected by helminths. Finally, *Heligmosomum moldavensis* Andr. and *Heterakis spalacis* Marcus have been observed in white-toothed mole rats. Mature forms of tapeworms are perhaps absent in mole rats. However, they are either hosts or intermediate hosts for nematodes.

The epidemiological significance of mole rats has not been sufficiently studied. It has been suggested that they could be the carriers of the infectious rabbit fever.

Significance of mole rats for man. Mole rats happen to be serious destroyers of field and orchard crops, stands of perennial grasses, gardens, grape orchards, and forest plantations. The loss caused by them to agriculture differs under different conditions. On virgin lands and wastelands, the destructive activity of mole rat is very insignificant and amounts to only the spoiling of pastures. However, the total area of such spoilt pastures is very small according to Beme (1931) (does not exceed 0.5 to 0.7% of the entire pasture area). Under conditions of intensive cultivation and forestation the destruction caused by mole rats is quite considerable.

Especially significant damage is caused by mole rats on the seedlings of vegetable crops. Thus, in the Spitak and Aginsk regions of Armenian SSR, if the mole rat Nehring is present at the rate of eight to nine individuals per hectare, the harvest of vegetables is reduced by 140 kg on a given area (Pogosyan, 1946). Usually, 15 to 18 kg of potatoes were found in their stores. As reported by Yu. V. Averin *et al.* (1962) in Moldavian SSR the white-toothed mole rat destroys potato fields intensively. Two to three individuals per hectare are capable of destroying 12 to 14 potato plants daily. The destruction caused by the mole rat can reach 13 to 15% of the whole plantation at places. Similar damage is caused by the white-toothed mole rat to the crops of fodder beet (*Beta vulgaris*), and sugar beet. For example, in some of the estates of the Sorokskii region of Moldavian SSR, the yearly damage caused to beet plantations may reach up to 600 kg per hectare (when there are eight individuals per hectare). The white-toothed and Bukovin mole rats cause an average reduction in beet harvest of 19 to 21% and of potato, about 15%, in a number of places around the Chernovitskii district in the Ukraine SSR (Yangolenko, 1965).

Considerable damage is done to the plantings of perennial grasses and hay harvests. Besides the direct damage done to the plantations, mole rats damage the contour of the forest land so badly that not only do they create serious obstacles in the moving of harvesting machines, but also even hand harvesting is made difficult because each mound thrown out has to be individually removed. The damage done to various grasses by the direct and indirect activity of these rodents around the Chernovitskii district could reach up to 10% (Yangolenko, 1965). A plantation of lucerne on 67 hectares around the right bank steppes of the Ukraine SSR suffered a two per cent damage due to the death of plants caused by the destruction of their root system by the Podolsk mole rat (Abelentsev, 1951). A shrub count on measured tracts around this area showed that as a result of the activity of mole rats, the destruction amounted to four to ten per cent in four years. In addition, the whole lucerne was covered by numerous mounds of excavated earth which proved to be a serious handicap in harvesting the crop because workers had to remove them by hand, and only then start the harvesting machines.

Compared to vegetable crops and perennial grass stands, field crops suffer less from the destructive activity of mole rats. Maize is most affected. Thus, according to E. I. Yangolenko (1965) the losses in maize sustained in some estates of the Chernovitskii region amount up to 10%.

Considerable damage is caused to forestation by mole rats. This damage is considerably increased on field protecting belts and forest plantations in parks in the territory of the southern European part of the USSR. Hence, according to Silant'ev (cited by Ognev, 1947) roots of oak seedlings have been predominantly found in the stores of the common mole rat living in the territory of Veliko-Anandolskii forestation of the Donets region. V. I. Abelentsev (1951) observed that on some estates in the Kherson region, in forest belts planted on not very deeply ploughed soil, the Podolsk mole rat can destroy up to 30 to 43 seedlings of different species of wood. The destruction of the roots of the field-protecting forest belts of 15 to 30 years standing has been observed; mole rats gave preference to basic species—elm, oak, and acacia.

Mole rats cause damage to fruit meadows. A. F. Anisimov (1938) also observed damage caused by the giant mole rat to the roots of grapes.

It should also be noted that mole rats influence soil fertility by their activity, by bringing up the lower layers of black soil to the surface. The damaging activity of mole rats is evident also in irrigation works. Water from irrigation canals usually penetrates the burrows of the rodent, thus pushing it out from the irrigation mesh.

The damage mentioned above increases the need for working out measures to fight these rodents. However, because of the peculiarities of their way of life the use of different control measures is accompanied by considerable difficulty. Gas as a method of destroying mole rats has not yet been very successful. The most promising method appears to be that of poisoned baits which cannot scare the cautious animals away. According to Yangolenko (1965), this method gave very good results in the Chernovitskii region. Zinc phosphate and sodium arsenate were used as poisons and beets, carrots, tubers of potatoes, and some wild vegetation served as baits. The effectiveness of these methods increased in early spring and autumn. However, in the right bank steppes of Ukraine SSR, the baits poisoned by zinc phosphate were not eaten by the Podolsk mole rat (Abelentsev, 1951). The most effective method to this day remains the mechanical catching of animals by digging up the burrows and using arc trap No. 1 and mole traps.

Some agroclimatic methods—the foremost being that of deep ploughing—play a great role in checking the number of mole rats.

A SHORT OUTLINE OF THE GEOGRAPHICAL DISTRIBUTION OF MOLE RATS

The family of mole rats (Spalacidae) is at present exclusively distributed in the Palearctic regions, to be more exact in the region of the Mediterranean Sea with some species extending out of this boundary because of their living primarily in the European portion of the USSR. The area (range of distribution) of the family includes a number of regions in North Africa, all of Central Asia, Asia Minor, Caucasia, all of southeastern Europe from the Balkan and Pre-Balkan regions in the west, to the Volga in the east and similarly from north Pre-Caspian to the Ural River, and possibly other parts of the Caspian. The northern boundary of the distribution of the groups reaches the northern Volga region, central regions of the European parts of the USSR, the northern parts of the Ukraine, southwest Poland and Hungary (Figure 31). The zone of distribution lies mainly in desert parts, semi-arid areas, steppes, parts of forest steppes, and a part of the forest zones. However, in the areas around the forest steppes and forest zones, mole rats have a tendency to come out into open areas.

The distribution of mole rats in the past almost completely coincides with the zones of their present distribution, extending out of these boundaries only in the Far East and Northwest. This is particularly so of the most recently extinct representatives of the species of ancient mole rats whose remains are abundantly found in the sediments of the superficial Pliocene of Prikarpate in Poland and Czechoslovakia.

The territory of distribution of Spalacidae at present and in the past is the ancient Mediterranean Sea, the region which was an area of intensive hill formation—the so-called Alpine Orogenetic phase—in the time of neogenesis which caused a permanent change in the contours of the ancient sea basins like the Sarmatian, Miocean, and Pontiac seas preceding the Mediterranean Sea into the present Black, Azov, and Caspian seas. The permanent change in the contour of these basins is related, perhaps, to those distinct factors which mainly pre-decided the distribution (including colonization) of various groups of mole rats in the past, and the basic regulation of its present-day distribution (in the areas of the family). Thus, the clarification of basic regulations for the origin of the fauna of mole rats in various regions of the Mediterranean Sea and the areas around it, and changes in these due to times and genetical relationships, should be based firstly on a clear understanding about the distribution of different groups of mole rats in the past geological periods in the history of the earth, together with an idea of all the intricate peculiarities of the paleogeographical state within these territories, all of which happen to be arenas of evolution for the group as a whole. A study of the fossil and present-day

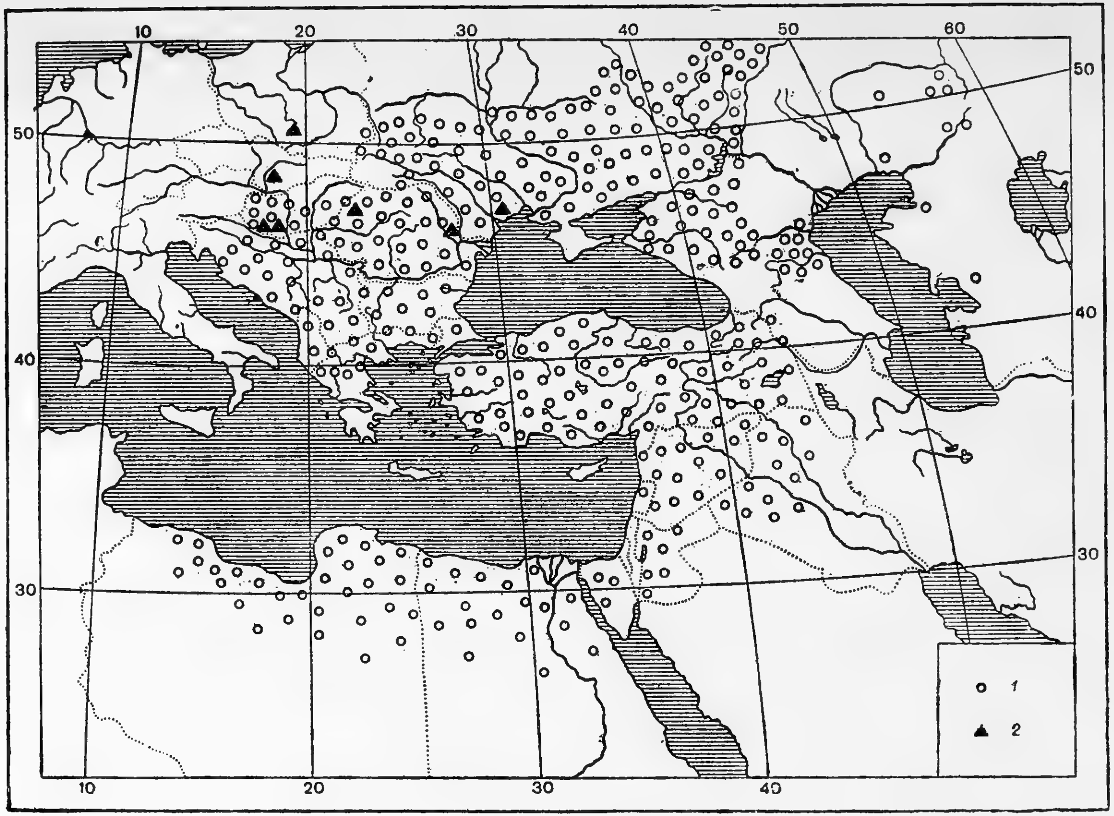

Figure 31. Distribution of subfamilies of Spalacidae.

1—Spalacinae; *2*—Prospalacinae.

fauna of mole rats in this aspect allows one to discover certain features in the distribution of the subfamilies, genera, subgenera, and individual species of these rodents, and we are taking the liberty of explaining these in detail below.

The subfamily of the ancient mole rats (Prospalacinae) succeeding the most primitive representatives of the family, ancestoral (in relation to the contemporary mole rat Spalacinae), and completely extinct by the end of the Pliocene epoch, is known at present by only the very latest forms. Their remains are restricted mainly to the middle and lower strata of the Late Pliocene northwest of the Black Sea region, and combined territories of Rumania as well as Hungary, Czechoslovakia, and south of Poland. It can be presumed that this group of mole rats was widely represented in the Late Oligocene, Miocene, and Early Pliocene of Europe, perhaps also North Africa. With regard to the already known representatives of ancient mole rats, these existed in the Middle and Late Pliocene of Europe with more highly specialized true mole rats of the Middle Pliocenic European species of the Nominal subgenera of the genus *Microspalax*. Around the northeastern Black Sea region of the USSR and combined territories of Rumania, the zones of distribution of ancient and contemporary mole rats are identical. This is proven by the finds of remains of both types in the Central Pliocenic Kuchurgan deposits (found in the valley of the Kuchurgan River, Odessa region) and contemporary strata in territories of Rumania (the place of the find was Malushteni, right bank of the Pruta River on its lower current). However, the frequency of finds of both remains under similar conditions is extremely rare when compared to the same for present-day mole rats.

Among the Late Pliocene fauna of North Rumania, Hungary, Czechoslovakia, and southern Poland, Spalacidae is represented only by a group of ancient mole rats. The absence of true mole rats here perhaps led to the frequent occurrence and subsequent discovery of abundant remains of Prospalacinae as compared to the contemporary sediments of the northwestern Black and Azov Sea areas. The preservation of most of the later representatives of ancient mole rats in the given area can be explained most likely, first of all, by paleogeographic factors. Foremost among such factors are perhaps the distinct influence of the Pannonski Basin and intensive organic processes in the raised region of Karpatiya and Tatranskii existing almost throughout neogenesis. As a result, in the Late Miocene period and throughout the Pliocene epoch, i.e., during the time of intensive sedimentation and settling of the true mole rats in the northwest Black Sea and Azov Sea regions, the old mole rats living in the region of Tatranskii and Karpatiya could have been isolated because of real insurmountable obstacles. All this facilitated the preservation of a number of Miocenic relics in the Pliocene fauna of the given region to a great degree. In addition to ancient mole rats, perhaps it is better to add ancient wrinkle-toothed hamsters (*Cricetus cricetus*) from the genus *Trilophomys* Deperet, *Baranomys* Kormos and others, and the primitives (*Ungaromys* Kormos and *Germanomys* Heller) which are totally extinct here but have preserved their numbers significantly up to the present in the northwest Black sea region.

In fact, the area of distribution of the subfamily of the true mole rats almost completely corresponds to the region of distribution of the family as a whole. Only some finds of the remains of Prospalacinae in southern Poland and Czechoslovakia have been found outside its boundaries.

The most ancient and primitive representatives of this group of true mole rats are the fossil and present-day species placed under the Nominal subgenera of the genus Microspalax (Figure 32). The only living species, *M. ehrenbergi*, is prevalent in the North African and Central Asian Mediterranean Sea area (northern regions of Libya, United Arab Republic, Israel, Jordan, Lebanon, Syria, Iraq, and possibly the southern regions of Turkey). However, at the end of the Miocene epoch and during almost all of the Pliocene, this subgenus was widely spread in Europe where lived other species like *M. compositodontus* (end of Late Miocene in northwest Black Sea region, USSR), *M. macoveii* (first half of the Middle Pliocene in the northwest Black Sea region of USSR and Rumania), and *M. odessanus* (second half of the Middle and Late Pliocene in the northwest Black and Azov sea region of USSR). It should be remembered that the subgenus *Microspalax* is represented in the Middle Pliocene of Europe by species which were already highly specialized in a greater number of traits than even the present-day *M. ehrenbergi*. This fact allows one to assume a considerably wider distribution of this subgenus during the latter part of the neogene, and to decide that the time of separation into areas with close proximity was the Early Pliocene.

If we consider the present-day *M. ehrenbergi* as relics of the Neogenic age, and if it is proved beyond doubt that their ancestors lived within the boundaries of their present distribution zone (based on the level of specialization of the species and the paleogeographical condition of the given territory at the end of the neogene era), at least from the end of the Early and the beginning of the Middle Pliocene, then taking into consideration the European fossil finds, the areas of distribution of the subgenus from the end of the Miocene epoch and during the whole of the Pliocene, in addition to North Africa, Middle East and possibly Asia Minor, extended to all the territory of southeast Europe situated south and east of the Pontiac basin going westward up to Northeast Rumania. Naturally, the contour of the area (zone of distribution) changed during different geological times in close proximity to the permanent changes in the configuration of the ancient sea basins in the areas of the present Mediterranean, Black, and Azov seas. Knowledge about the eastern boundary of the

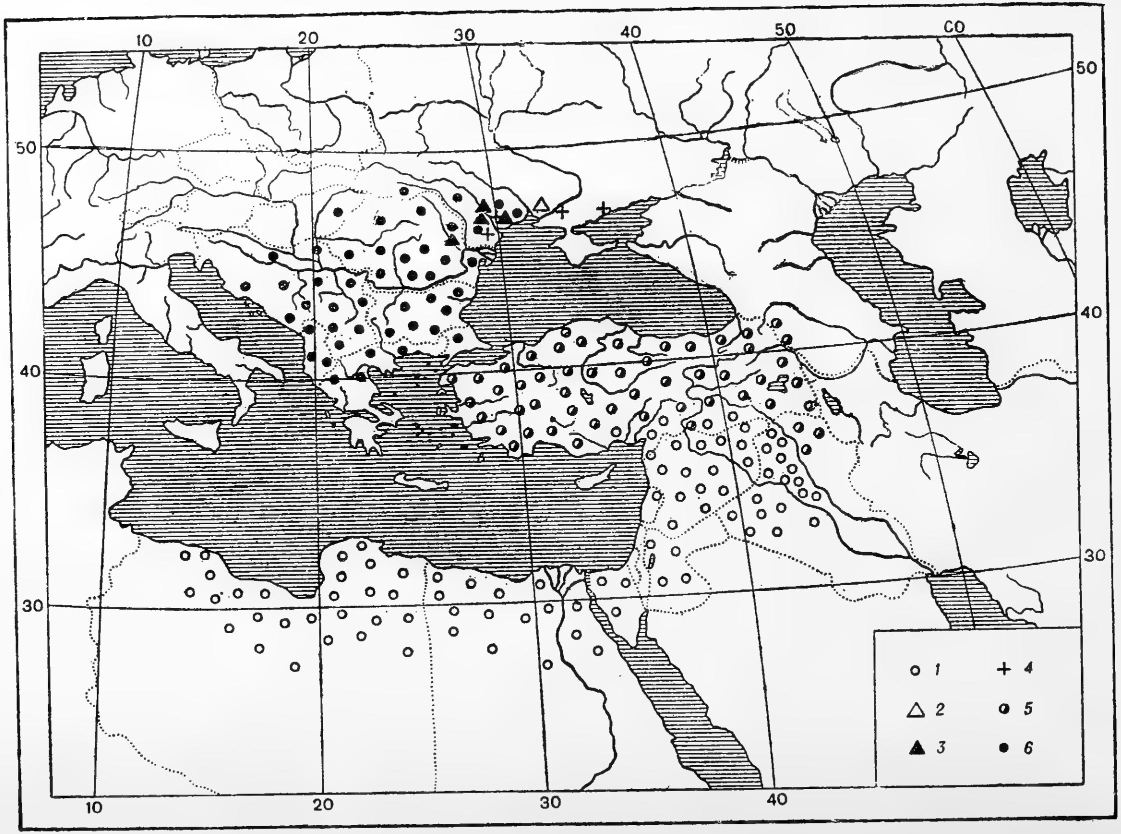

Figure 32. Distribution of species of the genus *Microspalax*.

1—M. ehrenbergi; 2—M. compositodontus; 3—M. macoveii; 4—M. odessanus; 5—M. nehringi; 6—M. leucodon.

distribution zone of the subgenus varies and is limited due to insufficient studies of the Neogenic fauna of rodents in the eastern territories. The Azov region near the Ukraine is the latest known farthest eastern point, recently determined from the finds of remains of the Pliocene European Microspalax.

The question of the final separation of the Afro-Asian and European *Microspalax* is of considerable interest. As shown by research, the permanent molar teeth of the living Afro-Asian mole rats of Ehrenberg fall in a middle category in respect to the degree of specialization, between the molars of Miocene and certain Middle Pliocene European representatives of the subgenus. Thus, it can be concluded that *M. ehrenbergi* represents, perhaps, a special Afro-Asian branch of the subgenus which separated from the main stem of *Microspalax*. Keeping in mind that in the Middle Pliocene of Europe there existed a species which had a number of better developed traits than the present-day *M. ehrenbergi*, perhaps it could be assumed that the final separation of the Afro-Asian and European branches of *Microspalax* took place somewhere in the beginning of the Pliocene period. Most probably the transgression of the Pontiac basin played a specifically distinct role here. Until this, perhaps the area of the subgenus was one as a whole; moreover, the joining of the Afro-Asian and European zones at the end of the Miocene epoch could have taken place only in the region of ancient Aegean land. Further, after the Pontiac period, the dry land communication between Central Asia and Asia Minor, and Europe in the region of the Balkan was perhaps restored; however, the further contact of Afro-Asian and European branches of *Microspalax* obstructed the appearance and colonization on the territory of Asia Minor and the Balkan of representatives of another still highly specialized subgenus of the genus *Microspalax* (*Mesospalax*) which is genetically related to the Afro-Asian branch of *Microspalax*.

The youngest branch of the genus *Microspalax* subgenus *Mesospalax*, which is represented by two species, *M. nehringi* and *M. leucodon*, is perhaps of Asia Minor–Balkan origin. The first is, at present, spread on the whole territory of Asia Minor and partly in Caucasia; the second, mainly around the Balkan and Pre-Balkan regions of Eastern Europe, penetrating only a little into Hungary, the northeastern Black Sea region, and the Karpate (Soviet Bukovina). The fossil remains, mainly of the obgoicene age, have been found entirely, without exception, in the region where modern species have spread. Thus based upon the zone of distribution and morphological peculiarities of the living representatives of the given subgenus, two branches fall within its composition—the one from Asia Minor represented by *M. nehringi*, and the European represented by *M. leucodon*. Of the aforementioned species, *M. nehringi* appears to be more primitive. In addition, a number of characteristics in its organization point toward a genetic relationship with Afro-Asian representatives of the subgenus *Microspalax*.

A sharp increase in the degree of specialization is observed in *M. leucodon*, steadily increasing in the subspecies toward the West. The degree of digging adaptability in the structure of the masticatory apparatus in mole rats of this species reaches its maximum in the farthest western nominal subspecies, *M. l. leucodon*, and is expressed to a lesser degree in *M. l. monticola* of the Balkan. The time of complete separation of the Asia Minor and European branches of *Mesospalax* in the region of the dry lands of the Bosphorus has not been finally decided, primarily because of an almost complete lack of paleontological documentation. However, considering the quite significant differences between the species indicated, the distinctions of the zone of distribution for the subgenus in the Late Pliocene can be assumed with a certain probability. There is absolutely no contact between the Asia Minor and European branches of the subgenus *Mesospalax* through the Caucasus and all the Black Sea region. This is contradicted by the already mentioned fact of the rise in the level of specialization in the European subspecies of *S. leucodon*[1] in eastern direction, and the paleontological data most undisputedly says that in the Late Pliocene deposits of the cis-Black Sea and cis-Azov parts of the Ukraine, the ancient mole rats of the subgenus *Microspalax* (*M. odessanus* and forms close to it) were immediately replaced by the highly specialized representatives of the genus *Spalax*. All the known reference material on the remains of *M. leucodon* in the Pliocene and Lower Anthropogene deposits of the above-mentioned region, are based exclusively on unreliable identifications, and the remains provisionally classified as belonging to this species were found, on closer examination, to belong to either Pliocene representatives of the subgenus *Microspalax* or to Late Pliocene–Early Anthropogene *Spalax*.

If in the Balkans the mole rats of the European branch of the subgenus *Mesospalax* are apparently autochtonic since the end of the Pliocene period, then they are comparatively late arrivals in their present habitat on the territory of the cis-Black Sea region of the USSR and possibly adjoining regions of Rumania. The period of penetration of this group in the territory mentioned is, most probably, approximately the end of the Pleistocene and Early Holocene era. The latter has been fairly reliably documented by paleontological finds in the limits of the present distribution of the species on the territory of the cis-Black Sea region of the USSR. In particular, it has already been mentioned that on the territory of the entire northern cis-Black Sea and cis-Azov regions in the deposits of the transitional zone between Neocene and Anthropogene, the mole

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[1] This should be *M. leucodon*—Editor.

rats of the subgenus *Microspalax* are immediately replaced by the early *Spalax*. This also relates to the region of the present distribution of *M. leucodon* in the limits of the Odessa region and Moldavia. In the deposits of the lower and middle sections of Anthropogene within the limits of the habitat of *M. leucodon* in the cis-Black Sea region, one comes across remains of representatives of the genus *Spalax* exclusively which are as if identical in their species affinity to the present-day *S. polonicus*. Reliable finds of remains of *Mesospalax* in this region relate only to the uppermost Anthropogene strata, most possibly to the end of the Pleistocene, if, of course, the remains of *M. leucodon* from Ilinka, Odessa region (Pidoplichko, 1956) are not of more recent origin. Otherwise, the distribution of this species on the territory mentioned above should be dated to the Holocene. Such a late penetration of *M. leucodon* in the northwest cis-Black Sea region is explained, most likely, by the presence in the past of the constant insurmountable barrier in the form of an aquatorium of different types linked with the Danube and its basins. Apparently, this species appeared to be more adaptable to the conditions of the xerophyte steppes than the earlier mole rat inhabitants of the species *S. polonicus* in this region, which undoubtedly facilitated the almost complete extinction of the latter from the region of the present distribution of *M. leucodon* in the northwest cis-Black Sea region of the Soviet Union. At present the valley of the Dunai and Tissa forms a natural boundary for the distribution of two present-day subspecies—Nominal and Balkan.

The Late Pliocene and Anthropogene autochtones of the southern and partly central belts of eastern Europe are mole rats of the genus *Spalax*. The areas of their present and past distribution encompass regions of the cis-Black Sea and Caspian lands from the Soviet Bukovina and adjacent areas of Rumania in the west, to the Volga, the north Caspian east of the Ural River, and partly the trans-Caspian in the east. The northern boundary of the habitat of this genus passes through the extreme southeast of Poland, northern regions of the Ukraine SSR, except the extremely northern parts, adjacent areas of the Chernozem belt of the Russian Federation to the Central Volga, roughly up to the latitude of the Samara Luk, and moving into the recent past, into the southern districts of the Gorkii region (Figure 33). In the Late Pliocene, the habitat of the genus also included the Crimea. The genus is genetically[1] linked with European Pliocene representatives of the subgenus *Microspalax*, among which we should possibly search the basic forms of the given group.

The genus includes two groups differing sharply in morphological features as well as in regions of their present distribution: group giganteus, represented by the present *S. giganteus* and the phylogenetically close *S.*

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[1] Should be phylogenetically—Editor.

arenarius, and close to the latter, early Anthropogene species and the group Microphthalmus, with three present-day (*S. graecus, S. polonicus* and *S. microphthalmus*), one fossil (*S. minor*) species. Among the foregoing subdivisions, the most primitive group constitutes the mole rats of the giganteus group. It consists of two clearly differentiated branches, viz., the western branch represented by *S. arenarius* and forms closely related to it from the lower Anthropogene deposits adjoining the present habitat of desert mole rats in the cis-Azov region of the Ukraine SSR, and the eastern branch including present-day *S. giganteus*.

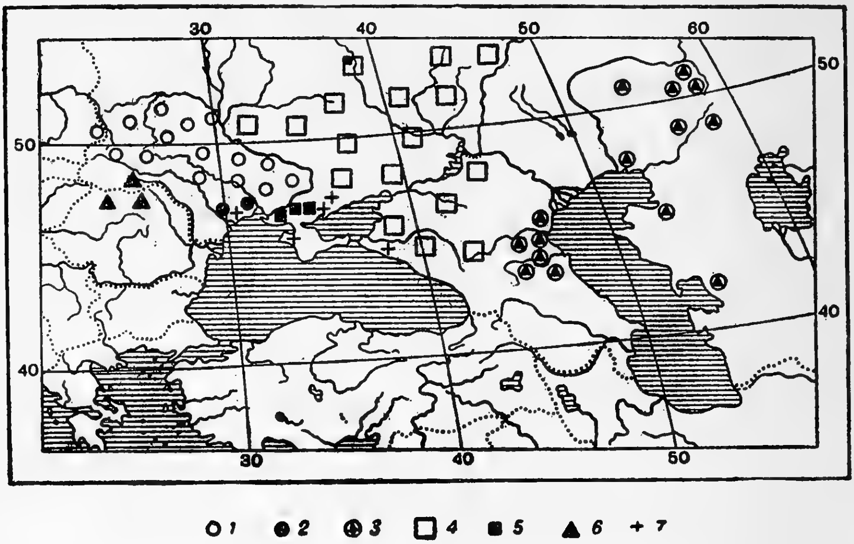

Figure 33. Distribution of species of the genus *Spalax*.

1—S. polonicus; 2—the same, Holocene*; 3—S. giganteus; 4—S. microphthalmus; 5—S. arenarius; 6—S. graecus; 7—S. minor.*

The distribution of the species of the western branch is restricted now to a small area of the lower Dnieper sand belt (left bank of the lower Dnieper, south of Kakhovka). Fossil remains of possibly closer species are known from the lower Anthropogene deposits of the village Tikhonovka (near Militopol') Zaporozh'e region, east of the present habitat of the species. The latter evidently points to a wider distribution in the past of mole rats of the given branch of the group giganteus. It should be noted that although representatives of the western branch have retained in their physiognomy various primitive features pointing to their phylogenetic link with *S. giganteus*, nevertheless in the course of subsequent evolution they have reached a considerably higher level of specialization than representatives of the eastern branch, thereby approaching, in this respect, the most highly organized species of this genus from the group *microphthalmus*. This, apparently, must serve as proof of a comparatively early separation of these branches, the roots of which pass to the end of the Pliocene era.

Of all the known mole rats of the genus *Spalax*, the most primitive physiognomy has been retained by representatives of the eastern branch of the giganteus group, i.e., the present-day giant mole rats. This species, in its level of specialization, is much inferior even to the comparatively primitive earliest representatives of the microphthalmus group like the late Pliocene *S. minor*. This, naturally, contradicts the suggestion of a comparatively early branching of the above-named groups of the genus *Spalax* (apparently beginning with the late Pliocene) and the relict nature of the present *S. giganteus* in the limits of their present-day distribution. It is known that the habitat of giant mole rats includes two areas isolated from each other, viz., eastern cis-Caucasus and the northern Caspian, and partly, the trans-Caspian east of the Ural River. In the lower Volga region and on the entire interfluve territory of the lower Volga and Ural Rivers, this species, like other representatives of the genus, is generally not found. Observations of V. S. Bazhanov (1930) and A. S. Stroganova (1954) on the presence of mole rats in the region of the Smolenka village, Pugachevskii region, based on the verbal information of collectors from local organizations for the procurement of wool, need additional proofs or confirmation. Thus, the distribution of the species is confined to the zone of stable changes in the course of the Late Pliocene and almost the entire Anthropogene of the ancient marine basins, preceding the present Caspian. It may be suggested that the isolating action of these basins in the course of various sections of the Late Pliocene and Early and Middle Anthropogene is the chief factor which, in the ultimate analysis, predetermined the present distribution of the species. Probably, the leading role in the separation of the western and eastern branches may have been played by the Manych Strait (Pidoplichko, 1951), the effect of which, as shown by the data of geologists, was apparently retained till the Pleistocene. It may also be assumed that the division of the habitat of the giant mole rat into two areas, observed in the present period, is, to a great extent, stipulated by the Pleistocene Khazar and subsequent Khvalin transgressions of the Caspian Sea. Before this, if we take into account the data of L. A. Vardanyants (1948), both the areas were undoubtedly linked, since in the early Quaternary period, in view of the contraction of the Caspian basin, the entire area in the limits of the present habitat of the giant mole rat from Dagestan to Emba was dry land.

Thus, if the eastern branch of the giganteus group, in view of the specific nature of the paleogeographical conditions of the past, remained insignificantly changed from at least the end of the Pliocene, then the western branch of this group in the course of Anthropogene evolved in the same direction as representatives of the microphthalmus group. This greatly facilitated the successful competition between them. Apparently, sandy mole rats were even more adaptive to the specific conditions of the sandy area of the lower Dnieper which greatly predetermined the conservation of this species in the limits of this area.

As mentioned above, the microphthalmus group includes, at the present stage of our knowledge, one fossil and three present-day species. Remains of the Late Pliocene *S. minor* are found throughout the deposits of the second half of the Upper Pliocene and partly the Lower Anthropogene along the length and breadth of the cis-Black and cis-Azov Sea parts of the USSR, including the Crimea, from the western state boundary in the east right up to the Taman Peninsula. Special attention should be paid to the fact that finds of remains of *S. minor* have been reported from the Crimea which documentally prove the existence of mole rats on the peninsula in the Late Pliocene. The latter is more interesting because in the Pleistocene and Holocene fauna (including present-day forms) of the Crimea, mole rats are apparently absent. The only (unfortunately unverified) mention of the discovery of *Spalax* remains of the Pleistocene age here in present times (Merezhkovskii, 1880), has not been confirmed by the research of Byalinitskii-Birulya (1930) and Gromov (1961) conducted on the massive paleontological material of the late Pleistocene and Holocene eras of the Crimea. Thus, the disappearance or, at least, a considerable reduction, in the population of mole rats in the Crimea in the course of the Middle and Late Anthropogene, should evidently be considered a secondary phenomenon. The reason for this probably lies in the substantial changes of paleogeographic conditions prevalent in the Crimea at the end of the Early, and the beginning of the Middle, Anthropogene. The causes stipulating these changes and their nature have not been explained thoroughly even to this date. It can only be suggested that they were associated with the intensification of tectonic disturbances in the Crimean hills, which ultimately led to the loss of land connecting the Crimea with adjoining areas of the cis-Black Sea and the cis-Azov Sea dry land. This, in turn, was accompanied by the emergence of new natural conditions, most unfavorable for the existence of these rodents. Soon afterwards (possibly at the end of the Pleistocene and Holocene) when natural conditions within the Crimean steppes appeared conducive again, the influence of the island's past isolation phase continued, apparently causing the retention of insurmountable barriers such as sea washes and edaphic factors linked to strong salinization and the formation of solonchaks in the isthmus of the earlier sea bottom.

In such a wide habitat, the remains of mole rats of the group *S. minor* are nevertheless practically undifferentiated, which apparently testifies to their affinity to a single species. Therefore, it may be assumed that the appearance of the present-day species grouped under microphthalmus group was prevalent only in the Anthropogene era. Evidently, these three present branches of the groups—*S. graecus*, *S. polonicus* and *S. microphthalmus*—were already formed at the end of the Early, and the beginning of the Middle, Anthropogene, since in the deposits of the upper strata of the Middle Anthropogene, one finds remains of fully differentiated forms which, from a species aspect, are possibly identical to present-day ones.

Today, the region of distribution of *S. graecus* encompasses a small area of the Soviet Bukovina and the adjacent regions of Rumania; that of *S. polonicus*, the extreme southeast Poland, the entire right bank portion of the Ukraine, except the northernmost parts of its territory occupied by *S. graecus* and *S. leucodon*[1] and finally, *S. microphthalmus* occupies the entire area of the interfluve of the Dnieper and Volga (except the lower Volga) reaching in the north up to Kiev, southern parts of the Chernigov region, eastern parts of the Kursk and Orlov regions, southern districts of the Tula and Tambov regions, Mordov ASSR and the Ul'yanov region (fossil Holocene remains have also been found in the southern parts of the Gorkii region), and in the south along the Kakhovka-Azov coast to the Krasnodar and Stavropol areas. The area of the species encompasses mostly the steppe zone and forest steppes penetrating in strips into the forest zone. Major factors greatly predetermining the present habitation of mole rats of the microphthalmus group and its evolution as an independent species are, apparently, insurmountable barriers in the form of fresh-water aquatoria in the limits of Pradnester and the middle Dnieper, existing here in the course of almost the entire Early and Middle Anthropogene. The presence of a fresh-water lake or group of lakes in the Pleistocene on the territory of the entire present middle Dnieper has been quite correctly established by geological studies (Pidoplichko, 1956). At this time, the role of insurmountable barriers in the distribution of the above enumerated species is played by the present valleys of Dnestr for *S. graecus* and *S. polonicus*, and that of Dnieper for the latter and *S. microphthalmus*. Of present-day representatives of the microphthalmus group, apparently the most ancient branch, is *S. graecus* which, to a great extent, has retained in its physiognomy the primitive features bringing it closer to the Late Pliocene-Early Anthropogene *S. minor*.

Thus, based on the above historical geographic account of the distribution of mole rats in the world, we cannot accept the migrational concept put forth by Mehely (1909) and accepted further without any revision by S. I. Ognev (1940, 1947). It concludes exclusively North African and possibly Asian origin for the entire group with subsequent habitation by

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[1] It should be *M. leucodon*—Editor.

its individual representatives on the territory of Europe and Asia, occupied by the family at present. Also paleontological data do not correspond to the hypothesis of the penetration of mole rats into Europe through the Caucasus range. There are contradictions (only for representatives of the family *Spalacidae*) in the Iranian course of penetration (Menzbir, 1934).

AN OUTLINE OF THE PHYLOGENY AND GEOLOGICAL HISTORY OF MOLE RATS. IMPORTANCE OF THE REMAINS OF SPALACIDAE FOR A STRATIGRAPHIC DESCRIPTION OF NEOCENE AND ANTHROPOGENE CONTINENTAL DEPOSITS OF EUROPE

The phylogenetic links of the family Spalacidae have not been firmly established in view of the high level of specialization of its representatives. The only dependable criterion for establishing the similarity could be studied in the field of teeth development since the establishment of other such structures in the skull and skeleton inherent in mole rats in the course of evolution proceeded only for the specialized group. Consequently, in most primitive representatives of the family, closer to the ancestral forms, these features must be in the initial stage of development. This, naturally, to a great degree complicates the elucidation of these features with the help of usual morphometric methods. With regard to the origin of mole rats, the opinion of Stehlin and Schaub (1951) and Schaub (1958) may be considered the most acceptable viewpoint to this date. It holds that Spalacidae, like the closely related family Rhizomyidae, originate from the general root which separated somewhere in the Eocene from the primitive Cricetidae, for which the pterydomidal plan of structure of permanent molars was typical. The Miocene Anomalomyinae should apparently be considered as forms of hamster-like rodents, if not as being first in relation to mole rats and Rhizomyidae, then at least as being closely related to the latter. The structure of the permanent molars in this group of hamster-like rodents is characterized by extreme similarities with primitive representatives of Spalacidae (sub-family Prospalacinae) and with the most ancient specimens of present-day mole rats. In fact, the differences in them almost exclusively lead to the complicated structure of M^2 and M_1 to M_2 in Anomalomyinae (Figure 34). Moreover, as shown by Petter (1961), significant similarities with original mole rats are found in the permanent molars of the relict group of Madagascar hamsters of the subfamily Nesomyinae, which are close to Anomalomyinae. Besides similarity in the structure of permanent molars, Anomalomyinae are characterized by a longitudinal ridge of enamel on the lower incisors. Such formations have been retained on similar teeth in Prospalacinae and the most primitive representatives of the subfamily of present-day mole rats.

Between the two viewpoints on the origin of Spalacidae, the hypothesis of Winge (1887) is worthy of consideration. It brings mole rats closer to the jerboa (Dipodidae). At first glance this closeness would seem to be proof enough. Particularly, besides the fact that representatives of both families have permanent molars with a pterydomidal plan, the primitive mole rats of the subfamily Prospalacinae are characterized also by the presence of a closed sub-occipital canal in the skull which is inherent in a number of contemporary Palearctic Myoidea jerboas. However, if we consider that hamsters separated from the general stem of Dipodidae and the branch of mole rats, and Rhizomyidae in turn take their start from the most ancient Cricetidae, then we can rightly assume that the latter must still retain the sub-occipital canal lost by representatives of this family in the subsequent period. Consequently, this hypothesis could also serve as an addendum to the earlier referred viewpoints of Stehlin and Schaub throwing light on the peculiarities of structure of the original group for Spalacidae.

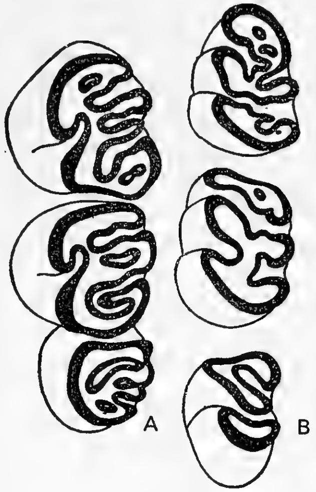

Figure 34. *A*—upper and *B*—lower rows of permanent molars of *Anomalomys gaudryi* Teillard (by Grasse, 1955).

The family of bamboo rats, Rhizomyidae, is close to mole rats. Both families apparently originate from common ancestors. A proof of this could be the considerable similarity in the structure of the lower jaw of the Oligocene Rhizomyidae, Rhizospalacidae (genus *Rhizospalax* Miller and Gidley), and primitive mole rats of the subfamily Prospalacinae. As shown above (page 66), in Prospalacinae the lower jaw in a sense has retained the Rhizomyidal plan of structure (Figure 40). There is no single opinion on the systematic position and phylogenetic links of the Oligocene Rhizospalacidae in current literature. It is known that the genus *Rhizospalax* was described by Miller and Gidley (1919) from the late Oligocene of France. These authors have absolutely correctly noted the general similarity of the lower jaw of *Rhizospalax* with the same in Rhizomyidae, particularly in *Tachyoryctes*, simultaneously viewing similarities with mole rats in respect to peculiarities of structure of the permanent molars. The latter conclusion is highly risky since the remains of the skull and the lower jaw at the disposal of these investigators belonged to old animals whose teeth were in that stage of rubbing when rubbed surfaces in all Myoidea acquire outlines similar in structure to the permanent molars of the Rhizomyidal plan. Attempts to explain identical features and differences between *Rhizospalax* and bamboo rats on the one hand, and mole rats on the other, in the structure of the retained portion of the hard palate, at present also calls for doubt since in the structure of this section, as shown by an examination of a series of skulls in Spalacidae and Rhizomyidae, no clear differences have been exhibited. However, we may agree in principle with the interpretation of the systematic position and phylogenetic links of *Rhizospalax* given by the above authors. If in his earlier work, Miller (1918) erroneously brought *Rhizospalax* close to the Spalacinae (subfamily according to Tullberg's system followed by the above authors), then later he refrained from similar interpretations by suggesting that these Oligocene rodents could be identified as an independent subfamily related to Rhizomyidae (Miller and Gidley, 1919). Somewhat later, Stehlin (1923) fully subscribed to this opinion. He significantly revised the description of the genus based on newer material. Like earlier authors, while correctly noting the Rhizomyidal structure of the lower jaw in genera of *Rhizospalax*, Stehlin gave, however, an absolutely unreliable viewpoint, on the structure of the permanent molars in this group of Oligocene rodents, by relating the structural characteristics of these teeth (without justification) of Oligocene Rhizospalacidae to the similar ones in mole rats. As opposed to Miller and Gidley who had only highly rubbed out permanent molars of *Rhizospalax* Stehlin had a small series of teeth more or less reflecting all the major stages of rubbing. This material has been pretty well described by him (1923). The data permits us to conclude that the Oligocene *Rhizospalax*, like Rhizomyidae, were characterized by well-expressed folded structures in the initial stages of rubbing of the permanent molars; at the same time, in mole rats, including highly specialized forms, the tubercular structure is more expressed on evenly rubbed teeth. Thus, molars in *Rhizospalax* are at a higher stage of specialization than in all the later fossil and present-day spalacidae, although more primitive than in fossil and living Rhizomyidae. Therefore, we do not see any contradiction in bringing Oligocene Rhizospalacidae close to bamboo rats, and feel that the schemes suggested by Simpson (1945) and Schaub (1955) are fully justified. These schemes view the rodents in question as belonging to the family of bamboo rats. True, it is quite likely that in future, with the availability of new material, these rodents may have to be separated into a special subfamily of ancient Rhizomyids—Rhizospalacinae—as suggested by Miller and Gidley.

As noted above, considerable similarities with Rhizomyidae, especially with ancient Oligocene Rhizospalacidae, are found in the structure of the lower jaw of primitive mole rats from the subfamily Prospalacinae. Therefore, it may be suggested that the ancestral form of Spalacidae should apparently be searched among the given group of Oligocene rodents. The latter does not at all mean that we consider this form as the only one known at present, as representatives of Rhizospalacidae, genus *Rhizospalax*, since its permanent molars are at a considerably higher level of specialization than even in the most specialized mole rats. At the same time, it is quite likely that types, as yet unknown, representative of this group of rodents, which retained the primitive plan of structure of the permanent molars, can give rise to the subfamily of ancient mole rats which, in turn, became ancestors to the highly specialized present-day mole rats. Thus, the phylogenetic links of Spalacidae with some other families of rodents belonging to the group Myoidea are seen by us in the form of a scheme presented in Figure 35. According to this scheme, the separation of the group Spalacidae from the genera stem occurs in the Middle Oligocene, since by the end of this era there already existed representatives of Rhizospalacidae with a degree of specialization of molars higher than that conditional level which had to be present in the suggested ancestors of mole rats.

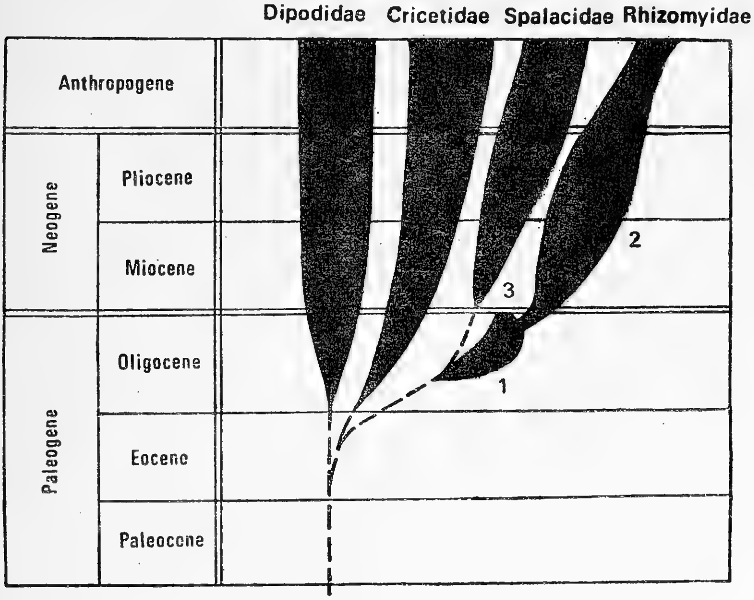

Figure 35. A scheme of phylogenetic relationships of Spalacidae.

1—Rhizospalacinae; *2*—Rhizomyinae; *3*—*Rhizospalax.*

As for the phylogenetic relationships of various groups of mole rats within a family, the scheme suggested by Mehely (1909), somewhat supplemented and corrected by S. I. Ognev (1940), and to a lesser extent the scheme of E. G. Reshetnik (1941), are the most popular ones in literature.

The real drawback in both systems is that they do not take the geologic factor into account at all. Moreover, the phylogenetic structure is based almost exclusively on a study of morphological peculiarities and the distribution of the present representatives of the family, without due consideration for paleontological material (Mehely, 1909; Ognev, 1940, 1947). In such cases when paleontological material was used to explain the affinity of various groups within the family (Reshetnik 1941), it was done without due interpretation and revision of the systematic position of fossil forms, in view of which the suggested scheme contains various serious factual inaccuracies.

The Mehely-Ognev scheme reflects in general the level of knowledge during their time. It includes major trends in the evolution of the family, although the interpretation of position in the system and affinity links of some taxa is highly disputable. However, if we discard the migrational hypothesis of the above authors, which in the light of the present level of knowledge of the paleogeography of the Mediterranean and Pontiac Caspian in the Neogene and Anthropogene is highly unacceptable, then the above scheme clearly defines two major lines of development in present-day mole rats corresponding to the genera *Microspalax* (subgenus *Mesospalax*) and *Spalax* (Figure 36). It has been very correctly pointed out that both branches take their start from the most primitive representatives of present mole rats, combining the Nominal subgenus of the genus *Microspalax*. However, an examination of the present-day *M. ehrenbergi* as a direct ancestor of *Mesospalax* and *Spalax* is justifiable doubtfully at

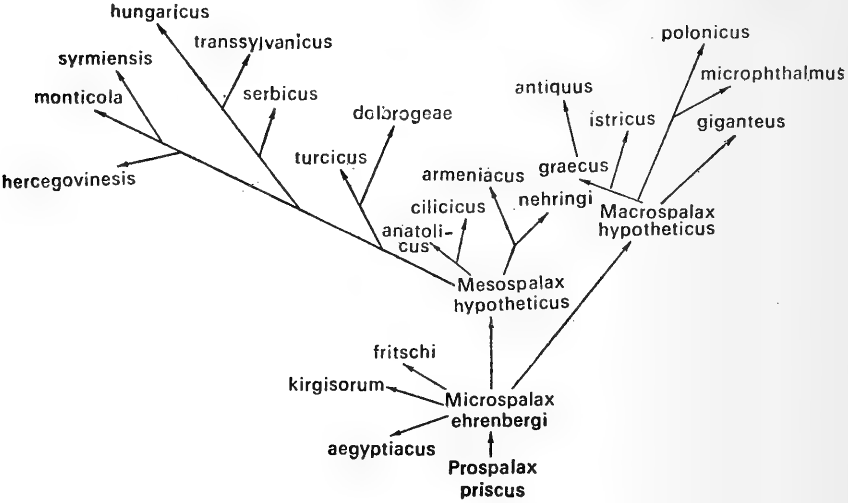

Figure 36. A scheme of phylogenetic relationships within the family Spalacidae (by Mehely, 1909).

this time. In our opinion, the most conspicuous drawback to the scheme is an attempt to derive present-day subspecies from other similar present-day forms. In addition, the number of the latter is unjustifiably high (see page 6). The substantial effect of the phylogenetic scheme of Mehely-Ognev is also an attempt to view the highly specialized *P. priscus* as direct ancestors of all living mole rats, though the phylogenetic link of the subfamily of ancient mole rats to which *P. priscus* and present-day mole rats belong, has been correctly noted in general.

The following inaccuracies are brought forward in the phylogenetic scheme suggested by Reshetnik (1941) (Figure 37).

1. The genus *Rhizospalax* should not be considered as a general ancestor of Rhizomyids and mole rats (pages 113–14).

2. The phylogenetic series *Miospalax*[1] Stromer—*Prospalax priscus*—

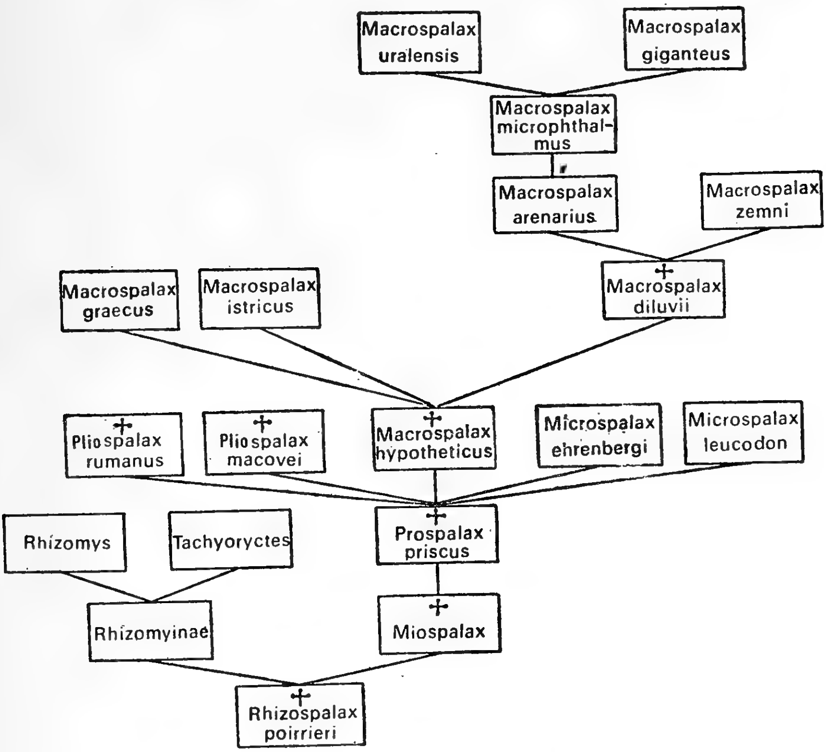

Figure 37. A scheme of phylogenetic relationships within the family Spalacidae (by Reshetnik, 1941).

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[1] *Nomen praeoccupatum* in relation to the generic group of zukors *Myospalax* Laxmann, 1769.

Macrospalax (= *Spalax* sen. str.) is artificial. Investigations show that *Miospalax monacensis* Stromer from the Late Miocene of Bavaria, in its general plan of structure of the upper permanent molars, is closest to the fossil hamsters of the subfamily Anomalomyinae and, most probably, must be considered as a part of the latter. The differences between the most specialized representatives of the subfamily of present mole rats forming genus *Spalax* and ancient mole rats are so great that it is difficult to visualize the direct ancestral link of the former with the latter, bypassing the intermediate group such as representatives of the Nominal subgenus of the genus *Microspalax* and especially its Miopliocene representatives with regard to the structure of the skull, the permanent molars, and the bones of limbs which exhibit similarity with *Spalax*.

3. The inclusion of *P. rumanus* in the genus *Pliospalax* (one of the synonyms for *Microspalax*) is based on the nomenclatural confusion associated with an incorrect translation of the paper written by Kormos (1932) which described the genus *Pliospalax* (details on page 203). In fact this species should be considered under the genus *Prospalax*.

4. The phylogenetic links within the genus *Spalax* do not correspond to reality since the level of specialization of individual species has been ascertained arbitrarily. In addition, the reasons are not absolutely clear as to why it was necessary for this author to conclude the phylogenetic series of forms of the genus *Spalax* with giant mole rats standing, as will be shown later on, at a lower level of specialization, based on the whole group of features, than *S. microphthalmus*, which is considered as a direct ancestor of *S. giganteus*. It is also not clear why the Bukovin mole rat (*S. graecus*) has been identified in an independent evolutionary line.

Thus, the above phylogenetic relationships appear mostly obsolete today. More so because, in recent years, significant new paleontological material has accumulated which can throw some light on the different stages of evolution within the family. Admittedly, this material is far from complete. Furthermore, we are deprived of exhaustive paleontological documentation characterizing the stage of separation of branches of ancient and present-day mole rats. Besides, any paleontological indications whatsoever of the time of emergence of the ancestors of the group of specialized forms of the genus *Microspalax* (subgenus *Mesospalax*) are totally absent. However, a comparative analysis of morphological features and the distribution of fossil and living mole rats permits us to identify series of branches combining forms with close adaptive characteristics and to identify various groups as independent subfamilies, genera, and subgenera. In our opinion, the scheme suggested below (Figure 38) reflects more reliably the trends in the evolution of the family and the phylogenetic links of subfamilies, genera, subgenera, and in some cases, even species and, consequently, may serve as the foundation for the classification of Spalacidae described in this book.

The fossil subfamily of ancient mole rats—Prospalacinae—is the most primitive and apparently the oldest group among Spalacidae. As has been repeatedly pointed out in the preceding sections of this book, the representatives of Prospalacinae with regard to the structure of the lower jaw have, to a great extent, retained the features of Rhizomyidae to the fossil Oligocene Rhizospalacinae. Among the features characteristic of Rhizomyidae, mention must be made first of the position of the angular process of the lower jaw in relation to the articular and alveolar ones, the comparatively lesser height of the latter, and also the clearly expressed ridge of the lower masseter plate in ancient mole rats. In addition, the facial portion of the skull of ancient mole rats, in general, acquired an outline, inherent in representatives of the family Spalacidae. Substantial features make it possible to readily differentiate the ancient mole rats from Rhizomyids: the presence in the former of a low, wide rostral section of the

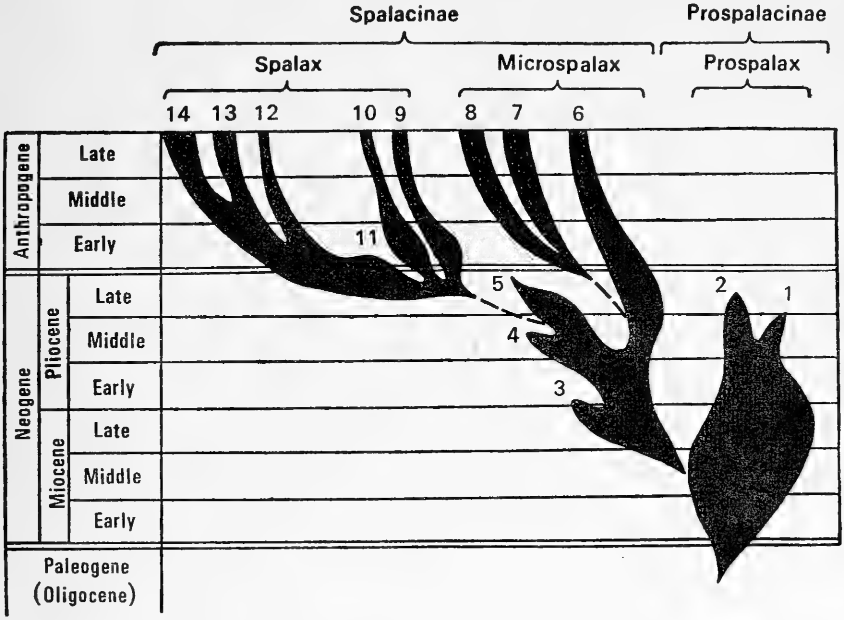

Figure 38. A scheme of phylogenetic relationships within the family Spalacidae.

1—Prospalax rumanus Sim.; *2—P. priscus* (Nehr.); *3—Microspalax compositodontus* sp. nov.; *4—M. macoveii* (Sim.); *5—M. odessanus* sp. nov.; *6—M. ehrenbergi* (Nehr.); *7—M. nehringi* (Sat.); *8—M. leucodon* (Nord.); *9—Spalax giganteus* Nehr. *10—S. arenarius* Resh.; *11—S. minor* W. Top.; *12—S. graecus* Nehr.; *13—S. polonicus* Meh.; *14—S. microphthalmus* Güld.

skull, the width of which considerably exceeds its least height; an elongation and contraction of the nasal bones; a large, comparatively narrow suboccipital cavity, the greatest diameter of which is roughly equal to the length of the two anterior permanent molars; a low placed, in relation to the teeth-rows, zygomatic arch base; incisor cavities shifted backward; a shortened masseter plate of the skull located almost in a horizontal plane, the anterior borders of which, furthermore, do not reach the sutures between the premandibular and mandibular bones, and their lengths being less than the same in M^1 to M^2; a highly deviated backward articular process of the lower jaw, the longitudinal axis of which agrees roughly with the same of the horizontal branch, and the more expressed tubercular plan of structure of the upper and lower permanent molars. Thus, there is no doubt that the subfamily of ancient mole rats is a connecting link between the highly specialized present-day mole rats and the ancestral group of ancient Rhizomyids—the Oligocene Rhizospalacinae.

Unfortunately, the fossil Prospalacinae is presently known only from the remains of comparatively later representatives, *P. priscus* (end of the Middle and first half of Late Pliocene) and *P. rumanus* (Middle Pliocene) with features of high specialization in the structure of the permanent molars. In particular, the molars of the aforementioned forms are even simpler than in the most ancient of the present mole rats of the Miopliocene group, i.e., *compositodontus* mole rats from the Nominal subgenus of the genus *Microspalax*. Therefore, it is quite natural that the above noted species cannot be considered as most primitive among Spalacinae. This is contradicted also by the fact of finding remains of present-day mole rats in deposits older than those in which the remains of *P. rumanus* and *P. priscus* have been found. Thus, remains of the primitive *M. compositodontus* were excavated from the strata of the Upper Miocene (Meotes) of the northwest cis-Black Sea region of the Ukraine SSR. Consequently, the roots of the subfamily Spalacinae, combining the most highly specialized forms of mole rats, apparently pass still deeper in the depths of the upper portion of the Middle Miocene, and the initial forms for the present-day mole rat group from the subfamily Prospalacinae should most probably be searched among the Middle Miocene species which are more primitive than the ones known at present (*P. rumanus* and *P. priscus*). Their remains have not yet been found due primarily to a far too incomplete study of Miocene rodents in general.

