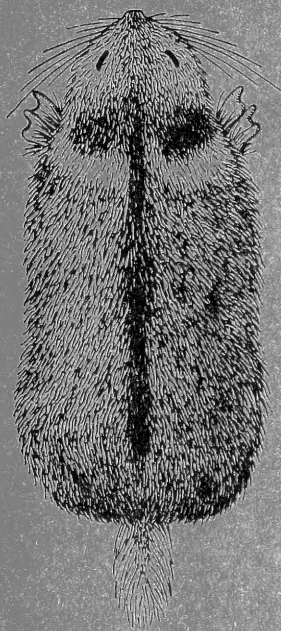

FAUNA OF THE USSR

MAMMALS

Volume III, No. 8



VOLES
(Microtinae)

I.M. GROMOV

I.Ya. POLYAKOV

This monograph is about the sub-family of voles (Microtinae)—a group of rodents which are of great practical importance as pests of agricultural crops as well as carriers and reservoirs of pathogens of several infectious diseases of animals and man. The introductory section describes the body structure and its adaptive characters, the geographic distribution, history of study, and phylogeny of the group. The taxonomic section presents characteristics of more than 130 extant and extinct species, representing 42 genera and 8 tribes. The monograph concludes with a special section (author Prof. I.Ya. Polyakov) containing detailed descriptions of the biology of individual groups of voles, including data on the structure and dynamics of their populations, economic importance, and control measures under various natural conditions.

Voles (Microtinae)



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LETTER FROM THE DIRECTOR OF THE UNIVERSITY OF CHICAGO

TO THE DIRECTOR OF THE UNIVERSITY OF CHICAGO

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JULY 15 1950

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FAUNA OF THE USSR

MAMMALS

Volume III, No. 8

Voles (Microtinae)

I.M. Gromov and I.Ya. Polyakov

Scientific Editors

Douglas Siegel-Causey

Robert S. Hoffmann



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and

The National Science Foundation
Washington, D.C.

1992

TT 81-52180

Fauna SSSR: Mlekopitayushchie, Vol. III, No. 8,
Polevki (Microtinae)

Akademiya Nauk SSSR
Zoologicheskii Institut
New Series, No. 116
Nauka Publishers
Leningrad, 1977

Translated from the Russian
Translators: Dr. B.R. Sharma and Dr. D. Siegel-Causey
General Editor: Dr. V.S. Kothekar
Scientific Editors: Douglas Siegel-Causey
Robert S. Hoffmann

© 1992 Oxonian Press Pvt. Ltd., New Delhi

Library of Congress Cataloging-in-Publication Data

Gromov, I.M.

[Polevki (Microtinae). English]

Voles (Microtinae) / I.M. Gromov and I.Ya. Polyakov; scientific editors
Douglas Siegel-Causey and Robert S. Hoffmann.

p. cm.—(Fauna of the USSR. Mammals; v. 3, no. 8)

Translation of: Polevki (Microtinae)

Bibliography:

Supt. of Docs. no.: SI 1.2:F27/v. 3/no. 8

1. Voles—Soviet Union. 2. Mammals—Soviet Union. I. Poliakov,
I. I. A. (Il'ia Iakovlevich) II. Siegel-Causey, Douglas.
III. Hoffmann, Robert S. IV. Title. V. Series: Mlekopitayushchie.
English; v. 3, no. 8.

QL737.R638G7613 1988

89-600011

599.32'33—dc 19

CIP

Translated for the Smithsonian Institution Libraries, pursuant to an
agreement with the National Science Foundation, Washington, D.C.,
by Amerind Publishing Co. Pvt. Ltd., 66 Janpath,
New Delhi 110 001, India.

Printed at Pauls Press, New Delhi, India

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Academy of Sciences of the USSR

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Foreword to the English Edition

The Smithsonian Institution Libraries, in cooperation with the National Science Foundation, has sponsored the translation into English of this and hundreds of other scientific and scholarly studies since 1960. The program, funded with Special Foreign Currency under the provisions of Public Law 480, represents an investment in the dissemination of knowledge to which the Smithsonian Institution is dedicated.

This volume is part of a series entitled *Fauna of the USSR*. The *Fauna* project, sponsored by the Academy of Sciences of the USSR, is a very extensive effort involving all groups of animals. The series is subdivided into taxonomic categories, and that to which the present volume belongs, *Mammals*, has seen a number of volumes published. Some have already been translated into English by the Smithsonian Libraries Translations Program.

The present volume on voles encompasses the group of rodents in the USSR that contain the largest number of species. Some of the species also occur in North America, or have close relatives there. This is, therefore, a volume of great value to English-speaking mammalogists. The treatment is thorough and up-to-date as of the time of its publication in Russian. It should be noted that since the time of the original publication, papers have been published on certain new developments concerning the scope and relationships of some of the genera treated here.

We have taken great care to ensure that this translation is an accurate reflection of the original text and have kept glosses at a minimum. The format employed by the authors has been retained for the most part, but some liberties were taken for readability, especially in certain diagnostic sections.

July 1989

Douglas Siegel-Causey
Museum of Natural History, University of
Kansas, Lawrence, Kansas

and

Robert S. Hoffmann
Assistant Secretary for Research, Smithsonian
Institution, Washington, D.C.

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Preface

3 For a decade since the publication of the volume of *Fauna of the USSR* on ground squirrels, for which I wrote the taxonomic section and several general sections, I have worked (with a long interruption to discharge scientific and administrative responsibilities) on the next volume of this series dealing with the subfamily of voles (Microtinae).

During this decade in the USSR, as in all Northern Hemisphere countries, mammalogists have intensively studied voles, mainly their biology and paleontology. The major objective of most studies of the first topic was to understand the various aspects of population composition and dynamics in order to develop reliable methods of forecasting population numbers of harmful species and rational methods for their control. Studies on the second topic were primarily of morphological and taxonomic focus; data on systematics and evolution were used for constructing a natural system for the group and through stratigraphic application, for interpreting geological sequences.

During this time, I did not stop the field work that provided new and interesting information on the history of the group and thus had an opportunity to use extensively the paleontological material collected by my colleagues. However, utilization of the vast biological data, especially the so-called applied information, was clearly beyond me. Fortunately, this part of the work was also favorably resolved. Prof. I.Ya. Polyakov, a specialist in rodents, who headed the Laboratory of Forecasting of the All-Union Institute of Plant Protection for many years, kindly agreed to write a special biological section, which is included here as an independent section. This arrangement was also followed for the *Fauna* covering mice and rats (Vol. III, No. 5). At the same time, for completeness of the remaining text, it was considered desirable to retain the brief outline of the biology of voles written by me. In it, I have described the characteristic features of the life styles of voles, which are important for understanding the adaptive significance of their distribution and the major pathways in their evolution.

Extensive development of cytogenetic studies in the last decade has focused the attention of mammalogists of all countries on the study of rodent chromosomes, mainly chromosomal number and their external structure. In our country, this line of work has been successfully developed in particular by N.N. Vorontsov, V.N. Orlov and their students. Voles were the favorite objects of cytogenetic study because the significance of differences is relatively easy to verify through hybridization tests, which provide reliable information for assessing the independent species status of the forms studied.

4 Since the postwar period, M.N. Meier has been intensively engaged in karyosystematic studies and conducting experiments on hybridization in the Laboratory of Mammals of the Zoological Institute, USSR Academy of Sciences, which to date have covered many Russian species of the genus *Microtus*. In preparing the present book, besides other literature, I had an opportunity to use both the published and unpublished data of M.N. Meier. For so-called "disputed" species, the results of these studies have confirmed, on the one hand, Vinogradov's (1933) and Vinogradov and Ivanov's (1945) opinions regarding their independent species status and, on the other, have permitted confirmation of the species status of some "well-known (better)" subspecies (Meier and Orlov, 1969) and "sibling" species (Meier, Orlov and Scholl, 1972a, b). The need to restudy such forms was thus brought to the attention of taxonomists who use "classical" characters in their studies.

Thus, my idea about the number of extant species of microtines, at least in Russian fauna, has a sufficiently reliable basis. The question of the number of extinct species is much more complex.

I have already presented my views (Gromov, 1959, 1972) on the correspondence between the taxonomy of extant and extinct rodents and on other more general questions of phylogenetic studies. Here I will only emphasize the fact that despite a vigorous increase in paleontological data we are still not able, in a large number of cases, to resolve the question: Are we dealing with characters of several extinct species or with chronoclinal morphotypic variability of infraspecific forms? The limited number of characters used by the paleomammalogist (mainly details of tooth structure) determine different scales of results of studies on the extant and extinct members of the group. On the other hand, it is well-known for purely taphonomic reasons that primarily the remains of numerous and flourishing forms become preserved for study. This is a bias that makes it difficult to discover the initial stages of diver-

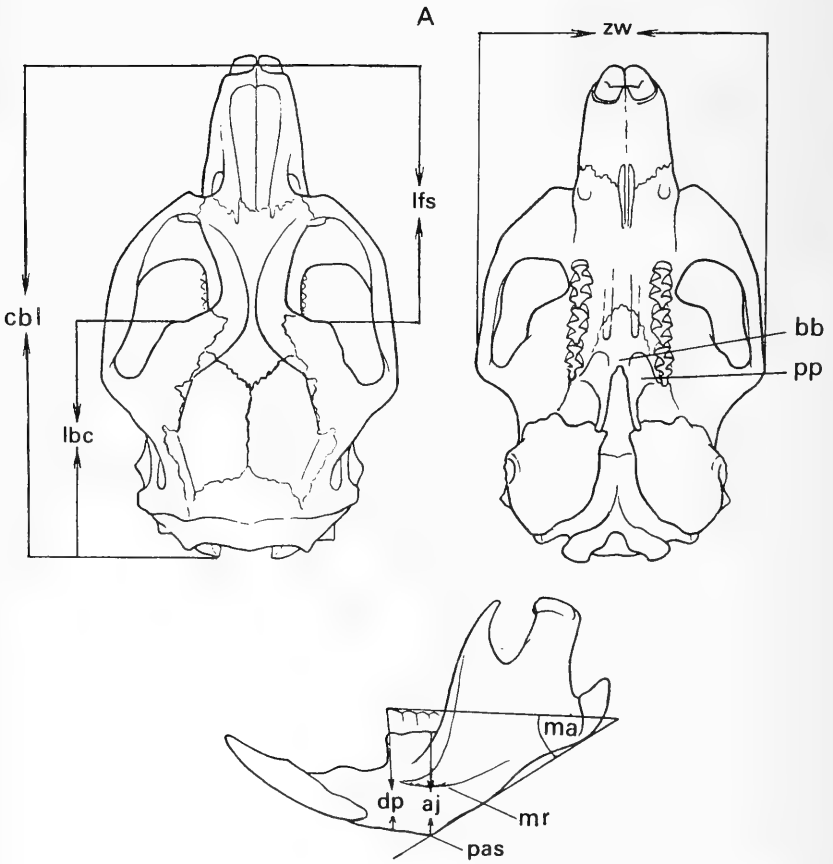
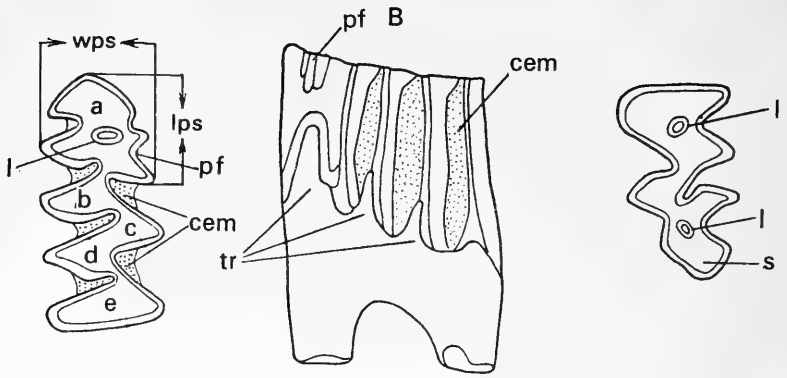
gent evolution, something about which we must judge from indirect evidence.

Unfortunately, several paleomammalogists used trivial characters and seldom explored the limits of chronocline and individual variability, and gleefully described new "species" on the basis of isolated fossil fragments. They forget that once a given name acquires priority in accordance with existing rules, essentially it only pollutes the systematics of a group and makes further study difficult and inefficient. I do not mean here those unfortunate cases still observed wherein the investigator clearly introduces a "nomen nudum".

Unlike most mammalogists who work with living and fossil material, I am not in favor of enlarging the rank of supraspecific taxa and instead consider voles a subfamily of the large family of cricetids (Cricetidae). The subfamily has been examined here at the generic level within the scope of the world fauna; all the species of genera found in the USSR are reviewed here and those not present simply listed. Of the total number of supraspecific taxa—genera and subgenera—I lacked material for three extant and four extinct taxa. Most of the present-day Palearctic species were represented by a series of tens to hundreds of individuals. It should also be borne in mind that the nature of this publication does not permit coverage, with an equal degree of detail, of the data on extant and extinct species; consequently, the latter, especially from other countries, are treated more schematically.

In decisions about taxonomic names, I tried to follow, not so much in letter as in spirit, the well-known Article 23 of the "International Code of Zoological Nomenclature" concerning the rule of priority. Its formal application has already generated a special literature and category of scientists who prefer to study not the objects themselves but how they were named by earlier systematists. According to this rule, the forest voles *Clethrionomys* (until recently, we called them *Evotomys*!) should more correctly be named *Myodes*. However, I see no rationale in such a change. For these reasons, only the most essential synonymies are given in this book.

In addition to the live, dry, and alcohol-preserved collections of the Zoological Institute, I had the wonderful opportunity to use the collections stored in the Zoological Museum of Moscow State University, the Zoological Institute of the Academy of Sciences of Kazakh SSR, the Institute of Biology of the Academy of Sciences of Kirgiz SSR, the paleontological material of the Institute of Zoology of the Academy of Sciences of Ukraine SSR, the Geological In-



stitute of the Academy of Sciences of the USSR, the Institute of Biology of the Siberian Division of the Academy of Sciences of the USSR, the Geological Institute of the Bashkirian Branch of the Academy of Sciences of the USSR, and the Department of Paleogeography of Moscow State University. I thank the heads of these institutes and their laboratories for their kind response and assistance.

In attempting to include the most current material, I probably tried the patience of my colleagues by seeking permission to publish the results of their manuscripts or even unpublished data even "on the day of study." I am deeply grateful to A.K. Agadzhanian (Moscow), L.I. Galkina (Novosibirsk), M.A. Erbaeva (Ulan-Ude), V.S. Zazhigin (Moscow), M.N. Meier (Leningrad), I.G. Malaeva (Sverdlovsk), V.P. Sukhov (Ufa), and V.A. Topachevskii (Kiev). Without the data they provided from their current studies, the present monograph would have been outdated even before its publication. To my great regret, in finalizing the manuscript I could no longer benefit from the advice of my dear mother, Prof. V.I. Gromova, who until her last day was keenly interested in the progress of my work.

Scientists at the Laboratory of Mammals of the Zoological Institute and the Laboratory of Forecasting of the All-Union Institute of Plant Protection (VIZR)—G.I. Baranova, M.N. Naumova, V.A. Fokanov, T.S. Gladkina, and E.N. Golovanova—provided much help to both authors during preparation of the manuscript for press, and S.V. Vasil'ev and G.E. Sergeev helped in the statistical analyses for the section written by I.Ya. Polyakov.

Prof. A.A. Strelkov assumed the task of scientific editing of the entire manuscript and brought it in line with the requirements of

Figure 1. Scheme of cranial and dental measurements of voles.

A—skull: cbl—condylobasal length; lbc—length of braincase; lfs—length of facial section; zw—zygomatic width; bb—bony bridge of hard palate; pp—postpalatine pits; aj—angle of lower jaw at symphyseal junction; dp—height of dental plane of lower jaw at anterior margin of M_1 ; pas—posterior angle of symphysis; mr—masseteric ridge; ma—mandibular angle. B—dentition: lps—length of paraconid section of M_1 ; wps—width of paraconid section of M_1 ; I—"island"; pf—prismatic fold; cem—outer cement; a—paraconid; b—metaconid; c—protoconid; d—entoconid; e—hypoconid; tr—dentine tracts; s—sole of M^3 .

the series publication, a tradition he has maintained for many years and successfully developed.

All illustrations, including those borrowed from my other publications as well as tracings, were prepared by artist S.L. Shmuilovich with great professional skill and enviable tact in simultaneously meeting author and printing requirements.

I express my gratitude to each and all those persons mentioned above.

The method of measurement for those parts, where it requires explanation, as well as the corresponding abbreviations, can be seen in Figure 1. As in my other publications, numbers are used in the text to indicate indices and, unless otherwise mentioned, refer to the alveolar length of the dental row; mean values (*M*) are given in italics and the number of specimens (*n*) is 10, unless mentioned otherwise. In the taxonomic account, organization of the individual sections differs slightly for extant and extinct species. Unable to provide a fresh differential diagnosis for each taxon investigated, I have, wherever possible, identified the major diagnostic characteristics. However, a complete examination of the latter for all taxonomic members of a single rank could not be followed consistently. All other structural details are included in the section "Description". The sequence in which the taxa are listed corresponds to my ideas on evolution and, as a rule, I begin with the more ancient forms.

- 7 The same open [geochronological] terminology is used as in the monograph on ground squirrels (Gromov *et al.*, 1965). Unlike the latter terminology, here I support not three, but four principal divisions of the Pleistocene into Ancient, Early, Middle, and Late period. I include under the first fauna, the so-called Villafrancan deposits (the Khaprovsk faunal complex) and their analogues, and I consider the Late Pliocene Moldavian faunal complex, the so-called "Moldavia Russillen," as Late Pliocene.

With rare exceptions, I have not introduced Russian common names for the taxa. Identification keys were prepared only for present-day members of Russian fauna and are most reliable for adult forms.

I.M. Gromov

List of Species

Subfamily MICROTINAE Cope

- †I. Tribe MICROTOSCOPTINI Kretzoi, 1955, stat. nov.
1. Genus *Microtoscopes* Schaub
 1. *M. praetermissus* Schaub 160
 2. *M. tjuvanensis* Zazhigin sp. nov. 161
 2. Genus *Goniodontomys* Wilson
- II. Tribe PROMETHEOMYINI Kretzoi, 1955, stat. nov.
- †1. Genus *Stachomys* Kowalski
 2. Genus *Prometheomys* Satunin
 1. *P. schaposchnikovi* Satunin 167
- III. Tribe ONDATRINI Kretzoi, 1955
- †1. Genus *Pliopotamys* Hibbard
 - †2. Genus *Dolomys* Nehring
 1. *D. nehringii* Kretzoi 173
 2. *D. milleri* Nehring 174
 3. Genus *Ondatra* Link

† Extinct taxa.

IV. Tribe CLETHRIONOMYINI Hooper and Hart,
1962 (= MYODINI Kretzoi, 1955)

Subtribe PLIOMYI Kretzoi, 1959, stat. nov.

†1. Genus *Pliomys* Mehely

1. <i>P. kowalskii</i> Schevtschenko	183
2. <i>P. ucrainicus</i> Topačevski and Scorik	184
3. <i>P. hungaricus</i> Kormos	185
4. <i>P. episcopalis</i> Mehely	186
5. <i>P. lenkii</i> Heller	187

2. Genus *Dinaromys* Kretzoi

†1. <i>D. dalmatinus</i> Kormos	190
†2. <i>D. posterior</i> Janossy	192
3. <i>D. bogdanovi</i> V. and E. Martino	192

†3. Genus *Pliolemmus* Hibbard

Subtribe ALTICOLI I. Gromov, nov.

4. Genus *Alticola* Blanford

Subgenus *Alticola* Blanford

1. <i>A. (A.) roylei</i> Gray	198
2. <i>A. (A.) argentatus</i> Severtzov	198
3. <i>A. (A.) stolizkanus</i> Blanford	199

9

Subgenus *Platycranius* Kastschenko

4. <i>A. (P.) strelzovi</i> Kastschenko	202
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Subgenus *Aschizomys* Miller

5. <i>A. (conf. Asch.) smithii</i> Thomas	204
6. <i>A. (Asch.) macrotis</i> Radde	205

5. Genus *Hyperacrius* Miller

6. Genus *Anteliomys* Miller

Subtribe CLETHRIONOMYI I. Gromov, nov.

7. Genus *Clethrionomys* Tilesius

†1. aff. <i>C. kretzoi</i> Kowalski	215
†2. <i>C. acrorhiza</i> Kormos	216
†3. <i>C. sokolovi</i> Topačevski	217
†4. <i>C. hintonianus</i> Kretzoi	218
†5. <i>C. esperi</i> Heller	219
6. <i>C. rufocanus</i> Sundevall	219
7. <i>C. andersoni</i> Thomas	222
8. <i>C. sikotanensis</i> Tokuda	223
9. <i>C. glareolus</i> Schreber	224
10. <i>C. frater</i> Thomas	230
11. <i>C. rutilus</i> Pallas	232
12. <i>C. gapperi</i> Vigors	236
13. <i>C. occidentalis</i> Merriam	236

8. Genus *Eothenomys* Miller

V. Tribe LAGURINI Kretzoi, 1955

†1. Genus *Jordanomys* Haas†2. Genus *Prolagurus* KormosSubgenus *Lagurodon* Kretzoi

1. <i>P. (L.) arankae</i> Kretzoi	245
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Subgenus *Prolagurus* Kormos

2. <i>P. (P.) praepannonicus</i> Topačevski	247
3. <i>P. (P.) pannonicus</i> Kormos	248
4. <i>P. (P.) posterius</i> Zazhigin	248

3. Genus *Lagurus* Gloger

†1. <i>L. transiens</i> Janossy	249
---------------------------------	-----

	2. <i>L. lagurus</i> Pallas	250
	4. Genus <i>Eolagurus</i> Eversmann	
	†1. <i>E. argyropuloi</i> I. Gromov and Parfenova	253
	†2. <i>E. simplicidents*</i> Young	254
	3. <i>E. luteus</i> Eversmann	255
	4. <i>E. przewalskii</i> Büchner	258
	5. Genus <i>Lemmiscus</i> Merriam	
VI.	Tribe DICROSTONYXINI Kretzoi, 1955	
	†1. Genus <i>Praedicrostonyx</i> Guthrie and Matthews	
	1. <i>P. hopkinsi</i> Guthrie and Matthews	267
	2. conf. <i>P. compitalis</i> Zazhigin	268
	2. Genus <i>Dicrostonyx</i> Gloger	
	†1. <i>D. renidens</i> Zazhigin	269
	†2. <i>D. simplicior</i> Fejfar	269
	†3. <i>D. guilielmi</i> Sanford	272
	4. <i>D. hudsonicus</i> Pallas	273
	5. <i>D. torquatus</i> Pallas	273
10 VII.	Tribe LEMMINI Gray, 1825, stat. nov.	
	1. Genus <i>Lemmus</i> Link	
	1. <i>L. lemmus</i> L.	283
	2. <i>L. sibiricus</i> Kerr	284
	3. <i>L. amurensis</i> Vinogradov	287
	2. Genus <i>Myopus</i> G. Miller	
	1. <i>M. schisticolor</i> Lilljeborg	289
	3. Genus <i>Synaptomys</i> Baird	

*Consistently spelled thusly throughout Russian text—Editors.

†Subgenus *Metaxyomys* Zaczewski

Subgenus *Pliotomys* Suchov

1. *S. (P.) mimomiformis* Suchov 294

Subgenus *Synaptomys* Baird

Subgenus *Mictomys* True

VIII. Tribe MICROTINI Miller, 1896

†1. Genus *Ischymomys* Zazhigin gen. nov.

1. *I. quadriradicatus* Zazhigin sp. nov. 306

†2. Genus *Aratomys* Zazhigin gen. nov.

1. *A. multifidus* Zazhigin sp. nov. 308

†3. Genus *Ogmodontomys* Hibbard

†4. Genus *Cosomys* Wilson

†5. Genus *Villanyia* Kretzoi

1. *V. praeungarica* Schevtschenko 315

2. *V. fejevaryi* Kormos 316

3. *V. hungarica* Kormos 318

4. *V. eleonora* Erbajeva 318

5. *V. laguriformes* Erbajeva 319

6. *V. exilis* Kretzoi 320

7. *V. steklovi* Zazhigin 321

†6. Genus *Ophiomys* Hibbard and Zaczewski

†7. Genus *Promimomys* Kretzoi

1. *P. stehlini* Kormos 325

2. *P. moldavicus* Kormos 326

3. *P. baschkirica* Suchov 328

†8. Genus *Mimomys* F. Major

Subgenus *Mimomys* F. Major

	1. <i>M. (M.) pliocaenicus</i> F. Major	331
	2. <i>M. (M.) minor</i> Fejfar	332
	Subgenus <i>Kislangia</i> Kretzoi	
	3. <i>M. (K.) rex</i> Kormos	334
	Subgenus <i>Microtomys</i> Mehely	
	4. <i>M. (? Micr.) conf. coelodus</i> Kretzoi	335
	5. <i>M. (Micr.) newtoni</i> F. Major	336
	6. <i>M. (? Micr.) pseudintermedius</i> Erbajeva	338
	7. <i>M. (Micr.) intermedius</i> Newton	339
	8. <i>M. (? Micr.) cantianus</i> Hinton	341
	9. Genus <i>Arvicola</i> Lacépède	
	† 1. conf. <i>A. mosbachensis</i> Schmidtgen	346
	† 2. conf. <i>A. greenii</i> Hinton	346
11	† 3. <i>A. chosaricus</i> Alexandrova	347
	† 4. <i>A. abboti</i> Hinton	347
	† 5. <i>A. gracilis</i> Heller	348
	6. <i>A. sapidus</i> Miller	348
	7. <i>A. terrestris</i> L.	349
	10. Genus <i>Proedromys</i> Thomas	
	† 11. Genus <i>Allophaiomys</i> Kormos	
	1. <i>A. pliocaenicus</i> Kormos	354
	2. ? <i>A. terrae-rubrae</i> Teilhard	357
	12. Genus <i>Microtus</i> Schrank	
	† 1. <i>M. (subgen. ?) deceitus</i> Guthrie and Matthews	362
	Subgenus <i>Neodon</i> Hodgson	
	2. <i>M. (N.) leucurus</i> Blyth	364
	3. <i>M. (N.) juldaschi</i> Severtzov	367

4. <i>M. (N.) irene</i> Thomas	369
5. <i>M. (conf. N.) millicens</i> Thomas	370
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Introduction

BRIEF BIOLOGICAL ACCOUNT

13 The subfamily Microtinae includes rodents, most of which are well-adapted to burrowing, only rarely to a semifossorial (*Prometheomys*) or to a semiaquatic mode of life in water bodies that freeze during winter (*Arvicola*, *Ondatra*, *Neofiber*). The life styles of forest voles (*Clethrionomys* and *Phenacomys*) are closest to that of the ancestral forms, and they have retained the capacity to climb (found feeding and even nesting in trees up to a height of 12 m), to reside in burrows for mobility under forest soil, and to burrow in layers of moss and forest litter. Montane voles that live among crevices in rocks and stony scree (*Alticola*, *Chionomys*, *Dinaromys*) and lemmings (*Lemmus*, *Dicrostonyx*) represent unique and, in many ways, primitive "living forms," which have adapted to life in the moss and turf layer of tundra at low air and soil temperatures, with unique light and burrowing conditions.

Voies inhabit open environments of mountains and plains, primarily in the temperate belt up to an elevation of 4,500–5,000 m and prefer to live in very moist habitats, including semimarshy, grass and shrub-covered biotopes. From these they have penetrated into desert and semidesert zones. Only some species (*Lagurus*, *Eolagurus*, *Blanfordimys*) have adapted to life in open environments of the hot belt of Eurasia.

Voies are active throughout the year and only a few species sharply reduce their activity during winter. They are mainly active at dawn and at night, although many montane forms and plain inhabitants are also active during the day during the season of storing food and in winter. One species—Brandt's vole (*Lasiopodomys brandti*)—is diurnal and lives in colonies and displays behavioral patterns (vocalization, sitting rigidly in an erect posture) typical of ground squirrels. As in the case of other mouse-like rodents, voies are characterized by complex hierarchical "intrafamily" relationships—behavioral patterns governing the establishment of individual territories and composition of the "micropopulation".

The burrows of Microtinae are generally shallow underground

shelters, with a network of surface runways connecting the openings to underground tunnels, which are often very complex but usually restricted to the thickness of the soil layer. Only when the soil is thin or totally absent are the burrows located in subsoil. Most of the runways are food-collection paths that allow the animals to gather stores of vegetative material from a large area. The dwellings of individual families may merge to form "colonies" that grow peripherally during periods of population explosion in many species and during crowded conditions; such colonies sometimes spread over hundreds of hectares.

- 14 All voles readily change over to life in the turf layer, where they cut runways similar to tunnels in the soil. During winter, in regions with sufficiently deep and stable snow cover, they live simply on the soil surface amidst dried vegetation where microclimatic conditions are more favorable. In the case of lemmings, some of the burrows are built directly in the lower part of the snow. The ability of voles to dig burrows in grassy turf and also to mine through moss cover and forest litter enables them to move easily in haystacks and hayracks and may lead to their possible use during winter. Some species that live in humid, marshy biotopes may switch fairly readily to a semiaquatic mode of life. In these forms, the nest-building instinct is highly complex: instead of the usual small spherical grass nests typical of voles, they build underground nests during the warm period of the year and on-ground or above-ground nests during the cold period (e.g. "hanging" nests of the marsh species, especially in tundra and forest-tundra habitats). The water vole and *Ondatra* spp. build spacious nests which, in the case of the latter group are in the form of a small "hut," a comparatively complex structure built on the bank or as a "floating" construction among broken reeds, floating mats, etc. In the construction of these nests, not only herbaceous plants but also twigs are used. Nests of twigs are also built on shrubs and trees by water voles, which live in them during the period of prolonged floods, as do the American forest voles *Phenacomys* spp. A unique method of building shelters is exhibited by the high-montane vole *Alticola strelzovi*, which protect their area of a talus from constant winds by plugging the slits with a unique cement prepared from their urine, feces, soil and small pebbles. This attests to its ancient association with biotopes having taluses and eroded rocky areas.

The results of the digging activity of voles are less noticeable than those of larger burrow dwellers (i.e., shallow burrowers) such as ground squirrels; however, in view of their high population den-

sity, the total effect is quite significant. This is obvious in a large form such as the water vole, especially during the winter period. Mixing of soil and subsoil layers in the process of transportation of material from deeper layers to the surface, gnawing of turf, breaking of twigs into small pieces, as well as transfer of nitrogen-rich material into the soil—all of these can have a significant influence on soil formation. The ultimate result of this influence varies under different natural conditions and may be favorable or unfavorable causing, in particular, salinization of desert soil.

All species of voles are phytophagous. Animal food, unlike for members of the related subfamily of hamsters, does not form a permanent or even a significant part of their diet. The only exception is the water vole. During the vegetative period, the above-ground parts of the plant are a major source of food for all species; at the end of the vegetative period, the underground parts of the plant—rhizomes, tubers and bulbs—become important for several species. Forest species of voles and some montane species (*Alticola*, *Chionomys*) and lemmings (*Lemmus*, *Dicrostonyx*) feed always on seeds, including those of conifers, as well as berries, twigs and shrub bark.

Some specialization is also observed among plant feeders. Thus, steppe lemmings (*Lagurus* spp.) primarily eat narrow-leaved grasses and most common voles (*Microtus* spp.) eat broad-leaved grasses and herbs. During winter all species readily adapt to feeding on bark of trees and shrubs, often eating the bark up to the level of the snow cover. The quantity of food consumed depends upon its caloric value. As much as 100 g of green vegetation is consumed
 15 by small species and 200 g by large species. Most species eat food on the surface, often in sheltered places. Places where the animal feeds regularly can be easily identified by the accumulated food waste and excreta; for voles, these are called “eating tables”. Such tables are often formed at the entry of open food runways where the rodents drag partly eaten plants or their parts. Such habits have led to the evolution of the instinct for storage. Actually, it is expressed in most vole species to a varying degrees.

In some species, all degrees of food storage are observed, from small, temporary stocks of roots, tubers and above-ground plant parts to large winter reserves, the preparation of which is associated with complex activity, e.g., drying, piling of hay, or plugging cracks and crevices in rocks etc. “Stores” of roots and tubers are found underground as well as on the surface, filling the runways cut through the turf of large hummocks (montane species of *Pitymys*).

Under favorable food and climatic conditions, voles are capable of reproduction throughout the year. In the sub-Arctic region, reproduction takes place even when the animals are living under the snow. The litter size varies for different species, depending on annual weather conditions, from one (subspecies of *Alticola*) to six or even seven (*Microtus arvalis*), and the young animals of the first, and sometimes second litters, reproduce in the year of their birth. Sexual maturity in most species occurs at the age of 1.5 months; the number of neonates in a litter averages five but may reach eight to ten.

The population of most species, particularly of plain dwellers, fluctuates sharply and may reach maximum density for mammals in general, increasing 100–200-fold the usual and then fall to 1/1,000 or even less. Mass reproduction resumes after one to two years, when warm as well as cold periods of the year are favorable for young animals to breed (abandoned food, warm winters, low floods, etc.). In forest, montane and subterranean species, population size is more constant and rarely increases compared to species living in open environments. With an increase in population, young voles colonize diverse biotopes, even including atypical ones. In some species, mass reproduction is accompanied by migrations—the rapid spread of many young animals beyond the borders of their usual habitats over tens or even hundreds of kilometers. During periods of population decline, voles survive in a few places that are particularly favorable relative to protection and food conditions, the so-called “survival habitat”.

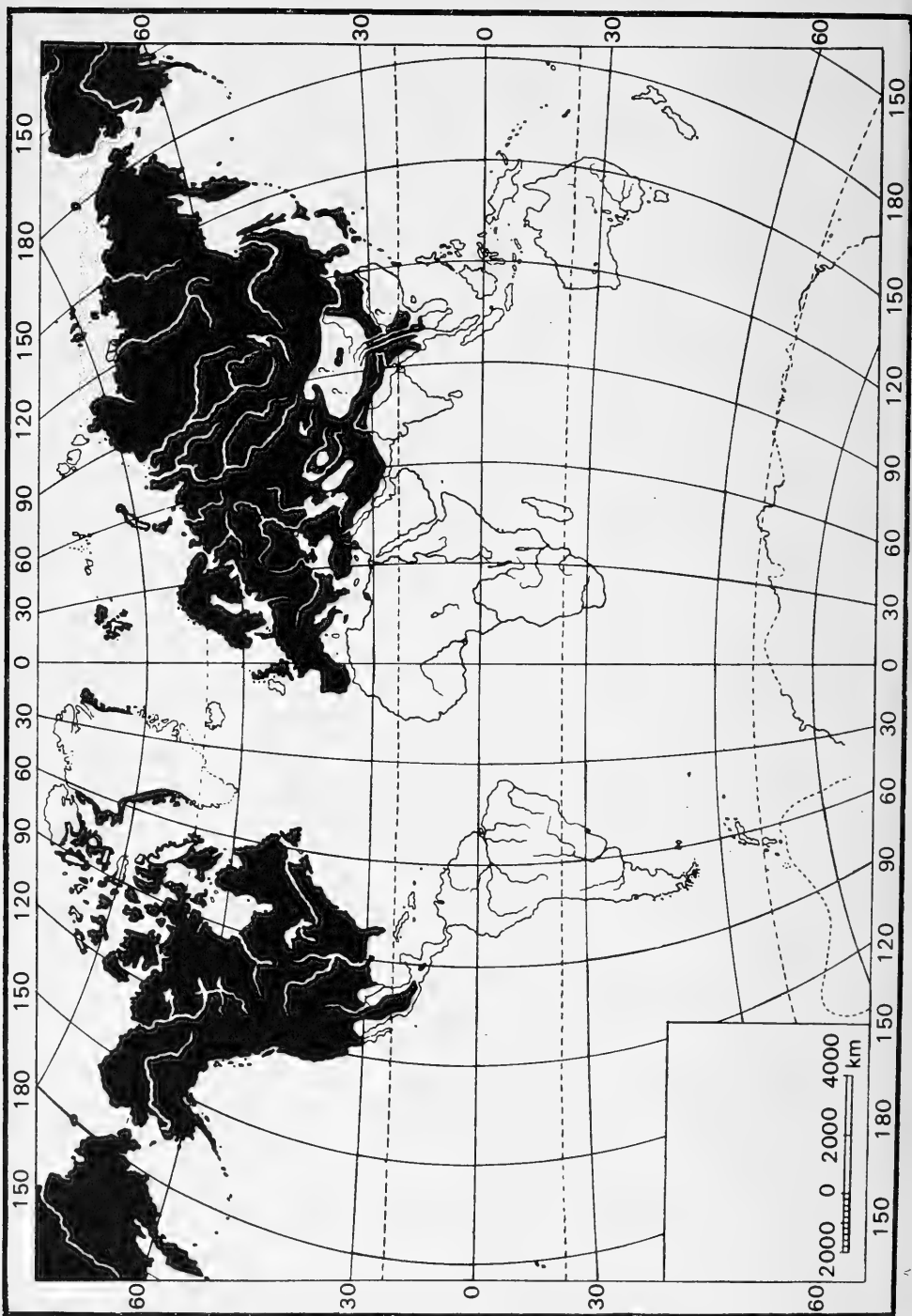
All voles are subject to high mortality from feathered and quadrupedal predators, for many of whom (owls and foxes) they serve as a major food item in all seasons of the year. Voles are an important food base for economically valuable species of predatory mammals, in particular martens of the forest zone. Microtines are hosts for numerous forest parasites and are also carriers of dangerous infectious diseases of man and domestic animals, such as encephalitis (forest voles), tularemia (water voles), leptospirosis (some common voles), infectious nephrosonephritis, etc. Voles constitute a substantial portion of the so-called mouse-like rodents that destroy a high percentage of grain crops, especially during years of population explosion; they damage pastures by eating favored fodder plants. A special survey, census and prognosis of animal populations under the Institute of Plant Protection, Lenin All-Union Academy of Agricultural Sciences, has been formed to forewarn of imminent spurts of large-scale reproduction and to develop biological control measures for

16 pests, including voles. More sophisticated agronomic practices and regular prophylactic measures greatly reduce the damage caused by them. Control measures include mechanical (trapping), chemical (poisonous baits) and bacteriological methods, manual as well as mechanical, including airplanes. In spite of several years' experience with such controls, the expenditure incurred in agricultural zones of all Northern Hemisphere countries is still very high.