Among Spalacinae, the mole rats of the genus *Microspalax* form the most primitive group. The most ancient representatives of living mole rats, i.e., species of the subgenus *Microspalax*, also belong to this genus. The latter is represented mostly by fossil forms, remains of which are found in deposits starting from the Upper Miocene to the Upper Pliocene inclusively, and also the only present-day representative of Asia Minor and

North Africa, *M. ehrenbergi*, whose relict nature at present is undisputed. In one of the preceding sections (page 64) we have discussed the major adaptive changes of the skull and the skeleton in the evolution of mole rats. It was shown that the leading trend in the evolution of the family was the specialization to search of food underground and the multifarious adaptations to burrowing and feeding. If we examine representatives of the subgenus *Microspalax* from this aspect, then to the number of features pointing to a primitive organization of the latter, we must add first of all the following features: very weakly developed sagittal and lambdoid crest of the skull, relatively wide parietal bones (a feature correlating with the degree of development of the sagittal ridge), a very sunken occipital bone, shortened upper and lower diastemata, considerable isolation of the angular process of the lower jaw, the comparatively small height of its alveolar process, the contraction of lower and upper incisors, and the most complicated permanent molars, the roots of which, furthermore, are the least reduced among all of the present-day mole rats. To the number of primitive features we should also add the presence of three longitudinal ridges on the lower incisors in representatives of the given subgenus. This peculiarity of structure has so far not been subjected to functional analysis and apparently relates to features inherited by representatives of the subgenus *Microspalax* from their direct ancestors, the extinct Prospalacinae. Thus, mole rats of the subgenus *Microspalax*, based on the series of indices enumerated above, are precisely that link which connects the extinct primitive Prospalacinae with the more highly specialized representatives of Spalacinae of the subgenus *Mesospalax* on one hand, and the most highly organized among present mole rats, the genus *Spalax* on the other.

The phylogenetic links of the different species of the subgenus *Microspalax*, considering their level of specialization, can be viewed in the following manner. The most primitive group in the subgenus most probably constitutes the late Miocene European *compositodontus* mole rats, namely the cis-Black Sea *M. compositodontus*. The name is derived from the complexity of their permanent molars, primarily because the upper and lower front ones still retain a free mesocone on M^1 and a mesoconid M_1. In addition, molars of the enumerated species as compared to the Middle and Late Pliocene *Microspalax* are characterized by great isolation, next to the paracone on the upper and the entoconid on the lower front permanent molars, a less reduced M^3, and also by less reduced roots. The Late Miocene *compositodontus* mole rat, in all probability, is the earliest group in relation to all the remaining European fossil *Microspalax*. It is most likely that in the evolutionary process of the subgenus, there was even a direct phylogenetic series of *M. compositodontus*—*M. macoveii*—a form close to *M. odessanus*, since in this species a constant increase in adaptation to burrowing and feeding is demonstrated in the structure of the masticatory apparatus. Moreover, in the degree of specialization of incisors *M. compositodontus* considerably excels the living *M. ehrenbergi* which naturally complicates conclusions about their direct ancestral link.

A further stage in the evolution of the group is represented by the Mid-Pliocene species *M. macoveii* and *M. odessanus*. The structure of their permanent molars illustrates most clearly the tendency during evolution as indicated earlier toward simplification in the structure of their grinding surfaces. Thus, both species, as distinct from the late Middle Miocene *compositodontus* mole rats, have already totally lost the mesocone on M^1, having retained a mesoconid on the front lower permanent molar in the initial and partly in the middle stages of wearing off (*M. macoveii*) or only in the very vestigial stage (*M. odessanus*). Thus *M. macoveii* is still characterized by a comparatively larger mesoconid on M_1, and in *M. odessanus*, the same is usually found only in a vestigial state or is even totally absent. Further, if the entoconid on M_1 in Late Miocene *compositodontus* mole rats is not fused with the posterior collar until after maturity, then in *M. macoveii* these loops are fused already in the initial stages of tooth wearing in adults, and in *M. odessanus* the free entoconid is generally observed only in very young specimens. In addition to the foregoing primitive peculiarities in the structure of permanent molars, *M. macoveii* also has various other features of a comparatively primitive organization. Mention must first be made of the presence of a relatively short diastema on the lower jaw of this species, a shortened symphytic tubercle, a well-expressed jaw angle, and a highly deviated, downward and sharply demarcated angular process. Moreover, as far as the specialization of incisors is concerned *M. macoveii* surpasses all the presently known species of the subgenus *Microspalax*. This makes it impossible to consider it as a direct ancestor of the later *M. odessanus*, not to speak of the present-day *M. ehrenbergi*.

M. odessanus should be considered as the most highly specialized representative of the subgenus *Microspalax*. Its remains have been excavated from deposits of the uppermost middle and lower depths of the Upper Pliocene. In addition to the characteristics already mentioned in the structure of permanent molars, a considerable widening of the skull in the region of the incisors and the entire rostrum as a whole, the absence of a longitudinal slit-like cavity on the nasal bones, the straight line of the forehead—nasal and forehead, jaw sutures, and a relatively high and thick horizontal branch of the lower jaw—are characteristics of this species. The upper and lower incisors, although not as widened as in *M. macoveii*, nevertheless demonstrate a very high level of specialization. Moreover, the species has retained the whole range of primitive characteristics in the structure of the skull and the lower jaw. Furthermore, except for features determining its subgenus affinity, the lower jaw of *M. odessanus* has still retained many structural characteristics bringing it close to *M. macoveii*, although they are expressed to a lesser degree in the latter (sharp demarcation of symphytic tubercle, well-expressed jaw angle, considerable separation of the angular process). It must be emphasized that despite the retention of a series of primitive features in the structure of the skull and the lower jaw, the *odessanus* mole rats, in their degree of development of burrowing adaptations, stand at a higher level than even some primitive members of the subgenus *Mesospalax*, particularly *M. nehringi*, not to speak of the recent *M. ehrenbergi*. This is equally true in respect of the above discussed facts relating to *M. macoveii*, and they totally exclude the possibility of viewing the group of Middle Pliocene European *Microspalax* as ancestral in relation to *Mesospalax*. Moreover, this group is apparently ancestral in relation to the most highly specialized representative of the subfamily of present-day mole rats of the genus *Spalax*. A proof of this could be the considerable similarity between the listed groups in individual details of structure for skulls and bones of limbs (shortened non-branched portion of the sagittal ridge, indistinct posterior palatine pits in the hard plate, and others) expressed more strongly than, for example, between *Spalax* and *Mesospalax*. Moreover, very primitive representatives of the genus *Spalax*, for instance from the group of giant mole rats, have retained in their organization other features of similarity with *Microspalax*. Thus, in *S. giganteus* the upper and lower diastemata are very short, the incisors are narrower than in the most highly specialized *Mesospalax*. Furthermore, the lower jaw in this species, as also in representatives of the subgenus *Microspalax*, has retained an alveolar process which in its height is only just equal to the articular one.

Among the species of the subgenus *Microspalax*, living representatives and the North African *M. ehrenbergi* have a special place. Together with features of higher evolutionary status (relatively longer sagittal ridge of the skull, smooth symphytic tubercle and jaw angle of lower jaw, separation of its angular process less expressed as compared to the Middle Pliocene *Microspalax*.), this species has retained many primitive features found in a lower level of specialization than in the Middle Pliocene and, in some cases, even in Late Miocene representatives of the given subgenus. In addition, the Ehrenberg mole rats are the only representatives of the subgenus that have retained longitudinal ridges not only on the lower but also on the upper incisors. Moreover, the species is characterized by the narrowest incisors among representatives of present-day mole rats. In the degree of complexity of permanent molars, *M. ehrenbergi* occupies an intermediate place between the Late Miocene *compositodontus* mole rats and the Middle Pliocene *M. macoveii* on the one hand and *M. odessanus* on the other. Thus, despite the fact that the front upper and lower permanent molars have already lost the mesocone and mesoconid respectively, the entoconid on M_1 remains unfused with the posterior collar in later stages of wearing than in the Pliocene Odessa mole rats. Considering what has been said above and also such an important factor as the present distribution of the species, it may be concluded that *M. ehrenbergi* is, apparently, a special Afro-Asian branch of the subgenus separating equally from the general stem of *Microspalax.* Considering that in the Middle Pliocene of Europe there were already species which stood at a higher level of specialization than the present *M. ehrenbergi* with regard to a series of features, we have to obviously assume that the separation of the Afro-Asian and European branches of *Microspalax* took place somewhere in the beginning of the Pliocene. Quite likely, a specific disjunctive role was played in this case by the transgression of the Pontiac basin.

At present, there are many inaccuracies in the knowledge of the origin of mole rats of the subgenus *Mesospalax.* This is first of all linked to the inadequacies of paleontological documentation due to a poor study of the territory of Asia Minor and the Balkans in this respect. This group most probably has an Asia Minor–Balkan origin. Results of comparative anatomical studies on the skull and the lower jaw in present-day species —*M. nehringi* and *M. leucodon*—point immediately to the phylogenetic link of this group with the Afro-Asian branch of *Microspalax.* Furthermore, the most primitive representative of the subgenus *Mesospalax*, the Asia Minor *M. nehringi*, has mostly retained even now features similar to *Microspalax* (the presence of slit-like cavities on the nasal bones, a relatively narrower rostral section of the skull, contracted upper and lower incisors). The proof of a closer relationship between the above listed groups lies apparently in the fact that the specialization of the skull in *Mesospalax*, and equally in the Afro-Asian *Microspalax*, as distinct from the European fossil *Microspalax* and *Spalax*, proceeded in the direction of an increase in overall length of the unbranched part of the sagittal ridge. In the more highly specialized European *Mesospalax* (*M. leucodon*) similarity of features with the initial type has been lost to a great extent. Here, the differences reach a maximum in the easternmost Nominal subspecies *M. l. leucodon*, while the Balkan form, *M. l. monticola*, mostly retains features similar to *M. nehringi*, being, as it were, the connecting link between the latter and *M. l. leucodon*. This apparently also points to the close relationship between the Asia Minor *M. nehringi* and the European *M. leucodon*. The period of separation of the Asia Minor and the European branches of *Mesospalax* has not been established finally. It may be assumed that the disjunction of the above species in the region of the Aegean land took place for the second time somewhere on the border between the Pliocene and Anthropogene.

It was noted above that the most probable ancestral group in relation to the genus *Spalax*, combining the most highly specialized representatives of the subfamily of present-day mole rats, is the Middle Pliocene European *Microspalax*. These mole rats have mostly an East European distribution and origin, only partly entering the North Caspian east of the Ural River and the trans-Caspian. Precisely, the area of evolution of the genus was parts of the Caspian land. Reliable remains of representatives of the genus *Spalax* are known at present, beginning from the second half of the Late Pliocene in the limits of the cis-Black Sea and cis-Azov Ukraine and Taman. However, these remains belong to species standing at a higher level of specialization than, for example, the present *S. giganteus*. Consequently, roots of the group probably pass still deeper toward the beginning of the Late, and the end of the Middle Pliocene.

Of the number of species of *Spalax* known presently, the most primitive facial outline is retained by the living giant mole rat. In the structure of its masticatory apparatus, it shows many features similar to the European Pliocene *Microspalax*. This species is characterized in particular by the presence of relatively shorter upper and lower diastemata, shortened incisors, and a lower alveolar process in the lower jaw. All this makes it possible to assume the comparatively earlier separation of the eastern branch of the genus, the group of giant mole rats, from the western branch to which we relate *S. Microphthalmus* and forms close to it. Most probably the roots of this group pass to the beginning of the Late Pliocene, and the retention of such primitive representatives as *S. giganteus* up to the present time is apparently explained by the isolating influence of the Manych Strait which existed since the Late Pliocene and possibly up to the Pleistocene inclusively.

In the other representatives of the group of giant mole rats, the present-day *S. arenarius*, the primitive features in the structure of the masticatory apparatus which brought mole rats of this group closer to the ancestral forms have been almost completely lost. The individual features of organization retained were only in the structure of the rostral section of the skull and partly the permanent molars. It may be suggested that the ancestral forms of this branch of giant mole rats, being isolated by the Manych Strait from the Caspian branch ancestral to *S. giganteus*, developed under conditions of the northeast Black Sea region in the same direction as mole rats of the *microphthalmus* group. Documentarily, the roots of the group of the above-mentioned mole rats are traced from the present time to the beginning of the Anthropogene inclusively. For example, in the lower Anthropogene deposits of the village Tikhonovka, Zaporozh'e region, remains of the species have been found which are very much closer to the now living *S. arenarius*.

Among the most highly specialized mole rats of the *microphthalmus* group, the most ancient and apparently primitive form, *S. minor*, is from the Late Pliocene of the north Black and Azov Sea. The present-day *S. graecus* has retained a number of features similar to it. This species has most probably retained to a considerable extent the facial outline of the form ancestral to more highly specialized forms of Middle and Late Anthropogene, including the present ones, *S. microphthalmus* and *S. polonicus*. As for the latter, their differentiation, considering the very small range of differences, took place somewhere on the border of the Early and Middle Anthropogene. In any case, in the Late Pleistocene the complete differentiation of the above-listed forms of present times has been confirmed documentarily by paleontological data.

In conclusion, the author feels it expedient to present a brief outline of the geological history of mole rats against the background of the development of faunal complexes of mammals, mostly smaller ones, the remains of which are most suitable for the purpose of bio-stratigraphy and paleogeography on the territory of Eastern Europe. Similar data, it appears to us, is not only of theoretical interest but also has a particular practical importance since it forms a suitable basis for a stratigraphic delineation of the remains of mole rats found in continental deposits of Neogene and Anthropogene, and their corresponding correlation within the limits of geographically remote areas.

It was noted above that the most primitive and apparently the most ancient group of mole rats combined in the subfamily Prospalacinae is presently known only from the comparatively late highly specialized representatives, *P. rumanus* and *P. priscus*. The remains of the former have been found in Middle Pliocene deposits of the Kuchurgan valley (Ukraine SSR, Odessa region) and territorially adjacent deposits of Rumania of the same age (the well-known Malushteni Kovurlui region, right bank of the Prut River and its lower reaches). In both places remains of mammals jointly constituting the so-called Kuchurgan Middle Pliocene faunal complex whose analogue in western Europe is the Middle Pliocene Russilion fauna of France, were likewise found. The following are the characteristics of the Middle Pliocene fauna of smaller mammals of the northwest Black Sea region:

1. Qualitative predominance of remains of rabbit-like animals over rodents.

2. Archaic rabbit-like fauna on the whole (rabbits being represented by genera *Alilepus* Dice and *Pliopentalagus* Gureev and Konkova; and pica of the genera *Prolagus* Pomel, *Proochotona* Chomenko, and the most ancient representatives of the genus *Ochotona* Link—*O. antiqua* Pidopl.).

3. Presence of beavers of the genus *Steneofiber* Geoffroy and *Promimomys-Dolomys* complex of a species of Rhizomyid field rats. The latter are represented in the Kuchurgan fauna by species *Promimomys moldavicus* (Kormos) and *Dolomys* aff. *milleri*. Nehr.

4. Absence of Rhizomyid cementodontus field rats of the genus *Mimomys* F. Major.

In deposits of this type, remains of *P. rumanus* have been found along with Middle Pliocene mole rats of the genus *Microspalax—M. macoveii.* Considering the above-noted distribution of the finds of *P. rumanus,* we may assume the specificity of the given species for deposits of the Kuchurgan stage.

P. priscus was apparently distributed over a wider time interval than *P. rumanus* within the area adjacent to the USSR, i.e., the countries of western Europe. Presently, its remains are known from various locations in Rumania (Beralt Kepeni, Transylvania), Hungary (Beremend, areas 4, 5, 7; Charnota, areas 1 to 3; Nadkhoroshan, area 1; and Villan, areas 3, 5, 11—all in south Hungary, Villan Hills, and also Kishlanga), Poland (Venzhe, area 1; Rembelitsy Krulevskie), and Czechoslovakia (Ivanovsky, near Trenchina, Slovakia). The geological age of most of the above-noted locations has been determined as Astian and Willifrank which most probably correspond to different time sections of the Middle and Late Pliocene in our interpretation. The Kuchurgan fauna of Chernotana, Hungary is closest. Thus, according to the data of Kretzoi (1956), in its composition *P. priscus* also follows *Promimomys* and *Dolomys* groups—*P. moldavicus, D. milleri, D. hungaricus* Kormos. Moreover, the fauna is widely represented by folded-toothed hamster-like rodents belonging to the genus *Baranomys* Kormos. All this allows us to place, with a high degree of probability, the Chernotana deposits parallel to deposits of the Kuchurgan Shield (Topachevskii, 1965). The later, i.e., Willifrank, stage of development is represented by the fauna of Beremend (areas 5, 7), Nadkhoroshan (area 1), Villan (areas 3 and, probably 5 and 11) where the remains of *P. priscus* are found along with cementodontus Rhizomyid field rats of the genera *Mimomys* and *Kislangia* Kretzoi—*M. pliocaenicus, F. Major, M. fejervaryi* Kormos, *M. pusillus* Mehely, *M. newtoni* F. Major, *K. rex* (Kormos) and Rhizomyid noncementodontus ones, *Villanyia* Kretzoi—*V. exilis* Kretzoi, *V. petenyii* (Mehely), *V. hungaricus* (Kormos). In certain locations they are also associated with remains of the more ancient *D. milleri.* Probably, this group of locations in Hungary corresponds in the limits of the Soviet Union to the deposits containing fauna of the Khaprov faunal complex (lower horizon of Kryzhanovka, Odessa region; middle layer of alluvial deposits exposed along the left bank of the Khadzhibei estuary near Avgustovka village, Odessa region; and depressions on Yalpukh Lake, Odessa region). A still later phase in evolution of the Late Pliocene fauna of rodents reflects the complexes from the locations Beremend 4, Villan 5, and Kishlanga, where the remains of *P. priscus* are associated with non-Rhizomyid field rats laguridna (*L. arankae* Kretzoi) and the cementodontus-allophajomys group (*Allophajomys* Kormos). This association, in geological age in the limits of the USSR, is apparently close to strata containing rodent fauna of Odessa, Nogai, and complexes closer to them.

The Astian phase of development of the Pliocene faunal complexes of West Europe is probably reflected by the fauna of Venzhe, area 1 in Poland. Remains of *P. priscus* have been found here according to Sulimski (1964) and Kowalski (1960b) along with similar ones of folded-toothed hamsters of the genera *Trilophomys* Deperet and *Baranomys*, primitive mole voles of the genera, *Ungaromys* Kormos and *Germanomys* Heller, non-Rhizomyid field rats of older types—genus *Dolomys*, *Villanyia*, *Cseria*. Kretzoi brings this group closer to faunal complexes of the north-west Black Sea region of the Ukraine SSR, particularly with the Kuchurgan one by the presence of Petauristin in its composition. As for such locations as Rembelitsy, and Krulevskie in Poland, their age most probably corresponds to Willifrank (Kowalski, 1960a, 1960b; Fejfar, 1957).

Thus, based on what has been said above, it is quite evident that within the limits of countries adjacent to the USSR and Poland (Precarpathia), Czechoslovakia, Hungary and Rumania (Transylvania), the remains of representatives of the subfamily of ancient mole rats are found in deposits which, in the northwest Black Sea region of Rumania and the adjacent territory of the Ukraine SSR and Moldavia as well as the Azov Sea region, already contain similar remains of present-day mole rats from the genera *Microspalax* and even *Spalax*. Consequently, it may be suggested that representatives of both subfamilies in the course of the entire Middle and almost the entire Late Pliocene coexisted in time within the limits of different regions of Europe. In view of this, the remains of mole rats could be used only to a restricted degree for correlation of the corresponding strata of Poland, Czechoslovakia, Hungary and the northwest regions of Rumania with similar aged strata of continental remains of the northwest Black Sea and Azov Sea regions.

The most ancient recoveries of remains of present-day mole rats (*Spalacinae*) in Europe are well known presently from the limits of the northwest Black Sea region of the USSR, starting apparently from the Meotes. In particular, remains of the comparatively primitive *M. compositodontus* have been found in gravels exposed near Andreevka village, Berezansk district, Nikolaevsk region of the Ukraine SSR. These gravels lie apparently within Pontiac limestone. The remains of *M. compositodontus* in the range of this locality coexist with fauna including *Steneofiber* hamster-like rodents, dormice (*Myoxidae*), and large *Muridae*. Similar fauna is presently known from the lower strata of alluvial beds exposed along the left bank of the Khadzhibei estuary near the Avgustovka village, Odessa region (Topachevskii, 1965). Here osteoferous gravels lie in gray-dove colored clays at a hypsometric level of eight to ten meters above sea level, directly under the place of fossilization of Hipparion fauna, the age of which, as determined by Korotkevish, relates to the latest Meotes.

The remains of *M. macoveii* in the limits of the north-western Black Sea region are confined to the strata of the Astian stage which in the opinion of N. A. Konstantinova (1965) includes the Kuchurgan deposits and probably the strata from Moldavia which are similar in age and contain fauna similar to that of the Russilion, France. Here in the Kuchurgan deposits, they are associated with isolated remains of ancient mole rats. We have already discussed the characteristics of the Kuchurgan Middle Pliocene faunal complex. As for fauna of smaller mammals of the Moldavian Russilion, it is quite similar to that of the Kuchurgan. The difference lies in not finding here the field voles of the genus *Promimomys* and the addition of smaller forms from the genus *Dolomys—D. kowalskii* Schevtschenko, although close to the Hungarian *D. hungaricus*, apparently differs from it in the primitive outline of the frontal section of the worn out surface of M_1 (unpaired anterior palate and the paraconid complex), and noncementodontus Rhizomyid field voles of an ancient type from the polymorphic composite group *Villanyia-Cseria*. If we compare this complex with the fauna of field voles of the Hungarian Charnotana, then we do not find any principal differences between them.

The remains of *M. odessanus*, confined to the territory of the north-western Black Sea region to the strata apparently completing the Astian phase of deposition (the Odessian karst hollows), are found in abundance in the sediments of the Willifrank stage (Kotlovina village on Yalpuk Island; lower horizon of Kulyalnits deposits of the village Kryzhanovka near Odessa; middle horizon of the old alluvial bed exposed along the left bank of the Khadzhibei estuary near the Avgustovka village, Odessa region) and rarely in the Upper Pliocene, post-Willifrank deposits (village Kaira, Gornostaev district, Khersonsk region of the Ukraine SSR; lower layer of the Nogai bed). In the first case, they are associated with the lagomorph-Cricetidae complex of smaller mammals which contain field vole forms from the group *D. hungaricus*. In the Willifrank-Khaprov faunal complex, the remains of *M. odessanus* have been found along with rich *Microtidae* fauna which already include Rhizomyids cementodontus field voles from the genera *Mimomys* (*M. pliocaenicus* and *M. reidi*), and *Kislanagia*, as well as comparatively later *Dolomys* from the group *hungaricus-episcopalis* and *ucrainicus* with the retention of primitive noncementodontus Rhizomyid field voles of the polymorphic group *Villanyia-Cseria*, close to the Hungarian *V. petenyii* (Mehely), (*M. tenaitica* Schevtschenko, *M. lagurodontoides* Schevtschenko, *M. praehungaricus* Schevtschenko), and *Cseria gracilis* Kretzoi, as well as the ancient *D. milleri*. Finally, in the post-Willifrank they are associated with the Kair and the

Nogai complexes of field voles which include non-Rhizomyid field voles of Microtid (*Allophajomys*) and lagurid (genus *Lagurus*, subgenus *Lagurodon* Kretzoi) groups.

In the deposits of the post-Willifrank phase of the Late Pliocene, mole rats of the genus *Microspalax* immediately replaced the specialized early representatives of the genus *Spalax* (*S. minor*) and forms close to them. The remains of mole rats of this group have recently been found in the limits of the Black Sea region of the Soviet Union in the strata containing smaller mammalian fauna belonging to the so-called Odessian (the upper horizon of the Kuyalnits deposits of Kryzhanovka; alluvial beds exposed along the right bank of the Kuyalnits estuary on the territory of the health resort bearing the same name in Odessa) and the Nogai faunal complexes (Azov coast near Nogaisk, Zaporozh'e region; Tarkhankut near the settlement Chernomorskoe in Crimea; lower portions of the upper layer of the Khadzhibei deposits; and Tsimbal in Tamani). In the first case, they are associated with *Lagurodontus-Allophajomys* complexes of field voles which retained the Willifrank relicts represented mostly by *M. pliocaenicus* and, to a lesser extent, the Rhizomyid non-cementodontus field voles of the genus *Villanyia*. In the second case, they are associated roughly with the same *Lagurodontus-Allophajomys* complexes but with the association of later *Mimomys* (*M. intermedius* Newton). It should also be noted that *S. minor* in the limits of the cis-Black Sea and Azov Sea regions of the Soviet Union apparently lived till the beginning of the Anthropogene. This is testified to by findings of remains, although not in large number, in the lower Anthropogene strata exposed near the village Tikhonovka, Novo-Vasil'evskii district, Zaporozh'e region, along with finds of early *Arvicola* Lacepede, *Microtus* Schrank (including the subgenus *Pitymys* Mc. Murtrie), and highly specialized Lagurids of the subgenus *Lagurus* Gloger and *Eolagurus* Argyropulo. The remains of this fauna are also associated with mole rats close to the present-day *S. arenarius*. It should be emphasized, however, that the early Anthropogene mole rats are one of the least studied groups.

Finally, in the deposits of even later sediments of the Anthropogene starting from the Pleistocene, we come across the remains of species close to present representatives of the genus.

The stratigraphic affinity of the remains of mole rats found on the territory of USSR and in Western Europe is represented in the scheme in Figure 39.

CLASSIFICATION

In the present work we have done the classification of the family Spalacidae somewhat differently from the one used in the works of most

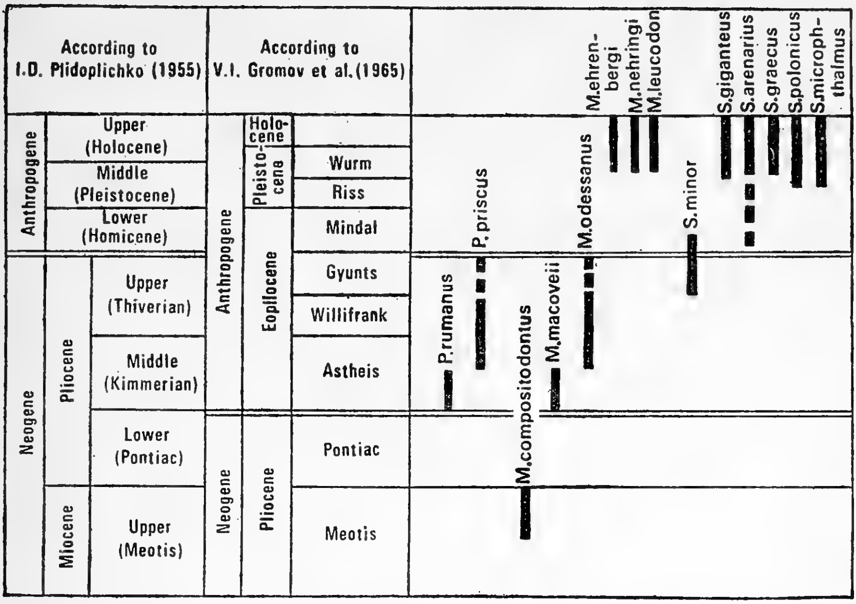

Figure 39. A scheme of distribution of *Spalacidae* in time and space.

of our predecessors. This system has been considerably revised on the basis of new data on classification by Mehely (1909). The basis for such a revision was the morphologic and systematic study in depth not only of present-day but also fossil representatives of the family with due consideration to their geographic distribution, geological periods, and phylogenetic links. As a result, it was possible to identify a new subfamily, acquire new knowledge on generic and subgeneric grouping, and also identify new taxa of the species range based on fossil material.

Below, we reproduce the classification of Spalacidae in which the relation of individual groups of these animals to their present-day counterparts most correctly reflects their phylogenetic relationship.

Family Spalacidae Gray, 1821; Late Miocene-recent; Europe, Asia, North Africa.

- †Subfamily Prospalacinae subfam. nov.; Late and Middle Pliocene of Europe.
  - †Genus *Prospalax* Mehely, 1908; Late and Middle Pliocene of Central and East Europe.
    - †*P. priscus* (Nehring, 1897); Middle and Late Pliocene; Polish Carpathian, Czechoslovakia, South Hungary, Rumania (Transylvania).

†*P. rumanus* Simionescu, 1930; Middle Pliocene (Astian); Rumania (lower reaches of Prut river), northwest Black Sea region of the Soviet Union.

Subfamily Spalacinae Gray, 1821 (= Spalacinae Thomas, 1897); Late Miocene-recent; Europe, Asia, North Africa.

Genus *Microspalax* Nehring, 1897; Early Miocene-recent; Europe, Asia and North Africa.

Subgenus *Microspalax* Nehring 1897; Late Miocene, Late Pliocene of Europe; Pleistocene-recent of northeast Africa, Middle East and partly Asia Minor.

M. ehrenbergi (Nehring, 1897); Pleistocene-recent; northern regions of Libya and UAR, Israel, Jordan, Livan, Syria, Iraq, possibly northern regions of Turkey.

†*M. compositodontus* sp. nov.; end of Late Miocene; northwest Black Sea region of the Soviet Union.

†*M. macoveii* (Simiionescu, 1930); Middle Pliocene; northwest Black Sea region of the Soviet Union and the adjoining regions of Rumania (right bank of the Prut River in its lower reaches);

†*M. odessanus* sp. nov.; end of Middle Pliocene and Late Pliocene; northwest Black Sea region and the north Azov Sea region of the Soviet Union.

Subgenus *Mesospalax* Mehely, 1909; recent; Transcaucasus; Asia Minor, the Balkans, Carpathian regions of Hungary, Soviet Bukovina, northwest Black Sea region (Rumania, Bulgaria, Moldavian SSR, Odessa region of the Ukraine SSR).

M. nehringi (Satunin, 1898); recent; Turkey, North Iraq, Transcaucasian region of the USSR.

M. leucodon (Nordmann, 1840); recent; Yugoslavia, north Greece, European Turkey, Bulgaria, Hungary, Rumania, Moldavian SSR, and the adjacent areas of the Odessa region of Ukraine SSR, Soviet Bukovina.

Genus *Spalax* Güldenstaedt, 1770; Late Pliocene-recent; Eastern Europe including cis-Caucasus and north Caspian, entering into Transcaspian region.

S. giganteus Nehring, 1897; recent; semi-deserts of Caspian regions of the northeast cis-Caucasus, north Caspian and Transcaspian regions.

S. arenarius Reshetnik, 1938; recent; left bank of lower Dnieper, South of Kakhovka.

S. microphthalmus Güldenstaedt, 1770; Pleistocene-recent; territory between Dnieper and Volga except lower Dnieper, west cis-Caucasus.

S. polonicus Mehely, 1909; Pleistocene-recent; right bank of

Ukraine, except its northernmost areas and the Soviet Bukovina.

S. graecus Nehring, 1898; recent; Soviet Bukovina and adjacent regions of Rumania.

†*S. minor* W. Topachevskii, 1959; Late Pliocene-Early Anthropogene; northwest Black Sea and Azov Sea regions of the Soviet Union.

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PART II

TAXONOMY

KEY FOR IDENTIFICATION OF SUBFAMILIES OF THE FAMILY SPALACIDAE

1 (2). The suborbital canal is always closed. On the frontal bones there is a small supraorbital foramen near the external border of the orbit. The alveolar process of the lower jaw is considerably shorter than the articular. The angular process is situated at the base of the articular and has a common border with it. Sella externa is absent .... 1. **Prospalacinae** subfam. nov.
(Mid Pliocene and beginning of the Late Pliocene).

2 (1). The suborbital canal and the supraorbital foramen are always absent. The alveolar process of the lower jaw exceeds in height the articular one, or is approximately equal to the latter. The angular process is placed outside and is on the external wall of the alveolar process and does not have a common border with the articulated member. Sella externa is always present .... 2. **Spalacinae** Gray.
(Late Miocene to present day).

1. Subfamily **PROSPALACINAE** W. Topachevskii subfam. nov.
ANCIENT MOLE RATS

Type genus. Prospalax Mehely, 1908; southern Poland, Czechoslovakia, Hungary, Rumania, northwestern Black Sea regions of the Ukraine SSR; Mid-Pliocene and beginning of Late Pliocene.

Diagnosis. The suborbital canal (bony canal for the branch of the trigeminal nerve) is always closed (Figure 40, No. 2). The small for. supraorbitalis is situated on the temporal bones near the external edges of the orbit (Figure 40, No. 1). The alveolar process of the lower jaw is considerably shorter than the articular one. The angular process is situated on the base of the articular one and has a common border with it. Sella externa is absent (Figure 40).

Additional description. Measurements are mostly small and close to the measurements of the then-living *M. ehrenbergi*; the length of the upper line of the permanent molars is, as a rule, less than 7.5 mm, and that of the lower, 8.0 mm. The upper and lower distances are short. The masseter area of the lower jaw is sharply defined. The lower incisors are relatively narrow and are characterized by the presence of usually three (sometimes two) prolonged ridges on the front side. The upper and lower permanent molars are longer and narrower than in the representatives of the subfamily Spalacinae Gray.

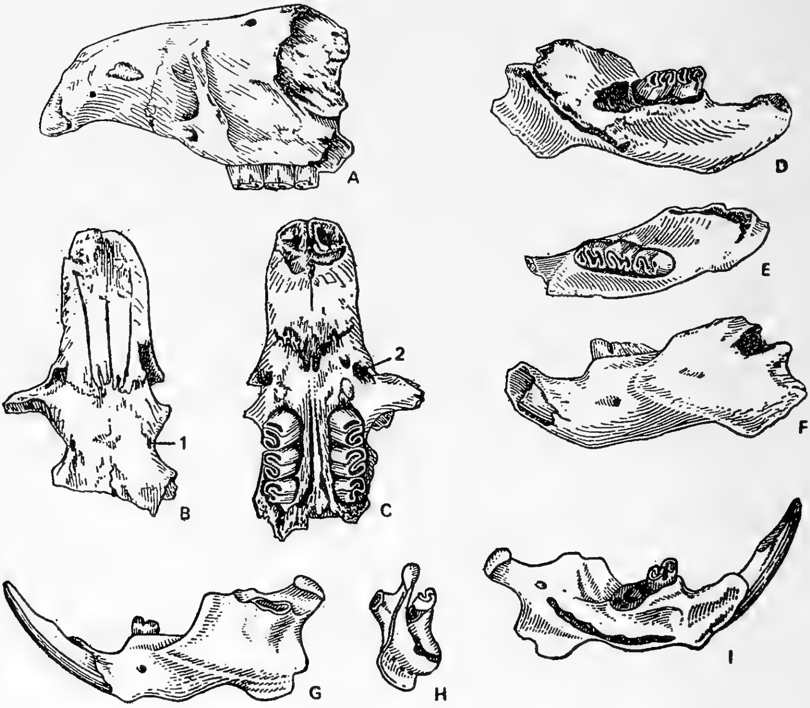

Figure 40. *Prospalax priscus* (Nehr.).

A—axial skull, lateral view; *B*—the same, from above; *C*—the same, from below; *D*, *I*—lower jaw, inner view; *E*—the same, from above; *F*, *G*—the same, outer view; *H*—the same, posterior view; *A* to *F*—by Sulimski, 1964; *G* to *I*—by Mehely, 1908. *1*—supraorbital foramen; *2*—suborbital canal.

Comparison. They can be clearly differentiated from the representatives of the subfamily Spalacinae by:

1. The usual presence of a closed infraorbital canal. It is always absent in Spalacinae.
2. The usual presence of for. supraorbitalis on the temporal bones. This is absent in Spalacinae.
3. The shorter alveolar process of the lower jaw is considerably less in height than the articular one. In Spalacinae, the alveolar process is almost

equal in height to its articular one and, in the majority of cases, it notably exceeds the latter.

4. The angular process is situated at the base of its articulated member, having a common border with it (the posterior section of the lower jaw). In Spalacinae the angular process is placed externally on the external wall of the alveolar border and does not have a common border with the articular process.

5. The absence of sella externa. This is always present in Spalacinae.

Formation of the subfamily. This is represented by the single genus, *Prospalax* Mehely, 1908, from the Middle and Late Pliocene of Europe.

Distribution and geological age. Southern Poland (Prikarpate), Czechoslovakia, Hungary, Rumania, northwestern Black Sea region of the Ukraine SSR (Odessa region); Mid-Pliocene and beginning of Late Pliocene.

1. Genus **PROSPALAX** Mehely, 1908—ANCIENT MOLE RATS

Mehely, 1908: 305–316, Table II, Figure 1–3; Table IV, Figure 1–3.

Genotype. Prospalax priscus Nehring, 1897; south Hungary (Villan Mountains), the Beremend near Villani, Committee of Baran; Late Pliocene.

Diagnosis. Same as for the subfamily.

Description and comparison. In addition to the traits described earlier for the subfamily, the following special characteristics are typical for the genus in respect of the structure of the permanent molars.

1. The protocone on M^1 in the early and middle stages of wear is always fused with the anterior collar and, along with the latter, is separated from the rest of the parts of the crown in the shape of a kidney (Figure 41). The paracone is largely fused with the hypocone, and the latter, in turn, is fused with the metacone to form a V-shaped figure on wearing. The fusion of the protocone with the hypocone in the later and final stages of wearing does not occur independently as in representatives of present-day mole rats (genera *Microspalax* and *Spalax*), but through the anterior collar and paracone, as a result of which the worn out grinding surface assumes either an S- or Z-like appearance. Subsequently, the tooth has two open intruding folds in the outer line only at the unfused protocone and hypocone and assumes an S- or Z-shaped appearance changing the W-like appearance which is characteristic of all Spalacinae without exception though at only the very early stages of erosion.

2. A similar phenomenon is also observed on the two lower and last permanent molars (M_{2-3}), the hypoconid of which is fused with the posterior collar in successive stages of erosion and is separated, along with the latter, from the rest of the parts of the crown in the form of a kidney, and the fusion, each with the protoconid of metaconid and entoconid, forms a V-shaped figure due to wearing. The fusion of the

protoconid and hypoconid again does not take place independently as in *Microspalax* and *Spalax*, but through the posterior collar thus giving the S- or Z-shaped appearance of the mastication surfaces. All the permanent molars in the later and final stages of erosion are, without exception, generally similar to the permanent molars of *Microspalax* and *Spalax*, if certain clear differences are not to be considered in the general proportions of the crowns.

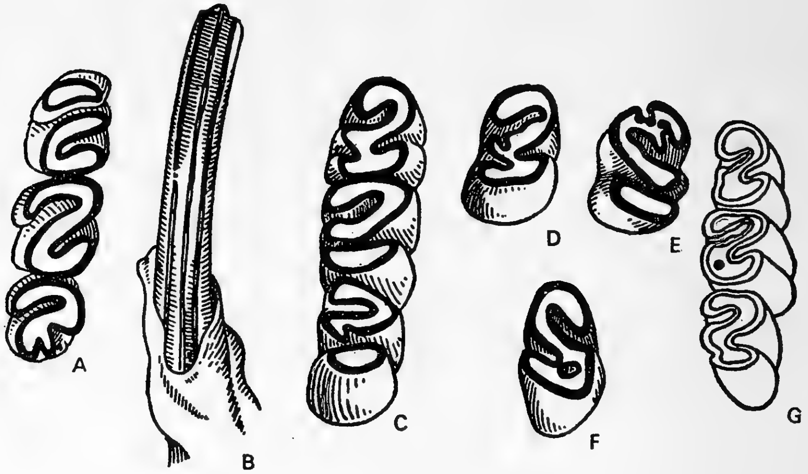

Figure 41. *Prospalax priscus* (Nehr.).

A—upper row of permanent molars (by Sulimski, 1964); *B*—incisor of lower jaw (by Mehely, 1908); *C*—lower row of permanent molars; *D* to *F*—isolated M_1 (by Sulimski, 1964); *G*—lower row of permanent molars (by Mehely, 1908).

3. The structural folds are more predominantly present on all the permanent molars without exception than in *Microspalax* and *Spalax*. In addition, the molars of the representatives of the genus *Prospalax* are, in general, rather simpler than in true mole rats.

Note. Considering the simplicity of the permanent molars of *Prospalax*, and its weakly developed tuberculoid type of structure for the permanent molars in the early stages of wear as compared to *Microspalax* and *Spalax*, a deviation from the opinion of Mehely (1908) appears imminent, i.e., not considering this given genus as a direct ancestor of true mole rats and proposing for it a place in the adjacent branch in the family group which was, in its time, indicated by Stehlin and Schaub (1951); Schaub, (1958). The presence of remains of true mole rats along with the similar Prospalacinae appears to be contradictory, and in some cases even the finds of the former in rather older sediments than the most ancient sediments containing the remains of *Prospalax* have been found. Thus, for example, the remains of true mole rats are known to have occurred from the Upper Miocene-meotes of the northwestern Black Sea region of the Ukraine SSR (please see further, page 188). All the aforesaid proves that in the Mid-Late-Pliocene of Europe, we come across only highly specialized last representatives of the once most populous subfamily of ancient mole rats which lived in their time in regions where the more adaptive present-day mole rat could not penetrate because of specific paleogeographical reasons. It can also be assumed that Prospalacinae were more widely spread out in the Miocene of Europe and possibly of north Africa, and Asia Minor, and their origin may be traced in the Oligocene period. In addition, considering the intermediate position of the subfamily between the Oligocene Rhizospalacinae and true mole rats, it is highly probable that one could discover the direct ancestors of Spalacinae in this very subfamily among ancient, yet unknown genera, less specialized than the only presently known genus *Prospalax*. However, all this has to be decided in the future as the study of the history of the group in the time prior to Mid-Pliocene faces considerable difficulties related primarily to the non-availability of paleontological material.

Composition of the genus. Two species—*P. priscus* (Nehring, 1897) from the Middle and Late Pliocene of southern Poland, Czechoslovakia, Hungary, and north Rumania, and *P. rumanus* (Simionescu, 1930) from Mid-Pliocene of the Black Sea region of Rumania. Perhaps the remains of *Prospalax* from the Mid-Pliocene of the northwestern Black Sea region of Ukraine should be added to the last mentioned species (Kuchurgan sediments, stratigraphically identical and mixed territories with corresponding sediments of Rumania in which the remains of *P. rumanus* have been found).

Distribution and geological age. Southern Poland (Prikarpate), Czechoslovakia, Hungary, Rumania, northwestern Black Sea region of Ukraine SSR (Odessa region); Mid-Pliocene and beginning of Late Pliocene.

KEY FOR IDENTIFICATION OF SPECIES OF THE GENUS PROSPALAX

1 (2). Length of the angular process of the lower jaw is less than the total length of M_1–M_2 . . . . 1. **P. priscus** (Nehring).
(Middle and Late Pliocene).

2 (1). Length of the angular process of the lower jaw exceeds the total length of M_1–M_2 . . . . 2. **P. rumanus** (Simionescu).
(Mid-Pliocene).

1. **Prospalax priscus** (Nehring, 1897)—**Original Mole Rats**

Nehring, 1897: 174–176, Abb. 4, Figure 3.

Holotype. Geological regulation in Budapest, No. 0 = 4722; the lower jaw (mandibula sin), the preserved articular process, the angular and considerable part of the alveolar process, and of the teeth—the incisor and the anterior permanent molar; south Hungary (the place of the find is Beremend, near Villani, Committee of Baran); Late Pliocene.

Diagnosis. The angular process of the lower jaw is short; its length is less than the total length of the two anterior permanent molars (M_1–M_2).

Description. The measurements are medium, a little larger than the then-living *M. ehrenbergi*; the length of the upper rows of the permanent molars is 6.0–7.5 mm, and that of the lower ones is 6–8–9 mm. The skull is narrowed in the molar region; the relation of the incisorial width to the length of the row of permanent molars is 71.3. The rostral part is wedge-shaped; its edges gradually close in anteriorly; the width of the rostrum at the level of the anterior edges of the for. sub-orbitalis exceeds the similar width in the middle. The nasal bones are shorter than the supermaxillary bones and are bifurcated from behind (Figure 40). The temporo-premaxillary sutures are directed outward and forward, forming an angle, the apex of which is directed back with the temporo-nasal suture. Along the borders of the temporal bones there are small for. sub-orbitalis. The sagittal ridge on the temporal bones is absent. The upper diastema is comparatively short. The magnitude of the diastema-tooth index is 151.0. The suborbital canal is always closed and in some instances it is divided in two. The alveolar protuberances, as can be judged by the figure given in the work of Sulimski (1964), are well expressed and are in immediate proximity from the anterior edges of the alveolus M^1 when removed, and are of considerably less length than the anterior permanent molar. The masseter area is short; its length is perhaps less than the distance from the anterior edge of the latter to the suture between the premaxillary and maxillary bones. The hard palate is narrow at the level of the anterior permanent molars, and its width is about equal to M^1. The middle ridge of the palate is well developed and wide. The pillar-like process is large and blunt. The fossae behind the palate are long and narrow.

M^1 (length 1.6–2.4–2.7 mm; width 1.3–1.7–2.1 mm) is long and narrow, the ratio of the width to length is, on an average, 71.0; $n = 93$ (Sulimski 1964). In true mole rats, the magnitude of this index in all the given cases is considerably greater than 80.0 or approaches to this value. The protocone is fused with the anterior collar in the early and middle stages of wearing, and is separated along with the latter from the rest of the parts of the crown in the shape of a kidney. The paracone is usually connected with the hypocone and the latter with the metacone; taken together they form a V-shaped figure during erosion. At a given stage the relationship of teeth is characterized by the presence of two outer and one inner intruding fold; moreover, the anterior outer and inner folds form a continuous fissure. During erosion, the anterior collar fuses with the paracone as a result of which the masticatory surface assumes an S- or Z-form. In this stage of wearing, the tooth has an intruding fold in both the outer and inner lines; the inner line, because of the type of fusion during erosion described above, deeply penetrates into the masticatory surface and its inner portion is not separated into the anterior mark. The length of the inner intruding fold in the just described stage of erosion usually exceeds two-thirds the total length of the width of the crown, whereas in true mole rats this measurement is about half the width of the latter. The mesocone and posterior collar are always absent. There are three molars—a large inner and two weakly developed outer.

M^2 (length 1.5–2.1–2.5 mm; width 1.3–1.8–2.2 mm) like the previous molar is, perhaps, relatively narrower than in true mole rats (the ratio of crown width to its length is 85.7; $n = 79$; whereas in Spalacinae the lowest values of the given index lay in the range of 90.0 and in the majority of given instances, the width of the tooth exceeds its length). The form of the wearing surface is S-shaped, quite similar to that of true mole rats because the anterior collar is fused with the paracone and the latter, in turn, with the hypocone. However the closure of the internal portion of the intruding fold of the inner line in the anterior mark, which is characteristic of the families of the genus *Microspalax* and *Spalax* in the middle and late stages of erosion in corresponding teeth, perhaps does not occur. The root structure is similar to that of the previous molar.

M^3 (length 1.2–1.6–2.0 mm; width 1.1–1.4–1.6 mm) like the previous permanent molars is, on an average, narrower than in true mole rats (the ratio of the width to length is 87.5; $n = 41$) in which the width of the crown of the tooth in the majority of cases exceeds its length (with the exception of Mio-Pliocenic *M. compositodontus* and Mid-Pliocenic *M. macoveii* which also have comparatively narrow upper permanent molars). M^3 is similar to the previous molar in the general outline of the grinding surface. The number of roots in the majority of instances does not exceed three—a large inner and two weakly developed outer. In individual cases, there are remains of a small fourth external crust.

The lower jaw has a shortened diastema (the value of the diastema tooth ratio is 66.0; 67.7) and a shortened angular process (length less than the total length of the anterior permanent molars). The ridge dividing the crown-alveoli, judged by the figures given in the work of Mehely (1908), is low and blunt. The lower ridge of the masseter surface is large and forms an acute angle (Figure 40) along with the prolongation of the anterior edge of the incoming branch. The horizontal branch is comparatively not high;

its height at the level of the posterior edge of the alveoli of M_1 is less than the length of the lower line of permanent molars. The mandibular foramen is somewhat shifted toward the edge of the coronary articulating groove and is situated far from the latter, a little exceeding half the length of the condylus.

The lower incisor is comparatively narrow (ratio of the width to antero-posterior cross section is 78.4; 80.8) with two to three longitudinal ridges on the dorsal surface (Figure 41). Regarding general proportions and details, the structure is very similar to the incisors of European Mio-Pliocenic fossils differing only in the lesser absolute width.

M_1 (length 1.6–2.4–2.8 mm; width 1.3–1.7–2.0 mm) is long and short (relation of width of crown to length is, on an average, 71.0; $n = 122$). The hypoconid and the posterior collar have been separated at very early stages of erosion in the form of a kidney. Furthermore, the metaconid shows a tendency to separate from the protoconid in the same stage of wearing on the crown of the tooth, or is completely separated from it. It has to be noted, however, that in semi-mature individuals, a complete fusion of the metaconid with the protoconid takes place, and also a formation of a bridge between the fused hypoconid and the posterior collar from one side, and between the rest of the parts of the crown on the other. The entoconid is always well developed in the early and middle stages of erosion and the mesoconid is always absent. It is clear from the foregoing description that in *P. priscus*, immature individuals and those in the early stage of maturation, M_1 is characterized by the presence of one intruding fold in the outer line and two in the inner lines. Due to further erosion, the intruding folds are closed in the marks in the following order: the posterior inner (with formation of posterior mark), the anterior inner, and finally the outer one. During this, the posterior mark usually completely vanishes with old age, the entoconid completely fuses with the posterior collar, and the grinding surface clearly takes up a well-defined S- oı Z-form and further, an E-form (at the complete closure of the anterior inner fold) and finally, an oval shape at the complete closure of the only outer). It has to be stressed however that in *P. priscus* as, perhaps, in all representatives of the genus, the formation of marks (stars) on permanent molars takes place in somewhat later stages of erosion than in true mole rats and, further, the complete closure of the outer intruding fold fades away only in very old age. The tooth is characterized by having two roots.

M_2 (length 1.5–2.2–2.6 mm; width 1.2–2.0–2.2 mm) like the previous molar is, on an average, narrower than in true mole rats (relation of width of crown to length is 90.9; $n = 144$). The hypoconid along with the posterior collar is separated from the rest of the parts of the crown at the initial and middle stages of erosion in the form of a kidney. The fusion of metaconid, protoconid, and entoconid forms a V-like shape on erosion.

The tooth has one intruding fold at the indicated stage of wear in the outer line, and two in the inner line; moreover, the posterior one is closer. During further erosion, there is a reduction of the posterior inner intruding fold because the entoconid fuses with the posterior collar and that is how the anterior mark is formed—by the closure of the corresponding fold of the inner line. As for the outer deep intruding fold, it perhaps remains open almost up to very old age. The tooth, like the previous molar, is characterized by the presence of two roots.

M_3 (length 1.3–2.0–2.2 mm; width 1.2–1.7–1.8 mm; relation of width to length is, on an average, 85.0; $n = 65$) is like M_2 in general, differing from the latter only by small absolute dimensions.

Comparison. It differs from the Mid-Pliocenic *P. rumanus* by:

1. A shortened angular process of the lower jaw, the length of which is less than the total length of M_1 to M_2. In *P. rumanus* it is longer than the latter.

2. Average large absolute dimensions (length of lower rows of permanent molars is 6.0–8.0–9.0 mm against 6.0; 6.2 in *P. rumanus*).

3. A wider lower incisor on an average (relation of width to the antero-posterior cross section is 78.4; 80.8 against 68.6 in *P. rumanus*).

Measurements. Length of upper rows of permanent molars, 6.0–7.5 mm; width of upper incisor, 1.7–1.9–2.2 mm; lower diastema, 4.4 mm; length of row of permanent molars, 6.0–8.0–9.0 mm; height of horizontal branch at level of posterior edge of alveolus of M_1, 6.3 mm externally; width of lower incisor, 1.6–1.8–2.1 mm; antero-posterior cross section of lower incisor, 2.55 mm.

Note. The presence of a shortened angular process of the lower jaw and comparatively wider lower incisors in *P. priscus* indicates, perhaps, a higher degree of specialization in the species for digging activity as compared to the Mid-Pliocenic *P. rumanus*.

Distribution and geological age. Poland (Prikarpate) (place of find Venzhe near Dzyaloshina; Rembelitsi Krulavskie, Klobutskova uezda), Czechoslovakia (Ivanovtsi near Trenchin), south Hungary (group of places of finds in Villanski Mountains; Beremend, sites No. 4, 5, and 7; Charnota, sites No. 1 to 3; Nad'khorshan', site No. 1 and Villan, sites No. 3, 5 and 11—all in the Committee of Baran'; in addition to around Hungary, the remains of this species have been found in the Late Pliocenic fauna of Kushlang); Rumania (Transylvania; place of find, Beralt-Kepeni) (Kretzoi, 1956; Kowalski, 1960b; Sulimski, 1964); Late and partly, perhaps, Middle Pliocene. Remains of this species are not found around the USSR. Information on this point available in literature is mainly based on some uncertain findings; the remains belonging to *P. priscus* were ultimately found to be those of *M. macoveii* after closer examination (Simionescu). Details are given below (pages 199–200).

2. **Prospalax rumanus** (Simionescu, 1930)—**Rumanian Mole rats**

Simionescu, 1930: 20, 21; Figures 29 and 30; Tab. II, 2.

Holotype. University in Yassakh (Rumania), number of the find has not been fixed; the lower mandible (mandibula sin.) without the rising branch, the angular process has been preserved and also the two permanent molars (M_1–M_2) (Simionescu, 1930). Rumania with Malushtein; Mid-Pliocene.

Additional data. Lower mandible from the Kuchurganskii sediments without the rising branch and the angular process, preserved incisor and complete line of alveoli of permanent molars; S. Novopetrovka of Frunzanskii region near Odessa; Mid-Pliocene. It is preserved in the collections of the Zoological Institute AN Ukraine SSR. The jaw was found during the paleontological expedition of the Zoological Institute AN Ukraine SSR in 1964, and is actually the only authentic find of remains belonging to representatives of the genus *Prospalax* in the USSR.

Diagnosis. The angular process of the lower jaw is elongated; its length exceeds the total length of the two anterior permanent molars (M_1–M_2).

Description. The measurement are, on the average, smaller than those of the previous species. The alveolar length of the lower row of permanent molars is 6.0, 6.2 mm. The lower diastema, as in *P. priscus*, is shortened; the value of the diastema-tooth index is 66.7 (holotype) and 74.3. The angular process is long; its length considerably exceeds the total length of M_1–M_2. The structure of the masseter area is the same as that of *P. priscus*. The lower incisor is, on the average, perhaps comparatively narrower than the one found in previous species; the relation of the width to the antero-posterior cross section is 68.6. There are three longitudinal ridges on the anterior surface. Unfortunately, the lower permanent molars in all the specimens known at present of this species are considerably worn out (Figure 42), i.e., they are in such a stage of erosion that it is very difficult to determine the species differences. From the general appearance, the grinding surfaces are very similar to the permanent molars of *P. priscus*.

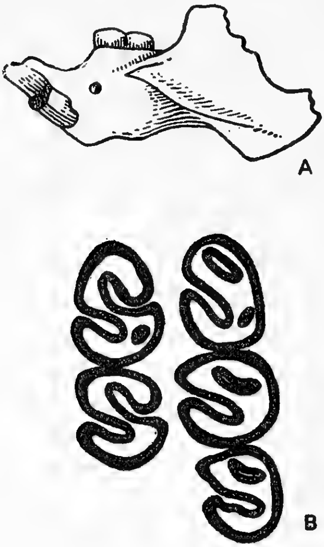

Figure 42. *Prospalax rumanus* Sim. (by Simionescu, 1930).

A—lower jaw, external view, holotype; *B*—lower rows of permanent molars.

Comparison. Completely given on page 161.

Measurements. Length of lower row of permanent molars 6.0, 6.2 mm; length of lower diastema 4.0, 4.6 mm; height of horizontal branch at the level of the posterior edge of alveolus of M_1 from outside, 5.0, 5.8 mm; thickness of the horizontal branch at the level of M_2, 3.0, 3.3 mm; width of lower incisor, 1.5 mm; antero-posterior cross section of lower incisor, 2.2 mm.

Note. This species in comparison with *P. priscus* has nearly all the above-mentioned peculiarities in the construction of the angular process of the lower jaw and incisors which, perhaps, points to its lesser specialization toward a burrowing type of life.

Distribution and geological age. Mid-Pliocene of northwest Black Sea region (Odessa), Kuchurganskii sediments and its analogues around mixed regions of Rumania (Malushteni Levoberezh'e (left bank) of the Pruta River along its lower current).

2. Subfamily **SPALACINAE** Gray, 1821
TRUE MOLE RATS

Type genus. Spalax Güldenstaedt, 1770; the steppes and forest steppes of Eastern Europe from the northwestern regions of Rumania, Soviet Bukovina and eastern regions of the Pre-Caspian to east of the Ural River and Trans-Caspian; Late Pliocene to present day.

Diagnosis. The suborbital canal and the supraorbital foramen are always absent. The alveolar process of the lower jaw in the majority of cases considerably exceeds the articular process in height or is approximately equal to it. The angular process is constricted from outside, and being on the external wall of the alveolar process, does not have a common edge with the articular one. Sella externa is always present.

Additional description. The measurements are mainly average and large. The upper and lower diastemata are elongated. The masseter area of the lower jaw is without a sharply defined ridge. The lower incisor is, on the average, relatively wider; in the majority of cases it is without a longitudinal ridge on the anterior surface (present only in representatives of the most primitive subgenus *Microspalax* Nehring—the then-living *M. ehrenbergi* and its Mio-pliocene fossil representatives). The upper and lower permanent molars are shorter and wider than in the species from the subfamily Prospalacinae.

Comparison. The comparison of the subfamily has been given fully on page 154.

Composition of the subfamily. This subfamily is represented by two recent genera—*Microspalax* Nehring, 1897; and *Spalax* Güldenstaedt, 1770.

Distribution and geological age. North Africa (northern region of Libya and United Arab Republic), Asia Minor (Israel, Jordan, Lebanon, Syria, Iraq, Turkey, Soviet Zakavkaz, and its southwestern regions), southeastern Europe, from Balkan and Pre-Balkan regions in the west, up to the Volga on the east Pregkavkaze, the northern Pre-Caspian region up to east of the Ural River and in Zakaspii; Late Miocene to present day.

KEY FOR IDENTIFICATION OF THE GENERA OF THE SUBFAMILY SPALACINAE

A—Based on the skull

1 (2). The for. supracondyloideum is always present though it is above one of the occipital condyles, usually above both. The tuberculum pharyngeum laterale are broad; being broad, they occupy almost all the place between the auditory bulbe at the place of contact of the basal wedge and the base of the occipital bone (Figure 43). The base of the skull has a sharply defined fissure because the basis-phenoid and the base of the occipital bone are situated at an angle. . . . . 1. **Microspalax** Nehring. (Late Miocene to present day).

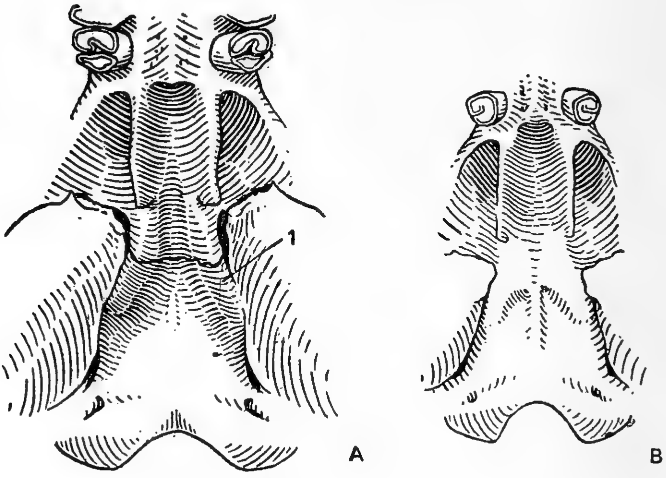

Figure 43. Base of the skull. ×2.75.

A—Spalax; *B—Microspalax*. *1*—lateral occipital tubercles.*

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*Probably a mistake in the original. By all accounts this refers to the lateral pharyngeal tubercle—Editor.

2 (1). For. supracondyloideum is always absent. The tuberculum pharyngeum laterale are compact, stretched in the shape of narrow ridges along the edges of the basic wedge-shaped bone and the base of the occipital bone; the base of the skull is concave and V-shaped. The basisphenoid and the base of the occipital bone lie on one level because of which the fissure in the base of the skull is not defined. .... 2. **Spalax** Güldenstaedt. (Late Pliocene to present day).

B—Based on the lower jaw

1 (2). The ridge of the coronary-alveolar groove is hardly defined; it is blunt or is absolutely unidentifiable. The depression (between ridges of the coronary-alveolar and coronary-articular process) is not deep, usually opening anteriorly and externally. The angular process is well separated and is inclined from the external wall of the alveolar process. The area on its external surface is represented by only a prolongation of its free edge and actually restricts the place of attachment of the posterior portion of the musculus masseter lateralis (Figure 61). The sella externa is placed below the sella interna (Figure 44)..................... 1. **Microspalax** Nehring.

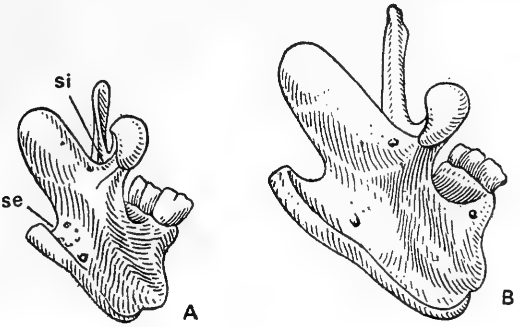

Figure 44. Lower jaw, posterior view. ×2.75.

A—Microspalax; *B—Spalax*. *se*—sella externa; *si*—sella interna.

2 (1). The ridge of the coronary-alveolar groove is strongly developed and is sharp. The fossa between the ridges is deep and is always closed. The angular process completely adheres to the alveolar process and is slightly inclined from the external wall of the latter. The area on its external surface is exhibited all along its free edge including the zones of attachment of the posterior as well as anterior

portions of the musculus masseter lateralis. The sella externa is placed approximately at the same level as the sella interna........ ....2. **Spalax** Güldenstaedt.

C—Based on the vertebrae

1 (2). The antero-posterior length of the dorsal arch of the first cervical vertebra—the atlas—is less than the height of the canal for the medula oblongata measured at the anterior side. The length of the neural spine of the second cervical vertebra—axis—measured from the anterior end, less than twice exceeds its least width (Figures 45 and 46). The 4th to 5th sacral vertebrae are always in contact (either

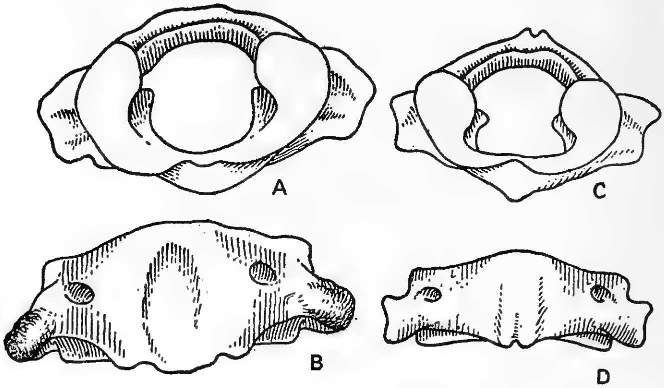

Figure 45. Atlas. ×3.6.

A, B—Spalax; *C, D—Microspalax*; *A, C*—anterior view; *B, D*—from dorsal arch.

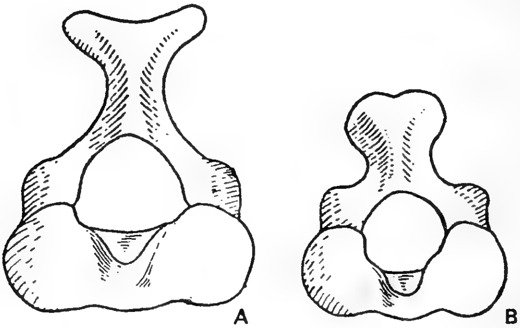

Figure 46. Axis, anterior view. ×3.7.

A—Spalax; *B—Microspalax*.

fuse or touch each other) with the spina ischiadica of the pelvic bone as a result of which the large sacral groove along with the sacrum forms a closed opening (Figure 49).. 1. **Microspalax** Nehring.

2 (1). The antero-posterior length of the dorsal arch of the first cervical vertebra—the atlas—is approximately equal to the height of the canal for the medula oblongata. The length of the neural spine of the second cervical vertebra—the axis—twice or more exceeds the least width of this process. The sacrum never comes into contact with the spina ischiadica of the pelvic bone and, as a result, the large ischial groove is open from behind.. 2. **Spalax** Güldenstaedt.

D—Based on the scapula

1 (2). The medial surface of the bone is flattened anteriorly (in the neck region). Its caudal edge is not wide because the caudal ridge (crista caudalis) is weakly developed; the maximum length of the caudal edge is more than three and a half times less than the maximum width of the scapula. The width of the acromion process is more than twice less its length (Figure 47)...... 1. **Microspalax** Nehring.

2 (1). The medial surface of the bone is highly concave anteriorly. Its caudal edge is broadened because of the great development of the caudal ridge. The maximum height of the caudal ridge is only three times less than the maximum width of the scapula. The width of

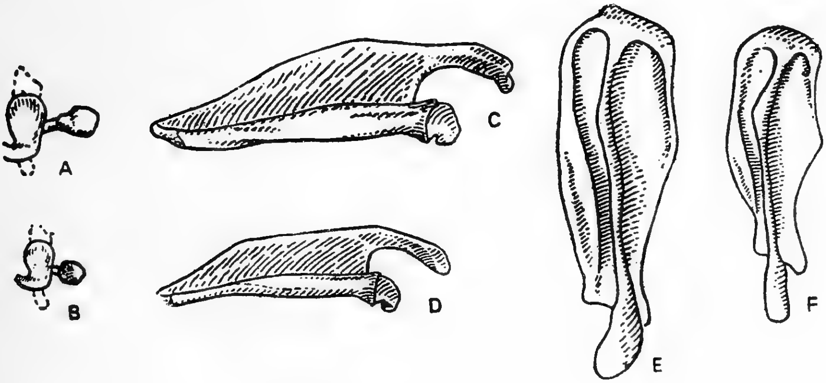

Figure 47. Scapula. ×1.7.

A, C, E—Spalax; *B, D, F—Microspalax*; *A, B*—from the side of the articulating fossa; *C, D*—from the side of the caudal tubercle; *E, F*—from lateral sides.

the acromion process is less than twice or more its length.........
..................................2. **Spalax** Güldenstaedt.

E—Based on the humerus and bones of the forearm

1 (2). The width of the diaphysis of the humerus is greater than the deltoid process by approximately one and a half times the antero-posterior cross section measured at the same level (Figure 48). The maximum width of the proximal epiphysis of the olecranon of the elbow bone is less than the length of this process. The maximum width of the crescent-shaped groove at the level of the ulna joint is approximately equal to its width at the level of the lower border of the coracoideus process. The least width of the ulna at the base of the proximal epiphysis is twice less than the width of the latter. The maximum width of the distal epiphysis of this bone is less than the width of the proximal epiphysis or is approximately equal to it.................................1. **Microspalax** Nehring.

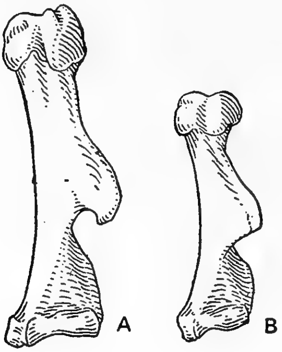

Figure 48. Humerus, anterior view. ×1.7.

A—Spalax; *B—Microspalax*.

2 (1). The width of the diaphysis of the humerus is greater than the deltoid process. It is always more than 2.5 times the antero-posterior cross section. The maximum width of the proximal epiphysis of the olecranon process of the radius* is less than 2.5 times the length of the olecranon. The maximum width of the crescent-shaped groove at the level of the ulna joint always exceeds the same at the level of the lower border of the coracoideus process. The least width of the ulna is about twice less than the width of the proximal epiphysis. The maximum width of the distal epiphysis of this bone always exceeds the similar width of the proximal epiphysis......
..................................2. **Spalax** Güldenstaedt.

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*Should read ulna—Editor.

F—Based on the pelvic bones

1 (2). The length of the ilium (measured up to the anterior edge of the articulating cavity) considerably exceeds the length of the ischium (by more than half the length of acetabulum). Measurements of spina ischiadica and tuber ischiadicus approximately coincide. The ischial axis always contacts the wings of the sacrum as a result of which the great ischial groove, along with the sacrum, forms a closed opening (Figure 49).....................1. **Microspalax** Nehring.

2 (1). The length of the ilium is about equal to the length of the ischium (even if it exceeds the latter, it does not do so more than half the length of the acetabulum). Measurements of the ischial axis are half or even less than those for the tuber ischium. Because of this, the ischium never contacts the wings of the sacrum

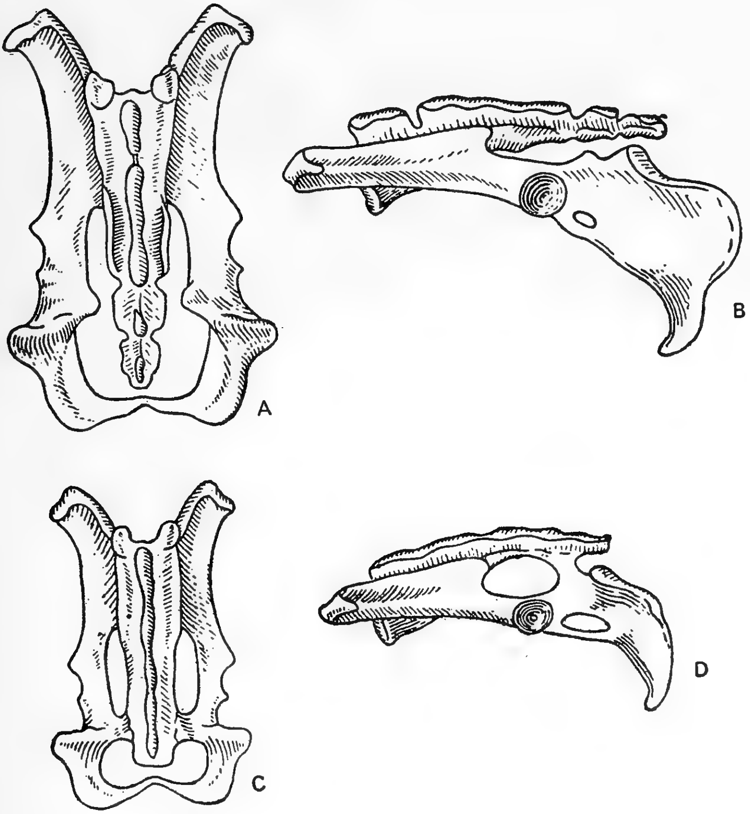

Figure 49. Pelvic bones and sacrum. ×1.6.

A, B—Spalax; *C, D—Microspalax*; *A, C*—from above; *B, D*—lateral view.

and the large ischial groove is not closed posteriorly.............
..................................2. **Spalax** Güldenstaedt.

G—Based on the femur, knee joint, and bones of the tarsus

1 (2). The width of the diaphysis of the femur at its narrowest part less than one and a half times exceeds its antero-posterior cross section at the same level. The width of the bone at the level above the articulating process is less than the intercondylary space or is approximately equal to it (measured between the external edges of the condyles). The length of the knee joint exceeds the width more than twice. The crista tibiae is massive and sharp all along. The medial ridge is absent or is faintly defined. The width of the proximal epiphysis of the fibula is two-thirds (or even less) of the width of the proximal epiphysis of the tibia........................
..................................1. **Microspalax** Nehring.

2 (1). The width of the diaphysis of the femur exceeds at its narrowest part one and a half times and more the antero-posterior cross section at the same level. The width of the bone at the level of processes above articulation always exceeds the intercondylary width. The length of the knee joint exceeds its width not more than two times. The crista tibiae in all the given cases is absent or is rarely faintly defined. The medial ridge is well developed and is sharp. The width of the proximal diaphysis of the fibula is two and a half times less than the width of the proximal epiphysis of the tibia.............
..................................2. **Spalax** Güldenstaedt.

1. Genus **MICROSPALAX** Nehring, 1897—SMALL MOLE RAT

Nehring, 1897: 168 (*nomen nudum*); Mehely, 1909: 22–25. *Nannospalax* Palmer, 1903, Sci. vol. XVII: 873 (*nomen praeocupatum*). *Ujhlyiana* Strand, 1922: 142. *Pliospalax* Kormos, 1932: 194–198, Abb. 1.

Genotype. Spalax ehrenbergi* Nehring, 1897; present day; eastern Mediterranean.

Diagnosis. The for. supracondyloideum is always present though it is above one of the occipital condyles, or usually above both. The tuberculum pharyngeum laterale are wide; they occupy almost all the space by width between the auditory bullae at the place of contact of the basal wedge and the base of the occipital bones (Figure 43). The base of the skull is concave because the basisphenoid and the base of the occipital bone are arranged at an angle. The auditory foramens are large. The

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*Should be *Microspalax ehrenbergi*—Editor.

length of the auditory bulla exceeds less than four times the largest diameter of the auditory foramen, usually 3.5 times (3.1–3.5–3.9). The lower portion of the lacrimal fossa in the majority of cases is pushed below the upper edge of the malar process of the mandibular bone, or is situated on the same level as the latter. The skull is placed low; its height at the level of the anterior edge of M^3 is half or even less than the length from the nasal bone up to the apex of the occipital process. The parietal bones form either a perpendicular trapezium or are at least triangular. The sagittal ridge is long; its height is only about one and a half times less than the length of the nasal bones (1.3–1.5–1.8) and concave (subgenus *Mesospalax*). In case the sagittal ridge is short (length of nasalia exceeds its length thrice or more), then there appear three longitudinal ridges of enamel (subgenus *Microspalax*) on the lower incisor. The ridge of the coronary-alveolar groove of the lower jaw (situated on the upper edge of the alveolar process all along its anterior half) is hardly defined, blunt, or is not marked absolutely (Figure 50). The fossa between the ridges (coronary-alveolar and the coronary-articular) is shallow and is usually open anteriorly and externally. The angular process is well separated and inclined from the external wall of the alveolar and in the majority of cases is a sharpened process at the end and considerably projects back in relation to the proc. alveolaris; its apex in mature and aged individuals is, as a rule, situated behind the posterior wall of the alveolar process or is situated at the level of the latter. The area on the external surface of the angular process is represented only along an inconsiderable length of its edge (near the apex actually) contouring only the place of attachment of the posterior portion of the musculus masseter lateralis. The sella externa is situated considerably below the sella interna. The alveolar process is placed low; its height at the inner edge in mature and aged animals is almost always less than the length of the lower row of permanent molars or is approximately equal to it. The dorsal arch of the first cervical vertebra (atlas) is narrower and has remnants of a neural spine in the shape of a bifurcated knob; its antero-posterior length is usually less than the height (anterior) of the canal for the medula oblongata. The neural spine of the second cervical vertebra (axis) is wide and low; its length, measured along the anterior border, exceeds its least width by less than twice. The neural spines of the thoracic vertebrae are short and wide. The sacrum is not ossified in the posterior portion; its width exceeds anteriorly less than thrice the same in the region of the fifth sacral vertebra. The neural spines and transverse processes are fused and form dorsal and transverse ridges (wings). The fifth sacral vertebra in males and females always contacts the spina ischiadica of the pelvic bone (comes in contact in females and fuses in males), as a result of which the large ischial groove is closed from behind (Figure 49). The medial surface of the scapula is flattened anteriorly. Its caudal edge is not widened because of a weakly developed crista caudalis; the maximum height of the caudal edge is more than three and a half times less than the maximum width of the scapula (3.6–3.9–4.6). The acromion ridge in mature and aged individuals is step-shaped, because the acromion tubercle (tuber spinae) is clearly defined (Figure 47). The acromion process is narrow; its width is more than twice less than its length. The cranial edge of the scapula has a sharp projection because its anterior and posterior cuts are equally well developed. The diaphysis of the shoulder bone is slightly flattened in the antero-posterior direction; its width is more than the proc. deltoideus (the free part of the crista tuberculi majoris) and approximately two and a half times exceeds the antero-posterior cross section measured at the same level (1.3–1.4–1.6). The deltoid process itself is, on an average, relatively longer and lower than in representatives of the genus *Spalax*; its lateral edge is, as a rule, situated at about the same level with similar lateral condyles, less bent, and the extent of the base always exceeds the distal width of the bone (measured from the lateral edge of the distal block up to the most protruding medial point of the medial condyle). The medial condyle is short and not wide; its length (slanting measurement) and the antero-posterior cross section (measured from the anterior edge of the medial portion of the block) only slightly exceeds half of the posterior width of the distal block. The elbow process of the elbow bone is constricted from above. The maximum width of its proximal epiphysis is greater than the length of the olecranon more than 2.5 times (2.6–2.7–2.9). The maximum width of the crescent-like groove at the level of the ulna joint is approximately equal to the width at the level of the edge of the proc. coronoideus because the proc. coronoideus ulnae is weakly developed. Furthermore, the olecranon is, on an average, shorter than in *Spalax*. The lateral fossa—the place of attachment of the long abductor of the pollux (M. abductor pollicus longus) and the M. extensor pollicus longus—is deep and clearly defined; its upper edge goes behind the lower edge of the proc. coronoideus at a distance approximately equal to the height of the crescent-like groove. The radius is, on an average, more slender than in representatives of the genus *Spalax*; its least width (at the base of the proximal epiphysis) is less than half the width of the latter (2.2–2.4–2.6). The distal epiphysis is weakly widened; its greatest width is less than the width of the proximal epiphysis or is approximately equal to it. The ilium is elongated in length (measured up to the anterior edge of the articulating process) and significantly exceeds the length of the ishium. The for. obturatum is large (Figure 49); its length exceeds the length of the articulating fossa or is approximately equal to the latter. Measurements of the spina ischiadica and of the tuber ischiadicus approximately coincide. As has been said before, the spina ischiadica always coalesces (in males) or touches (in females) with the wings of the sacrum. The femur has a diaphysis which is narrow and slightly flattened antero-posteriorly; the width of the bone at its narrowest less than one and a half times exceeds the antero-posterior cross section at the same level (1.0–1.2–1.4). The tubercles above the articulation are weakly developed; the width of the bone at the tubercles in the majority of cases is less than the width between condyles, or is approximately equal to it. The knee joint is long and narrow; its length more than twice exceeds the width. The crista tibiae is massive and sharp all along. The medial ridge is absent or is faintly defined. The anterior bend of the bone is more sharply defined than in representatives of the genus *Spalax*. The proximal epiphysis of the fibula is widened; its width is one and a half times less than the width of the proximal epiphysis of the tibia (1.2–1.3–1.5). The symphysis of the tibia and fibula is short, about two and a half times less than the full length of the tibia (2.3–2.5–2.8). The free portion of the fibula is bent back externally more sharply than in all the species of the genus *Spalax*.

Comparison. The differences between the genera *Microspalax* and *Spalax* stand out clearly if their diagnostic characteristics are compared. In addition to the characteristics noted in these pages, representatives of the genus *Microspalax* differ, on an average, from species of the genus *Spalax* by small absolute measurements, by shortened upper and lower diastemata, by compact (narrowed) upper and lower incisors, and also by more complicated wearing surfaces on permanent molars, especially the front ones, in the majority of cases cited. At the same time, the amount of reduction in roots of permanent molars is exhibited to a lesser degree than in species of the genus *Spalax*.

Composition of the genus. Two subgenera—*Microspalax* Nehring, 1897, and *Mesospalax* Mehely, 1909, with three present-day and three fossilized Mio-Pliocenic species: *M. ehrenbergi* Nehr., 1897; *M. compositodontus* sp. nov.; *M. macoveii* (Simionescu, 1930); *M. odessanus* sp. nov.; *M. nehringi* (Satunin, 1898); *M. leucodon* (Nordmann, 1840).

Until recently, the small mole rats from the subgenera *Microspalax* and *Mesospalax* were taken to be under the genus *Spalax*. However, the differences in the structure of the skull, lower jaw, and bones of the postcranial skeleton of these animals are so clear cut and great that their separation into independent genus, in our opinion, is well deserved.

Distribution and geological age. Eastern Mediterranean (northern Libya, Syria), Asia Minor (Turkey, Iraq), Soviet Trans-Caucasus, Balkan and Pre-Balkan regions (Yugoslavia, Hungary, Greece, Bulgaria, and European Turkey), northwest Black Sea region (Rumania, Moldavian SSR, Odessa region of the Ukraine, SSR), Prikarpate of Hungary, Rumania, and Chernovits region of Ukraine SSR (Soviet Bukovina); modern. Late Miocene—the Middle and Late Pliocene of the northwestern Black Sea region (Rumania, Moldavian SSR, Odessa, Nikolaev, and Kherson regions of the Ukraine), Azov region of Ukraine SSR.

KEY FOR IDENTIFICATION OF SUBGENERA OF MICROSPALAX

1 (2). The lower incisor has three longitudinal ridges on the anterior surface. The lambdoid and sagittal ridges are weakly developed even in the mature and aged. The sagittal ridge is represented only on the parietal bones and is faintly defined on the temporal bone. The width of both parietals approximately exceeds thrice the length of the upper row of permanent molars. The width of each of the parietal bones in mature and old individuals is approximately equal to its length, or even appreciably exceeds that of the latter. The alveolar process of the lower jaw is about equal to the articular one in height.............................1. **Microspalax** Nehring. (Late Miocene to present day).

2 (1). The anterior surface of the lower incisor is smooth without longitudinal ridges. The lambdoid and sagittal ridges in mature and old individuals are well developed; the sagittal ridge is present equally on the parietal and temporal bones. The width of both parietals exceeds significantly less than twice the length of the upper line of permanent molars; the width of each of the parietal bones in mature and old individuals is quite less than its length. The alveolar process of the lower jaw significantly exceeds the articular one in height. ....2. **Mesospalax** Mehely. (Holocene, including the recent period).

1. Subgenus **MICROSPALAX** Nehring, 1897

Nehring, 1897: 168. *Nannospalax* Palmer, 1903, Sci., vol. XVII: 873. *Pliospalax* Kormos, 1932: 194–198.

Genotype. *Spalax* ehrenbergi* Nehring, 1897; present day; eastern Mediterranean (northern regions of Libya and United Arab Republic, Israel, Jordan, Lebanon, Syria, southern regions of Turkey).

Diagnosis. The subgenus contains the smallest representatives of the subfamily Spalacinae. The lower incisors have three longitudinal ridges on the anterior surface. The lambdoid and sagittal processes of the skull are weakly developed even in adult and old individuals; the sagittal ridge is represented only on the parietal bones and is hardly defined on the temporal. The parietal bones are quite wide; the width of the parietale

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*Should be *Microspalax ehrenbergi*—Editor.

approximately exceeds twice the length of the upper row of permanent molars. In addition, the width of each of the parietal bones in adult and old individuals is about equal to its length or even appreciably exceeds the latter. The alveolar process of the lower jaw is low, and is about equal to the articular one in height.

Comparison. Microspalax Nehring, 1897 differs from representatives of the subgenus *Mesospalax* by:

1. Permanent presence of three longitudinal ridges on the anterior surface of the lower incisors. These are always absent in *Mesospalax.*

2. Weakly developed lambdoid and sagittal ridges. In *Mesospalax* the corresponding ridges are developed significantly stronger; moreover, the sagittal one in mature and old individuals is present on the parietal as well as on the temporal bones.

3. Widened parietal bones. In *Mesospalax* the width of the parietale in mature and old individuals less than twice exceeds the length of the upper row of permanent molars, and the width of each parietal bone is considerably less than its length.

4. A low alveolar process which is about the same height as the articular one. In *Mesospalax,* the alveolar process is considerably higher up than the articular one. The relation of height in the alveolar process to the condylary length of the lower jaw is equal to 9.0–15.3–21.0 in *Microspalax,* as against 12.3–20.0–26.5 in *Mesospalax.*

Differences between *Microspalax* and *Mesospalax* are also found in the average values of the proportions of the following sections of the skull and lower jaw:

1. The occipital bone is relatively lower (the relation of its height to the condylobasal length is 30.0–33.3–37.0 against 31.0–43.4–51.0 in *Mesospalax*).

2. The upper diastema is shorter (the value of the diastema-tooth relation is 141.4–179.4–221.5 as against 160.0–206.1–280.3).

3. The nasal bones are relatively narrower (the relation of their width to the length of the permanent molar rows is 62.6–72.6–79.7 as against 67.1–83.0–100.0).

4. The molar width is less (its relation to the condylobasal length is 70.0–72.0–75.0 as against 72.0–77.2–83.0).

5. The M^3 is comparatively longer and narrower (relation of length of M^3 to the same in the preceding molar, and width of the third permanent molar to its length is equal to 70.8–87.3–105.0 and 72.2–102.8–123.5 against respectively 56.0–78.0–100.0 and 88.2–108.9–125.0).

6. The lower diastema is relatively shorter (the value of the diastema-tooth index is 61.5–75.0–93.4 as against 70.0–89.6–125.4).

Composition of the subgenus. One present-day and three fossil Mio-Pliocenic species—*M. ehrenbergi* (Nehr., 1897), *M. compositodontus* sp.

nov., *M. macoveii* (Simionescu, 1930), and *M. odessanus* sp. nov.

Distribution and geological age. Eastern Mediterranean (northern regions of United Arab Republic, Libya, Israel, Jordan, Lebanon, Syria, Iraq, and possibly the southern regions of Turkey); present-day; Late Miocene; Middle and partly Late Pliocene, northwestern Black Sea region (Rumania, Moldavian SSR, around the Black Sea, and regions around the Azov in the Ukraine).

KEY FOR IDENTIFICATION OF SPECIES OF THE SUBGENUS MICROSPALAX

1 (2). The upper incisors have two longitudinal ridges on the anterior surface. The nasal bones have a sharply defined longitudinal slit-like depression in the region of the sutures between them. The symphysis tubercle of the lower jaw is flattened, the mandibular angle is weakly defined, and the angular process is slightly bent downward. .... 1. **M. ehrenbergi** (Nehring). (Holocene, including recent).

2 (1). The anterior surface of the upper incisors is smooth and devoid of longitudinal ridges. The nasal bones have no longitudinal slit-like depression (being smooth or a little concave). The symphysis tubercle of the lower jaw is sharply defined, the mandibular angle is well developed, the angular process is sharply bent downward.

3 (4). The mesocone on M^1 is well developed in almost all stages of tooth erosion (vanishes only in very old age). The entoconid on M_1 is not fused with the posterior collar, the posterior mark is absent until very old age; separate from the metaconid and entoconid, the well-developed mesoconid is always present and, along with the latter, forms a characteristic inner fork, the neck width of which exceeds one-third the general length of the wearing surface of the tooth or is about equal to the last one (Figure 6). M^3 has three roots. .... 2. **M. compositodontus** W. Topachevskii, sp. nov. (Late Miocene).

4 (3). The mesocone on M^1 is always absent. The entoconid on M^1 is fused with the posterior collar in old age, as a result of which the posterior intruding fold of the inner line forms a posterior mark; the mesoconid is not fully developed (the free mesoconid is found in some species in young age; however, in this case the width of the neck of the internal fork does not exceed one-fourth the total length of the wearing surfaces of the tooth). M^3 has two roots.

5 (6). The width of the hard palate between M^1 is less than the width of the alveoli of the anterior permanent molar or is about equal to it;

the central ridge of the palate is faint, in the shape of a slender cylinder, or is totally absent. M_1 has an independent mesoconid (in the young) or an anterior mark (in semi-mature and mature); the width of the neck of the inner fork is about one-fourth the total length of the grinding surface of the tooth; the posterior mark appears only in the mature. The symphysis tubercle of the lower jaw is short; its length is approximately equal to the two similar anterior permanent molars........3. **M. macoveii** (Simionescu). (First half of Mid-Pliocene).

6 (5). The width of the hard palate between M_1 exceeds the width of the alveolus of the anterior permanent molar; the central ridge of the palate is larger and wider. The mesoconid on M_1 is not fully developed, the anterior mark is absent; the width of the neck of the internal fork (if it is present at all) is considerably less than one-fourth the total length of the grinding surface of the tooth; the posterior mark is present in all stages of wearing (with the exception of very young individuals) (Figure 60). The symphysis tubercle of the lower jaw is elongated; its length is about equal to the length of a full line of permanent molars..4. **M. odessanus** W. Topachevskii, sp. nov. (Second half of Middle and Late Pliocene).

1. **Microspalax ehrenbergi** (Nehring, 1897)—**Ehrenberg Mole Rat**

Spalax ehrenbergi Nehring, 1897: 178–180. *S. typhlus* Fritsch, 1893, Abhandl. Naturforsch. Gesellsch. Halle: 79, 80 (*nomen praeocupatum*). *S. kirgisorum* Nehring, 1897: 176–178, Abb. 5. *S. aegyptiacus* Nehring, 1897: 180, 181. *S. intermedius* Nehring, 1897: 181–183. *S. Fritschi* Nehring, 1902: 78–87, Figure 1, *S. berytensis* Miller, 1903: 162.

Holotype. Institute of special Zoology and Zoological Museum of the University of Humboldt in Berlin, No. 5119 (Nehring, 1897: 178, Abb. 6); described from the spirit-preserved specimen from the vicinity of Tel-Aviv (Israel).

Material investigated. Thirty skulls and skins obtained around Egypt, Syria, Lebanon, Jordan, and southern regions of Turkey. They are preserved in the collections of the Zoological Museum of the University of Humboldt in Berlin, the Paris National Museum, and the Zoological Institute of the Academy of Sciences of the USSR.

Diagnosis. This is the smallest of the known representatives of the subfamily Spalacinae (length of body, 130 to 160 mm; condylobasal length of skull, 31.0–38.1–43.9 mm; length of upper row of permanent molars, 6.5–7.4–8.3 mm; length of lower row of permanent molars, 6.4–7.3–7.9 mm). The upper incisors have two longitudinal ridges on the anterior surface. The nasal bones have a sharply defined longitudinal slit-like depression in the region of the sutures between them. The temporo-nasal and temporo-maxillary sutures form a clear angle with a backwardly-directed apex.

The hard palate between M^1 is narrow; its width is approximately equal to the width of the alveoli of the anterior permanent molars. The central ridge of the palate is well developed and slightly widened. The mesocone on M^{1-2} and mesoconid on M_1 is always absent. The coalescence of the entoconid with the metaconid does not take place until old age, as a result of which the anterior mark is absent in young, semi-mature, and mature individuals. The entoconid of this tooth is not fused with the posterior collar until old age; the posterior mark is absent, almost throughout life.

Description. The skull is wide in the infraorbital and narrowed in the incisorial and rostral parts (the relation of the infraorbital, incisorial and rostral width to the length of the upper row of permanent molars is equal to 78.9–96.4–110.6, 69.2–76.4–86.1, and 97.3–108.6–126.0) with a relatively short diastema (value of diastema-tooth index is 141.4–179.4–213.5). The nasal bones are narrow with a sharply defined slit-like longitudinal depression (the relation of their width to the length of the lines of permanent molars is 62.6–72.6–79.7). The temporo-nasal and temporo-maxillary sutures form an angle with a backward-directed apex. The nasal opening is high and narrow (relation of its width to the length of lines of permanent molars is 49.3–60.2–66.7; of height to width, 61.0–73.3–81.6). The palate at the level of M^1 is narrow (its width is approximately equal to that of the alveoli of the anterior permanent molars). The central ridge of the palate is well defined and is slightly broad. The foramens behind the palate are clearly marked throughout the life span. The cut behind the palate is wide; its width is approximately equal to the length of the third permanent molar. The molar arches are constricted; the relation of the molar width to the condylobasal length is 70.0–72.0–75.0. The parietal bones are wide; the width of the parietale measured up to the lambdoid ridge approximately exceeds twice the length of the permanent molars; the width of each of the parietal bones in mature and old individuals is approximately equal to its length or even considerably exceeds the latter (Figure 50). The lambdoid and sagittal ridges in mature and old individuals are weakly developed; moreover, the latter is clearly defined only on the parietal bones and are faintly marked on the temporals. The occipital bone is low (the relation of its height to the condylobasal length is 30.0–33.3–37.0). The dental row is relatively long (relation of length to condylobasal length of skull is 17.0–18.7–22.0).

The upper incisors are narrow (relation of width to antero-posterior cross section is 76.0–83.2–94.0) with two longitudinal ridges on the anterior surface.

M^1 (length, 2.3–2.6–2.9 mm; width, 1.8–2.3–2.7 mm; relation of width

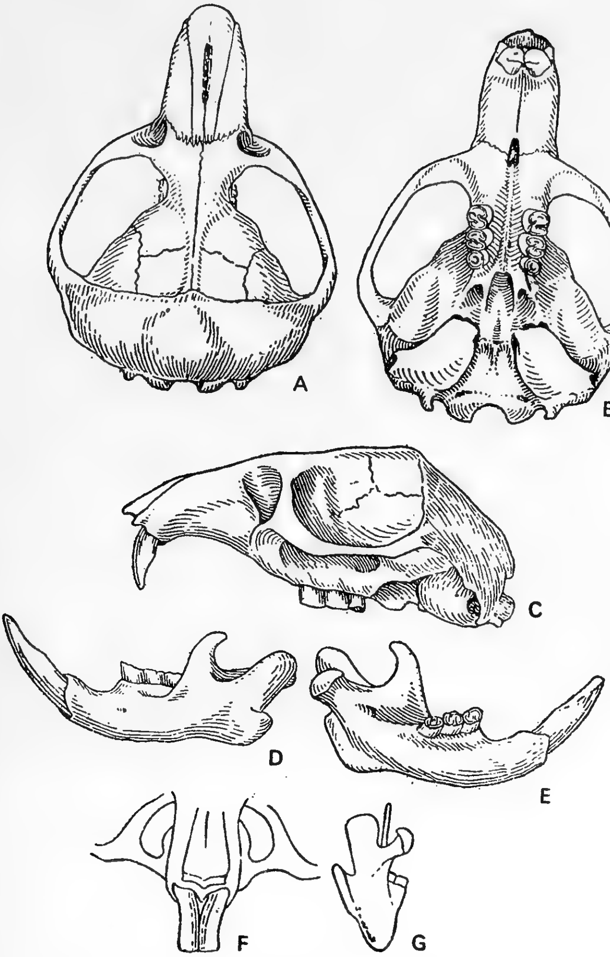

Figure 50. *Microspalax ehrenbergi* (Nehr.). ×1.6.

A—axial skull, from above; *B*—the same, from below; *C*—the same, from the side; *D*—lower jaw, from outer side; *E*—the same, inner view; *F*—rostral section of skull, anterior view (schematic); *G*—lower jaw, posterior view (schematic).

to length, 78.3–88.3–108.3) has no trace of the mesocone. The paracone is not fused until old age with the anterior collar (Figure 51). The degree of fusion of the metacone with the posterior collar varies; they are either fused or partially separated (Figure 51); there are two or three intruding folds on the outer line (when the metacone is not fused) and on the inner line, one only. The process of closure in the intruding folds into marks ends earlier in the outer line because of tooth erosion, than in the inner lines. The arrangement of formation of marks is as follows: the posterior (vanishing in the old), the anterior external, the central external, and finally, the internal. In very old individuals, the marks could be absolutely absent. The protocone and hypocone are approximately equal in magnitude. There are three large roots with marks of bifurcation on the internal and two external, out of which the posterior is less developed than the anterior (Figure 52).

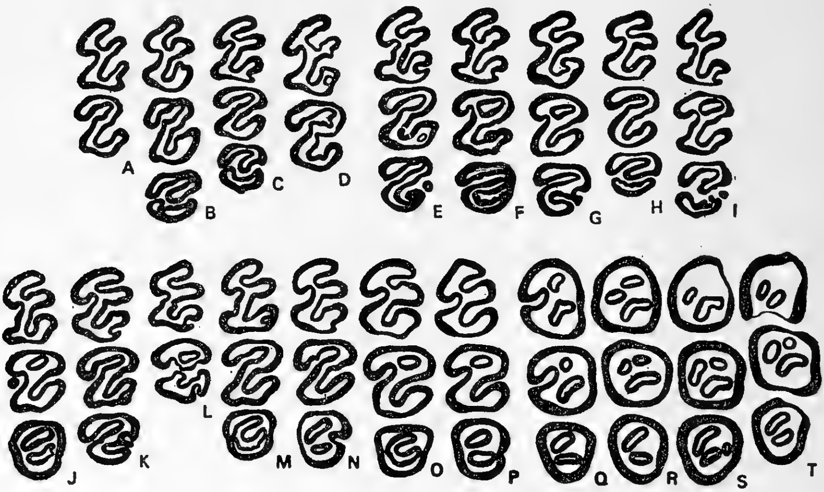

Figure 51. *Microspalax ehrenbergi* (Nehr.), upper line of permanent molars. ×8.

A to D—young; *E* to *I*—semi-mature; *J* to *P*—adult; *Q* to *T*—old.

M^2 (length, 1.8–2.2–2.4 mm; width, 1.8–2.3–2.6 mm; ratio of width to length, 95.5–107.3–135.3) is, on an average perhaps, more broadened than in the European Pliocenic *Microspalax*. The mesocone is completely reduced. The metacone, as a rule, is fused with the posterior collar. The tooth has a deep intruding fold on each side, because of which the wearing surface in the majority of cases is S-shaped. Sometimes, the inner intruding fold forms an anterior mark. The order of closure for intruding folds and the formation of marks is as follows: the inner portion of the intruding fold, the external, and finally, the rest of the portion of the inner one. There are three roots—the massive inner and two weakly developed external ones. In the fissure (depression) between the protocone and hypocone there is sometimes an additional tubercle (Figure 50).

M^3 (length, 1.6–1.9–2.3 mm; width, 1.6–2.0–2.2 mm) is wide (ratio of width to length is 81.8–105.7–123.5). The form of the wearing surfaces is exceedingly variable. The variations are as follows: (a) hypocone and metacone are isolated from the rest of the parts of the crown of the tooth (Figure 51); (b) the posterior lobe of the crown (hypocone and metacone) is fused with the anterior one, as a result of which the wearing surface assumes an S-shaped form; and (c) usual variations related to the formation of the marks by closure of the intruding folds. On the whole, the tooth has an intruding fold on each side. However, the complete closure

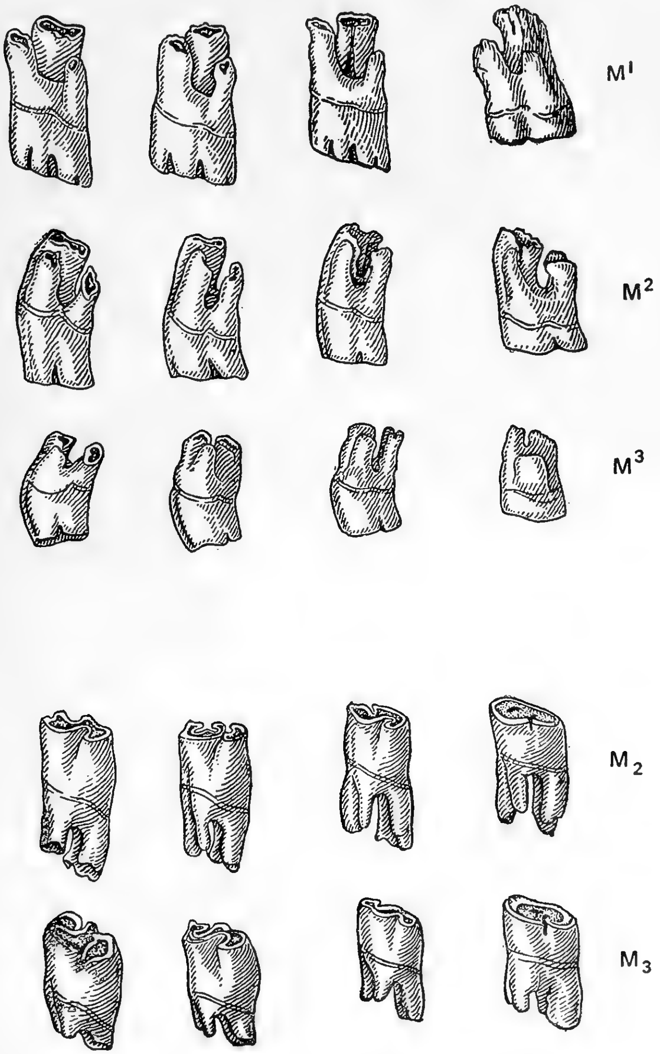

Figure 52. Structure of roots of upper and lower permanent molars of *Microspalax ehrenbergi* (Nehr.) (Mehely, 1909).

of the inner fold, differing from the preceding permanent molar, perhaps takes place earlier than that of the outer fold. The roots are usually three —the massive posterior and two anterior ones of normal size (Figure 52). Rarely the roots of the anterior molars exhibit a tendency toward fusion.

The lower jaw has a relatively elongated diastema (for representatives of the subgenus *Microspalax*) and a low horizontal branch; the ratio of the length of the diastema and the height of the horizontal branch at the level of the center of the alveolus of the anterior permanent molar to the length of the line of M_1–M_3 is respectively 61.5–77.0–93.4 and 78.5–88.1–101.3. In addition the horizontal branch is typically relatively less thick at the level of M_2. Thus, the value of the ratio of the corresponding measurement to the length of the lines of the permanent molars is equal to 37.5–45.7–57.8. The symphysis tubercle is flattened and elongated; its length is approximately equal to the length of the full row of permanent molars. The ridge in the space between the symphysis tubercle and the angular process is always present. The mandibular angle is weakly defined (Figure 50). The lower edge of the masseter area terminates directly near the alveolar edge. The angular process is more weakly defined than in the European Pliocenic *Microspalax* and is less inclined below with a relatively long base (ratio of length of the latter to length of the lines of permanent molars is 94.2–112.4–133.3). The alveolar process is low, and is approximately equal in length to the articular one. The mental (at the chin) foramen is somewhat shifted toward the alveolar edge. The coronary tubercle is saddle-shaped, tapering posteriorly in relation to the horizontal branch. The row of the permanent molars is relatively elongated (relation of length to condyle length of the lower jaw, 25.0–28.6–33.0).

The lower incisor is narrow (relation of width to antero-posterior cross section, 64.0–74.5–86.2), with three elongated ridges on the anterior surface.

The mesoconid on M_1 is absent. The entoconid is not fused until old age with the metaconid and the posterior collar respectively, because of which the anterior and posterior marks are absent on the teeth of the young, semi-mature, and mature animals. On the whole, the wearing surface is characterized by the presence of one outer and two inner intruding folds (Figure 53). The order of closure of the intruding folds into marks because of tooth erosion is as follows: the posterior inner fold, the inside portion of the anterior inner fold, and the outer one. The measurements of the protoconid exceed the measurements of the hypoconid less than two times. There are two roots: the posterior one is rather more massive than the anterior; is flattened in an antero-posterior direction; and has evidences of bifurcation. Tooth measurements are as follows: length, 2.2–2.5–2.9 mm; width, 1.9–2.2–2.5 mm; relation of width to length, 77.0–86.2–95.6.

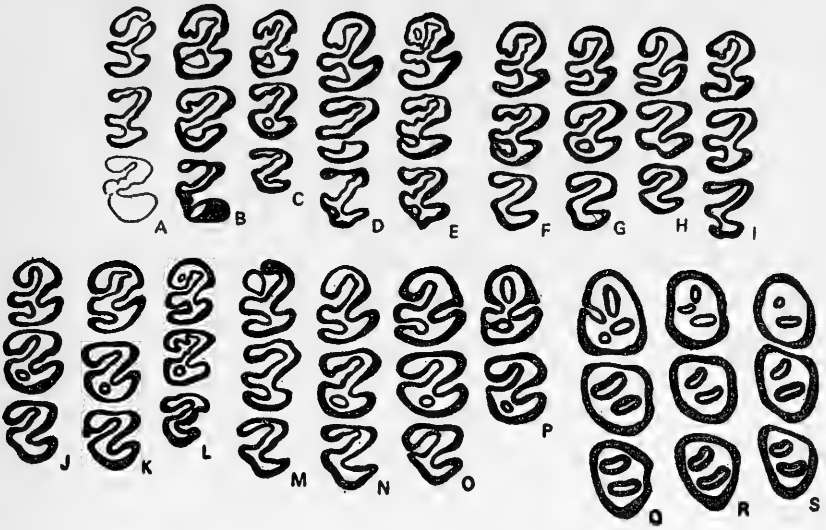

Figure 53. *Microspalax ehrenbergi* (Nehr.), lower row of permanent molars. ×8.

A to *E*—young; *F* to *I*—semi-mature; *J* to *P*—adult; *Q* to *S*—old.

M_2 (length, 1.8–2.1–2.7 mm; width, 1.9–2.2–2.5 mm) is, on the average perhaps, relatively wider than in the Pliocenic European *Microspalax* (relation of width to length, 80.0–104.3–125.0). The form of the wearing surfaces varies very much. In all the given cases, the tooth either has a posterior mark and an intruding fold—each in the outer and inner lines—or it is not fused with the posterior collar of the entoconid and the two intruding folds in the inner and one in the outer lines. The different variations are as follows: (a) the posterior collar and the hypoconid are isolated from the rest of the parts of the crown; (b) the entoconid is fused with the posterior collar and the posterior mark with the external intruding folds, because of which the wearing surface has an S-shaped form, i.e., it is characterized by the presence of a deep intruding fold in both the outer and inner lines. The order of the closure of the intruding folds into marks is as follows: the posterior inner, the anterior inner, and the outer. The tooth has two antero-posteriorly flattened roots with clear signs of bifurcation. The posterior root is rather more massive than the anterior one.

M_3 (length, 1.6–2.1–2.8 mm; width, 1.7–2.0–2.2 mm) is also relatively wider than in the European Pliocenic *Microspalax* (relation of width to length, 70.0–96.4–116.7). The form of the wearing surfaces for the majority of the given cases was S-shaped. The presence of an additional posterior intruding fold was rare (present only when the entoconid was not fused with the posterior collar). The closure of the intruding folds into marks took place more quickly in the inner line than in the outer. The tooth has two roots; moreover, the anterior one has a bifurcated end (Figure 52).

Comparison. It differs from all the fossil European species of the subgenus *Microspalax* by:

1. The presence of two longitudinal ridges on the anterior surface of the upper incisors. They are always absent in European species.

2. On an average, narrower upper and lower incisors (ratio of width to antero-posterior cross section is equal to 76.0–83.2–94.0 for the upper, and 64.0–74.5–86.2 for the lower incisors, against respectively 82.6–90.0–95.0 and 75.7, 80.6, 84.6, 87.5 in *M. compositodontus*; 95.4, 100.0, 100.0 and 70.3–86.2–93.5 in *M. macoveii*; and finally 83.3–89.7–95.8 and 71.4–81.2–90.0 in *M. odessanus.*

3. On an average, a wider M^3_3; the magnitude of the ratio of width of the last permanent molar to its length is equal to 81.8–105.7–123.5 for the upper, and 70.0–96.4–116.7 for the lower tooth as against respectively 77.8 and 72.7 in *M. compositodontus*; 88.9 and 87.5, 90.5, 95.6 in *M. macoveii*; and finally 95.0–100.0–115.0 and 82.7–89.8–95.6 in *M. odessanus.*

In addition to the traits described above, *M. ehrenbergi* differs from the Late Miocene–Early Pliocene *M. compositodontus* by the absence of a mesocone on M^{1-2} and of a mesoconid on M_1; of additional intruding folds on the inner line and tubercle at the base of the paracone on M^2; and also by a weakly developed hypocone on M^{1-2} and protocone on M_1—the measurements of which exceed respectively less than twice the protocone and hypoconid (in *M. compositodontus* the difference in the aforementioned tubercles is more clearly expressed).

The presence of three roots on M^1 and M^3 in *M. ehrenbergi* could be taken as an additional peculiarity of the lower jaw to the ones already mentioned which helps in differentiating *M. ehrenbergi* from the Mid-Pliocene European species of the given subgenus, *M. macoveii* and *M. odessanus* (in their Mid-Pliocenic European forms, there are two, as a rule); the flattened symphoidal tubercle and faintly defined mandibular angle; on an average, a relatively higher and thicker horizontal branch (relation of its height at the level of M_1 and thickness at the level of M_2 to the length of the row of permanent molars is equal to 78.5–88.1–101.3 and 37.5–45.7–57.8 against respectively 81.8–97.6–108.0 and 46.0–54.0–62.7 in *M. macoveii*; and 80.0–96.0–107.6 and 42.0–51.4–55.0 in *M. odessanus*); and also the process which is saddle-shaped and considerably steeply inclined backward in relation to the alveolar edge of the horizontal branch (in fossil European forms, this process is slanting, steeply placed in relation to the horizontal branch and its apex is almost not bent backward). Finally, average smaller measurements than the above-mentioned species' also differentiate it from others.

It is better to add to the above that this species differs from *M. macoveii* by a long lower diastema (the magnitude of the diastema-tooth ratio is 61.5–77.0–93.4 against 62.5–70.8–75.0); a long symphoidal tubercle of the lower jaw (its length is approximately equal to the length of a full line of permanent molars and in *M. macoveii* the magnitude of this measurement approximately corresponds to the length of M_1–M_2); the supramaxillary foramen is shifted to the alveolar edge (in *M. macoveii* it is situated equidistant from the alveolar and the lower edges of the horizontal branch); an elongated lower edge of the masseter area (in the mole rat of Ehrenberg it terminates in the immediate vicinity from the alveolar edge, and in *M. macoveii* approximately at the level of the supramaxillary foramen); absence of a free mesoconid or the anterior mark on M_1; and also of an additional intruding fold in the inner line on M_3 of young, semi-mature, and mature animals. It differs from *M. odessanus* by the presence of a clearly defined longitudinal depression on the nasal bones, in the shape of temporo-nasal and temporo-maxillary sutures (in *M. ehrenbergi*, it forms an angle with its apex pointing backward; in *M. odessanus*, it is in the shape of a straight line); a narrow hard palate between M^1 (its width is approximately similar to the width of alveolus of the anterior permanent molar; in *M. odessanus*, it is wider than the latter); a constricted skull in the incisorial and rostral sections; a wide groove behind the palate (width of this groove in *M. ehrenbergi* is approximately equal to the length of the last permanent molar; in *M. odessanus*, it is less than the latter); and an absence of a posterior mark on the M_1 of young, semi-mature and mature individuals.

Measurements. Condylobasal length of skull, 31.0–38.1–43.9 mm; basic length, 28.3–35.7–41.9 mm; length of nasal bones, 13.9–16.4–19.2 mm; total length of parietal and temporal bones, 13.9–16.3–19.5 mm; length of parietal bones, 5.7–7.2–9.1 mm; length of upper diastema, 9.9–13.2–15.9 mm; length of hard palate, 18.6–23.4–27.8 mm; length of upper row of permanent molars, 6.5–7.4–8.3 mm; width of nasal opening, 3.7–4.2–4.8 mm; incisorial width, 4.5–5.7–6.8 mm; width of nasal bones anteriorly, 4.4–5.3–5.9 mm; rostral width, 7.1–8.0–9.7 mm; width behind the eyes, 6.2–7.1–8.1 mm; width of both parietals, 11.4–12.8–14.8 mm; width of parietal bone along lambdoid ridge, 6.0–7.0–8.8 mm; malar width 22.9–27.2–32.8 mm; width of occipital (largest width), 22.1–25.5–27.9 mm; width of auditory bullae, 8.7–10.3–11.6 mm; length of auditory bullae, 6.6–7.0–7.7 mm; width of upper incisor, 1.5–1.9–2.4 mm; antero-posterior cross section of upper incisor, 1.7–2.2–2.7 mm; height of occipital bone, 10.4–13.2–15.5 mm; height of nasal cavity, 2.4–3.1–3.6 mm; angular length of lower jaw, 22.0–25.1–29.3 mm; condylary length of lower jaw, 20.1–23.9–27.7 mm; length of lower diastema, 4.8–5.6–6.9 mm; length of lower row of permanent molars, 6.4–7.3–7.9 mm; height of horizontal branch at the level of center of alveolus of M_1, 5.8–6.4–7.4 mm; thickness of horizontal branch at the level of M_2, 2.7–3.3–4.4 mm; height of alveolar process from inside, 2.0–3.9–5.1 mm; width of lower incisor, 1.4–1.9–2.5 mm; antero-posterior cross section of lower incisor, 1.8–2.5–3.0 mm.

Note. M. ehrenbergi is the only recent representative of the subgenus *Microspalax.* In addition to highly specialized traits, it has preserved a number of primitive characteristics in the construction of the skull, the lower jaw, and the permanent molars. Before the traits which determine the subgeneric disposition of the species, the combination of morphological structures which indicate a lesser adaptability toward a burrowing type of life has to be enumerated first (the narrowed upper and lower incisors, and the relative characteristics of the facial skull and the lower jaw). As far as the masticatory apparatus is concerned, its primitiveness is determined by the complexity of the picture of the wearing surfaces of first, the permanent molars, that of M_1, and then the roots which are reduced to a lesser extent. From the degree of development of adaptation to burrowing, the mole rat of Ehrenberg stands on a rather lower evolutionary step than even the Mid-Pliocenic and Late Pliocenic fossils of the European *Microspalax*; from the viewpoint of the degree of specialization in teeth, the fossil Mid-Pliocenic *M. odessanus* exceeds it. All this makes easy a statement about the comparatively early (perhaps beginning of the Pliocene) separation of the Asia Minor and European branches of the subgenus, each of which developed further independently. It can also be presumed that the indicated species has greatly preserved the characters of the original type common for *Microspalax* of Asia Minor and Europe.

In his first description of the species, Nehring (1897) included in the group of Asia Minor *Microspalax* three more species—*M. kirgisorum* (Nehr.), *M. aegyptiacus* (Nehr.) and *M. intermedius* (Nehr.)—besides *M. ehrenbergi* by erroneously considering individual and age variables in the structure of permanent molars as taxonomic traits. In his work, the description of *M. kirgisorum* has been done before that of *M. ehrenbergi.* However, there was some dispute over the fixation of habitat for the typical example of *M. kirgisorum.* Nehring obtained the skull and skeleton from Shlyuter by "unfair means"; Shlyuter indicated that they were found in the steppes of Kirgiziya, near the Volga (Rinpeski, western Kazakhstan region; Ognev, 1947), i.e., around the present day area of *S. giganteus* Nehr. By the way, the fact that the skull belonged to *Microspalax* was beyond doubt and Mehely indicated this in his time (1909). This is shown by such traits as comparatively smaller dimensions, the presence of very narrow upper and lower incisors with longitudinal ridges on the anterior surface, weakly developed sagittal and lambdoid ridges, a narrow facial section, nasal bones with a sharply defined longitudinal slit-like depression, and a number of other peculiarities of construction of the skull and the permanent molars (the lower jaw and the post-cranial skeleton were not described by Nehring). Taking all this into consideration and remembering that at present only *S. giganteus* is found in the Volga region, it can be said confidently that the specimen described by Nehring was not found in the Volga area. In this way, the place of the find of the holotype *M. kirgisorum* remains unknown. All the aforesaid forces us not to use this nomenclature for the species, and out of the three remaining synonyms, select the next one in order of description, i.e., *M. ehrenbergi.*

Mehely (1909) also did not recognize *M. kirgisorum*, *M. aegyptiacus* and *M. intermedius* as independent species, considering the first two as variants of *M. ehrenbergi* and the last one as a synonym for *M. e. kirgisorum* (this subspecies, in the opinion of Mehely, includes mole rats living in the region of Israel, Syria, Jordan, and Lebanon). However, as will be shown below, the separation of variants was done by them exclusively on a territorial principle, without sufficient basis for morphological differences. Thus, the differences attested to for the nominal subspecies and *M. e. kirgisorum* Nehring, which according to the opinion of Mehely (1909; 24, 25) are contained in the different number of ridges on the anterior surface of the lower incisors, the magnitude and degree of the pointedness of the angular process of the lower jaw and, also, in the details of construction of the roots of permanent molars and measurements, have not been confirmed on a series of skulls.

Nehring (1902) described a new species, *M. fritschi* Nehring on the basis of a lower jaw found in Holocene sediments of Lebanon. There is no doubt that this lower jaw belonged to the subgenus *Microspalax* which is shown by comparatively smaller measurements and the presence of three longitudinal ridges on the anterior surface of the incisor. Nehring, and after him even Mehely (1909) thought that the angular process on the jaw from Lebanon was on the whole more massive and rather more acutely inclined outward than in the then-living *M. ehrenbergi.* However, this was not confirmed during a comparison with a typical example from the series of lower jaws of the modern *M. ehrenbergi.* The traits described by Miller (1903) in his diagnosis of *M. berytensis* (Miller) from Libya (around Beirut) also fall within the range of individual variability. Thus, all the aforesaid makes us regard even these names as synonyms of *M. ehrenbergi.*

Distribution and Geological age. The northern regions of Libya and the United Arab Republic, Israel, Jordan, Libya, Syria, Iraq, possibly the southern regions of Turkey. Recent; fossil remains are known only from the Holocene sediments of Libya.

Subspecies 1. *M. e. ehrenbergi* Nehring, 1897 (including *M. e. kirgisorum* Nehring, 1897). Distributed in Israel, Jordan, Libya, Syria and possibly in southern regions of Turkey.

2. *M. e. aegyptiacus* Nehring, 1897. It differs from the nominal subspecies by, on an average, a narrower rostral section of the skull, elongated nasal bones, and a more strongly developed proc. naso-basalis. It is distributed in North Africa (Egypt and possibly from Libya up to Tripoli).

2. **Microspalax compositodontus** W. Topachevskii, sp. nov.—**Complex-toothed Mole Rat**

Holotype. Institute of Zoology, AN Ukraine SSR, No. 41–712; isolated left upper first permanent molar (M^1 sin.); around the Black Sea of Ukraine, Andreevka of Berezan district of Nikolaev region; Late Miocene.

Paratypes. Isolated permanent molars—M^2 sin. (No. 41–713), M^3 dex. (No. 41–714), M_1 sin. (No. 41–715) and M_3 sin. (No. 41–716). All are preserved in the collections of the Institute of Zoology, AN Ukraine SSR.

Additional Material. Isolated incisors: upper, seven samples; lower, five samples. These are preserved at the same place.

Diagnosis. Measurements are small: length of M^1 is 2.3 mm; of M_1 is 2.6 mm. The mesocone of M^1 is well developed at almost all stages of tooth development (perhaps it becomes completely complex as compared to similar permanent molars of other representatives of the genus). M_1 entoconid of this tooth is not fused with the posterior collar. The massive mesoconid is separated from the metaconid and the entoconid is always present; along with the latter, it forms a characteristic inner fork; the neck width of which exceeds one-third the length of the wearing surface of the tooth, or is approximately equal to it. The upper incisors are without two longitudinal ridges on the anterior surface.

Description. Remains of the skull and lower jaw are not known. The upper incisors are narrow; the relations of width to antero-posterior cross section is 82.6–90.0–95.0. The enamel on their anterior surface is smooth, without longitudinal ridges.

The paracone on M^1 in young, semi-mature, and mature individuals is not fused with the anterior collar (perhaps it fuses only in very old age). In addition, this fold is completely separated from the neck which also connects the inner anterior (protocone) and posterior (hypocone) folds (Figure 6). The mesocone is well developed and is completely separated from the paracone. During tooth erosion perhaps, the mesocone fuses with the paracone but during this fusion, the former is preserved up to old age in the shape of a well-developed process on the posterior wall of the latter. At the same time, perhaps, the fusion of the paracone with the neck which connects the protocone with the hypocone, also has a considerable meaning and, as a result, a portion of the anterior intruding fold forms a mark. The hypocone is almost twice longer than the protocone. The metacone at a given stage of wearing is still separated from the posterior collar though a tendency toward their fusion has been quite clearly observed. The general measurements of the tooth (length, 2.3 mm; width, 2.1 mm), the corresponding height of the crown, and the peculiarities of construction of the preserved parts of the base of the roots, prove that they belong more to very old individuals than to semi-mature, and least of all to young animals.