Together with wild ungulates, voles until recently served as an important factor in regulating wild vegetation in the steppe zone, contributing to the organic cycle of the soil, aeration of its upper layer, thinning of the turf and so forth. Only a few large-sized species provide fur of low value. However, *Ondatra*, which has been successfully acclimatized even in the USSR, occupies an important position in the fur industry, similar to its role in its homeland, North America. In recent years, on the basis of the value of fur produced, this vole has come to occupy one of the top positions among other fur-bearing animals of Russian fauna.

GEOGRAPHIC DISTRIBUTION AND BRIEF HISTORY

The present range of the subfamily does not extend beyond the limits of the Holarctic (Figure 2); even fossil remains of Microtinae have not been found to date beyond these limits. In the Nearctic, an isolated, extremely southeastern location (about 92° E) is known for the only species of the subgenus *Herpetomys*, which lies in western Guatemala at 4–5° E of the area of continuous microtine distribution, which in eastern Mexico consists of the Mexican vole (subgenus *Microtus* s. str.). In the Palearctic, the southern boundary is determined by the distribution of the genera *Chionomys* and *Microtus* (subgenus *Microtus* s. str., *Pitymys*) in the west, by the subgenus *Neodon* and the genera *Alticola* and *Hyperacrius* in its central part, and predominantly *Microtus* s. str. and some *Alticola* and *Clethrionomys* in the east. The southern boundary passes along the montane region of the Mediterranean, including some of its islands, northwest Asia and Asia Minor, northern parts of India, Indo-China, southwestern China, the Japanese islands and the Kurile and Aleutian islands. It must be mentioned that ancient microtine forms, as well as some other rodents and lagomorphs, have long survived on the islands of the Mediterranean but that insular forms of the Atlantic and Pacific coasts of North America, as well as several islands of the Polar and Far East seas, are Recent forms, whose differences from their continental ancestors do not



exceed the limits of subspecies. In all these cases, it may be concluded that their age is younger than the age of the last marine transgression.

There are few elements of similarity between the modern microtine fauna of the two parts of the Holarctic. The circumpolar genus *Dicrostonyx* represents a probable descendant of the sub-Arctic Beringian fauna, the elements of which were recently discovered in the Ancient Pleistocene faunas of Chukotka and Alaska (Guthrie and Matthews, 1971; Sher, 1971). According to karyotypic results, it has successfully differentiated into several closely related but distinct species (Kozlovskii, 1974). Their independent status should be verified by hybrid analysis. It is quite possible that at least two genera of the tribe Lemmini (*Lemmus* and *Synaptomys*) already existed within this Beringian fauna. Remains of *Synaptomys* were recently found in the Ancient Pleistocene (Mimomysian) faunas of northern Mongolia (Zazhigin, 1974), and stem forms that are similar in level of specialization were found in faunas of similar age from the Ufim-Ural region (Sukhov, 1977). The components of similarity among members of *Clethrionomys* and *Microtus* should be considered at several "levels of antiquity". The more ancient forest voles of the New World have differentiated up to the species level (*C. gapperi*). They can probably be considered an independent

18 line of development of ancient pliomysines, whereas *C. rutilus* is the result of one of the last invasions of Siberian fauna into North America. The history of distribution and evolution of the genus *Microtus* is far more complex. Besides forms which entered the New World late (for example, *M. oeconomus*), *Microtus* undoubtedly had an ancient faunal nucleus in the north (insular species *M. abbreviatus* as the probable "splinter" of the same Beringian fauna) as well as in the south, right up to the central part of the continent. The stem group of *Microtus* gave rise to several ecological vicariates having similar morphological specialization at the species as well as at higher taxonomic levels. Their fossil history has only recently been documented or is completely absent. Aside from the Beringian species, an Atlantic phylogenetic relationship has not been excluded for some species.

The vole fauna of Sakhalin Island and islands of the Japanese

archipelago is of special interest, since the ancient Asian nucleus and later "accumulations" can be identified, indicating the chronological variation in links with the continent and between various islands.

The richest microtine fauna is seen in areas of maximum variability of biotopes of open environments, which coincide with the upland territories of the central parts of the Holarctic. Zonal species are distributed in all environmental zones and their corresponding vertical belts. In the tropics, voles inhabit either montane regions or the intrazonal biotope of the lowlands, for example, *Neofiber* in the tropical marshes of Florida.

The zonal microtines of tundra habitats are lemmings of the genera *Dicrostonyx* and *Lemmus* as well as the narrow-skulled vole *Microtus (Stenocranius)*. *M. oeconomus* and the water vole *Arvicola terrestris* penetrate the tundra along interzonal biotopes of river valleys, as does the Siberian red-backed vole *Clethrionomys rutilus* in areas of shrubby growth. In hilly tundras of northeastern Siberia, lemming-like voles of the genus *Alticola* (subgenus *Aschizomys*) are found, and the unique species *Microtus miurus* is found in Alaska.

The later formation of ecosystems in montane regions and low-lying tundras is well-known. However, individual faunal-floral groupings were formed even in the Pleistocene and present-day zonal vole species of tundra have been found in the mammalian faunas of open environments of the pre-Riss period in submontane regions of central Western Europe, and from the Würm period all along the central belt of Eastern Europe and western Siberia in the region of modern forest-steppe and the southern part of the forest zone. It is quite possible that at the end of the Pleistocene, lemmings, being primarily montane forms, were interzonal species of so-called "mixed faunas" in which steppe voles were predominant. The "lemming faunas," with a predominance of tundra lemmings and rare species of *Microtus*, were formed at the boundary of the source of cooling as it retreated northward. In this context, it is assumed that unique ecological niches were provided at this time by the coastal shelves of eastern and western North America, which became dry land with regression of the sea, thus connecting islands and the mainland that were later separated (Cameron, 1962; Youngman, 1967).

Microtinae of the forest zone include forest voles of the genera *Clethrionomys* and *Eothenomys*, the forest lemming *Myopus*, as well as the contemporary endemics of the Nearctic, *Phenacomys*

and *Synaptomys*. The subzones of broad-leaved forest in the mountains and plains of Europe and western North America are characterized by the shrub voles *Pitymys* and *Pedomys*, which are replaced in the forests of Asian mountain ranges by some species of *Phaiomys*. Open habitats of the forest zone, depending on degree of their swampiness, are populated by common voles (*Microtus*) or water voles (*Arvicola*) in the Old World and by *Ondatra* in the New World. In mountains, intrazonal meadow-forest sections and taluses are inhabited as follows: first, by species of *Stenocranius*, *Phaiomys*, and *Pedomys*, and second, by *Alticola*, *Chionomys*, and *Dinaromys*. Unlike the tundra zone, the forest zone—an ancient landscape formation—witnessed the initial stages of evolution of Microtinae, which were evidently associated with the natural conditions of this biotope. The Late Pliocene forests of the Holarctic were inhabited by vole-toothed [*sic*] hamsters; the more numerous species of voles of the Dolomian-Pliomian and ancient Mimomian forms should be considered forest forms, an ecological occurrence that is more reliably judged from the composition of associated species. During the Pleistocene, forest species always existed in the fauna of the middle and partly southern latitudes, becoming more dominant during cooling periods, which, it is thought, attests to the presence of mixed woodland-grasslands during this period. Such a combination of forms (mostly of forest voles of *Clethrionomys*) is particularly significant and constant in the Western European Pleistocene and in Western Siberia.

From the end of the Pleistocene and throughout the Holocene (i.e., during the last ten millenia) forest voles rapidly colonized the present-day range and secured their position in the forest cenosis. The Holocene warming and northern advancement of forests left imprints on the vole fauna as well, for example, as isolated pockets of bush voles (*Pitymys*) in European taiga, far north of broad-leaved forest.

Forest-steppe, like forest-tundra, is devoid of typical species and the vole fauna here is mixed. Open steppe-type niches are inhabited by xerophilic species of common voles (*Microtus* s. str.) and the steppe lemming (*Lagurus*), and meadow habitats by mesophilic species of *Microtus* and by water voles (*Arvicola*), which are particularly dense here. The bush voles (*Pitymys*) and forest voles (*Clethrionomys*) live in insular forests. "Extinct environments," such as the Pliocene "savanna" and the cold Pleistocene forest-steppe, which spread over vast areas in central parts of Eurasia and North America, were forest-steppe-like in the past. These should

be considered unique environmental zones with typical fauna. The Pliocene "savanna" underwent a long evolution from a subtropical nature with summer-deciduous arboreal vegetation through a vegetational form of the Mediterranean type to the cold forest-steppe—the forest-tundra of Pleistocene cooling. The special features and evolutionary paths of its vole fauna are not entirely clear. It is quite likely however, that under these conditions, microtines with rootless teeth in several stages appeared; this process was delayed in zonal species of the forest up to the present time.

The biotopic affinity of individual species of the Pliocene Dolomian-Promomian [*sic*] and Mimomian faunas can be reconstructed with some degree of certainty only for subgenera as a whole. Such an averaged ecological index does not exclude the possibility that individual species could be distinguished by their ecological characteristics. However, this distinction could hardly be more pronounced than in members of modern subgenera. Judging from the composition of the accompanying fauna and bearing in mind the conditions of fossilization of rodents in contemporary alluvial deposits, it can be thought that voles of the genus *Villanyia* inhabited open biotopes of Pliocene "savanna" and those of the genus *Promimomys* occurred in forest or forest-meadow biotopes. In Late Pliocene faunas, innumerable species of *Mimomys* s. str. inhabited
 20 floodplain forests and meadows. As for the genera *Dolomys* and *Pliomys*, many of their species may have belonged to forest habitats, in particular the montane-forest forms. The Late Pliocene *Allophaiomys* is probably an ecological analogue of the water vole or, at best, the American *Neofiber*; whereas, ancient lagurids are undoubtedly inhabitants of open biotopes. It can be assumed that certain voles of the New World, whose teeth exhibit primitive levels of specialization, as mentioned above, also occupied similar habitats.

In the Pleistocene forest-steppe fauna, beginning in the Middle Pleistocene members of certain genera disappeared and the surviving *Stenocranius*, *Lagurus*, *Eolagurus* and *Clethrionomys* initially exhibited differences from modern genera at the species and then subspecies level. We have already noted the greater role of forest species in the western and eastern Palearctic.

In broadly latitudinal, mountainous regions of Eurasia, the forest belt changes from dense stands at places of sufficient Atlantic humidity in the west to a complete absence in interior regions where open environments of submountainous regions continuously merge with mountain steppes and meadows of the alpine belt. Under intermediate conditions, mountain forest-steppes and

plain forest-steppes can develop and are characterized by a mixed fauna. Only montane meadows above the upper forest boundary are inhabited by endemic species, for example, *Prometheomys*, the long-clawed mole vole from the Caucasus, the semifossorial vole *Hyperacrius* from Central Asia, and *Orthriomys* from North America. Pliocene paleontological data for microtine faunas of high mountains are not available. During the period of Pleistocene cooling, the remains of high-montane voles, together with other rodent species, were found in the so-called "lower Alps" faunal association in middle and low mountain belts: *Chionomys* in Western Europe, *Phaiomys* in Central Asia and *Alticola* in Trans-Baikal.

The steppe zone of the plains, including the grassy region (prairie) of the Great Plains of North America and mountain steppes, are inhabited primarily by species of the subgenus *Microtus* s. str., including drought and heat-tolerant forms as well as moisture-loving species which occupy humid locations near river floodplains and along lake banks. Specific types of steppe voles are the steppe lemmings (*Lagurus*) and, in Central Asia, members of *Lasiopodomys*. In spite of such low endemism, and that too only in the eastern part of the steppe zone, there is no doubt that evolution of Microtinae with rootless teeth occurred in association with the formation of open grasslands and mixed grass-herbaceous associations. Such forms originated within Pliocene savanna-like environments that formerly covered the area of present-day steppe and forest-steppes. It is noteworthy that many modern steppe forms were adapted to significant climatic fluctuations and could achieve very high population densities in a short period. The Pleistocene history of steppe microtines is associated with differentiation of the above-mentioned "mixed faunas," as well as with reduction in area occupied by steppes west of the Ural range and south-central North America. The range modifications of several Palearctic species, caused by these habitat contractions, are quite evident, as exemplified by the range of *Lagurus*, which extends up to France and includes Hios Island.

Holarctic deserts contain few voles and some types of voles are totally absent. Desert species have nevertheless remained in steppe-covered semideserts and in humid biotopes along river and lake banks. The former include the yellow steppe lemming *Eolagurus*, voles of the genus *Lasiopodomys*, and some species of *Alticola* (subgenus *Platycranius*). Some forms of *Stenocranius* and *Microtus* from the *oconomus* and *socialis* groups are also found in humid biotopes. The high-mountain, stony-pebbled deserts of the subnival

zone of Central Asia are inhabited by *Phaiomys* and *Alticola*. At present, there is no paleontological record of the evolution of desert voles. In Palearctic deserts, voles that are mesophilic in nature probably are recent faunal elements, confirming the southerly shifting of desert zones during periods of Atlantic moistening and suggesting the earlier distribution of some steppe forms in desert areas.

The above data support the nonsimultaneous (heterochronic) environmental changes of the Palearctic during the Pleistocene. Such biomes were more stable in the south and east but underwent substantial modification in the north and west, a difference which influenced not only the rate of change in the composition of the vole fauna but also the rate of evolution of individual species. As a result of this process, a decisive role was played by restructuring of the mixed Plio-Pleistocene faunas that contained the ancestral elements of three modern open biotopes of temperate and hot zones. Of these, the tundra belt was already completely separated from the two other forest zones around the end of the Pleistocene. The origin of the vole fauna of the tundra zone is not yet fully understood due to the absence of critical paleontological information.

EXTERNAL MORPHOLOGY AND SKELETON

External appearance: Depending on the degree of adaptation to a semifossorial life style, the ancestral "rat-like" appearance of voles underwent changes resulting in reduction of tail, limbs, and pinnae; a poorer differentiation of pelage and plantar pads; and increase in claw size on the forefeet. The neck region became poorly differentiated and less noticeable in living voles, as did the distal parts of the limbs. The body proportions of the ancestral type have been retained in semiaquatic and climbing forms (including rock-dwelling species), although structure of the pelage, paws and tail has acquired definite specializations. The largest number of ancestral skeletal characters has been retained, on the one hand, by voles of the forest zone (*Clethrionomys*, *Phaenacomys*, *Ondatra*) and on the other, by the more specialized subterranean forms (*Prometheomys*).

Size: Ranges from very small to medium, which is typical for rodents. The largest voles are adapted to a semiaquatic life style, evidenced in several genera (*Arvicola*, *Neofiber*, *Ondatra*) and in different species of the same genus (*Microtus oeconomus*, *M. fortis*). The smallest forms inhabit forests and open environments of the warmer zone. The size of a species may increase northwardly

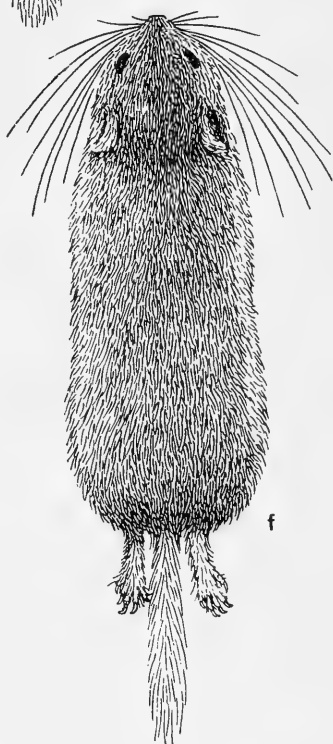
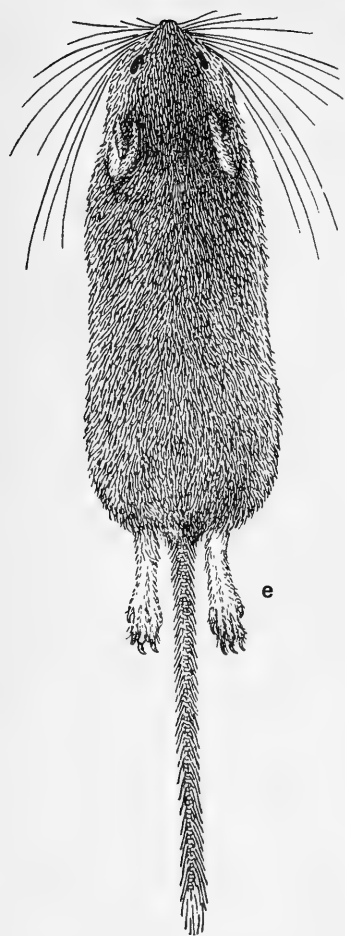
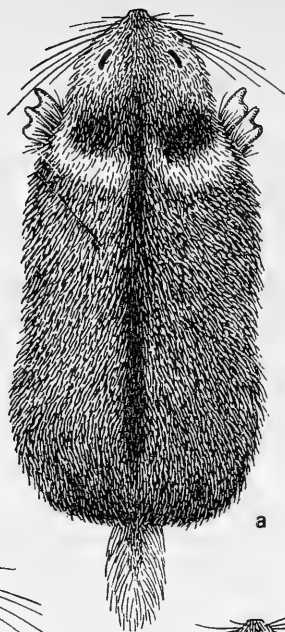
(*Stenocranius*), or towards the south (*Arvicola*), west (*Pitymys*), and east (several species of *Microtus*), probably in accordance with the so-called "Law of Optimum".* Similar changes are also observed with increases in altitude.

Color: Most voles are monochromatic. Striped or spotted patterns are not found. A black stripe along the middle of the back may be retained as an exception in such species as the steppe lemming (*Lagurus*), some steppe forms of narrow-skulled voles (*Stenocranius gregalis*), and lemmings of the genera *Dicrostonyx* and *Lemmus*. Except for true lemmings (*Lemmus*), contrasting patches of light and dark areas are not found in voles. The contrast in dorsal and ventral coloration is usually not pronounced; a more or less sharply demarcated border is observed only in a few forms, for example, in lemmings in which bichromatism has developed. The prevalent colors are bright brownish-gray, varying from fairly light gray or yellowish-gray (*Chionomys*, *Alticola*) to dark brown (*Arvicola*). Yellow-ocher tones are more typical of voles from southern latitudes and also both genera of lemmings; reddish shades, sometimes fairly bright, are seen in forest voles (*Clethrionomys*). Sharp seasonal changes in color, except for Arctic lemmings (*Dicrostonyx*)—which turn white in winter—and the lemming vole (*Aschizomys*) are not known, although most species are lighter in color in their denser winter pelage than during summer.

Molting: All voles in which molting has been studied undergo two seasonal molts (during spring and in autumn) in addition to the juvenile molt when the fur of young animals is replaced by the primary pelage of adults. Only in the long-clawed subterranean mole vole has spring molt not been firmly established. Autumn molt is generally more extensive and prolonged than the one in spring. As in many other mammals, molt is delayed in lactating females and juvenile molt more rapid in later litters than in earlier ones. The last stages of juvenile molt are often superimposed on the initial phase of autumn molt.

A.I. Kryltsov (1962) established that the sequence of fur replacement in all Old World voles is quite uniform. New hairs appear on the ventrolateral parts of the body and head and spreads to the ventral and dorsal surfaces. The dorsal surface of the head and posterior part of the back are the last to molt. Such a sequence is displayed both during juvenile and seasonal molts. Minor devia-

*This is usually understood to relate clinal variation to environmental conditions; the largest forms are found in the "optimal" environments—Eds.



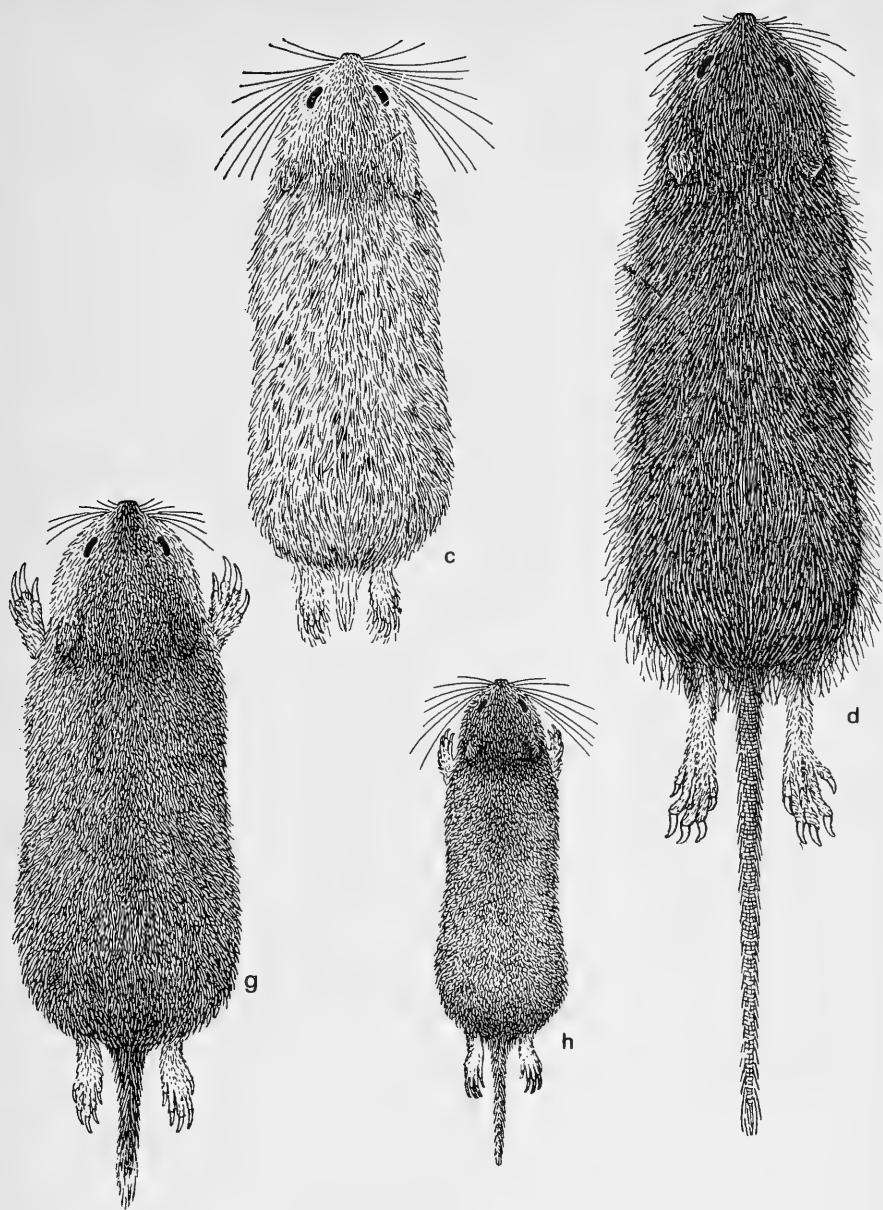


Figure 3. Body proportions and color patterns of voles.

a—Arctic lemming (*Dicrostonyx torquatus* Pallas), summer pelage; b—same, winter pelage; c—yellow steppe lemming (*Eolagurus luteus* Eversmann); d—Florida water vole (*Neofiber alleni* True); e—Balkan high-montane vole (*Dinaromys bogdanovi* V. and E. Martino); f—silver vole (*Alticola argentatus* Severtzov); g—long-clawed mole vole (*Prometheomys schaposchnikovi* Satunin); h—Central Asian high-montane vole (*Eothenomys melanogaster* Milne-Edwards).

tions do occur in the sequence as well as rate of molting of the head, middle and posterior parts of the back. Only in certain voles with rooted molars (*Clethrionomys* and *Phenacomys*) and the Norwegian lemming (*Lemmus lemmus*), do all or some species molt according to the cephalo-sacral type. The sequence of fur replacement in this case is the reverse of the one just described. It commences at two oval areas in the posterior part of the back and spreads from there toward the head; the sides and abdominal surface are the last to molt. Older animals in all species exhibit diffused molting in which no regular sequence is observed.

Pelage: Differentiation of the pelage into guard hairs and underfur is particularly well-developed in semiaquatic forms (*Ondatra*, *Neofiber*, *Arvicola*) in which four kinds of hair are clearly distinguished: straight, vibrissae, intermediate, and fur. To a lesser extent, these differences are discernible even in comparisons of different biological species within a single genus, for example, the common vole (*Microtus arvalis*) and the tundra vole (*M. oeconomus*). Structural differences of the superficial layer of hair of all categories are not discernible under a light microscope within the limits of the family. The cuticle is covered with bands of right-angled and irregular polygonal scales which, depending on hair thickness, may be arranged in one to four rows.

The pelage becomes more uniform in subterranean species. In *Prometheomys*, only sparse guard hairs and almost equally long hairs of the underfur can be distinguished. These exhibit no specific molting sequence and do not obstruct movement of the animals (*Prometheomys*, *Eothenomys*) in their underground passages. In addition to differences in nature of pelage, digging and swimming forms are also characterized by strong development of hard brush-like hairs near the snout, on the labial lobes, and on the lateral and dorsal surfaces of the foot, palm, and toes. Marginal tufts (*Ondatra*) or long bundles of hair masking the claws (*Dicrostonyx*) often form on the phalanges and become particularly dense during winter. Such stiff, brush-like hairs help prevent soil from entering the mouth by serving as an obstruction, by increasing the working surface of the limbs during digging and swimming, and by protecting the nails from rapid wear.

As a rule, specialized hairs, the vibrissae, appear earlier than others in one- to two-day-old neonates (subgenus *Microtus*); however, not all groups of vibrissae are equally well-developed in various members of the subfamily. Cheek vibrissae (pilli zygomatici) are probably totally absent. Furthermore, some vibrissae break easily

and may escape notice in older animals, particularly on dry museum specimens. The upper-lip vibrissae (p. labiales superiores) are always well-developed, numerous and long, especially in voles living in talus (*Chionomys*, *Alticola*, *Dinaromys*). Some may be half the trunk length (most *Microtus*) and reach back to the base of the pinnae. A large number of short, hard vibrissoid hairs may occur at the base of the upper-lip vibrissae. The lower-lip vibrissae (p. l. inferiores) are usually sparse, thin and short; the vibrissal pair at each side of the mouth is the longest and the difference quite pronounced in some forms (*Ondatra*). Long, well-developed lower-lip vibrissae are found in the water vole (*Arvicola*). Paired, more often solitary, chin vibrissae (p. submentales) are always present but sometimes indistinct (*Lemmus*, *Dicrostonyx*); they are well-expressed in the yellow steppe lemming (*Eolagurus*) and the water vole. Supra-orbital vibrissae (p. supraorbitales) are present in all voles; they are weaker in the forest vole (*Clethrionomys*) than in others and long and numerous in high-montane voles (*Alticola*). The solitary oral angle or cheek vibrissae (p. angulares) are present in some but probably not all members of Microtinae. For example, they are not found in any genus of lemmings but are long and thin in *Eolagurus*. The line connecting the tips of the longest vibrissae circumscribes the so-called "tactile field" (Kratochvil, 1956), the shape and size of which can be used as a distinct morpho-biological index. It is best developed in rock-dwelling forms, in which the horizontal cross-section of the field may equal the length of the body; it is least developed in semiaquatic forms.

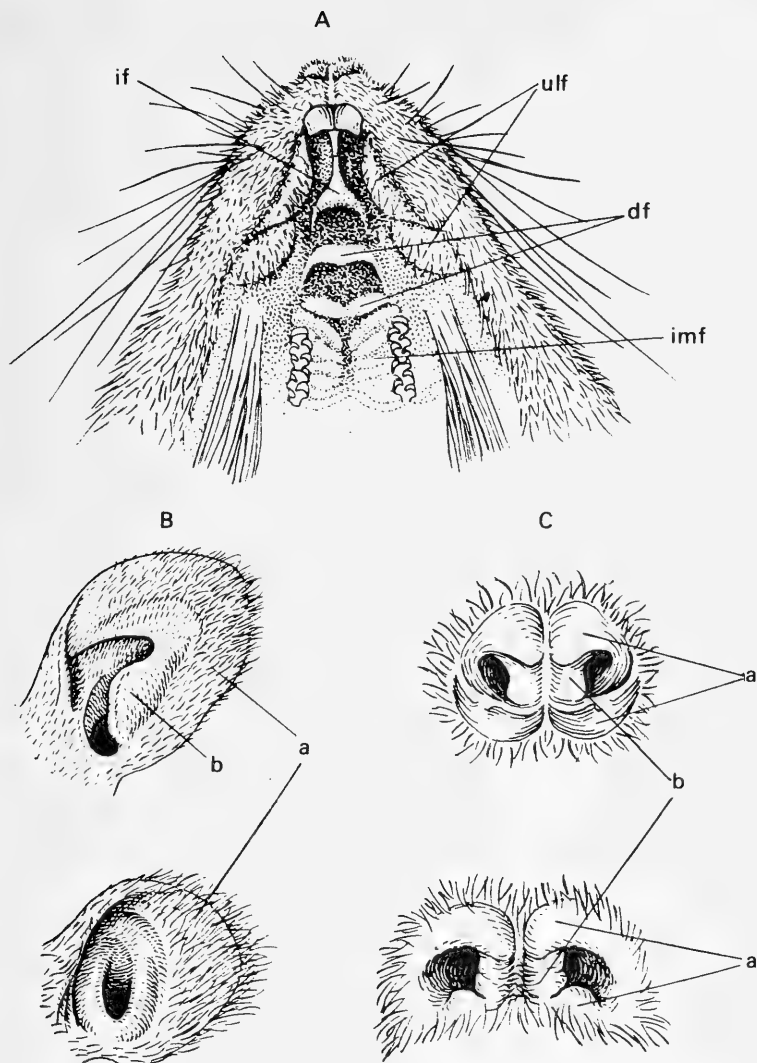
Lastly, many voles have two, or rarely more, carpal vibrissae located on the lower outer side of the wrist. If they are bent forward, they may reach the base of the middle finger in some species. Carpal hairs are especially long in *Alticola*, *Dinaromys*, and *Eolagurus*. Thus, a strong development of bristles is characteristic both of aquatic voles and of voles living in rocky screes. In both cases, the most probable reason is a greater need for tactile perception.

Tail length varies from barely longer than the hind foot (*Myopus*, *Synaptomys*, *Lagurus*), or even shorter (*Dicrostonyx*, *Lemmus*, *Lasiopodomys*), to slightly less than half trunk length (most voles of *Microtus*), or rarely somewhat longer (*Dinaromys*, *Ondatra*). Tail length reflects the degree of adaptation to a semisubterranean or semifossorial life style; a tendency toward tail reduction is observed in northern forms as well as those living in areas with a more severe climate (*Alticola*, *Stenocranius*, *Microtus* s. str.). The tail in many northern animals is also more densely covered with hair and may

26 possess terminal hairs longer than the tail *per se*. All the differences observed in voles are also seen in many other mammals; they reflect adaptations of the energy balance of a population during lean periods.

Pinna: Pinnae are variable in shape and size (Figure 4, B). They may strangely resemble the lobe of a shell (scapha) with a flat inner surface (*Eolagurus*, *Dicrostonyx*) or may be well-developed, protruding notably above the head pelage with an inner appendage of variable size and shape. Moreover, the pinnae may be covered with hair of variable density and length only on the outer side (*Dinaromys*), or be sparsely covered with hair on the inner surface as well (most forms). Sometimes the pubescence is evenly dense, at least along the margins and upper third (*Arvicola*). The external auditory meatus in most genera is covered by a broadly triangular or rectangular antitragus; the tragus is usually separated by a cleft—the helix—from the interior fold of the scapha. In *Ondatra*, a well-developed skin fold is located close to the inner margin of the lobe and has an acute-triangular shape that is free along its posterior edge. This fold possibly should be considered a tragus, although I am not aware of a similar structure in other Palearctic Microtinae. It is interesting that in *Ondatra* there is a depression on the inner surface of the pinnae corresponding to this fold. A somewhat unusual structure is also found in the same region in the water vole, in which a separate projection—the antihelix—occurs on the anterior wall of the scapha. In both cases, a more complete cover is provided for the external auditory meatus. In voles with a greatly reduced antitragus (*Myopus*), or none at all (*Lemmus*, *Dicrostonyx*, *Lagurus*, *Eolagurus* and others), there occurs a dense bundle of stiff hairs at the base of the outer ear replacing the antitragus and may cover not only the base but also the entire scapha.

Rhinarium (Figure 4, C): This region bears cuticular structures surrounding the external nares and contiguous narial depressions. These are the paired nasal wings (alae nasalis), which typically border (e.g., *Microtus*) the upper and partially the lateral (a. n. superiores) and the lower (a. n. inferiores) sides of the nares, together forming the “nasal mirror”. Anteriorly, the nares are covered by the paired upper labial flaps, often with lobed and frilled outer margins. The upper labia are variably fused along the midline of the snout with the alae nasalis triangle located above them and bordering the lower margin of the narial depressions; their posterior edges form several isolated lobes of varying development. The alae nasalis are mobile and can close the external nares and narial depressions.



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Figure 4. Structure of some soft parts of the vole head.

A—transverse folds (rugae palatinae) of mucous membrane in species of *Microtus*; ulf—upper labial flaps (inflexum pellitum labii superiores); if—incisorial fold; df—diastemal fold; imf—intermolar folds. B—Pinna: a—scapha; b—antitragus. C—nasal “mirror”: a—alae nasalis (upper and lower); b—upper labial lobe (B and C: upper figures—*Microtus*; lower figures—*Lagurus*).

A most unique arrangement is found in the fossorial genus *Prometheomys*. The narial depressions are absent in this animal and the nasal triangle and upper labial flaps are well-developed with the former bearing a uniquely incised upper margin. The adjoining part of the snout is covered with short, dense, stiff hairs.

The nasal "mirror" [= rhinarium]* has a simple structure in lemmings. The Arctic lemming (*Dicrostonyx*) has dense stiff hairs on the upper margin of the snout that cover it tightly—an adaptation that is quite understandable if we keep in mind the amount of this vole's activity under snow. The water vole and *Ondatra* have upper labial lobes and a well-demarcated narial pit on the lower side. In *Ondatra*, the alae nasalis are well-developed; they
27 are large, fleshy and mobile, and firmly close the entrance to the nasal cavity when the animal is under water. Skin lobes border the narial pits on their lower and outer sides; they are especially large in high-montane (*Alticola*) and forest (*Clethrionomys*) voles. Furthermore, in these voles the lower alae nasalis are very weakly folded, fused in pairs, and poorly separated along the midline of the snout. The outer parts of the alae nasalis are directed downward and somewhat forward. The rhinarial structure is similar in the steppe lemming (*Lagurus*), but the nares are widely open on the outer side and densely bordered with hairs.

Fore- and hind feet: These are elongate in swimming and climbing forms, including rock-dwellers (*Alticola*, *Chionomys*) and are short and broad in digging forms. Accordingly, there are differences
28 in phalangeal length, nails, size and structure of the plantar pads, and extent of pelage on the sole and palm.

The third finger on both limbs is usually the longest; the other digits are shorter in length in the sequence IV, II, V, I. As an exception, the fourth finger on the hind limb of some swimming forms (*Ondatra*, *Neofiber*) may be the longest; this has also been noted for voles living in talus (*Chionomys* and *Dinaromys*). There is a tendency toward elongation of the fourth and second fingers. For example, in many subgenera of *Microtus*, in *Myopus*, and in high-montane voles (*Alticola*), the fourth finger is almost equal to the third and in many others (*Clethrionomys*, *Eolagurus*, *Dicrostonyx* and others) the fourth finger is equal to the second, especially on the hind limbs. In this case, because of the three middle digits the foot resembles a symmetrically pointed shovel. Such a structure has been noted for the forelimb of Palearctic forms only in the

*"Mirror" used for rhinarium throughout—Eds.

long-clawed mole vole (*Prometheomys*), which is fossorial. The first finger (pollex) of the forelimb is reduced in many voles. A normal length and a well-formed nail are retained in only a few, including the digging (*Prometheomys*) and swimming forms (*Ondatra*, *Neofiber*). In the process of digit reduction, the nail may become small, flat and blunt, not protruding beyond the outer margin of the claw bed (*Eolagurus*, many subgenera of *Microtus* including *Microtus s. str.*), or more often may be totally lost (*Clethrionomys*, *Alticola*, *Lagurus*, *Dicrostonyx* and others). In *Lemmus* and *Myopus*, a unique nail that is laterally flattened and slightly bifurcate at the tip occurs on the large finger of the forelimb. Some reduction, primarily of the basal phalanx, is also observed in the first finger (hallux) of the hind limb. For example, this finger with its nail may reach only up to or slightly beyond the base of the second finger, half its length, or even up to the claw base (*Lemmus*).

The size and shape of nails are highly variable. Their variability and close dependence upon life style in a single or among related species have been well-demonstrated by Vinogradov (1946). Nail length usually constitutes about half the finger length or may be slightly more, but is rarely less than half (*Lagurus*). Nail elongation occurs in forms that dig with their forelimbs; here the nails on the three middle fingers are equal to the total length of the last digit (*Lasiopodomys*, *Prometheomys*), or even longer (*Dicrostonyx*). Small, pointed, and sharply curved nails are found in *Alticola*. Variations in nail curvature are also observed among *Microtus s. str.* and forest voles (*Clethrionomys*), which, for the latter, probably reflect adaptation to climbing.

The number of plantar pads or tubercles is no more than six on the fore- and hind limbs. Usually a large pad covers the base of the third and fourth digits and one each occurs at the base of the remaining digits. Two posterior pads are located on the outer and inner margin of the sole and palm and are particularly variable in shape and size.

In species with a subterranean or semisubterranean life styles, the interdigital pads are small. In the Arctic lemming and the yellow steppe lemming, these pads (only those of the third and fourth fingers retained in the latter) are fused into a single hard pad. Reduced interdigital pads are also found in true lemmings (*Lemmus*). Among all the listed forms, palmar pads are well-developed only in *Prometheomys*. In voles of rocky habitats such as *Alticola* (especially subgenus *Platycranius*), *Chionomys*, *Dinaromys* as well

29 as in *Ondatra*, the palmar pads are particularly enlarged. In the

first three genera, these may play the role of unique adhesive structures during locomotion over stones but their primary role is to hold plants near the mouth. In this respect, the differences between the two subterranean species—the mole vole and the long-clawed mole vole—are typical. The mole vole feeds underground mainly upon plant roots and has reduced and poorly demarcated palmar pads. Emerging from its burrow, the long-clawed mole vole uses well-developed palmar pads to shred and eat plants as other voles do; its food caches are located underground near the burrow entrance. Very large pads, like the thick but laterally flattened ones found in *Ondatra*, possibly help the animal build small shelters and nests by giving a better grip on building materials. The palmar surface is unique in Brandt's vole (*Lasiopodomys brandti*), which is diurnal. The thickened tissue comprises well-developed pads at the base of the fingers (interdigital pads) and two large pads on the palms (palmar pads).

The structure of the plantar pads of the hind limbs of voles is more uniform. In forms that dig well, semisubterranean or subterranean forms including *Ondatra*, the interdigital pads (and, in some cases, the metatarsal pads) are less developed than in other species, especially those which climb (rock-dwelling and forest species). In the Arctic lemming, the interdigital pads of the hind feet are also fused into a single pad like in the forefeet, while the metatarsal pads are absent. A large isolated finger pad and a small metatarsal pad are found in Brandt's vole and *Chionomys*. In several *Microtus*, the inner metatarsal pad is small or absent, and in some species is found only in some individuals.

The significance of pad development, as well as their associated glands (whose secretion serves for marking territory) deserves special study in voles.

The smaller the metatarsal pads of both limbs, the more densely they are covered with hair. The hair cover is more dense in Arctic, true and yellow steppe lemmings. The development of a tough pelage in amphibious and some digging voles has been described above.

Upper and lower labial flaps (Figure 4, A): These well-developed furred infoldings separate the incisors from the oral cavity. Their adaptive importance in Microtinae in connection with incisor action during digging (and also probably gnawing under water) was studied 50 years ago by Vinogradov (1926a, b). The upper labial flaps (inflexum pellitum labii superiores) may vary in shape from more or less triangular (*Myopus*, *Prometheomys*), to

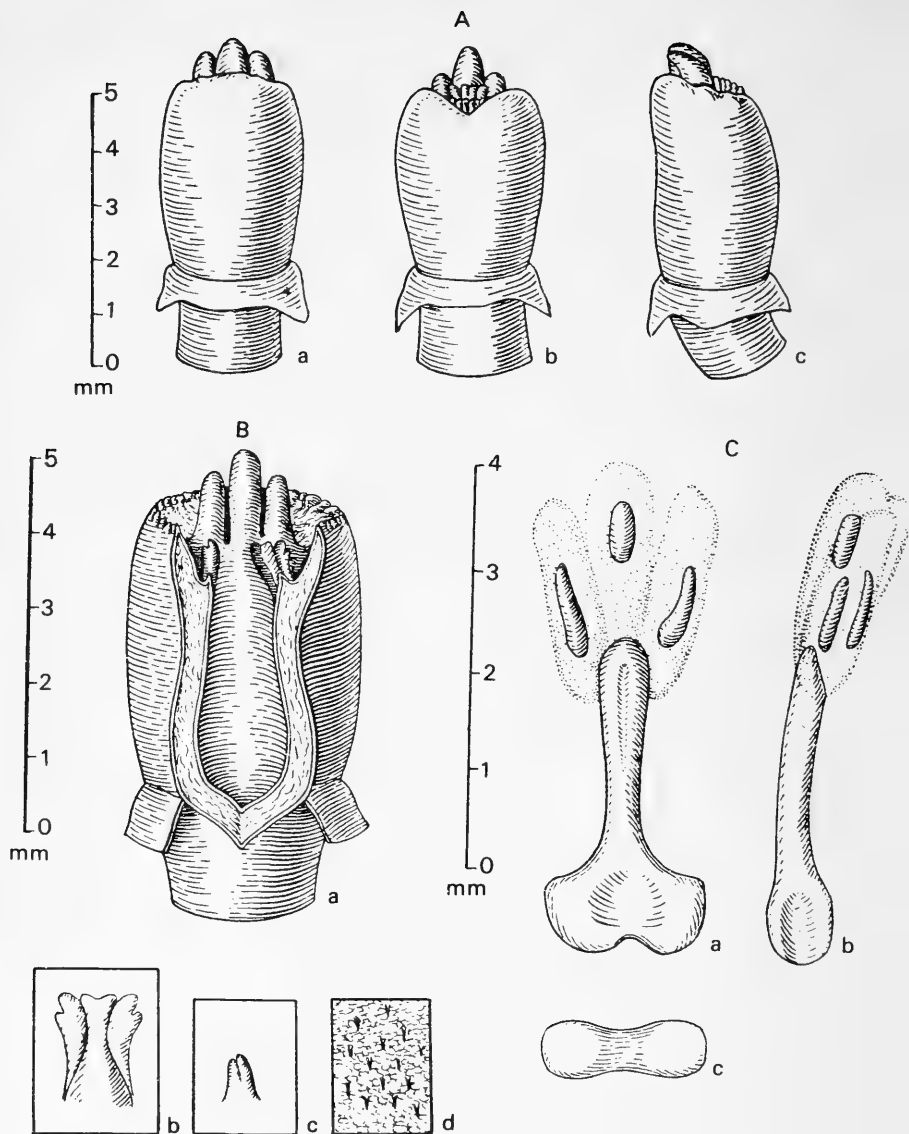
rounded, to rounded-right-angled, or more precisely, trapezoid with angles that are rounded to a variable degree. These flaps either are contiguous along the diastemal midline behind the incisors or terminate short of the midline leaving a sometimes large gap between them (*Dicrostonyx*, *Prometheomys*). More often, a fairly narrow slit is present (*Microtus* and many other genera). When the mouth is closed, the upper surface of the tongue overlaps the slit (except for the incisor part); when the mouth is open, the slit may close with the stretched skin of the lips. Closing of the slit is also effected by hairs covering the entire surface of the labial flaps. Such hairs are longer on the inner flap margins and are directed medially. However, immediately behind the upper incisors an opening still remains to accommodate the tips of the lower incisors.

The lower labial flaps (i. p. labii superiores*) resemble two hair-covered leathery lobes, similar to the upper ones, with a mucous margin located behind the incisors. These flaps are particularly well-developed in *Ondatra*, the long-clawed mole vole, and the common lemming (*Lemmus*), but are not fused as in the mole rat (*Spalax*); the tongue is located immediately behind these flaps. Generally speaking, the lower labial flaps are not well-differentiated in voles.

Transverse folds of mucous membrane of hard palate (Figure 4, A, rugae palatinae): These folds can be divided on the basis of their location into incisorial and diastemal folds; they are located in the region of the diastema and usually number three, while the intermolar folds number four to six. The first or incisorial fold may be fused with the incisorial papilla (papilla incisiva) and form a symmetrical cushion-like structure of complex profile that covers the incisorial opening (foramina incisiva), which is partly covered by the upper labial flaps. The second fold behind the incisors is usually complete, but the third one is deeply incised or divided, a condition seen in the two anterior intermolar folds. The structure of the palatal folds may be used for characterizing a large number of microtine taxa, although variability in this feature is fairly high.

External genitalia of male (penis): The penis is a small cutaneo-muscular structure (Figure 5) with a small bone (baculum) located inside its distal part (glans penis). The maximum length of this organ is equal to half the hind-foot length, and the ratio of its width to length varies from 50 to 75%. The penis tip is directed backward; and it is directed forward only after erection. In this state, its usual

*[sic]; should read "i. p. labii inferiores"—Eds.



30 Figure 5. Structure of external genitalia of voles (*Dinaromys bogdanovi* V. and E. Martino).

A—structure of glans penis (external view): a—dorsal view; b—ventral view; c—lateral view. B—structure of glans penis (slit open): a—dorsal view; b—urethral process (processus lingualis); c—dorsal process (pro. dorsalis); d—section of surface epithelium. C—structure of baculum (os penis): a—ventral view; b—lateral view; c—basal view.

dorsal surface becomes the ventral surface. To avoid confusion, we consider that surface along which the urethra passes to be ventral. The glans surface is covered with minute epidermal plates bearing spinules. The shape, size, and location of the lobes at the tip of the glans are used as specific and generic diagnostic characteristics (Tokuda, 1941; Hooper and Hart, 1962). They are manifested as a relatively large dorsal lobe and much smaller ventral lobes connected by lateral folds with a few small papillae along their margins. These structures cover the depression in which three partially protruding papillae are located: a large middle papilla, corresponding to the central of the three small distal bones of the baculum (for details, see page 39), are two smaller lateral papillae corresponding to the small lateral bones of the "trident". The inner surface of the dorsal lobe has one or two dorsal papillae (papilla dorsalis) and the ventral lobes correspondingly have urethral papillae (p. utheralis).

Skull: Dorsally the skull is uniformly rounded and supraorbital processes are absent. The maximum width across the zygomatic arches usually occurs medially or at the base of the anterior third; rarely, the arches diverge slightly (*Blanfordimys*, *Chionomys*) or converge somewhat posteriorly (*Stenocranius*, older specimens of *Lemmus*). The dorsal profile of the skull is relatively straight. Its highest point occurs at the anterior margin of the zygomatic arches; towards the rostrum it may slope downward quite steeply (Lemmini, *Eolagurus*), and in the interorbital region may slope down gently. The length of the braincase, measured from the most posterior point of the occipital to the middle of the line connecting the anterior margins of the postorbital processes (or plates), is greater than its maximum width, sometimes markedly so (*Stenocranius*). This length is approximately equal to the length of the facial part (from the middle of the above line to the end of the nasals or premaxillae). The braincase is flattened dorsally, especially in between the parietal crests, rarely bulging somewhat uniformly (*Phenacomys*, *Clethrionomys*). The rostrum may be notably reduced (*Lagurus*, *Arvicola*, *Blanfordimys*, *Pitymys*) and crests are poorly developed. The occipital (lambdoidal) crest is usually incomplete, terminating along the hind margin of the interparietal. The smaller the interparietal (*Lemmus*, *Eolagurus*, *Neofiber*, *Prometheomys*), the shorter the distance between the posterior end of the parietal crests. The latter border on the parietals and form a variably-expressed irregular polygonal shape. The frontals may have two distinct crests that form a depression between them (*Dicrostonyx*, *Lagurus*, *Eolagurus*, *Phenacomys*) and

32 may touch one another in older animals. Interorbital crests may occur in the interorbital region of some genera (*Lemmini*, *Arvicola*, *Stenocranius*, *Lasiopodomys*, some species of subgenus *Microtus*), but the interorbital region is usually flat. A continuous arrow-shaped crest is present only in older *Prometheomys*. In voles with well-developed vertical crests, the postorbital processes are also more distinct. They may be in the form of triangular plates forming the posterior margin of the orbit. Part of the temporal muscle is inserted here. The sagittal crest on the occipitals is weak, but more distinct in its upper part. It is more prominent in *Dicrostonyx*, *Lemmus*, *Myopus*, and *Eolagurus*.

The length of the upper diastema in voles constitutes on the average about one-third the condylobasal length of the skull. It is considerably longer in *Ondatra* and *Arvicola*, but shorter in *Dicrostonyx* and *Clethrionomys*. About half of the diastema (56%) is spanned by the incisive foramina. They are relatively longer in *Clethrionomys* and lemmings (except *Dicrostonyx*) and shorter in *Arvicola*.

The zygomatic process of the maxilla is shorter than the zygomatic process of the squamosal. The jugal connecting them is significantly long in *Lemmus* and *Phenacomys*. The masseter tubercles in the former slightly overlap the infraorbital foramen in its lower part and form an angle to its remaining part. The masseter tubercles are higher and more vertical in Arctic and true lemmings and comparatively low and inclined forward in steppe lemmings (*Lagurus*), some montane voles (*Phaiomys*), and especially *Alticola* (subgenus *Platykranius*).

The hard palate widens posteriorly, more strongly so in true lemmings than in the others. In some forms, its posterior margin either terminates at the level of the pterygoids (*Ondatra*) or forms a plate of variable thickness, often with a median falcate process that variably covers the bases of the alae nasalis (*Alticola*, *Clethrionomys*, *Antelionomys*, *Lemmus*). In most present-day microtines, the posterior part of the palate rises gradually posteriorly and terminates at the paired posterior palatine foramina, and is separated by a bony bridge of variable length and width. The foramina may be poorly developed (e.g., in *Lagurus*, *Dinaromys*, *Pliomys*, *Allophaiomys*).

The pterygoids overlap the antero-medial ends of the tympanic bullae and are particularly broad in *Ondatra* and *Neofiber*, almost reaching the alveolar margin of the upper jaw.

The orbit is relatively small and slightly variable in size. Its diameter is about one-fifth the condylobasal length of the skull, larger in the Arctic and common lemmings and smaller in the yellow steppe lemming (*Eolagurus*). The squamosal part of the orbit is not demarcated and its anterior margin may be shifted to the level of the postorbital process or plate. The position of the orbit and the angle formed by it with the horizontal plane is more variable. In voles, with rare exception the orbit is located somewhat behind the middle of the skull: the length of the anterior orbital line (distance from prosthion to hind margin of the orbit) is 12% greater than the distance from its hind margin to the dorsal rim of the foramen magnum. The orbit is situated most posteriorly in *Neofiber*, *Ondatra* and the Arctic lemming, and most anteriorly in bog lemmings (*Synaptomys*), in which it is located forward of the skull's midpoint and the ratio is reversed. The orbital angle is smallest in the high-montane vole *Alticola* (*Platycranius*) *strelzovi*, i.e., 23° (average angle of inclination within the subfamily is about 40°) and is greatest in species of the nominal subgenus *Alticola*, forest voles (*Clethrionomys*), and steppe lemmings (*Lagurus*).

33 It should be mentioned that the size of the eyeball, which occupies about two-thirds of the orbit, does not always correspond to the size of the orbit. Thus, in yellow steppe lemmings (*Eolagurus*), with the smallest index of relative size, the eyeball size is largest among voles as a whole (19% of the length from the tip of the snout to the anteroventral corner of the scapha). This proportion is greater than that found in the comparatively large-eyed rats of the genus *Rattus* (average 18%). On the other hand, the smallest eyeball is found in the long-clawed mole vole and *Chionomys*; it is located in sockets of moderate size in the former and in sockets of large size in the latter. Because of differences in eyeball size, a significant difference is also observed in the extent of development of intraorbital glands surrounding it. In Microtinae, including those with reduced eyes, orbital glands are better developed than in squirrels (Sciuridae) and mice (Muridae), and in most species, they form an almost circular "pad" around the eyeball. However, in some cases (e.g., *Eolagurus*), these glands are small, and the eyeball directly adjoins posteriorly on the inner part of the temporal muscle and anteriorly on the medial masseter muscle that passes through the infraorbital foramen (pars anterior).

The tympanic bullae vary in size and shape; they are usually somewhat flat laterally and high posteromedially. The bony auditory meatus is barely perceptible on the anterolateral margin

of the ear opening. The bullae are comparatively small in semi-aquatic forms (*Lagurus* and *Antelionomys*) and large in *Lemmus*, *Chionomys*, *Blanfordimys*, and *Eolagurus*; in members of the last two genera, the mastoid is also inflated. The bullar cavity may be completely filled with spongy bony tissue with small pores—a result of the formation of numerous bony septa (common and Arctic lemmings, *Lagurus*, *Eolagurus*, *Lemmiscus*). Often, and especially in these forms, the auditory meatus and pinnae are reduced. In other species, only the ventral convex part of the bulla is filled with large-pored spongy bony tissue, the remainder of the cavity being empty (*Arvicola*, most *Microtus* species). The thin-walled bulla is empty in *Neofiber*, *Dinaromys*, *Prometheomys*, and some others. The papilla-like paroccipital processes are small and, even in species with small bullae, do not protrude downward to the lower bullar surface. In *Dinaromys* and *Prometheomys*, these processes are relatively small. In Arctic lemmings, as distinct from other voles, the tips of the paroccipital processes are notably directed backward.

The occipital region in the horizontal plane of the alveolar margin of the jaw and masticatory surface of the molars (which corresponds to the horizontal direction of the optical axis, and determines the anatomical position of the head) is nearly vertical. Rarely, the part above the foramen magnum lies at an acute angle of 30–35° (*Neofiber*, *Ondatra*, *Arvicola*). The occipital condyles are directed backwards beyond the plane of the occiput, and only in rare cases are they masked by the mastoid and not visible from the sides (*Lemmus*, *Myopus*).

34 The lower margin of the mandibular rami forms an angle of about 15° with the horizontal plane of the molar row. However, in *Neofiber*, *Arvicola*, and *Eolagurus*, the angle may be 45°, while in *Dolomys* and *Dicrostonyx*, it may not exceed 10°. The length of the symphysis region is always greater than the length of the molar row. Depending upon the position of the incisor in the lower ramus, the posteromedial junction of the symphysis may be closer to the lateral plane or turned inward at an obtuse angle. The symphyseal junction is particularly distinct in lemmings (except *Synaptomys*), *Neofiber*, and *Ondatra* and is comparatively poorly developed in *Dolomys* and *Eolagurus*; other voles are structurally intermediate. The length of the incisorial part and the steepness of its ascent, as well as flatness of the ventral margin of the rami, are variable. These features also depend upon the position of the incisors, their curvature, and the nature of their free part. Anteriorly broad and ventrally flat rami are characteristic of lemmings (except *Synapto-*

mys) and lagurids; in these forms the incisor passes on the inner side of each ramus and is laterally flat. In *Neofiber*, the incisor forms the ventral margin of the jaw. The configuration of the incisor and ventral margin of the jaw in other voles is intermediate in development.

The tip of the coronoid process does not extend above the tip of the articular process. It is almost level with the tip of the latter in *Neofiber*; in older water voles (*Arvicola*), the coronoid process almost reaches the lower margin of the articular condyle; in *Dicrostonyx* and *Lemmus*, it is reduced and does not extend to this level. The long, relatively narrow articular process is well-demarcated by deep notches from the coronoid and angular processes in all four genera of lemmings, forest voles (*Clethrionomys*), and *Neofiber*; it is shorter and broader in most members of *Microtus* and *Eolagurus*. The angular process is weakly demarcated from the ventral margin of the jaw in *Lemmus*, *Myopus*, *Synaptomys* and *Eolagurus*; the separation is more distinct in *Clethrionomys* and some members of *Microtus*. When the jaw is closed, the angular process notably extends beyond the hind margin of the articular process; the posterior extension is less pronounced in the long-clawed mole vole. The masseteric ridge usually terminates somewhat before the anterior margin of M_1 and rarely reaches this level (*Lemmus*, *Myopus*). The coronoid crest terminates somewhat above and usually posterior to the masseteric ridge; this crest is a continuation of the anterior margin of the coronoid process; only in *Prometheomys* are the two situated at the same point.

Incisors: The posterior part of the lower incisor may form a knob on the inner margin of the ramus (lemmings), on the margin of the crescent-shaped notch (*Eolagurus*, some members of *Microtus*), or on the lateral surface of the articular process, but it never resembles an isolated process as seen in *Ellobius* or *Spalax*. The crown of the lower incisors usually has a more or less curved anterior surface and a "teardrop" profile in cross section. In *Ondatra*, the lower incisors are flatter on the labial side than in other voles; in yellow steppe lemmings, they flatten towards the front; and in *Dicrostonyx*, they are laterally compressed. The position and length of the lower incisors are more variable than in the upper ones. In most voles (except lemmings) with rootless molars, the incisors are long, laterally curved in their posterior part, and pass between the roots of M_2 and M_3 in such a manner that both anterior molars are located on the labial side of the incisor with M_3 on its lingual side. The roots of the first two molars in more hypsodont species

may form knobs below the masseteric ridge, while M_3 is located in a lingually-directed bony socket. In lemmings, comparatively short and straight incisors pass on the medial side of the rami, terminating from the level of the posterior margin of M_1 to the middle of M_3 . In microtines with open-rooted molars, the posterior tip of the incisor either reaches the margin of the crescent-shaped notch [angular notch] (*Neofiber*, *Eolagurus*) or, in most cases, extends along the ascending ramus to the lower margin of a similar notch [sigmoid notch], or penetrates the body of the articular process.

Among voles with rootless molars, the simplest condition is observed in the American forms *Neofiber* and *Lemmiscus*, in which the incisor is neither shifted inward nor turned outward at its posterior end but passes along the ventral margin and terminates near the apex of the crescent-shaped notch. In New World voles with rooted molars—*Phenacomys* and *Ondatra*—the incisor is not only shifted inward relative to the ventral margin of the ramus but it also passes under the molar roots, deviating slightly laterad at its posterior end to terminate below the mandibular foramen. In this case, the incisor alveolus does not form a swelling on the lingual surface of the ascending ramus. In voles with rooted molars, the incisor alveolus borders the posterior side of the trough for insertion of the temporal muscle. In the long-clawed mole vole (*Prometheomys*), all molar roots are located laterad to the incisor, the anterior of which is shifted inward and the posterior curved outward. Voles with rooted molars of the genera *Clethrionomys* and *Dinaromys* occupy an intermediate position. The incisor alveolus either passes under the posterior root of M_3 , or between the two roots of M_3 , so that the anterior root is located on the outer side and the posterior one on the inner side of the incisor. A similar condition is observed in different groups of fossil voles with rooted molars, in which this character is given great taxonomic importance (detailed description is given in the characterization of various groups). It should be noted that the position of the root relative to the incisor is subject to age-dependent changes: in young animals, the posterior root "sits" on the incisor and in adult animals, it slides downward. In *Dinaromys*, the incisor is shorter than in *Clethrionomys* and does not reach the margin of the crescent-shaped notch.

The upper incisors are shorter and more sharply-curved than the lower ones and, usually, terminate near the root of M^1 . Their crowns have a yellowish-orange tinge that is particularly intense in semiaquatic and semisubterranean forms (*Prometheomys*); in the Arctic lemming, the crowns are uniquely greenish. The ante-

rior surface of the upper incisors often has a shallow longitudinal groove that is best developed in *Lemmus*, *Myopus*, and *Synaptomys*. The edge of the incisor is laterad to the groove and usually describes a distinct dihedral angle to the medial edge. Since the medial portion of both incisors wears out faster than the lateral part, a crescent-shaped notch or inverted "W" (as viewed ventrally) is formed on their common cutting edge and a fairly long groove-shaped depression is formed on their posterior surface. In addition to the aforementioned lemmings, such a structure is characteristic of the long-clawed mole vole and is also found to a lesser extent in several other members of the subfamily. In the Arctic lemming, the upper incisors lack a groove; however, their anterior surfaces form a distinct sharply-acute dihedral angle with its apex directed forward. Accordingly, their combined cutting edge forms a notch that becomes triangular in shape with grinding; however, the groove-shaped depression on the posterior surface of each incisor is lacking. We may also note that in Arctic lemmings the upper and lower incisors are relatively narrower than in any other voles.

*Molars**: As in members of other [cricetid] subfamilies, voles also have three true or posterior molars lodged in each side of the jaw. The medial side of the mandibular ramus has a bony socket that covers the root of M_3 only in certain voles with hypsodont molars. In *Eolagurus* and some members of *Phaiomys*, the lower end of this socket may protrude somewhat beyond the ventral edge of the ramus and be visible in a lateral view.

The prismatic teeth of voles originated from the tuberculate, low-crowned molars of their hamster-like ancestors. The tubercles of the grinding surface, positioned alternately or oppositely, increased in height and became triangular prisms whose shorter sides are directed towards the midline of the tooth. In the alternate condition, these prisms are fused along the angles and in the opposite condition, along the bases. Simultaneously, the cingula of the tuberculate teeth formed unpaired columns on the anterior or posterior ends of the teeth and became acutely-angled, bifaceted folds separating the prisms. A characteristic pattern of alternate or opposite triangles of various size forms on the grinding surface of such prismatic teeth, with an unpaired semicircular loop on the anterior or

*In this section the author uses different terms for the same loop structures. Basically, there are triangular loops and semicircular loops; the former are paired, opposite or alternate. Often the triangular loops are simply called triangles. To avoid confusion, we have used the term "triangle" for the triangular loops and "loop" for the unpaired anterior or posterior loop—Eds.

posterior end; the loops are enamelled laterally and dentine medially and each loop separated by acutely-angled folds. Cement may be deposited at the bottom of these folds, partly or entirely along their length.

In the simplest case, the enamel layer of the molars is uniformly thick throughout the crown and the lower margin of the enamel forms a straight line on the lateral surface of the teeth. Differences in enamel thickness may occur due to its thinning at the bottom of the folds, along the outer ridge of the prism, or along one side of the prism, anterior or posterior. Thus the enamel layer on the grinding surface may be uniformly thick along the perimeter of the tooth, or may become thinner in the region of the bottom of the folds, or may differ in thickness on the anterior or posterior ends of the triangles. In the last case, the pattern is reversed on the upper and lower molars. Finally, when the enamel thins along the ridges and sides of the prisms, "tongues" of dentine (tracts) form that narrow gradually towards the occlusal surface. Often, due to intense erosion at the apices of the triangles, the enamel layer is interrupted, a condition also seen on the anterior wall of the anterior unpaired loop of M_1 . The probable functional significance of enamel differentiation is discussed below (page 40).

With increasing crown height, a threshold is reached when the growth process continues mainly due to generative changes of the root portion of the tooth. The beginning of root formation is shifted to later stages of postembryonic growth, with the result that roots gradually stop developing completely and the pulp cavity remains open throughout the animal's life. Thus a constantly growing high-crowned, hypsodont tooth similar to the incisors is formed, an adaptation seen in many other rodents. The last stage which completes the process of increase in crown height is distinctly seen in voles during ontogeny as well as in the phylogeny, based on analogous judgments about the initial evolutionary stage of hypsodonty as observed in other subfamilies of Cricetidae. Thus the transition from low-crowned (Brachyodont) tuberculate and medium high-crowned (Mesodont) tuberculate prismatic teeth to fully prismatic teeth can be observed in different species of Gerbillinae (genus *Gerbillus*) and hamsters.

Somehow the ontogenetic development of vole teeth continues from the front teeth to the back ones (the animals are born with more or less well formed and ossified M_1^1 , weakly ossified M_2^2 and without M_3^3). The same sequence is also observed for each tooth—the anterior elements develop before the posterior. The first ele-

ments to appear are either the unpaired terminal structure or the first pair of opposite prisms. Thus the last elements to form in the dental row are the posterior columns of M_3^3 . In some modern molar types (*Prometheomys*), these become visible only when the anterior sections of the teeth wear out.

Evolutionary changes have led to greater complexity of the crown structure, i.e., increase in number of constituent elements, primarily in the anterior part of M_1 . This has led to a simultaneous simplification of the rooted part of the molars and a reduction in the number of roots and even their complete disappearance in some forms. The triangles of the grinding surface and the folds separating them are indicated by numbers, letters, or their combination; 37 often the terminology of cones and conids, conventionally adopted for the teeth of other mammals, is used. Differences in terminology reflect the views of authors about the homology of these elements with the tuberculate teeth of other rodents. In the most generalized form, mammalogists speak about the closed (isolated) or fused triangles of the occlusal surface (their outer angles are sometimes called denticles), about the folds separating them, and also about the unpaired loops at the ends of each molar. Some paleontologists also use abbreviated letter symbols for the main measurements of the molars; a uniform scheme has not been devised to date.

The structure of M_1 is the most complex. Three so-called basal triangles are located on its masticatory surface ahead of the posterior unpaired loop (hypoconid plus the posterior cingulum of the tuberculate tooth). The triangle on the outer side is termed the protoconid and the two triangles on the inner (medial) side the metaconid and entoconid, of which the former adjoins the paraconid section of the tooth (see Figure 1). In the simplest case, the paraconid consists of one anterior unpaired loop with more or less symmetrical (*Prometheomys*) or asymmetrical depressions near its base, indicating the beginning of elongation of the first pair of triangles. From this simple tooth, a second stage is seen in *Arvicola*, *Allophaiomys*, and the extinct *Jordanomys*. The paraconid section in these species has a symmetrical trifoliate structure, with the medial lobe larger than the lateral ones. This is also seen in true lemmings but the medial lobe is narrower and sometimes shorter than the lateral ones (*Synaptomys*). Further complexity involves complete separation at the base of the paraconid section of the first pair of triangles, which may remain fused to some degree or may be separate from each other; in the next stage, similarly separated loops form a second pair of triangles. The first molars of

many representatives of the subfamily are at this stage. The anterior unpaired loop in this process may be symmetrical or variously asymmetrical, with folds that may be similar or variable in depth on the outer and inner sides of the tooth. Complete or almost complete isolation of the second pair of triangles of the paraconid is observed in *Ondatra* and *Dicrostonyx* and, among extinct forms, in the Late Pliocene *Dolomys* and some species of *Pliomys*. Paleontological material shows that the simple structure of the paraconid section may also result from secondary simplification that occurred after the formation of the first pair of triangles, by means of closure of the lateral fold between the first and second pair of triangles. In the intermediate stages, an "island" is formed at the apex of this fold and denticles are seen along the outer margin of the paraconid, with the so-called mimomyic or prismatic fold retained between them. The entire sequence is clearly seen in different species of the extinct genera *Mimomys* and *Promimomys* or in different stages of ontogenetic development of individual teeth, which appear to represent adult teeth of different species of these fossil genera (Figure 6).

38 It should be kept in mind that, in addition to the true prismatic folds and "islands" described, false folds and "islands" may also be observed in the paraconid section of M_1 . Among the latter, a distinction is made between the false outer [lateral] "island," inner [medial] "island" (in some extinct American genera), and the anterior "island". The anterior "island" is always present, for example, in *Microscoptini*, which have a primarily simple M_1 , as well as in some other modern and extinct microtines at early developmental stages of individual teeth. Morphologically, such "islands" represent the bottom of juvenile folds that are observed at the edge of the anterior unpaired loop in young animals of many species. At the same time, one of the posterolateral folds may form a structure which is analogous (but not homologous) to the true prismatic fold, e.g., in the extinct *Stachomys* or early members of *Microtus* and *Arvicola* (further details given in generic descriptions).

A process of secondary simplification, similar to that seen in the anterior part of M_1 , is also observed in M^3 , but since it represents a reverse image of M_1 , the simplification takes place not in its anterior but in its posterior part. In the simplest case, the anterior unpaired loop of this tooth is followed by one lateral and one medial triangle; posteriorly, the occlusal surface touches an unpaired heel, which has a more or less isolated denticle on its posterolateral angle (*Arvicola*, *Eolagurus*). In the next stage, triangles are differentiated on the heel in an anterior to posterior direction,

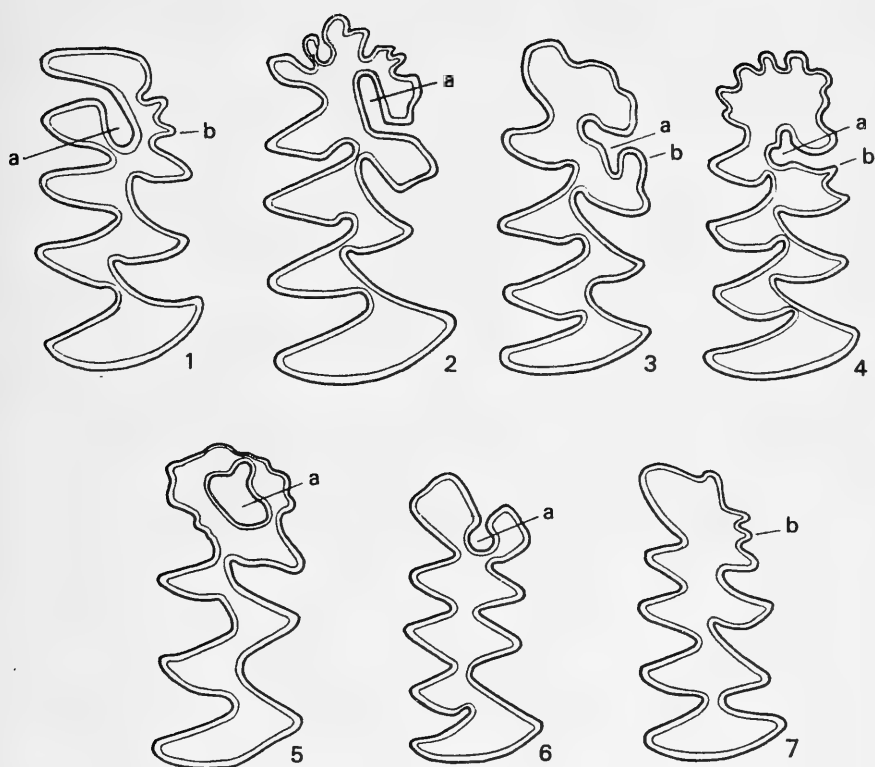


Figure 6. Structure of M_1 in different genera of Cricetidae.

1—*Pliopotamys*; 2—*Ogmodontomys*; 3—*Cosomys*; 4—*Mimomys*;
 5—*Baranomys*; 6—*Microtoscopes*; 7—*Stachomys*: a—"island";
 b—prismatic fold.

the first one being from the outer denticle. The process usually proceeds faster on the medial side and, in the most complex case (*Antelionomys*), this side may be completely double-folded with an additional denticle, indicating the isolation of a third pair of triangles. Secondary simplification of M_3^* is seen in its anterior section on the lateral side and in its posterior section on the medial side. In the first case, the anterior fold is closed and, in contrast to M_1 , completely disappears; after the "island" disappears, only a depression,

*[sic] should read " M^3 "—Eds.

which is much shallower than the next fold, remains in the place of its bottom. Such a terraced structure of the first two folds of M^3 characterizes living members of *Alticola* and, among extinct forms, 39 representatives of *Pliomys*. In the next stage, the last posteromedial fold is completely closed or rarely, the posterolateral fold forms an "island". This latter type of simplification is more common among voles, and only in rare cases is it also observed in the anterior and posterior segments of the tooth (*Pliomys*). The last upper molar is even more simply constructed in *Prometheomys* than in *Arvicola* or *Eolagurus*. Immediately behind the anterior unpaired loop, which may have a small lateral depression, there occurs a simple heel that rarely bears denticles nor forms complete triangles. The M^3 of true lemmings (Lemmini) is uniquely structured. The anterior unpaired loop is divided into two lobes by a deep fold that extends from the lateral side almost to the opposite tooth wall. The next pair of triangles is either divided (*Lemmus*) or fused (*Myopus*, *Synaptomys*); in *Synaptomys*, only the lateral fold is maintained. The heel of the tooth in all three genera has the appearance of an elongate transverse loop that touches the tooth only at its lateral margin ("Baranomys" structure).

The simplification sequence of M_1 and M^3 described here proceed faster in M_1 in ontogeny as well as phylogeny. For example, in the fossil *Mimomys* (the *M. intermedius* group), which has a completely simplified M_1 and M^3 , an "island" can still be noted in the posterior section of these teeth. Sometimes, the island appears as a transient wear formation where the posterior segment of the tooth joins the anterior one. It may be noted that in the most ancient microtine, *Ischymomys*, the posterior "island," which rapidly disappears with age, is also observed in both M_1 and M^3 .

Whereas M^1 and M_2^2 are simple and uniform, M_3 is somewhat more complex. In all cases, the complexity in the upper molars occurs in their posterior segment and that of the lower molars in the anterior segment. The structure of M^1 is most constant, with two pairs of triangles in addition to the anterior unpaired loop. Only *Dicrostonyx* has three pairs of triangles, but the posterior pair is poorly developed, and the posterior end of the tooth often has a small lingually-directed loop and a corresponding thin enamel lining throughout its height. Both anterior triangles are more often alternate to some extent than opposite and are fused. Among living voles, total fusion (up to complete opposite placement) is observed in the tribes Prometheomyini and Microscoptini.

In the case of individuals with two paired structures, the posteromedial end of M^1 often has a small additional triangle that reaches the dimensions of the major ones only in rare cases (*Eothenomys*). In living forms with rooted molars, this tooth has two roots, a comparatively large and anteroposteriorly flattened anterior root and a smaller rounded posterior root. In many extinct voles of *Mimomys* and *Dolomys*, a small third inner root is also present and the anterior one is apically bifurcate. Traces of this third root are observed in *Phenacomys* in which it is fused with the anterior root and occupies a common alveolus. In the most ancient microtines, such as *Aratomys* and *Ischymomys*, M^1 has four roots. The occlusal surface of M^2 has three triangles besides the anterior unpaired loop; in some members of *Microtus*, a small additional triangle is also present on the outer side. In *Dicrostonyx*, M^2 has one more pair of triangles, the posterolateral of which resembles that of M^1 . Fusion of the major triangles of M^2 is observed in the same taxa that exhibit fusion of M^1 .

The structure of M_2 and M_3 is similar: besides the posterior unpaired loop, their masticatory surface has two pairs of alternate or opposite triangles. Opposite triangles are generally observed in
40 more ancient forms and are more usual in M_3 than M_2 ; in the latter, the anterior pair of triangles are more often opposite than the middle pair. A complex anterior end is again characteristic of both M_2 and M_3 of *Dictrostonyx*: the occlusal surface on the inner side of M_3 or on both sides of M_2 has rudimentary triangles and corresponding cingula-plates all along the tooth height. Simplification of M_3 structure is found in *Prometheomyini*.