M^2 (Figure 6) belonging to mature animals is complex like the preceding permanent molar. The mesocone, differing from the same on M^1, is fused with the paracone at a given stage of wearing. Moreover, the paracone is fused with the collar. The fusion of the paracone at a given stage of wearing takes place in addition to the fusion of the latter with the anterior collar. The fusion of the paracone with the neck, connecting the protocone with hypocone, does not take place. As a result, the anterior outer intruding fold forms a mark which has a form of a crescent. The complexity of the wearing surface takes place also because of the remains of an additional inner intruding fold placed anterior to the protocone and the external additional tubercle at the base of the paracone. The hypocone, as in M^1, approximately twice exceeds the protocone. The metacone is fused with the posterior collar. There are three roots—the massive inner and two weakly developed outer. The measurements of the tooth are as follows: length 2.2 mm; and width 2.0 mm.

M^3 (Figure 6) is strongly drawn out (elongated) in a longitudinal direction (length, 1.8 mm; width, 1.4 mm; relation of width to length, 77.8) and has an S-shaped form on the wearing surface. Notwithstanding the fact that the tooth belonged to a considerably mature animal, all the intruding folds are open. There are three roots—the massive inner and two rather weak outer (Figure 54). There is no fusion of roots.

The lower incisor is narrow (relation of width to antero-posterior cross section, 75.7; 80.6; 84.6; 87.5) with three longitudinal ridges on the anterior surface. The central ridge sometimes exhibits a tendency toward bifurcation. The anterior surface of the incisor is very convex.

M_1 (Figure 6) is complex. The entoconid is not fused with the posterior collar in almost all stages of wear. The mesoconid is represented by a well-developed independent fold fused neither with the metaconid nor with the entoconid. It forms, along with the latter, a characteristic inner fork, the neck width of which exceeds one-

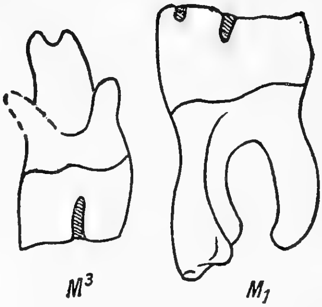

Figure 54. Structure of roots of permanent molars of *Microspalax compositodontus* sp. nov., Late Miocene of South Ukraine.

third the length of the wearing surface of the tooth, or is approximately equal to it. The protoconid is approximately twice greater than the hypoconid. In the anterior portion of the tooth, there is a mark representing a linked portion of the anterior inner intruding fold. There are two roots—the massive antero-posteriorly flattened posterior one, and a weakly developed anterior. The posterior root has a tendency toward bifurcation. The tooth belonged to a mature animal. Measurements were: length 2.6 mm; width 2.3 mm.

M_3 is elongated in a longitudinal direction (length, 2.2 mm; width, 1.6 mm; relation of width to length, 72.7) and has a characteristic S-shaped form on the wearing surface with two anterior and one posterior mark. Additionally, all the permanent molars of *M. compositodontus* have, without exception, a relatively lower crown.

Comparison. The basic characteristic by which *M. compositodontus* differs from all other species of the subgenus *Microspalax* is the presence of many folds on its permanent molars which make the structure of the latter more complex. In addition, there are other differences related, first of all, to the general proportions of the teeth, corresponding measurements of their separate parts, and the structure of their roots. A detailed comparison of the *compositodontus* mole rat with contemporary and fossil representatives of the subgenus *Microspalax* has been given below.

The *compositodontus* differs from all the presently known species of the subgenus *Microspalax* by:

1. The presence of mesocone on M^1 and M^2. It is absent in other species.

2. The presence of remains of a middle inner intruding fold on M^2, and a tubercle at the base of the paracone. It is absent in other species.

3. The presence of a massive free mesoconid on M_1 in maturity which is not fused with the metaconid, and a wide inner fork, the neck width of which either exceeds one-third the length of the whole wearing surface of the tooth or is approximately equal to it. In other species, the mesoconid is absolutely absent (*M. ehrenbergi*), is underdeveloped (*M. odessanus* sp. nov.), or finally, is present in young animals but fuses with the metaconid in mature age [*M. macoveii* (Simionescu)]. In the last two instances the width of the neck of the inner fork does not exceed one-fourth the total length of the wearing surface.

4. The more strongly developed hypocone on M^1 and M^2 and the protoconid on M_1 almost twice exceed the protocone and hypoconid respectively. In the remaining representatives of the subgenus *Microspalax*, differences in the respective measurements of the above-mentioned parts of these teeth are not that significant.

5. The more elongated and longitudinal direction of M^3_3. Thus the magnitude of the ratio of width of tooth in *M. compositodontus* is 77.8 for

M^3 and 72.7 for M_3 against, respectively, 81.8–105.7–123.5 and 70.0–96.4–116.7 in *M. ehrenbergi*; 88.9 and 87.5, 90.5, 95.6 in *M. macoveii*; and finally, 95.0–100.0–115.0 and 82.7–89.8–95.6 in *M. odessanus*.

Furthermore, the *compositodontus* mole rat differs from *M. ehrenbergi* by, on the average, wider upper and especially lower incisors (the range of relation of width of incisors to antero-posterior cross section is equal to 82.6–90.0–95.0 for upper, and 75.7, 80.6, 84.6, 87.5 for lower incisors in *M. compositodontus* against, respectively, 76.0–83.2–94.0 and 64.0–74.5–86.2 in *M. ehrenbergi*); and from *M. macoveii* and *M. odessanus* by a lesser degree of reduction of roots for M^3 (in the last two species, the number of roots of this tooth, as a rule, does not exceed two). It should be remembered that in the *compositodontus* the entoconid of M_1 is not fused with the posterior collar until after very old age, differing from the Mid-Pliocenic *M. macoveii* and *M. odessanus*, whereas in the latter two, the process of fusion ends either in the mature (*M. macoveii*) (Figure 56) or even in the young (*M. odessanus*) (Figure 60).

Note. From the description given above of *M. compositodontus* and its comparison with fossil and living species of the subgenus *Microspalax*, it is seen that the given species out of the presently known representatives of the subfamily *Spalacinae* had the most primitive permanent molars according to their structure. This can be deduced from the general complexity of the wearing surface of the molar teeth and a lesser reduction of their roots—a fact which puts the complex-toothed mole rat in a specific category to the forms which are original for *Spalacinae*. According to the degree of complexity in the molar teeth, *M. ehrenbergi* is most closely-related to *M. compositodontus*, though in this species, the permanent molars on the whole are more simplified. This similarity is due mainly to the presence of an entoconid on M_1 up to very old age in the mole rat of Ehrenberg which is not fused with the posterior collar.

In addition, according to the degree of development of adaptation to a burrowing way of life in the structure of the incisors, the *compositodontus* considerably exceeds not only the present-day *M. ehrenbergi*, but even certain more primitive representatives of the subgenus *Mesospalax* which have a greater specialization for a burrowing existence and also the *M. nehringi* from Asia Minor and around Kavkaz. This throws some light on the different trends of development in adaptation toward feeding and a burrowing way of life, as well as on the limitations for examining the *compositodontus* as a type—original for all the fossil and present-day species of the subgenus *Microspalax*, notwithstanding its considerable geological antiquity. At the same time, it can be successfully taken as an ancestral type of the European Pliocenic *Microspalax*—*M. macoveii* and *M. odessanus*. This is as if proven by the gradual simplification of the structure of permanent molars, and the growing degrees of reduction of their roots through comparatively minor changes in the structure of incisors in the evolutionary lines of *M. compositodontus—M. macoveii* and species closely related to it—types closer to *M. odessanus.*

Habitat. Village Andreevka (near Tiligulo-Berezanki), Berezan region. Nikolaev region, right bank of Tiligulo-Berezan estuary; ancient alluvial sands lying under Pontiac limestone.

Distribution and geological age. Around the Black Sea of the Ukraine; Late Miocene.

3. **Microspalax macoveii** (Simionescu, 1930)—**Mole Rat of Macovei**

Prospalax Macoveii Simionescu, 1930: 21, 22, Figure 31–33, Tab. 2, Figures 3, 4. *Pliospalax simionescui* Kormos, 1932: 194–198, Abb. 1.

Holotype. University of Yassakh (Rumania); the number of the exhibit was not fixed; lower jaw (mandibular sin) with an intact incisor, two anterior permanent molars (M_1–M_2), the articular process and the angular one (Simionescu, 1930: 22, Figure 33, Table 2, Figure 4); Rumania, Malushten, Kovurlui region; Mid-Pliocene.

Paratypes. Fragments of the lower jaw (mandibular dex.) from Malushten and Bereshti (Simionescu, 1930: 22, Figure 32, Table 2, Figure 3; Kormos, 1932: 195, Abb. 1); Rumania; Mid-Pliocene; preserved in the collections of the University in Yassakh; the number of samples had not been fixed. Lower jaw (mandibular dex.) with completely preserved incisors, row of permanent molars (M_1–M_3), and the angular process; Ukraine SSR, Novopetrovka of Odessa region; Mid-Pliocene; preserved in the collections of the Institute of Zoology AN Ukraine SSR, No. 37–970.

Additional Material. Fragment of palatal portion of the skull with alveoli of M^{1-2}; lower jaws and their fragments, samples 14; isolated teeth—upper incisors, samples 3; M^1, samples 4; M^3, one sample; lower incisors, samples 13; M_1, samples 3; M_2, samples 2; M_3, one sample; a few fragments of limb bones.

Diagnosis. Measurements are minimal (within the boundaries of the subgenus *Microspalax*); length of the lower row of permanent molars, 7.4–7.9–8.6 mm. The mesocone on M^1–M^2 is absent. The width of the hard palate between M^1 is less than the width of the alveoli of the anterior permanent molar, or is approximately equal to it; the central ridge is weak, in the shape of a narrow ridge, or is absolutely absent. The free mesoconid on M_1 is present only in young animals. In mature animals it fuses with the metaconid; the inner side of the anterior fold of the lingual line encloses into a mark which is stretched in a longitudinal direction. The neck width of the inner fork is approximately equal to one-fourth the total length of the wearing surface of M_1. The entoconid is free in young individuals; in maturity it fuses with the collar which encloses the posterior intruding fold of the inner line in the shape of a mark. The anterior surface of the upper incisors is smooth, without longitudinal ridges.

Description. The structural peculiarities of the hard palate have been noted in the diagnosis. The upper incisor is, on an average perhaps, wider than in the preceding species and in *M. ehrenbergi.* The relation of the width of the incisor to the antero-posterior cross section is 95.4, 100.0, 100.0. The anterior surface of the incisors is smooth, without longitudinal ridges.

M^1 has no sign of a mesocone. The paracone is not fused with the anterior collar in young, semi-mature and mature animals. The fusion takes place only toward old age (Figure 56). The metacone fuses with the posterior collar in the early stages of wearing. The number of intruding folds in the outer line is two; in the unfused metacone, three; and in the inner line, one. Because of tooth erosion the process of closure of the intruding folds into marks ends earlier in the outer lines than in the inner lines. The order of closure is as follows: the posterior external, the anterior external, the central external, and finally, the inner one. In very old individuals, marks on teeth are absolutely absent. The hypocone usually exceeds the protocone less than twice. There are two roots—the massive antero-internal and a comparatively weak postero-external (Figure 57). The antero-internal root with a canalicular posterior wall exhibits a tendency toward bifurcation. Rarely, the number of roots of M^1 may reach to three. In this case, their disposition in the alveolus would look as follows: the massive inner and two approximately equally developed external ones. Reduction takes place due to a coalescence of the anterior outer and inner roots. The measurements of M^1 are: length, 2.7, 2.7, 2.9 mm; width, 2.2, 2.3, 2.6 mm; relation of width to length, 81.5, 85.2, 89.6. Possibly, this tooth is, on the average, more elongated in a longitudinal direction than in other representatives of this subgenus.

M^3 (length, 1.8 mm, width, 1.6 mm; ratio of width to length, 88.9) is less elongated in a longitudinal direction than in previous species. The inner intruding fold closes into marks in the early stages of tooth erosion, though it remains fused for a long time with the outer intruding fold. Because of this, the wearing surface of both has a C-shaped form. At a given stage of wearing, an additional tubercle is still preserved at the base of paracone. The roots have not been preserved.

The lower jaw has a short diastema and a relatively big horizontal branch. The relation of the length of the diastema and the height of the horizontal branch at the level of center in the alveolus of M_1, measured from outside, to the length of the row of permanent molars is respectively equal to 62.5–70.8–75.0 and 81.8–97.6–108.0. The symphoidal tubercle is clearly defined (Figure 55) and short; its length is considerably less than the length of permanent molars (approximately equal to the length of

M_1–M_2). The ridge on the space between the symphoidal tubercle and the angular process is absent. The ridge on the masseter area terminates at a considerable distance from the alveolar edge, a little above the mental foramen. The angular process is clearly defined, sharply bent down, and has possibly a shortened base (relation of the length of base to length of row of permanent molars is 88.7, 104.8). The alveolar process is low and is approximately equal to the articular one. The mental foramen does not blend with the alveolar edge; it is situated approximately at an equal distance from the alveolus and the lower edges of the jaw. The coronary process is slanted and its apex has practically no backward incline. The body of the mandible is relatively thick (ratio of thickness at the level of M_2 to length of row of permanent molars is equal to 46.0–54.0–62.7).

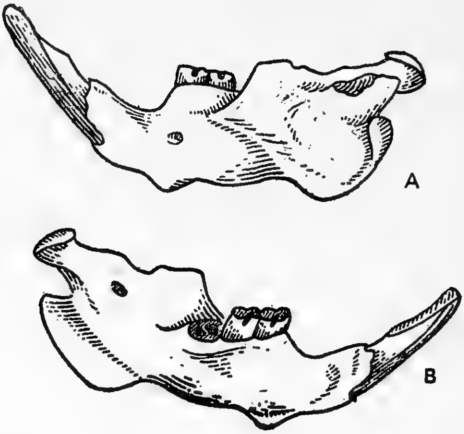

Figure 55. *Microspalax macoveii* (Sim.). × 1.7.

A—lower jaw, external view; *B*—the same, internal view.

The lower incisor is, perhaps, wider than in all the presently known representatives of the subgenus *Microspalax* (the relation of width of incisor to antero-posterior cross section is 70.3–86.2–93.5), with three longitudinal ridges on its surface.

The mesoconid on M_1 is free in young individuals (Figure 56). In mature animals, it is fused with the metaconid. During this, a portion of the anterior intruding fold of the inner line closes as a mark elongated in a longitudinal direction. The width of the inner fork is approximately equal to one-fourth the total length of the tooth. The entoconid in young animals is not fused with the posterior collar, but exhibits a tendency toward fusion in mature animals. It should also be noted that the protoconid and anterior collar (which are fused in mature animals) are disconnected. The protoconid exceeds the hypoconid less than twice. There are two roots—the posterior one is rather more strongly developed than the anterior, is flattened in an antero-posterior direction, and has vestiges of bifurcation. The measurements of M_1 are as follows: length, 2.4, 2.7, 2.7, 2.7 mm; width 2.0, 2.2, 2.3, 2.4 mm; relation of width to length, 81.5, 83.3, 85.2, 88.9. The order of closure for the intruding folds and the marks is as follows: the posterior and interior part of the anterior plate of the inner line, the anterior internal, and finally, the external. The marks are totally absent in very old age.

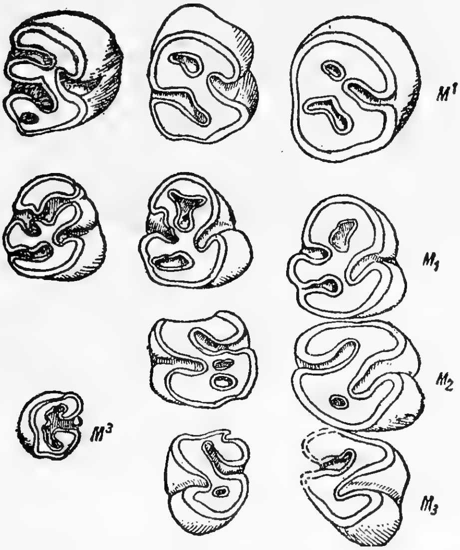

Figure 56. *Microspalax macoveii* (Sim.), upper and lower permanent molars. Mid-Pliocene of South Ukraine and Moldavia.

The entoconid on M_2 in mature animals is fused with the posterior collar. During this, the posterior intruding fold of the inner line closes as a mark. The mark vanishes with age. On the whole, the work surface is characterized by the presence of one outer and one or two (in an unworn condition) intruding folds. The order of their closure into marks is the same as in the preceding molar. The protoconid and hypoconid are approximately of the same size. There are two roots. Of them the posterior is better developed than the anterior. Both roots have vestiges of bifurcation which indicates their complex nature (each was formed in the process of fusion of two roots—the external and internal); they are flattened in an antero-posterior direction. The end of the anterior root is bifurcated in the shape of a fork; there is a socket for each end of the fork in the alveolus. The measurements of the tooth are as follows: length, 2.2, 2.2, 2.4, 2.6 mm; width, 2.1, 2.2, 2.4, 2.6 mm; relation of width to length, 84.0, 100.0, 108.3, 109.1.

M_3 (length, 2.1, 2.3, 2.4 mm; width, 1.9, 2.1, 2.2 mm) is relatively longer (relation of length of M_3 to length of the preceding permanent molars is 95.8, 109.1) and elongated in a longitudinal direction (relation of width to length is 87.5, 90.5, 95.6). The shape of the wearing surfaces are, as a rule, S-shaped though in some cases the inner portion of the external intruding fold closes into a mark. In young and semi-mature animals, vestiges of an additional fold of the inner line, placed anterior to the metaconid, are present (Figure 56). The tooth is characterized by the presence of two roots which are fused all along and flattened in an antero-posterior direction, each of which has clear marks of bifurcation. The terminus of the anterior root has even two free ends for each of which there is a socket in the alveoli.

Comparison. It differs from *M. ehrenbergi* by:

1. Average large absolute measurements.

2. A weakly developed central ridge of the hard palate (wider in *M. ehrenbergi*).

3. Absence of longitudinal ridges on the anterior surface of the upper incisors (always present in *M. ehrenbergi*). In addition, the upper and lower incisors of *M. macoveii* are, on an average, wider than in *M. ehrenbergi* (relation of width of incisor to its antero-posterior cross section in *M. macoveii* is equal to 95.4, 100.0, 100.0 for the upper, and 70.3–86.2–93.5 for the lower tooth as against respectively 76.0–83.2–94.0 and 64.0–74.5–86.2 in *M. ehrenbergi*).

4. Presence of two and not three roots for M^1–M^2 in the majority of the given cases.

5. The M^3 is more elongated in a longitudinal direction (relation of width to length is 88.9 against 81.8–105.7–123.5 in *M. ehrenbergi*).

6. A relatively short lower diastema (relation of diastema-tooth is 62.5–70.8–75.0 against 61.5–77.0–93.4 in *M. ehrenbergi*).

7. On an average, a relatively higher and thicker horizontal branch at the level of M_2 (relation of its height on the level of the antero-permanent molar, and thickness at the level of M_2 to the height of line of permanent molars is equal to 81.8–97.6–108.0 and 46.0–54.0–62.7 in *M. macoveii*, as against respectively 78.5–88.1–101.3 and 37.5–45.7–57.8 in *M. ehrenbergi*).

8. A clearly defined, downward bent, short symphoidal tubercle (length is approximately equal to the length of the two anterior permanent molars), and a well-expressed mandibular angle; in *M. ehrenbergi*, the symphoidal tubercle is flattened and elongated (its length is approximately equal to

the length of a full row of permanent molars), and the mandibular angle is expressed faintly.

9. A mental foramen which is separate from the alveolar edge (placed approximately equidistant from the alveolar and lower edges of the horizontal branch). It is placed nearer to the alveolar edge in *M. ehrenbergi.*

10. The ridge on the masseter surface does not reach up to the alveolar edge of the horizontal branch (it terminates approximately at the level of the chin opening in *M. macoveii*). In *M. ehrenbergi*, it almost reaches the alveolar edge.

11. A coronary process steeply placed with respect to the horizontal branch, the apex of which is practically non-inclined behind. In *M. ehrenbergi*, the coronary process is bent, saddle-shaped, and more tapered in relation to the horizontal branch.

12. A clearly defined angular process which is sharply bent down. It is flattened, and slightly bent down in *M. ehrenbergi.*

13. Presence of a mesoconid on M_1—free in young animals and fused with the metaconid in mature animals (it is altogether absent in *M. ehrenbergi*). Furthermore, in *M. macoveii*, the entoconid exhibits a tendency toward fusion with the posterior collar in mature animals (in *M. ehrenbergi*, they are not fused up to old age).

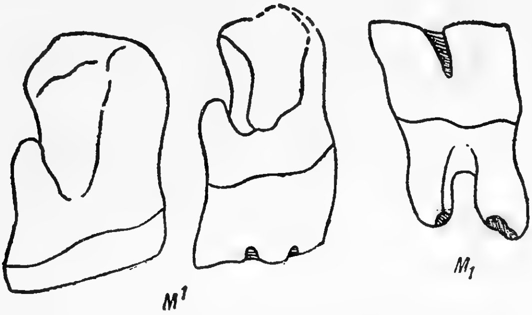

Figure 57. Structure of roots of permanent molars of *Microspalax macoveii* (Sim.). Mid-Pliocene of South Ukraine and Moldavia.

14. Presence of an additional fold of the inner line and posterior mark (absent in *M. ehrenbergi*); on M_3 of young and semi-mature individuals; and also by the fused roots of this tooth almost all along the row (in *M. ehrenbergi*, the anterior and posterior roots are not fused and the tendency toward bifurcation in each of them is rarely expressed). In addition, the M_3 in *M. macoveii* is, on an average, more elongated in a longitudinal direction than the similar permanent molars of *M. ehrenbergi* (the relation of width of tooth to length is equal to 87.5–90.5–95.6 as against 70.0–96.4–116.7 in *M. ehrenbergi*).

The most important differences from *M. compositodontus* may be summarized as follows:

1. The mesocone on M^1–M^2 is absent.

2. The vestiges of an anterior inner intruding fold and an additional tubercle at the base of the paracone are absent on M^2.

3. The mesoconid in mature animals is fused with the metaconid and the width of the neck of the inner fork does not exceed one-fourth the total length of the wearing surface. In the *compositodontus* mole rat, the mesoconid is free up to very old age, and the width of the neck of the inner fork exceeds one-third the length of the wearing surface, or is approximately equal to it. In addition, the entoconid of the first lower permanent molar in mature animals has a tendency to fuse with the posterior collar (in *M. compositodontus* it is not fused until up to very old age).

4. The hypocone on M^1 and M^2 and the protoconid on M_1 are weakly developed. These dimensions are exceeded less than twice by the measurements of the corresponding protoconid and hypoconid.

5. M^3_3 are less elongated in a longitudinal direction (relation of width to length is equal to 88.9 for upper, and 87.5, 90.5, 95.6 for lower, as against respectively 77.8 and 72.7 in *M. compositodontus*). Furthermore, the M^3 of *M. macoveii has*, perhaps, not more than two roots; in *M. compositodontus* there are three.

6. The upper and lower incisors are, on the average, wider than in *M. compositodontus* (relation of width of incisor to antero-posterior section is equal to 70.3–86.2–93.5 for the lower, and 95.4, 100.0, 100.0 for the upper teeth, as against respectively 75.7, 80.6, 84.6, 87.5 and 82.6–90.0–95.0 in *M. compositodontus*).

Finally, it differs from the Mid-Pliocene *M. odessanus* as follows:

1. A narrow inter-dental space in the anterior portion (width of the hard palate between M^1 is less than the width of the alveolus of this tooth, or is approximately equal to it); and a weakly developed central ridge of the palate (which may be absolutely absent). In *M. odessanus*, the width of the alveolus of the anterior permanent molar, and the central ridge is massive and broad.

2. The presence of a mesoconid on M_1 which is free in young individuals, and fused with the metaconid in mature ones, with the formation of an anterior mark by a relatively wide inner fork (the neck width of which is approximately equal to one-fourth the length of the masticatory surface); and by a late fusion of the entoconid with the posterior collar. In *M. odessanus* the mesoconid is reduced, the entoconid and posterior collar are fused even on the teeth of young individuals, and the width of the inner fork (if it is present at all) is considerably less than one-fourth the total length of the masticatory surface. Furthermore, the fusion of the entoconid with the metaconid takes place in *M. macoveii* through the

mesoconid, as a result of which the anterior mark (representing the inner portion of the anterior intruding fold of the inner line) forms even on the teeth of young animals. In *M. odessanus* the fusion of the corresponding folds takes place directly with each other and that, too, in very old age; and the anterior intruding fold of the inner line does not form an anterior mark.

3. The M^3 which is, on the average, more elongated in a longitudinal direction (relation of width to length, 88.9 as against 95.0–100.0–115.0).

4. A shortened symphoidal tubercle of the lower jaw, the length of which is approximately equal to the length of the two anterior permanent molars. In *M. odessanus,* it is approximately equal to the length of a complete line of permanent molars. In addition, the ridge in the space between the symphoidal tubercle and the angular process which is well developed in *M. odessanus,* is absent in *M. macoveii.*

5. A shortened lower ridge of the masseter area which approximately terminates at the level of the mental foramen. In *M. odessanus,* this ridge is placed considerably above the for. mentale.

6. Apparently wider upper and lower incisors (relation of width of tooth to antero-posterior cross section is equal to 95.4, 100.0, 100.0 for the upper, and 70.3–86.2–93.5 for the lower, as against respectively 83.3–89.7–95.8 and 71.4–81.2–90.0 in Odessa mole rats).

7. The presence of vestiges of an additional intruding fold on M_3 in young and semi-mature individuals (absent in *M. odessanus*).

8. On an average, smaller absolute dimensions.

Measurements. Condylar length of lower jaw, 24.3 mm; angular length of lower jaw, 25.4 mm; length of lower diastema, 5.0–5.7–6.1 mm; length of lower row of permanent molars, 7.4–7.9–8.6 mm; height of the horizontal branch at the level of M_1, 7.0–7.8–9.2 mm; thickness of horizontal branch on the level of M_2, 3.8–4.3–4.7 mm; width of upper incisor, 2.1, 2.2, 2.6 mm; antero-posterior cross section of upper incisor, 2.2, 2.2, 2.6 mm; width of lower incisor, 1.9–2.5–2.9 mm; antero-posterior cross section of lower incisor, 2.4–2.9–3.5 mm.

Note. From the above description of the Mid-Pliocene *M. macoveii* and its comparison with fossil and living representatives of the subgenus *Microspalax,* it is quite clear that the given species takes up an intermediate position in regard to the degree of specialization of permanent molars, between the Late Miocene–Early Pliocene *M. compositodontus* and the still later Mid-Pliocene *M. odessanus.* Its permanent molars have simpler structures as compared to *M. compositodontus,* and more complex on the whole, than in *M. odessanus.* In addition to the primitive characteristics in the structure of the permanent molars mentioned above, *M. macoveii* has also a comparatively primitive organizational structural set up. The presence of a comparatively short diastema and ridge on the masseter area, a shortened symphoidal tubercle, a well-defined maxillary angle, and a sharply defined angular process which is strongly bent down, are some of these structures. It follows that in the given case, we apparently come across a species which is very primitive on the whole. Furthermore, in the degree of specialization in incisors, *M. macoveii* is superior to all the presently known species of the subgenus *Microspalax*. This inclines us to presume the impossibility of taking it as a direct ancestor of the more ancient *M. odessanus*.

There is a known confusion even at present with regard to the taxonomy of this species. It occurs primarily because the majority of authors who carried out investigations on the remains of mole rats from the Mid-Pliocene of South Ukraine SSR, Moldavia SSR, and mixed regions of Rumania (Simionescu, 1930; A. I. Argiropulo, 1940; E. G. Reshetnik, 1939, 1941) did not differentiate the genera *Prospalax* and *Microspalax*. Even in current literature there are references to the presence of *Prospalax* in Pliocenic fauna of the catacombs of Odessa, the Kuchurgan sediments, and the territorial Mid-Pliocenic sands and gravels of Moldavia. Along with these authentic remains of representatives of this genus, as has been said above, were first found within the territory of the USSR only in 1964. The descriptions of finds of *Prospalax* in the USSR (Argiropulo, 1940; Reshetnik, 1939, 1941) are based on unauthentic determinations and the very remains on closer examination, appear to belong to *Microspalax*—a species identical, or closely related to *M. macoveii*. This can be explained by the fact that the said authors concentrated exclusively on the presence of three longitudinal ridges on the lower incisors in the Mid-Pliocenic mole rats of Odessa, Kuchurgan and Moldavia (a trait which is equally characteristic of *Prospalax* and of the most primitive species of the genus *Microspalax*), and paid less attention to the morphologic peculiarities of the outgoing branch and the angular process of the lower jaw, the differences in the structure of which are basic not only between the genera *Prospalax* and *Microspalax*, but even between the subfamilies Prospalacinae and Spalacinae. It should also be noted that A. I. Argiropulo (1940) and E. G. Reshetnik (1939) who had material from the Karst caves of Odessa and Moldavia, represented mainly by lower jaws identical to *M. macoveii* (Moldavia) as a species, and to a closer species—*M. odessanus* (Odessa)—very correctly ascribed some of their resemblances to the presently living *Microspalax*. However, inadequate review of works by Mehely (1909) who separated the genus *Prospalax*, or of Simionescu (1930) who described the species *M. macoveii*, and Kormos (1932) who reviewed the taxonomical position of the finds in Rumania and described the genus *Pliospalax*, led Argiropulo to an incorrect conclusion about the morphologic similarity of the genera *Prospalax* and *Microspalax*. As far as the report of A. I. Argiropulo (1940) on the find of remains of

Microspalax in Tiraspole is concerned, it is apparently based on a misunderstanding because these remains from the gravel of Tiraspole have yet to be found. S. I. Ognev (1947) differentiated the genera *Prospalax* and *Microspalax* however, due to an incorrect translation of the work of Kormos (1932); he confused the problem of the generic position of Rumanian mole rats from Malushten and Bereshti which were described by Simionescu. The author also (1965) did not differentiate the typical Kuchurgan and Moldavian *M. macoveii* and *M. odessanus* from the red-gray loam (clay) finds of the Karst caves in Odessa and much later sediments. In order to clarify this problem it would seem proper to look at the generic position and synonyms of European Mid-Pliocenic *Microspalax* in detail.

The species *M. macoveii*, as has been said above, was first described by Simionescu (1930) from the Mid-Pliocene of Rumania (place of find —Malushten); moreover, the said author mistakenly took it to be in the genus *Prospalax*. Simionescu (1930) described the remains as *Prospalax rumanus* which undoubtedly belonged to the genus *Prospalax* as Kormos (1932) indicated at that time. As far as *M. macoveii* is concerned, however, inclusion of this species in the genus *Prospalax* is absolutely unfounded. The following peculiarities of the construction of the lower jaw of *M. macoveii* are against this:

1. The alveolar process is somewhat longer than its articular one, or is approximately equal to it. In *Prospalax* it is shorter than the latter.
2. The angular process is shifted outward, placed on the lateral walls of the alveolar process, and is separated from the latter by a well-defined sella externa. In *Prospalax*, this process is not situated on the lateral wall of the alveolar, but at the base of its articular process, and has a common edge with it. The sella externa is absent.

The given peculiarities of the structure of the lower jaw of a typical *M. macoveii* from Malushten bring it close to representatives of the typical subgenus of the genus *Microspalax*, and sufficiently clearly fixes the position of the given species in the composition of this genus. This was also observed by Kormos (1932); however he quite wrongly brought *M. macoveii* closer to the modern highly specialized representatives of the genus *Spalax* sensu str. (= *Macrospalax* Mehely). The mistaken interpretation of the taxonomical position of *M. macoveii* could have been easily and clearly proven by comparing the peculiarities of structure of the lower jaw of this species with a modern representative of the genera *Microspalax* and *Spalax*, the results of which have been given below. The similarity of the lower jaw of *S. macoveii* to the jaw of a modern *Microspalax* on the one hand, and their difference from the same bones of the present Bering *Spalax* on the other, can be summarized as follows:

1. The angular process is quite separated and inclined from the external wall of the alveolar process, tapered at one end, and strongly moved back

in relation to the proc. alveolaris; moreover, its apex in mature and old representatives is situated behind the posterior wall of this process or, at most, is placed at the level of the latter. In *Spalax,* this process is almost completely adhered to the alveolar process, is rounded off at the end, and is inclined somewhat forward in relation to the latter, as a result of which its apex is situated in front of the posterior wall of the proc. alveolaris.

2. The sella externa is placed considerably below the base of the articular process. In *Spalax* the sella externa and the base of the proc. condyloideus are placed almost on the same level.

3. The alveolar process is connected to the coronary by a low blunt ridge. In *Spalax* the ridge joining the alveolar and coronary processes is higher and is sharp all along the edge.

Thus, there is no doubt about the fact that *M. macoveii* belongs to the group of species of the genus *Microspalax.* Furthermore, traits such as the presence of three longitudinal ridges on the lower incisors, a relatively lower alveolar process (approximately equal in height to its articular one, or slightly higher), a short diastema and the complex wearing surfaces of the permanent molars—quite clearly fixes its place in the compositions of the subgenus *Microspalax.*

It has been said above that Kormos (1932) described a new genus of mole rats—*Pliospalax*—from the Mid-Pliocenic sediments of Rumania found near Bereshti, and stratigraphically identical sediments of Malushten, from a single fragment of the lower jaw with a piece of an incisor and completely preserved permanent molars. Kormos was not confident about showing the similarity of the mole rat from Bereshti and the *M. macoveii* from Malushten, because of which he proposed to name the typical species of the new genus *Pliospalax simionescui* Kormos—with the reservation that if the mole rat from Bereshti should appear similar in species to the *M. macoveii* of Malushten, then the name given by Simionescu (1930) should be retained for the typical species. The reason for the separation of the genus was the presence of an anterior mark on the M_1 of the mole rat from Bereshti which the said author mistook for a vestige of the additional anterior intruding fold of the outer line. The jaw described by Kormos belonged to a semi-mature animal, proven by the recently started wearing process of M_3, whereas the remains of a typical *M. macoveii,* for that matter even the holotype described by Simionescu, belonged to old animals on whose teeth the process of closure of the intruding fold into a mark had almost come to an end. Hence, it is very logical to presume that Kormos took one of the variables of age as a taxonomical trait. The likelihood of such an assumption becomes clear if the nature of age changes in the structure of the wearing surface of M_1 on a series of teeth for *M. macoveii* (Figure 56) and representatives of the subgenus *Microspalax* which is closely related to it—i.e., the Mid-

Pliocenic *M. odessanus* (Figure 60) and the recent *M. ehrenbergi* (Figure 53), is reviewed. It has been said above that the anterior intruding fold of the inner line of the first lower permanent molar in primitive representatives of the subfamily Spalacinae forms the anterior mark by way of folding in its inner portion. This process takes place either by the fusion of the mesoconid (if it is present) with the metaconid (in *M. macoveii*) or by direct fusion of the entoconid with the metaconid (in *M. odessanus* and *M. ehrenbergi*, on the teeth of which the mesoconid is not fully developed or is completely reduced). The speed of completion of this process in Mid-Pliocenic and modern *Microspalax* is, apparently, directly dependent on the degree of development of the mesoconid. By the way, the formation of the anterior mark on the teeth of *M. macoveii* takes place already in semi-mature animals, whereas in *M. odessanus* and *M. ehrenbergi* this process takes place only in old age. Thus, if it is considered that the anterior mark is found on the teeth of Mid-Pliocenic *M. odessanus* and *M. ehrenbergi* where it represents the folding of the internal part of the anterior intruding fold of the inner line, then, it is not understood how it could be proven that this formation in the mole rat from Bereshti represents a vestige of an additional anterior buccal fold. As a result, *Pliospalax simionescui* is nothing but a young form of *M. macoveii.* With the known similarity between *M. macoveii* and *P. simionescui*, naturally, there is no necessity for their separation into independent genera. It also has to be mentioned that the lower incisor of the mole rat from Bereshti is, on the whole, identical to the incisor of a typical *M. macoveii*, i.e., it has three longitudinal ridges of enamel on the anterior surface. That the lower jaw from Bereshti belongs to a representative of the genus *Prospalax* is impossible because on the M_1–M_2 of the latter, the hypoconid and the posterior collar are folded in the shape of a bud away from the rest of the portions of the corona at this stage of wearing (Kowalski, 1960b). In conclusion, it has also to be noted that in the works of S. I. Ognev (1947) and Reshetnik (1939, 1941), *Prospalax rumanus* and *M. macoveii* have been presented under a common generic name—*Pliospalax*—with a reference to the work of Kormos (1932). This is explained by an absolutely inaccurate translation of the corresponding places in the paper by Kormos. The latter never wrote anywhere about the inclusion of *Prospalax rumanus* in the genus separated by him, thus accepting its previous generic disposition (Kormos, 1932: 194). He merely discussed a possible similarity of the typical species *Pliospalax simionescui* and *M. macoveii.*

It has also been stated above that in his earlier works, the author (Topachevskii, 1965) did not differentiate between *M. macoveii* and the rather late *M. odessanus.* In the present work, the differences between these species have been looked into in detail (pages 198-99), and also in the portion where the Odessa mole rat has been described. Remains of *M.*

macoveii were restricted only and exclusively to the most ancient sediments of the Mid-Pliocene-Kuchurgan sands and gravel, and in sediments stratigraphically identical to it around Moldavia SSR, and in the valleys of the Salchi and Kagul rivers.

Place of find. Around the villages Novo-Petrovka and Veliko-Mikhailova, of Frunzenskii area, of Odessa region; right bank of the Kuchurgan River; Kuchurgan sediments—sands and gravel of the alluvial period. Around the village Grebenniki, Razdelnyanskii area, Odessa region; alluvial sands and gravel similar to Kuchurgan's. Around the villages Musaid (right bank of the Salchi River) and Gavonosy (right bank of the Kagul River), Moldavia SSR; alluvial sands and gravel, possibly similar to Kuchurgan's.

Distribution and geological age. Northwest of the Black Sea region; first half of the Mid-Pliocene.

4. **Microspalax odessanus** W. Topachevskii, sp. nov.—**Odessa Mole Rat**

Holotype. Institute of Zoology AN Ukraine SSR, No. 8442; skull without occipital and parietal portions and zygomatic arch; Black Sea region of Ukraine, Odessa; Mid-Pliocene, second half.

Paratypes. Fragment of facial skull with completely preserved permanent molars; Nos. 4582 and 4584; Odessa, second half, of the Mid-Pliocene. All are preserved in the collections of the Institute of Zoology AN Ukraine SSR.

Additional material. Lower jaws and their fragments, 14; isolated teeth —upper incisors—10; M^1, 7; M^2, 6; M^3, 3; lower incisors—10; M_1, 4; M_2, 6; M_3, 5; and a few fragments of limb bones. Many series of isolated teeth from Pliocenic sediments of the village Kotlovina of the Odessa region. Individual incisors and permanent molars from the lower horizon of the village Kryzhanovki, Odessa region; village Kairy, Kherson region; and Nogaisk city, Zaporozhie region.

Diagnosis. The largest of the presently known representatives of the subgenus *Microspalax* (length of upper and lower rows of permanent molars is respectively equal to 7.9, 8.3, 8.4 mm and 7.9–8.4–8.8 mm). The nasal bones are devoid of a sharply defined longitudinal depression in the region of the suture between them (flattened or slightly concave). The temporo-nasal and temporo-maxillary sutures form an almost straight line. The hard palate between M^1 is wide (its width exceeds the width of the alveoli of the first permanent molar); the central ridge of the palate is well developed and wide. The mesocone on M^1 and M^2 is absent. The mesoconid on M_1 is not fully developed; the neck width of the internal fork (if one is present at all) is considerably less than one-fourth the total length of the wearing surface. The fusion of the entoconid with the metaconid does not take place up to old age, and so the anterior mark in young, semi-mature, and old animals is absent. The entoconid of this tooth is fused in the early stages of wearing with the posterior collar, as a result of which the posterior mark is present almost throughout life. The anterior surface of the upper incisors is flattened (smooth) without any longitudinal ridges.

Description. The skull is wide in the incisorial, behind the eyes, and the rostral section (relation of width behind the eyes, the incisors, and the rostrum to length of upper row of permanent molars is respectively equal to 81.0, 102.5, 96.4, 97.6, 100.0 and 105.0; 143.3). The peculiarities of the structure of the nasal bones, temporo-nasal and temporo-maxillary sutures, and partly of the hard palate, have been mentioned in the diagnosis. In addition, the posterior palatine groove is narrow (its width is less than the width of the third permanent molar), and the opening behind the palate is almost completely overgrown even in the young.

The upper incisors are, on the average, apparently less wide than in the preceding species (relation of width of the incisor to the antero-posterior cross section is 83.3–89.7–95.8). The anterior surface of the incisor is smooth and without longitudinal ridges.

In the structure of the worn surface and roots, M^1, on the whole, is similar to the permanent molars of *M. macoveii*, i.e., it has a completely reduced mesocone and paracone, and a hypocone which until a later age is not fused with the anterior collar and less than twice exceeds the protocone; its metacone is fused with the posterior collar in the early stages of erosion; it has two roots—a massive anterior inner and a comparatively weaker posterior outer (rarely, the number of roots could be three) (Figure 58). Furthermore, the tooth is, on the average, relatively wider than in the

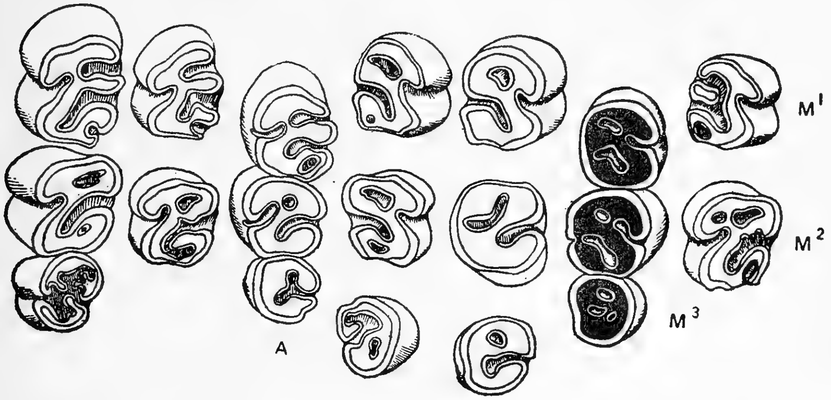

Figure 58. *Microspalax odessanus* sp. nov., upper permanent molars. ×8. Mid-Pliocene of South Ukraine, Odessa.

A—holotype.

preceding species. The measurements of M^1 are as follows: length, 2.3–2.6–3.0 mm; width, 2.2–2.3–2.6 mm; relation of width to length, 80.0–90.3–100.0. The order of closure of the intruding folds into marks is the same as in the previous species. The paracone, in the majority of the given examples, is fused with the neck connecting the inner anterior (protocone) and the posterior (hypocone) folds. Rarely is the fold separated.

M^2 is moderately wide (length, 2.1–2.3–2.4 mm; width, 2.1–2.4–2.6 mm; relation of width to length, 95.8–102.8–108.7). The hypocone less than twice exceeds the protocone. The anterior mark (the constricted inner portion of the intruding fold of the inner line) is formed in the early stages of tooth erosion. The metacone fuses with the posterior collar forming a posterior mark (preserved up to old age) in the very early stages of the wearing process. The tooth has one outer and one inner intruding fold. In the process of erosion, the outer fold closes into a mark earlier than the inner one (Figure 58). There are three roots—a massive inner and two weakly developed outer.

M^3 is relatively wider; its width is approximately equal to its length (length, 1.9–2.0–2.2 mm; width, 1.8–2.0–2.3 mm; relation of width to length, 95.0–100.0–115.0). The inner and outer intruding folds in young animals are open and are fused with each other (Figure 58). The fusion of the protocone with the hypocone, together with the closure of the inner intruding fold into a mark, takes place with age. During this, the wearing surface of the tooth assumes either a C-shaped or an E-shaped form. The tooth has two roots which are fused approximately up to two-thirds their length. The anterior root is massive, flattened in an antero-posterior direction with marks of bifurcation. The posterior root is weak and rounded in the cross section.

The lower jaw has a relatively high horizontal branch (relation of height of horizontal branch at the center level of the alveolus of M_1 to the length of row of permanent molars is 80.0–96.0–107.6). The diastema is apparently longer than in the preceding species, but is shorter than in *M. ehrenbergi* (magnitude of diastema-tooth index, 62.5–74.4–81.0). The symphoidal tubercle is clearly defined (Figure 59) and elongated, its length being approximately equal to the length of a full row of permanent molars. The ridge in the space between the symphoidal tubercle and the angular process is well developed. The mandibular angle is well expressed, apparently a little less than in the previous species; however, it is better defined than in the modern mole rat of Ehrenberg. The ridge on the masseter area is elongated, and terminates considerably above the supramaxillary foramen in the direct vicinity of the alveolar edge. The angular process is sharply defined, strongly bent down, and elongated at the base (the relation of the length of the base of the angular process to the length of the row of permanent molars is 104.5–114.3–130.3). The alveolar process is low, and almost equal to its articular one in height. The supramaxillary foramen is somewhat displaced above on the side of the alveolar edge. The coronary process is placed steeply, its apex is almost non-inclined backward. The horizontal branch is relatively thick (relation of its thickness at the level of M_2 to the length of row of permanent molars is 42.0–51.4–55.0).

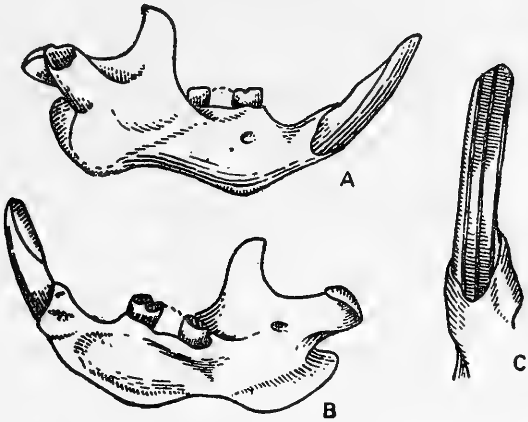

Figure 59. *Microspalax odessanus* sp. nov. ×1.7. Mid-Pliocene of South Ukraine, Odessa.

A—lower jaw, external view; *B*—the same, internal view; *C*—lower incisor.

The lower incisor is, apparently, less in width, on the average, than in the preceding species (relation of width to antero-posterior cross section, 71.4–81.2–90.0) with three longitudinal ridges on the anterior surface.

The mesoconid on M_1 is almost completely reduced; its marks are sometimes preserved in the shape of a small protuberance on the anterior wall of the entoconid (Figure 60). In the last case, the neck width of the inner fork is considerably less than one-fourth the total length of the wearing surface of the tooth. The fusion of the entoconid and the metaconid takes place only in very old age, as a result of which the anterior intruding fold of the inner line of young, semi-mature, and mature animals does not form the anterior mark. The entoconid and the posterior collar are fused even on the teeth of young individuals, as a result of which the posterior mark is present almost throughout life. The protoconid and the hypoconid are of about equal magnitude. There are two roots: the posterior is more massive than the anterior with marks of bifurcation. Teeth measurements are as follows: length, 2.4–2.6–2.9 mm; width, 2.1–2.3–2.5 mm; relation of width to length, 78.5–86.0–95.8. The order of closure of the intruding folds into marks is as follows: the posterior inner, the inside portion of the anterior inner, the anterior inner, and finally, the outer.

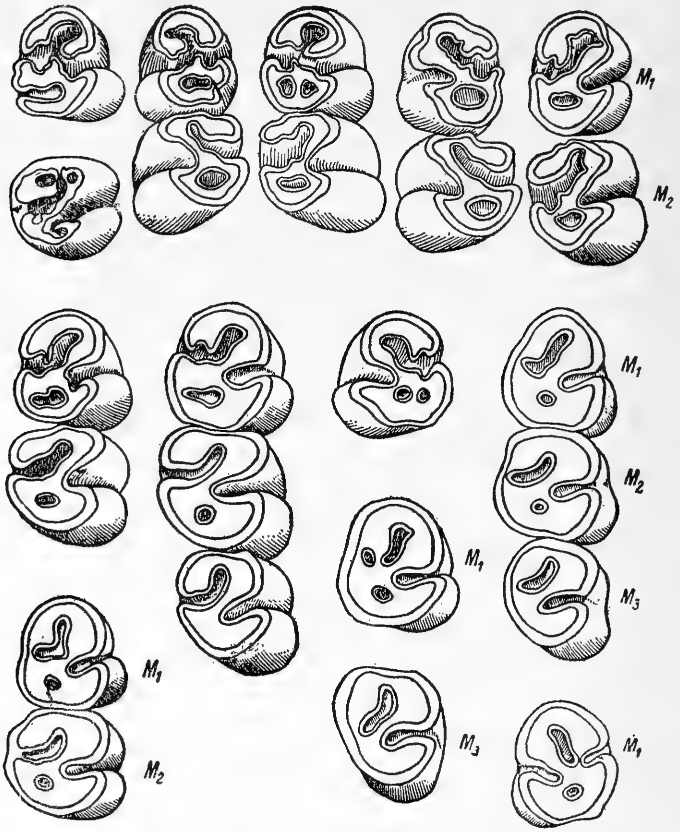

Figure 60. *Microspalax odessanus* sp. nov., lower permanent molars. ×8. Mid-Pliocene of South Ukraine, Odessa.

On the whole, M_2 is similar to the preceding species. The measurements are as follows: length, 2.2–2.4–2.9 mm; width, 2.1–2.3–2.6 mm; relation of width to length, 89.6–98.2–109.1. The entoconid is fused with the posterior collar in the early stages of wearing; subsequently, the posterior mark is present throughout life. There are two roots. Both are flattened in an antero-posterior direction with marks of bifurcation; moreover, the tendency to bifurcation is more strongly expressed on the anterior root than on the posterior, which is also seen in the structure of the alveolus.

M_3 (length, 2.2–2.4–2.9 mm; width, 2.0–2.2–2.4 mm) is elongated (relation of length to length of preceding molar, 100.0; 109.1), and drawn out in a length-wise direction (relation of width to length, 82.7–89.8–95.6). The wearing surface is S-shaped. The closure of the inner intruding fold into a mark takes place only in old age (Figure 60). Marks of an additional intruding fold of the inner line, which is placed anterior to the metaconid, are absent. The anterior and posterior roots are fused almost all along as a result of which the tooth is, in fact, characterized by the presence of one complex root. The anterior and posterior parts in turn also show a tendency toward bifurcation. On the anterior portion, traces of bifurcation are expressed more sharply, as a result of which the corresponding socket in the alveolus shows a tendency toward the formation of two lunes.

Comparison. It differs from the present, living *M. ehrenbergi* by:

1. Absence of two longitudinal ridges on the upper incisors (always present in *M. ehrenbergi*). Furthermore, the upper incisors of the Odessa mole rat are wider (relation of width of incisor to antero-posterior cross section, 83.3–89.7–95.8 as against 76.0–83.2–94.0 in *M. ehrenbergi*).

2. Absence of a sharply defined longitudinal depression on the nasal bones.

3. Almost straight temporo-nasal and temporo-maxillary sutures (in *M. ehrenbergi*, the temporo-nasal and temporo-maxillary sutures form an angle with the apex directed backwards).

4. A widened hard palate, the width of which in the region of the anterior permanent molars considerably exceeds the width of the alveolus of this tooth. In *M. ehrenbergi* the width of the hard palate between M^1 is approximately equal to the similar alveolus of the anterior permanent molar.

5. A skull widened in the incisorial and rostral sections (relation of incisorial and rostral width to length of line of permanent molars is equal to 81.0–102.5 and 105.0–143.0 as against respectively 69.2–76.4–86.1 and 97.3–108.6–126.0).

6. A narrow post-palatal opening (width is less than the length of the third permanent molar). In *M. ehrenbergi*, it is approximately equal to the length of M^3.

7. A horizontal branch which is, on the average, higher and thicker at the level of M_2 (relation of its length at the level of M_1 and thickness at the level of M_2 to the length of row of permanent molars is equal in *M. odessanus* to 80.0–96.0–107.6 and 42.0–51.4–55.0, as against respectively 78.5–88.1–101.3 and 37.5–45.7–57.8 in *M. ehrenbergi*).

8. Presence of two roots for M^1 and M^3 in the majority of the given cases. There are three roots in *M. ehrenbergi*.

9. A clearly defined, bent down, symphoidal tubercle and a well-expressed maxillary angle. In *M. ehrenbergi* the symphoidal tubercle is flattened and the maxillary angle is expressed faintly.

10. A coronary process which is steeply placed in relation to the

horizontal branch, the apex of which is almost not bent backward. In *M. ehrenbergi*, the coronary process is concave like a saddle and is more tapered in relation to the horizontal branch.

11. Wider lower incisors (relation of width to antero-posterior cross section is equal to 71.4–81.2–90.0 as against 64.0–74.5–86.2 in *M. ehrenbergi*).

12. Presence of a posterior mark on M_1 throughout life (formed as a result of the fusion of the entoconid with the posterior collar). In *M. ehrenbergi*, it appears only in old age.

13. The M_2 and M_3 are, on the average, apparently more drawn out in a length-wise direction (the relation of the width of tooth to its length is equal to 89.6–98.2–109.1 for M_2 and 82.7–89.8–95.6 for M_3, as against respectively 80.0–104.3–125.0 and 70.0–96.4–116.7 in *M. ehrenbergi*).

14. Larger absolute measurements.

The differences between *M. odessanus* and *M. compositodontus* and *M. macoveii* have been examined above.

Measurements. Length of upper diastema, 14.1, 15.0, 17.5 mm; length of hard palate, 24.8–26.8 mm; length of upper row of permanent molars, 7.9, 8.3, 8.4 mm; incisorial width, 7.0, 8.0 mm; rostral width, 2.6, 2.7, 3.0 mm; width behind the eyes, 7.9, 8.0, 8.2 mm; width of upper incisor, 1.8–2.1–2.4 mm; antero-posterior cross section of the upper incisor, 2.0–2.4–2.6 mm; condylar length of lower jaw, 29.3, 29.9, 31.6 mm; angular length of lower jaw, 27.5, 28.3, 30.1 mm; length of lower diastema, 5.6–6.4–6.9 mm; length of lower row of permanent molars, 7.9–8.4–8.9 mm; height of branch at the level of M_1, 6.7–8.1–9.0 mm; thickness of horizontal branch at the level of M_2, 3.7–4.2–4.9 mm; width of lower incisor, 1.6–2.1–2.7 mm; antero-posterior cross section of lower incisor, 2.0–2.6–3.3 mm.

Note. M. odessanus is the most highly specialized representative of the subgenus *Microspalax*. This is indicated by the presence of a wide skull in the incisorial and rostral region of this species, nasal bones without a longitudinal slit-like depression, a straight sutura maxillo-naso-frontalis, a relatively high and thick horizontal branch of the lower jaw, widened upper and lower incisors, a grinding surface of the permanent molar which is very simple in structure and by a high tendency toward reduction of roots with formation of teeth having long period of growth. With regard to the advanced development of some of the above-mentioned traits, primarily concerned with adaptations toward burrowing (widening of incisors, related changes in the structure of the skull and lower jaw), *M. odessanus* surpasses not only the living *M. ehrenbergi*, but also the most primitive representatives of the subgenus *Mesospalax*, the present *M. nehringi*, which is highly specialized as a whole. At the same time, this species still preserves a number of primitive characteristics in the structure of the skull and the lower jaw. In particular, besides the traits which determine its position in a subgenus about which much has been said in the preceding sections, *M. odessanus* is further characterized by a quite sharply defined symphoidal tubercle, a well-developed maxillary angle, and a well-separated and strongly bent down angular process of the lower jaw. The foregoing forces us not to accept the Odessa mole rat as an original form of the living representatives of the subgenus *Mesospalax*. This is, perhaps, further proven by the fact that the representatives of the subgenus *Microspalax* immediately give place to species of the genus *Spalax* within the boundaries of the present distribution of *M. leucodon* in the Late Pliocene (second half) and, moreover, in some excavations their remains have been found together (lower horizon of the Nogaisk geological strata). All this also proves the rather later penetration of *M. leucodon* (which spread up not before the Pleistocene) in the region of the northwest Black Sea of the USSR (Ukraine, Moldavia), i.e., the regions which, as is well-known, are the easternmost part of the area of the subgenus *Mesospalax* in Europe.

Place of find. Odessa, red-gray gravel, aggregates of Karst caves and craters in Pontiac limestone (catacombs of Odessa); ancient, alluvial layer which opened up near the village Kotlovina of the Odessa region (right bank of Lake Yalpukh); lower horizon of alluvial sediments near the village Kryzhanovki of the Odessa region; alluvial layers of the village Kairy of the Kherson region; and Nogaisk of the Zaporozhie region.

Distribution and geological age. Northwest Black Sea of Ukraine SSR; Mid-Pliocene (latter half); Late Pliocene (rare in the sediment lying above the Willafrank strata).

2. Subgenus **MESOSPALAX** Mehely, 1909

*Genotype. Spalax typhlus leucodon** Nordmann, 1840; recent, around the city of Odessa.

Diagnosis. Measurements are average. The anterior surface of the lower incisor is smooth, without longitudinal ridges. The lambdoid and sagittal ridges are well developed in mature and old individuals. The sagittal ridge is equally prominent on the parietal and temporal bones. The parietal bones are contracted; the width of the two parietale is considerably much less than twice the length of the upper row of permanent molars. In addition, the width of each of the parietale, individually in mature and old representatives, is significantly less than its length. The alveolar process of the lower jaw is high and considerably exceeds its articular one in height.

Comparison. A detailed comparison of the subgenera of the genus *Microspalax* has been given above (page 175).

*Should be *Mesospalax typhlus leucodon*—Editor.

Composition of the subgenus. Two modern species—*M. nehringi* (Satunin, 1898) and *M. leucodon* (Nordmann, 1840).

Distribution and geological age. Zakavkaz, Asia Minor, Balkan, northwest Black Sea region (Rumania), Moldavia SSR, Odessa region, Prikarpate regions of Hungary, Rumania and Ukraine SSR (Bukovina); Holocene including recent period.

KEY FOR IDENTIFICATION OF SPECIES OF THE SUBGENUS MESOSPALAX

1 (2). The nasal bones have sharply defined longitudinal slit-like depressions in the region of the sutures between them (Figure 61) pointed anteriorly. The temporal nasal and temporo-maxillary sutures form an angle with its apex bent backward. The edges of the rostrum are almost parallel and do not meet in a forward direction. The foramina behind the palate are small. The fossae behind the palate are not present. The central ridge of the palate forms a lamellar broadening at the level of the foramina behind the palate.........
....1. **M. nehringi** (Satunin).
(Holocene, including recent).

2 (1). The nasal bones are without a longitudinal slit-like depression (Figure 65) and are rounded or blunted anteriorly. The temporonasal and the temporo-maxillary sutures form an almost straight line, or an angle with its apex directed forward. The edges of the rostrum meet sharply in a forward direction. The foramina behind the palate are comparatively large. The fossae behind the palate are sharply defined and drawn out in a longitudinal direction. The central ridge of the palate, at the level of the foramina behind the palate, does not form a lamellar broadening...................
..................................2. **M. leucodon** (Nordmann).
(Holocene, including recent).

1. **Microspalax nehringi** (Satunin, 1898)—**Mole Rat of Nehring**

Spalax Nehringi Satunin, 1898: 314, 315, Figures 1–3. *S. monticola nehringi* Mehely, 1909: 70–79, Tab. I, Figure 2, Tab. XXII, Figures 1–14. *S. monticola armeniacus* Mehely, 1909: 79–84. *S. monticola cilicicus* Mehely, 1909: 84–88. *S. monticola anatolicus* Mehely, 1909: 88–100. *S. monticola turcicus* Mehely, 1909: 105–114. *S. labaumei* Matschie, 1919: 35–38. *S. leucodon nehringi* Ognev, 1947: 627–633, Figure 309.