Limb bones: The length of the scapula is, on average, one-fourth the combined length of the thoracic and lumbar regions of the backbone. It varies comparatively little in relative length but varies highly in shape: from narrow and long (width less than half length) in *Lemmus* to narrow and broadly triangular in *Ondatra* and *Eo-lagurus*. The posterior margin of the scapula is usually straight and only in *Dicrostonyx* is it anteriorly convex. The maximum width of the bone varies from 90% of its length (*Ondatra*) to slightly more than half of it (*Lagurus*). Broadening with age primarily results from better development of the suprascapular fossa in *Ondatra* and *Prometheomys* and of the infraspinous fossa in *Lagurus*; more often the fossae are approximately even. The length of the acromion process varies widely, from 30 to 50% of the scapular length. The minimum values are characteristic of *Chionomys* and *Dicrostonyx*; the highest values have been noted for *Microtus* and *Arvicola*. The

spine of the scapula is highest in *Lemmus* and lowest in *Lagurus* and *Microtus*.

Upper arm and forearm bones: These are equal in length, constituting slightly more than one-third the total length of the free part of the limb. A marked difference is observed only in *Dicrostonyx* because of the greater length of its humerus; the latter is relatively short in *Ondatra* and *Arvicola*. Besides Arctic lemmings, a massive diaphysis is present in *Prometheomys* and the yellow steppe lemming (*Eolagurus*); the humerus is thin and slender in *Microtus* s. str. and *Myopus*. The head of the humerus is almost spherical (width more than 80% height) in *Microtus* s. str., *Arvicola*, and *Eolagurus*; it is elongated along the longitudinal axis in *Ondatra* and *Lagurus*. The ridge of the greater tuberosity is high in microtines, comparatively well-isolated from the diaphysis and notably deflected outward; it is higher in *Ondatra* and *Dicrostonyx* and shorter in *Clethrionomys* and *Alticola*. The medial epicondyle is best developed in *Ondatra*, *Lagurus*, and *Eolagurus* and small in *Chionomys* and *Microtus* s. str. The trochlear condyles are well-differentiated (high ridges and narrow body of the trochlea) in *Microtus* and *Prometheomys* and least differentiated in *Clethrionomys* and *Alticola*. The forearm bones are more variable in length than the humerus. The ulna and radius are usually rigidly joined as a syndesmosis or sychondrosis. The forearm is relatively short in *Clethrionomys* and *Chionomys*, and long in *Ondatra* and the long-clawed mole vole. Both forearm bones arc forward, the arc being more distinct in *Microtus* and *Arvicola*; rarely, they are straight (*Ondatra*, *Dicrostonyx*). A widening of the diaphyses of the ulna, or of both forearm bones, in an anteroposterior plane and a simultaneous flattening in a transverse plane are often observed, especially in *Dicrostonyx*; these shape features are poorly expressed in *Clethrionomys*, *Chionomys*, and *Arvicola*. The olecranon process is longest in the long-clawed mole vole and *Ondatra* and shortest in *Clethrionomys* and *Alticola*.

Pelvis: Long, on the average more than 10% of the total length of the thoracic and lumbar vertebrae. The ilium constitutes, on average, about 60% of the pelvic length and is particularly long in *Ondatra* and *Arvicola*. The ilium is shortest in *Ondatra* but also short in *Lemmus* and *Myopus* and longest in *Dicrostonyx* and *Eolagurus*; it is broadest posteriorly (at midpoint of the obturator foramen) in *Microtus* and *Arvicola*. The pubic symphysis is short
41 in all microtines, but especially so in *Lemmus* and *Alticola*. The acetabular perforation tends to close in most forms; rarely, it re-

mains open throughout the animal's life (*Lemmus*, *Prometheomys*). The iliac tubercle is moderately developed; it is low and rounded in *Ondatra*, compressed dorsoventrally in most species, comparatively high in *Lemmus* and *Eolagurus*, and is barely separated from the acetabular margin in *Dicrostonyx*.

Femur: Always shorter than the tibia. The difference between them is greatest (about 9%) in *Ondatra* and *Lemmus* and least in *Dicrostonyx* and *Eolagurus*. Tibial length varies far less than femoral length. Of the aforementioned genera, it is relatively short in the first two and relatively long in the latter two. The condyle is massive in *Ondatra*, *Prometheomys*, and *Dicrostonyx*; in addition, the lower end is particularly broad in *Arvicola* and narrow in *Clethrionomys* and *Alticola*. The ridge of the third trochanter is relatively high and short in *Ondatra* and *Arvicola* but low in *Dicrostonyx* and *Eolagurus*; it gradually merges with the diaphysis in *Alticola* and *Chionomys*. The head of the femur is usually "sessile" with a short, broad neck, especially in *Dicrostonyx* and *Eolagurus*; however, in *Arvicola* and, to a lesser extent in *Myopus* and *Lemmus*, it is relatively long and narrow. As in all Myomorpha, the tibia and fibula are fused at their lower end. The extent of fusion constitutes, on average, 30% of the length of the bone; the fused segment is longest in *Chionomys*, *Alticola*, and *Myopus* and shortest in *Dicrostonyx*.

Baculum: This consists of a central shaft about 3.0 mm long that is broadened basally (up to 5.0 mm wide in *Ondatra*), and three separate digitate ossicles that are terminally connected to the shaft through a cartilaginous base and together form a unique trident (Figure 5, C). Ossification of the trident and shaft occurs later in ontogeny. However, in some microtines the trident ossifies peripherally (*Stenocranius*, some members of *Microtus*) and in others remains cartilaginous throughout life (*Dicrostonyx*). In all voles with rooted molars, the trident is well-ossified in adult animals. The proportions of the shaft as well as the relative length of the terminal ossicles are variable and specific size ratios are typical for different species and genera (Anderson, 1960; Aksenova, 1974). Thus the base of the shaft may be fairly massive, with its width exceeding half its length (*Lemmus*, some *Clethrionomys*), or constitute about half its length (*Chionomys*), or reach only one-third its length (*Dicrostonyx*). Narrowing of the shaft at its distal tip may be acute or gradual, and the surface of its base may be variably concave on one or both sides. The length of the terminal ossicles and the massiveness of the middle one are also variable.

Thus, the ossicles are relatively long in *Clethrionomys* and short in *Neofiber* and *Synaptomys*; massiveness of the middle ossicle is characteristic of many members of *Microtus* s. str.

PROBABLE ADAPTIVE SIGNIFICANCE OF SOME
SPECIALIZATIONS OF THE GNAWING, CHEWING,
AND LOCOMOTORY APPARATUS

The ecological series—from the most “general” type represented by Old and New World forest voles with rooted molars and minimal adaptation to life in burrows (*Clethrionomys*, *Phenacomys*) through the typical burrow dwellers (*Microtus* s. str.), to the semi-fossorial forms (*Prometheomys*)—corresponds to a morphological series of adaptive specializations that are most distinctly expressed in the skeleton. They have been best studied in their extreme expression in the subterranean forms (Vinogradov, 1926a, b; Gambaryan, 1960).

In the above series, adaptations to digging and to feeding are most obvious. With regard to the latter, the size, shape and location of the incisors are most relevant, as well as the corresponding cranial features that affect jaw action and maximum bite pressure during nibbling as, for example, the attachment of the masseter muscles, which control “cutting”. Since the incisors are used for cutting food as well as loosening soil, the mechanical requirements are partly the same. At the initial stages of adaptation, these functions cannot always be separated without involving other structures. Incidentally, prognathism of the upper incisors is probably always a consequence of their use in digging. Hardness of the food also influences the structure of the rest of the occlusal apparatus, namely, the molars, jaw articulation, zygomatic structure, and, as in the case of nibbling, generation of maximum grinding pressure, i.e., insertion of the “masticatory part” of the large masseter, temporal, and pterygoid muscles.

Conspicuous structural changes of the postcranial skeleton are found in the forelimbs. These changes began first with the nails and their horny sheaths (Vinogradov, 1946), then were seen in other limb parts that contact the ground, and with increasing specialization, spread to more proximally-located parts. Changes in the sense organs are highly-developed in the eco-morphological series mentioned above and include the size and location of the orbits and the shape and structure of the tympanic bullae. Differences in the structure of the nasal cavity are less obvious.

In the amphibious forms that have appeared among burrow-dwelling voles, a large number of features exhibit specializations parallel to those seen in digging forms whose morphology reflects their association with more solid substrate (including the use of incisors for digging); adaptations in terrestrial forms to swimming mainly led to changes in external structure, blood supply (Heran, 1964; Galantsev, 1965), and behavior.

Incisor Function

The structure of microtine incisors is quite variable and reflects their adaptive specializations to the same degree as is seen in the molars. However, sufficient attention has not yet been paid to their functional morphology, not only in voles but in rodents as a whole. Naturally, only the most general remarks can be included here.

In incisor action the predominant movement is their vertical displacement (together with the jaw) along the arch corresponding to their radius of curvature. In this motion, the lower incisors are more active. The lower incisors may be located either in a forward position with the edges opposite the upper incisors, or (rarely) in a posterior position wherein their edges are not opposite and the point of support (upper incisor tips) is located ahead of the point of force application (lower incisor tips). The former position is mechanically more effective. In both cases, either cutting and nibbling or scraping and planing is done in a single or multiple motion. A similar effect can also be achieved with opposite movement of the upper and lower incisors relative to one another, although the movement of the lower incisors is greater. This effect is particularly discernible along the length of the incisor "functional path" on the object being incised. Lastly, these movements can even be performed by the upper incisors alone with support on the fixed lower ones. A unique type of simultaneous action of the upper and lower incisors, characterized as a nibbling or cutting movement, is observed during eating voluminous and comparatively soft food as well as during digging. The act of nibbling itself is a combination of all types of movements, which replace each other in different sequences but with a clear predominance of any one motion, depending upon the nature of the substrate being handled and specializations of the incisor structure. There is little or no movement of the lower jaw in horizontal and lateral planes during nibbling; in a vertical plane, it is restricted anteriorly by the length of the articular surface [glenoid fossa] and posteriorly by the anterior wall of the auditory bulla (Vorontsov, 1963). The lower jaw may be re-

stricted frontally by the possible extension of the soft labial parts. The amplitude of opposing and independent cranial movements is restricted by the atlas-epistropheus joint [axis] and, to a lesser degree, by the atlas-occipital articulation (in both cases, the movements are short and strong), as well as by the cervical vertebrae as a whole. The restriction of the lower jaw is primarily effected by the temporal muscle, mainly by fibers of its inner (middle) part that continue from the coronoid process toward the occipital condyle. Mandibular movement is primarily effected by the posterior part of the medial masseter muscle, which extends from the masseteric ridge of the mandibular ramus to the lower margin of the zygomatic arch. Skull posture is maintained by a number of muscles attached to the occipital area of the skull and upper incisor movement is controlled by the flexors of the head: the long and straight muscles running from the transverse processes of the cervical vertebrae to the basioccipital.

The maximum mechanical advantage for nibbling a hard substrate depends upon the following: the moderately long free part of the incisors (the upper ones shorter but strongly curved) and their long alveoli placed high in an anteroposterior direction; the strongly laterally-compressed, anteriorly-flattened surface of the upper incisors and rounded surface of the lower ones; the large angle of contact; the straight line of the cutting edge of the upper incisors and the lower pointed incisors with their single common tip. The coronoid process is either pointed vertically or curved posteriorly, but in either case, the effect of vertical action is ensured by the site of origin of the temporal muscles on the axial skull; in both positions, suitable conditions are obtained for functioning of the temporalis during movement of the jaw and fixation of the mandibular articulation. The masseteric ridges on the mandibular rami are close to the zygomatic arches and are more or less parallel to their margin and provide insertion for the medial masseter muscles that raise the jaw. These adaptive features are best developed and their structural development unique in mice and tree squirrels who use their incisors on hard seed coats. In voles, there is a great diversity of food specialization with a predominance of biting and cutting of grass and sedge stems and, only in some groups, of twigs. This has led to considerable structural diversity of the incisors and the arrangement of the main muscles responsible for nibbling.

Four morphological types have been noted among microtines, which indicate the different directions of specialization of the nibbling apparatus. However, in various genera of voles, these fea-

tures are not manifested in "pure form" but with a predominance of traits of one type, or some other combination of features, even those most unexpected. These variations correspond to differences in phylogeny as well as in nature of individual adaptations among microtine groups.

1. Both pairs of incisors, especially the lower pair, are well-adapted for work on hard surfaces. The incisors are moderately long (at least in their free part), broad, slightly compressed anteroposteriorly and sharply curved; thus, their angle of contact is obtuse. The upper incisors are flat towards the front, and their lateral surfaces are small and rounded forming an indistinctly-dihedral angle with the anterior face. The lower incisors are comparatively strong and asymmetrically flat on the sides (the outer edge, particularly in the distal third, is broader than the inner one). The cutting edge of the upper incisors is somewhat M-shaped and the sharpening level on their posterior surfaces is comparatively shallow. The area of origin of the temporal muscle on the cranium is large: an arrow-shaped ridge or two lateral ones separated by a groove are present on the interorbital region; the parietals are well-defined and enclose a comparatively narrow pentagonal area; the postorbital processes or plates are strongly developed and, the coronoid process is high and vertical. The zygomatic arch is placed high on the skull and the area of origin of the medial masseter muscle is well-developed on its lower margin. The masseteric ridge of the lower jaw, whose contour describes the lower outline of the arch, is also well-developed. The occipital crest [lambdoidal ridge] is high, at least, in its lateral parts. The basioccipital is broadly triangular and pronounced in relief.

2. The upper pair of incisors is less adapted to nibbling than the lower pair. These are weak, narrow, and short (including their edges), more compressed anteroposteriorly, not so steeply curved, and the contact angle of the upper and lower incisors is the same or smaller. The anterior surface of the upper incisors is less flat and forms a distinct dihedral angle with the lateral surface; the cutting edge of these incisors is deeply M-shaped, mainly because of their lateral parts, and the posterior sharpening bevel is strongly notched. The lower incisors and the structural arrangement of the medial masseter are the same as in the preceding case; however, the frontal ridges are usually curved and the postorbital processes may be poorly developed. The lateral part of the occipital crest is short and low and the basioccipital is narrower.

3. Both pairs of incisors are comparatively poorly adapted to nibbling hard food and are meant for relatively soft substrates. The structural specializations of the upper incisors mentioned above reach their fullest development, so typical of members of the sub-family. The lower incisors are short, evenly curved, and slightly compressed laterally, and their contact angle with the upper incisors is small. The cranial ridges and postorbital processes are undeveloped or barely perceptible, the zygomatic arches are low and thin, the masseteric ridge of the lower jaw is weak, the basioccipital is narrow, and the lateral part of the occipital crest is short and low.

4. Both pairs of incisors are adapted for digging. They are longer, especially in their alveolar regions (the lower incisors are also longer in their distal segment), than in voles with all other incisor types; they are relatively broad and greatly compressed in an anteroposterior direction; and they have a flat anterior surface and uniformly rounded lateral surfaces. The lower incisors are neither narrow nor pointed at their tips. The curvature of both incisors is fairly smooth and the contact angle is small, on average not exceeding 100° —a prognathous condition. The profile of the cutting edge of the upper incisors is slightly M-shaped and the sharpening bevel on their posterior surface is broad and small. The ridges
45 on the interorbital region are moderately developed, more posteriorly placed than in other voles and the parietals are more inclined outward. Accordingly, the coronoid process is longer and more recurved than in other microtines. The origin of the medial masseter from the comparatively high zygomatic arch covers not only its lower margin but also continues onto its ventromedial surface. The masseteric ridge of the lower jaw is short but high in relief. The occipital crest is high and long, sometimes continuous. The base of the occipital is broadly triangular, with well-developed crests for muscle attachment.

The progressive sequence of differences in incisor structure and muscle attachment primarily reflects an increase in the quantity of grasses and sedges (i.e., stems and leaves) in the food and reduction in the proportion of arboreal/shrub food items (branches, bark, etc.). The capacity of a species to exist on either food class, particularly in a "lean" period, must have played a decisive role in survival of the species. Most probably, the ability of these animals to make runways not in soil, but in dense grass/sedge turf is associated with this type of feeding. The true lemmings are the most specialized "turf" form. However, features of the second type of feeding

are variably developed in some species of many other genera (high-montane species of *Pitymys*, some species of *Phaiomys*, etc.).

Masticatory Movements

After being cut by the incisors, food probably accumulates in the diastemal cavity where it is pushed by the tongue to the molars. But the probable accumulation of food in the diastemal cavity of voles should not be given undue importance. It depends on the degree of isolation of this region by soft tissue (pages 22–23) growing over the incisor segment of both jaws; with complete isolation of the diastemal cavity (in digging forms), food deposition in this region is not possible.

Unlike members of Cricetidae with tuberculate teeth, the molars of voles have a single flat masticatory surface and more specialized structure, but they have less complex masticatory movements, which mainly take place in an anteroposterior direction. In this case, hard cellulose-rich food is ground between two ridged surfaces formed by the molars, of which the upper one is fixed (the millstone principle). Grinding is apparently aided by the working of the tongue against the palatine folds. The lower jaw acts as a single unit whose main functional movement is directed posteriorly. During forward movement, the jaws are closed and the tongue removes the food from the occlusal surface of the molars. However, the movement of the mandibular halves at their symphysis is not only forward-backward but also lateral, which compels us to admit the possibility of their independent movement as well, although with a lower amplitude. Thus, more primitive forms ought to show elliptical as well as restricted lateral masticatory movements mostly in the posterior region of the tooth rows. We can judge that such movements take place on the basis of the structure of the last molar, namely, in those species in which M_3^3 are broader than M_2^2 , with fused opposite triangles and M_3 devoid of enamel. These features are best developed in the tribe Lemmini. Also, with their strongly posteriorly divergent tooth rows, the anteroposterior movements of the entire jaw would be disadvantageous in these voles, since a large part of the occlusal surface of their molars would not work against each other. Functional studies should reveal either
46 of the whole jaw over an elongate ellipse, a motion observed in some hamsters and possibly inherited by lemmings directly from a group of these rodents.

As noted above, the predominant masticatory movements of most voles are directed backward; however, masticatory pressure is not uniform over the entire surface of the tooth row. The tooth surface is curved: concave on the lower molars and convex on the upper. In addition, the slope of this surface—inward on the lower molars and outward on the upper—is variable and may restrict lateral movement during sliding. In species in which the slope is greater (mainly in forms with rootless molars), there is a corresponding greater size contrast between outer versus inner prisms and triangles, which are larger on the sloping surface. The difference is always more conspicuous on the lower molars than on the upper where it may not be manifested at all.

It must be noted that in many voles, particularly those with rootless molars, mobility of the symphysis may also allow a certain rotation of each mandibular ramus during its backward movement. As a result, the anterior molars are sharpened more in their inner parts and the posterior ones in their outer parts (an effect probably due to the contraction of the pterygoid muscles), and the entire occlusal surface acquires a mild propeller-type torsion in the horizontal plane. Such a picture of sharpening is observed to a greater extent in ground squirrels (Gromov *et al.*, 1965) in which the mandibular rami alternately participate in masticatory movements. The possibility of such movement in voles cannot be completely excluded.

Lastly, as in hamsters, the tooth rows of voles are only nearly parallel (their unique orientation in Lemmini was mentioned above). In most species they diverge slightly both in the anterior region because of a shift in the anterior prisms of M^1 , similar to the anterior pair of tubercles in cricetines, and in the posterior section because of a corresponding shift of prisms in M^3 . This is also observed in M_1 , whereas M_3 may be progressively shifted inward because of the insertion of the temporal muscle in the depression at the base of the ascending ramus.

N.S. Lebedkina (1949), showed that the magnitude of displacement of the lower jaw in relation to the upper during masticatory movement is such that with the existing kinematic possibilities determined by the extent of temporal-mandibular mobility (three degrees of freedom exist), the largest number of cutting enamel edges of the prisms are engaged. Usually, such displacement does not constitute more than two-thirds of M_1 length; it is believed that "empty movement" takes place with a greater displacement.

Maximum mechanical effect is also ensured by several structural details of the masticatory surface, some of which have already been mentioned.

1. The three-faceted shape of the prisms and their corresponding triangles on the masticatory surface are basally narrow and transversely elongate. With an increased number of prisms and triangles, the total length of the cutting edge and the working contact of individual dental parts increases.

2. The prisms and triangles of the occlusal surface are not opposite, as in the hamster-like ancestors of voles, but alternate and separate from each other. Closure of enamel triangles is absent or poorly developed in primitive microtines and is also observed in the early development of more specialized forms, proceeding faster in the anterior part of the tooth row.

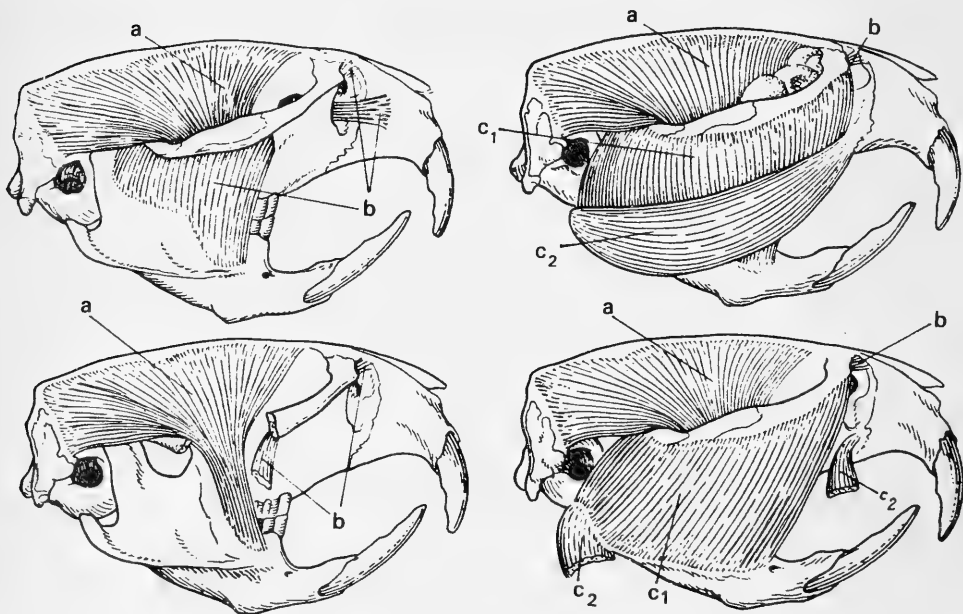
3. Three substances of different hardness—enamel, dentine, and in some forms cement—alternate on the masticatory surface in a definite sequence that causes alternation of raised enamel margins with both closed (dentine in the middle of the triangles) and open (cement at the bottom of folds) depressions.

47 4. The occurrence and maintenance of varying thicknesses of enamel (p. 32) provide a unique microrelief of the occlusal surface since sharpening is more pronounced where enamel is thinner.

At sites with undifferentiated enamel, the more rapidly-wearing dentine forms depressions on the inner surfaces of the triangles (semilunar type of wear); whereas, at sites with enamel at the bottom of folds (apices directed backward on the upper molars and forward on the lower), a distinct sequence of depressions and elevations is observed along the midline of the tooth rows. The occlusal surface resembles an obtuse dihedral angle with its apex downward on the lower molars and emergent on the upper (angular type of wear). If the enamel is thinner at the apices of the triangles (denticles) then a marginal type of grinding takes place. Finally, with different thicknesses of enamel on the anterior and posterior walls of the triangles, deeper dentine depressions (stronger wear) form near thin enamel margins and alternate with more raised (lesser wear) grinding surfaces at places of thicker enamel. In this process, because of the reversed structural configuration of the upper and lower molars, the areas of the upper teeth that are more resistant to wear erode the softer parts of the lower teeth. Since differences in enamel thickness occur along the height of the crown, this occlusal microstructure is maintained during grinding, forming a self-sharpening grate (progressive type of wear).

It is interesting to note that differences in enamel thickness on the cusps of some hamsters studied by N.N. Vorontsov (1967) ensure self-sharpening of the masticatory surface of their tuberculate molars during chewing. Such differences are believed to be inherited by some group of voles, particularly those forms with thicker anterior walls on the upper molars and thicker posterior walls on the lower molars.

The major power movement during grinding is generated by parts of the masseter muscles (*m. masseter**), which draw the jaw forward and upward and backward. Since the same muscles work in the anterodorsal movement as during nibbling, their total volume is much greater than those moving the jaw backward and forward. In anterodorsal movement, the two parts of the lateral masseter (*m. m. lateralis*) play a leading role: the anterior superficial part (*p. anterior*), which originates as a tendon from the tuberosity below the masseter [zygomatic] plate of the maxilla and inserts on the outer side of the angular process of the dentary and partly on



48 Figure 7. Main masseter muscles of voles (from Hinton, 1926).
 a—temporal muscle (*musculus temporalis*); b and c—masseter muscle (*m. masseter*): b—inner (*m. medialis*), c—outer (*m. lateralis*): c₁—deep part, c₂—superficial part.

*So given in the Russian original. However, the major retractor of the lower jaw is the digastric muscle, not the masseter—Eds.

its inner surface; and the posterior (deep) part (p. posterior), which originates along the ventral margin of the zygomatic arch and attaches to the masseteric ridge of the mandibular ramus (Figure 7, c_1 , c_2). Among the muscles important for backward jaw movement (jaw retraction) are the posterior part of m. m. medialis (p. posterior), attached from the lower margin of the middle zygomatic arch to the apex of the angular process, and the posterior part of the temporal (m. temporalis pars posteroventralis). The masticatory pressure developed by these muscles greatly determines the shape and mutual disposition of some parts of the skull, since the attainment of greater mechanical advantage is one of the significant evolutionary changes not only in the lineage from hamsters to voles (during transition from crushing masticatory movements to grinding) but also in the further evolution of voles. Vorontsov (1967) has noted the following in hamsters: an increase in height of the zygomatic plate and its more perpendicular reorientation in relation to the sagittal plane of the skull; a more anterodorsal placement of the tuberosity for the superficial masseter and dorsal extension of the angular process; and, a steeper slope of the masseteric ridge depending on the angle formed by the ventral margin of the rami of the jaws, which is close to a right angle. These and other structural specializations create ideal conditions for horizontal action of the masseter muscle, primarily of the anterior and inner parts of the lateral masseter (masseter lateralis). These characters are combined in various ways in different genera of voles; in individual phyletic lines of the subfamily, we find different stages of evolution that in totality ensure the most effective grinding of the typical foods consumed by the species. Thus, for example, a high zygomatic plate is found in *Lemmus*, *Dicrostonyx*, and *Eolagurus*, and a relatively lower one in *Lagurus*, *Lemmiscus*, *Pitymys*, and *Platycranius*. Its shape is nearly square in *Limmini*, *Ondatra*, *Lagurus*, *Pitymys*, and *Clethrionomys*, but its width slightly greater than its height in *Lemmiscus*. While its orientation is close to perpendicular in relation to the longitudinal skull axis in *Lagurus*, *Eolagurus*, *Lemmiscus*, and *Microtus*, it forms a large anterior dihedral angle with the sagittal plane in *Dicrostonyx*, *Synaptomys*, and *Myopus*.

In addition to the foregoing characters, other features likewise enhance the mechanical advantage of the masseter muscles in microtines, such as the vertically extended articular process, indicating a higher position of temporo-mandibular joint. This joint is located high in *Ondatra*, *Neofiber*, *Arvicola*, and *Eolagurus* and low in *Microtus* s. str., *Pitymys*, *Lagurus*, and *Alticola*.

- 49 Four types of morphofunctional complexes that allow "masticatory adaptations" can be identified within the subfamily.

The first type is characterized by relatively short, parallel tooth rows; the masticatory surface is slightly convex (or concave) in a longitudinal axis; the enamel is uniformly thick and wear pattern in semilunar; the molars are broad with broad prisms at their base, with no difference in size of lateral and medial prisms; M_1 is moderately long, M^3 relatively short; the ventral margin of the jaw rami strongly curved; and the mandibular symphysis relatively high. The probable predominant type of masticatory movement is independent transverse action of the mandibles with retraction of the jaw as the major working phase. Many ancient microtines, and *Prometheomys* and *Neofiber* among the modern members, belong to this type.

The second morphofunctional complex is characterized by relatively long and posteriorly divergent tooth rows; the masticatory surface is flat in its longitudinal axis and convex in the transverse; the enamel in the folds is sharpened and wear pattern is angular and marginal; the teeth are narrow with broad prisms at base, and the size difference of lateral and medial prisms marked in upper and lower molars; M_1 is reduced, M_3^* moderately long; the lower margin of mandibles moderately curved; and, the mandibular symphysis is moderately high. The probable predominant masticatory action is movement of the lower jaw as a whole along the relatively elongate chewing orbit with extension and retraction of the jaw as the major working phase. This type is present only in the tribe Lemmini.

The third type comprises voles with moderately long tooth rows that are slightly posteriorly divergent; the masticatory surface is more often distinctly (sometimes slightly) convex (or concave) in its longitudinal axis; enamel is uniformly thick and the wear pattern is semilunar; the teeth are narrow with narrow prisms at their base and no difference in size of lateral and medial triangles; M_1 and M^3 are variable in size; the lower margin of mandibles is usually moderately curved; and the mandibular symphysis is often high. The probable predominant masticatory action is anteroposterior, mostly by the entire jaw, with retraction of jaw the major working phase. This type is typical of members of Lagurini and Dicrostonyxini.

In microtines comprising the fourth type, the tooth rows are moderately, often relatively long, slightly divergent (posteriorly

*[sic]; should be M^3 —Eds.

more so); the masticatory surface is variably convex (or concave) in its longitudinal axis and often has a common propeller-like torsion; enamel is undifferentiated in certain ancient forms but becomes differentiated in descendants, the earlier forms among the later groups with thinner enamel in the folds and on the anterior walls of the upper molar prisms and posterior walls on the lower molars; the picture is reversed in the later forms of the later groups—accordingly, wear patterns are semilunar and angular, but are more often terraced; the length of M_1 and M^3 is variable, M^3 is always relatively long, the medial prisms usually larger than the lateral at least on the lower molars; the curvature of the lower jaw margin is slight, rarely moderate; and the mandibular symphysis is low or moderately high. The probable predominant masticatory action is the same as in species of the preceding type. This type comprises most extant and extinct microtines of Microtini and Clethrionomyini.

Adaptations of the teeth for feeding on cellulose-rich food have also appeared in different groups of the subfamily Cricetinae in particular, both in the to-and-fro movements of the jaws on flat, transversely-folded crowns and in the hypsodont molars with root formation only in very old individuals (*Neotoma*). N.N. Vorontsov (1967) proposed a similar sequence for hamsters of the Old and New World including the tribes Phyllotini, Sigmodontini, and Neotomini; in the last tribe, the corresponding adaptive specializations achieve a significant level of convergence to voles. This is also observed in some extinct genera (*Trilophomys*, *Baranomys*). However, even in members of specialized modern genera such as *Andinomys* of the Phyllotini, *Neotomys* of the Sigmodontini, and *Neotoma* of the Neotomini, the similarity relates only to individual characters and does not repeat the entire complex of characters typical of Microtinae. Thus, the extent of "vole-like tooth development" decreases in the dental rows anteroposteriorly; with very rare exceptions (*Neotomys*), M^3 and the reduced bilobate M_3 never attain the length and complexity typical of voles (an exception among voles are the hamster-like molars of *Prometheomys*); opposite placement of triangles of the occlusal surface dominates alternate placement; the anterior part of M_1 does not develop secondary complexity; and, the molars themselves do not attain the level of true hypsodonty.

Structural differences of the incisors are also significant for Cricetinae and are closer to those of Muridae, which are adapted for nibbling a harder substrate than voles do. In a vast majority

of vole-like forms, the incisors are more sharply-curved than in Muridae (at least for the upper incisors); they are more strongly laterally compressed, especially the uppers; their tips almost never form a dihedral angle; and the cutting edge is M-shaped in profile. The posterior end of the lower incisor in vole-like hamsters never continues into the articular [condyloid] process; if it forms a knob, then it is located at the midpoint of the coronoid process base or near the base of the anterior margin of the articular process. Accordingly, there are contrasts in the general structure of the lower jaw (for example, the very weak angular curvature at its lower margin) and skull (absence or very poor development of the postorbital process or ridge) that attest to a different, generally less prominent, muscular load during nibbling as well as chewing food. Thus, the hereditary morphophysiological basis in this subfamily did not suffice to allow the generally high level of food specialization that has been achieved by voles.

In conclusion, let us mention that wide use of radiographic and cine-radiographic methods of studying the nature and interactions of the morphological and biomechanical parameters involved in nibbling and mastication (Labas, 1968; Vorontsov and Labas, 1968) and also the mathematical expression of mastication (Resenberger, 1973) will in the future enable us to better understand their adaptive role and evolutionary significance of these parameters.

Limb Structure and Function

The major adaptive characteristics of limb bone structure in microtines as well as the proportion of individual limb elements depend upon the nature of the major movements they perform. These functions are common for all mammals. The hind limbs primarily push the body forward during locomotion—walking, running, jumping, and swimming—and support the body during forelimb activity. The forelimbs perform various movements associated with feeding, some specialized types of movements (climbing), digging, and, during rapid locomotion along a horizontal surface, serve for shock absorption upon landing (Gambaryan, 1972).

51 Unlike gerbils, no vole group is adapted to running fast. Even those voles which live in open environments move by slow or quick steps, or short jumps amidst fairly dense vegetation that is many times higher than their leaps. Only in open environments of the northern latitudes and high mountains, or in other areas only during the cold period of the year, may some species run over several hundred meters on the snow or on barren terrain. Judging from the

position of footprints, locomotion in this case may occur by jumps in which the hind limbs are brought ahead of the forelimbs. The adaptive mode of microtines reflects their life as burrow-dwellers who dig with their forelimbs and who move along the ground or in tunnels and natural hollows by a slow quadrupedal gait. The most specialized, and correspondingly the most universal, skeletal structure of this kind is observed in common voles of the subgenus *Microtus*. Enhancement of adaptations for digging and restricted burrow-dwelling (rare emergence on the surface since underground plant parts form a major food source) leads to the appearance of more sharply expressed structural traits typical of a fossorial animal as in the ecological series: *Microtus*—*Lagurus*—*Eolagurus*—*Dicrostonyx*—*Prometheomys*.

Two directions of change from the above-mentioned "general" type are the appearance of adaptations for running and climbing, which are less conspicuous but nevertheless evident. Cursorial habits are observed in true lemmings (*Lemmus*) and climbing in forest voles (*Clethrionomys*) as well as in *Alticola* and *Chionomys*; *Chionomys* is also capable of moving among scattered rocks. More basic changes are observed in the hind limb skeleton as a result of adaptation to swimming. Such changes are best developed in *Ondatra* and least developed in the water vole *Arvicola* (and probably in the American genus *Neofiber*), in which the forelimbs are heavily used for digging, aided to a small extent by the incisors.

Let it to be noted here that the structural characteristics of the limb bones *per se* may not always be interpreted unequivocally in a functional sense since different types of locomotion bearing a similar load may cause some structural changes. Thus, the increased mechanical load placed on the hind limbs during swimming or for enhanced support during digging causes increased massiveness of the tubular bones, especially their diaphyses; a stronger elbow joint or shoulder joint capable of freer movement is equally effective during digging as well as climbing. This makes it extremely difficult to understand the structural adaptations of the limb bones of extinct forms of microtines, especially the isolated taxa in which neither the animal's life style nor the bone structure of its related forms are known.

Thus, given that the nature of function determines the predominant mechanical load on the muscles and limb skeleton, the following three types of limb structure can be identified among the major life styles of microtines.

1. *Nonspecialized burrow-dweller type*: The limbs are moderately long,¹ and not designed for an extended reach nor for attaining high locomotory speeds. The hind limbs are moderately long relative to the forelimbs, which underscores the absence of specialized locomotion by jumping, running, or swimming. All tubular bones have relatively narrow diaphyses—an indication of comparatively low mechanical demands.

The humerus is short with a spherical head, a comparatively poorly-developed crest on the greater tuberosity, a short medial epicondyle, and a moderately high crest on the medial part of the trochlea, which is comparatively strongly-constricted. The ulna is long with a high olecranon process, a small anteroposterior diameter, and a narrow articular area for the radius. The synchondrosis region of both forearm bones is comparatively short, mostly along their upper third, and their anterior curvature is prominent. The hand is relatively short. Such a forelimb structure suggests fairly diverse movement at the shoulder joint, a comparatively weak development of muscles that pull the limb backward, and a small range of flexion and extension at the ulnar joint with rather firm articulation and strong extensors. The flexors and extensors of the fingers lack special development and the comparatively weak attachment of the forearm bones suggests little capacity for rotary movement. The forelimb also lacks special adaptations for digging. However, in many species included in this group, elongation of the arm has been noted in forms living on more compact ground as well as in those with excessive claw growth during winter (Vinoogradov, 1946). The femur is moderately long with a massive lower epiphysis and large patella, short crest on third trochanter, and a medium-sized neck. The tibia is also not elongate but has a moderately long lateral crest and a relatively long fusion with the fibula. The foot is short but not broad. Thus, specialized features of the hind limbs are absent; only the structure of the lower femur indicates the presence of sufficiently strong foot flexors and extensors, and the long region of fusion of the tibia-fibula points to greater strength of the lower hind limb.

The change from this nonspecialized structure to the initial stages of climbing adaptation in Palearctic voles involves the reduction of both fore- and hind limbs in relation to trunk length. Reduction in hind limbs is particularly noticeable in montane forms

¹In relation to the total length of the lumbar and thoracic region of the backbone.

living in loose rocky areas and can be considered an index of their jumping capacity. The arm bones are more massive than in species of the preceding group; however, the elbow joint, judging from the comparative size of the olecranon process, is smaller and much shorter and indicates a small movement span. Concomitantly, the thinner lower femur and patella point to a certain weakening of the foot extensors and the longer neck of the femur indicates much greater freedom of movement at the hip joint.

In contrast, some cursorial adaptations can be seen in true lemmings and to a lesser extent in the forest lemming (*Myopus*), which have relatively longer limbs with a short and narrow foot and short arm, long forearm and tibia, longer neck of femur and shorter tibial crest. Some of these characters are common to amphibious voles (see below), which can be explained by similarity in movements and mechanical load.

53 2. *Digging type of structure*: Enhancement of adaptations for forelimb digging, which attain maximum expression in the long-clawed mole vole (involving its entire skeleton) and Arctic lemmings (involving distal limb bones), is primarily reflected in: (a) shortening of the limbs, which evolves at a faster pace in the anterior than in the posterior ones (unlike ground squirrels in which the case is reversed and in which the least-specialized burrow-dwellers initially had longer hind limbs)—with such proportions, the movement force increases due to the range and speed of movement; (b) increased massiveness of all forearm bones, especially in the diaphyses of the tubular bones—an indicator of greater mechanical pressure; (c) an increased crest height of the greater tuberosity of the humerus, increased length of the medial epicondyle, and increased size of the medial part of the trochlea, all of which reflect stronger muscles for retraction of the entire limb; and, increased movement span in the elbow joint, and augmented digital and forearm flexure. Moreover, in highly specialized forms the trochlea of the humerus is shifted laterally and the humeral crests are directed obliquely relative to the longitudinal axis of the bone such that the forearm and hand form at obtuse angle to the shoulder region and digging motion is not so much along the body as to the sides (raking movements); (d) an increased length of the olecranon process and augmented mobility of articulation of both forearm bones with an increase in their anteroposterior diameters (especially the olecranon process), which indicates greater range and force of movement in the elbow joint with the absence of rotatory movement of the forearm, stronger digital flexors and extensors, as well as general

increase of the mechanical load upon the distal limbs; and (e) elongation of the hind limb. Compared with the nonspecialized type, structural changes of the hind limb are comparatively small; they attest to some strengthening of the muscles that anchor the body during forelimb action and restriction in movement of the hip joint.

It is interesting to note some specific characteristics of limb structure in mole voles (*Ellobius*) in view of their probable separate ancestry among burrow-dwellers of the hamster subfamily and the somewhat different nature of their fossorial adaptations. The limbs of this animal simply throw out soil loosened by the incisors. Differences primarily relate to limb proportions, which differ markedly from those in Microtinae. The relatively long forelimbs and short hind limbs (the ratio is reversed in voles) are almost equal in length. The broad foot is "spade-shaped" for throwing soil, and the head of the humerus is oval (allowing more uniform movement at the shoulder joint). The forearm bones are strongly upcurved and comparatively narrow in their anteroposterior diameter (less mobility of fingers and hand), and the neck of the femur is somewhat longer. A few other differences were noted by me earlier (Gromov *et al.*, 1963).

3. *Swimming type of structure in voles using their hind limbs:* Both pairs of limbs are long especially the hind ones, mainly due to elongation of the foot and are designed for strong long-sweeping movements. Compared with the hind limbs, the forelimbs are shorter than in other voles. All tubular bones are massive, having large diaphysis in both longitudinal and transverse axes; the diaphysis of the femur is more massive than in other voles, indicating a high mechanical load.

The humeral structure is similar in many respects to that of fossorial forms. However, the head of the humerus is notably longitudinally elongate, the trochlear crest is high, and the trochlea itself is slightly constricted in the middle; thus, movement at the shoulder joint is more uniform and the sweep of the elbow joint is comparatively large although the joint itself is not as strong as in digging forms. The ulna has a small anteroposterior diameter and is strongly fused with the radius; their combined curvature is variable and depends upon the degree of fossorial adaptation. The femur, as in the digging forms, has a massive lower section, a large patella, and in microtines best adapted to swimming (*Ondatra*), is relatively short with a strong third trochanter (strong hip-femur flexors). The tibia is short with a long outer crest, indicating strong flexors of the knee joint and extensors of the hip joint; the distal end of the

tibia is strongly emarginate and suggests strong development of the tendons of the digital flexors and extensors. Differences between the water vole (*Arvicola*) and *Ondatra* are quite significant: the hind limb in the former is less of a "swimming" type and the forelimb is more a "digging" type.

ORIGIN AND EVOLUTION OF THE SUBFAMILY

Our present understanding of the origin and evolution of voles is based mainly on dental data. Unfortunately, to date this is the only means for formulating comparative ideas regarding the group's evolution based on living as well as fossil material (Gromov, 1972).

As noted earlier, evolution of the initial tuberculate tooth in the entire series of families and genera of hamsters has led repeatedly to the appearance of a prismatic tooth of varying degrees of perfection. However, such evolutionary trends for the animal *per se* would appear nonadaptive since the general level of specialization typical of voles has not been achieved anywhere else except in this group. Such are the North American sylvan genus *Neotoma*, the South American *Phyllotis*, and *Brachytarsomys* of the Malagasian Nesomyinae, and among extinct forms, vole-toothed hamsters such as *Trilophomys*, *Baranomys*, and *Pannonicola*.

In the early 1930s,* Hinton (1926), while maintaining that a multituberculate molar structure is primitive, identified forms of mouse-like rodents whose molars had three rows of tubercles on the masticatory surface as probable microtine ancestors. Hinton observed traces of such a structure on the unworn molars in *Prometheomys*, *Dicrostonyx*, and *Arvicola*. According to him, the number of such tubercles including the most reduced ones of the middle row was 17 (*Dicrostonyx*) and may have been as many as 21 in the ancestral form. This raises doubts about the possible origin of the vole-like tooth from a secondarily simplified tooth with tubercles arranged in a double row, as seen in most Cricetidae.

The final solution to the problem requires a series of investigations on late embryonic and early postembryonic stages of molar development in a large number of "mouse-like" rodents, including extinct animals (difficult because of the poor fossilization of young animals) in order to explain the homologies of dental tubercles and prisms. Work of this kind has only begun but preliminary results contradict rather than support Hinton's views.

*[sic]; should read "late 1920s"—Eds.

In one way or another, the majority of mammalogists, including myself, hold the opinion that the direct ancestors of microtines were hamsters of the hesperomyid type, close to the three above-mentioned extinct genera from the European Mio-Pliocene, or forms such as *Ischymomys* from the Late Miocene of Asia. Whether some 55 genera of voles evolved independently in the New and Old World while others evolved from forms widely distributed in the northern Holarctic, cannot be completely ruled out.

Vole-toothed hamsters coexisted with late forms of hamsters of the family Cricetodontidae, many of which had lost their characteristic additional molar elements toward the Middle Pliocene and acquired a simplified tuberculate tooth typical of most true hamsters of the Old World. Therefore, and because of the similarity in other skull characters, several authors do not exclude the possible direct origin of voles from late cricetodontids (Kretzoi, 1969).

As already mentioned (p. 31), the prismatic tooth of voles and vole-toothed hamsters is in any case easily derived from the tuberculate tooth of Cricetinae. All early-wearing low tubercles and deeper valleys separating them form the initial opposite prisms and a unique "rhombodont" structure of the masticatory surface (Thaler, 1962); the cingulum of M_1 and of M^3 is an element of the paraconid section and "heel" respectively. Together with increased crown height and fusion and loss of roots, division of the tuberculate tooth into two areas—anterior and posterior—takes place. Concomitant with such changes and with the predominance of propalinal mastication, the attachment of the masseters also changes (Repenning, 1968). A qualitative jump in this common progression was the loss of roots and the formation of a persistent high-crowned tooth biomechanically suitable for action on fibrous food. Various combinations of archaic and more "advanced" structural characteristics many of which were described above (pp. 30–38) are used widely by the taxonomist as indices of stages of evolutionary development within the subfamily.

The first group includes the most ancient Mio-Pliocenic microtines. They are characterized by many cricetid dental characters as well as mandibles that already exhibit a clear predominance of vole characters. The molars are structurally primitive: the upper molars have at least three, sometimes even four roots; M_1 has a posterior loop, three basal triangles, and an anterior loop; M^3 has an anterior loop, two basal triangles, and a short heel. The enamel does not differ in thickness on the lateral molar surfaces nor on the anterior and posterior side of the loops; on M_1 the lower enamel margin

is straight. Structurally, the posterior triangles are mainly rhomboid and the middle triangles on all the teeth are either opposite or broadly contiguous. The "island" on M_1 , if present, is anterior or medial. There is no cement in the folds. Among present-day voles, the M_3^3 typical of this [first] group is retained only in the long-clawed fossorial mole vole. Incidentally, in some Lemmini a baranomyid type M^3 structure, rather than the vole type, can also be readily identified. Most probably, the masticatory adaptations of the foregoing voles were within the limits typical of the first morphofunctional type (p. 50).

The second group includes microtines with rooted teeth from the Plio-Pleistocene as well as modern forms whose molars are in different stages of root simplification and complexity of their primarily simple crowns. Members of this group that survived to modern times flourish in the forests of the Old World and in the aquatic-marshy biotopes of the New World. These are voles of the tribe Ondatrini, voles with rooted molars from the subtribes *Pliomyi* and 56 *Clethrionomyi* of the tribe *Clethrionomyini*, and *Villanyia* and possibly some species of *Mimomys* from the tribe *Microtini*. Among American microtines, the extinct genera *Pliophenacomys*, *Pliopotamys* (Ondatrini) and the modern genus *Phenacomys* should be included under this type. The third upper molar always has two roots; sometimes the same number is also present on the second molar (though this molar often has three roots) and the anterior molar tends toward a reduced third root in some forms. The anterior part of M_1 (the paraconid) is complex: one accessory loop or, in some cases, even a pair of accessory loops that are separated from each other, is present at the base of the anterior loop. The posterior section of M^3 is equally complex. Molar enamel varies in thickness and may be thinner on the occlusal surface either in the folds, at the apices of the triangles, or on one of the walls of the triangles. On M_1 the lower enamel margin is uneven with tongues of dentine extending upward along the lateral surface of the prisms. The triangles are alternate, although they may not be completely separated, with the exception of the more often widely-fused or opposite additional loops of the anterior section of M_1 and the posterior section of M^3 . There are no "islands" on M_1 with the rare exception of a false "island" in some individuals. Cement is either absent from the folds or varies in deposition.

The third group is characterized by secondary simplification of the anterior section of M_1 and the posterior section of M^3 through the loss of the "island" formed from the anterolateral fold and,

together with this island, a secondary prismatic fold on M_1 . This simplification commenced in sufficiently early stages of ontogeny of similar adaptive secondary specializations (in the ancient cementless forms of the genus *Promimomys*); in still earlier stages of ontogeny, it may be impossible to trace this simplification during postnatal ontogenesis. M_1 having lost the "island" through secondary simplification has acquired the appearance of a primitively simple tooth, a transformation that makes it difficult to determine the relationship between ancient animals and descendants with rootless molars. Only M^3 has retained a distinct trace of such simplification, as expressed in the significantly variable depth of the anterolateral fold and its adjacent fold. In addition to the specialized *Promimomys*, this morphology is also seen in *Mimomys* and the American genera *Cosomys* and *Ogmodontomys*.

The fourth group is characterized by a qualitative jump, namely the loss of roots, a transition in which they initially appear at later ontogenetic stages and finally do not form at all, the tooth becoming rootless. This trait has evolved independently from forms with rooted molars whose stage of crown complexity represents the second and third groups, e.g., the tribes Microtini and Lagurini. The process is completed fairly quickly in the geological sense and, as a result (and possibly for taphonomic reasons), reliable transitional forms are known only for *Mimomys* and the Lagurids *Arvicola* and *Villanyia*. Incidentally, some authors recognize *Villanyia* as the ancestor of most modern microtines with rootless molars (Chaline, 1972). As in voles of the second group, the degree of structural complexity may include complete additional loops on the paraconid section of M_1 and the posterior section of M^3 , variably formed additional triangles, variable differentiation of enamel thickness, and cement more or less deposited or completely absent. The molars of Arctic lemmings (*Dicrostonyx*) reach a maximum complexity that involves the posterior section of M^1 and M^2 and the anterior section of M_2 and M_3 . The most archaic structure of the first molar is found in true lemmings (the paraconid exhibits the beginning of complexity) and *Allophaiomys*. For the latter, however, it is not clear whether we are dealing with the beginning of complexity or with secondary simplification of the ancestral rooted molar. The question is important because many authors now associate the genus with the history of *Microtus* in a broad generic sense.

The nature of masticatory movements in the last three groups apparently differs and the morphofunctional groups identified earlier (p. 50) do not necessarily match systematic groupings. How-

ever, the four stages of dental differentiation undoubtedly reflect some still unexplained biomechanical advantages of cranial structure and evolution, the characterization of which is often not even based upon complete tooth rows but only on isolated molars. In their present systematics, such groups merely represent stages of phylogeny ("grades" of the American paleomammalogists) through which the different phyletic lines have passed and which they may only partially resemble.

Major Chronological Development of the Subfamily

End of Late Miocene—Middle Pliocene: During this period in the northern hemisphere, the hipparionid faunas of Europe include the first remains of vole-like hamsters (*Baranomys* and *Trilophomys*) and the ancient microtines themselves, together with numerous and widely-distributed cricetodontids. If we assume that the discovery of fossil remains implies in most cases the abundance of the group, then the appearance of ancient microtines possibly occurred in the Early Miocene. One of them, *Microtoscoptes*, is common to the Old and New World; the remains of two others, *Aratomys* and *Ischymomys*, have been found to date only in the central region of Asia, and the latter is the only distinctly Miocene genus. In the extensive literature on European Miocene faunas, mice and primitive hamsters are absolutely dominant; the absence of ancient voles during this period can hardly be considered incidental. Remains of *Promimomys* and *Pliomys* are known at the end of the Middle Pliocene in Europe and in North America at this time (if the correlation of strata is fairly precise). *Ogmodontomys*, with a first molar already at the stage of secondary simplification, has appeared in these strata.

The fate of vole-toothed hamsters in the Old and New World was different. In Eurasia, they probably could not compete with true voles, which were better adapted for living in open plains of the steppe environment. The remains of vole-like hamsters have not been found later than the Pliocene—Pleistocene boundary, when they occur together with highly-developed microtines of the genus *Mimomys*. In the New World, especially among the isolated theriofaunas of South America, vole-like specialization of hamsters occurred successfully even into the Recent epoch.

Late Pliocene—Ancient—Early Anthropogene: At this time, *Promimomys* and *Pliomys* are replaced by *Mimomys* of the Khaprovsk faunal association. Within this association are also found the first voles with rootless molars of the genera *Lemmus*

(Europe) and *Synaptomys* (Eurasia and North America). In the faunal association following the Khaprovsk and Tamansk complexes, species abundance decreases and frequency of *Mimomys* increases, and during this interval, mixed *Mimomys*–*Allaphaiomys* faunas are replaced by the *Allophaiomys*-type lagurodont.

In the Khaprovsk *Mimomys* fauna, genera with a complex as well as secondarily simplified M_1 structure predominate, while forms with cement are abundant in the later faunas. Fossils of *Dolomys* and *Pliomys* are also found but in small numbers, especially in more northern faunas. In some voles with rooted molars from the Late Khaprovsk faunas, root initiation takes place at later stages of individual development, a possible indication of the transition to rootless teeth. In the southern Great Plains of North America, the Blancan faunas (except the later) are the faunal analogue of the Villafrancan faunas. They contain genera that are near, if not identical to, the level of dental specialization seen in the above-mentioned rooted-toothed forms of the Old World. Such are *Mimomys* (stage *Cheria*) and *Ophiomys*, on the one hand, and *Dolomys*–*Pliomys* and *Pliopotamys*–*Pliophenacomys*, on the other. Cement appeared earlier in New World voles with rooted molars (the *Dolomys*–*Ondatra* line) than in Old World forms with rootless teeth.

In the Tamansk faunas, development of molars lacking roots and cement is represented by the lagurid lineage from the genus *Lagurodon* sensu lato, possibly through the West Asian genus *Jordanomys*, to voles of the genus *Villanyia* with rooted molars. Animals with cement and rootless molars, i.e., the genus *Allaphaiomys*, and also several water voles of the genus *Arvicola*, probably originated from the *intermedius* species group of *Mimomys*. These, as well as forest voles of the genus *Clethrionomys*, are the most common forms in Tamansk faunas. The faunal analogues of these later groups are the Late Blancan faunas of North America and the Wald-Arno faunas in Europe.

Early–Middle Anthropogene: This period is characterized by a rapid proliferation of microtines with rootless molars. In the Tiraspol and Khazarsk faunas of Eurasia, the teeth attain specialization typical of the third group as in most genera and subgenera of the tribes Microtini and Lagurini, whose remains numerically dominate deposits from this age. In sites from northeastern Siberia and Alaska, analogous to the Tiraspol faunas, the ancestors of living Arctic lemmings '*Praedicrostonyx*' have been found. These underwent rapid dental evolution in the direction of mod-

ern *Dicrostonyx* during the Early to Middle Anthropogene. Rooted-toothed voles from the ancient nucleus of this group can be considered the few surviving groups in these faunas. These are the later *Mimomys* (*intermedius* group) and *Pliomys*. At approximately the same time, species of *Microtus*, *Pitymys*, and *Pedomys* became dominant in North American late Irvingtonian faunas of Kansas, while fossil genera of voles with rooted teeth did not survive this boundary (Hibbard *et al.*, 1965). From this time onward, the earliest *Ondatra* as well as remains of endemic genera such as *Neofiber* and *Phenacomys* are known from America.

Finally, according to some paleomammalogists (Chaline, 1972), species of *Allophaiomys* extended their distribution into Western Europe at the end of the Middle Pleistocene, after which occurred the further rapid evolution of microtines with rootless molars and the formation of modern fauna.

The Khazarsk (Mindel-Riss) vole faunas contain almost exclusively living genera. It is true that in Europe the last members of *Pliomys* had survived in ancient faunas of this type (on Mediterranean islands they occur even in the Riss), as did *Lagurodon* among the rootless-toothed voles. Major differences from the more recent faunas are significant in areas of origin and occurrence of extinct species, many of which are immediate ancestors of modern species. The vole faunas of modern European tundras probably evolved during the pre-Riss period. In North America, the modern microtine fauna was also formed by the period of maximum 59 (Illinois) glaciation. Only the forest vole (*Clethrionomys*) has been found in North America since this time, which may indicate the comparatively rare penetration of this genus in the New World. Incidentally, Chaline (1972) has assumed an Early to Middle Pleistocene arrival in the New World for the ancestors of most modern American microtines of the genera *Microtus* and *Pedomys*.

Late Pleistocene–Holocene: Numerous well-preserved vole fossils from this time permit us to reliably conclude that the current distribution of extant species, some represented by extinct subspecies, occurred during this period. In the Palearctic this process is associated, on the one hand, with rearrangement and north-south shifts of environmental zones during cooling periods and at the beginning of warm (dry and humid) phases, and on the other, with a west-to-east change in open environments under the influence of the same factors. Such processes also took place in the New World; however, the zonal, and accordingly the faunal, changes were more complex because the initial picture varied more due to the exis-

tence of the large transverse Cordilleras. As in the case of other mammals, the most indicative evidence of such range shifts is the discovery of northern (present forest and tundra) species far south of the region of their present distribution; west-east change is indicated by a shrinking of the western distribution of forms known today only from the east.

Such distributional changes undoubtedly took place in microtines from older faunal groups; however, such faunas have not been reported because of insufficient study.

Thus, all available information on the modern and extinct members of the subfamily allows the following conclusions: (1) a date of at least the Late Miocene for origin of the subfamily; (2) a close affinity of ancestral microtines in the Old and New World and a similar direction of morphofunctional restructuring of their teeth; (3) a more primitive condition of geochronologically similar New World forms, which is readily explained by differences in the age of deposits containing these fossils: in Europe, the Pliocene–Pleistocene boundary passes higher than in America (Kretzoi, 1969); (4) the ancient endemic nature of both continents at supra-generic levels: Lagurini in Eurasia and, at a similar taxonomic level, the genera *Neofiber* and *Phenacomys* in North America; and (5) a rapid Pleistocene evolution and correspondingly greater generic differentiation of microtines in the Old World because of predominance of the tribes Microtini and Clethrionomyini in Eurasia.

BRIEF HISTORY OF TAXONOMY AND CLASSIFICATION

To date, rodent taxonomy has been poorly analyzed compared to other mammalian orders, and the information obtained in this field is far from sufficient to allow a natural (evolutionary) classification. At the same time, the paleontological history of microtines is quite complete and, in this case, should be viewed as a reliable basis for continued development of such a classification.

The phylogenetic position of voles among Myomorpha has been variously interpreted. Some authors consider voles a subfamily of the rat family (Muridae): G. Waterhouse (1842), E. Brandt (1855), G. Miller (1896), Trouessart (1897), L. Mehely (1914), M. Hinton (1926), B.C. Vinogradov (1933), J. Ellerman (1941), N.A. Bobrinskii, B.A. Kuznetsov, A.P. Kuzyakin (1944, 1965), C.E. Ognev (1948), C. Anderson (1960), E. Hooper and B. Hart (1962). Others consider them a subfamily of the small hamster

family (Cricetidae): B.C. Vinogradov and A.E. Argiropulo (1941),
60 G. Simpson (1945), B.C. Vinogradov and E.M. Gromov (1952), A.
Wood (1955), E. Hall and K. Kelson (1959), E.M. Gromov, A.A.
Gureev, G.A. Nobikov (1963), V.E. Flint, Yu.D. Chugunov and Y.M.
Smirin (1965), N.N. Vorontsov (1966, 1967), and the American
paleomammalogist C. Hibbard in many of his publications.
Finally, even since pre-Linnaean times, several mammalogists have
considered voles an independent family of Myomorpha: K. Illiger
(1811), K. Zittel (1893), T. Tullberg (1899), M. Kretzoi (1955b),
S. Schaub (1958), J. Kratochvil (1959), J. Chaline (1972, 1974,
1975), as well as G. Waterhouse in his earlier publications. The
higher taxonomic rank assigned to voles, especially in recent years,
is based on exhaustive studies of living and fossil forms.

The number of tribes listed for the family (or subfamily) varies
from three to six; moreover, three to four suprageneric groups
are also identified in the most extensive tribe (Microtini). The
number of genera also varies significantly, depending mainly on
whether generic or subgeneric rank is assigned to various groups
in *Mimomys* and *Microtus*.

Only in recent years have the first serious attempts been made
to formulate a natural classification of Microtinae that includes fos-
sil members and that considers extinct rooted-toothed voles ances-
tors in lineages giving rise to modern voles with rootless molars. As
yet, the fossil material required is far from complete. Nevertheless,
our knowledge has substantially increased during the last 10 to 12
years so that a natural ("vertical") classification of the major tribes
of Microtinae may be expected in the near future.

Before the publication of G. Miller's work (1896), which left
its imprint on many subsequent taxonomic studies of voles, mostly
artificial classifications were proposed that had the major shortcom-
ing of using only one character in diagnosis, viz., size of ears, num-
ber of plantar pads, or dental structure. Such an approach led to an
amusing combination of genera into higher groups. G. Miller's con-
tribution is that, having accepted the idea of complex characteristics
of supraspecific groups that was distinctly expressed in the classi-
fication proposed by the French mammalogist F. Lataste (1886),
he applied it to the whole group. How much importance Lataste
(1884) attached to this principle can be seen from his fairly sharp
dissension with the Russian mammalogist E.C. Polyakov (1881),
who ascribed major importance to dental structure in his taxonomic
review of Siberian voles published after G. Blasius (1857).

Miller identified two suprageneric groups of voles, viz., Lemmi and Microti, with three genera in the former and four in the latter; both groups have invariably figured in all subsequent classifications.

As for other rodent groups, we owe much to Schlosser (1884) and Major (1873), who tried to create a unified classification of modern and fossil forms. However, such attempts were sufficiently fruitful only in the case of Hinton (1910) and were further developed in his famous, but unfortunately incomplete, monograph, of which only the first volume was published (Hinton, 1926). Here mention may be made of the Mehely's classification (1914), which was most progressive for its time. In this classification, he separated the rooted-toothed voles as an independent subfamily, Fibrini, with two suprageneric groups. This underscored taxonomically the evolutionary irregularity of certain features, and the difficulty in constructing a natural classification of arvicolids. Mehely's classification also influenced the opinion of Russian mammalogists (Ognev, 1948; Vorontsov, 1967).

Hinton's classification, like Miller's, was fairly viable; it contained few changes but significant additions, especially at the generic and subgeneric levels, and remained unaltered through the 1950s. In his famous publication, Simpson (1945) raised both suprageneric groups of Miller and Hinton to the rank of tribe—Lemmini and Microtini. He further separated Ellobiini as an independent tribe. Among the 34 genera forming the subfamily according to Simpson, Lemmini comprises one extinct and four modern genera, Microtini—11 extinct and 16 modern genera, and Ellobiini—one extinct and one modern genus.

Further progress in the study of fossil voles, on the one hand, and of the comparative anatomy of modern forms, on the other, yielded several new interpretations. Two—Kretzoi's (1955b) and Hooper and Hart's (1962)—are quite interesting as they reflect opposite tendencies among modern classifications, not only for our interest group but also for rodents in general.

Kretzoi has classified the family Arvicolidae as follows:

†Subfam. Baranomyinae
 Gen. *Baranomys*
 Gen. *Microtodon*

†Subfam. Microscoptinae
 Gen. *Microscoptes*
 Gen. *Goniodontomys*

Subfam. Ellobiinae	† Gen. <i>Mimomys</i>
Gen. <i>Ellobius</i>	Gen. <i>Kislangia</i> *
† Gen. <i>Ungaromys</i>	† Gen. <i>Arvicola</i> **
† Gen. <i>Germanomys</i>	† Gen. <i>Villanyia</i>
Subfam. Prometheomyinae	† Gen. <i>Phaiomys</i>
Gen. <i>Prometheomys</i>	† Gen. <i>Allophaiomys</i>
Subfam. Lemminae	Tribe Ondatrini
Gen. <i>Lemmus</i>	Gen. <i>Ondatra</i>
Gen. <i>Synaptomys</i>	Gen. <i>Neofiber</i>
Gen. <i>Myopus</i>	Gen. <i>Dinaromys</i>
† Gen. <i>Pliolemmus</i>	† Gen. <i>Ogmodontomys</i>
Subfam. Myospalacinae	† Gen. <i>Pliomys</i>
Gen. <i>Myospalax</i>	† Gen. <i>Dolomys</i>
† Gen. <i>Prosiphneus</i>	Tribe Microtini
Subfam. Arvicolinae	Tribe Lagurini
(= Microtinae)	Gen. <i>Lagurus</i>
Tribe Arvicolini	Tribe Dicrostonychini
† Gen. <i>Promimomys</i>	

Besides the three “classical” suprageneric groups—lemmings, mole voles, and voles (accorded subfamilies by Kretzoi, since he ranked voles as a family)—we also accept the independent position of long-clawed mole voles (*Prometheomys*) and zokors (*Myospalax*, *Prosiphneus*), which Kretzoi combined with voles, and of two extinct groups based on the genera *Baranomys* and *Microscoptes*. The suprageneric group of voles *per se* (“Microti” of the old authors) is the most complex in composition, and divided into five groups of suprageneric rank (tribes according to Kretzoi and subtribes in other classifications). As in other groups, these also include modern and extinct genera, although they clearly belong to several lineages. Despite the drawbacks and the disputed position of individual taxa, Kretzoi’s classification contains many important improvements. These are the inclusion of Arctic lemmings, long-clawed mole voles, and mole voles under different suprageneric groups and, contrarily, the combination of genera such as *Ondatra*

*Extinct, but not so marked in Russian original—Eds.

**Extant, but marked extinct in Russian original—Eds.

and *Dolomys*, *Mimomys* and *Arvicola*, and several others into single groups. Kretzoi's classification is an attempt to create a natural (phylogenetic) classification, which is to be expected from a micro-paleomammalogist who adhered to Darwinian concepts.

The classification of Microtinae provided by Hooper and Hart is as follows:

Tribe Lemmini	Tribe Dicrostonychini
Gen. <i>Synaptomys</i>	Gen. <i>Dicrostonyx</i>
Gen. <i>Myopus</i>	
Gen. <i>Lemmus</i>	Tribe Neofibrini
	Gen. <i>Neofiber</i>
Tribe Clethrionomyini	Tribe Ondatrini
Gen. <i>Clethrionomys</i>	Gen. <i>Ondatra</i>
Gen. <i>Eothenomys</i>	
Gen. <i>Antelionomys</i>	Tribe Microtini
Gen. <i>Aschizomys</i>	Gen. <i>Lagurus</i>
Gen. <i>Alticola</i>	Gen. <i>Arvicola</i>
Gen. <i>Hyperacrius</i>	Gen. <i>Microtus</i>
Gen. <i>Dolomys</i>	
Gen. <i>Phenacomys</i>	Tribe Ellobiini
Tribe Prometheomyini	
Gen. <i>Prometheomys</i>	

Here, further separation of suprageneric groups is proposed among modern members of the family: tribe Neofibrini for the living American genus *Neofiber* and Clethrionomyini with eight genera. Other suprageneric categories of modern voles are the same as in Kretzoi's classification with the exception of zokors, which Hooper and Hart have rightly excluded from voles. A shortcoming of Hooper and Hart's classification is the absence of fossil forms; its indisputable advantage is that, of all known classifications, the largest number of morphological parameters have been taken into account in evaluating relationships, and these parameters are essentially the basic ones used by mammalogists with the addition of karyological analysis. They include structure of the male genitalia (including the shaft and bony parts), teeth (including incisors), the hard palate, basicranial bones, tympanic bullae, location of the mandibular foramen, number of planter pads, nipples, and various other "macrosomatic" characters. Unfortunately, shortage of material did not allow the authors to

classify the entire family. Furthermore, the conclusion drawn by Hooper and Hart is confusing. Thus, they propose that either the modern members of the family can be divided into eight tribes, or the modern and fossil members into two tribes (Microtini and Ellobiini), or with generally equal success even a "tribeless" classification. Such a position is equivalent to an acknowledgment of the futility of a phylogenetic classification, including solution of the problem of phylogenetic relationships within large taxa, at least at the present level of study. This, naturally, does not facilitate progress.

Development of Kretzoi's ideas presented above can be found in article on microtine classification published after almost 50 years of intensive study of extinct and modern forms (Kretzoi, 1969). Compared with his 1955 scheme, the essential changes are these: Microscoptinae, Baranomyinae, and Myospalacinae are separated from the vole family; two new tribes have been established within the subfamily Arvicolinae—Pliomyini and Myodini (= Clethrionomyini, following Hooper and Hart); and the tribes Arvicolini and Microtini are combined into a single tribe and 26 genera.

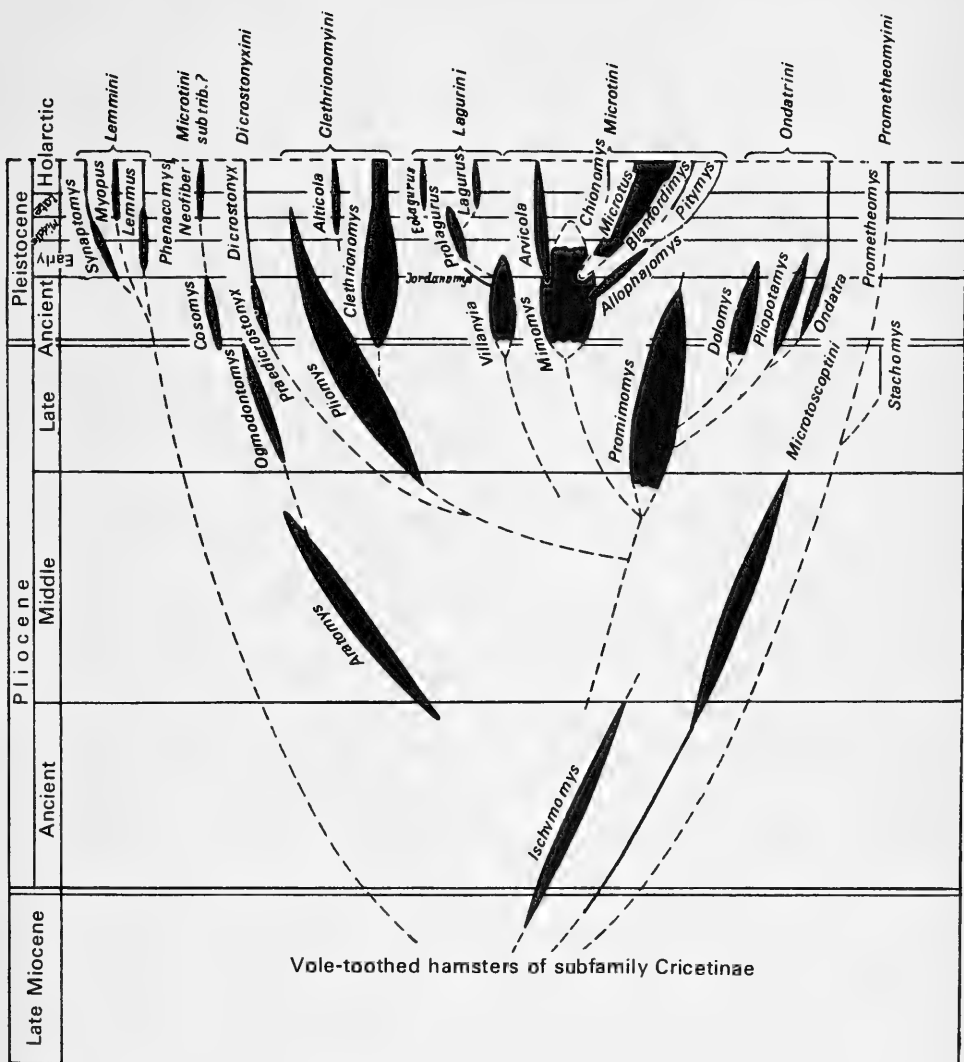
63 Lastly, the French paleomammalogist Chaline (1975), who extensively studied the extinct rodents of Western Europe in the last decade, separated from the Arvicolinae an independent subfamily, Dolomyinae which included the tribes Ondatrini, Pliomyini, Arvicolini, and Microtini. However, in my opinion this is not a natural unit and consequently Chaline's entire suprageneric classification should be considered a step backward compared to Kretzoi's (1969) classification. Actually, not considering the last two tribes (Arvicolini and Microtini), fewer structural features are found in the remaining tribes, which indicates a closer phylogenetic link between them than is found in tribes of other subfamilies accepted by Chaline following the classification of Kretzoi. At the same time, the composition of Chaline's tribe Pliomyini is more complete than Kretzoi's, at least with regard to Old World genera.

My article dealing with the supraspecific taxonomy of microtines was published in 1972. While the manuscript was in press, I learned of Kretzoi's second article and with great pleasure discovered that our publications were similar in recognition of suprageneric taxa. However, significant differences exist in the assignment of taxonomic rank and especially in their generic composition. For example, I considered the genus *Pliomys* as the only member of the subtribe Pliomyi of the tribe

Clethrionomyini, which includes the nominate subtribe with two genera and Alticoli with three. In addition, I kept MicrotoscOPTINI among the microtines, but excluded *Ellobius* (I now believe that the mole voles are vole-toothed hamsters which became fossorial). Earlier I considered *Microtodon* a member of another tribe of the subfamily (I now believe that this should be considered a subtribe whose position among Cricetidae is as yet unclear). During the last three years, my views on generic and subgeneric level, especially for broadly-defined taxa, have also changed, based on study of my own and material of my colleagues.

As argued earlier, I continue to hold that the only correct basis for constructing a classification is similarity based on affinity, which requires, as rightly emphasized by Vorontsov (1926) not only declarative recognition but also information from the three classical sources, viz., paleontology, comparative morphology, and embryology, including data on ontogeny and heredity. The fact that our present state of knowledge cannot provide a strict "vertical" (based on affinity) classification, instead of a "horizontal" (based on similarities) one, does not mean that we should reject schemes presenting a somewhat intermediate position. This should not weaken our research efforts, however, for factors that will bring us closer to the construction of a natural phylogenetic classification.

I am fully aware that such an "intermediate" system is presented in this book. A division of the subfamily into suprageneric groups has been accepted that combines the above-mentioned schemes to a variable extent: eight tribes with three Palearctic subtribes. Possibly, the rank of subtribe or even tribe should have been attributed to three endemic American genera—*Neofiber*, *Phenacomys*, and *Lemmiscus*. The 11 recognized suprageneric taxa contain 42 genera and 21 subgenera. Such a classification fully reflects my understanding at the time of completion of the manuscript (pp. xvii–xxv). The tribes (subfamilies) Myospalacini, Baranomyini, and Ellobiini of Kretzoi have been included under the hamster subfamily (Cricetinae). The tribe of rooted-toothed voles, Fibrini, lacks basis for independent status. Many of its extinct genera can now be considered ancestral rooted-toothed forms of different tribes. The tribe Microtini should also be viewed as composite in this respect. Thus, in addition to the three American genera mentioned above, the genus *Villanyia* must be placed at the base of the tribe Lagurini and different taxa from the *Mimomys* group at the base of the genera *Arvicola* and *Allophaiomys*; it is also necessary to separate subtribes in



64 Figure 8. Scheme of probable relationships in the subfamily of voles (Microtinae) (from Gromov, 1972, with modifications).

65 the tribe Microtini. Thus the artificial formation of the latter tribe will become significantly rearranged toward a more natural classification, which is partially reflected in the phylogenetic scheme in Figure 8.

It should be emphasized that the intrageneric taxonomy of microtines has progressed significantly in recent years, because the study of morphologic variability of rooted teeth in modern and extinct forms has proved fructuous. Such studies provide comparative data characterizing the evolutionary process in this part of the digestive system in time and space. It thus became possible to relate the appearance of new species to moments of qualitative change similar to the phenomena of chronocline, clinal, and other kinds of geographic variability (Chaline, 1972; Maleeva, 1976). Unfortunately, in his later publications, the French paleomammalogist Chaline (1974b, 1975) gave undue importance to the structural features of M_1 and M^3 for separating microtine subgenera. Most of the species groupings so formed appear extraordinary to a researcher who uses a larger number of characters for this purpose.