Holotype. Museum of Georgia in Tbilisi, No. 119 1/c-80; Zakavkaz, Kizikoporan, village of the Tandurek-Chaya River (tributary of the Araks).

Material investigated. More than 50 skulls and skins obtained from around the republic of Kavkaz (Caucasia) and Turkey. The material is preserved in the collections of the Zoological Institute AN USSR of Moscow State University and the Zoological Museum of the University of Humboldt in Berlin.

Diagnosis. The nasal bones have a sharply defined longitudinal slit-like opening in the region of the suture between them. The temporo-nasal and temporo-maxillary sutures form an angle with its apex directed backward. The upper and lower incisors are narrowed (relation of width and antero-posterior cross section, 72.2–87.2–95.8 for the upper, and 70.0–79.6–85.2 for the lower teeth).

Description. Measurements are average (length of body 170–191–225 mm; length of foot, 23.0–25.7–30.0 mm; condylobasal length of skull, 34.4–44.0–53.3 mm). The skull is narrow in the incisorial and rostral sections (relation of incisorial and rostral width and length of row of permanent molars is respectively equal to 67.1–83.0–98.8 and 98.7–115.7–135.0). The edges of the rostrum are almost parallel and do not meet in a forward direction (Figure 61). The constriction behind the eyes is clearly defined; the width behind the eyes is approximately equal to the length of the anterior permanent molars. With regard to the degree of development of this trait, the mole rat of Nehring is closer to the Balkan type of *M. leucodon* than the east European representatives of this species. The upper diastema is relatively short (magnitude of the diastema-tooth index, 160.0–202.7–247.0). In this respect, the species exhibits characteristics that are, after all, similar to the Balkan type of *M. leucodon*. In the east European *M. leucodon*, the diastema is relatively longer, the nasal bones have a clearly marked longitudinal slit-like depression, sharpened anteriorly and long; their length, as a rule, exceeds the total length of the temporal and parietal bones (a typical subspecies of the Caucasus), or is approximately equal to the latter (subspecies of Anatoliya). The temporo-nasal and temporo-maxillary sutures form an angle with its apex directed upward (Figure 61). The occipital bone is narrow; its width approximately twice exceeds the height measured from the upper edge of for. magnum up to the apex of the lambdoid process. The hard palate is narrow; its width between the anterior permanent molars is considerably less than the length of M^1. The openings (foramina) behind the palate are small. Depressions behind the palate are not present. The central ridge of the palate at the level of the foramina behind it form a lamellar broadening. The portion behind the palate is bifurcated into two by a well-developed styloid process. The alveolar bulges are absent or faintly marked. The ridges in the space between the anterior edge of the alveolus of M^1 and the incisorial openings are well developed. The structural characteristics of the upper incisors have already been given in the diagnosis.

In complexity, the grinding surface of the upper permanent molars resembles similar structures in the specialized representatives of the subgenus *Microspalax*, namely *M. ehrenbergi* and *M. odessanus*. The paracone

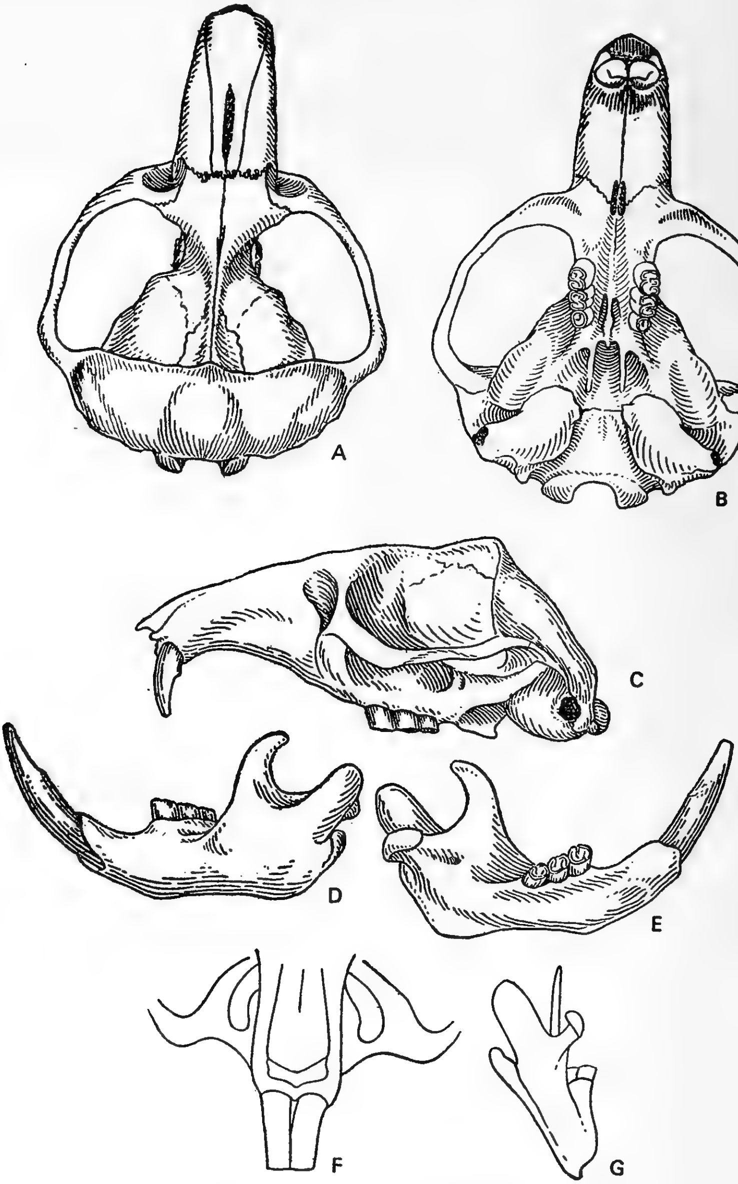

Figure 61. *Microspalax nehringi* (Sat.). ×1.6.

Legend is the same as in Figure 50.

on M_1 is not fused until old age with the anterior collar, as a result of which the tooth in these stages of wearing is characterized by the presence of two intruding folds in the outer line. However, it differs from representatives of the subgenus *Microspalax* in that the metacone and the posterior collar, as a rule, are completely fused in almost all stages of tooth erosion, as a result of which in the majority of cases, at least one of the marks of the additional outer intruding fold or posterior mark are absent (markings of this fold were only observed by us in some very young individuals from the series of fifty skulls). Figures 62 and 63 allow us to judge the characteristics of individual and age variability in the construction of the masticatory surfaces of the upper permanent molars.

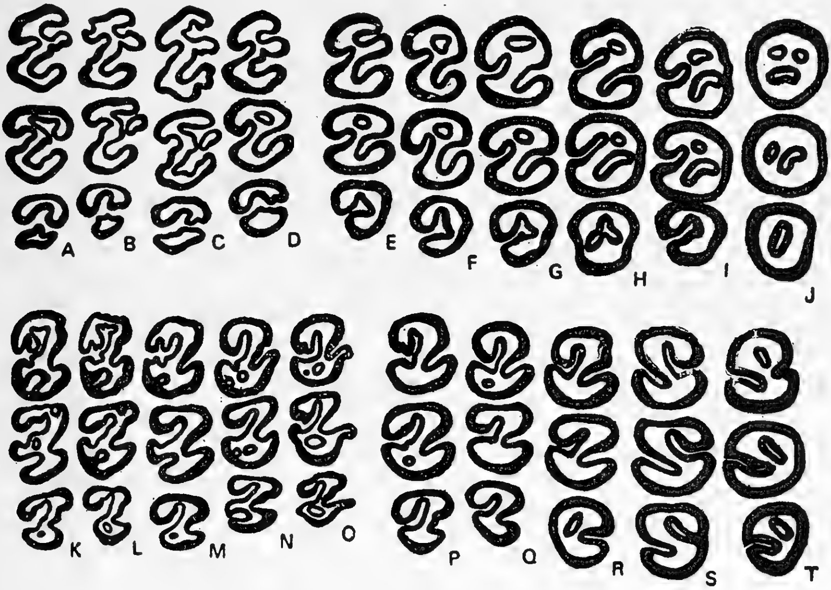

Figure 62. *Microspalax nehringi cilicicus* Meh. ×8.

A to *J*—upper, and *K* to *T*—lower rows of permanent molars; *A* to *D* and *K* to *O*—young and semi-mature; *E* to *J* and *P* to *T*—adult and old individuals.

The peculiarities in the structure of the roots of the upper permanent molars may be summarized as follows: M^1 and M^2 in the majority of cases are characterized by the presence of three roots—a massive inner and two weakly developed outer ones (Figure 64); the inner root, as a rule, has marks of bifurcation; the outer ones sometimes show a tendency to fuse with the inner. In some individuals, the anterior outer root is completely fused with the inner, as a result of which the teeth have two roots. However, on M^2 the general tendency toward root fusion is more apparent than on M^1. M^3 in the majority of cases has two roots because the postero-external is, as a rule, fused with the inner one. In individual cases the fusion of the respective roots does not take place and so three separate roots appear. The dimensions and proportions of the teeth are as follows: M^1—length, 2.2–2.7–3.2 mm; width, 2.0–2.3–2.7 mm; relation of width to length, 74.0–85.3–104.0; M^2—length, 1.9–2.2–3.0 mm; width, 2.0–2.3–2.6 mm; relation of width to length, 86.7–103.8–114.3; M^3—length, 1.4–1.7–2.1 mm; width, 1.5–1.9–2.2 mm; relation of width to length, 95.2–109.4–125.0.

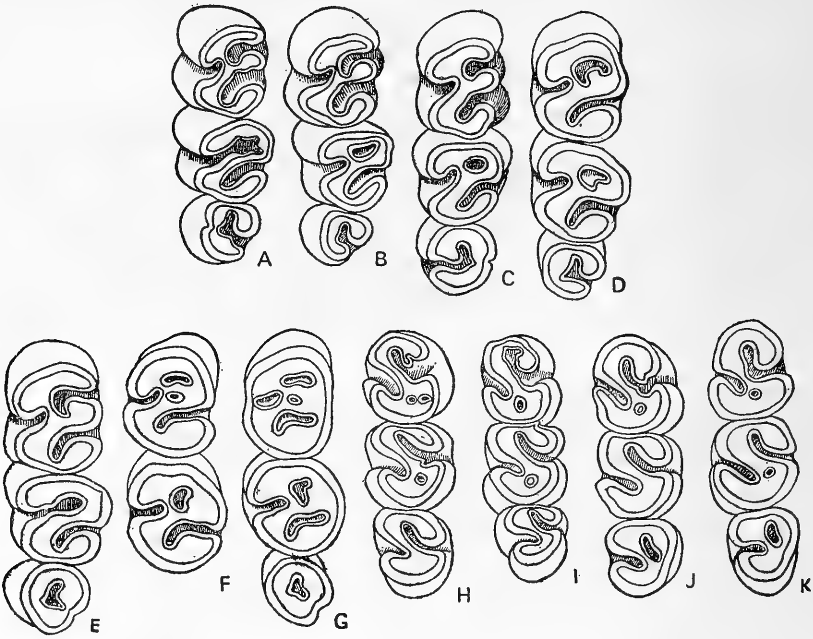

Figure 63. *Microspalax nehringi nehringi* Sat. ×10.

A to *G*—upper, and *H* to *K*—lower rows of permanent molars; *A* and *H*—semi-mature; *B* to *G* and *I* to *K*—adult and old individuals.

The lower jaw has a relatively high horizontal branch; the ratio of its height at the level of the anterior permanent molar to the length of row of M_1–M_3 is 80.0–96.5–113.9. The lower diastema is, on the average, relatively longer than in representatives of the subgenus *Microspalax*, and lower and shorter than in the most specialized species from the subgenus Mesospalax—the living *M. leucodon*; the magnitude of the diastema-tooth ratio is 70.4–87.0–106.3. The symphoidal tubercle is flattened, the maxillary angle is slightly expressed, the supramaxillary foramen is shifted to the lower edge of the jaw. With regard to the degree of development of these traits, the mole rat of Nehring is, after all, closer to the western Balkan form, *M. leucodon*, than the east European nominal subspecies.

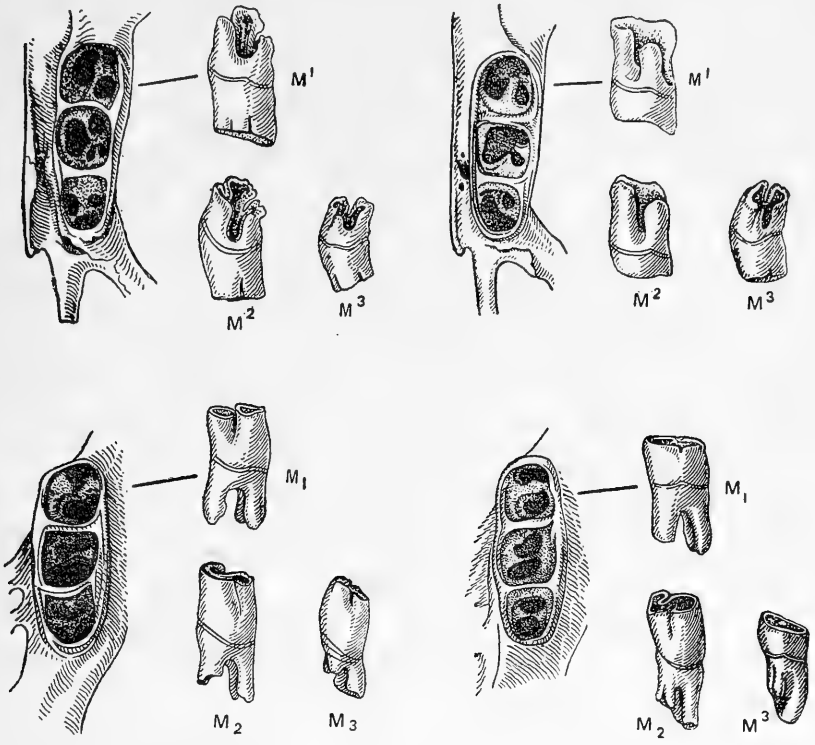

Figure 64. Structure of roots and alveoli of the permanent molars of *Microspalax nehringi* (Sat.) (Mehely, 1909).

The characteristics of the structure of the lower incisors have been described above in the diagnosis. The lower permanent molars are, on the whole, simpler compared to the same in representatives of the subgenus *Microspalax*. The entoconid on M_1 at all stages of wearing is fused with the posterior collar, as a result of which the tooth has characteristically only one intruding fold on the inner line. However, the vestige of this fold in the shape of one, or rarely, two posterior marks could be preserved up to very old age. The mesoconid is absent in old age in the majority of cases. In young animals its vestiges are represented in the form of a small tooth. The tooth is, on the average, narrower than in the European *M. leucodon*; the relation of width of the corona to its length is 68.0–86.5–95.8. The range of individual and age variability in the structure of the wearing surface of M_1–M_3 is very great; this can be judged on seeing Figures 62 and 63. The lower permanent molars in the majority of cases have two roots each. The posterior root on M_1 and M_3 and the anterior on M_2 and M_3 exhibit a tendency toward bifurcation. Sometimes, the ends of the respective roots are bifurcated in the shape of a fork, each portion of which has, often, a corresponding socket in the alveolus (Figure 64). Measurements and proportions of lower permanent molars are as follows: M_1—length, 2.2–2.5–3.1 mm; width, 2.0–2.2–2.4 mm; relation of width to length, 68.0–86.5–95.8; M_2—length, 1.9–2.2–2.5 mm; width, 2.1–2.3–2.4 mm; relation of width to length, 92.0–103.3–120.0; M_3—length, 1.7–2.0–2.3 mm; width 1.8–2.0–2.1 mm; relation of width to length, 86.3–101.7–123.5.

Comparison. It differs from the European *M. leucodon* as follows:

1. Presence of a clearly defined longitudinal slit-like depression in the nasal bones (always absent in *M. leucodon*).

2. Construction of temporo-nasal and temporo-maxillary sutures which, in *M. nehringi*, form an angle with an apex directed backward. In *M. leucodon* the corresponding sutures are straight (nominal subspecies) or form an angle with its apex directed forward (Balkan subspecies).

3. Narrow upper and lower incisors (relation of width to antero-posterior cross section is equal to 72.2–87.2–95.8 for the upper, and 70.0–79.6–85.2 for the lower teeth, as against respectively 86.4–101.5–119.0 and 80.0–92.1–115.0 in *M. leucodon*).

4. A skull which is narrow in the incisorial and rostral sections (relation of incisorial and rostral width to length of row of permanent molars is respectively equal to 67.1–83.0–98.8 and 98.7–115.7–135.0, as against 80.3–100.3–130.0 and 106.8–129.9–162.0 in *M. leucodon*).

5. A narrow occipital bone, the width of which approximately twice exceeds its height, measured from the upper edge of the for. magnum up to the apex of the lambdoid ridge (in *M. leucodon*, the first measurement exceeds the second by more than twice).

6. Relatively longer nasal bones which are pointed anteriorly and the length of which exceeds the total length of the temporal and parietal bones, or is equal to it. In *M. leucodon*, the nasal bones are rounded off anteriorly, are blunted, and their length is less than the total length of the temporal and parietal bones.

7. A narrowed hard palate, the width of which between the anterior permanent molars is considerably less than the length of M^1. In *M. leucodon*, the width of the palate at the same place exceeds the length of the anterior permanent molar or, at best, is equal to the latter.

8. Smaller measurements of the foramina situated behind the palate and by the almost undefined depressions behind the palate. In *M. leucodon*, the foramina behind the palate are comparatively large and the depressions behind the palate are deeper and elongated in a longitudinal direction.

9. The central ridge of the hard palate has a lamellar broadening at the level of the foramina behind the palate and of the depression behind the palate. In *M. leucodon,* the lamellar broadening of the central ridge is absent.

10. A well-developed styloid process which divides the area behind the palate into two portions (weakly developed or absent in *M. leucodon*).

11. On an average, weakly developed alveolar and more strongly developed ridges in the place between the anterior edge of the alveolus of M^1 and the incisorial opening.

Measurements. Condylobasal length of skull, 34.4–44.0–53.3 mm; basic length of skull, 34.8–40.4–47.5 mm; length of nasal bones, 14.8–19.3–25.6 mm; total length of parietal and temporal bones, 15.9–18.8–24.8 mm; length of the parietal bones, 6.7–8.7–10.6 mm; length of upper diastema, 11.2–17.0–25.0 mm; length of hard palate, 20.6–27.7–34.7 mm; length of upper row of permanent molars, 7.0–8.0–8.9 mm; width of nasal apertures, 4.0–5.0–6.0 mm; incisorial width, 4.9–6.6–8.6 mm; width of nasal bones anteriorly, 4.7–6.4–8.0 mm; rostral width, 7.3–9.5–11.3 mm; width behind eyes, 6.4–7.2–8.7 mm; width of two parietale, 7.6–11.0–13.2 mm; width of bones up to lambdoid process, 5.6–6.2–7.7 mm; molar width, 28.5–37.5–45.3 mm; maximum width of occiput, 23.4–29.7–35.0 mm; length of auditory bullae, 9.2–11.7–13.6 mm; width of auditory bullae, 6.7–7.6–8.4 mm; width of upper incisor, 1.6–2.0–2.7 mm; antero-posterior cross section of upper incisor, 1.9–2.5–3.2 mm; height of occipital bones, 11.1–18.7–24.2 mm; height of nasal aperture, 2.4–3.6–5.2 mm; condylar length of lower jaw, 22.7–29.0–36.1 mm; angular length of lower jaw, 20.7–27.0–32.6 mm; length of lower diastema, 5.0–6.6–8.4 mm; length of lower row of permanent molars, 6.4–7.6–8.3 mm; height of horizontal branch at the level of center of alveolus of M_1, 5.9–7.2–8.8 mm; thickness of horizontal branch at the level of M_2, 2.9–3.6–4.4 mm; height of alveolar processes from inside, 2.8–5.6–7.9 mm; width of lower incisor, 1.5–2.1–2.8 mm; antero-posterior cross section of lower incisor, 2.0–2.7–3.6 mm.

Note. M. nehringi is the most primitive representative of the subgenus *Mesospalax.* With regard to the degree of development of adaptations of the skull and the lower jaw for burrowing (relative width of incisors and morphologic characteristics of the rostral section of the skull related to them), it occupies a middle position, between *M. ehrenbergi* and the European *M. leucodon.* It has to be noted further that in the aspects noted above, this species looks more primitive than even the European Pliocenic representatives of the subgenus *Microspalax—M. compositodontus, M. macoveii,* and *M. odessanus.* In addition, it has all the peculiarities which are characteristic of the subgenus *Mesospalax* (complete disappearance of longitudinal ridges, presence of narrowed parietal bones, a higher alveolar process of the lower jaw, and others). All this leads to an assumption about the morphological closeness of *M. nehringi* with the forms original to *Mesospalax* and also, perhaps, about an early (Pliocene) bifurcation of the branches of *Microspalax* and *Mesospalax* with their further parallel development.

The species was first described by K. A. Satunin (1898); however, he took the characteristics of skull structure as differentiating features which are greatly subject to transgression in the newly described species and in some forms of the European *M. leucodon*. The latter fact made Mehely (1909), and after him, V. I. Radugin (1917), K. A. Satunin himself (1920), and S. I. Ognev (1947) examine it as a subspecies of *M. leucodon* (= *M. monticola* Nehr.). Mehely preserved the name given by Satunin during his first description of the nominal subspecies—the Caucasian mole rat—while separating the Armenian and a number of Asia Minor forms as independent subspecies (please see the section on subspecies, page 221). However, research on the skulls of Caucasian and Asia Minor mole rats permits a differentiation in the interdependence of traits which were not subjected to, or were less subjected to, transgression in the Asia Minor (including Caucasian) and European group of mole rats of the subgenus *Mesospalax*. Such traits were, first of all, the presence of sharply defined longitudinal slit-like depressions on the nasal bones of the Asia Minor *Mesospalax* and a number of specific peculiarities in the structure of the temporo-nasal and temporo-maxillary sutures of the rostrum as a whole, of the hard palate, and of the upper and lower incisors—all of which have been described in the previous sections of this work. Thus, we have no doubt about the necessity for reorganization in the species of *M. nehringi* which joins the Asia Minor and, for that matter, even the Caucasian *Mesospalax*. *M. labaumei* (Matschie, 1919) which differs from *M. nehringi* in regard to individual and age differences has to be examined.

Distribution and geological age. Turkey, North Iraq, Republic of USSR near Caucasus. Also found around the USSR region in Akhalkalskii, Aspindzskii, Tsalkinskii, and Bashkichetskii regions of Georgia and around Leninkana, Artiksk, Achinsk, Akhuryansk, Amasii, Tukasyansk, and Spitaksk and Talin region of Armenia SSR (boundary area between USSR and Turkey). Recent; fossil remains not known.

Subspecies. It has been said above that Mehely (1909) did not recognize *M. nehringi* as an independent species and considered it as a subspecies of *M. leucodon*. Furthermore, he described still four subspecies from the region of Caucasus and Asia Minor: *M. l. armeniacus* Meh., 1909 (southwest Armenia SSR, mixed regions of Turkey from the Arart Mountains in the east); *M. l. cilicicus* Meh., 1909 (central Tavr, place Bulgar Maden); *M. l. anatolicus* Meh., 1909 (west Turkey around Izmira); and *M. l. turcicus* Meh., 1909 (southwest Turkey, around Fekhti). Afterwards, Hinton* described more forms from the central regions of Turkey: *M. l. corybantium* Hinton and *M. l. captorum* Hinton. However, these authors had extremely scanty material (*M. l. turcicus* was described from six; *M. l. armeniacus* and *M. l. antolicus* from three; and *M. l. cilicius* from just one skull) which puts one in doubt about the actual presence of these species in reality. This has been proven in the works of S. I. Ognev (1947) who has shown that *M. l. nehringi* and *M. l. armeniacus* are identical. We had an opportunity to examine a collection of recent mole rats which were found in the geographical areas from where the forms *cilicicus*, *anatolicus*, *turcicus*, *corybantium* and *captorum* had been taken. On the basis of a related literature and a morphometrical examination carried out on the collection, it was found that Mehely and Hinton described individual and, partly age variables, as subspecies differences, whereas the number of subspecies should be reduced to two as given below.

1. *M. nehringi nehringi* Satunin, 1898 (including *M. n. armeniacus* Meh., 1909). It is characterized by comparatively large (within the subgenus) measurements (condylobasal length of skull, 40.3–46.3–53.3 mm; length of upper row of permanent molars, 7.5–8.1–8.8 mm; condylar length of lower jaw, 27.2–30.5–35.9 mm; length of lower row of permanent molars, 7.3–7.8–8.3 mm) by a relatively long upper diastema, by a skull which is constricted behind the eyes and widened in the incisorial and rostral sections, by comparatively wider and elongated nasal bones (their length exceeds the total length of the temporal and parietal bones in the majority of cases). It spreads up into the southern regions of Georgia SSR (Akhalkalakskii, Aspindskii, Tsalkinskii and Bashkichetskii regions) around Leninkana, Artiksk, Achinsk, Akhuryansk, Amasii, Tukasyansk and Spitaksk regions of Armenia SSR. On the east, up to Kurovakan; on the south, the whole of the Talin region; in the mixed regions of Turkey (from the Gelskaya basin-crater on the west up to the Arart mountains in the east). Perhaps, this form spreads up also into north Iraq (Reed, 1958).

2. *M. nehringi cilicicus* Mehely, 1909 (including *M. n. anatolicus* Meh., 1909; *M. n. turcicus* Meh., 1909; *M. n. corybantium* Hinton and *M. n. captorum* Hinton). This differs from the nominal subspecies by:

a. On the average, rather smaller absolute measurements (condylobasal length of skull, 34.4–40.6–47.2 mm; length of upper row of permanent molars, 7.0–7.7–8.2 mm; condylar length of lower jaw, 22.7–26.7–31.6 mm; length of lower row of permanent molars, 6.4–7.4–8.2 mm).

b. A shortened upper diastema (magnitude of diastema-tooth index, 160.0–190.9–239.7 as against 172.8–200.0–247.0 in the nominal subspecies).

c. A lesser incisorial width (relation of incisorial width to length of row of permanent molars is 67.1–77.0–97.4, as against 77.5–87.3–98.8).

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*Reference omitted from the bibliography—(G. Ed.).

d. Nasal bones which are narrow and relatively short. The relation of width of nasal bones anteriorly to length of row of permanent molars is 67.1–76.3–91.0 as against 72.7–82.4–92.5. In addition, the length of the nasal bones in *M. n. cilicicus* is approximately equal to the total length of the temporal and parietal bones (in *M. n. nehringi*, the former measurement as a rule exceeds the latter).

e. A lesser rostral width (relation of rostral width to length of row of permanent molars is 98.7–111.7–137.2, as against 103.7–118.5–135.0).

f. A larger width behind the eyes (relation of width behind the eyes to length of row of permanent molars is 83.7–97.2–105.1, as against 71.9–81.2–90.6).

It is distributed in the region of Asia Minor (Figure 32). The boundaries of the distribution of the indicated species have not yet been exactly determined.

2. **Microspalax leucodon** (Nordmann, 1840)—**Hilly or White-toothed Mole Rat**

Spalax typhlus leucodon Nordmann, 1840: 32–35. *S. typhlus hungaricus* Nehring, 1897: 173, Abb. 3. *S. hungaricus* Nehring, 1898a: 479–481, Figure 1. *S. monticola* Nehring, 1898 Sitzungsber. Gesellsch. naturforsch. Freunde Berlin: 6. *S. dolbrogeae* Miller, 1903: 161. *S. leucodon* Nordmann, Reshetnik 1939: 9, 17.

Holotype. Zoological Museum of Odessa University; skull from the collections of Nordmann; around the city of Odessa.

Material investigated. Above ninety skulls and skins in the custodial finds of the Zoological Institute AN SSSR, Institute of Zoology AN Ukraine SSR, Institute of Zoology AN Moldavia SSR, Kiev and Odessa Universities.

Diagnosis. The nasal bones are without a longitudinal slit-like depression. The temporo-nasal and temporo-maxillary sutures form almost a straight line or an angle with its apex directed forward. The upper and lower incisors are wide (relation of width to antero-posterior cross section, 86.4–101.5–119.0 for the upper, and 80.0–92.1–115.0 for the lower teeth).

Description. Measurements are average (length of body, 150–201–240 mm; length of foot, 19.0–24.5–27.5 mm; condylobasal length of skull, 35.7–43.8–51.4 mm). The skull is wide in the incisorial and rostral sections (relation of incisorial and rostral widths to length of row of permanent molars is respectively equal to 80.3–100.3–130.0 and 106.8–130.0–162.0). The edges of the rostrum meet anteriorly (Figure 65). The constriction behind the eyes is clearly defined in the Balkan types (width behind the eyes is approximately equal to the length of the two anterior permanent molars), and finally in the east European types (the first measurement is, as a rule, always greater than the second one). The upper diastema is relatively short in the Balkan subspecies (magnitude of diastema-tooth index, 162.5–201.7–240.0) and is elongated in the east European nominal

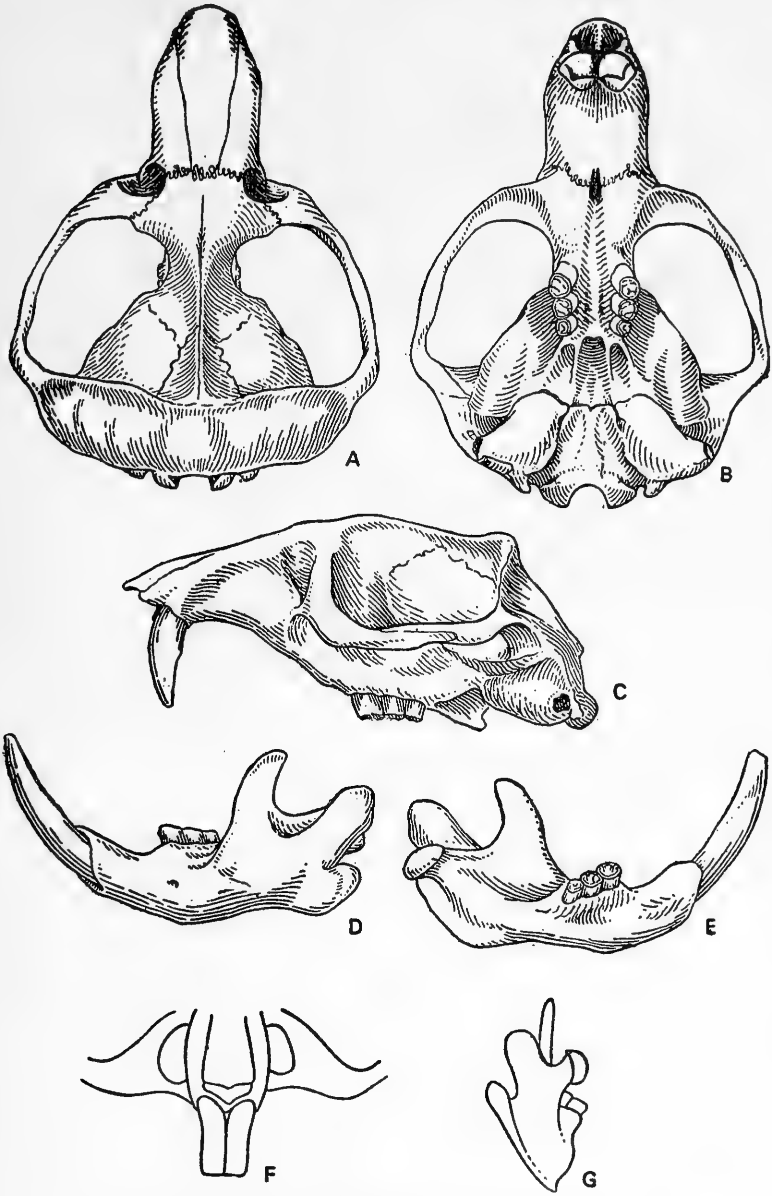

Figure 65A. *Microspalax leucodon monticola* Nehr. ×1.6.

Legend is the same as in Figure 50.

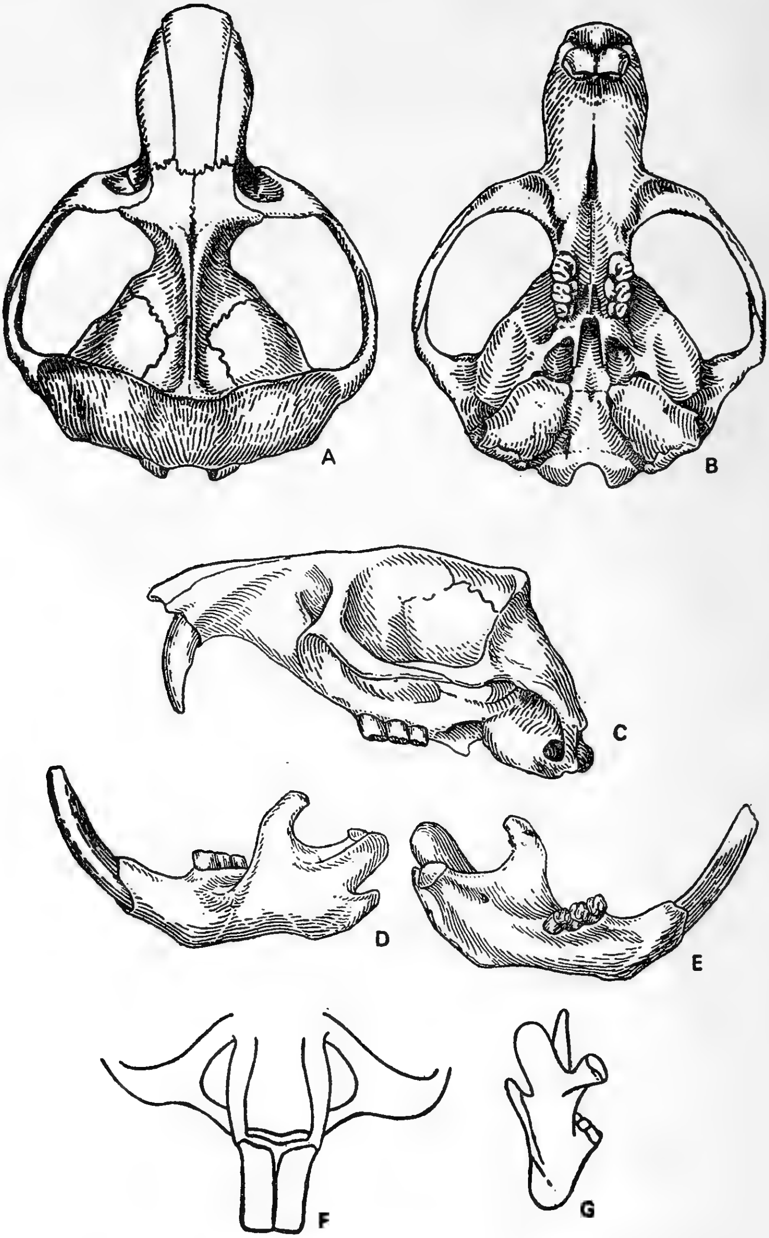

Figure 65B. *Microspalax leucodon leucodon* Nord. ×1.6.

Legend is the same as in Figure 50.

type (164.4–214.0–280.3). The nasal bones are without a longitudinal slit-like depression, rounded or blunted in front, and short; their length is less as a rule than the total length of the temporal and parietal bones. The temporo-nasal and the temporo-maxillary sutures form an almost straight line (nominal subspecies) or an angle with its apex directed forward (Balkan subspecies). The occipital bone is wide; its width in the majority of cases exceeds more than twice its height measured from the upper edge of the for. magnum up to the apex of the lambdoid process. The hard palate is wide; its width between the anterior permanent molars exceeds the length of M^1 or is approximately equal to the latter. The foramina behind the palate are sharply defined and elongated in a longitudinal direction. The central ridge of the palate at the level of the foramina behind the palate does not form a lamellar thickening. The styloid process of the palate is weakly developed, or is totally absent. The alveolar bulges in the majority of cases are well developed. The ridges in the space between the anterior edges of the alveoli of M^1 and the incisorial openings are weakly developed in old age and maturity. The structural characteristics of the upper incisors have been given in the diagnosis.

The general configuration of the grinding surface of the upper permanent molars is like that of *M. nehringi* as a whole. However, in some cases the anterior fold of M^1 is complicated by the presence of an additional outward layer (Figures 28 and 66). The roots of the upper permanent molars are constructed on the same principle as in the previous species. However, the tendency toward bifurcation of the inner root on M^1–M^2 is, perhaps, more clearly expressed (Figure 67). Three roots are often observed on M^3. The measurements and proportions of the upper permanent molars are as follows: M^1—length, 2.2–2.6–3.3 mm; width, 1.9–2.3–3.0 mm; relation of width to length, 71.4–88.2–104.0; M^2—length, 1.9–2.2–2.8 mm; width, 2.0–2.3–2.9 mm; relation of width to length, 88.0–105.9–123.5; M^3—length, 1.3–1.7–2.1 mm; width, 1.5–1.8–2.3 mm; relation of width to length, 88.2–108.7–125.0.

The horizontal branch of the lower jaw is, on the average perhaps, relatively higher and the diastema is relatively longer than in the preceding species (relation of height of horizontal branch at the level of the first permanent molar, and length of diastema to length of row of permanent molars are equal respectively to 84.0–101.7–127.1 and 70.0–91.0–125.4). The nature of the structure, the degree of development in the symphoidal tubercle, the jaw angle, and also the position of the supramaxillary foramen in the Balkan type are similar to the same in *M. nehringi*. In the nominal subspecies, the symphoidal tubercle is sharply defined, the maxillary angle is well developed, and the supramaxillary foramen is not shifted to the lower edge of the jaw.

The structural characteristics of the lower incisors have been noted in the diagnosis. The lower permanent molar (Figures 29, 67 and 68) are similar, on the whole, to the molars of the preceding species with regard to the structure of the grinding surfaces and the roots. However, on the

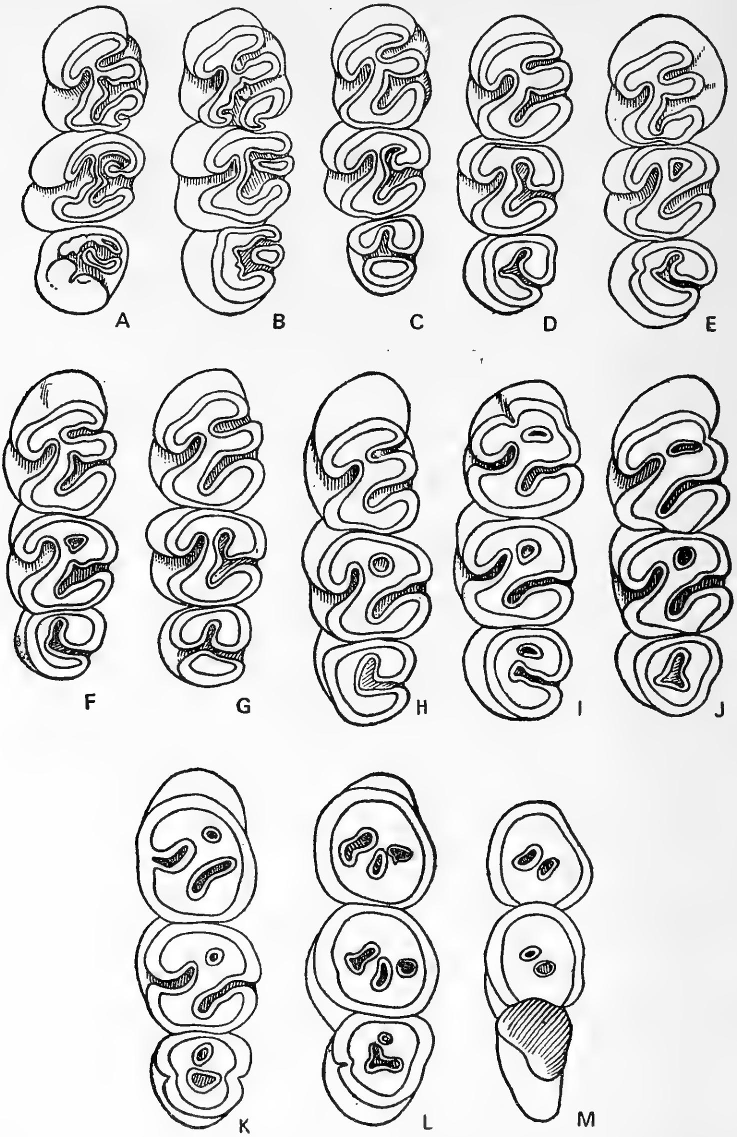

Figure 66. *Microspalax leucodon leucodon* Nord. ×10.

Upper row of permanent molars: *A* to *E*—young and semi-mature; *F* to *J*—adult; *K* to *M*—old individuals.

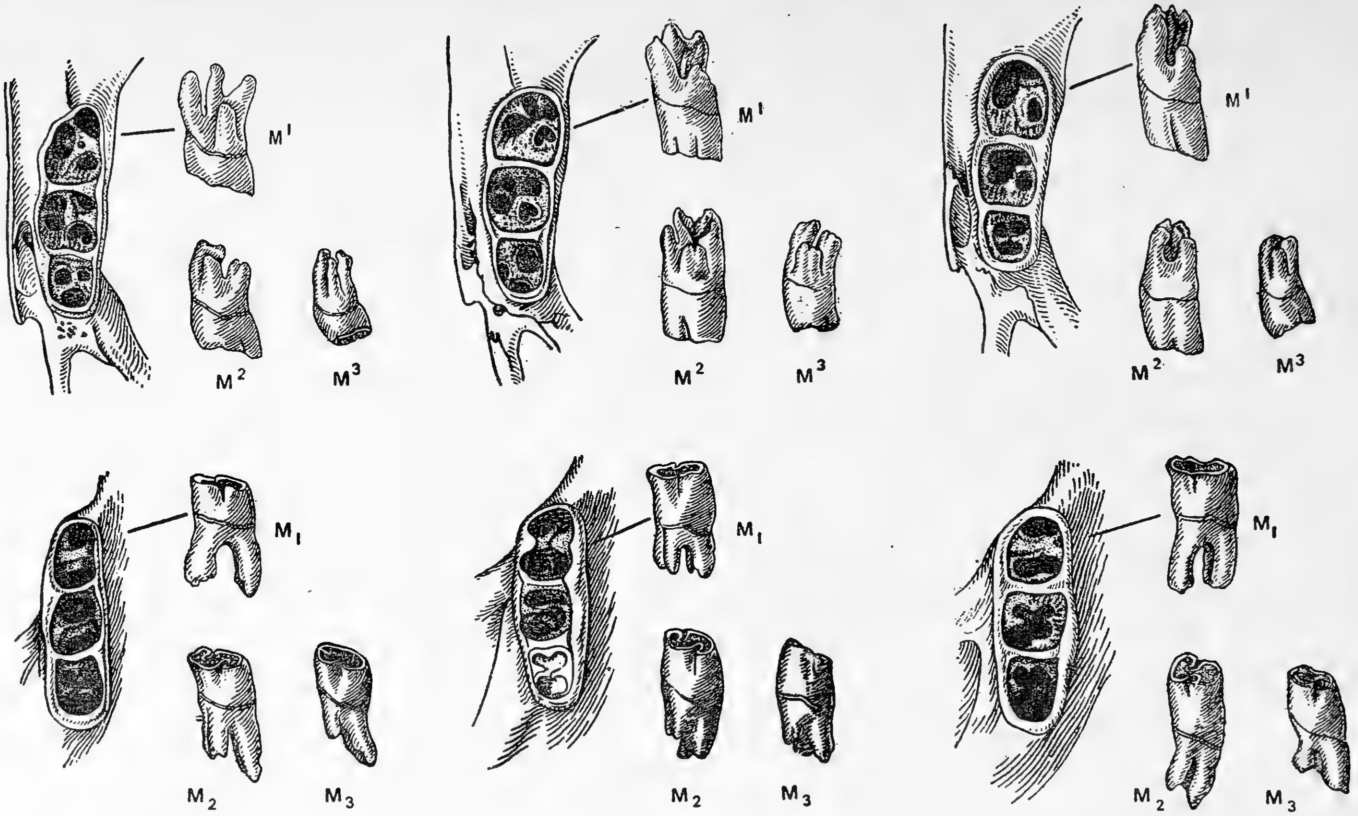

Figure 67. Structure of roots and alveoli of permanent molars *Microspalax leucodon* Nord. (by Mehely, 1909).

average, M_1 is relatively wider than in *M. nehringi* (relation of width to length, 83.3–95.1–122.2). The measurements and proportions of the lower permanent molars are as follows: M_1—length, 1.8–2.3–3.1 mm; width, 1.8–2.2–2.6 mm; relation of width to length, 83.3–95.1–122.2; M_2—length, 1.8–2.2–3.0 mm; width, 2.1–2.4–2.8 mm; relation of width to length, 87.0–108.1–130.0; M_3—length, 1.6–2.0–2.5 mm; width, 1.6–1.9–2.4 mm; relation of width to length, 81.0–96.1–129.4.

Comparison. A detailed comparison of *M. leucodon* and *M. nehringi* has been carried out above (pages 218-219).

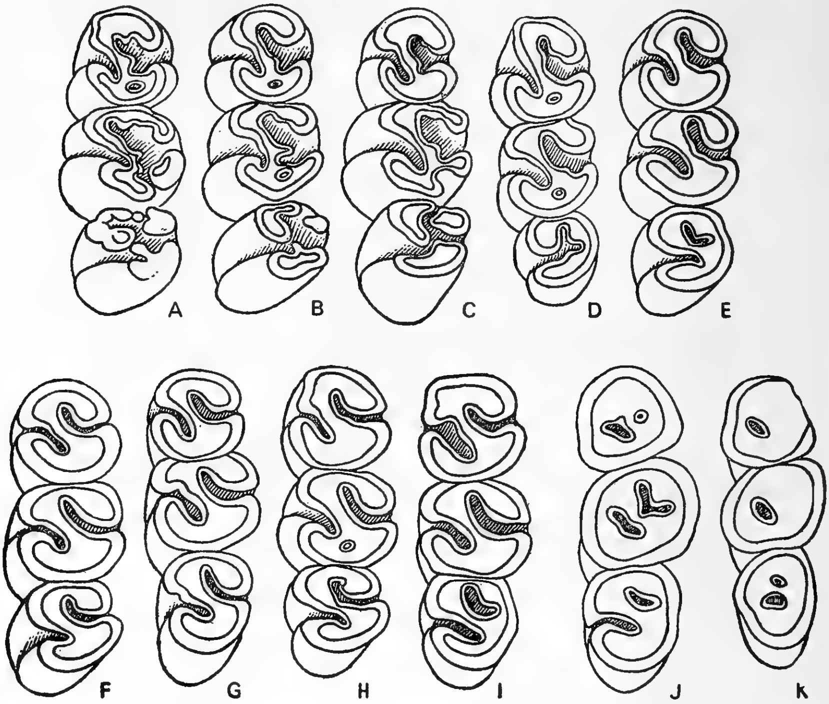

Figure 68. *Microspalax leucodon leucodon* Nord. ×10.

Lower row of permanent molars: *A* to *E*—young and semi-mature; *F* to *I*—adult; *J*, *K*—old individuals.

Measurements. Condylobasal length of skull, 35.7–43.8–51.4 mm; basic length of skull, 32.9–40.8–50.8 mm; length of nasal bones, 14.9–18.7–24.4 mm; total length of parietal and temporal bones, 15.3–19.0–23.0 mm; length of parietal bones, 5.8–8.2–10.6 mm; length of upper diastema, 12.5–16.1–20.5 mm; length of hard palate, 21.5–26.5–33.2 mm; length of upper row of permanent molars, 6.5–7.8–9.0 mm; width of nasal openings, 4.3–5.5–7.0 mm; incisorial width, 5.9–7.8–9.5 mm; width of nasal bones anteriorly, 5.2–7.3–8.1 mm; rostral width, 8.1–10.0–12.0 mm; width behind the eyes, 6.3–7.5–8.9 mm; width of two parietals, 8.5–12.0–15.0 mm; width of parietal bones up to lambdoid ridge, 5.2–6.6–8.6 mm; malar width, 27.1–34.6–41.4 mm; maximum width of occiput, 23.0–28.0–34.7 mm; length of auditory bullae, 10.2–11.6–13.7 mm; width of auditory bullae, 6.7–7.5–8.2 mm; width of upper incisor, 1.9–2.6–3.3 mm; antero-posterior cross section of upper incisors, 1.8–2.5–3.3 mm; height of occipital bone, 16.9–19.9–23.2 mm; height of nasal openings, 2.9–3.6–4.8 mm; condylar length of lower jaw, 23.8–28.7–35.5 mm; angular length of lower jaw, 22.4–27.7–35.8 mm; length of lower diastema, 5.0–6.8–8.8 mm; length of lower row of permanent molars, 6.7–7.4–8.7 mm; height of horizontal branch at the level of center of the alveoli of M_1, 6.0–7.5–8.9 mm; thickness of horizontal branch at the level of M_2, 3.1–4.1–5.1 mm; height of alveolar process from inside, 3.2–6.0–8.0 mm; width of lower incisor, 1.8–2.6–3.3 mm; antero-posterior cross section of lower incisor, 2.0–2.7–3.8 mm.

Note. M. leucodon is a highly specialized representative of the genus *Microspalax* for an underground way of life. Within the genus, it is characterized by the widest upper and lower incisors and the corresponding sections of the facial section, by the most elongated upper and lower diastemata, by a wide and low occipital section of the skull, by strongly developed sagittal and lambdoid ridges, and by a relatively high horizontal branch of the lower jaw.

The species was first described by Nordmann (1840) from an example found around Odessa. However, this work was ignored by research workers without due consideration. As a result, the species was rewritten several times, based on very scanty material from Yugoslavia and Hungary (Nehring, 1897, 1898a) and from Bulgaria (Miller, 1903, 1912), and moreover, the respective descriptions were done without a proper comparison with the east European forms described by Nordmann. Nehring (1898a, 1898b) and after him, Mehely (1909), considered that around the Balkan countries and around the adjacent regions of Hungary and Rumania, there lived two species of the genus *Microspalax*—*M. monticola* (Nehr.) (Yugoslavia, Greece, Bulgaria, and European Turkey) and *M. hungaricus* (Nehr.) (Hungary, Rumania). The peculiarities of M_3 were taken as differentiating traits by the authors. It was considered that *M. hungaricus* had only one inner intruding fold on the lower third permanent molar and not two (the external and internal), differing from *M. monticola* in this respect. However, as new data poured in, this trait was not confirmed.

Miller (1912) quite emphatically said *M. monticola* was synonymous with *M. hungaricus*; however, he mistakenly thought a type lived around Bulgaria which is principally different from *M. hungaricus*. Because of this, he maintained the name of *M. dolbrogeae* (Miller) given by himself in 1903 for the Bulgarian and Rumanian *Microspalax*. To prepare a basis for this, Miller (1912) made an unsuccessful attempt to discover the difference between the types mentioned above with regard to relative height of skull (in relation to condylobasal length), width of auditory bullae and suborbital foramen. However, the traits given by Miller (1903, 1912) in the diagnosis of the type and in the table determining it were found after further review to be nothing other than an expression of individual and age variability.

Mehely (1909) considered *M. dolbrogeae* as a subspecies of *M. monticola* Nehr. The name given by Nordmann was restored only later in the works of Reshetnik (1939, 1941) and Ognev (1947).

Distribution and geological age. Yugoslavia, north Greece, European Turkey, Bulgaria, Hungary, Rumania, Moldavian SSR and surrounding regions of Ukraine, Odessa region in the north approximately up to the Baltic, on the coast up to the Yuzhnogo Buga River, Soviet Bukovina. Authentic fossil remains up to the Holocene age are not known though, possibly, the Pleistocene mole rats from the sediments of south Austria (Brunner, 1936) and Hungary (Kormos, 1917) have to be added to this species.

Subspecies. Mehely (1909) and Hinton described nine subspecies of *M. leucodon* from very scanty data from different sources of the Balkan and Pre-Baltic regions. This was not confirmed in the comparative study on Martino's collections stored in the Zoological Institute of Academy of Sciences of the USSR. These collections refer to specimens from Yugoslavia, Hungary and Bulgaria, material from Moldavia and nearby territory of the Ukraine, and related literature. On this basis perhaps, there are not more than two subspecies which differ in their average magnitudes of measurements in regard to a number of traits of skull and lower jaw.

M. l. leucodon Nordmann, 1840 (including *M. l. transsylvanicus* Meh., 1909). It is characterized by comparatively smaller absolute measurements (body length, 158–185–230 mm; length of foot, 17–20–24 mm; condylobasal length of the skull, 36.7–42.5–50.4 mm; length of upper row of permanent molars, 6.5–7.4–8.0 mm; condylar length of lower jaw, 23.8–27.6–32.9 mm; length of lower row of permanent molars, 6.7–7.1–7.9 mm); by an elongated upper and lower diastemata; widened upper and lower incisors; relatively wider skull in the incisorial-rostral sections and in the section behind the eyes; by a lower, widened nasal opening; by faintly separated processes of the winged bones; by a sharply defined symphoidal tubercle; by a well-developed maxillary angle of the lower jaw; and by a supramaxillary foramen which is not shifted to the lower edge of the jaw.

It is distributed in Hungary on the west up to Tissa in Rumania, Moldavia SSR and surrounding regions of Cherenovitskaya region of the Ukraine SSR, in the Odessa region of the Ukraine SSR on the north approximately up to Balta, and on the east up to the Yuzhnogo Buga River.

M. l. monticola Nehr., 1898 (including types *M. l. hellenicus* Meh., 1909; *M. l. dolbrogeae* Miller, 1903; *M. l. hercegovinensis* Meh., 1909; *M. l. syrmiensis* Meh., 1909; *M. l. serbicus* Meh., 1909; *M. l. hungaricus* Nehr., 1898; *M. l. thermaicus* Hinton). It differs from the nominal subspecies by:

1. On an average, large, absolute measurements (body length, 170–201–245 mm; length of foot, 21.5–24.5–27.5 mm; condylobasal length of skull, 37.4–45.1–53.7 mm; length of upper row of permanent molars, 7.1–8.1–9.0 mm; condylar length of lower jaw, 25.0–29.9–33.9 mm; length of lower row of permanent molars, 6.9–7.7–8.7 mm).
2. A shortened upper diastema (magnitude of diastema-tooth ratio, 162.5–201.7–240.0, as against 164.4–214.0–280.3 in the nominal subspecies).
3. Narrowed upper and lower incisors (relation of width to antero-posterior cross section, 86.4–97.7–108.7 for the upper, and 80.0–89.5–100.0 for the lower, as against respectively 93.3–105.3–119.0 and 81.8–94.8–115.0).
4. A lesser width of skull in the incisorial, rostral, and behind the eyes sections (relation of incisorial, rostral and preorbital width to length of row of permanent molars, 80.3–95.3–111.7, 106.8–123.7–149.3 and 71.6–89.8–115.5, as against respectively 82.9–105.5–130.0, 112.3–136.0–162.0 and 85.0–102.8–124.3).
5. A high and narrow nasal aperture (relation of height of nasal aperture to its width, 56.7–72.2–82.6, and to width of row of permanent molars is 55.4–67.1–81.6, as against respectively, 45.1–59.7–79.0 and 60.0–76.7–91.7 in the nominal subspecies).
6. Widely separated processes of wing-like bones (distance between external edges, as a rule, exceeds the length of the two first permanent molars; in the nominal subspecies, the first measurement in the majority of given instances is less than in the second or, at best, equals it).
7. Shape of temporo-nasal and temporo-maxillary sutures (nasal bones are shorter than premaxillary because of which the sutures indicated form an angle with its apex directed anteriorly; in the nominal subspecies, the temporo-nasal and temporo-maxillary sutures form an almost straight line because the length of the nasal bones is approximately equal to the length of the premaxillary bones).
8. On the average, a short lower diastema (magnitude of diastema tooth index, 70.0–88.4–125.4 as against 74.0–93.6–117.3).
9. A flattened symphoidal tubercle, a faintly expressed maxillary angle

of the lower jaw and, similarly, a supramaxillary foramen which is somewhat shifted (situated at the lower edge of the horizontal branch closer than to the alveolar; in the nominal subspecies, it is situated closer to the alveolar edge).

It spreads up into Yugoslavia, north Greece, European Turkey, Bulgaria (up to Dunai on the north), Hungary (east up to Tissa).

2. Genus **SPALAX** Güldenstaedt. 1770—TRUE MOLE RAT

Güldenstaedt, 1770: 409–440. Mus (partim!) Schreber, 1792: 718–720. *Talpoides* Lacépéde, 1799: 10. *Aspalax* Desmarest, 1804: 24. *Anotis* Rafinesque, 1815, Analyse de la nature, on tableau de l'univers et de corps organises: 58. *Ommatostergus* Keyserling u. Blasius, 1840 (nomen nudum). *Myospalax* Hermann, 1873: 83. *Macrospalax* Mehely, 1909: 32–37.

Genotype. Spalax microphthalmus Güldenstaedt, 1770; recent; left bank of Ukraine, mixed regions of black soil, strips of RSFSR, right bank of Volga region except the lower, and the northwestern Caucasus.