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TAXONOMY

Subfamily MICROTINAE Cope, 1891

(= Arvicolinae Gray, 1821)—Voles

Diagnosis: The following basic set of characters enables the determination of the probable taxonomic affinity of living and fossil voles to the subfamily Microtinae, and the exclusion from this subfamily of several extinct suprageneric taxa of voles (Cricetinae) (*sensu lato*) assigned the rank of subtribes, tribes or even independent subfamilies (Baranomyini, Cricetodontidae,* etc.) by various authors.

1. Molars with triangles having pointed raised angles on flat masticatory surface and arranged oppositely (primary, "rhombodont" structure) or alternately (secondary, "deltodont"). This molar structure is evidence of origin from hamsters, in which molars have opposite tubercles with closed depressions between them.

2. M_3^3 with minimum of three segments, and not shorter, or slightly shorter, than M_2^2 . Third molar in hamsters is significantly shorter than second, consisting of two segments, or is sigmoid in shape.

3. Anterior margin of the ascending mandibular ramus, in lateral view, covers or almost covers M_3 . In hamsters, it overlaps the lower half of M_3 .¹

4. In voles, groove (place of insertion of p. anterior m. masseter medialis) is well developed and parallel to the anterior margin of the ascending mandibular ramus. This groove is generally lacking in hamsters.

5. Medial junction of the symphysis (insertion of m. digastricus) of the mandibular ramus is distinct; here, ventral margin of ramus forms an angle up to 120° but not more than 150° . In hamsters, the ventral margin is normally rounded and the angle greater than 150° .

* A family of vole-toothed hamsters and not a subfamily—Eds.

¹Characters 3 and 4 were established by Repenning (1968).

6. With secondary simplification of the anterior (paraconid) section of M_1 , the "island" on this molar forms an anterolateral fold as a result of incomplete closing, rarely an anteromedial fold, and an anterior fold only in the most primitive forms. If such a fold forms in hamsters, it is only of the anterior type.

7. When the lower incisor is long, it extends posteriorly up to the molar roots or variably beyond them. In hamsters, this incisor terminates posteriorly midpoint of the coronoid process.

Composition of the subfamily: One extinct and, at least, eight extant tribes: Microscoptini stat. nov. (foss.); Prometheomyini stat. nov.; Ondatrini Kretzoi, 1955; Clethrionomyini Hooper and Hart stat. nov.; Lagurini Kretzoi, 1955; Lemmini Simpson, 1945; Dicrostonyxini Kretzoi, 1955; Microtini Simpson, 1945. The last 98 tribe is a highly artificial grouping. Following Repenning (1968), I have excluded from the subfamily Microtinae the vole-toothed hamsters (the European genera *Microtodon* Miller, 1927; *Baranomys* Kormos, 1933; and *Pannonicola* Kretzoi, 1965) and mole voles (*Ellobius* Fischer, 1914).

Age and distribution: From Late Miocene to Early Pliocene in Asia, very Early (?) to Late Pliocene in Europe, from Middle Pleistocene in northern Africa. In the south, up to semideserts and subtropical forests; in the north, up to the Arctic tundra; and in the mountains, up to the subnival zone.

Taxonomic notes: It is natural that in the course of evolution of tuberculate-toothed Neogene hamsters, selection of microtine characters did not proceed simultaneously in all directions and the appearance of macromorphological features, including those listed above, must have preceded changes in energetics, behavior and so forth.

For the Miocene–Pliocene boundary, the geological and paleontological sequelae have provided us a complete series of vouchers attesting to the several evolutionary attempts among hamsters toward a microtine adaptive type. Because of the specificity of paleontological material, this is particularly clear in the structural characters of the molars. As in many other phytophagous mammals, these intensive "trials" of evolution were undoubtedly associated with significant changes in living conditions and a sharp depletion in Miocene fauna, including typical hamsters, due to the replacement of forest and shrubby landscapes and biotopes with open ones. As a result of these changes, free or relatively free ecological niches were formed. Their occupation by hamster-like rodents necessitated [a change to] processing a large volume of comparatively

less nutritious cellulose food instead of high-caloric seeds. This led to more powerful masticatory muscles and changed the direction and nature of their major movements from crushing to dominantly grinding. Vorontsov (1967) has traced features in cranial structure associated with these changes through an anatomical series covering primitive forms of hamsters to specialized voles. Naturally, the picture becomes much more complicated if we consider this series phyletically. Individual microtine characters, or an incomplete series of characters, or poorly defined characters, appear only in adaptive branches of the phylogenetic tree. Here, possibly, the genetic possibilities were absent or the required correlations, triggered by the same gene mechanism, simply did not develop. The appearance of a combination of fairly complex and variable features was the deciding factor; they are adequately reflected in the macro- and partially in the micromorphological characters seen in modern microtines. These characters, *in toto*, made it possible for voles to attain a comparatively high level of morphological development.

KEY TO TRIBES AND SUBTRIBES

- 1 (6). Tail significantly shorter than one-third trunk length, often shorter or only slightly longer than hind foot.
- 2 (5). Claws on at least the three middle digits of forelimb notably longer than each of them; if shorter, the plantar surface dark or ash-gray.
- 99 3 (4). Pinna rudimentary, resembles small skin fold near opening of auditory passage
..... VI. Tribe **Dicrostonyxini** (p. 262).
- 4 (3). Pinna present, though small, and covered with hair
..... VII. Tribe **Lemmini** (p. 277).
- 5 (2). Claws of three middle digits of forelimb not longer than each of them; plantar surface not dark, ash-gray
..... V. Tribe **Lagurini** (p. 239).
- 6 (1). Tail notably longer than one-third trunk length and always much longer than hind foot.
- 7 (8). Trunk length more than 250 mm; tail about three-fourths trunk length. Tail laterally flattened, covered with distinct small scales and sparse hairs
..... III. Tribe **Ondatrini** (p. 169).
- 8 (7). Trunk length less than 250 mm; tail less than three-fourths trunk length. Tail hairs variably developed and cover scales.

- 9 (10). Claw length of three middle digits of forelimb greater than length of each of them on hind limb II. Tribe **Prometheomyini** (p. 162).
- 10 (9). Claw length of three middle digits of forelimb less than length of each of them on hind limb.
- 11 (16). Molars of adult animals rooted or at least closed by dihedral angles of lateral surfaces at root end. If roots absent and angles not closed on ventral side, posterior margin of bony palate in form of straight transverse plate which barely covers posterior palatine foramina IV. Tribe **Clethrionomyini** (p. 177).
- 12 (15). Teeth rooted.
- 13 (14). Tail length much more than half trunk length. Gray tones dominant in color of back Subtribe **Pliomyi** (p. 181).
- 14 (13). Tail length about half trunk length. Brown tones with distinct rusty or rusty-red shade dominant in color of back Subtribe **Clethrionomyi** (p. 210).
- 15 (12). Teeth rootless Subtribe **Alticoli** (p. 194).
- 16 (11). Molars of adult animals rootless and folds of lateral surface open at root end. Posterior margin of bony palate in form of hollow bridge rising toward base of skull, separating posterolateral palatal pits VII. Tribe **Microtini** (p. 297).

I. Tribe **MICROTOSCOPTINI** Kretzoi, 1955, stat. nov. (foss.)

Diagnosis: Structure of hard palate not known. Molars rooted, cement absent in folds. No differences in size of lateral and medial triangles of lower molars. Enamel uniformly is thick throughout the entire lateral surface of molars. Paraconid section of M_1 is primarily simple, folded not more than once and incompletely. Unlike all other microtines, the anterior unpaired loop has a slightly asymmetric bilobate structure, and medial triangles, at least on all lower molars are opposite and isolated from anterior and posterior enamel fields. The length of M^3 is variable; it is without traces of secondary simplification; there are two dentine-enamel fields with one lateral and one or two medial folds located behind anterior unpaired loop. M_3 is moderately long; its position in molar row is not clear. Posterior end of incisor (its position more or less known for one species) continues into base of roots but, apparently, does not reach f. dentale.

100 *Composition of tribe:* Two extinct genera: *Microscoptes* Schaub, 1934 and *Goniodontomys* Wilson, 1937.

Description: Size small. Length of lower molars about 7.0 mm, M_1 from 2.2 to 3.2 mm. Posterior angle of mandibular symphysis moderate in size (*Microscoptes*); in *Goniodontomys* possibly lacking. Angle of ventral margin of mandibular ramus slight to moderate. With ramus horizontal, ventral margin covers tooth row commencing with second prism of M_2 . Distance between mental foramen and anterior angle of masseteric ridge large; this foramen may be significantly shifted toward upper surface of cutting section. Anterior part of M^1 projects slightly laterally; posterior part of M^3 not projecting; posterolateral section of latter almost rectangular. Roots form much before wearing of crown commences, their number in upper molars not less than three; in M^2 at least four in half of the specimens. Posteromedial root of M^1 is moderately or relatively long (*Microscoptes*). Of the two anterior processes, the lateral one is large and becomes angular in shape before medial one during wear. An "island" may form opposite the fold separating these two processes. Juvenile folds are present or absent; it is not known how long they are retained on M_1 . Unlike all other microtines, in most of these forms the posterior pair of triangles is fused with the posterior unpaired loop and demarcated from the two anterior triangles which are fused with each other. The structure of upper incisors not known. The crown section, particularly in *Goniodontomys*, is probably relatively long, and the incisor itself is massive. The alveolus of the lower incisor passes between M_2 and M_3 (*Goniodontomys*). Judging from one known fragment of the mandibular ramus, the posterior end of the lower incisor does not form a knob on the lateral surface of the ascending ramus.

Distribution and zonal affinity: Odessa, coast of Black Sea, eastern part of Kazakhstan, inner Mongolia, central part of North America. Composition of associate fauna provides no clue to probable ecological affinity of members of this tribe. Repenning (1968) may possibly be correct in concluding that these species were mostly inhabitants of riverine biotopes of the floodplains.

Evolution and phylogeny: Finds beyond the Late Miocene to Pliocene are not available to date. Except for Kretzoi (1969), all investigators from the time of Schaub (1934) are unanimous that *Microscoptini* are most probably a blind side-branch of microtines whose phylogeny is not clear. They combine structural features typical of *Microtinae* and *Cricetinae*. Such features are the asymmetric anterior loop of M_1 , formed by both anterior tubercles of this tooth

in hamsters; opposite anterior prisms of lower molars which coincide with corresponding tubercles in cricetines; an intact complete set of roots of M^2 ; and others. At the same time, crown height in some forms is not more than that in several vole-toothed hamsters of the New World and the structure of M^3 is much more complex. The ultimate solution about the position of *Microscoptini* in the hamster family lies in a study of new, more complete material, including at least the entire mandibular rami. Here the microtine and cricetine structure is quite distinct and the molar structure is similar, e.g., in living voles and vole-toothed hamsters of the New World. The considerable similarity between the two known genera underscores the uniqueness of Pliocene faunas of the Holarctic and does not contradict data known for other mammals.

101

1. Genus *Microscoptes* Schaub, 1934

Diagnosis: Mediolateral triangle of M^2 and M^3 at least half size of preceding one. Located against only medial fold of M^2 and tooth correspondingly has only two denticles on medial side. M^3 shorter than M^2 . Posterior section of M^3 simple in structure; triangular groove occurs behind anteromedial fold, bordered by heel of same shape as fold.

Composition of genus: Two species: *M. praetermissus* Schaub, 1934 and *M. tjuvanensis* Zazhigin sp. nov. (in litt.).

Age and distribution: Lower to Middle Pliocene in central part of Asia: Pavlodar site in Irtysh region, Tuva, northern Mongolia.

Taxonomic and ecological notes: The recent discovery of additional complete material in the USSR, which supplements the specimens from Mongolia that Schaub used in describing the type species, permits an assessment of the affinity of American and European members of the tribe that differs from Repenning's (1968). The two species warrant the rank of independent genera.

Associate fauna of the Pavlodar site in Irtysh is distinctly of the forest-steppe ("savanna") type.

1. *Microscoptes praetermissus* Schaub, 1934

Diagnosis: Size small: length of M_2 —2.2 mm, M_3 (M^2 ?)—1.8 mm. Deposition of enamel of M_1 , judging from Pavlodar specimen, retained until roots reach one-fourth to one-third crown height.

Age and distribution: Lower Pliocene of Mongolia (Ertemte, Olan, Khoreya) and, possibly, Pavlodar Irtysh region.

Taxonomic notes: Species described from M_1 intact in piece of jawbone and isolated M_3 or M^2 (M^1 according to Schaub, which is hardly correct). Judging from size (M_1 —2.5 mm) in this species, we can possibly include finds from Pavlodar suburbs where *Microscoptes* was first found in the USSR by P.F. Savinov in 1960.

2. *Microscoptes tjuvanensis* Zazhigin sp. nov. (in litt.)

Diagnosis: Size larger than preceding species: length of M_1 —3.0—3.1—3.2 mm (n = 4), M_3 —1.5—1.6—1.8 mm (n = 5). "Islands" absent on M_1 in material available.

Age and distribution: Middle Pliocene of southern Tuva ?, Late Miocene of the Ukraine.

Description: Only isolated teeth known; size: M_1 — M_2 —5.25 mm, M_2 —2.0—2.1—2.15 mm (n = 5), M^1 —2.4, 2.8 mm, M^3 —1.65 mm.

102 *Taxonomic notes:* Based on molar structure of this species, it is possible that more ancient forms of the genus were smaller and the "island" on M_1 retained for a longer time; this possibility does not contradict the evolutionary trend of molars among microtines.

2. Genus *Goniodontomys* Wilson, 1937

Diagnosis: Mediolateral triangle of M^2 and M^3 same size as preceding one. Faces corresponding triangle of medial side, where M^2 correspondingly has two folds and three denticles. M^3 longer than M^2 . Posterior section of M^3 with heel and retains rectangular profile only on lateral side; well-developed fold and two denticles present on medial side (Figure 9).

Composition of genus: One species: *G. disjunctus* Wilson, 1937.

Age and distribution: Middle Pliocene of North America.

Description: Repenning (1968), who studied fragments of the horizontal section of the left mandibular ramus pointed out that: (1) lower incisor passes under anterior root of M_3 and along lateral side of its posterior root; (2) upper crest of masseteric ridge not raised along anterior margin of ascending ramus, but approaches it not far from its anterior angle ("hamster"-type structure); and (3) posterior end of lower incisor does not extend to f. dentale. Length of M_1 —2.84 mm, M^1 —2.29 mm.

Paleoecological data: Associated fauna inhabits riverine biotopes of floodplains, which led Repenning to conjecture that this species may have been amphibious.

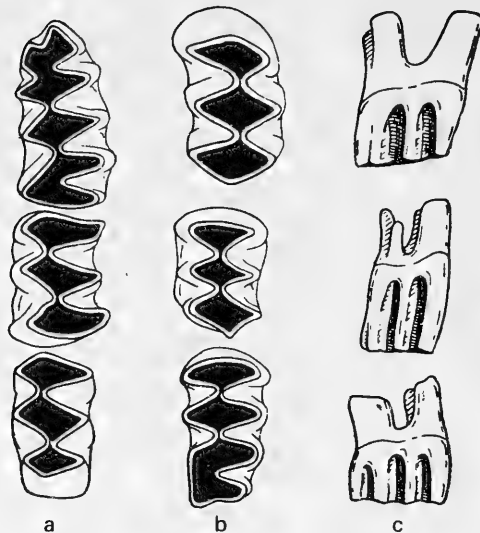


Figure 9. Molars of *Goniodontomys* (from Repenning, 1968).
a—lower molar; b—upper molar; c—same, lateral view.

II. Tribe PROMETHEOMYINI Kretzoi, 1955, stat. nov.

Diagnosis: Posterior section of hard palate (structure known only for extant genus) in form of broad bony constriction with barely perceptible posterior palatine foramina; margin of chonal groove with weak W-shaped notch at end of middle protuberance. Molars rooted, cementless. Lateral triangles of masticatory surface of lower molars somewhat smaller than medial ones; difference less perceptible in present-day animals. Enamel equal in thickness along margin of teeth. Paraconid section of M_1 primarily simple, with no more than one fold,* and that usually incomplete. Juvenile folds on lateral margin of anterior unpaired loop in extinct forms may reach half crown height. Triangles at base of this loop not completely demarcated, widely fused with each other. Antero-lateral triangle of M^2 , unlike all other microtines, much smaller than second triangle, its fold less than that of third triangle. M^3

*Throughout the text the author has used the expression "ascending angles" on the molars, which we have understood as referring to "folds". In the description of these folds, he has used the terms "first, second, and third complications," which could be interpreted as primary, secondary, and tertiary or first, second, and third order folds. We have preferred the latter terminology—Eds.

reduced or moderately long, its anterolateral fold smaller than succeeding fold (false secondary simplification). Posterior section of this tooth simple in structure: posterior unpaired loop with not more than two denticles, one fold on each side, one dentine-enamel field. Structure of M_3 , unlike majority of other microtines, similar to M^3 , but lower molar slightly reduced and without heel extending posteriorly. Bony cover lacking above root section of M_3 . Posterior end of lower incisor extends backward much above f. dentale (no known data for extinct forms).

103

Composition of tribe: Two genera: extinct—*Stachomys* Kowalski, 1960 and extant—*Prometheomys* Satunin, 1901.

Description: Similar to the tribe Ondatrini. External features in the solitary living member of long-clawed mole vole (*Prometheomys*) can hardly be considered typical for the extinct form, since adaptive modifications for a fossorial life style are no less significant than, for example, the amphibious adaptation in *Arvicola* of the tribe Microtini. Therefore, only structural features of the skull, mainly teeth, are presented below; other features are given in the generic description of *Prometheomys*.

Size: Moderate. Length of lower molars up to 7.8 mm, upper molars from 5.7 to 7.5 mm. Body length up to 140 mm (in present-day animals). Posterior margin of incisor alveoli far ahead of line joining anterior margin of alveolus of M^1 . Anterior margin of palato-maxillary suture next to posteromedial corner of M^1 . Longitudinal palatine grooves deep; section between them resembles keel with blunt apex. One pair of well-developed posterior palatine foramina present. Symphysis of mandible forms barely perceptible inner angle with ventral margin of jaw. Angle of lower margin of symphysis varies from small in *Stachomys* to rather large in *Prometheomys*. Ascending section broad: when mandibular ramus horizontal, its anterior margin covers molar row starting from second prism of M_2 ; posterior notch small. Articular process short (known for *Prometheomys*). Coronoid process extends at least to lower margin of articular process. Angular process short (*Prometheomys*), broad at base; if its posterior margin extends beyond posterior margin of articular process, does so only slightly. Distance between mental foramen and margin of crest of masseteric ridge relatively large. Upper tooth row anteriorly wide-set, relatively narrow, diverges slightly posteriorly; anterior section of M^1 projects slightly upward, posterior section of M^3 not projecting. Number of roots three in all upper molars (*Stachomys*) to three (in some individuals) in M^1 and two in M^2 — M^3 (*Prometheomys*). M_1 moderately long.

Juvenile folds one to two, sometimes retained throughout animal's life, and may form false prismatic fold. This structural feature is also found in mole voles (*Ellobius*), as is the partial fusion of the three basal triangles of M_1 into a single field, with the apex of the lateral triangle facing the bottom of the field separating the two medial ones. Formation of "islands" in the anterior section of M_1 , including the anterior or false "islands," is not known. Length of crown section of lower incisor large in *Prometheomys*; in *Stachomys*, most probably moderate, as is steepness of its bend. Alveolus of lower incisor passes under posterior root of M_2 or between M_2 and M_3 . Posterior end of lower incisor forms well-developed knob at base of condylar process (*Prometheomys*).

Distribution and zonal affinity: Present-day genus is montane and endemic to the western Caucasus Isthmus; extinct genus known from middle mountain ranges of Western Europe and foothills of Ufa region of the Urals (Sukhov, 1976). The possibility is not excluded that related forms also existed in the Early Anthropogene of North America (*Atopomys*). The literature is scant and not sufficiently explicit (Patton, 1965). Since the known members of the tribe are associated with hilly regions, perhaps the tribe was originally montane; remains of living forms have been found in the western part of the range together with remains of forest species. Incidentally, like the present-day *Prometheomys*, the possible existence of forest species in montane meadow conditions is not excluded.

104 *Evolution and phylogeny:* Remains of extinct members have been found in Early and Middle Anthropogene, but ancestral forms are not known. However, the closeness of *Stachomys* to ancestral vole-toothed hamsters, probably a unique group common with *Ellobius*, cannot be doubted. This is indicated by the structure of the last molars, the paraconid section of M_1 , location of the basal triangles of this tooth, and so forth. In both cases, primitive features must have been retained to a great extent because of their fossorial life style. The semifossorial *Prometheomys* shows closer affinity with typical microtines than *Ellobius*, which essentially better represents the vole-toothed hamsters. The reasons for extinction of this unique lineage of the subfamily possibly are related somehow to changes in the biomes during alpine orogenesis and mountain separations. The American *Atopomys* possibly might be the only unique representative of the extinct folded-toothed hamsters (*Baranomys*) in the New World.

1. Genus *Stachomys* Kowalski, 1960 (foss.)

Diagnosis: Upper molars with three roots. Posterior section of M^3 not reduced. Juvenile folds may be retained for sometime on margin of anterior unpaired loop, and, in some forms, one such fold may often form a false prismatic fold. Variable partial fusion of the triangles of the masticatory surface, especially in posterior sections of $M_1^1-M_2^2$ is rather common. Outer part of anterior surface of M^1 without longitudinal groove-like depression. Lower incisor passes under posterior root of M_2 (Figure 10).

105 *Composition of genus:* Species: *S. trilobodon* Kowalski, 1960. The various species among the series of M_1 from a single site have yet to be identified (Sulimski, 1964).

Age and distribution: Late Pliocene of Poland, Early Pleistocene of Ufa region of the Urals.

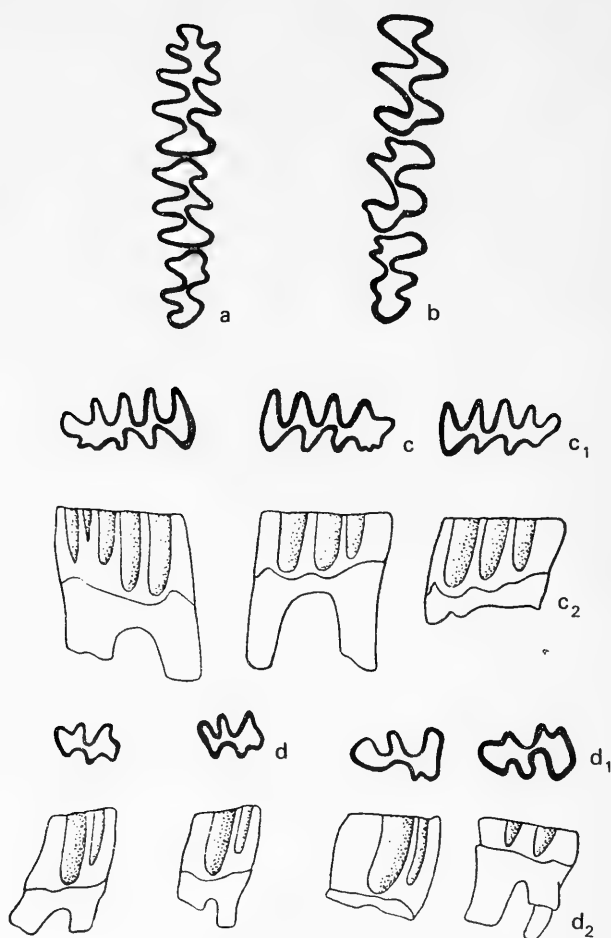
Taxonomic notes: Based on molar structure and known parts of the axial skull, this species is close to *Prometheomys*, and exhibits several primitive features. Based on structural similarity of M_1 , Kowalski has combined *Stachomys* with the genus *Germanomys* Heller, to which the Hungarian *Ungaromys* Kormos is also closely related. However, the structure of the upper molars is not yet known for either genus, and the structure of M_3 is likewise not known for *Germanomys*; hence merging these genera is not justifiable. In this book, these two genera are included under the tribe Ellobiini (subfamily Cricetinae) which, in any case, is sufficiently probable for *Ungaromys*.

2. Genus *Prometheomys* Satunin, 1901— Long-clawed Mole Voles

Diagnosis: Third root of upper molars found only in M^1 and only in some individuals. Posterior section of M^3 reduced. Shallow juvenile folds on lateral margin of anterior unpaired loop disappear during early phase of grinding and never form false prismatic folds. Partial fusion of triangles of the masticatory surface of molars less distinct than in *Stachomys*, occurs more often in old individuals. Outer part of anterior surface of M^1 with longitudinal groove-like depression, traces of which discernible even in old individuals. Lower incisor passes between roots of M_2 and M_3 .

Composition of genus: One present-day species: *P. schaposchnikovi* Satunin, 1901.

Distribution and zonal affinity: Alpine belt, subalpine meadows,



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Figure 10. Molars of *Stachomys* (from Kowalski, 1960).

a—lower molars; b—upper molars; c—anterior lower molars: view of masticatory surface (c_1) and lateral view (c_2); d—posterior upper molars: view of masticatory surface (d_1) and lateral view (d_2).

and upper part of forest belt in western Caucasus Isthmus, from northern slopes of main range up to northeastern Turkey.

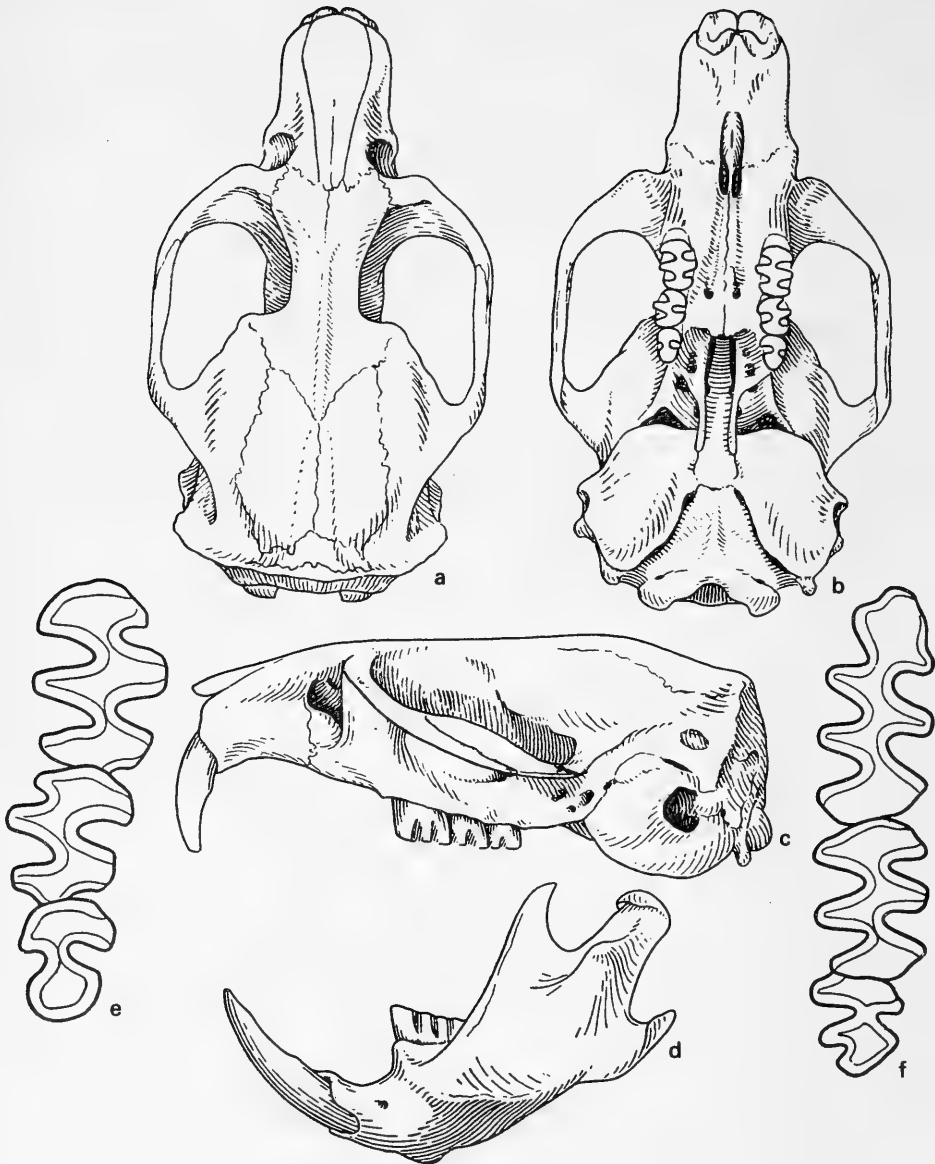
Evolution and phylogeny: Fossil remains are known from the Middle Pleistocene from the region of the present range (western Georgia). Based on molar structure, it is close to *Stachomys*; jaws exhibiting an M_3 structure identical to the jaw of this genus

have been found among the very early remains. More distant phylogenetic links are not clear. Vinogradov (1926b) visualized several structural features of the long-clawed mole vole according to which it appears intermediate between *Ellobius* and *Ondatra*. However, given our present knowledge regarding the evolution of these genera, affinity with the latter is less probable. But in addition to *Ellobius*, affinity with the type genus *Ischimomys* of ancient microtines of the tribe Microtini is apparent.

1. *Prometheomys schaposchnikovi* Satunin, 1901—
Long-clawed Mole Vole (Figure 11)

Description: Body length up to 140 mm, tail up to 53 mm (on average, about 30% to 40% of body length), upper row of molars 67–77–85 mm, lower row up to 8.3 mm, M_1 —3.1–3.3–3.5 mm. Coat color brownish-ocher, sharp boundary between color of back and belly absent. Guard hair sparse, soft, and barely longer than underfur; seasonal dimorphism of coat color not marked. Tail length about one-third trunk length. Tail monochromatic, often with white tip, fairly densely covered with comparatively long hairs. Eyeballs small, smaller than in any other microtine. Pinna with reduced lobe and small rectangular, fleshy antitragus. Rhinarium fairly large. Both alae nasalis separated into left and right halves, more distinct for lower than for upper. Margins of middle and lateral lobes of lower alae nasalis weakly lobate. Narial pit closed. Upper lip moderate in size, poorly demarcated, not touching sides of frontal unpaired tubercle; its tip and strongly developed anterior ridge covered with hairs. Lower labial lobes more strongly developed than in other microtines, although hairs on them, as on upper labial lobe, comparatively sparse. Third (hind) transverse fold of diastemic section of bony palate entire. Well-developed interdental folds of palate unique: four anterior ones interrupted while fifth (posterior) entire. Head with complete set of vibrissae, which, except for long buccal ones, are comparatively short, sparse, and stiff. Carpal vibrissae present. Forelimbs reduced (shorter only in *Dicrostonyx*). Carpus also relatively shorter and narrower than in other microtines (similar to *Arvicola*), and forearm long. Palm glabrous; foot with hairs behind pads. Pads poorly developed on forelimbs (except two carpal pads), well developed on hind limbs. Digits of forelimbs: III, II–IV, I; first digit with well-developed claw. Digits of hind limb: III, II, IV, V–I.

107 Claws on forelimbs much longer than digits, slightly curved and slightly grooved. Claws on hind limbs about half length of digits,



106 Figure 11. Skull of long-clawed mole vole (*Prometheomys schaposchnikovi* Satunin).

a—axial skull, dorsal view; b—same, ventral view; c—same, lateral view; d—outer lateral view of lower jaw; e—masticatory surface of upper molar teeth; f—same, lower molar teeth.

on fifth digit more than half.

Significant cranial features: (1) sagittal ridge complete; (2) braincase elongate with barely perceptible postorbital processes; (3) molar row relatively short, M^3 reduced; (4) ventral margin of jaw more inflected than in other microtines; and (5) upper incisors broad, slightly compressed anteroposteriorly, lower incisors with relatively long crown section (similar to *Arvicola* and *Blanfordimys*).

Distinguishing limb bone features: (1) scapula relatively narrow with broad prespinous area; (2) head of humerus narrow and high; (3) ulnar process short and ulnar plate relatively narrower (lower); (4) femur with broad distal section; and (5) fibula with relatively longer fused section than in other microtines. Chromosome no. $2n = 56$.

Evolution and phylogeny: Given in generic description.

III. Tribe ONDATRINI Kretzoi, 1955

Diagnosis: Postpalatine depressions small, sometimes almost imperceptible; bony bridge between them broad and flat. Molars rooted (in present-day genera, form only at time of cutting teeth), without cement deposition in folds or slight cementation. Medial triangles of masticatory surface of lower molars smaller than lateral ones. Enamel uniformly thick throughout or thin in upper folds. Maximum degree of folding of paraconid section of M_1 —1.5 times, rarely 2.0 times; "island" present on M_1 (in ancient members) or absent; prismatic fold absent; large number of juvenile folds may be retained until roots attain half crown height. M^3 reduced, simple in structure: anterior unpaired loop posteriorly with two denticles and one fold on each side. No traces of simplification of this tooth in anterior and posterior sections: anterolateral fold deep and narrow, without "island" because medial section elongate. Lower incisor extends to dental foramen or beyond it.

Composition of tribe: Three genera, closely related: extinct—*Dolomys* Nehring, 1898, *Pliopotamys* Hibbard, 1938; extant—*Ondatra* Link, 1795.

108 *Description:* If structural features of the molars and some known structural details of the palatal section of the skull are excluded, the description applies only to present-day members of *Ondatra*. However, it may be that typical features of the tribe are masked in *Ondatra* (unlike features of *Dinaromys* in the subtribe Pliomyi) by the maximum adaptation of microtines for

a semiaquatic life style. Therefore, most of the structural features are given in the generic diagnosis.

Size large. Length of molars from 8.5 mm in extinct forms to 16 mm in *Ondatra*, M_1^1 from 2.9–7.5 mm respectively, which corresponds to body length in extinct forms, which is not less than 270 mm. Posterior end of incisor alveoli slightly ahead of line connecting anterior margin of alveolus of M^1 (least in *Ondatra*). Anterior margin of palato-maxillary groove near posteromedial prism of M^1 . Longitudinal palatine grooves shallow, area enclosed between them flat. Two pairs of small posterior palatine foramina present. Posterior margin of bony palate in form of short flat plate, sometimes with rostriform process (*Ondatra*). Symphysis of mandible forms marked angle with ventral margin of jaw. Angle of lower margin of symphysis varies from small (*Pliopotamys*, *Dolomys* ?) to large (close to right angle) in *Ondatra*. Ascending section broad; when mandibular ramus horizontal, its anterior margin covers molar row commencing from second prism of M_2 ; posterior notch comparatively small. Articular process relatively long (length not known in *Dolomys*). Coronoid process extends to lower margin of articular surface of pr. articularis. Angular process long and broad at base, extends beyond posterior margin of articular process (position not known in *Dolomys*). Distance between mental foramen and anterior angle of masseteric ridge variable; foramen lies relatively high on lateral surface of jaw. Molar rows anteriorly wide-set, not diverging posteriorly; anterior section of M^1 and posterior section of M^3 not deflected outward or slightly deflected only in M^1 (*Ondatra*). Roots completely formed in ancient members even by time of cutting teeth. Roots vary from three in all upper molars (*Pliopotamys*) to two on M^2 and M^3 ; third (inner) root of M^1 may be variably reduced or even disappear in a large number of present-day *Ondatra*. In latter, difference between size of lateral and medial triangles of masticatory surface of lower molars less than in species of both extinct genera. M^1 moderately long. One pair of triangles at base of paraconid section in M^1 , second pair ahead of it variably developed (one of this pair may be incompletely developed or lacking) and variably shifted relative to each other. Anterior unpaired loop asymmetric, galleate; small transitory “islands” may develop on its lateral margin with disappearance of juvenile folds. M^3 sometimes with poorly formed lateral denticle. Crown of lower incisors long, comparatively highly curved in *Pliopotamys* and moderately long and sharply curved in *Ondatra*. Incisor alveolus passes under posterior root

of M_2 in *Dolomys* and between roots of M_2 and M_3 in *Ondatra*; corresponding data for *Pliopotamys* not known. Incisor terminates under f. dentale in *Dolomys*, at its upper margin in *Pliopotamys*, and much above this foramen in *Ondatra*; deflecting outward, incisor forms knob on outer surface of articular process, and above process is distinctly lingually-directed.

Distribution and zonal affinity: The present-day genus of
 109 *Ondatra* is intrazonal. Its members live in coastal biotopes and flowing or stagnant continental reservoirs throughout the Holarctic (introduced in Old World). Except for northern parts of tundra, it occurs up to 2,700 m above msl. *Dolomys* is a Plio-Pleistocene endemic in southern and southeastern Europe; *Pliopotamys* occurs in central North America. The greater part of the fossil remains of extinct species are recovered in forests of the Old and New World and a small percentage in ancient forest-steppes ("savannas"); in Europe, it has fairly narrow belt of distribution, from the Carpathians to western Cis-Caucasus; reliable fossils not known for the East. *Ondatra* has not been found in America outside the present range of the tribe.

Evolution and phylogeny: The most ancient fossil remains of the European members of the tribe have been dated to the Late Pliocene (Moldavian faunal association) up to the middle Early Pleistocene (Late Tamansk faunas). Found in the New World from about the same era (Late Plank faunas) up to the Recent. As shown by Hooper and Hart (1962), *Neofiber*, considered close to *Ondatra* by many authors, differs markedly. These authors include this genus under the tribe Microtini (p. 334). The genus *Dolomys*, with no descendants in the Old World, falls, in my opinion, within this tribe as proposed by Kretzoi (1955b).

Ancestral forms of *Ondatra* are not known, but ancient links with *Promimomys* are quite possible; separation into European and American branches must have occurred by at least the beginning of the Pliocene.

1. Genus *Pliopotamys* Hibbard, 1938 (foss.)

Diagnosis: Voles with cementless molars. Length of M_1 more than 4.0 (4.0–4.8 mm). M^1 – M^3 with three roots that are completely isolated in most members and with independent alveoli. M_1 with an "island" that is retained in ancient forms until roots reach half crown height; in later forms it has disappeared by the time of root initiation. "Island" narrow, elongate, and forms an acute angle with

longitudinal axis of tooth. Juvenile folds along margin of anterior unpaired loop may descend to half crown height and are retained as the animal ages for quite sometime. Position of lower incisor relative to roots of M_2 not known; posterior end of alveolus extends to upper margin of f. dentale, and articular process above this level distinctly linguallly-directed.

Composition of genus: Two species: *P. minor* Wilson, 1933 and *P. meadensis* Hibbard, 1938.

Age and distribution: Late Pliocene—Early Pleistocene of central North America.

Taxonomic notes and evolution: Hibbard (1938) described this genus and later (1959) found it differed from *Dolomys* only in number of roots of upper molars; in this respect, *Pliopotamys* is actually less specialized than the most ancient known members of *Dolomys*. Yet, as indicated by Mehely (1914), and later by Kretzoi (1955b), it is close to ancient cementless forms of *Ondatra*, which are probably its ancestors. Surprisingly, some species of *Pliopotamys* (e.g., *O. idahoensis* Wilson, 1958) have been included by various authors under one or another genus. Actually, extinct species of *Ondatra* did not differ from *Pliopotamys* either in size of molars or in absence of cement in their folds. However, except for isolated molars
110 other remains have not been recovered to date; thus it is not possible to check such characters as the relatively small diastemic length, which is typical of *P. minor*. Possibly, even this character, which confirms the high degree of adaptation to an amphibious life style, also changed over time: the diastema increased in length from ancient forms to present-day *Ondatra*.

2. Genus *Dolomys* Nehring, 1898 (foss.)

Diagnosis: Voles with cementless molars. Length of M_1 —3.1–3.5–4.4 mm. M^1 with three roots, M^2 – M^3 , at least in some individuals, also with three roots; roots not completely isolated, and without independent alveoli in ramus. M_1 without “island” (data on structure of molars up to commencement of wear not available). Juvenile folds along margin of anterior unpaired loop lacking even at initial stage of wear. Lower incisor passes under posterior root of M_2 and terminates under f. dentale. Articular process somewhat higher than incisor tip, and very slightly linguallly-directed.

Composition of genus: Two species: *D. nehringii* Kretzoi, 1959 and *D. milleri* Nehring, 1898. Probability of occurrence of third, *D. monrupinus* Kretzoi, 1955, not clear.

Age and distribution: Late Pliocene—Ancient Pleistocene of central and eastern Europe. In the USSR, fossil remains earlier than Moldavian faunas and late Early Tamansk faunas not known. Former species of this genus, as also species of *Promimomys*, are common and numerous.

Taxonomic notes and evolution: Kretzoi (1955b) was one of the first to note the fact that the extinct form differs from the extant "*Dolomys*" of the Balkan Peninsula and that the latter should be considered an independent genus, namely, *Dinaromys*. According to our taxonomic scheme, *Dinaromys* belongs to the tribe Celthronomyini (subtribe Pliomyi). *Dolomys* differs far less from *Ondatra* and somewhat more from the primitive present-day American genus *Pliopotamys*, which is closer to *Ondatra* (see above). However, separation of these three genera appears justified at the present time. Kretzoi, who earlier (1955b) considered *Pliopotamys* a synonym of *Ondatra*, now (1969) supports this view.

1. *Dolomys nehringii* Kretzoi, 1959

Diagnosis: Size comparatively small; length of M_1 usually less than 4.0 (3.1–4.0 mm). Anteromedial fold of paraconid section of this molar comparatively deep, wedged much higher than half crown height; fold absent not only in old but also some adult individuals. Posteromedial fold of M^3 directed medially, projects only slightly backward; heel relatively short and broad.

Age and distribution: Described from Late Pliocene Hungarian site, Charnota-2. In the USSR, it probably includes remains from Late Pliocene of Moldavia (Moldavian faunal association) and Ancient Khaprovsk faunas of Lower Don region. During the latter period of existence, it evolved in direction of *D. milleri*, a fact also noted in Hungary for the Charnota period (Kretzoi, 1962b) where remains of larger dimensions are known in upper layers. The insufficiently described species, *D. monrupinus* Kretzoi, 1955, has also been mentioned as a more primitive form (Kretzoi, 1955b).

111 *Description:* Size small. Paraconid section of M_1 comparatively less complicated. Molars relatively broad, and partial fusion of triangles of masticatory surface (variably evident on all molars) are primitive characters that can be used in comparison with *D. milleri* despite the small amount of material available. With more material, other differences could be compared, such as the less reduced roots of upper molars or extension of lower incisor between roots of M_2 .

Paleoecological data: Found in composition of unique alpine forest faunas of Late Pliocene, in which remains of field mice and

forest dormice dominant among tropical species of animals—monkeys, South Asian-type flying squirrels and giant salamanders. Collections are few throughout the USSR, and the associated forest-type fauna is poorly developed.

2. *Dolomys milleri* Nehring, 1898

Diagnosis: Size large. Length of M_1 usually more than 4.0 (4.0–4.4 mm). Anteromedial fold of paraconid section comparatively deep and wedged toward base of crown. Posteromedial fold of M^3 deviates strongly downward; heel of this tooth comparatively narrow and long.

Age and distribution: Described from Beremend in Hungary, probable age—lower Early Anthropogene (Ancient Villan and Khaprovsk faunas). Judging from size, *Dolomys* from stratotype of Khaprovsk faunal association (Liventsovka) is still closer to the preceding species; large forms began to appear among Late Khaprovsk faunas up to Ancient Tamansk faunas inclusively. Besides Hungary, a few remains are known from the Black Sea coast of Odessa, northeastern Azov region, and Tamansk Peninsula.

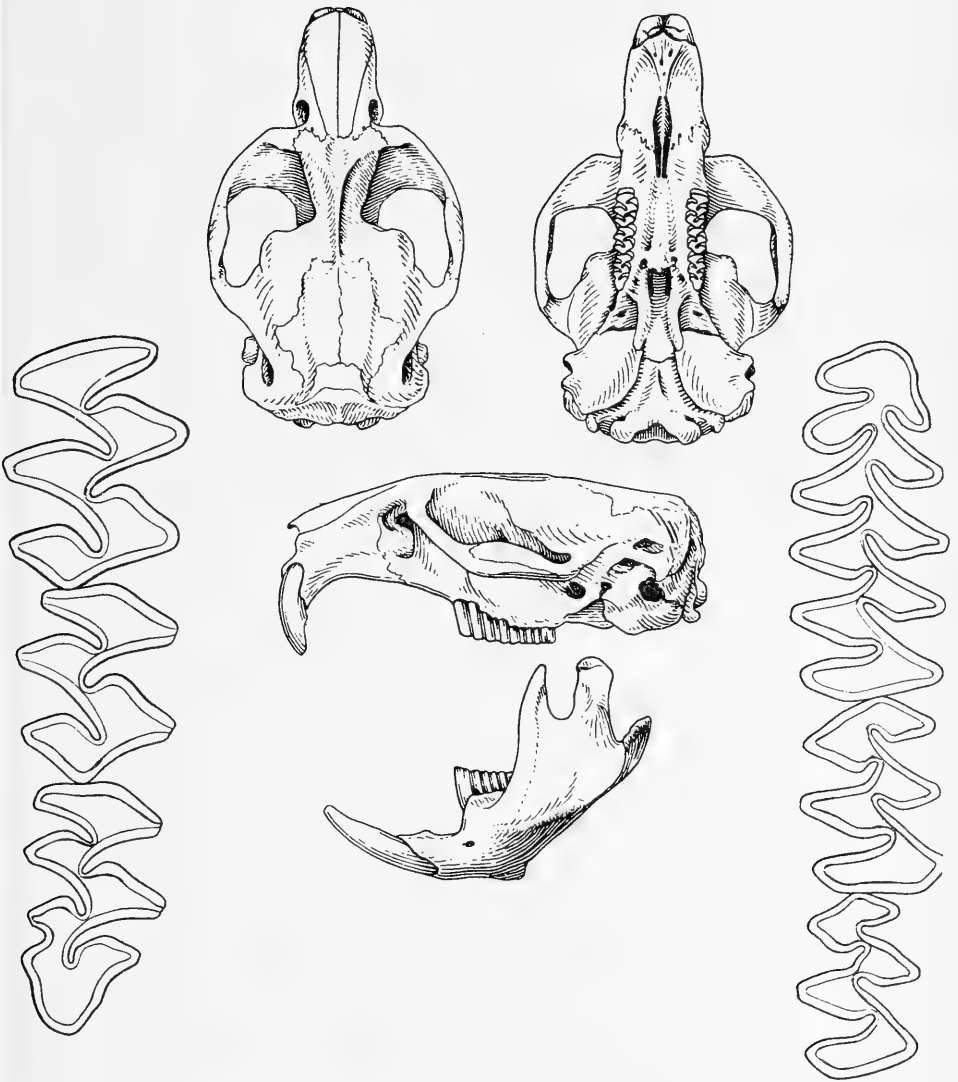
Description: Aside from individual molars, only a few other skull remains are known from Hungary to date. Judging from the small dimensions, the bony palate in the anterior section is comparatively broad and broader than in *Pliopotamys* and *Ondatra*. This species exhibits features indicating greater specialization in molar structure than seen in *D. nehringii*; some of these features have been described above.

Unlike the preceding species, *D. milleri* is largely found in “steppe” faunas.

3. Genus *Ondatra* Link, 1795 (Figure 12)

Diagnosis: Voles with cementless (extinct forms) and less cemented molars. Size largest among known forms of microtines. Length of M_1 more than 4.5 mm in extinct and 6.5 mm in extant forms (6.8–7.6–8.4 mm). M^1 – M^3 in present-day *Ondatra* have two roots; some individuals have three roots for front tooth which are not free throughout length. M_1 without “island”; juvenile folds along margin of anterior unpaired loop extend slightly downward along tooth wall and rapidly disappear during wear. Unlike other species of the other two genera of this tribe as well as extinct *Ondatra*, the paraconid section of M_1 is completely folded twice in present-day forms. Lower incisor passes between roots of

M_2 and M_3 ; posterior end of alveolus terminates above f. dentale, near outer surface of jaw; articular process above this level highly deflected lingually.



Composition of genus: One extant species—*O. zibethica* L., 1766 and three extinct—*O. annectens* Brown, 1908; *O. nebracensis* Holister, 1911; and *O. idahoensis* Wilson, 1933.

Description: Among all microtines, the present-day *Ondatra* are better adapted to a semiaquatic life style. Body length up to 360 mm and weight up to 1.3 kg. Coat monochromatic, from chocolate-brown, sometimes with rusty tinge, to almost completely black, with dorsal coloration merging gradually into ventral. Pelage sharply differentiated into guard hair and underfur; seasonal dimorphism of fur well-expressed. Tail length up to four-fifths trunk length; tail laterally flattened with short, stiff hairs and leathery ridge along dorsal and ventral surfaces. Tail laterally with fine scales masking three hard black bristles. Eyeballs medium in size, placed high, contiguous. Pinna small, covered with hair, with well-developed rectangular antitragus. Rhinarium comparatively large; division of both alae nasalis into left and right halves distinct; upper alae nasalis only slightly demarcated by shallow fold from lower ones. Middle and lateral lobes of latter entire or only slightly lobate. Narial pit closes readily. Upper labial lobes fleshy, rounded, with dense hairs, touching each other anterior to anterior palatine process, from which comparatively poorly developed anterior ridge continues toward incisor base. Lower labial lobes also well developed, usually pelage similar to upper lips. Third (hind) transverse fold of bony palate entire or interrupted. Head with complete set of vibrissae, although none, especially genal and lower labial (except corner ones) differentiated by strong development. Carpal vibrissae present. Limbs long; forelimbs relatively longer only in *Arvicola*; hind limbs longer than in other microtines. Hand moderately long for subfamily, relatively broad; foot longer than in other members but relatively narrow. Palm and plantar glabrous. Margins and digits of foot with crestate fringe of stiff hairs. Plantar pads well-developed on forelimbs but less so on hind limbs (heel pad on medial side more massive than other pads). Digits of forelimbs: III, IV, II, V, I; first digit, though small, with well-developed claw. Digits of hind limbs: IV, III, II, V, I. Claws on both limbs large, exceeding half length of digits (especially on hind limbs); claw on 5th digit extends more than half length of 4th digit.

Significant skull features: (1) orbits shifted posteriorly, plane close to horizontal; (2) upper diastema long; (3) bony palate narrow, especially in anterior section; (4) sagittal crest long; (5) jaw with strongly curved ventral margin; (6) long upper incisors greatly

flattened anteroposteriorly; and (7) masticatory surface of upper molars convex in longitudinal axis and laterally truncate, but concave and inwardly truncate on lower molars.

Distinguishing limb bone features: (1) highly developed crest of large trochanter of humerus, inner trochlea, third trochanter of femur, anterior crest of tibia—all relatively more massive than in other microtines; (2) inner epicondyle of humerus long; (3) ilia of pelvis short; and (4) scapula broad, mainly because of large width of prespinous fossa.

Distribution and zonal affinity: This genus is an original inhabitant of North America where it is distributed throughout the continent except in extreme northern and southern parts. In the Old World, related forms of the genus *Dolomys* became extinct even by the beginning of the Early Pleistocene. Adapting first to the climate in Western Europe, it extended its range into the USSR. At present, it inhabits the coastal biotopes of various bodies of water throughout the northern half of Eurasia. In Asia, the boundaries of its southern range have still to be determined.

Evolution and phylogeny: Fossil remains known from end of Pliocene (Late Blancan faunas). Direct ancestors can probably be searched among members of *Pliopotamys* (see above). Possibly the reason no amphibious forms arose among the *Dolomys* is the distribution of aquatic voles (*Arvicola*) in the Old World—the ancient group in which semiaquatic adaptations developed fairly early, possibly within the genus *Mimomys*. Naturally, competition with such
 114 an amphibious form at the early stages of evolution of a new species was difficult, more so because presumably the semiaquatic life style was also typical for the extinct *Allophaiomys*, whose range coincided with that of *Arvicola* over the greater part of western Eurasia. In the New World, both lineages of semiaquatic voles—*Ondatra* and *Neofiber*—have survived to the present time; in the Old World, there still remained the highly specialized members which facilitated the successful dispersal of *Ondatra*.

IV. Tribe CLETHRIONOMYINI Hooper and Hart, 1962 (= Myodini Kretzoi, 1955)

Diagnosis: Bony palate with usually small postpalatal depressions, either isolated by bony bridge in plane of hard palate, which gradually merges or projects step-wise toward margin of interpterygoid groove (“*Pliomys* type”), or covered by common border of palatals (“*Clethrionomys* type”). Molars rooted in most extinct

forms but rootless in majority of extant members; molars cementless in extinct forms and with or without cement in extant members. Size of lateral and medial triangles of masticatory surface on lower molars may or may not differ. Enamel poorly differentiated or undifferentiated in extinct forms, and undifferentiated to well-differentiated in modern forms. Paraconid section of M_1 folded once or twice (secondary fold often unilateral) and in some extinct forms even three times (third-order fold incomplete) and without secondary simplification. M^3 generally relatively long, with traces of secondary simplification in extinct as well as most modern genera; anterolateral fold smaller than successive fold. Alveolus of M_3 in rootless forms poorly isolated; anterior section of tooth not markedly shifted lingually. Lower incisor variable in length, extends to dental foramen or beyond it.

Composition of tribe: Three subtribes: Pliomyi stat. nov.; Clethrionomyi nov.; and Alticoli nov.

Description: Small or medium-sized voles with body length up to 90 mm in former and 150 mm in latter. Length of upper and lower molars respectively 4.5–5.5, 7.8–8.6, and 4.2–5.2, 7.4–8.2 mm. Color of dorsal surface from light or dark gray, often with brown tinge, to fairly dark brown and grayish-brown, often with admixture of fairly bright rusty tones. Seasonal dimorphism of coat color well-expressed: winter pelage longer, lighter, and often more rusty; some northern forms may turn completely white in winter. Tail length one-fifth to three-fourths body length. In forms with short tail, latter often densely pubescent (especially during winter) and terminal hairs reach half tail length; in long-tailed forms, tail often covered with short, sparse hairs. Eyes very small (in semifossorial members of *Hyperacrius*) to medium and large (some *Alticola*). Pinna very small, with reduced lobe and helix and weakly pubescent, fleshy antitragus (*Eothenomys*) to well-developed with highly leathery antitragus, rarely without it (*Dinaromys*). Head variably covered with hair protruding from fur. Rhinarium small. Separation of both alae nasalis into right and left halves as well as upper and lower variably expressed. Middle lobes of lower alae nasalis weakly, rarely distinctly lobate; outer parts well-developed, touching or contiguous with outer parts of upper lobes, as a result of which narial pit completely or almost completely closed. Lobes of upper lip moderately or well-developed, from narrowly-triangular to broadly-trapezoidal (their structure known only for *Clethrionomys* and *Alticola*) and in the latter type (in *Platycranius*) they touch the median line and rather compactly surround the incisor. Accord-

ingly, anterior palatine process and postincisor ridge covered, half open, or free. Upper labial vibrissae often long, genal and mental vibrissae reduced—the former may be absent; carpal vibrissae present, often long.

Data on relative length of limbs and their components available only for *Alticola* and *Clethrionomys*. Limbs relatively short (especially forelimbs) in *Alticola* and within average limits for the subfamily in *Clethrionomys*. Manus and pes moderately long or manus short (*Clethrionomys*); both narrow. Palm and sole variably with hairs behind planter pads (less in *Dinaromys* than in other members). Pads generally large and well-isolated; heel pad may be absent. Digits of forelimbs: III, IV, II, V, I; first digit rudimentary, without claw or with small flat claw; claws on other digits shorter than half length of digits, often steeply concave. In hind limbs, ratio of digit lengths similar to that in forelimbs, or 4th digit longer than 3rd. Claws on 3rd may be enlarged and more than half digital length.

Upper line of axial skull profile straight, with weak, rarely distinct dip in region of base of zygomatic arch. Interorbital space short, usually broad, with weak but often well-marked longitudinal and transverse depressions, with or without barely visible crests that may touch along midline in old individuals. Braincase juvenile in appearance—rounded and uniformly convex without crests, rarely weakly angular with short crests. Zygomatic arches weak, cylindrical, not wide-set except in *Eothenomys* and *Dinaromys*, in which they are comparatively strong and well-separated. Orbits medium in size, rarely small (*Eothenomys*) or large (*Platycranius*), and median in position relative to occipital section of skull. Angle formed by plane of orbit large, rarely small (*Dinaromys*). Postorbital processes small. Masseteric ridge of mandible low and broad. Outer angle formed by plane of this ridge with sagittal platform large: 1.5 times right angle or more. Auditory bullae variable in size and thin-walled. Symphysis of mandible forms weak angle with ventral margin of jaw. Angle of lower margin of symphysis varies from small to large (*Eothenomys*). When lower jaw horizontal, anterior margin of ascending section covers molar row starting from anterior or second prism of M_3 , rarely M_2 (*Eothenomys*); ascending section correspondingly narrow in first case and broad in second. Articular process variable in length. Coronoid process either much below articular or almost parallel. Angular process, if extends beyond margin of articular, only slightly so. Mental foramen closer to anterior angle of masseteric ridge and often markedly shifted

from upper surface of incisor section. Molar rows moderately, rarely wide-set anteriorly. Anterior section of M^1 and posterior section of M^3 of *Eothenomys* more strongly deflected outward than in members of other genera. Root sections of M^1 , especially of M^2 , with well-developed intraorbital projections. Relative length of M_1 variable: less to more than half length of molar row. Anterior triangles of paraconid section of M_1 may fuse variably between themselves and also with anterior unpaired loop. Shape of latter variable: broad, 116 rostriform, usually assymetric often oval, oriented obliquely relative to longitudinal axis of molar row or more or less parallel, with lateral angle shifted posteriorly and rostriform (many members of *Alticola*), or “*Lagurus*” in structure (*Pliolemmus*). Lower incisors with moderately long curved crown; their facing angle particularly large—about half right angle in *Dinaromys* and *Hyperacrius* (data not available for extinct forms). Upper incisors moderately broad, moderately compressed laterally (except probably in *Pliolemmus*), with longitudinal groove-like fold on slightly convex labial side. Combined cutting edge of incisors slightly and broadly M-shaped. In forms with rooted molars, lower incisor passes either under posterior root of M_2 so that it “sits” on incisor ridge, or between roots of M_2 so that posterior root appears on lateral side and anterior root from medial side, or between posterior root of M_2 and anterior root of M_3 .

Structure of postcranial skeleton known only for *Alticola* and *Clethrionomys* and highly similar in the two genera. Thus, *Alticola* characterized by low ischio-pubic section of pelvis, lower third trochanter of femur, relatively long fused section of fibula, short collar bone and scapula, low ridge of greater trochanter of humerus, and short ulnar process. *Clethrionomys* differs mainly in free section of hind limbs. Thus, in species of this genus neck of femur as well as tibia and anterior crest of tibia longer, but fused section of fibula shorter. Ulna also broader (high) in middle part.

Distribution and zonal affinity: Members of this genus live in forested plains and mountains of the Holarctic within the limits of temperate and partly subtropical zones, as well as unforested parts of mountains (including part of tropical zone); e.g., talus, alpine meadows, bare peaks, and montane tundra zones. In the north, they move into forest-tundra and the shrub-tundra subzone. In northeastern Siberia and the northern parts of North America they live along the upland biotope and the edges of river terraces up to the coastline. In the south, they are found in the insular forests and forest-covered valleys, and then penetrate far into the steppe

zone of the Old and New World. They are found from the Pyrenees and eastern part of the Mediterranean coast to northern Turkey and northwestern Trans-Caucasus; the forest-steppes of western Siberia and Kazakhstan; the montane forests of the Trans-Ili and Dzhungarian Alatai, Saur, and Tarbagatai ranges; the Altai Ranges (including the Mongolian Altai), the Sayans Range, the mountains of Central Asia (including Tibet as well as the Hindu Kush and its various ranges), India (Assam), Burma, Japanese islands (including part of Kuril' Islands), Kamchatka, and continental parts of eastern and northeastern Siberia. In North America, they are found up to northern California and New Mexico to the west and North Carolina and Florida to the east. The range boundaries of individual genera changed significantly in the Pleistocene: the southern edge of the distribution fluctuated, as did the lower boundary for montane forms into forest and open landscapes of alpine regions.

Evolution and phylogeny: The most ancient fossil remains have been found in Middle (?) and Late Pleistocene deposits (also including remains of the extant genus *Clethrionomys*), especially in the southern European part of the USSR. In that period, species of *Pliomys* were already specialized and, including primitive forms of *Promimomys*, were the common species of lagomorphs and subsequently of numerous species of *Pliomys-Dolomys* faunas. These species are linked with the tribe Microtini and the more distant species with Lagurini through the last genus and especially through the genus *Villanyis*. The three subtribes are poorly isolated and related to each other through the present-day relict genera of Clethriomyini from Central Asia.

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Subtribe PLIOMYI Kretzoi, 1969, stat. nov. (foss.)

Diagnosis: Posterior section of bony palate poorly differentiated (the "*Pliomys*," rarely "*Microtus*," type). Anterolateral fold of M^3 reduced. Anterior unpaired loop of this tooth fused with first lateral triangle, and width of medial fold equal to or slightly broader than its triangle.

Composition of subtribe: Two extinct genera: *Pliomys* Mehely, 1914 and, possibly, *Pliolemmus* Hibbard, 1937, and one extant genus—*Dinaromys* Kretzoi, 1955.

1. Genus *Pliomys* Mehely, 1914 (foss.)
(= *Apistomys* Mehely, 1914)

Diagnosis: Voles with cementless molars, rarely with some cementation. Length of lower molars 5.5–6.5 mm, M_1 —2.4–3.3 mm, M^3 —1.5–2.0 mm. Bony palate with poorly differentiated posterior section in which postpalatine foramina may remain open for a long time. Enamel same thickness along periphery of molars, rarely thins slightly in folds. M^1 with three roots and only in very recent forms are they incompletely fused. M^2 with three roots in more ancient forms and two in later forms; M^3 always with two roots. Anterior or posterior “islands” on M^3 occur rarely, and only in young individuals of some species. Paraconid section of M_1 without “islands” and long-retained juvenile folds on margin of anterior unpaired loop that, in one phyletic line, tend to form a double fold. M_3 with three transverse enamel fields (triangles not separated). Low incisor often extends much beyond dental foramen and forms distinct alveolar knob on outer surface of articular process. Mental foramen markedly shifted on upper surface of incisor section.

Composition of genus: About seven to eight species are known and form three natural groups in the western Palearctic; however, subgeneric designation for some of them (see Kretzoi, 1969), is hardly justifiable until the axial skull features have been thoroughly studied.

The species known in the Old World are: *P. episcopalis* Mehely, 1914; *P. ucrainicus* Topačevski and Scorik, 1967; *P. hungaricus* Kormos, 1934; *P. kowalskii* Schevtschenko, 1965; and *P. lenkii* Heller, 1930. North American species include: *P. parvus* Wilson, 1933; *P. meadensis* Hibbard, 1956; and, possibly, *P. deeringi* Guthrie and Matthews, 1972. Until recently, the North American forms (except the last) were combined in the genus *Pliophenacomys* (s. l.); in 1967, however, Hibbard and Zakrzewski (1967) placed them in a new genus, *Ophiomys*, even though the descriptions and diagrams are not adequate to warrant such a grouping or to support their generic independence; the latter fact was indicated by Kretzoi more than 20 years ago.

Age and distribution: Middle Pliocene, Middle Pleistocene, Kuchurgan to Late Hazara faunal associations of Eurasia; in the east, up to the Altai region of Siberia; reports of finds in Trans-Baikal (Pokatilov, 1966) need confirmation. Early Pleistocene of North America. In the eastern European part of the USSR, north up to

latitudes of Ufa, this genus includes species from forest and forest-steppe faunas.

Taxonomic notes and evolution: Ancestral forms are linked possibly by common origin with species of *Promimomys*. This is indicated in ancient species by the bifurcate margin of the outer prism of the paraconid section, which gives the corresponding triangle of the masticatory surface a forked appearance. However, unlike in *Promimomys*, closure of the fold anterior to this triangle normally does not occur with the formation of an "island," and has been mentioned only as a senile change. It may be noted that some younger individuals of *Promimomys* have been erroneously included under *Pliomys* (see description of "*Dolomys*" *gromovororum* Alexandrova, 1966) and, possibly, some individuals of the type series of *P. kowalskii* Schevtschenko. Judging from the molar structure, the ancestors of forest voles (*Clethrionomys*) may be found among the *episcopalis* group, and the ancestors of the Balkan mountain voles (*Di-naromys*) among the *hungaricus* group.

1. *Pliomys kowalskii* Schevtschenko, 1965

Diagnosis: Size small. Length of M_1 —2.65–2.75–2.90 mm, M^3 —1.55 mm. Specimens from type location (Moldavia, right bank of Bol'shaya Sal'cha River near village Moskovoi' Rezeshti) on average slightly larger (M_1 —2.8, 2.8, 2.75, 3.0 mm). Upper molars not known from type locality. In specimens from Odessa "catacombs," M^1 always with three roots and M^2 with two to three. Lower roots relatively narrow. Lateral and medial triangles of masticatory surface differ in size. Anterior part of paraconid of M^1 usually not completely demarcated from pair of triangles at its base. However, width of cingulum not greater than three times thickness of enamel. Anterior unpaired loop without traces of secondary fold, asymmetric (fungal-shaped), sometimes with barely perceptible depression on medial side; profile of this loop in tooth of old animals triangular and resembles that of *P. hungaricus*. Unlike other species of the genus, anterior prism of M_1 with longitudinal depression along lateral margin or with its ridge truncate; apex of corresponding triangle of masticatory surface bifurcate, with groove-like depression or blunt notch. M^3 in specimens from type locality not isolated and position of lower incisor not known. In species from reddish-brown loam soils of Odessa (catacombs), this tooth has a short broad heel and an "island" in its posterior section; at least in young animals, it is quite probable. Lower incisor extends below posterior root of M_2 .

Age and distribution: Middle (?) and Late Pliocene in southern Ukraine and Moldavia (fauna of "Moldavian Russellen"); also occurs in Irtysh region of Altai (Bazhanov *et al.*, 1968).

Taxonomic notes: I tentatively include here *Pliomys* from the reddish-brown cimberian (?) loam soils from the Odessa "catacombs." They differ from the type species in size, in the absence of a forked apex of the anterolateral triangle of M_1 , and the presence of a truncate apex in numerous individuals, which possibly corresponds to a more ancient stage in phylogeny (Shevtchenko, 1965). Kretzoi, who examined molars of *Pliomys* from the same locality, tentatively identified them as *P. odessanus* (nomen in collectio); this name should be used if/when the Odessa form is given an independent status. Some remains of *Pliomys* from the Late Pliocene to the Early Anthropogene faunas of Kotlovina village in southwestern Odessa district are also closely related to the Odessan form; judging from the structure of M_1 , this form occurred together with *P. ucrainicus*. As for Chaline's (1974) categorical statement that this species is identical to *P. hungaricus* Kormos, comparative analysis did not support this claim and, therefore, it has no taxonomic sanction.

119 2. *Pliomys ucrainicus* Topačevski and Scorik, 1967

Diagnosis: Size large. Length of M_1 —2.85–3.0–3.15, M^3 —1.7–1.8–2.0 mm. M^1 – M^2 not isolated and number of their roots not known. Molars relatively narrow. Ratio between size of lateral and medial triangles of the masticatory surface of molars and degree of isolation of anterior unpaired loop is similar to that of preceding species; secondary folds of paraconid section of M_1 present and disappear only in small number of very old individuals. In many molar specimens, inner margin of anterior unpaired loop with well-developed fold of third order, that is particularly distinct in remains of molars of young animals, in which the unpaired loop is asymmetrically situated. M^3 relatively long, with narrow and nearly isolated heel, without anterior and posterior "islands," and with equal-sized denticles bordering reduced anterolateral fold. Distinguishing features of lower incisor not known.

Age and distribution: Ancient Anthropogene in southern Ukraine and Moldavia (Khaprovsk faunal association).

Taxonomic notes: The authors (Topachevskii and Skorik, 1967) consider *P. ucrainicus* the ancestor of a later European species, *P. lenkii*; the former had a sufficiently complex anterior

section of M_1 and distinguishing features of M^3 by the end of the Pliocene.

3. *Pliomys hungaricus* Kormos, 1934

Diagnosis: Size large. Length of lower molars—6.5 mm (holotype, young animals), M_1 —2.8–3.0–3.3 mm, M^3 —1.6–1.7–1.75 mm (topotypes). M^1 – M^2 with three roots, molars relatively broad. Size difference of lateral and medial triangles of the masticatory surface of the lower molars distinct and greater than in the two preceding species. Anterior part of paraconid section in most cases almost completely isolated from first pair of triangles at its base, and latter isolated from each other. With growth, second-order fold of paraconid rapidly disappears (medial triangle always deeper than lateral) and triangles become equilateral with shorter side directed outward. M^3 relatively short, with reduced, short heel that fuses with section of anterior denticle; posterior “island” present in young animals. Anterior and posterior denticles bordering reduced anterolateral fold equal in size. Length of lower incisor and its position relative to roots of posterior molars in typical individuals not described. In *P. hungaricus* from Venge (southern Poland), lower incisor passes under posterior root of M_2 and its posterior end extends up to f. dentale.

Age and distribution: Late Pliocene and hilly regions of southeastern Europe (Hungary, Poland). Reliable remains have not been found in the USSR; indications of their occurrence in the Kuyal'nits deposits of the Black Sea coast of Odessa (Shevchenko, 1965) relate to *P. ucrainicus* (Topachevskii and Skorik, 1967).

Taxonomic notes: Kretzoi (1955b) proposed the generic name *Propliomys* for this species, but did not insist on it later (Kretzoi, 1965b). The specimen of *P. hungaricus* from Poland (Kowalski, 1960b; Sulimski, 1964) differs slightly from the typical Hungarian form in structural details of the anterior unpaired loop and, possibly (if the material is not mixed with *Promimomys*), in the presence of bifurcate and truncate angles of the anterolateral triangle of M_1 in some individuals.

120 Moreover, in the material from Venge (Poland), Sulimski (1964) separated a series of mandibular rami and individual molars (including more than 30 M_1), which are distinguished by the apex of the anterolateral fold of this tooth. It closes very readily to form an “island” that is retained in all adult stages, even in very old specimens in which traces of the prismatic fold is totally absent. Sulimski included these remains in the genus *Mimomys* with a

question mark. Even if considered an extreme case of variability of *P. hungaricus*, these remains indicate how a species similar to *Mimomys coelodus* Kretzoi could have evolved with an "island" on the paraconid section of M_1 but without the prismatic fold. This is similar to damaged specimens of subspecies of *M. pliocaenicus*, which are usually not separated by individual forms, or members of the subgenus *Kislangia*.

P. hungaricus is probably an ancestor of *Dinaromys*.

4. *Pliomys episcopalis* Mehely, 1914

Diagnosis: Size small. Length of lower molars 5.5–6.1 mm, M_1 —2.3–2.6–3.0 mm, M^3 —1.5–1.7–1.9 mm. M^1 with three roots, in later forms with two. M^2 always with two roots. Molars relatively broad; difference in size of medial and lateral triangles of masticatory surface of lower molars negligible. Triangles at base of paraconid section of M_1 completely or almost completely isolated (more distinctly so in molars of older individuals); medial triangle broadly fused with anterior unpaired loop in older individuals but isolated in younger ones. This triangle is asymmetric (fungus-shaped) with lateral angle directed down and back, and weak depression on lateral side. M^3 relatively long, with triangular heel well-demarcated from anterior part of tooth; posterior denticle adjoining reduced anterolateral fold smaller and shorter than anterior one. Anterior "island" retains typical shape on molar of young individuals. Lower incisor passes under posterior root of M_2 (typical form) or between roots of M_2 and M_3 (subsp. *bolkayi*) and extends upward beyond f. dentale, forming a distinct alveolar knob high on lateral surface of articular process.

Age and distribution: Early to Middle Pleistocene, mainly in southern part of Western Europe. In southern France (preserved up to Late Riss) and the European part of the USSR, remains have been found in the east, and north of the latitude of Ufa. It is found even in *Lagurus* and *Microtus* faunas.

Taxonomic notes: Two forms are included under *P. episcopalis*: (1) *P. bolkayi* Kormos, 1931 (Early Anthropogene from Podumtsa, Yugoslavia), which differs from the type specimen in late root development, poor enamel differentiation, increased length of anterior loop of M_1 (extending to roots of M^1), and the incisor extends between M_2 and M_3 —all features universally accepted as subspecific; and (2) *P. coronensis* Mehely, 1914, described as a species of an independent genus, *Apistomys* (Mehely, 1914; Early Anthropogene fauna of Brasso, Hungary). Opinion is not unanimous regarding the

taxonomic status and affinities of *P. coronensis*. Its distinguishing features (anterior part of bony palate broad, incomplete fusion of roots of M^1 , posterolateral angle of anterior unpaired loop of M_1 narrow, rostriform, and tendency toward isolation of anterior pair of triangles of M_2) do not allow us to consider it as an independent species much less a genus although differences in the axial skull are well-defined. Forms with poor cement deposition, closely related to *P. episcopalis* in structure of M_1 , have already been included under the genus *Clethrionomys*. However, because the *Pliomys* structure of M^3 is also found in some members of present-day species of this genus, such an affinity can only be considered when the posterior section of the hard palate of a fossil is available. Until then, the generic status of forms with sparse cementation can justifiably be considered tentative.

5. *Pliomys lenkii* Heller, 1930 (? = *coronensis* Mehely, 1914)

Diagnosis: Size medium. Length of lower molar row 6.45 mm, upper row 5.75, 6.1 mm (typical locality, Sakdillingen, FRG), M_1 —2.55—2.8—3.1 mm, M^3 —1.6—2.0 mm. Roots appear late. M^1 with three roots, anterior ones often fused. Molars relatively narrow; lateral and medial triangles of masticatory surface of lower molars equal in size. Anterior part of paraconid section of M_1 almost completely demarcated from triangles at its base; latter separate despite considerable fusion, especially in ancient forms. Second-order folds of paraconid section do not disappear with age, and in some individuals may form a fully-developed pair of fused triangles that are demarcated from rounded anterior unpaired loop (*progressus* type). Third-order folds absent, but in some individuals a juvenile fold defines M_1 with a corresponding indentation on the masticatory surface (*proavius* type). M^3 found in some specimens with M_1 . M^3 relatively long with narrow and almost isolated heel, without anterior and posterior "islands". Posterior denticle bordering anterolateral reduced fold much smaller than anterior one and may be minute. Anterior pair of triangles of M_2 with definite tendency toward isolation. Position of incisor relative to roots of M_2 and M_3 not described; posterior part of incisor extends much above i. dentale and forms well-developed alveolar knob on lateral surface of articular process.

Composition of species: *P. l. lenkii* Heller, 1930 (end of Early to Middle Pleistocene of FRG and Czechoslovakia), *P. l. ultimus* Fejfar, 1975 (Late Pleistocene, same locality), and *P. l. relictus* Chaline, 1975 (Middle to Late Pleistocene of France and Spain).

Age and distribution: End of Early to Middle Pleistocene of Western and Eastern Europe, west up to Transylvania. It has been found as a relict in Late Pleistocene in well-developed *Microtus* (including *Pitymys*) Würm faunas where *Mimomys* have not been found. Unlike the preceding species, it must be considered more a steppe than a forest form (Bartolomei, 1970). Reliable remains have not been found to date in the USSR and available reports (Shevchenko, 1965) apparently pertain to *P. ucrainicus*.