Diagnosis. The for. supracondyloideum is always absent. Vestiges of this foramen are observed only in two per cent of the individuals from the most primitive representatives of the genus *Spalax*—the modern Bukovin mole rat *S. graecus* Nehr. The tuberculum pharyngeum laterale are narrow, drawn out in the shape of narrow ridges along the edges of the main wedge-shaped bone and the base of the occipital bone, because of which the base of the skull in the region of the tuberculum pharyngeum laterale is convexly bent like a furrow (canal) in a longitudinal direction. The basisphenoid and the base of the occipital bone are in one plane; the crack in the base of the skull at the place of this contact (which is characteristic of *Microspalax*) is not expressed. The auditory aperture is small; the length of the auditory bulla exceeds more than four times the largest diameter of the auditory opening (4.1–5.6–8.0). The lacrimal fossa is placed low. Its lower edge is situated above the upper edge of the molar process of the mandible. The skull is high; the height at the level of the anterior edge of the last permanent molar is twice less than the length from the nasal up to the apex of the lambdoid ridge. The parietal bones form a pentagon or five-angled star (Figure 74). The sagittal ridge is short; it is twice or more shorter than the nasal bones (1.8–2.1–2.7) and is convex. The ridge of the coronary-alveolar site of the lower jaw is well developed and sharp. The depression between the ridges is deep and always closed. The angular process which almost always touches the alveolar process is rounded at the ends and shifted somewhat forward in relation to the latter; its apex, as a rule, is situated anterior to the posterior wall of the proc. alveolaris. The area on the external surface of the angular process is marked all along its border covering the places of attachment of the anterior and posterior parts of the musculus masseter lateralis. The sella externa is approximately situated at the same level as the sella interna or is placed even above it. The alveolar process is high; its height beginning from maturity exceeds the length of the lower row of permanent molars. If the height of the alveolar process should be less than the length of the lower tooth row or approximately corresponds to it, then the length of the body is more than 250 mm, and the condylobasal length of the skull exceeds 55 mm. The dorsal arch of the first cervical vertebra is wide; its antero-posterior length is equal to the height of the neural canal. Remains of the general spine are absent or are represented in the shape of a small protuberance. The neural spine of the second cervical vertebra is long and high; its length exceeds more than twice the least width. The neural spines of the thoracic vertebrae are long and narrow. The sacrum is greatly constricted in the posterior portion; its anterior width exceeds approximately twice or more the same in the region of the fifth sacral vertebra. The neural spines are not fused completely; the sagittal ridge is divided (Figure 49), though in some cases complete fusion of the respective processes is observed in the second, third, and rarely fourth sacral vertebrae. The horizontal wings are always divided in the region of the fifth sacral vertebra and sometimes in the region of the fourth. In males and females the sacrum never touches the ischial axis of the pelvic bone, as a result of which the large ischial arch is always widely open from behind. The medial surface of the scapula is strongly bent anteriorly. Its caudal edge is widened because of the great development of the caudal crest (crista caudalis); the greatest height of the caudal edge is less than the maximum width of the scapula by about three times (2.3–2.8–3.1). The acromion process in mature and old representatives is completely dissimilar because the acromion tubercle (tuber spinae) is flattened (Figure 47). The acromion process is wide and club-shaped; its width is shorter by twice or less its length. The cranial edge of the scapula is smooth or has a blunt tooth-like process because its posterior portion is not well defined. The diaphysis of the shoulder bone is considerably flattened in an antero-posterior direction; its width above the proc. deltoideus exceeds the antero-posterior cross section at the same level by more than one and a half times (1.6–1.8–2.0). The deltoid process itself is, on the average, relatively shorter and higher than in representatives of the genus *Microspalax*; its lateral edge, as a rule, considerably protrudes as compared to the edge of the lateral condyle, is strongly curved, and the general area of its base is less than the distal width or is approximately equal to the latter. The medial condyle is long and wide; its length and the antero-posterior cross section are approximately equal to the posterior width of the distal block. The tubercle of the radius is widened from above; the maximum width of its proximal epiphysis is two and a half times less than the length of the olecranon (2.0–2.2–2.5). The maximum width of the semi-circular notch at the level of the ulna joint always exceeds the same at the level of the lower edge of the hook-like process because the coronary process of the radius is well developed. Furthermore, the olecranon is, on the average, longer than in *Microspalax.* The lateral depression—the place of attachment of the long abductor of the pollux and the long flexor of the same —is shallow; it is wide in appearance; its upper edge in the majority of given cases is placed approximately at the same level as the lower edge of the hook-like process and even if it elevates, it does so at a distance which is considerably less than the height of the semilunar groove, The ulna is, on the average, thicker than in representatives of the genus *Microspalax*; its least width (at the base of the proximal epiphysis) is approximately twice less than the width of the latter (1.8–2.0–2.3). The distal epiphysis is greatly widened; its maximum width exceeds the similar width of the proximal epiphysis. The ilium is short; its length in all the given cases was approximately equal to the length of the ischium (even when it exceeds the latter, it does so at not more than half the length of the acetabulum). The abdurator in the majority of cases is almost completely overgrown; its length is considerably less than the length of the articulating fossa (Figure 49). However, in *S. microphthalmus*, the measurements of this opening approximate those in representatives of the genus *Microspalax.* Measurements of the ischial axis are twice or more less than the measurements of the tuber ischii. During this, the ischial axis never fuses and does not come in contact with the wings of the sacrum. The femur has a wide diaphysis greatly flattened in an antero-posterior direction; the width of the bone at its narrowest part exceeds more than one and a half times the antero-posterior cross section measured at the same level (1.4–1.6–1.8). The tubercles under the joint are well developed; the width of the bone at the tubercles is wider and the joint always exceeds the intercondylar width. The patella is short and wide; its length exceeds its width not more than two times. The tubercle of the femur in the majority of cases is absent or present as a vestige. The medial ridge is well developed and sharp. The bend of the bone is present but slight (considerably less than in *Microspalax*). The proximal epiphysis of the fibula is narrow; its width is less than the width of the proximal epiphysis of the tibia by more than one and a half times (1.6–1.9–2.3). The symphysis of the tibia and fibula is, on the average, longer than in *Microspalax*; its length is usually less than two and a half times the full length of the tibia (2.0–2.2–2.4). The free part of the fibula is slightly more curved from the external side than in representatives of the genus *Microspalax.*

Comparison. A comparison of the genus *Spalax* and *Microspalax* has been given above.

Composition of the genus. Five modern and one fossil Late Pliocenic species—*S. giganteus* Nehr., 1897; *S. arenarius* Reshetnik, 1939; *S. micro-*

phthalmus Güld., 1770; *S. polonicus* Mehely, 1909; *S. graecus* Nehr., 1898; and *S. minor* W. Topachevskii, 1959.

Distribution and geological age. Late Pliocene (middle and end of the period) to present day. Recent representatives are distributed in the Prikarpate regions of Rumania and Ukraine SSR (Bukovina), in all the territory of the Ukraine but for its northernmost parts, in the mixed regions of the black soil belt of the Russian Federation in the middle of the region around the Volga (right bank), in the Pre-Caucasus, North Caspian to the east from the Ural River and behind the Caspian. Fossil remains of the Pliocenic period are known only from around the Black Sea and Azov regions of the Ukraine. Anthropological remains are found everywhere within the boundaries of the distribution area of the genus, and even to the northern borders of its present-day area (Arzamaskii region, Gorkii district; Gromov and others, 1963).

KEY FOR IDENTIFICATION OF SPECIES OF THE GENUS SPALAX

1 (4). The rostral section of the skull is greatly widened and scapula-shaped. Its width at the level of the anterior edges of the suborbital opening and at the center is approximately the same (Figures 3 and 71) The total width of the nasal bones posteriorly is considerably less than the width of the premaxillary bones (individually), and the latter in turn considerably exceeds half of the anterior total width of the nasale. The temporo-parietal and forehead-to-temple sutures form a sharp angle (*giganteus* group).

2 (3). The length of the upper masseter exceeds approximately twice or more the least distance between the premaxillary and maxillary bones. The width of the hard palate, at the level of M^1 in adult and old individuals, is approximately equal to the length of the anterior permanent molar. The natural articulating fossa is wide with a flattened inner ridge. The alveolar process of the lower jaw in adult and old individuals is approximately equal in height to the articular one (Figure 3). The length of the body is 250 to 350 mm; condylobasal length of skull, 43.9–55.4–69.6 mm. The color is light pale-gray-yellow (straw); on the ventral side it is slightly more gray than on the back. . . . . .1. **S. giganteus** Nehring. (Holocene, including recent).

3 (2). The length of the upper masseter area is approximately equal to the distance between the anterior ridge of the latter and the suture between the premaxillary and maxillary bones. The width of the hard palate at the level of M^1 exceeds one and a half times or more

the length of this tooth. The natural articulating fossa is narrow with a sharply outlined inner ridge. The alveolar process of the lower jaw in adults and old individuals considerably exceeds the articulating one in regard to height (Figure 71). The length of the body is 190–234–275 mm; condylobasal length of skull, 42.4–51.0–59.0 mm. Comparatively darker shades of color predominate (dull gray); the ventral side is usually considerably more gray than the back..............................2. **S. arenarius** Reshetnik. (Recent).

4 (1). The rostral section of the skull slowly narrows in a forward direction and is wedge-shaped. Its width at the level of the anterior edges of the suborbital foramen always exceeds the width at the middle (Figures 74, 77 and 81). The total width of the nasal bones posteriorly is considerably more than the width of the nasale or is approximately equal to it. The temporo-parietal and forehead-to-temple sutures form a blunt or straight angle (*Microphthalmus* group).

5 (6). The anterior width of the nasal bones exceeds less than twice the width posteriorly. The groove between the nasal bones in the region of the temporo-nasal suture is well developed; its posterior ends are sharp and are bifurcated like a fork (Figure 81). The least width of the external wall of the suborbital foramen exceeds the length of the anterior permanent molar. The depression on the temporal bones in the place of the sagittal ridge is deep and sharply defined. The apex of the coronary process of the lower jaw is very much serrated...................................5. **S. graecus** Nehring. (Holocene, including recent).

6 (5). The anterior width of the nasal bones exceeds more than twice the posterior width. The groove between the nasal bones in the region of the temporo-nasal suture is absent or is slightly demarcated; the posterior ends of the nasale are blunt in the majority of cases and do not form a fork-like bifurcation (Figures 74 and 77). The greatest width of the external wall of the suborbital foramen is less than the length of the anterior permanent molar or is close to the latter. The depression on the temporal bone in the place of the displaced sagittal ridge, is absent or is faintly marked. The apex of the coronary process of the lower jaw is not serrated.

7 (8). The nasal bones are shorter than the premaxillary. The temporo-nasal and the temporo-premaxillary sutures form an angle with the apex directed forward (Figure 77). The length of the nasale is less than the total length of the temporal and parietal bones. The largest diameter of the auditory opening exceeds the length of the anterior permanent molar. The protocone and hypocone on M^1 of young

and semi-mature animals are always separated (Figure 78)........ .... 4. **S. polonicus** Mehely. (Pleistocene to recent).

8 (9). The nasal bones are of the same length as the premaxillary bones or even longer than the latter. The temporo-nasal and temporo-premaxillary sutures are straight (Figure 74). The length of the nasale is more than the total length of the temporal and parietal bones, or is equal to the last. The largest diameter of the auditory opening is approximately equal to the length of the anterior permanent molar. The protocone and hypocone on M^1 in the majority of cases are fused at the same stage of wearing (Figure 75).

9 (10). The total width of the parietal bones exceeds the length of the upper row of permanent molars. The width of the articulating surface of the condylus of the lower jaw exceeds half its length. The corono-alveolar groove is very step-like; its ridge in regard to height is close to the height of the corono-articulating groove. ....3. **S. microphthalmus** Güldenstaedt. (Pleistocene to recent).

10 (9). The total width of the parietal bones is less than the length of the upper row of permanent molars. The width of the articulating surface of the condylus of the lower jaw is less than half its length, or is approximately equal to it. The corono-alveolar groove is step-like; its ridge usually exceeds in height the height of the corono-articulating groove......... 6. **S. minor** W. Topachevskii. (Late Pliocene, Early Anthropogen).

1. **Spalax giganteus** Nehring, 1897—**Giant Mole Rat**

Nehring, 1897: 169–171, Abb. 2. *Spalax uralensis* Tiflov and Usov, 1938: 141–143.

Holotype. Institute of Special Zoology and Zoological Museum of the University of Humboldt, Berlin; the number of the example has not been fixed (Nehring, 1897: Abb. 2); around Makhachkaly, Dagestan.

Material investigated. Forty-five skulls and skins obtained in the vicinity of Pre-Caucasus and northern Pre-Caspian. They have been stored in the collections of Moscow State University, Zoological Institute of AN SSSR, Institute of Zoology AN Kazak SSR, and Kiev State University.

Diagnosis. This is the largest of the presently known representatives of the subfamily Spalacinae (length of body, 250 to 350 mm; length of hind foot 31.9 to 36.8 mm; condylobasal length of skull, 43.9–55.4–69.6 mm; length of the upper row of permanent molars, 9.1–10.5–11.7 mm., length of lower row of permanent molars, 9.3–10.2–11.0 mm). The rostral section of the skull is greatly widened and is shovel-shaped. The width of the nasal bones posteriorly is less than the width of each of the premaxillary bones; the latter, in turn, exceeds half the width of the nasale anteriorly. The temporo-nasal and the temporo-maxillary sutures form an angle with its apex directly forward. The antero-external edges of the molar arches are sharply bent down (Figure 3). The masseter area is long; its length exceeds approximately more than twice the least distance between the anterior ridge of the latter and between the inter-mandibular and mandibular sutures. The alveolar tubercles are separated from the anterior edge of the alveolus of M^1 at a distance which is considerably less than the length of the first permanent molar. The hard palate at the level of the anterior permanent molars is narrow. Its width in mature and old individuals is approximately equal to the length of M^1. The alveolar process of the lower jaw is approximately equal to its articular one in height.

Description. The rostral section of the skull is greatly widened because of the latitudinal bulge of the upper sections of the premaxillary bones. Its width at the level of the anterior edges of the suborbital foramen, and at the middle, is approximately similar. The edges of the rostrum greatly converge together anteriorly. The posterior portions are parallel and, rarely, slightly separate in the majority of cases. The total width of the nasal bones from behind is considerably less than the width of each premaxillary, and the latter, in turn, considerably exceeds half the total anterior width of the nasale. The nasal aperture is narrow and placed low. The ratio of its width and height to the length of row of permanent molars is respectively equal to 68.1–78.6–92.3 and 33.6–39.0–44.0 in mature and old individuals; and 62.2–70.5–75.5 and 33.6–35.0–36.3 in the young and semi-mature. The nasal bones are relatively narrow anteriorly; the magnitude of the relation of their anterior width to the length of row of permanent molars is 75.2–86.6–101.8 for mature and old individuals, and 65.3–76.1–87.9 for young and semi-mature animals. The length of the nasal bones in the majority of cases is less than the total length of the temporal and parietal bones. Furthermore, the nasale are shorter than the premaxillary bones because of which the temporo-nasal and temporo-maxillary sutures form an angle with its apex directed forward. It has also to be noted that the nasal bones of the giant mole rat are, on the average, relatively shorter than in all the modern species of the genus *Spalax*; the relation of their length to the length of row of permanent molars is equal to 201.9–226.6–263.4 in mature and old individuals, and 171.4–196.6–231.6 in young and semi-mature animals. The constriction behind the eyes is equally and strongly expressed in mature and old males and females; the relation of the width behind the eyes to the length of row of permanent molars is 58.5–75.6–95.6. The temporo-parietal section is short; the relation of total length of the temporal and parietal bones to the length of M^1–M^3 is 217.1–245.2–267.3 for mature and old individuals, and 208.7–222.4–235.7 for the young and semi-mature. The parietal bones are relatively longer and wider; the relation of length and width of each to the length of the row of permanent molars is respectively equal to 87.6–130.0–148.1 and 32.1–50.5–63.2 in mature and old individuals, and 124.2–142.0–204.3 and 65.0–78.0–89.1 in young and semi-mature animals. The depression on the temporal bone in the place of the displaced sagittal ridge is not expressed. The temporo-parietal and the temple-to-forehead sutures form a sharp angle (Figure 3). The upper diastema and the hard palate are relatively shorter than in all the presently known recent representatives of the genus *Spalax*. Thus, the magnitude of the diastema-tooth index is 194.4–216.0–247.3 in mature and old individuals, and 148.0–165.6–183.8 in young and semi-mature animals; the relation of the length of the hard palate to the length of row of permanent molars is respectively equal to 320.0–347.3–384.8 and 267.3–282.6–314.1. The masseter is long; its length approximately exceeds more than twice the least distance between the anterior ridge of the latter and between the suture of the premaxillary and maxillary bones. The alveolar tubercles are well developed and placed in the direct vicinity of the anterior edges of the alveolus of M^1 at a distance which is considerably less than the length of the anterior permanent molar. The hard palate at the level of the anterior permanent molars is narrow; its width in mature and old individuals is approximately equal to the length of M^1 in the majority of cases.

The zygomatic arches are very massive anteriorly. Their antero-external edges are sharply bent down forming a malar angle approximately equal to or exceeding 45°. The zygomatic arches are situated at the same level posteriorly to the articulating surfaces for the joint of the lower jaw. The external wall of the suborbital foramen is narrow from above (its least width is less than the length of the anterior permanent molar), and significantly widens below. The suborbital foramen is placed low; its height is approximately equal to the length of the lower row of the permanent molars and, in some cases, somewhat exceeds it. The inner edge of the fossa glenoidea is smooth, and the articulating surface itself is wide. The base of the occipital bone is narrow, as a result of which the auditory bullae are closer to each other. Thus, the greatest distance between the external edges of the tuberculum pharyngeum laterale approximately coincides with the length of M^2–M^3. The auditory bullae are relatively narrow; the relation of their width to the length of row of permanent molars is equal to 80.0–94.5–111.1. The occipital part of the skull is relatively low; the magnitude of the relation of the height of the occipital bone, measured from the upper edge of the for. magnum up to the apex of the lambdoid ridge, to the largest width of the occiput (measured near the base of the molar arches) is 33.4–41.2–48.9.

The upper incisors are relatively narrow (for representatives of the genus *Spalax*); the relation of width to antero-posterior cross section is

90.9–106.3–114.0. Their anterior surface is more complex than in all the presently known fossil and presently living species of the genus.

M^1 (length, 3.0–3.4–3.8 mm; width, 2.7–3.1–3.5 mm; relation of width to length, 77.8–91.8–97.2) in the young and semi-mature is similar to the M^1 of the previously described genus *Microspalax*; the paracone is still not fused with the anterior collar in the given stages of development, as a result of which the tooth has, characteristically, two intruding folds in the outer line (Figure 69). In mature animals, the middle external tubercle fuses with the anterior collar while closing the antero-external intruding fold, and thus forms a mark. In addition, vestiges of the metacone are better preserved on the teeth of young and semi-mature animals than in other species of the genus; the metacone is fused with the posterior collar and the posterior mark represents itself as a structurally constricted portion of the postero-external intruding fold. Such types of formations are alto-

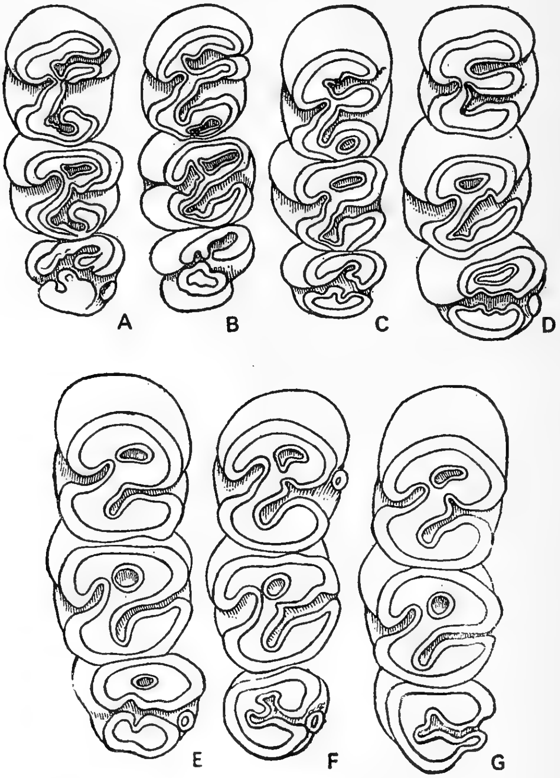

Figure 69. *Spalax giganteus* Nehr. ×10.

Upper row of permanent molars: *A* to *D*—young and semi-mature; *E* to *G*—adult individuals.

gether absent on the teeth of mature and old individuals. The order of closure of the intruding folds into marks because of tooth erosion is as follows: the antero-external, the inner portion of the postero-external, the postero-external, and finally, the inner. In the majority of cases, the tooth has two roots—the massive antero-internal which is formed because of the fusion of the antero-external and the internal roots, and the postero-external which is comparatively weakly developed. Quite often, all the roots fuse together because of which the tooth has only one complex root.

M^2 (length, 2.4–2.8–3.3 mm; width, 2.6–3.1–3.6 mm; relation of width to length, 100.0–109.7–120.7) is characterized by the presence of an anterior mark of one outer and one inner intruding fold (Figure 69). The anterior mark is formed in two ways. Most often it represents a constricted portion of the outer intruding fold, and rather rarely, inside portions of the inner intruding layer. The metacone and the posterior collar have a tendency to separate only in the teeth of young individuals. In semi-mature and mature animals, they are completely fused. The order of closing of the intruding folds into marks is as follows: the anterior inner portion of the outer, the inner portion of the inner, the outer, and finally, the inner. The number of roots often varies from one to two. The order of fusion of the roots is the same as in the preceding permanent molar.

M^3 (length, 1.8–2.2–2.7 mm; width, 2.4–2.7–3.3 mm) is relatively wider than in all the other species of the genus (relation of width to length, 90.9–120.3–144.4). In addition, this tooth is, on the average perhaps, relatively shorter than in the close *S. arenarius* (relation of length of M^3 to length of the preceding molar, 72.0–80.2–96.4). The protocone and hypocone in the majority of cases are not fused on lightly worn teeth. In the middle stages of erosion, the third permanent molar of the giant mole rat is also characterized by the presence of an anterior mark. It should be added to the aforesaid that in the majority of cases, there is also an additional external protuberance which fuses with the posterior intruding fold of the outer line with age, and completely vanishes in old age. Most often, the tooth is characterized by the presence of two roots—the massive posterior internal (formed as a result of the fusion of the internal and posterior external roots) and the weak antero-external. The degree of separation of the latter vary significantly.

The lower jaw has a shortened diastema and a relatively low horizontal branch. The values of the diastema-tooth index, and the relation of height of horizontal branch to the length of the lower row of permanent molars are respectively equal to 72.4–89.0–102.9; 103.0–113.5–127.9 in mature and old individuals, and 73.3–78.7–92.0; 88.7–103.0–113.0 in young and semi-mature animals. The alveolar process is low; it is equal to or slightly exceeds the articulated one in height. The height of the process measured from the internal side, even in mature and old individuals, is less than the length of the row of permanent molars. Thus, the values of the respective indices in the giant mole rat are 70.0–85.1–100.1 in mature and old, and 42.4–61.4–83.0 in young and semi-mature individuals. The incisura corono-alveolaris terminates near the base of the coronary process. Its ridge is, on the whole, more weakly developed than in other species of the genus *Spalax*. The coronary process is low with a smooth external surface in the majority of cases, because the lower edge of the coronary-alveolar groove does not reach the coronary process (a little encroachment is observed sometimes in very young individuals). The incisura corono-condyloidea is wrongly cut because of the shortness of its coronary edge as compared to the condylar edge. It has to be noted that the ridge of the corono-alveolar groove is considerably less in the degree of its development than the similar coronary articular groove, because of which the depression between them is considerably smaller anteriorly than in all the other fossil and recent representatives of the genus. The for. mandibulae is placed low and separated from the ridge of the corono-articular groove at a distance approximately equal to the length of the articulating surface of the condylus; in any case, it much exceeds two-thirds the length of the latter. The articulating surface of the condylus is wide; the relation of width to length is 47.5–53.1–60.3.

The lower incisor is relatively narrower than in all the modern species of the genus *Spalax*; the relation of its width to the antero-posterior cross section is 95.2–98.0–108.1.

M_1 (length 3.0–3.2–3.7 mm; width, 2.8–3.1–3.5 mm; relation of width to length, 86.5–96.2–106.4) in young, semi-mature, and partly in mature individuals is characterized by an almost constant presence of an anterior mark representing, most probably, a constricted anterior (additional) external intruding fold which in other modern species of the genus, except for *S. microphthalmus*, is completely reduced (Figure 70). The protoconid and hypoconid are separate in early stages of wear. Furthermore, the tooth is characterized by the constant presence of an additional tubercle at the base of the external intruding fold between the protoconid and hypoconid in young, semi-mature, and partly in mature animals. There is one outer and one inner intruding fold in mature individuals. There are two roots. Of them, the posterior one is more strongly developed than the anterior one and has vestigial marks of bifurcation.

M_2 (length, 2.6–2.8–3.1 mm; width, 3.0–3.3–3.7 mm; relation of width to length, 103.2–118.2–132.1) is relatively wide. It is characterized by the presence of one intruding fold in the outer and inner lines. The protoconid and the hypoconid are fused, though in early stages of wear they sometimes exhibit a tendency toward separation (Figure 70). Traces of an entoconid are absent (it is completely fused with the posterior collar). The tooth has two roots; moreover, the posterior is developed considerably stronger than the anterior one. Both roots exhibit a tendency toward fusion; in addition, the anterior one has marks of bifurcation.

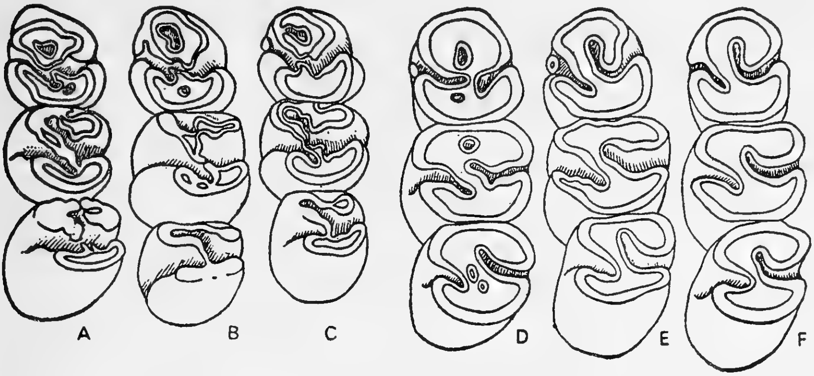

Figure 70. *Spalax giganteus* Nehr. ×10.

Lower row of permanent molars: *A* to *C*—young and semi-mature; *D* to *F*—adult individuals.

M_3 (length, 2.4–2.7–3.1 mm; width, 2.6–3.0–3.6 mm; relation of width to length, 93.1–112.9–128.0) is, on the average, relatively wider than in all the presently known modern representatives of the genus. In the majority of the given cases, it has an intruding fold in the outer line and one in the inner. Separation of the protoconid and the hypoconid is observed rarely in the very early stages of wear. There are two roots; the posterior one is larger than the anterior. Both roots fuse along almost their entire length. The anterior exhibits a tendency toward bifurcation which is proven by the structure of the alveolus.

Comparison. This mole rat sharply differs from those of the microphthalmus group in which we include the recent *S. graecus*, *S. polonicus*, and *S. microphthalmus* and the fossil Late Pliocene *S. minor*, by a widened rostral section of the skull which bulges along the edges of the rostrum as well as by considerably large absolute measurements. The width of the rostrum at the level of the anterior edges of the suborbital foramen and in the middle is approximately equal because of the fact that its edges are approximately parallel all along the posterior half of its length, and slightly approach each other in the anterior part; the rostral section, on the whole, has a more or less clearly defined shovel-shaped form. In mole rats of the microphthalmus group, the rostral section does not bulge along the edges, and the latter gradually meet in a forward direction because of which the rostrum, on the whole, has an almost wedge-shaped contour rather than a shovel-shaped form. The above-mentioned traits would look as follows: the width of the nasal bones posteriorly in *S. giganteus* is less than the width of the premaxillary (individually), and the latter considerably exceeds the total width of the nasal anteriorly. In mole rats of the microphthalmus group, the total width of the nasale posteriorly is greater than the width of the praemaxilla, and the latter is less than half of the anterior width of the nasal bones, or is approximately equal to it.

This species differs from its closely related species, the present-day *S. arenarius*, as follows:

1. Considerably large absolute measurements.
2. A relatively long masseter area, the length of which exceeds more than twice the least distance between the anterior ridge of the latter and the suture of the premaxillary and maxillary bones. In *S. arenarius*, the measurements are approximately the same.
3. Alveolar tubercles which are placed in the direct vicinity of the anterior edges of the alveoli of the first permanent molars, at a distance considerably less than the length of M^1. In *S. arenarius* the alveolar tubercles are separated from the anterior edges of the alveoli of M^1 at a distance exceeding (in young and semi-mature individuals) the length of the anterior permanent molar, or approximately equal to it.
4. The hard palate which is narrow at the level of M^1, and the length of which in both aged and mature individuals in the majority of cases is approximately equal to the length of the anterior permanent molar. In *S. arenarius*, its width exceeds the length of M^1 by more than one and a half times.
5. A wide fossa glenoidea with a flattened inner ridge. In *S. arenarius*, the inner ridge is sharply defined.
6. An occipital bone with a narrow base (the largest distance between the external edges of the tuberculum pharyngeum laterale is approximately equal to the length of M^2–M^3). In *S. arenarius*, the base of the occipital bone is wide (the indicated distance considerably exceeds the length of the last two permanent molars).
7. A lower alveolar process of the lower jaw (even in mature and old individuals, it is approximately equal to the articular one in regard to height). In *S. arenarius*, this process is considerably higher than its articular one. The indicated trait is quite clearly illustrated by the magnitude of the ratio of the inner height of the process to the length of the lower row of permanent molars. Thus, in *S. giganteus*, the alveolar process in the majority of the given cases is shorter than the row of M_1–M_3 or rarely approximately equal to the latter (70.0–85.1–100.0), whereas in *S. arenarius* it is always longer than the lower row of permanent molars (102.5–116.6–132.5).
8. An unfused coronary-alveolar groove with a faintly developed ridge (it is considerably weaker developed than the coronary articular one). In *S. arenarius* this groove is very step-like because of a well-developed ridge

in the lower portion of the proc. alveolaris which is not less in the degree of development of the coronary articular one, and because of which the fossa between them is considerably deeper than in the giant mole rat.

9. A low placed mandibular foramen (shifted from the edge of the coronary articular groove at a distance approximately equal to the length of the articulating surface of the condylus). In *S. arenarius*, it is situated at a distance considerably less than two-thirds the length of the condylus.

10. A widened articulating surface of the proc. condyloideus, the width of which in the majority of cases is approximately equal to half the length (47.5–53.4–60.3) or exceeds the same. In *S. arenarius*, the articulating surface of the condylus is constricted; its width is always less than half its length (38.8–45.2–48.2).

11. A lesser tendency for separation of the protocone and hypocone on M^1, and a greater tendency for separation of the metacone and the posterior collar than in similar permanent molars of *S. arenarius*.

12. An almost permanent presence of an additional inner tubercle on M^3. It is always absent in *S. arenarius*.

13. The metaconid of M_1 which is fused with the protoconid in all stages of wear. In *S. arenarius*, the metaconid is represented by an independent fold on the similar permanent molar in young and semi-mature individuals. In addition, the anterior mark and the additional tubercle at the base of the intruding fold between the protoconid and hypoconid are strongly developed on the anterior lower permanent molars of young, semi-mature, and partly in adult giant mole rats. The former is rarely found on similar molars in *S. arenarius* and the latter is always absent in this species.

Additional differences between the given species may be observed in the average values of the following traits:

1. The nasal bones in giant mole rats are relatively short (relation of their length to length of row of permanent molars, 201.0–226.6–263.4 in adult and old individuals, and 171.4–196.6–231.6 in young and semi-mature animals, as against respectively 241.0–250.6–257.9 and 210.5–214.5–216.9 in the sandy mole rat).

2. The total length of the temporal and parietal bones is relatively less (relation to length of M^1–M^3, 217.1–245.2–267.3 in adults and old individuals, and 208.7–222.4–235.7 in young and semi-mature animals, as against respectively 241.6–261.1–285.0 and 216.7–230.2–244.2 in *S. arenarius*).

3. The parietal bones are relatively longer (87.6–130.0–148.1 and 124.2–142.0–204.3, as against 105.2–125.2–137.5 and 131.1–124.5–130.1).

4. The upper diastema and hard palate are relatively shorter (value of the diastema-tooth index and the relation of length of hard palate to length of row of permanent molars, 194.4–216.0–247.3 and 148.0–165.6–

183.8; 320.0–347.3–384.6 and 267.3–282.6–314.1 as against respectively 230.0–249.9–266.7 and 178.3–184.2–195.2; 363.6–393.4–418.4 and 313.0–321.3–332.1 in the sandy mole rat).

5. The nasal aperture and the nasale are relatively narrower (relation of width of nasal aperture and both nasale anteriorly to length of row of permanent molars is respectively 68.1–78.6–92.3 in adult and 62.2–70.5–75.5 in old individuals, in young and semi-mature animals respectively 75.2–86.6–101.8; 65.3–76.1–87.9 as against 78.1–84.6–90.8; 71.8–75.3–79.5 and 87.5–94.7–100.0; 77.6–82.6–87.2 in *S. arenarius*).

6. The constriction behind the eyes in mature and adult specimens is expressed more sharply (relation of width behind eyes to length of row of permanent molars, 58.5–75.6–95.6 as against 71.6–81.3–89.3).

7. The parietal bones are comparatively wide (relation of width of each parietal bone to length of M^1–M^3, 32.1–50.5–63.2 in adult and old individuals, and 65.0–78.8–89.1 in young and semi-mature animals, as against 33.0–44.2–51.2 and 62.7–68.1–71.7 in the sandy mole rat).

8. The occipital section is relatively low (relation of height of occipital bone measured from the upper edge of the for. magnum to the largest width of the whole occipital section, 33.4–41.2–48.9 as against 47.9–52.8–59.3).

9. The upper incisors are relatively narrow (relation of width to antero-posterior cross section, 90.9–106.3–114.0 as against 108.3–119.0–130.0 in *S. arenarius*).

10. M^3 is relatively wider (relation of width to length, 90.0–120.3–144.4 as against 95.6–109.5–120.0).

11. The lower diastema is relatively shorter (magnitude of diastema-tooth index, 72.4–89.0–102.9 in adult and old individuals, and 73.3–78.7–92.0 in young and semi-mature animals, as against respectively 100.0–117.4–126.6 and 84.3; 101.3 in the sandy mole rat).

12. The horizontal branch of the lower jaw at the level of the posterior edge of the alveolus of M_1 is placed relatively low (relation of height to length of lower row of permanent molars, 103.0–113.5–127.9 in adult and old animals, and 88.7–103.0–113.0 in young and semi-mature individuals, as against respectively 118.1–123.0–132.0 and 111.3 in *S. arenarius*).

13. The lower incisor is relatively narrower (relation of width to antero-posterior cross section, 95.2–98.0–108.1 as against 100.0–103.9–109.0).

14. M_3 is relatively wider (relation of width to length, 93.1–112.9–128.0 as against 88.0–98.9–104.3).

Furthermore, the third permanent molar is, apparently, relatively short (relation of its length to length of M^2 is 84.0–95.5–111.5 as against 95.8–104.4–109.1).

Measurements. Condylobasal length of skull, 43.9–55.4–69.6 mm; basic length of skull, 40.0–53.4–65.6 mm; length of nasal bones, 16.8–22.9–31.4 mm; total length of parietal and temporal bones, 20.0–25.0–30.2 mm; length of parietal bones, 9.2–14.1–18.8 mm; length of upper diastema, 14.4–20.9–28.0 mm; length of hard palate, 23.6–34.0–43.4 mm; length of upper row of permanent molars, 9.1–10.5–11.7 mm; width of nasal aperture, 6.1–8.0–10.8 mm; incisorial length, 8.8–11.5–14.1 mm; width of nasal bones anteriorly, 6.4–8.7–11.7 mm; rostral width, 11.5–15.0–19.4 mm; width behind the eyes, 6.4–8.7–10.9 mm; width of two parietale, 6.9–10.8–15.8 mm; width of the parietal bone up to lambdoid to tubercle, 5.9–7.0–8.5 mm; malar width, 34.5–44.8–54.4 mm; maximum width of occiput, 31.0–38.1–45.4 mm; length of auditory bullae, 12.6–15.2–17.7 mm; width of auditory bullae, 8.8–9.9–12.0 mm; width of upper incisor, 2.8–3.9–4.9 mm; anterior posterior cross section of upper incisor, 2.7–3.6–4.6 mm; height of nasal opening, 3.1–4.0–4.9 mm; condylar length of lower jaw, 33.6–40.1–46.3 mm; regular length of lower jaw, 33.3–39.8–47.9 mm; length of lower diastema, 7.4–8.8–10.7 mm; length of lower row of permanent molars, 9.3–10.2–11.0 mm; height of horizontal branch at the level of posterior edge of alveoli of M_1 externally, 9.4–11.3–13.6 mm; thickness of horizontal branch at the level of M_2, 5.2–6.5–8.2 mm; height of alveolar process internally, 4.5–8.0–10.0 mm; width of lower incisor, 3.1–4.0–4.7 mm; antero-posterior cross section of lower incisor, 3.1–4.2–5.1 mm.

Note. As has been said above, the giant mole rat compared to the rest of the presently known living species of the genus has a shorter upper and lower diastema, a skull placed relatively low in the occipital region, narrow upper and lower incisors, a relatively low horizontal branch and alveolar process of the lower jaw; with an ill-developed ridge on the coronary-alveolar groove. Furthermore, apart from the above-mentioned traits, the species has other traits indicating a lesser specialization of the skull for burrowing activity.

In addition to this, the toothrows of *S. giganteus* are more complex as compared to the same ones in other modern representatives of the genus which together with traits indicating a rather stronger development of the masticatory musculature (details of the structures of the masseter area of the skull and partly of the zygomatic arches, etc., have been given above) proved the great adaptability of the species toward consumption of vegetative food which is rough in consistency. The latter fact is based, perhaps, on the life style of the giant mole rat who, as is known, feeds in more arid climatic zones compared to other recent species of the genus,

The foregoing account apparently shows that the species has preserved, even up to present times, the old way of life akin to certain fossil species which will be described below, in a way original for the group as a whole.

The species was described by Nehring (1897) from the Pre-Caucasus.

Afterward, V. E. Tiflov and Ya. A. Usov (1938) tried to report its eastern forms from Gurev and west Kazakhstan regions as an independent species —*S. uralensis* Tiflov and Usov. The reasons for such a separation were the rather smaller dimensions of the individuals from Kazakhstan, their rather darker color, and at times, a sharply defined angle between the temporo-nasal and the temporo-maxillary sutures, which was not confirmed by a series of data. All this permits one to completely agree with the opinion of S. I. Ognev (1947) who considered *S. uralensis* as synonymous with *S. giganteus*. However, the possibility of the Ural mole rat being an independent subspecies is theoretically feasible because the nominal and the Ural form of mole rats live at quite a significant distance from each other. We could not put our hands on enough data to solve this problem with finality.

Distribution and geological age. The semi-arid Pre-Caspian regions of northeastern Pre-Caucasus, mainly between the lower currents of the Kumu, Tereka, and Sulaka Rivers. On the north, it exists somewhat beyond the Kumu River, in the southern region of Kalmytskii ASSR to the south approximately in the line of Mahachakala-Gudermes. Isolated colonies are also known to occur to the east of the Urals in the eastern parts of west Kazakhstan, at the extreme northeast Gur'evskii, and also the Aktyubinskii regions along the Uilu, Temiru, and middle and upper currents of the Emby River. Recent. Fossil remains have not yet been found.

Subspecies. The geographical variability has not yet been studied though *S. g. uralensis* Tiflov and Usov could be taken as an independent subspecies.

2. **Spalax arenarius** Reshetnik, 1939—**Sandy Mole Rat**

Ognev, 1947: 615–620, Figures 296–301. *Spalax polonicus arenarius* Reshetnik, 1939: 11–12, Figure 3a. *S. zemni arenarius* Reshetnik, 1941: 31–33; Figures 6a–d, 7, 8. *S microphthalmus arenarius* Vinogradov and Gromov, 1952: 177.

Holotype. Institute of Zoology AN Ukraine SSR; No. 14, around the Black Sea, Ukraine SSR; around the city Golaya Pristan, Kherson region.

Material investigated. Forty-two skulls and twenty-five skins obtained in the region of Aleshkinski sands (lower Dnieper). All stored in the collections of the Institute of Zoology AN Ukraine SSR.

Diagnosis. Measurements are considerably smaller than in the giant mole rat (body length, 190–234–275 mm; hind foot, 22–26–30 mm; condylobasal length of skull, 42.4–51.0–59.0 mm; length of upper row of permanent molars, 8.3–8.7–9.9 mm; length of lower row of permanent molars, 7.8–8.1–8.7 mm). The rostral section of the skull is very wide and is shovel-shaped. The relative width of the nasal and premaxillary bones is similar to that of the preceding species. The temporo-nasal and temporo-maxillary sutures, as in the giant mole rat, form an angle with its apex directed forward. The antero-external edges of the zygomatic are sharply bent down. The masseter area is shortened; its length is approximately equal to the distance between the anterior ridge of the latter and between the suture of the intermandibular and maxillary bones. The alveolar tubercles are placed farther from the anterior edge of the alveolus of M^1 at a distance exceeding the length of the first permanent molar, or is approximately equal to it (in young and semi-mature animals). The hard palate at the level of the anterior permanent molars is wide; its width in adults and old individuals exceeds the length of M^1 by one and a half times and more. The alveolar process of the lower jaw considerably exceeds the articular one in regard to height (in adult and old individuals).

Description. The rostral section of the skull is, on the whole, like that of *S. giganteus.* The nasal aperture is wide and high; the relation of its width to length of permanent molars is respectively equal to 78.1–84.6–90.8 and 38.6–43.2–50.0 in adult and old individuals, and 71.8–75.3–79.5 and 35.7–38.0–40.0 in young and semi-mature individuals. The nasal bones are relatively narrower anteriorly; the value of the relation of their anterior width to the length of permanent molars is equal to 87.5–94.7–100.0 for adult and old individuals, and 77.6–82.6–87.2 for the young and semi-mature. The length of the nasal bones, as in the giant mole rat, in the majority of cases, is less than the total length of the temporal and parietal bones. The structure of the temporo-nasal and temporo-maxillary sutures, is, on the whole, as in *S. giganteus.* However, the nasal bones are, on the average, longer than in the preceding species; the relation of their length to the length of M^1–M^3 is 241.0–250.6–257.9 in adult and old individuals, and 210.5–214.5–216.9 in young and semi-mature animals. The constriction behind the eyes is, perhaps, expressed more faintly than in the giant mole rat; the relation of the width behind the eyes to the length of row of molars is 71.6–81.3–89.8 in adult and old individuals, and 96.5–99.5–102.3 in young and semi-mature animals. The temporo-parietal section is elongated; the relation of the total length of temporal and parietal bones to the length of M^1–M^3 is 241.6–261.1–285.0 in adult and old individuals, and 216.7–230.2–244.2 in young and semi-mature animals. The parietal bones are short and narrow; the relation of their length and width (individually) to the length of row of permanent molars is 105.2–125.2–137.5 and 33.0–44.2–51.2 in adult and old individuals, and 113.1–124.5–130.1 and 62.7–68.1–71.1 in young and semi-mature animals. The relation of the structure of the sagittal ridge, the temporo-parietal and temporo-frontal sutures is similar to the preceding species. The upper diastema and the hard palate is elongated; the magnitude of the diastema-tooth index is 230.0–249.9–266.7 in adult and old animals, and 178.3–184.2–195.2 in young and semi-mature animals; the relation of the length of the hard palate to the length of the row of permanent molars is respectively equal to 363.6–393.4–418.4 and 313.0–321.3–332.1. The structural characteristics of the masseter area, the alveolar tubercles, and the hard palate have been given in the diagnosis. It may be added to the aforesaid that the alveolar tubercles in the sandy mole rat are, as a whole, more weakly developed than in the giant mole rat. The structure of the anterior sections of the zygomatic arches in general are as in *S. giganteus*. Their antero-external edges are strongly bent down, forming a malar angle equal to 45° or exceeding it (Figure 71). The external wall of the suborbital foramen in adult and old animals is slightly broadened; its least width is equal to the length of the anterior permanent molar or even considerably exceeds it. The suborbital foramen itself is relatively higher than in the preceding species; its height exceeds the length of the upper row of permanent molars. Only in some cases do these measurements coincide. The inner ridge of the fossa glenoidea is sharply defined; the articulating surface itself is narrow and elongated. The base of the occipital bone is wide, because of which the auditory bullae are widely separated. Thus, the largest distance between the external edges of the tuberculum pharyngeum laterale considerably exceeds the length of M^1–M^3. The structure of the auditory bullae is, on the whole, similar to that of the giant mole rat; the relation of width to length of line of permanent molars is 90.6–96.1–103.4. The occipital section of the skull is relatively high; the magnitude of the relation of the height of the occipital bone, measured from the upper edge of the for. magnum to the largest width of the occiput, is 45.4–51.0–59.3.

The upper incisors are wide; the relation of width to the antero-posterior cross section is 108.3–119.0–130.0. Their anterior surface is flattened and smooth.

M^1 (length, 2.4–2.6–2.9 mm; width, 2.4–2.5–2.9 mm; relation of width to length, 85.7–96.3–108.3) is, on the average perhaps, relatively wider than in the previous species. The configuration of the enamel fold of the grinding surface resembles the similar molar of the giant mole rat. However, the tendency of separation of the protocone and hypocone is sharply expressed (Figure 72). The metacone is fused with the posterior collar in all stages of erosion. The order of closure of the intruding folds into marks is similar to that of the preceding species. In the majority of cases, there are two roots—the massive postero-internal (formed by the fusion of the postero-external and the inner roots) and the weak antero-external.

M^2 (length, 2.1–2.3–2.5 mm; width, 2.3–2.6–2.9 mm; relation of width to length, 100.0–113.3–126.1) in regard to the nature of the structure of the grinding surface is, as a whole, as in the giant mole rat. There are two roots—the massive antero-internal (the fused antero-external and the inner roots) and the faintly developed postero-external.

M^3 (length, 1.8–1.9–2.4 mm; width, 2.0–2.1–2.4 mm) is, on the average,

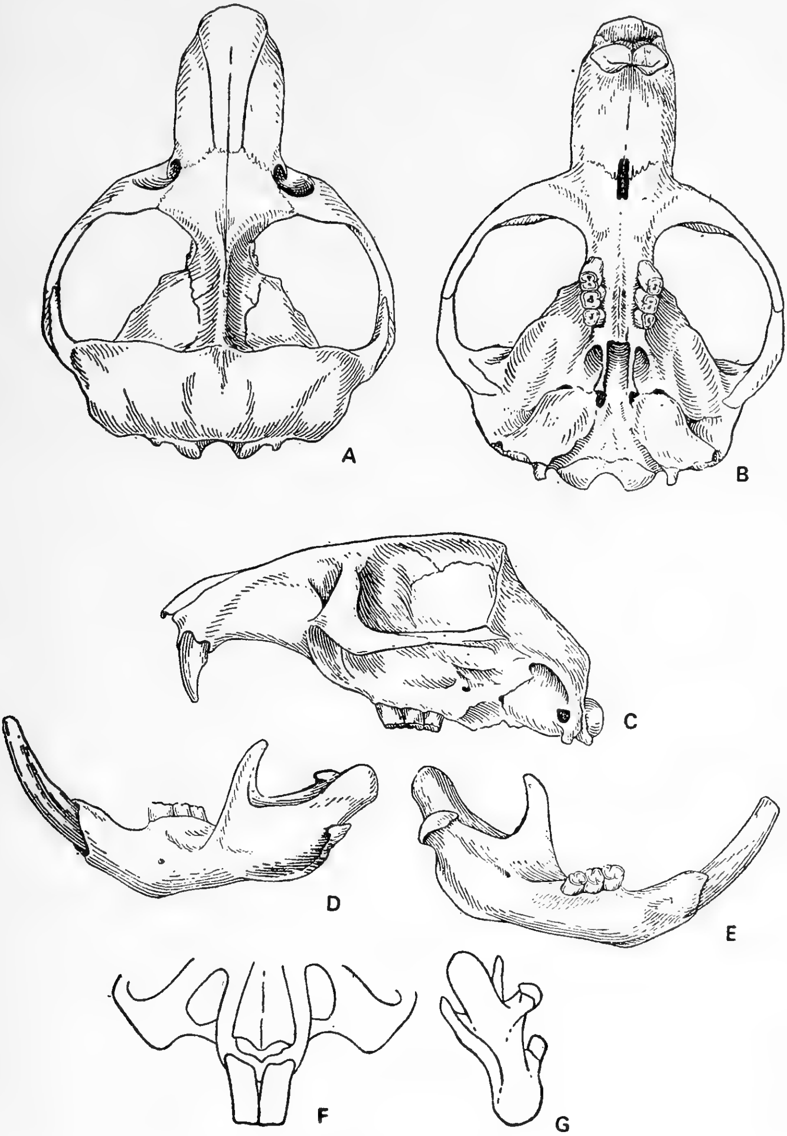

Figure 71. *Spalax arenarius* Resh. ×10.

Legend is the same as in Figure 50.

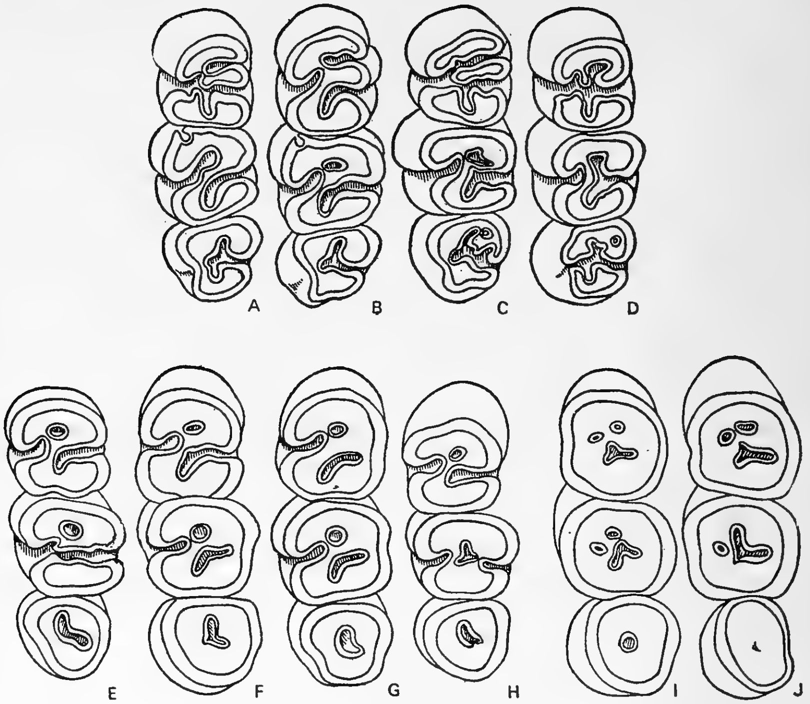

Figure 72. *Spalax arenarius* Resh. ×10.

Upper row of permanent molars: *A* to *D*—young and semi-mature; *E* to *H*—adult; *I*, *J*—old individuals.

relatively narrower and longer than in the preceding species; the relation of width to length, and length to length of the preceding molar is respectively equal to 95.6–109.5–120.0 and 80.0–87.9–100.0. In young and semi-mature animals, the protocone and hypocone were fused in the majority of the given cases, because of which the tooth is characterized by the presence of only one intruding fold in the outer line. The external additional tubercle is always absent. The anterior and posterior outer roots are fused almost along their entire length with the inner root.

All the upper permanent molars are considerably smaller than similar molars of the giant mole rat.

The lower jaw has an elongated diastema; the value of the diastema-tooth index is 100.0–117.4–126.6 in adult and old individuals, and 84.3–101.3 in the young and semi-mature. The horizontal branch is relatively high; the relation of its height measured at the level of the posterior edge of the alveolus of M_1 to the length of the lower row of permanent molars is 118.1–123.0–132.0 in adult and old individuals, and on the average, 111.3 in young and semi-mature animals. The alveolar process is high in adult and aged individuals and considerably exceeds the articular one with regard to height. The height of this process, measured from the inner side, always exceeds the length of the lower row of permanent molars (the value of the respective index in the sandy mole rat is 102.5–116.6–132.5). The incisura corono-alveolaris is step-like because of the strong development of the anterior tubercle of the alveolar process which considerably overlaps the coronary process. The latter, in the majority of cases, is higher than in the preceding species, though in individual cases, a type of structure akin on the whole to the condition in the giant mole rat is observed. The outer surface of the proc. coronoideus is step-like due to its being overlapped by the tubercle of the corono-alveolar groove. The nature of the structure of the coronary articular groove varies depending on the height of the coronary process; it is asymmetrical when the proc. coronoideus is elongated. The ridges of the corono-alveolar and coronary-articular groove are developed approximately to a similar degree anteriorly, as a result of which the depression between them is considerably deeper than in the preceding species. The mandibular foramen is raised to the border of the coronary-articulate groove, away from the tubercle of the latter, at a distance considerably less than two-thirds the length of the condylus. The articulating surface of the proc. condyloideus is narrow; the relation of width to length is 38.8–45.2–48.2.

The lower incisor is wide; the relation of width to antero-posterior cross section is 100.0–103.9–109.0.

M_1 (length, 2.4–2.7–2.8 mm; width, 2.4–2.5–2.7 mm; relation of width to length, 88.9–93.1–100.0) in young and semi-mature individuals is characterized by non-fusion with the anterior collar and, as a result, also with the protoconid and the anterior inner tubercle, the metaconid (Figure 73). In addition, the tooth has vestiges of an entoconid in the early stages of wear. The protoconid and hypoconid are fused in all the stages of erosion; however, a tendency for separation is, after all, observed in very young animals. The additional tubercle on the outer intruding fold is always absent. Because the tooth has a free metaconid in the early and middle stages of wear, the number of intruding folds in the inner line in young and semi-mature animals is two. Because of the fusion of the metaconid with the anterior collar, the anterior intruding fold is reduced. The order of closure of the intruding folds into marks is given in Figure 73. The tooth has two roots; of them, the posterior one is more strongly developed than the anterior. The roots sometimes exhibit a tendency for fusion.

M_2 (length, 2.2–2.3–2.4 mm; width, 2.6–2.7–2.8 mm; relation of width to length, 113.0–117.2–127.2) as in the previous species is wide. It is, on the whole, similar to the same tooth in the giant mole rat with regard to the configuration of the grinding surface and the structural nature of the roots.

M_3 (length, 2.3–2.4–2.6 mm; width, 2.1–2.3–2.6 mm; relation of width to length, 88.0–98.9–104.3) is relatively narrow. On the whole, it is similar to the M_3 of the giant mole rat; however, it differs in that the protoconid and hypoconid on the teeth of young and semi-mature animals, in the majority of cases, are separate. The tooth is characterized by having two roots. In the majority of cases, they are fused along the entire length.

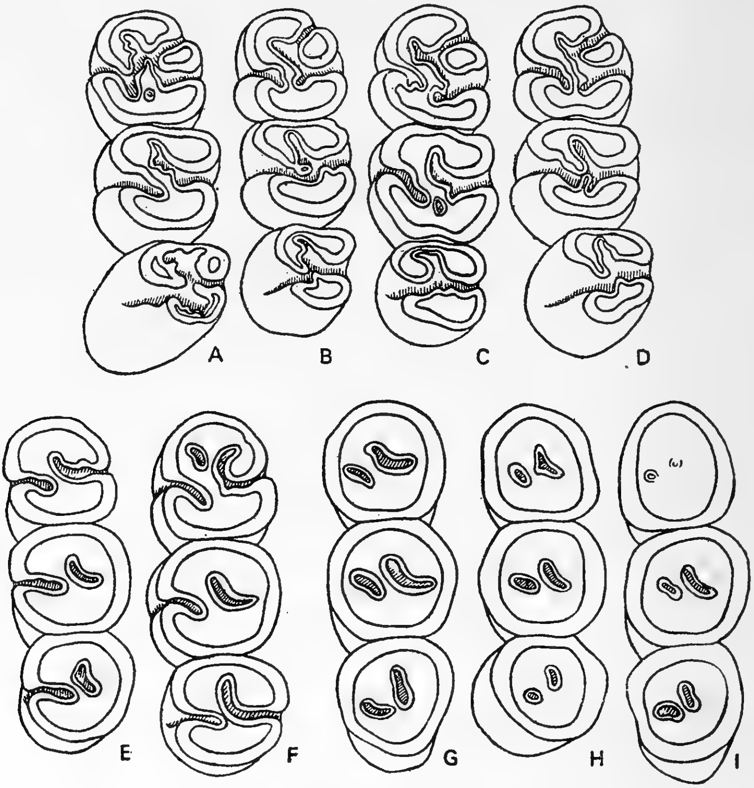

Figure 73. *Spalax arenarius* Resh. ×10.

Lower row of permanent molars: *A* to *D*—young and semi-mature; *E*, *F*—adult; *G* to *I*—old individuals.

Comparison. A detailed comparison of *S. arenarius* and *S. giganteus* has been made above. (Please turn to the corresponding section of characteristics for *S. giganteus*.) The basic differences from mole rats of the *microphthalmus* group are the same as for the giant mole rat.

Measurements. Condylobasal length of skull, 42.4–51.0–59.0 mm; basic length of skull, 39.6–47.4–56.0 mm; length of nasal bones, 17.7–20.8–23.9 mm; total length of parietal and temporal bones, 18.2–21.8–24.9 mm;

length of parietal bones, 9.5–10.8–12.7 mm; length of upper diastema, 15.2–19.8–24.4 mm; length of hard palate, 26.5–32.2–38.6 mm; length of upper row of permanent molars, 8.3–8.7–9.6 mm; width of nasal aperture, 6.1–7.1–8.0 mm; incisorial width, 7.8–9.5–11.2 mm; width of nasal bones anteriorly, 6.6–7.9–9.6 mm; rostral width, 10.4–12.6–14.7 mm; width behind the eyes, 6.8–7.7–8.8 mm; width of two parietale, 4.9–8.0–12.6 mm; width of parietal bone up to the lambdoid tubercle, 2.9–4.5–6.1 mm; malar width, 31.3–39.9–45.6 mm; greatest width of occiput, 29.2–33.5–40.1 mm; length of auditory bullae, 10.8–12.8–15.0 mm; width of auditory bullae, 7.7–8.4–9.1 mm; width of upper incisor, 2.6–3.3–4.0 mm; antero-posterior cross section of upper incisor, 2.2–2.7–3.6 mm; height of nasal aperture, 3.1–3.5–4.8 mm; condylar length of lower jaw, 31.8–36.2–39.0 mm; angular length of lower jaw, 32.6–36.4–38.2 mm; length of lower diastema, 7.0–9.0–10.1 mm; length of lower row of permanent molars, 7.8–8.1–8.7 mm; height of horizontal branch at the level of the posterior edge of the alveolus of M_1 externally, 8.6–9.7–10.4 mm; thickness of the horizontal branch at the level of M_2, 4.7–5.3–5.9 mm; height of alveolar process internally, 7.4–9.2–10.6 mm; width of lower incisor, 3.0–3.5–4.0 mm; antero-posterior cross sections of lower incisor, 3.0–3.4–3.9 mm.

Note. The sandy mole rat is more specialized toward a burrowing type of life than the previously described species. The presence of an elongated upper and lower diastema, a skull relatively high in the occipital region, widened upper and lower incisors, a relatively high horizontal branch and alveolar process of the lower jaw, are the proofs; moreover, the latter is characterized by a strongly developed tubercle of the corono-alveolar groove in its anterior portion.

In addition, this species has still preserved the complex permanent molars like those of *S. giganteus* which indicates not only the relative primitiveness of it as a whole, but also its special adaptation of feeding on rather hard, rough vegetative foods or, in other words, to living in conditions of more arid climate than mole rats from the microphthalmus group. This is partly proven also by the already described structural characteristics of the upper masseter area (it assumes a medium position in regard to the degree of development, between the giant mole rat and the species of the microphthalmus group), and the zygomatic arch (massive and sharply bent down in the antero-external section).

The status of this species was confirmed by S. I. Ognev (1947). Until then, the sandy mole rat was primarily taken as a subspecies of *S. polonicus* (Reshetnik, 1939, 1941). Ognev put *S. arenarius* close to *S. microphthalmus*. As has been shown above, the species takes a middle position between the giant mole rat and the species from the microphthalmus group. The structure of the rostral section of the skull, the zygomatic arches, and partly the permanent molars, put it close to the former; whereas the elongated upper and lower diastema, widened upper and lower incisors, the height of the occipital section of the skull, the wide hard palate, the base of the occipital bone, a number of structural peculiarities in the lower jaw, and foremost, its alveolar process, put it close to the latter. Further, without sufficient basis for all this, the species was taken to be a subspecies of *S. microphthalmus* (Vinogradov and Gromov, 1952; Gromov *et al.*, 1963).

Distribution and geological age. The lower Dnieper sandy area (Aleshkinskie Piski). The western boundary, the bank of the Dnieper and estuaries of the Dnieper; the eastern boundary, approximately in line with Kakhovka-Brilevka; the southern boundary, along the lines of Brilevka-Ivanovka. The area of the species is apparently relict. Recent; fossil remains are not known.

Subspecies. Because of the small area, it is represented only by a nominal subspecies, *S. a. arenarius* Reshetnik.

3. **Spalax microphthalmus** Güldenstaedt, 1770—**Common Mole Rat**

Güldenstaedt, 1770: 409–440, Tab. XV, Figures 1–10. *Spalax Pallasii* Nordmann, 1839: 200. *Spalax typhlus xantodon* Nordmann, 1840: 35. *Mustyphlus* Pallas, 1778: 154–165, Tab. VIII. *Ommatostergus Pallasii* Keyserling and Blasius, 1840.

Holotype. Described from a find in the Zadone Steppes (Novokhoper). Number of samples and place of storage not known.

Material investigated. More than 300 skulls and skins obtained within the boundaries of Ukraine SSR, mixed region of Russian Federation and northern Caucasus; stored in the reserves of the collections of the Institute of Zoology AN Ukraine SSR, Moscow State University, Kiev State University, and the Zoological Institute AN SSSR.

Diagnosis. Measurements are, on the average, similar to those of the sandy mole rat (body length, 197–232–290 mm; length of feet, 23.0–26.3–30.0 mm; condylobasal length of skull, 37.2–49.8–58.4 mm; length of upper row of permanent molars, 7.3–8.2–9.0 mm; length of lower row of permanent molars, 6.8–7.6–8.4 mm). The rostral section of the skull gradually narrows in an anterior direction and is wedge-shaped. The width of the nasal bones posteriorly is more than the similar width of each of the premaxillary bones, and the latter, in turn, is less than half of the anterior total length of nasale, or approximately equal to it. In addition, the width of the nasal bones anteriorly exceeds approximately twice or more their posterior width (in all cases, it was measured at the level of the temporo-premaxillary sutures). The temporo-nasal and the temporo-premaxillary sutures are straight, usually slightly step-like because of the bifurcation of the nasale behind the line of the temporo-premaxillary sutures. The groove between the nasal bones in the region of the temporo-nasal sutures is absent or is lightly defined, because of which the posterior ends of the nasale are blunt. The length of the nasal bones exceeds the total length of the parietal and temporal bones. The antero-external edges of the zygomatic arches are practically not bent down. The masseter area is short and has a slightly developed anterior tubercle; its length is approximately equal to the distance between the anterior ridge of the latter and the suture of the intermaxillary and maxillary bones. The external wall of the suborbital process is narrow; its least width is less than the length of the anterior permanent molar. The alveolar tubercles in adult and old individuals are hardly defined, and are placed apart from the anterior edge of the alveolus of M^1 at a distance exceeding the length of the tooth. The auditory opening is small; its greatest diameter in the majority of cases is less than the length of M^1, and is rarely equal to it. The alveolar process of the lower jaw considerably exceeds its articulate one in regard to height (in adult and old individuals). The coronary process is high. The corono-alveolar groove is slightly step-like. The closed foramen of the pelvic bone is large; its length approximately coincides with the length of the acetabulum.

Description. The rostral section of the skull is not wide and gradually narrows down anteriorly. Its width at the level of the anterior edges of the suborbital foramen always exceeds the same at the center. The total length of the nasal bones posteriorly is always more than the width of the premaxillary bone, and the latter, in its turn, is less or equal to half of the total anterior width of the nasale. In addition, the nasal bones are strongly narrowed in the posterior section; the total anterior width of the nasale exceeds twice or more the posterior width. The groove in the region of the temporo-nasal suture is absent or slightly marked, because of which the posterior ends of the nasal bones are blunt and do not form the sizable bifurcation characteristic of *S. graecus* (Figure 74). It should also be mentioned that the nasal bones of the common mole rat are, on an average, relatively longer than those of the giant mole rat and, perhaps, even those of the sandy mole rat. The relation of their length to the length of row of permanent molars is 231.0–259.5–306.0 in adult and old individuals, and 205.0–220.0–231.0 in the young and semi-mature. Furthermore, the nasale, as in *S. arenarius*, are apparently relatively wider anteriorly, on the average, than in the giant mole rat; the relation of their total width to the length of M^2–M^3 is equal to 84.5–96.4–121.0 in adult and old individuals, and 77.1–82.1–87.0 in the young and semi-mature. The length of the nasal bones, as a rule, exceeds the total length of the temporal and parietal bones; the magnitude of the relation is 95.0–106.5–120.0 for adult and old individuals, and 94.2–101.9–106.7 for young and semi-mature animals. The structural characteristics of the temporo-nasal and temporo-maxillary sutures have been given in the diagnosis. The nasal openings are relatively narrow though, on the average, probably wider than in the giant mole rat. The relation of their width to the length of row of permanent molars is 70.8–88.0–101.0 for adult and old individuals, and 70.8–77.2–80.7 for young and semi-mature animals. The constriction behind the eyes is slightly more expressed than in mole rats from the

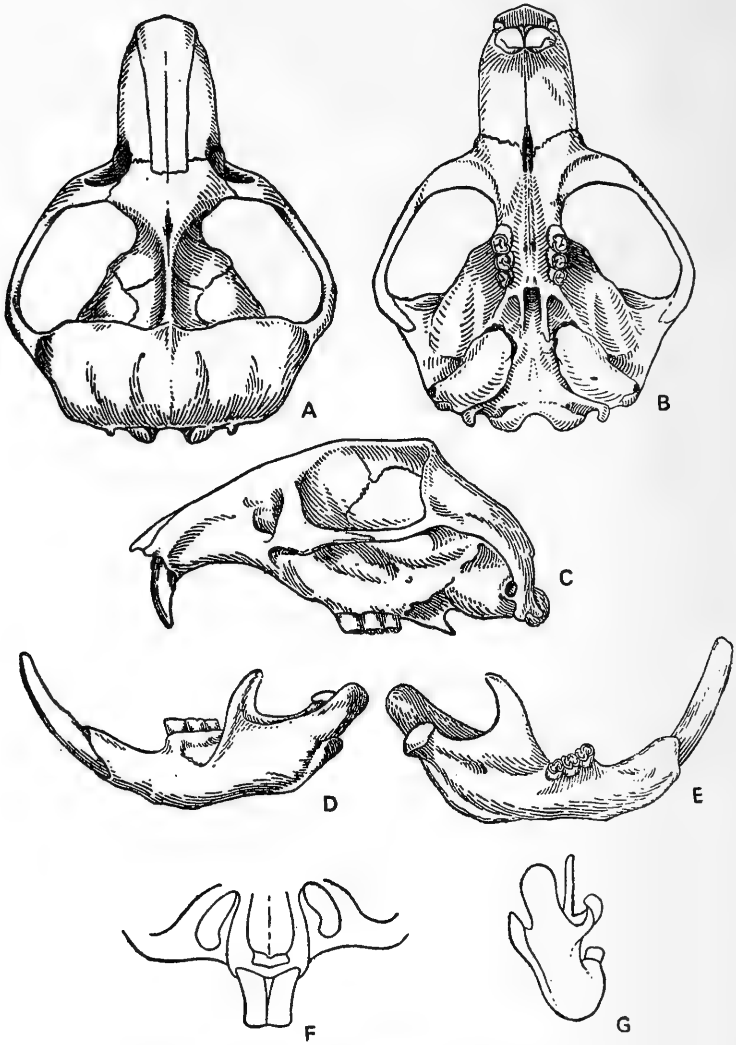

Figure 74. *Spalax microphthalmus* Güld. Natural size.

Legend is the same as in Figure 50.

giganteus group; the relation of width behind the eyes to length of row of permanent molars is 77.9–94.2–114.0 for adult and old individuals, and 166.0–176.0–195.0 for the young and semi-mature. The temporo-parietal section is shortened; the ratio of the total length of the temporal and parietal bones to the length of M^1–M^3 is respectively equal to 218.0–233.5–302.0 and 209.0–218.0–227.0. The parietal bones are relatively longer and greatly widened; the relation of length and width for each of them to the length of row of permanent molars is respectively equal to 107.0–130.0–156.0 and 45.3–68.4–92.9 in adult and old individuals, and 116.0–128.0–134.0 and 71.9–86.2–94.2 in young and semi-mature animals; the relation of the total width is 80.2–140.0–179.0 in adult and old individuals, and 166.0–176.0–195.0 in the young and semi-mature. Their sutures form a pentagon or five-pointed star. The triangular depression on the temporal bones in the area of displacement of the sagittal ridge is absent (Figure 74). The temporo-parietal and temporo-frontal sutures form a blunt angle. The upper diastema and hard palate are elongated. Thus, the magnitude of the diastema-tooth index is 204.0–241.0–317.0 in adult and old individuals, and 177.0–192.0–214.0 in the young and semi-mature. The relation of length of hard palate to length of row of permanent molars is respectively equal to 334.0–378.0–463.0 and 302.0–322.0–347.0. The structural characteristics of the masseter area and of the alveolar tubercles have been discussed fully in the diagnosis. The hard palate, on the whole, is apparently wider than in the giant mole rat at the level of the anterior permanent molars, and narrower than in the sandy mole rat. Its width in adult and old individuals only slightly exceeds the length of M^1. The zygomatic arches are thin anteriorly. Their antero-external edges are almost not bent down. The malar angle is considerably less than 45°. The external wall of the suborbital foramen is constricted; its least width is considerably less than the length of the anterior permanent molar.

The suborbital foramen itself is high; its length considerably exceeds the length of the upper line of permanent molars. The zygomatic arches are considerably elevated posteriorly in relation to the fossa glenoidea. The suture between the malar processes of the maxillae and the frontale (situated near the outer wall of the suborbital foramen) is strongly tapered. The inner crest of the fossa glenoidea is marked more sharply than in the giant mole rat, and less so than in the sandy mole rat. The articulating surface itself is wide. The base of the occipital bone is wide because of which the auditory bullae are widely separated. Thus, the greatest distance between the external edges of the tuberculum pharyngeum laterale considerably exceeds the length of M^1–M^2. The auditory bullae are, on the average perhaps, relatively wider than in representatives of the giganteus group. The relation of their width to length of the permanent molar is equal to 92.8–101.5–116.0. The structural characteristics of the auditory opening have been discussed in the diagnosis. The occipital section of the skull is, on the average perhaps, relatively higher than in all the presently living representatives of the genus; the magnitude of the relation of the occipital bone measured from the upper edge of the occipital foramen to the largest width of the occiput, is 52.5–55.0–66.1.

The upper incisors are relatively narrow (for representatives of the genus); the relation of width to antero-posterior cross section is 104.4–112.0–120.8. Their anterior surface is flattened.

M^1 (length, 2.4–2.7–3.2 mm; width, 2.1–2.5–3.0 mm; relation of width to length, 80.6–91.1–107.1) has a type of structure in the grinding surface of the teeth akin only in very young animals to the same in giant and sandy mole rats, and a number of representatives of the microphthalmus group in *S. graecus* (the paracone is not fused with the anterior collar but is isolated from the neck which joins the protocone and hypocone; two intruding folds are in the outer line; Figure 75). In the majority of the cases, the central external tubercle is fused with the anterior collar, but separated from the neck joining the anterior and posterior internal tubercles, as a result of which the tooth is characterized by the presence of only one intruding fold in the outer line in early and middle stages of wear (in young, semi-mature, and partly in adult animals). The antero-internal part of the outer intruding fold closes into a mark as age advances. The protocone and hypocone in the majority of cases are fused and rarely separated. The remnants of the metaconid are rarely preserved at very early stages of tooth erosion. The grinding surface in adult and old animals is similar, on the whole, to the one in the giant mole rat and the sandy mole rat. The intruding folds close into marks due to tooth erosion in the following order: the inner part of the external, the external, and finally, the internal one. There are two roots—the massive antero-internal (formed by the fusion of the antero-external and the internal roots), and a weakly developed and free postero-external. The antero-internal root has no markings or bifurcation. Perhaps, the fusion of the postero-external root with the antero-internal does not take place.

M^2 (length, 2.1–2.4–2.8 mm; width, 2.1–2.5–2.9 mm; relation of width to length, 92.3–105.3–124.0) is similar to the same molar in the sandy mole rat in regard to structure of the wearing surface. However, it is perhaps relatively narrower, on the average. It is quite different from the same in mole rats of the giganteus group by a constant presence of three roots—the massive internal, and the weakly developed anterior and posterior externals.

M^3 (length, 1.6–2.1–2.4 mm; width, 1.9–2.2–2.6 mm; relation of width to length, 90.5–107.0–120.0) is like the previous molar, on the whole, and similar to the same one in the sandy mole rat. However, in the common mole rat, the completely separated anterior and posterior tubercles are often observed and, similarly, a considerable tendency toward complexity in the grinding surface is observed on the teeth of young animals because of the formation of additional tubercles and layers. Besides, a lesser degree

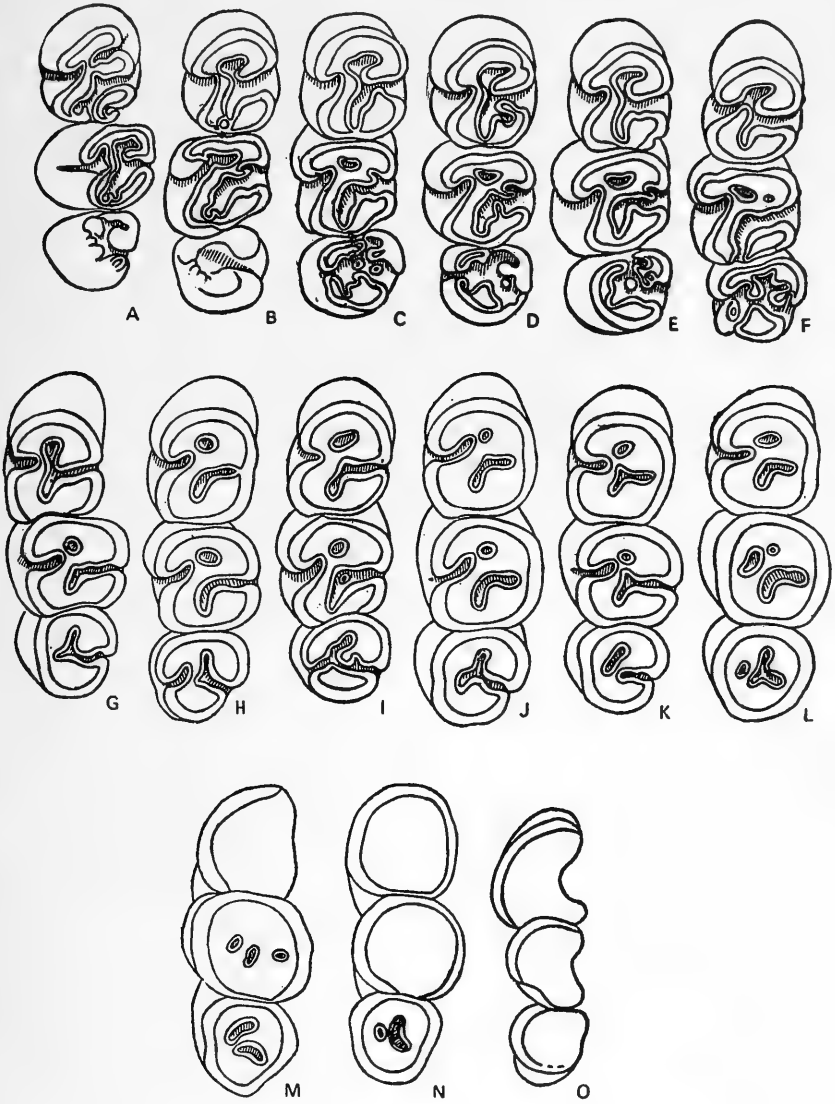

Figure 75. *Spalax microphthalmus* Güld. ×10.

Upper row of permanent molars: *A* to *F*—young and semi-mature; *G* to *L*—adult; *M* to *O*—old individuals.

of reduction of the antero-external root is characteristic of the M^3 of *S. microphthalmus*. The latter is almost always not fused with the postero-internal root (the fused postero-external and the single internal root), and is represented in the alveolus by an independent socket.

The lower jaw has an elongated diastema; the value of the diastema-tooth index is 98.9–117.0–138.7 in adult and old animals, and 92.0–106.0–125.0 in the young and semi-mature. The horizontal branch is relatively high; the relation of its height to the length of the lower row of permanent molars is 109.0–129.2–146.4 in adult and old animals, and 92.0–106.0–125.0 in the young and semi-mature. The alveolar process, as in the sandy mole rat, is high and exceeds the articulating one in both adult and old animals in this regard. The height of the process from the inner side beginning from mature conditions, as a rule, considerably exceeds the length of the lower row of permanent molars (value of the corresponding index in common mole rats, 95.0–114.4–138.6). The incisura corono-alveolaris, as in previous species, is slightly step-like; its anterior edge goes into the coronary process. The coronary process is high. The external surface of it is step-like which, as has been shown above, is related to the encroachment of the ridge of the corono-alveolar groove. Because of the approximate coincidence of the height of the coronary and the length of the upper edge of the articulating process, the corono-articular groove is correctly divided (Figure 74). The common mole rat and the sandy mole rat do not differ from each other in regard to the structure of the corono-alveolar and the corono-articulating ridges, the anterior fossa between them, and also in regard to the position of the mandibular foramen in relation to the edge of the incisura corono-condyloidea. The articulating surface of the proc. condyloideus is wide; the relation of width to length is 50.0–57.0–66.7.

The lower incisor is, on the average, probably relatively wider than that of all the presently known representatives of the genus. The relation of the width of the antero-posterior cross section is 100.0–109.5–120.7.

M_1 (length, 2.2–2.5–3.0 mm; width, 2.1–2.4–2.7 mm; relation of width to length, 79.3–94.5–108.3) differs from M_1 of the sandy mole rat by the process of an additional anterior intruding fold in the outer line, or its vestige in the shape of an anterior mark, and also, on the average, a less reduced entoconid in young and semi-mature animals (Figure 76). In addition, the metaconid is fused with the anterior collar in the given stages of wear, and through it with the protoconid also. In some cases, the neck of the antero-internal tubercle at the place of fusion with the anterior collar shows the marks of division. The protoconid and hypoconid are fused in all stages of wearing. Because the tooth in young and semi-mature animals has an additional outer (almost always) and inner intruding (rarely) fold, the number of the latter in the outer and inner lines at given stages of wear may vary from one to two. In adult and old animals, the tooth always has an inner and outer intruding fold. The order of closure of the intruding folds into marks is as follows: the antero-internal and

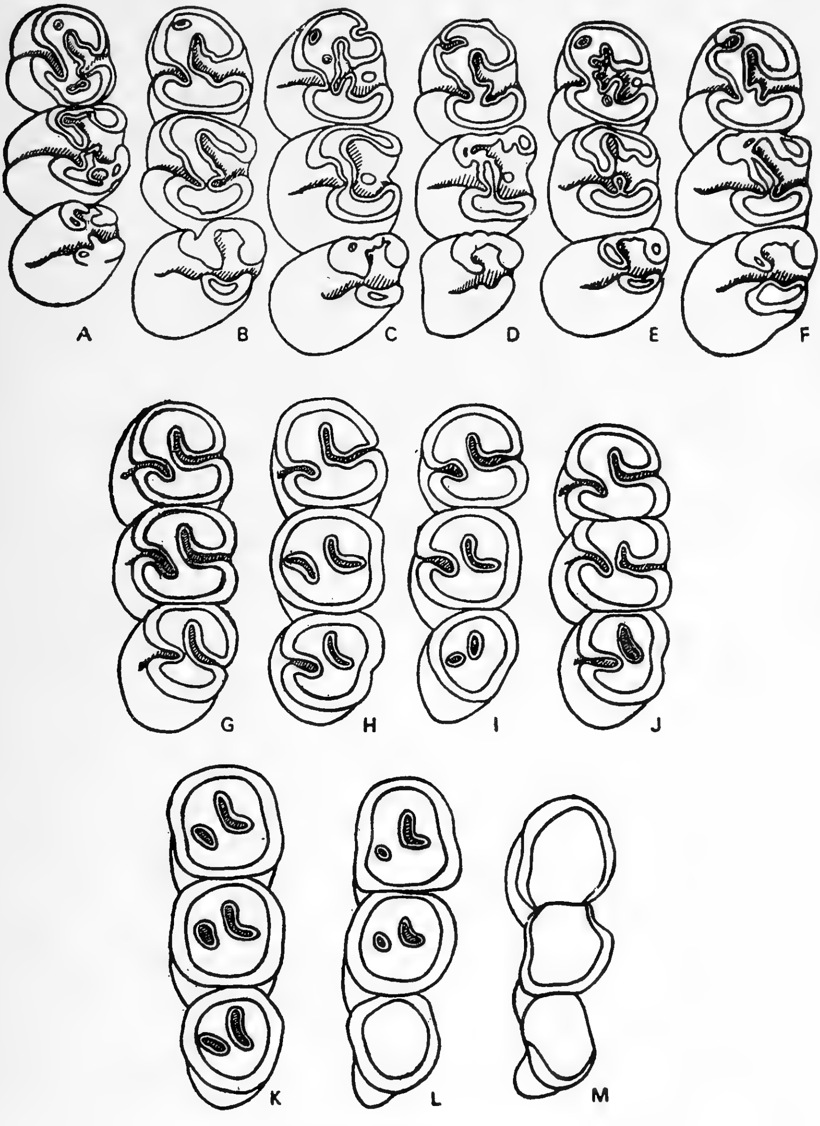

Figure 76. *Spalax microphthalmus* Güld. ×10.

Lower row of permanent molars: *A* to *F*—young and semi-mature; *G* to *J*—adult; *K* to *M*—old individuals.

external additional in the given order, the main internal, and finally the main external. The tooth has two roots; the posterior is better developed than the anterior one.

M_2 (length, 1.9–2.2–2.7 mm; width, 2.1–2.5–2.9 mm; relation of width to length, 95.4–110.7–128.5) is, on the average, probably relatively wider than in the preceding species. In regard to the general configuration of the grinding surfaces, it is generally similar to the M_2 (permanent molar) of sandy and giant mole rats. There are two roots; the posterior is more developed than the anterior. Sometimes the roots exhibit a tendency toward fusion.

M_3 (length, 1.9–2.2–2.5 mm; width, 1.7–2.2–2.7 mm; relation of width to length, 81.8–101.4–121.0), like the preceding molar, is principally similar to the permanent molar of the sandy mole rat in regard to its relative width of the corona, and the nature of the structure of the grinding surface and roots.

Comparison. The traits common for all the representatives of the microphthalmus group which allow one to differentiate them from the species of the giganteus group, were discussed above (page 243). As far as the common mole rat is concerned as a species, the following differences need to be considered in addition to those observed earlier.

1. The temporo-frontal and temporo-parietal sutures form a blunt angle; in mole rats of the giganteus group, the temporal bones are placed on the border of the parietals and the frontale at an acute angle (the trait is clearly exhibited in adult and old animals).

2. The temporo-nasal and temporo-premaxillary sutures form a line that is almost straight in common mole rats; in giant and sandy mole rats, they form an angle with its apex directed forward.

3. The almost unbent downward anterior outer borders of the zygomatic arches and a malar angle that is much less than 45°; in representatives of giganteus group, the anterior outer borders of the zygomatic arches are considerably shifted downward and the malar angle is almost equal to or slightly more than 45°.

4. In mature and adult animals, the temporal bones widen in the front, forming a figure resembling a regular pentagonal star (Figure 74) to some extent; in giant mole rats, and to a lesser degree in sandy mole rats, these bones are constricted, because of which the pentagon is elongated in a longitudinal direction with a highly elongated anterior ray.

5. An elongated nasale whose length exceeds the combined length of the temporal and parietal bones, as a rule; in mole rats of giganteus group, an inverse relationship is observed in the majority of cases.

6. In the majority of cases, a fused paracone and anterior collar in the early and middle stages of wear of the first permanent molar of the upper jaw; in giant and sandy mole rats, the middle outer tubercle is not

fused with the anterior collar though it communicates with the suture connecting the protocone and hypocone.

In the remaining features, *S. microphthalmus* is identical with the sandy mole rat although some differences are observed in the average values of indices for the skull structure, the lower jaw, and the permanent molars. These differences are readily observed on comparing the descriptions of both the species given earlier; therefore, it appears to us that there is no urgency to discuss them in detail. The most substantial differences, in addition to those mentioned, could be the following:

1. In the common mole rat the external wall of the infraorbital foramen is narrow; its width in the narrowest part is considerably less than the length of the anterior permanent molar. In the sandy mole rat, the bony bridge above the for. infraorbitale is slightly widened; the least width is approximately equal to the length of M^1 or clearly exceeds it.
2. A broadened fossa glenoidea with a weakly developed inner ridge, and a correspondingly short and wide articulating condyle of the lower jaw (width of the condylus exceeds half its length or, rarely, is approximately equal to it; the values of the corresponding relations are 50.0–57.5–66.7). In *S. arenarius*, the articulating fossa on the skull is narrowed with a highly developed internal ridge. Correspondingly, the condyle of the lower jaw is narrow and long. Its width is considerably less than half its length (38.8–45.2–48.2).
3. The antero-internal tubercle—the metaconid on M_1—of young and semi-mature animals is fused with the anterior collar (independent in the sandy mole rat). In addition, the anterior permanent molar of the common mole rat is characterized in the early and middle stages of wear by the presence of an additional intruding fold in the outer line, or its vestige (always absent in the sandy mole rat).

It differs quite clearly from *S. polonicus* which is a close species by:

1. Elongated nasal bones and a shortened temporo-parietal of the skull. The length of the former, with rare exception, exceeds the total length of the temporal and parietal bones. The trait mentioned can be quite clearly seen while comparing such traits as the relation of the length of the nasale, and the total length of frontale and parietale to the length of the row of permanent molars. The former value in the common mole rat is 231.0–259.5–306.0, and of the latter, 218.0–233.5–302.0 as against 208.1–235.4–260.0 and 240.0–270.9–296.6 in *S. polonicus*.[1]
2. The shape of the temporo-nasal and temporo-premaxillary sutures (almost a straight line in the common mole rat, with an angle that has an apex directed forward in the Podolsk mole rat).
3. A fused protocone and hypocone on M^1 in the early and middle

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[1] The indices here and afterward are given only for adult and old animals because the author did not possess a sufficient number of young and semi-mature *S. polonicus*.

stages of wear in the majority or cases (always separated in the Podolsk mole rat).

4. Complex anterior lower permanent molars in young and semi-mature animals. M_1 of the common mole rat is characterized in early and middle stages of wear by the presence of an additional external intruding fold, or its vestige in the shape of a small anterior mark which is absent in *S. polonicus.*

5. A comparatively small auditory opening, the greatest diameter of which, in the majority of cases, is less than the anterior permanent molar and sometimes is approximately equal to the latter. In the Podolsk mole rat, the said measurements always exceed the length of M^1.

In addition, the differences between the common mole rat and the Podolsk mole rat can be seen in the average values of the following traits:

1. The parietal bones and the upper diastema are relatively longer; the relation of the length of the parietale to the length of the row of permanent molars, and the diastema-tooth index, is respectively equal to 107.0–130.0–156.0 and 204.0–241.0–317.0 in the common mole rat, as against 78.4–114.1–135.8 and 198.8–230.4–263.6 in the Podolsk mole rat.

2. The nasal bones are narrower anteriorly (84.5–96.4–121.0 as against 87.2–102.5–113.6).

3. The total width of the parietale is relatively greater (80.2–140.0–179.0 as against 84.0–117.0–142.7).

4. The nasal bones are placed relatively low (33.3–37.4–45.2 as against 36.6–44.8–51.1).

5. The occipital bone is relatively higher; the relation of its height measured from the upper edge of the foramen magnum to the greatest width of the occipital is 52.5–55.0–66.1 as against 43.0–50.1–53.8.

6. The upper incisors are relatively narrower; the relation of width to antero-posterior cross section is 104.4–112.0–120.8 as against 110.3–119.5–130.7.

7. The lower diastema is relatively longer; the value of the diastema-tooth ratio is 98.9–117.0–138.7 as against 100.0–109.3–122.0.

8. The horizontal branch is relatively higher; the relation of its height, at the level of the posterior edge of M_1 externally, to the length of the lower row of permanent molars is 109.0–129.2–146.4 as against 106.1–122.1–134.7.

9. M_2 is relatively narrower (relation of width to length is 95.4–111.0–128.5 as against 113.0–117.2–127.2).

Finally, the common mole rat differs from the presently living Bukovin mole rat, *S. graecus,* by:

1. Nasal bones which are narrowed posteriorly and widened anteriorly (width anteriorly exceeds twice and more the width posteriorly). In *S. graecus,* the total anterior width of the nasale exceeds considerably less

than twice the posterior width. Furthermore, the posterior groove on the nasal bones of the common mole rat is absent or faintly present and the ends of the nasale are blunt. In common mole rats, the latter is always well developed, the posterior ends of the nasal bones are sharpened, and the nasal bones themselves are greatly bifurcated posteriorly.

2. A narrow external wall in the infraorbital foramen, the least width of which is considerably less than the length of the anterior permanent molar. In the Bukovin mole rat, the width of the wall of the infraorbital foramen in its narrowest part considerably exceeds the length of M^1.

Furthermore, the infraorbital foramen itself in the common mole rat is relatively higher. Its height considerably exceeds the length of the upper row of permanent molars whereas in the Bukovin mole rat, the values of these measurements approximately correspond to each other.

3. A greatly tapered position of the sutures between the frontale and the malar process of the maxillary bone in relation to the longitudinal axis of the external wall of the infraorbital foramen. In *S. graecus* it is weakly tapered or even placed in a transverse position.

4. The absence of a three-angled fossa in lieu of the displacement of the sagittal ridge. It is always present in the Bukovin mole rat.

5. A weakly developed upper alveolar tubercle.

6. Slender, almost not bent down, antero-external edges of the zygomatic arches, and a malar angle which is considerably less than 45°. In *S. graecus* the zygomatic arches are massive, sharply bent down, and have a malar angle which approaches or is roughly equal to 45°.

7. Widened parietal bones; the relation of the total width of the two parietale to the length of row of permanent molars is 80.2–140.0–179.0 as against 41.1–60.1–85.5 in the Bukovin mole rat.[1]

8. A less step-like coronary-alveolar groove in the lower jaw. It is step-like in *S. graecus* because of the great development of its ridge. This trait equally differentiates the common mole rat from the fossil Late Pliocene *S. minor*.

9. The non-serrated apex of the coronary process. It is quite serrated in the Bukovin mole rat.

10. A simplified structure of the anterior permanent molar. In *S. graecus*, M^1 is similar to the same molar in *S. giganteus* and *S. arenarius* in regard to complexity.

The differences between the above-mentioned species could also be found in the average values in the number of structural traits of the skull and the lower jaw. Thus, for example, the common mole rat compared to the Bukovin mole rat has a relatively short temporo-parietal section of the skull, elongated and widened parietal bones, a comparatively low

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[1] As in the case of *S. polonicus*, measurements are for adult and old animals only, because we did not possess a series of skulls for young and semi-mature animals.

nasal aperture and high occipital bone, an elongated lower diastema and a high horizontal branch of the lower jaw, and widened lower incisors. The said differences stand out more clearly when the respective indices are compared, the values of which can be found in the section devoted to them. In some cases, the trend of these changes coincides with similar ones in the Podolsk mole rat (a relatively wide rostrum and parietale).

The common mole rat takes up a middle position between the Podolsk and Bukovin mole rat in regard to a number of traits because, in the latter, the individual differences have a great importance. In particular, the nasal bones in *S. microphthalmus* are, on the average, shorter than in *S. graecus*; the relation of their length to the length of row of permanent molars is 231.0–259.5–306.0 as against 249.0–273.0–296.0.

Measurements. Condylobasal length of skull, 37.2–50.0–58.4 mm; basal length of skull, 34.3–46.8–54.2 mm; length of nasal bones, 15.8–20.9–25.9 mm; total length of parietal and temporal bones, 15.9–19.9–24.0 mm; length of parietal bones, 8.9–10.7–12.8 mm; length of upper diastema, 13.4–19.4–24.7 mm; length of hard palate, 23.0–30.7–37.1 mm; length of upper row of permanent molars, 7.0–8.2–9.0 mm; width of nasal aperture, 5.3–7.1–8.5 mm; incisorial width, 7.0–8.7–10.3 mm; width of nasal bones anteriorly, 5.4–7.8–9.6 mm; rostral width, 9.3–11.6–14.7 mm; width behind the eyes, 6.7–7.9–9.9 mm; width of two parietale, 8.7–11.8–15.4 mm; width of parietal bones up to the lambdoid ridge, 3.9–5.4–6.7 mm; malar width, 31.1–39.7–45.9 mm; maximum width of occiput, 26.3–33.9–38.8 mm; length of auditory bullae, 10.7–12.7–14.5 mm; width of auditory bullae, 7.4–8.2–9.1 mm; width of upper incisor, 2.2–2.9–3.4 mm; antero-posterior cross section of upper incisor, 2.0–2.6–3.3 mm; height of nasal aperture, 2.4–3.0–4.0 mm; condylar length of lower jaw, 24.2–33.0–40.1 mm; angular length of lower jaw, 23.3–32.2–39.8 mm; length of lower diastema, 6.7–8.8–10.4 mm; length of lower row of permanent molars, 7.3–7.6–8.4 mm; height of horizontal branch at the level of the posterior edge of the alveolus of M_1 externally, 7.3–9.6–11.2 mm; thickness of the horizontal branch at the level of M_2, 3.5–4.7–6.5 mm; height of alveolar process internally, 3.7–8.2–11.2 mm; width of lower incisor, 2.1–3.1–3.8 mm; antero-posterior cross section of the lower incisor, 1.8–2.9–3.7 mm.

Note. The common mole rat is approximately on the same level of specialization toward a burrowing type of life as *S. arenarius.* Traits like an elongated upper and lower diastema, widened upper and lower incisor, a skull which is relatively high in the occipital portion, a comparatively high horizontal branch, and an alveolar process of the lower jaw, are proofs of this: moreover, the latter, as in the sandy mole rat, is characterized by a sufficiently well-developed ridge of the corono-alveolar groove. In addition, the species has a simplified structure of permanent molars, the roots of which are less reduced than in the sandy mole rat. The latter, along with rather weak development in the sites of attachments of the masticatory muscles (masseter area of the skull, the antero-external portions of zygomatic arches, and others) proves, perhaps, the trend of development toward adaptation to eating more succulent and soft vegetative food.

It has also to be noted that the common mole rat considerably preserved characteristic resemblances to the fossil Pliocene *S. minor* from around the Azov Sea. This permits one to consider with a high degree of probability that this species is a direct descendant of the latter.

Distribution and geological age. It spreads up from the Dnieper west to the Volga and Pre-Caucasus in the east (in the Dnieper region, it is absent in the Aleshki Sands portion). The northern borders of the spread pass through approximately the Kiev region along the southern part of the Chernigovskaya region; in the eastern portion through the Kursk and Orlov regions, in the southern portion through Tula, the Tambovsk region and Moldov ASSR, along the southern portion of the Ulyanov region. The southern border is approximately in line with Kakhovka, the Azov shore up to the Krasnodar and Stavrapol regions, but for their southern parts. Holocene, recent. Holocene remains from the excavation, related to the mole hill forest, are found everywhere within the area of the species. Finds of closely related forms are also known from Pleistocene sediments (mole hill forest).

Subspecies. Geographical variability has not been studied at all. The northern Caucasian form could very well be an independent subspecies.

4. **Spalax polonicus** Mehely, 1909—**Podolsk Mole Rat**

Mehely, 1909: 34, 35, 194–202. *typhlus* Kessler, 1850: 74–77 (nomen praeocupatum). *diluvii* Nordmann, 1858; 164. *podolica* Troussart, 1898: 570 (nomen nudum). *zemni* Reshetnik, 1941: 28–31, Figures 4, 5, 8a, 12. *Microphthalmus podolicus* Bobrinskii *et al.*, 1944: 362. *Microphthalmus polonicus* Vinogradov and Gromov, 1952: 177. Podolian Marmot Pennant, 1771: 274 (nomen nudum). *Glis zemni* Erxleben, 1777, Systema Regni Animalium, I: 370–371 (nomen nudum). *Mus typhlus* Dwigubski, 1804: 78–80 (nomen praeocupatum).

Holotype. Teachers Museum of L'vov, No. 261/430, Ukraine SSR, around Krements city (village Vishnevets), Ternopolsk region.

Material investigated. Twenty-five skulls and skins found in and around Nikolaev, Odessa and Dnepropetrovsk regions (recent), right bank portion of Kiev and Zhitomir regions (subfossil). All stored in the collections of the Institute of Zoology AN Ukraine SSR.

Diagnosis. Measurements are, on the average, close to that of *S. microphthalmus* (body length, 200–280 mm; length of foot, 25–30 mm; condylobasal length of skull, 39.3–49.2–56.5 mm; length of upper row of permanent molars, 7.3–8.2–8.8 mm; length of lower row of permanent molars, 7.2–7.6–8.2 mm). The skull, as a whole, is similar to that of the common mole rat. It differs in regard to the shortened nasal bones, the length of which is considerably less than the total length of the temporal and parietal bones, the line of the temporo-nasal and temporo-premaxillary sutures forming an angle with its apex directed forward, a relatively large auditory aperture, the maximum diameter of which exceeds the length of the anterior permanent molars. The closed foramen of the pelvic bone is almost completely overgrown; its length is considerably less than the length of the acetabulum.

Description. The rostral section of the skull is not broad and gradually narrows in an anterior direction as a wedge-shaped structure, as in the common mole rat. Its width at the level of the anterior edges of the infraorbital foramen always exceeds the same in the center. The total length of the nasal bones posteriorly is always more than the length of the premaxillary bone, and the width of the latter, in turn, is less or approximately equal to half of the anterior width of the nasale. Furthermore, the nasal bones are primarily in the posterior section; the width of the nasale exceeds anteriorly twice or more times the width posteriorly. As in *S. microphthalmus*, the groove in the region of the temporo-nasal sutures is absent or is slightly marked because of which the posterior ends of the nasal bones are blunt and do not form a fork-like bifurcation (Figure 77). However, the nasal bones are considerably shorter than in the common mole rat. As has already been mentioned in the diagnosis, their length is considerably less than the total length of the temporal and parietal bones (the value of the corresponding index is 79.2–86.4–95.0 in adult and old animals, 76.3 and 92.8 in the young and semi-mature), and the ratio of the length of nasale to the length of row of permanent molars is 208.1–235.4–260.0. Additionally, the nasale are probably wider, anteriorly, on the average, than in *S. microphthalmus*; the relation of their anterior total width to the length of row of permanent molars is 87.2–102.5–113.6 in adult and old animals, and 87.7 and 92.5 in the young and semi-mature. The structural characteristics of the temporo-nasal and temporo-premaxillary sutures have been mentioned in the diagnosis. The nasal aperture is comparatively wide; the relation of its width to the length of row of permanent molars is 80.2–93.4–105.0 in adult and old individuals, and 82.2 and 91.3 in the young and semi-mature. The constriction behind the eyes is, on the average, possibly more strongly expressed than in the common mole rat; the relation of the width behind the eyes to the length of M^1–M^3 is 77.3–88.5–101.2. The temporo-parietal section is elongated; the relation of the total length of the temporal and parietal bones to the length of row of permanent molars is 240.0–270.9–296.6 in adult and old animals, and 242.5 and 283.5 in the young and semi-mature. The parietal bones are short and narrow; the relation of the length of each and their total width to the row of permanent molars is respectively equal to 78.4–

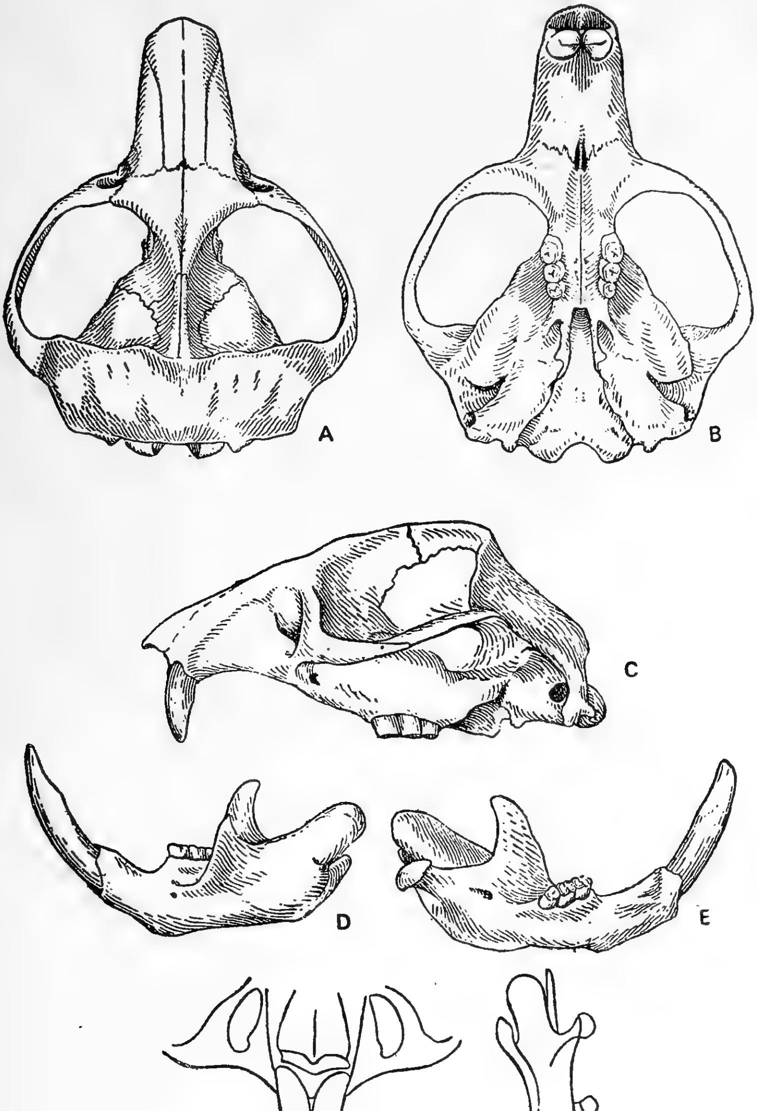

Figure 77. *Spalax polonicus* Meh. Natural size.

Legend is the same as in Fig. 50.

114.1–135.8 and 84.0–117.0–142.7. As in the preceding species, it forms a pentagon suggesting a five-angled star. The triangular depression on the temporal bone, in lieu of the displacement of the sagittal ridge, is not expressed. The temporo-parietal and the temporo-frontal sutures form a blunt angle; rarely, this angle is almost straight. The upper diastema and hard palate are, on the average, probably shorter than in the common mole rat; the values of the diastema-tooth and palate-dental indices are respectively equal to 198.8–230.4–263.6 and 331.4–369.3–408.0. The structure of the masseter area, the alveolar tubercles, the hard palate, the zygomatic arches, the infraorbital foramen and its external wall, the sutures between the maxillary and temporal bones, the fossa glenoidea, the base of the occipital bone, and the auditory bullae is, on the whole, similar to the same in *S. microphthalmus*. However, the auditory aperture in the Podolsk mole rat is considerably larger than in the common mole rat; its maximum diameter always exceeds the length of the anterior permanent molar. The occipital section of the skull is probably, on the average, relatively lower than in *S. microphthalmus*; the relation of the height of the occipital bone, measured from the upper edge of the for. magnum, to the maximum width of the occiput is 43.0–50.1–53.8.

The upper incisors are widened; the relation of the width to the antero-posterior cross section is 110.3–119.5–130.7. The anterior surface is flattened.

M^1 (length, 2.5–2.6–2.9 mm; width, 2.2–2.4–2.7 mm; relation of width to length, 82.1–90.9–103.8) in regard to the configuration of the grinding surface is similar to the same permanent molar of the common mole rat. Thus, the paracone in all stages of wearing is fused with the anterior collar because of which the tooth is characterized by the presence of only one intruding fold in the outer line (Figure 78). In addition to this, it differs from *S. microphthalmus* in that the protocone and hypocone in the early stages of wearing (in young and semi-mature, and even in some old individuals) are separated, as a result of which the outer and inner intruding folds fuse at the ends of each other. With age, the intruding folds close into marks approximately in the same order as that of the similar permanent molars of the common mole rat (the inner part of the external, the external, and finally, the internal). Furthermore, the fusion of the anterior and posterior external tubercles takes place. The fusion of the roots is expressed to a greater extent than in *S. microphthalmus*. In the majority of cases, the tooth is characterized by the presence of only a complex root formed by the fusion of the massive inner, and the weakly developed anterior and postero-external. During this, the vestiges of the fusion of the antero-external and the inner roots are altogether absent. However, the marks of the fused postero-internal root are almost always evident on the very root, and also in the structure of the alveoli.

M^2 (length, 1.9–2.3–2.5 mm; width, 2.2–2.5–2.7 mm; relation of width to length, 104.0–108.9–117.4), like the preceding molar, is principally similar in regard to the nature of the structure of the wearing surface to the similar permanent molar in the common mole rat. However, it differs from the latter in that a complete separation of the protocone and hypocone is observed in the young and semi-mature. Furthermore, the closure of the antero-internal section of the intruding fold of the outer line into mark in the Podolsk mole rat takes place, perhaps, in rather later stages of tooth erosion than in the common mole rat; the fold itself is simpler, on the whole, because of a rather weakly developed pleating of its walls. The order of the closure of the inner folds into marks because of tooth erosion is, perhaps, the same as in the preceding molar. It should also

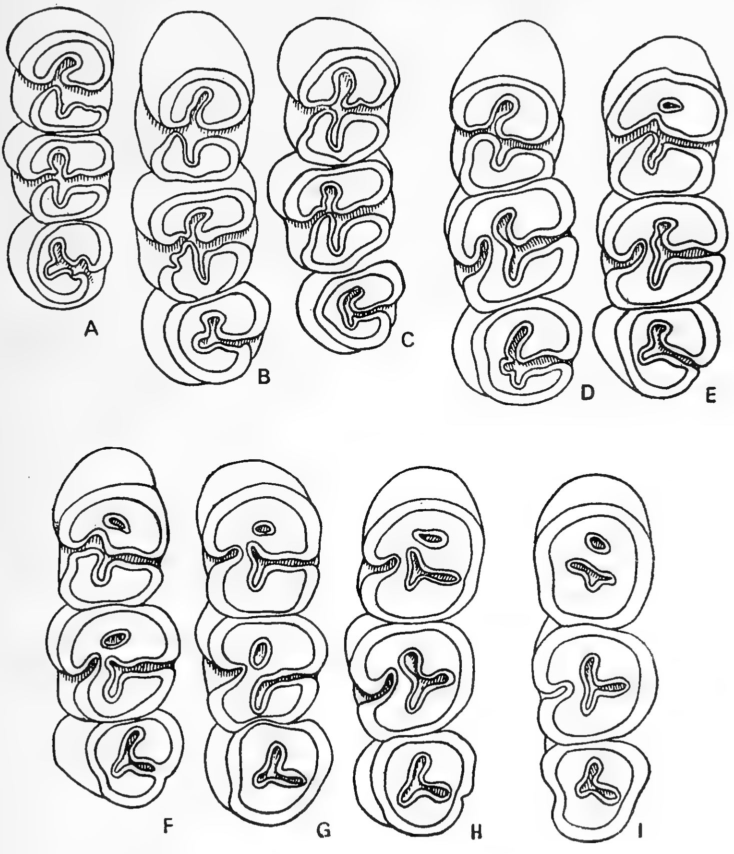

Figure 78. *Spalax polonicus* Meh. × 10.

Upper row of permanent molars: *A* to *C*—young and semi-mature; *D* to *H*—adult; *I*—old individual.

be noted that as distinct from the common mole rat, the anterior and posterior outer root of the tooth completely fuse with the single inner one, although traces of fusion are fairly clearly expressed on the root itself as well as on the structure of the alveolus.

M^3 (length, 1.8–1.9–2.4 mm; width, 2.0–2.1–2.4 mm; relation of width to length, 96.8–111.4–122.2), in young and semi-mature animals, has a more simplified grinding surface as compared to the same molar of the preceding species. Because of the presence of only one intruding fold and fused anterior and posterior internal tubercles, the degree of complexity more closely resembles that of adult *S. microphthalmus* than in the young and semi-mature. In addition, the roots of the tooth differ from similar teeth in the common mole rat, by showing a greater tendency toward fusion. The antero-external and the complex postero-internal roots are fused, though marks from the fusion area are clearly seen on the roots and in the alveolus.

The lower diastema is shortened; the value of the diastema-tooth index is 100.0–109.3–122.0. The horizontal branch is, on the average, relatively lower than in the common mole rat; the relation of its height to the length of the lower row of permanent molars is 106.1–122.1–134.7. As in the desert mole rat and the common mole rat, the alveolar process is high; in adult and old animals it considerably exceeds the articulating one in height. Its height from the inner side, at a mature stage, exceeds, as a rule, the length of the lower row of permanent molars (100.0–114.1–133.6). The structure of the coronary-alveolar and the coronary-articular grooves, and the ridges of the coronary and its articulating process, are, on the whole, similar to the same in the common mole rat.

The lower incisor is wide; the relation of its width to the antero-posterior cross section is 97.0–104.3–110.7.

M_1 (length, 2.2–2.4–2.7 mm; width, 2.4–2.5–2.7 mm; relation of width to length, 92.3–101.0–118.2) is, on the average perhaps, relatively wider than in the common mole rat. In regard to the general structure of the grinding surface, it is very close to the same permanent molar in *S. microphthalmus* (the metaconid in all stages of wearing fuses with the anterior collar and weakly developed entoconid, Figure 79). It differs from the earlier mentioned species by a permanent absence of an additional intruding fold in the outer line, or any of its markings, because of which the number of intruding folds does not exceed one on each side of the corona. If the additional fold is not taken into consideration, then, as has been shown above in the teeth of common mole rats, the closure of the intruding folds into marks due to tooth erosion in both species takes place in the same general order. The tooth has two roots; the posterior is more strongly developed than the anterior.

M_2 (length, 1.9–2.2–2.4 mm; width, 2.6–2.7–2.8 mm; relation of width to length, 113.0–121.8–137.6) as in the previous molar, on the average, is probably relatively wider than in the common mole rat. In the remaining aspects, it is not possible to differentiate the said permanent molars in the Podolsk and common mole rat, though it is possible that in the former the entoconid, on the average, is more strongly developed than in the latter.

M_3 (length, 2.0–2.1–2.4 mm; width, 2.1–2.2–2.5 mm; relation of width to length, 91.6–105.4–115.0) is also, on the whole, similar to the same permanent molar of the common mole rat.

Comparison. A detailed comparison of the Podolsk and common mole rat was done above (see page 265).

Because, as has been shown, the skull and the lower jaw of the Podolsk mole rat is akin in basic structure to the same in *S. microphthalmus*, then, the differences of the said species from *S. graecus* coincide, on the whole,

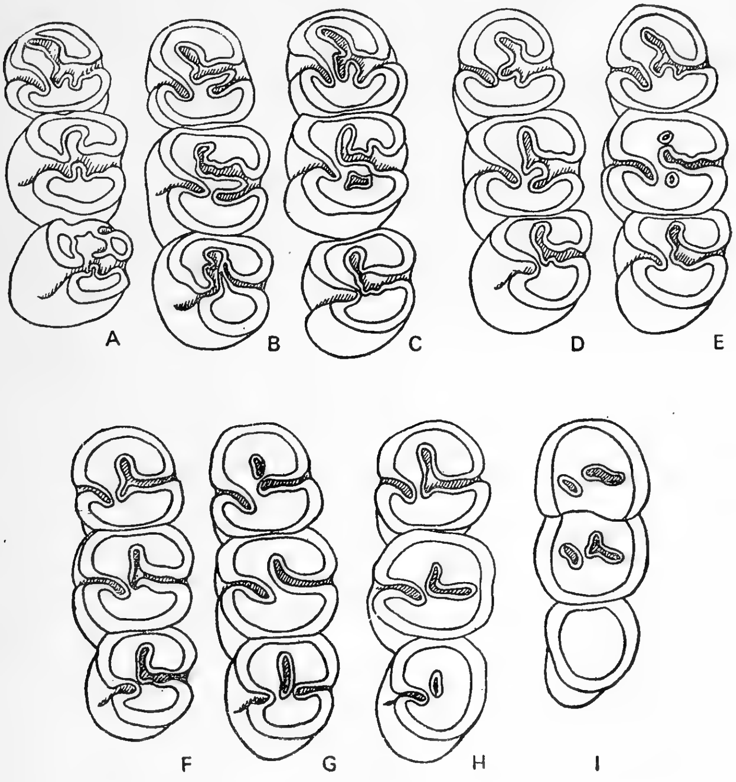

Figure 79. *Spalax polonicus* Meh. ×10.

Lower row of permanent molars: *A* to *C*—young and semi-mature; *D* to *H*—adult; *I*—old individual.

in all the ten main points (pages 266–67). To the traits which allow differentiating the Podolsk mole rat from the Bukovin mole rat may be added the shape of the temporo-nasal and temporo-premaxillary sutures which form an angle anteriorly directed in the former. In *S. graecus*, the temporo-premaxillary sutures are straight or directed in relation to the temporo-nasal suture externally and slightly forward, as a result of which their line in the expected intersection should form an angle directed backward.

Furthermore, the difference between the Podolsk and Bukovin mole rat could be found in the average values of the following traits:

1. The nasal bones are relatively short; the relation of their length to the length of row of permanent molars is 208.1–235.4–260.0 as against 249.0–273.0–296.0 in the common mole rat.
2. The rostrum is relatively narrow (132.5–145.5–158.0 as against 142.0–160.0–172.0).
3. The constriction behind the eyes is more pronounced (77.3–88.5–101.2 as against 90.5–98.8–111.0).
4. The parietal bones are relatively wider (relation of their total width to length of row of permanent molars, 84.0–117.0–142.7 as against 51.1–60.1–85.5).
5. The lower diastema is relatively long (the value of the diastema-tooth index is 100.0–109.3–122.0 as against 82.8–100.3–107.8).
6. M_1 and M_2 are relatively wide (relation of their width to length, 92.3–101.0–118.2 for M_1, and 113.0–121.8–137.6 for M_2, as against respectively 82.8–92.0–100.0 and 100.0–108.6–118.2 in the common mole rat).

It differs from the Late Pliocene Nogaisk *S. minor* by the shape of the temporo-nasal and temporo-premaxillary sutures (the angle with an apex directed forward in Podolsk mole rat, and an almost straight line in *S. minor*), by a slightly step-like corono-alveolar groove (quite step-like in *S. minor*), and by a widened, relatively short articulating surface of the proc. condyloideus (its width in the Podolsk mole rat in the majority of cases is half as long as the cord; in *S. minor*, it is less than half the length).

Measurements. Condylobasal length of skull, 39.3–49.2–56.5 mm; basic length of skull, 36.5–46.1–53.6 mm; length of nasal bones, 15.8–19.3–22.7 mm; total length of parietal and frontal bones, 20.6–22.4–26.1 mm; length of parietal bones, 6.9–9.3–11.9 mm; length of upper diastema, 14.2–18.7–23.2 mm; length of hard palate, 26.5–30.2–35.9 mm; length of upper row of permanent molars, 7.3–8.2–8.8 mm; width of nasal aperture, 6.0–7.6–9.0 mm; incisorial width, 7.0–8.6–9.8 mm; width of nasal bones anteriorly, 6.4–8.3–9.8 mm; rostral width, 9.8–11.9–13.9 mm; width behind the eyes, 6.8–7.5–9.1 mm; width of two parietale, 7.3–10.2–12.1 mm; width of parietal bones up to the lambdoid ridge, 3.9–5.7–8.1 mm; malar width, 30.0–38.6–46.8 mm; maximum width of occiput, 28.3–34.5–

40.0 mm; length of auditory bullae, 10.8–12.6–13.9 mm; width of auditory bullae, 7.5–8.5–9.2 mm; width of upper incisor, 2.4–3.0–3.4 mm; antero-posterior cross section of upper incisor, 2.1–2.5–2.9 mm; height of nasal aperture, 3.0–3.6–4.5 mm; condylar length of lower jaw, 31.2–33.1–37.2 mm; angular length of lower jaw, 30.3–33.4–38.9 mm; length of lower diastema, 6.9–8.1–9.0 mm; length of lower row of permanent molars, 7.2–7.6–8.2 mm; height of horizontal branch at the level of the posterior border of the alveolus of M_1 externally, 7.9–9.3–10.5 mm; thickness of horizontal branch at the level of M_2, 4.4–4.9–5.6 mm; height of alveolar process internally, 7.6–8.7–10.3 mm; width of lower incisor, 3.0–3.3–3.8 mm; antero-posterior cross section of lower incisor, 2.8–3.2–3.8 mm.

Note. The Podolsk mole rat is, on the whole, similar to the common mole rat in regard to the degree of specialization to a burrowing way of life. The basic differences—related to the shortening of the nasal bones of the former, as has been shown above, which is perhaps related to another trait, namely, the shape of the temporo-nasal and temporo-premaxillary sutures (the common line of them depends upon whether the premaxillary bones are shorter or longer than the nasal bones)—are for the time being inexplicable from the viewpoint of stabilizing selectivity which, in Spalacidae on the whole, is directed toward progressive adaptations to burrowing. A proposal for taking these traits as characteristics of a less expressed specialization could be put forth because the traits indicated are, no doubt, related to the degree of elongation or of shortening of the rostral section of the skull as a whole. The adaptive character of the first trait can, perhaps, be proven by comparing the structure of the respective section of the skull in different ecological forms within the limits of one taxonomical group of rodents burrowing with help of incisors. For this, the forms have only to be compared within the limits of a family which has an exclusively underground way of life, and burrowers living partly underground but obtaining their food on the surface. In this respect, the family of field voles represents very good material for relating innumerable numbers of different zoological forms. A comparison of the relative length of the rostral section of the skull in the group of Ellobii and other field voles, as it were, confirms the opinion already expressed. The Ellobii are characterized by a relatively drawn out narrow rostral section in comparison to other Microtidae (short, wide). The foregoing makes us examine the given differences between the Podolsk mole rat and the common mole rat as an index of the comparatively lesser degree of specialization in the former to a burrowing way of life. This is confirmed even by such structural characteristics of the skull and the lower jaw of the Podolsk mole rat as a relatively short upper and lower diastema. However, from the structure of the upper incisors, the said species perhaps stands on a rather higher level of specialization than the common mole rat (upper incisors in *S. polonicus* are, on the average, wider than in the latter).

At the same time, the Podolsk mole rat is characterized by more specialized permanent molars compared to the common mole rat (structure of the grinding surface is simplified, reduction of roots is more pronounced) which, with a known degree of probability, may be seen as a compensatory reaction for a shortened diastema (forward carrying of the burrowing organ which, in this case, is the incisor), and related to its general elongation, provides rather easier isolation of the buccal cavity from falling gravel during digging.

The differentiation of the said species took place, perhaps, somewhere on the border between the Early and Middle Anthropogene. At any rate, we have skulls with complete formation of permanent traits from sediments of the end of the Pleistocene epoch which allow unmistaken differentiation of the Podolsk and common mole rat.

The name of the species is greatly confused. At present, three names appear in literature: *S. podolicus* (Pennant), *S. zemni* (Erxleben), and *S. polonicus* Mehely. The first name, introduced in literature casually by Troussart (1898), relates to the first part of the Podolian Marmot (Pennant, 1771) as the name of a species; as Troussart did not give even a short description, this name should be undisputedly cast out as a *nomen nudum*. Moreover, in the work of Pennant, the nomenclature of the species given in the translation is not in accord with the rules of bionomial nomenclature.

An attempt to confirm the name *S. zemni* (Erxleben) (in the first description, *Glis zemni* Erxleben, 1777) was done by S. I. Ognev (1940, 1947), and after him even by Reshetnik (1941). However, the description of *Glis zemni* subjects "mole rat" to considerable strain. To substantiate the above, a translation in Russian given in the work of Erxleben (1777, cited by Ognev, 1947) is given here: "Measurement based upon squirrel. Head is large, rostrum is short. The first lower teeth are of half the length of the upper ones. The eyes are small, covered with hair. The ear holes are short. The rounded paws have four fingers. The feet have five fingers. The tail is short." From this description, we feel that even this nomenclature should not be used, that is a *nomen nudum*, since we have a right to doubt whether the description is that of a mole rat at all.

The name *S. typhlus* (Pallas) under which this species has been introduced in the works of Dwigubski (1804) and Kassler (1850) also cannot be used because it is synonymous with *S. microphthalmus* Güld.

The name *S. diluvii* Nordmann, 1858, may be rightly retained because it has been described elaborately though quite superficially. Moreover, E. G. Reshetnik (1941) in his time proved that the subfossil *S. diluvii* and *S. polonicus* were identical, and this is completely in line with our findings.

However, *S. diluvii* was forgotten for some time and we feel that resurrecting it now is not necessary.

In fact, the species was first described in detail by Mehely (1909) under the name *S. polonicus* Mehely. This happens to be the only correct nomenclature at present.

In our literature, there is currently an unjustified tendency for taking the Podolsk mole rat as a subspecies of the common mole rat (Bobrinskii *et al.*, 1944; Vinogradov and Gromov, 1952; Kuzyakin, 1963; Gromov *et al.*, 1963). However, as has been shown above, the Podolsk mole rat has permanent traits which do not transgress and which formed during a long geological history (throughout the Anthropogen), in addition to the structure of the skull and permanent molars which allow an unmistakable differentiation of this species from *S. microphthalmus*. Add to the aforesaid that the Podolsk mole rat also has genitals basically different from the same of *S. microphthalmus* (Figure 80), then separating this form as an independent species is fully justified (Pidoplichko, 1930; Kuntze and Scynal, 1933; Libich and Nezabytovskii,* 1934; Migulin, 1938; Reshetnik 1939, 1941; Ognev, 1940, 1947).

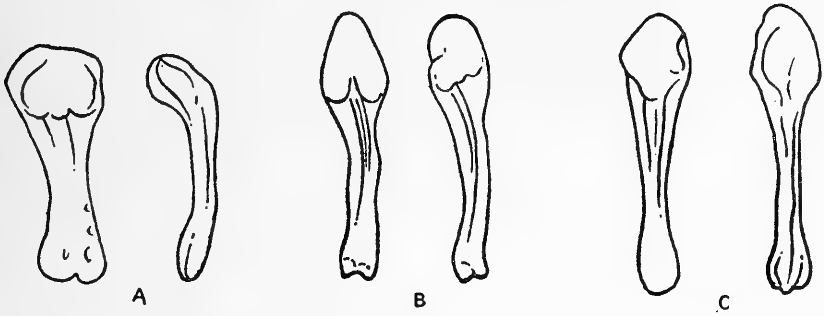

Figure 80. *Os* penis from above and from the side.

A—Spalax polonicus, Meh.; *B—S. microphthalmus* Güld.; *C—S. arenarius* Resh. (by Ognev, 1947).

Distribution and geological age. The distribution has been studied only in very general terms. Perhaps it inhabits a large portion of the right bank of the Ukraine besides the northernmost parts of the Volynsk Zhitomirsk and Kiev regions. The western boundary passes from the San River in the Peremyshlya region along the Dnestra approximately up to Kotovsk in the line Kotovsk-Pervomaisk, and further south along the South Bug River. It was not found in the Odessa and Nikolaev region west from the South Bug River within the limits of the present distribution of *M. leucodon*, though fossil and subfossil remains were found around the region

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*Reference omitted from the bibliography—(G. Ed.).

mentioned. The remains described by Nordmann (1858) from around Odessa are one of these. In addition, skulls of this species were found in layers of VI–I ages to A.D. and I–V ages A.D. during excavations of the ancient city Ol'viya (situated near the village Parutino of the Ochakovsk region, Nikolaev district) around its periphery (Pidoplichko, 1956; Topachevskii, 1956) as well as in fresh sediments on the right bank of the Kuchurgan River between the inhabited regions of Veliko-Mizailovka and Novo-Petrovka of the Frunzenskii region, Odessa district. All this helps in assuming the presence of the Podolsk mole rat in the region even now, though its number is very low. There is another species, *S. graecus*, living west from Dnestra around the Chernovitskii region. The north boundary of the area goes through, perhaps, in the line of Peremyshl, Yavorov, Rovno, Novograd-Volynsk, Kiev (somewhat to the north of the latter). The eastern boundary of the distribution is the Dnieper River.

Recent; remains of close forms are known starting from the Pleistocene. It has been found everywhere in subfossil conditions within the limits of the present-day distribution.

Subspecies. It is represented by only the nominal subspecies, *S. polonicus polonicus* Mehely, 1909.

5. **Spalax graecus** Nehring, 1898—**Bukovin Mole Rat**

Nehrin, 1898b; 228–230, Figure 1–2. *istricus* Mehely, 1909: 34, 186–194, Tab. II, Figure 4, Tab. III, Figure 6, Tab. XXVIII, Figures 9–16.

Holotype. University in Munich (Federal Republic of Germany); number of item is not fixed (Nehring, 1898b); place from which the holotype obtained, not known.

Material investigated. Twenty skulls and skins from the collection of Yangolenko obtained from Chernovits, Storozhnitskii, and Glybokskii regions, Chernovits district. Stored in collections of the Zoological Institute of AN USSR and the Institute of Zoology AN Ukraine SSR.

Diagnosis. With regard to measurements, it is close to the common mole rat and the Podolsk mole rat (condylobasal length of skull, 49.9–53.0–55.1 mm; length of upper row of permanent molars, 8.1–8.5–9.0 mm; length of lower row of permanent molars, 7.7–8.4–8.9 mm). The rostral section of the skull gradually narrows in an anterior direction and is wedge-shaped. The width of the nasal bones posteriorly is greater than the width of each of the premaxillary, and the latter in turn is less or approximately equal to half of the anterior total width of nasale. However, the width of the nasal bones anteriorly less than twice exceeds their posterior width. The temporo-premaxillary and temporo-nasal sutures are straight or form an angle directed backwards and, rarely, an angle directed forward. The groove between the nasal bones in the region of the temporo-nasal suture is highly developed; the posterior extremities of the nasale are sharp and bifurcated like a fork. The length of the nasale bones exceeds the total length of the temporal and parietal bones. The external wall of the infraorbital foramen is wide; its least width exceeds the length of the anterior permanent molar. The auditory opening is small; its maximum diameter is approximately equal to the length of M^1. The alveolar process of the lower jaw in adult and old individuals considerably exceeds its articulating one in regard to height. The coronary alveolar groove is step-like.

Description. The structure of the rostral section of the skull, and the corresponding width of the nasal and premaxillary bones on the whole, are similar to the same in the earlier described species—the common mole rat and the Podolsk mole rat. However, this species differs from the other two in that the *nasale* are not constricted in the posterior portion; their width anteriorly, less than twice exceeds the width posteriorly. In addition, the groove on the nasal bones in the region of the temporo-nasal suture is well developed; the posterior end of the nasal is sharp and forms a characteristic fork-like bifurcation which is not present in all the other fossil and present-day representatives of the genus (Figure 81). It has also to

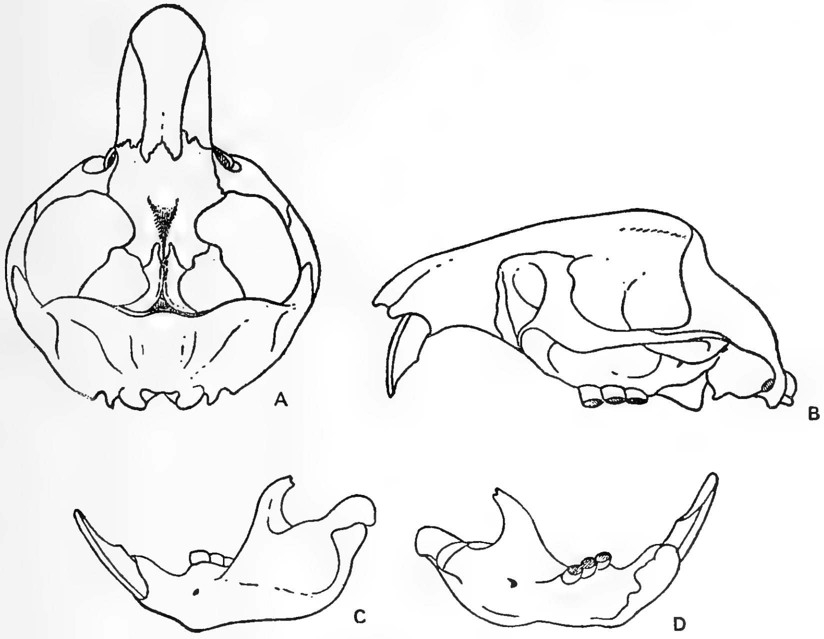

Figure 81. *Spalax graecus* Nehr. Natural size.

Legend is the same as in Fig. 50.

be noted that the nasale in the common mole rat are, on the average, relatively longer, and the rostrum is relatively wider at the base, than in other species from the genus *Spalax*. Thus, the relation of the length of the nasal bones and rostral width to the length of row of permanent molars is respectively equal to 249.0–273.0–296.0 and 142.0–160.0–172.0. As in the Podolsk mole rat, the nasal bones anteriorly are relatively wide; the relation of the total anterior width to the length of row of the permanent molar is 98.8–103.0–109.0. Respective measurements of the nasal bones with regard to the parietal and temporal bones have been given in the diagnosis. The temporo-premaxillary sutures are directed outward in relation to the temporo-nasal sutures, and slightly forward, as a result of which their lines in the expected intersection form an angle with its apex directed posteriorly. Rarely, the shape of the temporo-premaxillary and the temporo-nasal sutures is similar to the same in the common mole rat (straight) or in the Podolsk mole rat (angle with apex directed forward). On the whole, the sutura praemaxillo-nasofrontalis in the Bukovin mole rat, because of a considerable development in the grooves, one of which has already been described, has rather sharper contours than in other species of the genus. Also, in the Podolsk mole rat the nasal apertures are relatively high and wide; the length of the row of permanent molars is respectively equal to 36.4–43.6–53.0 and 91.1–94.4–98.0. The constriction behind the eyes is expressed in about the same degree as in the common mole rat. The relation of the width behind the eyes to the length of row of permanent molars is 90.5–98.8–111.0. The temporo-parietal section is elongated; the relation of the total length of the temporal and parietal bones to the length of row of permanent molars is 245.0–274.0–301.0. The parietal bones are short and narrow. The relation of their length and the total width of length of M^1–M^3 is respectively equal to 101.0–113.0–125.0 and 51.1–60.1–85.5. In view of the elongation of the parietal bones in a longitudinal direction, the pentagon formed by them acquires a corresponding form. The triangular depression on the temporal bones in the place of displacement of the sagittal ridge is well developed. The non-bifurcated portion of the sagittal ridge is shorter than in all the presently known fossil and present-day representatives of the genus; its length is twice or more less than the length of the nasal bones. The temporo-parietal and temporo-frontal sutures form a sharp or straight angle. As in the common mole rat, the upper diastema and hard palate are, on the average perhaps, relatively longer than in the Podolsk mole rat. The value of the diastema-tooth index and the ratio of the length of the hard palate to the length of row of permanent molars are respectively equal to 217.0–238.0–258.0 and 351.0–378.0–404.0. The alveolar tubercles in the majority of animals are more strongly developed than in the common mole rat and the Podolsk mole rat, are closer to the anterior edge of the alveolus of M^1, and situated at a distance which is less than the length of the first permanent molar, or is approximately equal to it. The masseter surface is shortened; its length is approximately equal to the distance between the tubercle of the latter and the suture between the premaxillary and maxillary bones. However, it differs from the common mole rat and the Podolsk mole rat in that the anterior tubercle of the masseter area is massive and sharply defined. The zygomatic arches are widened anteriorly (Figure 81). Their antero-external edges, as in mole rats from the giganteus group, are strongly bent down. The malar angle approaches to 45°. The external wall of the infraorbital foramen is wide. Its least width considerably exceeds the length of the anterior permanent molar. The infraorbital foramen itself is low, its length is approximately equal to the length of the row of permanent molars. The zygomatic arches are considerably lifted posteriorly in relation to the fossa glenoidea. The sutures between the malar process of the maxillary bone and the frontal pass almost in a transverse direction to the former. The hard palate is wide; its width at the level of the anterior permanent molar exceeds one and a half and more times the length of M^1. Its posterior edge often carries markings of the styloid process in the shape of a small diodontus. The inner ridge of the fossa glenoidea is flattened and the articulating fossa is wide. The base of the occipital bone is wide and the auditory bullae are widely separated. The greatest distance between the external edges of the lateral pharyngeal tubercles considerably exceeds the total length of the two last permanent molars, in some cases approaching to the full length of the tooth row. The auditory bullae are wide; the relation of their width to the length of row of permanent molars is 96.6–102.0–106.0. The auditory aperture is small; its greatest diameter is approximately equal to the length of the anterior permanent molar. The occipital portion of the skull, as in the Podolsk mole rat, on the average perhaps, is lower than in the common mole rat. The relation of the length of the occipital bone measured from the upper edge of the foramen magnum to the maximum width of the occiput is 47.1–50.2–53.2.

The upper incisors are wide; the relation of width to antero-posterior cross section is 110.3–115.8–133.0. Their anterior surface, as in all representatives of the microphthalmus group, is flattened.

M^1 (length, 2.8–2.9–3.0 mm; width, 2.5–2.6–2.8 mm; relation of width to length, 83.3–89.4–96.4) with regard to the nature of the structure of the grinding surface is similar to the same molar in representatives of the giganteus group. In particular, in young, semi-mature and even partly in old individuals, the paracone is not fused with the anterior collar, as a result of which the tooth has two intruding folds in the outer line (Figure 82). The order of closure of the intruding folds into marks, because of tooth erosion, is the same as in the already described common mole rat and the Podolsk mole rat. The roots are less reduced than in all the present-day representatives of the genus. The number of roots of this tooth varies from three to two. In the first case, only the internal and the antero-external roots are fused incompletely, because of which each of them has a corresponding independent socket in the alveolus. In the second case, the fusion is complete; however, the markings of the fusion of the said roots are always expressed more clearly than on the same permanent molars of the common mole rat. A fusion of the postero-external and the internal roots never takes place.

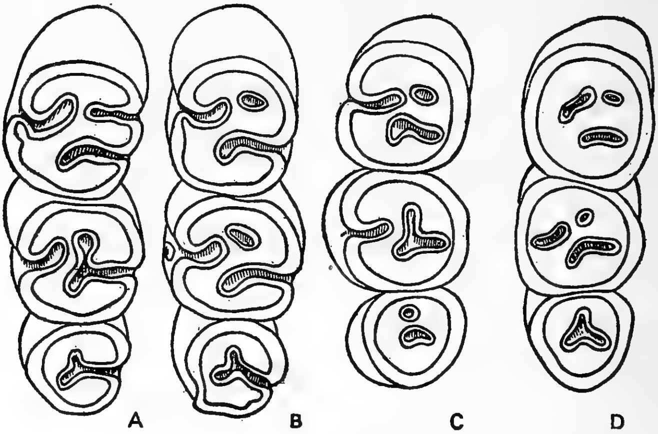

Figure 82. *Spalax graecus* Nehr. ×10.

Upper row of permanent molars: *A* to *C*—adult; *D*—old individual.

M^2 (length, 2.2–2.5–2.8 mm; width, 2.5–2.6–2.8 mm; relation of width to length, 96.3–105.6–122.7) by the structure of its grinding surface is more akin to the similar molar in the sandy mole rat than the common mole rat or the Podolsk mole rat. In particular, it differs from *S. microphthalmus* by less defined foldings of the walls of the outer intruding fold in the young and semi-mature; and from *S. polonicus*, by the presence of anterior and posterior internal tubercles which, in the initial stages of erosion, are fused with each other. The roots are less reduced than in all the presently living representatives of the genus. As in the common mole rat, M^2 in all cases is characterized by the presence of three independent roots—a massive internal one and weakly developed anterior and posterior external ones; moreover, each root has an independent socket in the alveolus.

However, it differs from *S. microphthalmus* in that some individuals have a tendency toward bifurcation of the end of the internal root, as a result of which the number of cavities in the alveolus may reach up to four.

M^3 (length, 1.8–2.0–2.3 mm; width, 2.1–2.2–2.3 mm; relation of width to length, 100.0–109.0–116.7) is, on the whole perhaps, similar to the same permanent molar of the common mole rat and the Podolsk mole rat, possibly differing from the latter in its average smaller relative length. Thus, the relation of the length of M^3 to the length of the preceding molar in the Bukovin mole rat is 73.1–79.7–86.4 as against 71.4–84.2–100.0 in the common mole rat, and 78.2–83.4–100.0 in the Podolsk mole rat. In addition, it differs from the similar permanent molar in *S. microphthalmus*, perhaps, by a rather simpler structure of the grinding surface in the early and middle stages of wear. The roots, in the majority of cases, also have a structure similar to that of the same permanent molar of the common mole rat. They are usually two—a massive postero-internal (the fused internal one and the posterior external) and the free antero-external. In such cases, the number of cavities in the alveolus is two. In some cases there is a tendency toward bifurcation of the end of the postero-internal root, as a result of which the number of cavities in the alveolus may reach up to three.

The lower jaw has a short diastema. The latter is, on the average perhaps, shorter than in all the presently living representatives of the genus, except for the comparatively primitive giant mole rat. Thus, the value of the diastema-tooth index in the Bukovin mole rat is 82.8–100.3–107.8, that is, approximately equal to the length of the lower row of permanent molars. As in the Podolsk mole rat, the horizontal branch is, on the average, relatively lower than in the common mole rat; the relation of its height at the level of the posterior edge of the alveolus of M_1 is 108.0–119.4–126.7. The alveolar process in adult and old individuals, with regard to height, considerably exceeds its articulating one. The height of the process from the internal side in the said age, as a rule, considerably exceeds the length of the lower row of permanent molars (97.7–113.3–124.4). However, it differs from the sandy mole rat, the common mole rat, and the Podolsk mole rat, because the alveolar process of *S. graecus* is often complex; a tubercle is formed on its posterior surface which, in some cases, attains the degree of development of a ridge (Figure 81). Such forms are met in 70 percent of adult and old individuals, and significantly change the contours of the upper portion of the process. Thus, if in the sandy mole rat, the common mole rat, and the Podolsk mole rat, the apex of the alveolar process laterally in a cross section has an appearance more or less of a semi-circle, then in the Bukovin mole rat, because of the aforesaid, this does not happen. In fact, the upper section of the alveolar process of *S. graecus* looks to be somewhat flattened posteriorly (Figure 81). In this respect, the given species exhibits characteristics similar to those of the giant mole rat because in the latter, the alveolar process of the lower jaw also carries markings of similar structures, though it does not reach the degree of development characteristic of the Bukovin mole rat. The incisura corono-alveolaris is step-like because of the great development of the anterior ridge of the alveolar process (Figure 81). Its anterior edge encroaches considerably on the coronary process. The coronary process is high and wide, with a step-like external surface related to its being encroached upon by the anterior edge of the corono-alveolar groove. The corono-articulating groove is correctly cut because of the approximate coincidence of the height of the coronary process and the length of the upper edge of the articulating one. The ridge of the coronary-alveolar groove in the majority of cases is more strongly developed than the ridge of the coronary-articular one; rarely, the degree of their development is approximately similar. Because of a more strongly developed coronary-alveolar ridge, the fossa contoured by its anterior extremity and the coronary alveolar ridge is, on the whole, deeper than in the sandy mole rat, common mole rat, and the Podolsk mole rat. Furthermore, it differs from the species mentioned above in that the mandibular foramen is placed low and apart from the edge of the coronary-articulated groove, at a distance approximately equal to the length of the articulating surface of the condylus; in any case, it considerably exceeds two-thirds the length of the latter. With regard to the degree of development of this trait, the Bukovin mole rat comes nearer to the primitive *S. giganteus* after all. The articulating surface of the condylus is widened: its width in the majority of cases is equal to half the length or even considerably exceeds the length (relation of width to length is 44.0–52.0–59.0).

The lower incisor is, on the average perhaps, narrower than in the common mole rat; the relation of the width to the antero-posterior cross section is 100.0–101.2–103.0.

M_1 (length, 2.7–2.8–2.9 mm; width, 2.4–2.5–2.7 mm; relation of width to length, 82.8–92.0–100.0) in the structure of its wearing surface bears a similarity to the teeth of the sandy mole rat and the common mole rat. The tendency toward separation of the metaconid and the anterior collar in the initial stages of tooth erosion and the almost completely reduced entoconid take it close to the first; the presence of an additional intruding fold in the outer line in the corresponding stages of wearing takes it close to the second. The tooth has two roots—a massive, wide posterior and a weakly developed anterior. Sometimes, the posterior root exhibits a tendency toward bifurcation.

M_2 (length, 2.2–2.4–2.6 mm; width, 2.4–2.6–2.7 mm; relation of width to length, 100.0–108.6–118.2), with regard to the structure of the wearing surface and the general proportions of the corona, is similar to the same permanent molar of the common mole rat. However, it differs from the latter by becoming more complex in the very early stages of wearing (in very young individuals), because of the presence of an additional intruding fold in the outer line. There are two roots; moreover, both of them either exhibit a tendency toward bifurcation or are even characterized by forked ends. In the first instance, the anterior and the posterior cavities of the alveoli have a well-developed fold, and in the second case, each of the cavities is divided into two.

M_3 (length, 1.9–2.2–2.4 mm; width, 2.2–2.3–2.5 mm; relation of width to length, 95.6–103.7–115.8), with regard to the general characteristics of the wearing surface, proportions of the corona, and the nature of the root structure, does not differ from the same permanent molar in the common mole rat (Figure 83).

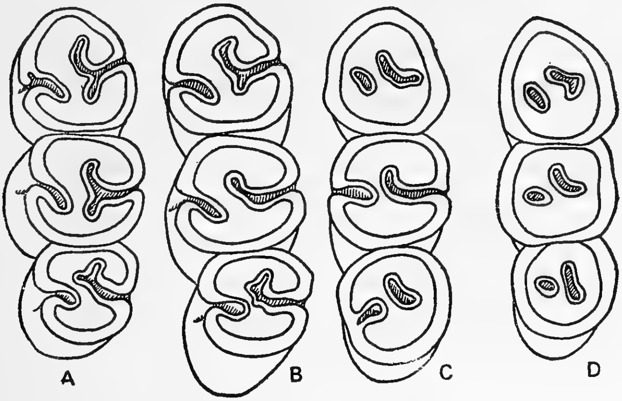

Figure 83. *Spalax graecus* Nehr., lower row of permanent molars. ×10.

A to *C*—adult; *D*—old individual.

Comparison. A detailed comparison of the Bukovin mole rat was made above.

Measurements. Condylobasal length of skull, 49.9–53.0–55.1 mm; basal length of skull, 46.1–49.3–51.5 mm; length of nasal bones, 21.2–23.5–25.3 mm; total length of parietal and temporal bones, 22.1–23.0–24.4 mm; length of parietal bones, 8.7–9.7–11.3 mm; length of upper diastema, 19.0–20.4–21.7 mm; length of hard palate, 29.9–32.5–34.8 mm; length of upper row of permanent molars, 8.1–8.5–9.0 mm; width of nasal aperture, 7.8–8.1–8.3 mm; incisorial width, 8.4–9.3–10.3 mm; width of nasal bones anteriorly, 8.6–8.9–9.2 mm; rostral width, 12.1–13.7–14.8 mm; width behind the eyes, 7.3–8.5–9.6 mm; width of two parietale, 3.3–5.2–7.7 mm; width of parietal bone up to lambdoid ridge, 4.8–5.3–6.1 mm; malar width, 39.8–42.7–45.5 mm; width of occiput, 36.4–37.7–39.5 mm; length of auditory bullae, 12.1–12.9–13.9 mm; width of auditory bullae, 8.5–8.7–9.2 mm; width of upper incisor, 3.0–3.2–3.6 mm; antero-posterior cross section of upper incisor, 2.5–2.8–3.1 mm; height of nasal opening, 3.1–3.7–4.3 mm; condylar length of lower jaw, 33.9–35.2–39.1 mm; angular length of lower jaw, 32.6–35.5–41.4 mm; length of lower diastema, 7.2–8.4–9.1 mm; length of lower row of permanent molar, 7.7–8.4–8.9 mm; height of horizontal branch at the level of the posterior edge of the alveolus of M_1 externally, 9.4–10.1–10.9 mm; thickness of horizontal branch at the level of M_2, 4.8–5.4–6.1 mm; height of alveolar process internally, 8.5–9.5–10.7 mm; width of lower incisor, 3.1–3.4–3.9 mm; antero-posterior cross section of lower incisors, 3.0–3.4–3.8 mm.

Note. From the above description of the Bukovin mole rat and its comparison with fossil and presently living representatives of the genus, it is very clear that in the given case we are dealing with the least specialized species from the *microphthalmus* group from the viewpoint of a trophic as well as a burrowing capacity. This group preserved, along with highly specialized traits characteristic for the group as a whole, some primitive traits taking it closer to the most primitive representative of the giganteus group—the giant mole rat, and from the number of species of the microphthalmus group—the Pliocene *S. minor*. Such traits in the structure of the skull, the lower jaw, and the permanent molars of the Bukovin mole rat are: structural characteristics of the alveolar tubercles and the zygomatic; a highly developed anterior ridge in the masseter area; a shortened lower diastema; a relatively low horizontal branch of the lower jaw; a typical structure of the upper end of the alveolar process; a lower position of the mandibular foramen, possibly relatively narrower lower incisors; and also complex upper and, to a certain extent, lower anterior permanent molars, the roots of which are less reduced than in all the presently living representatives of the genus *Spalax*. Furthermore, individual specimens of Bukovin mole rats rarely preserve markings of the for. epicondyloideum which actually push it toward the boundary between *Microspalax* and *Spalax*. In the rest of the traits, the species is characterized by all traits inherent in the highly specialized mole rats from the genus *Spalax*, and foremost from the species of the highly developed group *microphthalmus*. The foregoing helps in taking it to be a species which has, to a considerable degree, preserved the characteristics original for the group *in toto*.

The species was first described by Nehring (1898b). In place of its *terra typica*. Nehring supposedly indicated only the region around Athens because the etiquette of the holotype did not offer a possibility to exactly fix the place of its find. Afterwards Mehely (1909) doubted the possibility of finding this species in Greece because all the rest of the finds were discovered exclusively in the Karpate region of the Pricarpate regions of the Chernovits district of Ukraine SSR (Bukovina), and the adjacent regions of Rumania. However, in the work of further researchers up to Miller (1912) the findings of Nehring (1898b) and especially of Mehely

(1909) were forgotten, and the presence of the species around Athens was taken to be an established fact not needing additional proof. As a result, Greece and Bulgaria are included in the present-day area of the species: true, sometimes with a footnote that the species is presently extinct there (Ognev, 1947). By the way, it could be confirmed adequately that during the determination of the *terra typica* of the Bukovin mole rat as well as the *M. kirgisorum*, a great misunderstanding with regard to etiquette prevailed. Hence, we feel the *terra typica* of the species may be taken as the region around the city of Chernotisi from where Mehely (1909) described two skulls belonging to the given species which could be rightly taken as paratypes of the species. At present, the habitat of this species within Soviet Bukovina is restricted to the hilly landscape on the right bank of the Prut River (Yangolenko, 1959). The mole rat of this species obtained from adjacent territorial regions in Rumania (around Borshi and Bistritsi, Northeastern Klusha) were separated by Mehely (1909) as an independent species—*S. istricus* Mehely. However, a comparison of the skull of Rumanian mole rats with a series of skulls obtained from the region of Soviet Bukovina makes it possible to determine the presence of considerable transgression in respect to all the traits which Mehely took to be specific for the species (structural characteristics of the temporo-nasal and temporo-premaxillary sutures, the corresponding length of the premaxillary and nasal bones, the degree of reduction of roots on the permanent molars). On this basis, a separation of it as a separate species, in our opinion, does not have enough basis. In addition, it is possible that these differences will be taken into further consideration in the average of the serial data which serves as a basis for the preservation of this nomenclature as a subspecies. The presence of an independent subspecies in the vicinity of the indicated regions of Rumania is quite possible theoretically because the main ridge of the Karpate hills could play the role of a geographical fence between the Rumanian and Bukovin forms. However, at present, this question remains unsolved because we do not have a series of skulls for the Rumanian *S. graecus*.

Distribution and geological age. In Soviet Bukovina, spread up on the right bank of the Prut River, occupying the northwestern portion of the near hills and hilly zones. It has been found around the village Zavoloki, Mikhalcha, Kamenka, Chagor, Valya Kuzmina of Chernovitsk region, and also in a number of centers of the Storozhintsk and Glybovskii regions; around the adjacent regions of Rumania near Borsh and Bistritsi (northeast of Kluzha). Recent; subfossil remains of the Holocene period have been found in and around the present regions of its spread near Turda.

Subspecies. Geographical variability has not been studied; however, it is quite possible to have two subspecies.

1. *S. g. graecus* Nehring, 1898—Bukovin subspecies; distributed around Soviet Bukovina along the northeastern slant of Karpate and their foothills.

2. *S. g. istricus* Mehely, 1909—Rumanian subspecies; differs from the nominal form, perhaps, by a lesser degree of reduction of roots on the permanent molar. It is distributed along the southwestern slant of the Karpate hills within the limits of Rumania. *S. g. antiquus* Mehely, 1909, from the Holocene sediments of Rumania (Turda) is absolutely similar to this form.

6. **Spalax minor** W. Topachevskii, 1959—**Small Mole Rat or the Nogaiskii Mole Rat**

Topachevskii, 1959: 1263–1266, Figures 1, 2, 7, 8. *microphthalmus minor* Topachevskii, 1957a: 144–145.

Holotype. Institute of Zoology AN Ukraine SSR, No. 27–92; lower jaw (mandibula sin.) without the coronary and alveolar processes; from the permanent molars, only the complete line of alveoli has been preserved; Late Pliocene Nogaisk.

Paratypes. Skull is without temporal and occipital sections and the zygomatic arches, No. 27–980; lower jaw with a fully preserved row of permanent molars, without coronary and upper portion of the alveolar processes, No. 27–981; lower jaw without teeth, with disturbed coronary and alveolar processes, No. 27–215. All the remains are from Upper Pliocene sediments, hidden near the city Nogaisk, Primorsk region, Zaporozh'e district, and are stored in the collections of the Institute of Zoology AN Ukraine SSR.

Material investigated. The lower jaws at different degrees of preservation and their pieces—4 items; isolated teeth—incisors of the upper jaw —10, M_1—13; M^2—7; M^3—5; lower incisors—20; M_1—12; M_2—7; M_3—4. All these remains come from the Upper Pliocene sediments of Nogaisk. In addition, the author had individual broken pieces of the lower jaw, and a small series of teeth from a number of places of finds of the Late Pliocene in the region of Odessa and Kryma.

Diagnosis. It is the smallest of all the presently known representatives of the genus. The skull is generally similar to the skull of the Bukovin mole rat. It differs by narrowed parietal bones, the total length of which is less than length of the upper line of permanent molars, and also by, on the average, a shortened upper diastema, a hard palate, row of permanent molars, and a reduced width behind the eyes. The lower jaw has a high diastema section, elongated and narrowed articulating surfaces for the condylus (width is less than half its length or is approximately equal), and a step-like corono-alveolar groove. In addition, the upper and lower incisors, and the anterior permanent molars are, on the average, relatively narrower than in all the presently living representatives of the genus.

Description. The rostral section of the skull is similar to the same as in the common mole rat and is wedge-shaped (its width at the level of the anterior edges of the infraorbital foramen exceeds the width at the center. The total length of the nasal bones posteriorly exceeds the length of the premaxillary, and the latter, in turn, is approximately equal to half the anterior total width of the nasale. The nasal bones are greatly narrowed in the posterior section; total width of the nasale anteriorly, approximately twice exceeds the width posteriorly. The groove in the region of the temporo-nasal suture is faintly marked; however, the posterior ends of the nasal bones are slightly sharpened and exhibit a tendency toward forming a fork-like bifurcation, typical as was shown above, of the presently living Bukovin mole rat (Figure 84). The nasal bones are elongated; their length slightly exceeds the total length of the temporal and parietal bones. The temporo-premaxillary and temporo-nasal sutures are straight; however, the posterior ends of the nasale are slightly curved

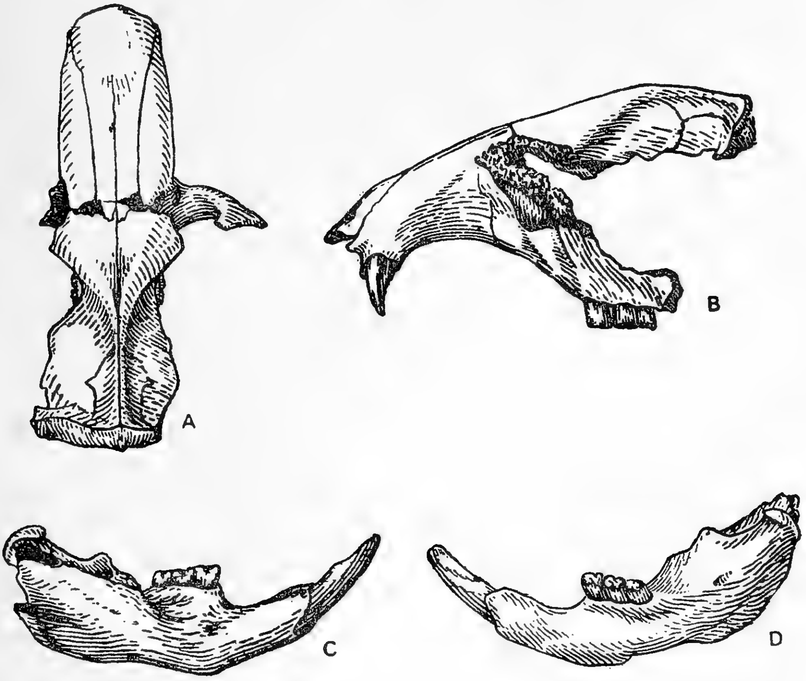

Figure 84. *Spalax minor* W. Top. × 1.6. Late Pliocene of South of Ukraine, Nogaisk town, Zaporozh'e district.

Legend is the same as in Figure 50.

back in relation to the former. The constriction behind the eyes is expressed more clearly than in the common mole rat. The relation of the width behind the eyes to the length of skull from nasion to apex of the lambdoid is 16.0[1] as against 16.4–19.4–22.4 in *S. microphthalmus*. The parietal bones are narrow; the relation of their total width to the length of row of permanent molars is 86.1 as against 80.2–140.0–179.0 in adult and old *S. microphthalmus*. It has also to be taken into account during this that the dental row in *S. minor* is shortened and, as a result, the value of the given trait in it is dependent on it. The parietal bones form a pentagon drawn out in a longitudinal direction like a five-angled star. The triangular depression on the temporal bones in the place of displacement of the sagittal ridge is almost not expressed. The temporo-parietal and the temporo-frontal sutures form a blunt angle. The upper diastema and the hard palate are short; the relation of their lengths to the length of the skull from nasion to apex of the lambdoid ridge is 42.4 and 67.8 as against respectively 43.1–48.1–52.2, and 68.1–75.6–81.3 in the common mole rat. The masseter area is shortened; its maximum width is equal to the distance from the anterior tubercle of the latter up to the suture between the premaxillary and maxillary bones. The anterior ridge of the masseter area is weakly developed. The alveolar tubercles are absent. The hard palate at the level of the anterior permanent molars is narrowed; its width only slightly exceeds the length of M^1. The upper row of permanent molars is short (16.4 as against 18.4–20.2–22.7 in *S. microphthalmus*). The zygomatic arches, the posterior portion of the base of the skull, and the frontal and occipital sections have not been preserved, because of which the comparison of their structure with similar organs in the Bukovin mole rat is out of question.

The upper incisors are, on the average, narrower than in the common mole rat; the relation of the width to the antero-posterior cross section is 100.0–104.2–108.6 as against 104.4–112.0–120.8. Their anterior surface is flattened.

M^1 (length, 2.0–2.3–2.5 mm; width, 1.7–1.9–2.1 mm; relation of width to length, 75.0–84.6–95.0) is smaller in regard to absolute measurements than the similar permanent molar in all presently living representatives of the genus. Furthermore, it is, on the average, comparatively narrower. A great similarity is observed between the permanent molars of mole rats from the giganteus groups in regard to the structure of the grinding face

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[1] Here and afterward the indices of the skull differ from the earlier described species in being measured against the length of the skull from nasion to apex of the lambdoid ridge, and not to the length of the upper row of permanent molars, because the latter in the Nogaisk mole rat in comparison with presently living species is shortened and, as a result, even the values of the corresponding relations, if they are to be brought to this number, will be dependent to a considerable extent. In cases where the index is taken from the length of M^1–M^2, a corresponding note is given in the text.

in young, semi-mature, and partly in old animals, and among representatives of the microphthalmus with the Bukovin mole rat. This similarity is due mainly to the presence of a paracone that is not fused with the anterior collar, as a result of which the tooth is characterized by two intruding folds in the outer line (Figure 85). The types of structures characteristic of the common mole rat (paracone fused with the anterior collar but separated from the neck, joining the protocone with the hypocone; one intruding fold in the outer line, the protocone and the hypocone fused) and the Podolsk mole rat (protocone and hypocone isolated) are rarely seen. It has also to be noted that the closure of the intruding fold into a mark in the Nogaisk mole rat takes place, perhaps, in rather later stages of tooth erosion than in all the present-day and fossil quaternary species of the genus. It differs from all the presently living representatives

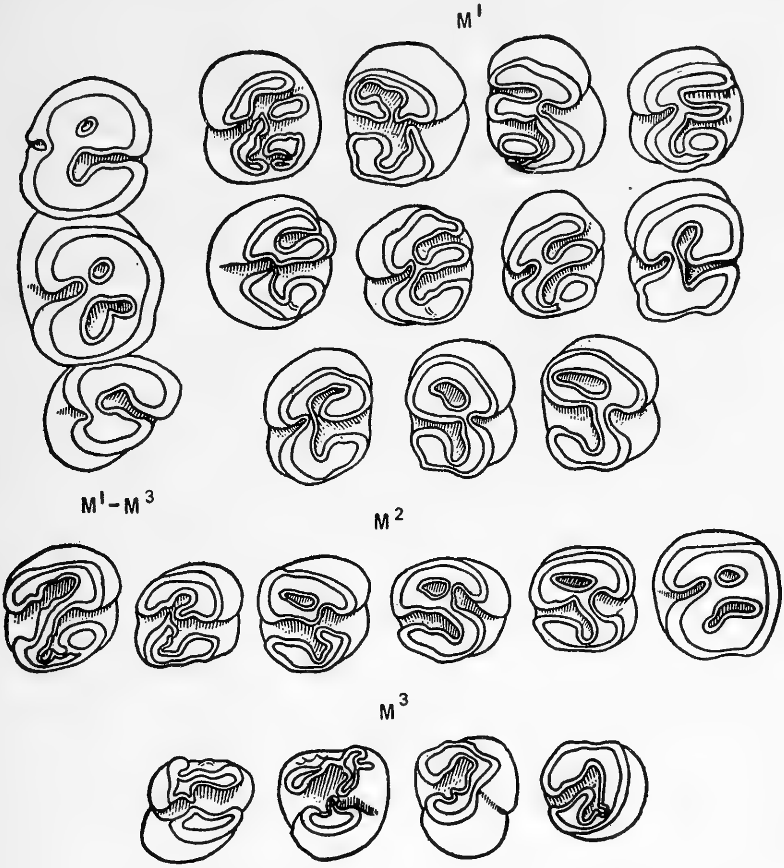

Figure 85. *Spalax minor* W. Top., upper permanent molars. ×10.

of the genus in that the metacone and posterior collar express, perhaps, a greater tendency for separation; moreover, in individual cases the posterior external tubercle may even have the form of an independent fold, as a result of which the tooth will be characterized by the presence of three intruding folds in the outer line. The grinding surface of the said teeth from the moment of the closure of the intruding folds into marks assumes a form very similar to that on the same permanent molars in recent representatives of the genus, because of which the differentiating characteristics at a given stage of wearing (in part, of adult and old animals) will reduce to only smaller absolute measurements and somewhat other proportions in the structure of the corona. The number of roots in the majority of given cases, as in Bukovin mole rats, does not exceed two—the massive antero-internal (the fused internal and the external), and a comparatively weakly developed posterior external. In some animals, the antero-external and the internal roots are not fused, as a result of which the tooth is characterized by the presence of three roots. On the whole the roots on the anterior permanent molars of the Nogaisk mole rat are more reduced than in the common mole rat which, to a certain extent, puts it closer to *S. graecus*.

M^2 (length, 1.8–2.0–2.2 mm; width, 1.8–2.0–2.2 mm; relation of width to length, 95.0–100.0–104.8), on the average, is smaller and perhaps relatively narrower than in the present-day *S. microphthalmus*. The structure of the wearing surface is similar to that of the recent common mole rat. However, the degree of reduction of roots is generally expressed more strongly. This varies in the Nogaisk mole rat from one to two as against three in the common mole rat.

M^3 (length, 1.6–1.7–1.9 mm; width, 1.7–1.8–1.9 mm; relation of width to length, 95.0–106.8–112.5), in regard to the character of the structure of the wearing surface, and general proportions of the crown, is, on the whole, similar to the same molar in the common mole rat, differing only in the average lesser absolute measurements. However, as in the preceding molar, the degree of reduction of roots is expressed more strongly than in *S. microphthalmus*. This tooth in the Nogaisk mole rat, in the majority of cases, is characterized by the presence of only one root. In present-day common mole rats, there are usually two roots.

The lower jaw is, on the whole, similar to the lower jaw of the presently living *S. microphthalmus*, differing by a rather high diastema-section and an outgoing branch. Thus, the values of the height of the jaw along the center of the diastema and the outgoing branch to the condylar length, respectively, are equal to 16.7, 17.8, 18.1 and 36.5 as against 13.0–14.3–16.2 and 30.7–33.4–35.5 in *S. microphthalmus*. In addition, the horizontal branch of the lower jaw of the Nogaisk mole rat is perhaps thicker at the level of M_2; the relation of its thickness to the condylar length is 15.7, 16.3, 17.4 as against 13.4–14.3–15.8. The coronary alveolar groove is steplike because of the greater development of the alveolar ridge in the alveolar process than in the common mole rat. With regard to the development of this trait, the Nogaisk mole rat is closer to the present-day *S. graecus* than to the rest of the representatives of the microphthalmus group. Particularly clear differences between *S. minor* and the common mole rat are observed in the structure of the articulating surface of the condylus. The latter in the Nogaisk mole rat is, on the average, relatively longer and narrower than in *S. microphthalmus*. This trait is well seen during a comparison of the values of the relation of width of the articulating surface to its length, which in *S. minor* is respectively equal to 47.8, 48.1, 49.1, 52.3 as against 50.0–57.0–66.7 in *S. microphthalmus*. The said peculiarity of the structure of the lower jaw, to some extent, draws the Nogaisk mole rat nearer to the recent *S. arenarius*.

The lower incisor is, on the average, relatively narrower than in all the presently known representatives of the genus, except for the giant mole rat. The relation of the width to the antero-posterior cross section is 90.0–97.7–104.1 in the Nogaisk mole rat and 88.9, 92.3, 96.0 and 96.4 in Krym mole rats. However, it differs from the giant mole rat in that the anterior surface of the incisor is flattened and not convex. Furthermore, the incisors of the Nogaisk mole rat differ from the same in *S. giganteus* by considerably smaller absolute measurements.

M_1 (length, 1.9–2.2–2.5 mm; width, 1.5–1.9–2.0 mm; relation of width to length, 78.3–84.1–90.9), on the average, is smaller and narrower than the same permanent molar in all the presently known recent representatives of the genus. In the initial stages of wearing (in very young individuals), there is quite a similarity in the structure of the wearing surface with the same permanent molar of the sandy mole rat and the Bukovin mole rat, because the metaconid and the anterior collar are not fused (Figure 86). However and further (in young, semi-mature, and partly in old individuals), the masticatory surface of the tooth assumes a form which is characteristic of the common mole rat and the Podolsk mole rat. It differs from the first in that the markings of an additional intruding fold in the outer line (observed by us only in one instance, Figure 86) are rarely observed on the anterior permanent molars of the Nogaisk mole rat. As far as the Podolsk mole rat is concerned, the said teeth in it are, on the average, considerably wider than in the common mole rat, not to speak of the Nogaisk mole rat. The protoconid and the hypoconid in the majority of cases are fused. The entoconid is developed to approximately the same degree as that in the common mole rat and the Podolsk mole rat. Rarely, this tubercle fuses with the posterior collar forming a posterior mark characteristic, as was shown above, of the same permanent molar in representatives of the genus *Microspalax*. The structure of the root on the whole, is similar to the same on the anterior lower molars of the common mole rat.

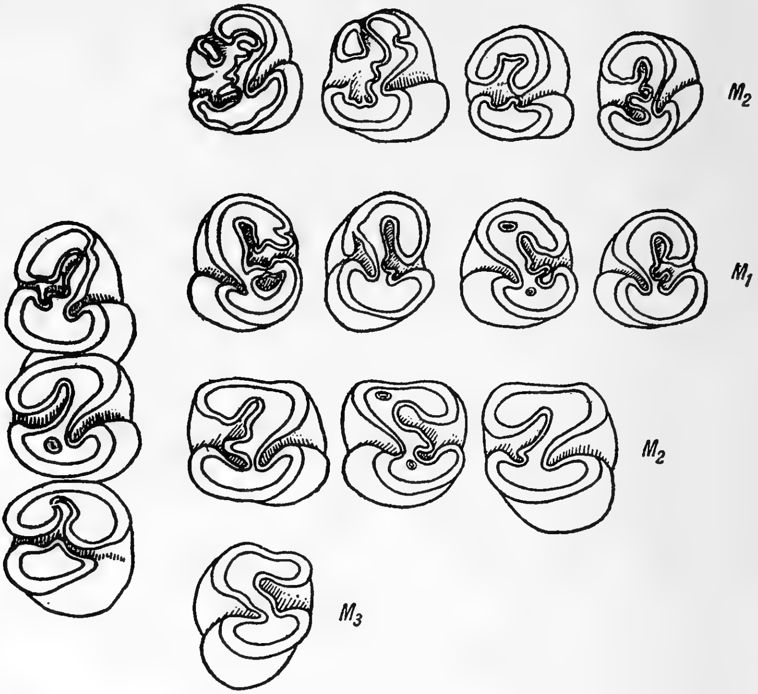

Figure 86. *Spalax minor* W. Top., lower permanent molars. ×10.

M_2 (length, 2.1–2.2–2.3 mm; width, 1.9–2.1–2.3 mm; relation of width to length, 82.6–96.8–104.8), with regard to the general characteristics of the wearing surface and the structure of the roots on the whole, is similar to the same permanent molar of the common mole rat and the Podolsk mole rat. It differs from all the presently living species of the genus by lesser absolute measurements and by a narrowed crown.

M_3 (length, 1.8–1.9–2.0 mm; width 1.8–1.9–2.1 mm; relation of width to length, 94.7–102.7–105.1) is similar to the same permanent molars of the present-day species from the microphthalmus group.

Comparison. Characteristics of similarity and difference between the Nogaisk and the common mole rat have been looked into above. While summarizing the foregoing, it has to be underlined that *S. minor* differs from all the recent representatives of the microphthalmus group by a long and narrow articulating surface of the condylus of the lower jaw, and also by, on the average, relatively narrower upper and lower incisors and permanent molars, primarily, M_1^1–M_2^2. Furthermore, it differs from *S. polonicus* as follows:

1. Elongated nasal bones, the length of which exceeds the total length of the temporal and parietal bones (in the Podolsk mole rat, the relationship is reversed).

2. Shape of the temporo-nasal and temporo-premaxillary sutures (almost a straight line in Nogaisk mole rat, with an angle whose apex is directed forward in the Podolsk mole rat).

3. A protocone and hypocone on M^1, fused in the majority of cases in the early and middle stages of wear, and also the paracone which is not fused at a given stage of wear with the anterior collar (in Podolsk mole rat, the first are always isolated and the second ones are fused).

4. A step-like form in the corono-alveolar groove (faintly stepped in *S. polonicus*).

Finally, besides the above-mentioned characteristics in the structure of the articulating process of the lower jaw and the permanent molars, it differs markedly from the Bukovin mole rat by a weakly developed groove on the nasal bones in the region of the temporo-nasal sutures and by the triangular depression on the temporal bones in lieu of the displacement of the sagittal ridge.

Measurements. Length of nasal bones, 22.9 mm; total length of parietal and temporal bones, 21.7 mm; length of parietal bones, 10.9 mm; length of upper diastema, 18.6 mm; length of hard palate, 29.7 mm; length of upper row of permanent molars, 7.2 mm; width of nasal aperture, 7.9 mm; incisorial width, 8.3 mm; width of nasal bones anteriorly, 8.3 mm; rostral width, 12.0 mm; width behind the eyes, 7.0 mm; total length of parietale, 7.7 mm; width of parietal bones up to the lambdoid ridge, 4.0 mm; width of upper incisor, 2.3–2.6–2.9 mm; antero-posterior cross section of the upper incisor, 2.2–2.4–2.8 mm; height of nasal aperture, 4.3 mm; condylar length of lower jaw, 26.9, 29.9, 31.2 mm; length of lower diastema, 7.0, 8.1, 8.3 mm; length of lower row of permanent molars, 6.8–7.0–7.2 mm; height of horizontal branch at the level of the posterior edge of the alveolus of M_1 externally, 7.1, 7.8, 8.8, 8.8 mm; thickness of horizontal branch at the edge of the M_2, 4.2–4.6–5.2 mm; width of lower incisor, 2.3–2.6–3.0 mm; antero-posterior cross section of lower incisor, 2.3–2.6–2.9 mm.

Note. From the description given above about the mole rat from Nogaisk, and comparing it with fossil and presently living species of the genus *Spalax*, there is no doubt that in the given case we are dealing with an already completely formed representative of a most highly specialized group within the limits of the microphthalmus group which has preserved in its structure a number of primitive traits that place this species closer to the last specialized representatives of the group—the present-day *S. graecus*, and in regard to some traits, even closer to the species from the giganteus group—the giant mole rat and the sandy mole rat. However, it has to be underlined that the Nogaisk mole rat, in regard to a number of structural characteristics of the skull, the lower jaw, and the permanent molars, stands closer to the common mole rat than to the Bukovin mole rat. This, first of all, concerns the degree of reduction of roots on the permanent molars which in *S. minor* is expressed in a greater manner than in *S. graecus*. Thus, taking into consideration the highly expressed trophic adaptability of the Nogaisk mole rat as compared to the Bukovin mole rat, the comparatively early separation of these took place, perhaps, somewhere toward the end of the Late Pliocene. In addition to this, with regard to the degree of development of adaptations to burrowing (relative width of the incisors) the Late Pliocene Nogaisk *S. minor* sharply differs from all the presently living representatives of the genus except for *S. giganteus* which, perhaps, indicates a lower degree of specialization in the species in this regard. Relative to the development of this trait, the Nogaisk mole rat takes up a middle position between representatives of the primitive genus *Microspalax* and the highly specialized *Spalax*.

It has also to be underlined that the considerable similarity of the Nogaisk mole rat with present-day *S. microphthalmus* and, to a lesser extent, with *S. polonicus*, allows one to look to it with a known degree of probability as a form close to the ancestral with regard to the said species separation which, as has already been mentioned, took place perhaps only in the Anthropogene.

The Nogaisk mole rat is the most ancient of the presently known species of the genus *Spalax*. In sediments more ancient than the Nogaisk sediments (Villapransk and below), mole rats have been represented by remains of representatives of the genera *Microspalax* and *Prospalax*. Thus, the type of structure of the skull, lower jaw incisors, and permanent molars inherent in all fossil and presently living *Spalax* completely took shape, perhaps, in eastern Europe only at the end of the Pliocene epoch. The remains of closer forms, considering the past and present distribution of the genus, should be found in the corresponding sediments of western Europe also (Rumania, Hungary, Czechoslovakia, Poland). In this regard, Kretzoi's report (1941) about finding in the Upper Pliocene sediments in Hungary (place of find, Betfiya near Nagivard, Inner Karpate) the incisors of a mole rat of the *Spalax* species, which did not have on the anterior border the three additional ridges of enamel characteristic of the European Pliocenic *Microspalax* and representatives of the genus *Prospalax*, is significant. Unfortunately, the foregoing author does not give the measurements of width and the antero-posterior cross section of the incisors. Hence, there is insufficient basis for assuming that this mole rat from Betfiya belonged to a species closer to *S. minor* and not to a form from the subgenus *Mesospalax*. It has also to be noted that Kretzoi (1956) gives it the name *S.*

advenus Kretzoi. Remains of this species orginate from the Upper Pliocene sediments of Hungary, possibly stratigraphically identical or at least close to the Nogaisk mole rat. Unfortunately, in the absence of at least a short description, we cannot compare *S. minor* with *S. advenus.*

Distribution and geological age. End of Late Pliocene and, perhaps, early fossils around the Black Sea and the Azov Sea of USSR, including Krym. Besides Nogaisk, remains of this species have been found in the Upper Pliocene sediments of mysa Tarkhankut in Krym (near the village Chernomorskoe) and on Tamani (place of find, Tsimbal). Perhaps some portion of the remains from the lower fourth of the sediments in the village Tikhonovka of the Novo-Vasilevsk region, Zaporozh'e district, could be related to this species. Very scanty remains of the close, if not identical form are known at the present time from the sediments of the right bank estuary of Kuyal'nitsk around the city of Odessa (Zhevakhova hills, territory of Kuyal'nitsk hill station), and from down under the upper layer of the ancient alluvial soil, hidden in the left bank of the estuary of Khadzhibeisk near the village Avgustovka, Odessa region, Odessa district (Topachevskii, 1965). In the first case, they are accompanied by fauna more ancient than that of Nogaisk which has been separated by A. I. Shevchenko (1965) in the so-called Odessa Late Pliocene complex. In the second case, the remains of the mole rat having a shape very close to the Nogaisk's were found in adjacent sediments.

Special attention should be given to the discovery of this species in Krym, giving documentary evidence of the presence of mole rats in the territory of the peninsula in the Late Pliocene. The latter is more interesting because among the Pleistocene and Holocene (including present-day forms), fauna of Krym, mole rats, perhaps, are absent. Unfortunately, the only one unconfirmed report on the habitation of the fossil remains of *Spalax* of the Pleistocene period (Merezhkovskii, 1880) was not confirmed by the research of A. A. Byalinitskii-Birulya (1930), and I. M. Gromov (1961), who carried out research on masses of paleontological material from the Pleistocene and Holocene of Krym. Thus, the disappearance, or at least a considerable reduction, in the number of mole rats in Krym through the Anthropogene makes us look at it perhaps as a secondary event, the reason for which is most probably hidden in the significant changes of a paleogeographical nature which took place in Krym at the end of the Early Anthropogene and in the beginning of the Pleistocene. The reasons bringing about these changes and the nature of the latter are not clear even up to the present time.

Spalax Species

Spalax aff. *microphthalmus* Topachevskii, 1965: 139.

Material investigated. Isolated teeth: M^1—1 only; M^3—1 only; lower incisors—7; M_1—3. All the remains originate from the lower Anthropogene sediments excavated near the village Tikhonovka of the Novo-Vasilevsk region, Zaporozh'e district.

Description and comparison. The author has already reported in earlier works the fact of the discovery of two types of mole rats among the early Anthropogene fauna of Tikhonovka (Topachevskii, 1965). A portion of the remains from this place of discovery (mainly, isolated incisors and permanent molars) appeared to be absolutely identical to those of *S. minor* and, in all probability, should be attributed to this species. In addition, it was possible to separate these series of teeth sharply differing from the similar remains of the Nogaisk mole rat, by large general measurements, somewhat different proportions in the structure of the crown of the permanent molars, and perhaps, by a less expressed degree of reduction in the roots of the latter. This form was earlier placed close to *S. microphthalmus* by us. However, during a detailed study of the material, we had to retract this because it was possible to note a number of significant differences in the Tikhonovka large mole rat from this species. The traits taken together indicate, first of all, that in the given case we are dealing with a less specialized form than the recent species which, perhaps, takes an intermediate place in the evolutionary line between the Nogaisk mole rat and the presently living species from the microphthalmus group. Because these finds are interesting from the point of view of understanding history of stabilization in the group as a whole, we take the liberty of putting forward a short description of the remains, though the very scanty material available with the author does not allow describing the Tikhonovka mole rat as an independent taxon at the species or subspecies level.

M^1 (length, 2.5 mm; width, 2.3 mm; relation of width to length, 92.0 mm) is larger and mainly, relatively wider than the same permanent molar in the earlier described Late Pliocene Nogaisk mole rat, and approaches in regard to development of the said traits to presently living representatives of the genus. There were no differences in the structure of the grinding surface between *S. minor* and present-day species of *Spalax* because both belong to aged individuals (the anterior fold or the inner portion of the only fold of the external line closed into a mark), and the configuration of the masticatory surface of the permanent molar in all mole rats of this genus, as has already been said, at these stages of advanced age has a very similar shape. The structure of the roots is basically similar to the common mole rat. The tooth has two roots—a massive antero-internal and a weakly developed postero-external.

M^3 (length, 1.9 mm; width, 1.9 mm; relation of width to length, 100.0), with regard to general features of the grinding surface, proportions of the crown, and absolute measurements, is similar to the same permanent molar of the Nogaisk and the common mole rat. However, the presence of two roots sharply differentiates it from the former.

The lower incisors are larger than in the Nogaisk mole rat, and approach to the same in *S. microphthalmus* in regard to absolute measurements (width of incisor, 3.2–3.4–3.8 mm; antero-posterior cross section, 3.1–3.3–3.4–4.0). However, they are, on an average, relatively narrower than in the common mole rat (relation of width to antero-posterior cross section, 94.1–98.1–103.2), which brings the Tikhonovka mole rat closer to *S. minor* and the giant mole rat.

M_1 (length, 2.3–2.4–2.5 mm; width, 2.2–2.2–2.2 mm; relation of width to length, 88.0–91.7–95.6), on the average, is apparently larger and relatively wider than in the Nogaisk mole rat, resembling, because of this, the same molars in the recent representatives of the genus. With regard to the general characteristics of the grinding surface, it exhibits many characteristics that are similar to the same permanent molars of the Nogaisk mole rat because, in the initial stages of wearing, the metaconid and anterior collar are completely separated (Figure 87). The said teeth could also belong to *S. arenarius* though in the semi-mature animals the antero-internal tubercle and the anterior collar fuse together. In the sandy mole rat, isolation of the metaconid and the anterior collar is preserved even in semi-mature animals.

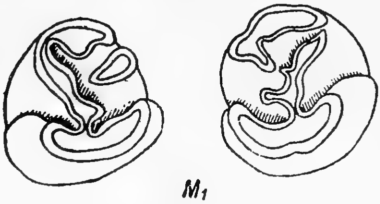

Figure 87. *Spalax* sp. ×10. Early Anthropogene, South of Ukraine, Village Tikhonovka, Zaporozh'e region.

Thus, on the basis of the Tikhonovka Early Anthropogene mole rat, we come across a type of structure which has considerably preserved the style of the Late Pliocene forms and which, at the same time, is highly specialized like the presently living species from the microphthalmus group. The presence of less reduced roots on the permanent molars, as compared to *S. minor*, greatly reduces the obstacles in the way for seeing this species as an ancestor in relation to the common mole rat and to the species close to it.

Distribution and geological age. Early Anthropogene, the Azov Sea region in the Ukraine SSR.

INDEX OF LATIN NAMES[1]

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[1] Bold face numbers denote pages on which a description is given; an asterisk refers to pages with diagrams; italics indicates synonyms.

(Contd. from front flap)

Neocenic and Anthropogenic continental deposits in the southern region of the European part of the USSR and adjacent territories. Taking into consideration also the Pontiac origin of the Mediterranean Sea and the present distribution of Spalacidae, it is self-evident that the evolution and geographical distribution of the family in the past, and at present, were dictated by a distinct influence—mainly by the contours (Sarmatian, Miocean, and Pontiac Seas) of these basins during their entire geological history.

The book reviews fossil and present-day mole rats of the family Spalacidae (Rodentia, Mammalia) from all over the world. The general characteristics of the family, the basic adaptive characteristics of its ancestors and the occurrence of basic adaptations in phylogeny and postembryonic ontogeny are given. Data are presented on the distribution of this group in the past and at present. The phylogeny of the family has been worked out. A reconstruction of the taxonomy of mole rats has been made. A separation of subfamilies and certain genera has been done for the first time.