Taxonomic notes: Probable ancestral form—*P. ucrainicus* (Topachevskii and Skorik, 1967). Several forms are close to *P. lenkii*, some of which are described as independent species. Some are age variants distinguished by depth of second-order folds of paraconid section and especially of anterior unpaired loop [depressa, intermedius, inflexa, tenuis—separated by Heller (1968)], others are variants of morphologic or individual variability, often described on the basis of individual specimens known to date (*progressus* Kretzoi, *proavius* Heller, *zimmermanni* Brunner, *soergeli* Brunner).

2. Genus *Dinaromys* Kretzoi, 1955—Balkan High-montane Voles

Diagnosis: Voles with rooted molars with sparse or normal cementation. Length of lower molar row 5.5–6.5 mm, M_1 —2.8–3.8 mm, M^3 —2.3–2.7 mm. Posterior palatine foramina smaller than in *Pliomys*. M^1 with three roots in extinct *Dinaromys dalmatinus* and two roots in present-day *D. bogdanovi*; sometimes anterior root with traces of longitudinal separation. M^2 and M^3 with two roots. M_1 and M^3 without “islands”. Paraconid section of M_1 sometimes retains rather long juvenile prismatic fold. A second-order fold may appear on both lateral and medial sides (in present-day forms) of anterior unpaired loop in M_1 . All molars, including M_3 , with complete isolation of triangles of masticatory surface only in present-day forms. Lower incisor extends almost to dental foramen and does not form alveolar knob on lateral surface of articular process. Position of mental foramen similar to that of *Pliomys*.

Composition of genus: One extant species—*D. bogdanovi* V. and E. Martino, 1922 (Mirić, 1970). Extinct species allied to this genus are: *D.* (conf. *Pliomys*) *dalmatinus* Kormos, 1931 and *D.* (conf. *Pliomys*) *posterior* Janossy, 1969.

Description: Size large. Body length up to 140 mm, length of upper molar row up to 8.6 mm. Fairly dark and ash-gray tones dominant on dorsal surface; ventral surface light-colored; distinct boundary between colors absent. Winter pelage distinctly

longer than summer. Tail length may reach three-fourths trunk length and always more than half. Tail light-colored with grayish longitudinal stripe along dorsal surface. Pinna large, with large lobe, well-developed helix, but without antitragus. Eyeballs small. Rhinarium small. Middle groove separating nasal filtrum into left and right halves distinct, but that of upper and lower alae nasalis faint. Middle and outer lobes of lower alae nasalis entire or slightly lobate. Narial pit closed. Labial flaps small, rounded-triangular, not contiguous with midline of palate, and sparsely covered with hairs. Third (posterior) fold of bony palate isolated.¹ Data on relative length of limbs, foot, and hand not available. Palm and plantar glabrous. Digits of hind limbs: IV, III, II, V, I.

The external structure of the male genitalia, not known earlier for this species, is described below (prepared by T.G. Aksenova at my request). Glans penis (Figure 5) medium in size (length 4.5, width 2.7, thickness 2.5 mm), with cylindrical head, and slightly flattened dorsoventrally. Surface of glans penis folded-tuberculate, with uniform epithelial spinules that are larger near base of head. Dorsal ridge and digitate processes not well-developed. Middle and lateral appendages protrude by half their length from opening of head, with distal end curved dorsally. Urethral papilla (pr. lingualis) trilobate, each lobe apically bifurcate. Dorsal papilla (pr. dorsalis) biapical and tightly adjoins dorsal fold of middle appendage.

Upper line of axial skull profile with very slight dip at bases of zygomatic arch; bases of latter high in middle section. Skull without depressions in interorbital region (Figure 13). Orbit medium in size; angle formed by its plane with horizontal plane moderate. Symphysis of mandible forms moderate angle with ventral margin of jaw. When mandibular ramus horizontal, anterior margin of coronoid process covers molar row commencing from second prism of M_3 . Posterior notch of jaw deep and, as a result, ascending section correspondingly narrow. Apex of coronoid process does not extend to tip of articular process, and angular process only slightly extends above its posterior margin. Upper dental row anteriorly moderately wide-set. Relative length of M_1 about half length of molar row. Anterior unpaired loop of paraconid section of M_1 broadly-triangular, often asymmetric because lateral angle directed backward. Facing

¹Variability has not been taken into account in describing the "soft" parts since the description is based (like the genital structure) on just one alcohol-preserved specimen, kindly loaned to me by Prof. B.M. Petrov (Belgrade) to whom I am sincerely grateful.

angle of upper and lower incisors large, about 1.5 times right angle. Lower incisor passes under posterior roots of M_2 .

- 124 Shape of os penis (baculum) (Figure 5) typical for microtines. Baculum body (length 6.4 mm) broad at base (3.0 mm), distal part in form of trident comprising ossified middle and lateral protuberances. Broader part of base with slight terminal notch; dorsal and ventral notches equally poorly-defined. Shaft or lever of baculum with small depression in middle part of distal section. Not clear whether remainder of trident completely ossified; this process was probably not well-studied in specimen found.

Structure of postcranial skeleton not described.

Distribution and zonal affinity: These are inhabitants of Dinarides and Balkan ranges; these species live in taluses and among rock outcrops at height ranging from 1,700 to 2,400 m above msl, near and above the upper boundary of forests. Remains of the aforementioned extinct forms from the Middle Pleistocene were found in the Carpathians in northern Italy, outside the present-day Balkan range of distribution.

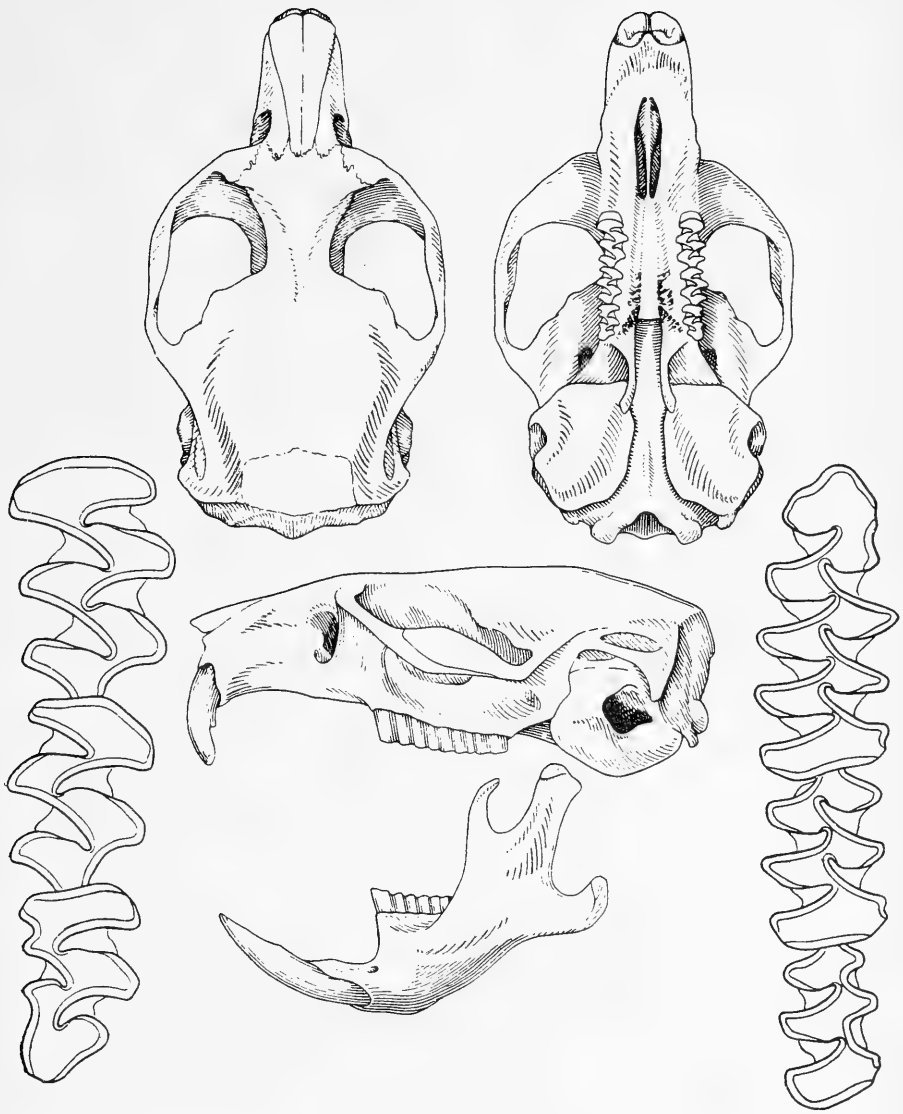
Evolution and phylogeny: The genus is known from Middle Pleistocene and possibly also Early Pleistocene. The need for its separation from the genus *Dolomys* is recognized by most mammalogists. Following Kretzoi (1955b), I have included several extinct European species of the tribe Ondatrini (p. 173) under *Dolomys* s. str.

1. *Dinaromys* (conf. *Pliomys*) *dalmatinus* Kormos, 1931 (foss.)

Diagnosis: Size medium. Length of M_1 — M_3 —6.4 mm, M_1 —2.8—3.0—3.2 mm (n = 10), M^3 —1.3—2.0—2.1 mm (n = 11) (Podumtsy, northern Dalmacia, Yugoslavia). M^1 with three roots. Anterior unpaired loop of M_1 broadly triangular; both triangles at base of paraconid of this molar highly shifted relative to each other, but often rather broadly fused. M^3 usually shorter than M^2 , and its medial triangle incompletely isolated from anterior and posterior part of molar. Cement deposition negligible or lacking.

Age and distribution: Early Pleistocene of the Balkans (northern Dalmacia).

Taxonomic notes: Intermediate position between the genus *Pliomys* (*hungaricus* group) and *Dinaromys* has been reported by various authors. Kowalski (1958a) has analysed the type location; Hibbard (1970c), after examining regional material, has provided some precise information about this species, and paid particular attention to the sparse cement deposition in the folds of the molars.



123 Figure 13. Skull of Balkan high-montane vole (*Dinaromys bogdanovi* V. and E. Martino).

2. *Dinaromys* (conf. *Pliomys*) *posterior* Janossy, 1969 (foss.)

Diagnosis: Length of M_1 —2.8 mm (holotype; Uppon, northern Hungary). Upper molars not known. In M_1 , anterior unpaired loop rounded-triangular, and triangles at base of paraconid section almost exactly opposite and widely fused (“*Pitymys*” structure). Cement deposition negligible.

Age and distribution: Middle Pleistocene of the Hungarian Carpathians.

Taxonomic notes: To date, this form is known only from the holotype (fragment of mandibular ramus with M_1 — M_2). The structure of M_1 indicates possible relationship with *Pliomys* from the *lenkii* group, and the fused “*Pitymys*” triangles suggest an earlier stage in evolution than for any known morphotypes of this species. Incidentally, Chaline (1974) drew attention to the fact that the fusion of triangles might be largely the result of incorrect reconstruction of the broken tooth.

3. *Dinaromys bogdanovi* V. and E. Martino, 1922

Diagnosis: Length of M_1 — M_3 —5.5—6.5 mm, M_1 —3.0—3.8 mm, M^3 —2.3—2.7 mm ($n = 10$). M^1 with two roots. Anterior unpaired loop broadly-triangular, often with well-developed folds (second-order fold of paraconid); triangles completely isolated at base of loop. M^3 normally longer than M^2 , and its medial triangle completely isolated. Cement deposition comparatively extensive.

Composition of species: Yugoslavian mammalogists have identified six subspecies (Mirić, 1970) and described some as independent species inhabiting various mountain ranges. Todorovic (1956) combined them into two population groups: the *grebenscikowi* group (mountain ranges of the Hindu Kush) and the *bogdanovi* group (the Dinara Alps); a third group might also exist (e.g., *preniensis*).

Description: Given in generic diagnosis. Todorovic (1956) drew attention to the difference between the two groups of forms (see above) with reference to extent of the shift of the anterior pair of folds of M_1 relative to each other; however, he did not attribute taxonomic importance to this feature lacking more abundant material. Chromosome no. $2n = 56$.

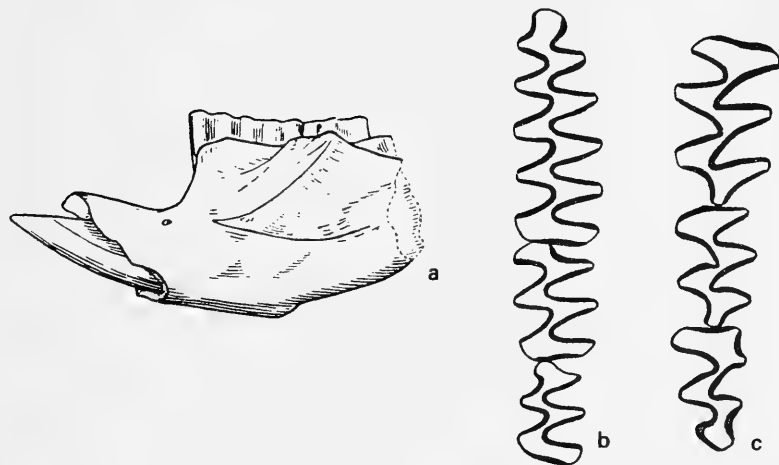
Distribution and zonal affinity: Same as for genus.

Evolution and phylogeny: Fossil remains known from the Middle (?) Pleistocene (northern Italy). *D. bogdanovi* is the only extant member of the subtribe *Pliomyi*.

3. Genus *Pliolemmus* Hibbard, 1937 (foss.) (Figure 14)

Diagnosis: Voles with rootless, cementless molars. Length of lower molar row about 6.4 mm, of upper row about 6.6 mm, M_1 —2.5 mm (holotype *P. antiquus*), 3.0, 3.3 mm, M^3 —1.8, 1.9, 2.0 mm (all dimensions, except that of holotype, determined from diagrams). Posterior sections of bony palate better differentiated than in members of other genera of the subtribe: two fairly deep postpalatal depressions isolated by a comparatively-broad bony bridge (as in *Microtus*). M^3 and M_1 without "islands". M_1 most probably without juvenile folds along margin of anterior unpaired loop, with complete second-order folds in paraconid section in numerous individuals, and with third-order folds at least on lateral margin of anterior loop. Enamel in middle of M_3 divided into two triangles. Position of posterior end of lower incisor not known. Mental foramen shifted to upper surface of incisor section, although not as strongly as in *Pliomys*.

Composition of genus: *P. antiquus* Hibbard, 1937.



127 Figure 14. Part of skull of *Pliolemmus* (from Skinner and Hibbard, 1972).

a—anterior part of left mandibular ramus, lateral view; b—lower molars; c—upper molars.

Description: Upper diastema much longer than molar row. Incisor alveoli do not narrow posteriorly and are only slightly short of anterior margin of alveolus of M^1 . Lower diastema comparatively short, incisura smoothly-curved; angle of curve of ventral margin of jaw not large. Triangles of masticatory surface of molars narrow, sharp; lateral ones on lower molars smaller than medial; all triangles isolated, except anterior pair of M_3 in adult individuals, and partly fused in molars of young individuals. Posteromedial triangle of paraconid of M_1 may also fuse with anterior unpaired loop. Posterior end of M^1 , and especially of M^2 , with additional digitate process that sometimes manifests tendency to separate into minute secondary lobes. Enamel thin on upper triangles, on lateral and medial margins of unpaired loops, and on anterior and posterior ends of M_1 and M^3 , rapidly disappearing during wear. M^3 of *Pliomys* type with narrow, thin elongate posterior loop. Posterior denticle on anterolateral reduced fold of this tooth larger than anterior one. Lower incisor passes between roots of M_2 and M_3 , highly deflected outward near former and, apparently, forms alveolar knob on lateral surface of jaw. M_3 slightly shifted inward relative to longitudinal axis of molar row and wall of its alveolus forms inflated bony capsules.

Age and distribution: Early Pleistocene in plains of North America (Blancan fauna).

Taxonomic notes and evolution: This species is a unique member of the subtribe, exhibiting some molar features (e.g., complicated M_1 , secondary structures on the posterior ends of anterior upper molars, unique differentiation of enamel layer), similar to those of present-day *Dicrostonyx*, that indicates possible affinity of Arctic lemmings with ancient *Pliolemmus*. However, the sharp differences in structure of M^3 are very conspicuous. *Pliolemmus* and *Synaptomys* are the first voles with rooted molars known in the New World; because they are already quite highly specialized, as rightly pointed out by Hibbard (1956a), they must have had a rather lengthy Pliocene evolution.

Subtribe ALTICOLI nov.

Diagnosis: Posterior sections of bony palate well-differentiated ("Clethrionomys" type). Anterolateral fold of M^3 reduced. Anterior unpaired loop of this molar fused with first lateral triangle. If isolated, width of fold on medial side notably smaller than width of its lobes (relationship usually reversed).

Composition of subtribe: Three extant genera: *Alticola* Blanford, 1881; *Antelionomys* Miller, 1896; and *Hyperacrius* Miller, 1896.

4. Genus *Alticola* Blanford, 1881—Asian High-montane Voles

Diagnosis: Voles with rootless molars, with sparse cement or cementless (?). Body length up to 140 mm, length of upper molar row 5.2–7.1 mm. Enamel from poorly to distinctly differentiated. Triangles of masticatory surface of upper molars variably fused only on M^3 , isolated on M_1 in lower molars, and completely fused on M_3 and often on M_2 (mainly anterior pair of triangles). Paraconid section of M_1 with more than one fold. Number of folds on each side of M^3 up to three; if only two, posterior part of molar narrow and elongate. Lower incisor extends to dental foramen and only rarely reaches its outer margin along margin of posterior notch of jaw ramus; alveolar knob not formed. Mental foramen not shifted notably to outer surface of incisor section.

Composition of genus: Three subgenera: *Alticola* Blanford, 1881; *Platycranius* Kastschenko, 1901; and *Aschizomys* Miller, 1898. Taxonomic status and affinity of the last genus is under debate.

127 *Description:* Pelage usually dense, long, and soft (guard hair comparatively thin), rarely shorter and stiff. Color in most individuals comparatively light, sandy-yellow or chocolate-brown to ocher tones, rarely rather dark and brown. Seasonal dimorphism of pelage well-apparent. Some forms turn white in winter. Tail length from one-fifth (slightly longer than hind leg) to almost half body length; variably covered with hairs. Pubescence in short-tailed forms dense, terminal hairs long. Plantar pads five on fore- and six on hind limbs. Eyes medium or large. Pinna protrudes from head pelage to variable extent. Upper labial flaps broadly-trapezoid; touching midline of palate, they cover anterior unpaired tubercle of soft palate and large part of postincisor ridge. Tubercular protuberance present on latter immediately behind incisor.

Interorbital space with distinct longitudinal and sometimes with transverse depressions without crests; crests absent on parietals. Symphysis of mandible forms gentle angle with ventral margin of jaw.

Distribution and zonal affinity: This genus inhabits hilly regions up to 6,100 m above msl in treeless regions, but in the presence of favorable biomes—rock outcrops, taluses, or loose vegetation on pebbled-rubble areas—species occur at elevation of 150 to 200 m,

even down to sea level. Species are found in mountain ranges in eastern Eurasia: ranges in Pamir, Altai, Tien-Shan, southern Siberia and Mongolia, Central Asia and eastern and northeastern Siberia, where by way of rocky regions and gravel terraces of rivers they reach the ocean.

Evolution and phylogeny: Fossil remains are known from the early Middle Pleistocene (foothills of Zeravshan range, Trans-Baikal region ?). The report of *Alticola* in the Middle Pleistocene fauna of Choukoudyanya I. (north of Beijing) (Young, 1934) is not reliable. What probably was described were the remains of a juvenile *Clethrionomys rufocanus* before the formation of molars. Animals lacking a complicated paraconid section of M^1 (the *episcopalis* group), which is similar to the early sparsely-cemented members of *Clethrionomys*, indicates a probable affinity with *Pliomys* spp. The transitional characters linking *Alticola* with forest voles are particularly distinct in species of the subgenus *Aschizomys* which, probably, should be considered a *Clethrionomys* that has lost its [molar] roots as in the genus *Antelionomys*.

KEY TO SUBGENERA OF SPECIES OF GENUS *ALTICOLA*

- 1 (2). Height of skull at anterior margin of alveolus of M^1 notably smaller than length of upper molar row. M^3 longer than M^1 Subgenus *Platycranius* Kastschenko (p. 201).
One species: *A. (P.) strelzovi* Kastschenko.
- 2 (1). Height of skull at anterior margin of alveolus of M^1 equal to, or greater than length of upper molar row. M^3 not longer than M^1 .
- 3 (4). Enamel coat of molars thick; apices of triangles of masticatory surface rounded. Anterior unpaired loop of M^3 isolated from rest of tooth .. Subgenus *Aschizomys* Miller (p. 202).
One species: *A. (A.) macrotis* Radde.
- 4 (3). Enamel coat of molars thin; apices of triangles of masticatory surface acute. Anterior unpaired loop of M^3 fused with rest of tooth Subgenus *Alticola* Blanford (p. 197).
- 5 (6). Brownish tones dominant in long silky dorsal pelage. Tail light-colored, monochromatic; length half or more trunk length *A. (A.) argentatus* Severtzov.
- 6 (5). Brownish-ash tones dominant in comparatively short, stiff dorsal pelage. Tail sharply bichromatic, dark on dorsal surface and lighter on ventral; length not more than half trunk length *A. (A.) roylei* Gray.

Subgenus *Alticola* Blanford, 1881

Diagnosis: Skull relatively high, its height at anterior margin of alveolus of M^1 equal to, or more than length of upper molar row. Interorbital space and braincase not highly flattened. Enamel thin; apices of triangles of masticatory surface of molars acute. M^3 shorter than, or equal to M^1 . M_3 with two lateral folds; difference in depth of folds large. Medial folds of M^3 broader than triangles; anterior unpaired loop usually not isolated from rest of tooth. Number of chromosomes, $2n = 56$.

Composition of subgenus: Up to 20 species have been described, many from a single specimen or a small series from inaccessible areas of Central Asian and northern Indian mountains. V.G. Heptner and O.L. Rossolimo (1968) examined a few of these specimens and have presented their view regarding the affinities of the species within the genus based on their concept of polytypic species. If their view is compared with the findings of Ellerman (1947), who examined all the material from the British museum, and the findings presented in more recent publications, one is compelled to conclude that it is hardly possible to solve the problem of the actual number of species of this subgenus using the old method of "museum taxonomy," even through simultaneous examination of the
 129 entire material available in collections. At present, in the opinion of Soviet scientists, the following three species (probably species groups) may be accepted: *A. argentatus* Severtzov, 1879; *A. roylei* Gray, 1842; and *A. stolizkanus* Blanford, 1875 (= *stracheyi* Thomas, 1880). In this context, it should be kept in mind that all three of the taxonomic characters selected show a distinct clinal variability: tail length decreases, color becomes gray, and structure of M^3 simplifies to the south and east.

Distribution and zonal affinity: Typical habitats of *Alticola* are occupied by the above-named species, up to the upper limits of distribution of the genus in the Pamir-Alai, Tien-Shan, and Altai-Sayan ranges, Central Asia and eastern Mongolia up to Bogdo-ula (eastern Mongolia), Nan-Shan, the upper reaches of the Golubaya River and eastern Nepal. By clinal variability, long-tailed forms mainly occupy the northern and western parts of the range, and short-tailed forms the central and southern parts, but they also penetrate northeast (Altai) where species from both groups are sympatric. Fossil remains were found in the Pleistocene much below the present-day range; in the USSR they were recovered from the northern fringes of the Tien-Shan and Pamir-Alai ranges.

1. *Alticola (Alticola) roylei* Gray, 1842

Diagnosis: Tail at least one-third trunk length but not more than half, bichromatic—dark on dorsal surface and light on ventral; rarely, not distinctly bichromatic. Predominant type of M^3 structure complicated: three medial denticles, although third (posterior) one may be barely perceptible or even lacking in some individuals. Gray tones dominate brown on dorsal surface. All these features less well-defined in northeastern forms in southwestern forms.

Composition of species: Ellerman (1947) reported four subspecies; later Ellerman and Morrison-Scott (1954) doubled the number: *A. (A.) r. roylei* Gray, 1842; *A. (A.) r. blanfordi* Scully, 1880; *A. (A.) r. montosa* True, 1894; *A. (A.) r. albicauda* True, 1894; *A. (A.) r. phasma* Miller, 1912; *A. (A.) r. cautus* Hinton, 1826; *A. (A.) r. acmaeus* Schwarz, 1910; *A. (A.) r. glacialis* Miller, 1913. Based on its sharply bichromatic tail, *A. bhatnagari* (Biswas and Khajuria, 1955) should also be included, while the short-tailed *albicauda* and long-tailed *phasma* appear doubtful.

Distribution and zonal affinity: This species ranges along southern boundary of Tibet from Kara-Korum mountain system to eastern Nepal. In the northwest, it borders the species described below and is found along the northern boundary with *A. stolizcanus* Blanford, with which it is sympatric in a relatively narrow belt and where the two are possibly isolated ecologically. Other details of distribution are not known.

Evolution and phylogeny: Fossil remains are not known. The Tien-Shan and Pamir-Alai species *A. argentatus* Sev. is the closest related group. According to the penetrating analysis of V.G. Heptner and O.L. Rossolimo (1968), who directly compared *A. roylei*, *A. blanfordi*, and *A. cautus* with the Pamir and Tien-Shan animals, their "... differences are so significant that the possibility of *roylei* as an independent species cannot be excluded" (p. 80)—a conclusion I also endorse.

2. *Alticola (Alticola) argentatus* Severtzov, 1879—Silver Vole (Figure 15)

130 *Diagnosis:* Tail about half trunk length or slightly longer, monochromatic, rarely slightly bichromatic, white or gray. The predominant type of M^3 structure is as in the preceding species. Brownish-pale tones dominate gray. Heptner and Rossolimo (1968) have reported another important character: the pelage in the entire *argentatus* group is long and silky, while that in the *roylei* group is short and stiff.

Composition of species: The above-mentioned authors indicate this distribution: *A. (A.) a. argentatus* Severtzov, 1879 (Pamir-Alai range, western and central Tien-Shan, Dzhungarian Alatau); *A. (A.) a. tuvinicus* Ognev, 1950 (eastern and southern slopes of western Tannu-Ola range, Tuva, and possibly Ol'khon Island of Baikal); *A. (A.) a. semicanus* G. Allen, 1924 (eastern Mongolia); and *A. (A.) a. alleni* Argiropulo, 1933 (southeastern Tuva and basin of Lake Ubsu-nur to Hangai range, almost up to 106° E). The independent status of the Pamir-Alai and Tien-Shan form is not clear: *rosanovi* Ognev, 1940; *leucurus* Severtzov, 1873; and *saurica* Afanasjev and Bazhanov, 1939, as well as *kosogol* Litvinov, 1973 (northern part of Lake Ubsu-nur basin). It is also not clear which of the exotic forms belong to the *argentatus* group (*A. phasma* Miller, 1912 ?).

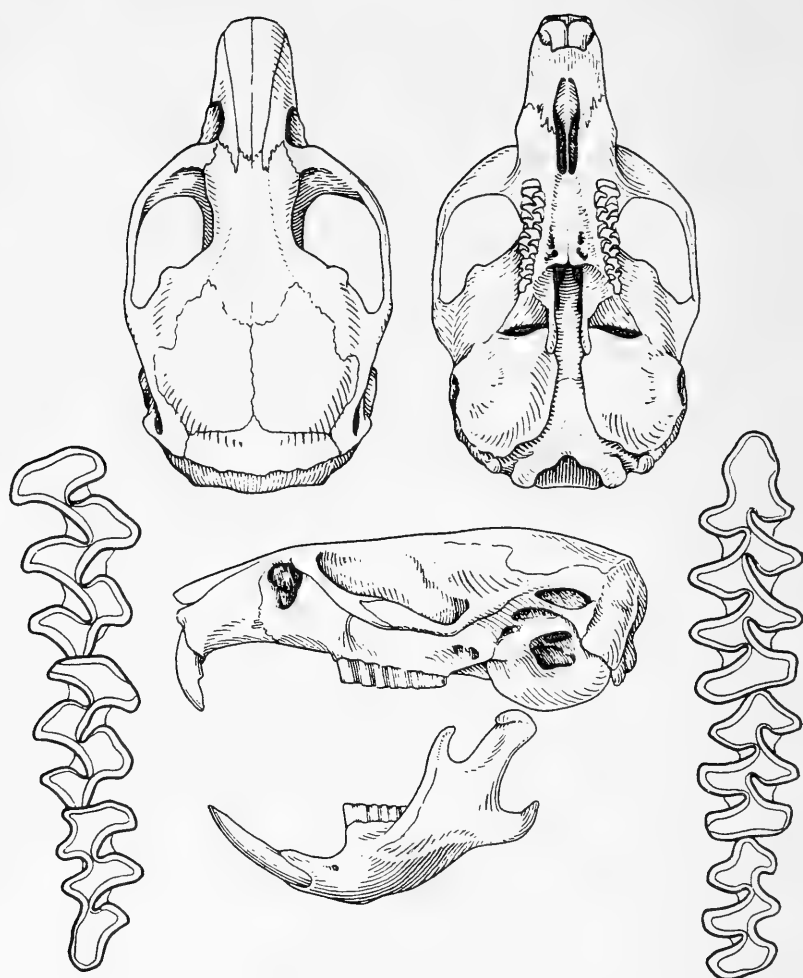
Distribution and zonal affinity: Mountain systems of Pamir-Alai, Tien-Shan (including the Saur and Tarbagatai), Altai-Sayan mountain area, Hangai, Kentai, and smaller uplands of Mongolia within the limits of the eastern part of the area of distribution of the subgenus. Elevations from 300–400 m above msl to snow level. Coexists in the area of distribution in the northeastern zone with *A. macrotis* Radde, in the Mongolian Altai and along the southern border of the Tibetan plateau with forms belonging to *stolizkanus*, and in the Kara-Korum mountain system with members of the *roylei* group.

Taxonomic notes: The status of *A. argentatus* as an independent species has already been discussed. Hinton (1926) is of a similar view, and consider the long-tailed members of *Alticola* from Tien-Shan and Pamir-Alai as an independent species.

3. *Alticola (Alticola) stolizkanus* Blanford, 1875 (= *stracheyi* Thomas, 1880)

Diagnosis: Tail less than one-third trunk length, often slightly longer than hind limb, pure white on dorsal and ventral surfaces, but laterally slightly bichromatic. Predominant type of M³ structure simple, usually only two medial denticles (third not developed, rarely more or less weakly so). Brownish tones dominant on dorsal surface; southern forms light-colored, sandy-yellow. Pelage otherwise as in preceding species.

Composition of species: Six to seven subspecies: *A. (A.) s. stolizkanus* Blanford, 1875 (Kun'lun', northern Ladakh); *A. (A.) s. stracheyi* Thomas, 1880 (Ladakh-Kumaon); *A. (A.) s. lama* Barrett-Hamilton, 1900 (western Tibet); *A. (A.) s. acrophilus* Miller, 1899 (Kara-Korum range); *A. (A.) s. kaznakovi* Satunin, 1903 (upper reaches



131 Figure 15. Skull of silver vole (*Alticola argentatus* Severtzov).

of Golubaya River); *A. (A.) s. nanshanicus* Satunin, 1903 (Nan-Shan); and *A. (A.) s. barakschin* Bannikov, 1948 (Mongolian and Gobi Altai).

Distribution and zonal affinity: Tibet and mountain ranges along its northern borders; Mongolian Altai where it is sympatric with *A. argentatus* (the two probably are isolated ecologically).

Taxonomic notes: Ellerman (1947) confidently included *A. stracheyi* as a subspecies of *A. stolizkanus*, although in a postscript he indicated that he did not examine the nominal form of the latter. Actually, it is indicated in the description of *A. stolizkanus* (Blanford, 1875) that the tail length is about one-fifth trunk length and only slightly greater than half foot length. The western Tibetan species, *A. lama*, is also indisputably included with this group, but the position of *A. acrophilus* is less clear. As for the last two subspecies described by Satunin (1903) and Bannikov (1948) as independent species, the authors have already correctly determined their place in the *stolizkanus* group, and the independent species status of the Gobi-Altai vole should be considered quite probable. The taxonomic status of *A. kaznakovi* Satunin (1903) from southern Tibet (upper reaches of Golubaya River) remains unclear. This is a white-tailed vole with a long tail (20 mm), slightly longer than length of hind foot (18.4 mm), and is known from two semiadult specimens (collections of the Zoological Institute, Academy of Sciences USSR). One of them had been preserved in alcohol and then stuffed, thereby losing its natural color, while the second had a brownish-gray juvenile coat. M^3 in the type specimen (skull damaged) is simple in structure with two medial denticles, a barely perceptible third, and a very long "heel".

Subgenus *Platycranius* Kastschenko, 1901

Diagnosis: Skull low: height at anterior margin of alveolus of M^1 notably smaller than length of upper molar row. Interorbital space of braincase highly flattened. Enamel thin; apices of triangles of masticatory surface of molars as in members of preceding subgenus and acute. M^3 longer than M^1 . Third lateral fold of M^3 , if present, rudimentary; differences in depth of anterolateral and medial folds large. Anterior unpaired loop of M^3 usually not closed; medial fold wider than adjacent triangles.

Composition of subgenus: One species: *A. (P.) strelzovi* Kastschenko, 1899.

Distribution and zonal affinity: This species occupies typical habitats of *Alticola* from foothills to lower hills, up to an elevation of 3,000 m above msl, from outlying upland and hilly regions in eastern Kazakhstan to the Saur, Tarbagatai, and Altai Ranges and northwestern Mongolia.

133 4. *Alticola (Platycranius) strelzovi* Kastschenko, 1899—
Flat-skulled Vole (Figure 16)

Diagnosis: Differs greatly from other members of the subgenus *Alticola* in such external characters as thick and comparatively densely pubescent tail with long brush of terminal hairs. Skull structure with maximum tendency for flattening among members of this genus: entire braincase flattened, including auditory bullae. Molars with shorter crown, highly conspicuous compared to size of intraorbital alveolar processes; lower incisors weaker, thinner, though with long crown. Mandibular rami low, with narrow articular process, weak coronoid process, and narrow angular process at base.

Composition of species: Probably no more than two subspecies: *A. (P.) s. strelzovi* Kastschenko, 1899 (= *desertorum* Kastschenko, 1901) (Kazakhstan hilly region, Tarbagatai, Altai) and *A. (P.) s. depressus* Ognev, 1944 (southeastern Altai, Mongolia).

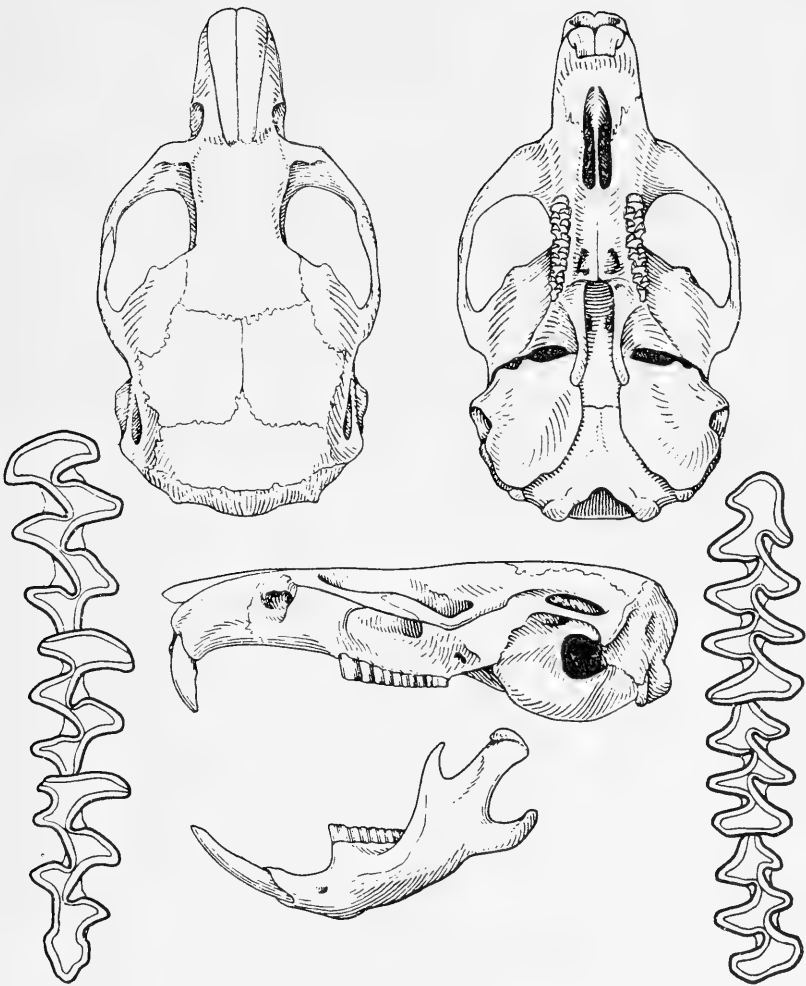
As noted by Heptner and Rossolimo (1968), subspecific characters are the color and the dip of the frontals which form a distinct wedge. Eastern forms are lighter in color and the dip of the frontals is more pronounced.

Distribution and zonal affinity: The distribution coincides with those of the subgenus. Western and northwestern boundaries in Kazakhstan pass approximately along the line of the Zharykas, Ermantau, and Bayanaul Ranges; the southern boundary includes the hill region of Kazakhstan, encircles the basins of Alakul' and Zaisan lakes, and moves into the Altai Range, including Mongolia.

Taxonomic notes: Fossil roots have not been found. Indirect indications of Bol'shekov (1960) that the Kazakhstan hill region is the center of origin of this species can scarcely be credited. The routes and rate of evolution of specific behavioral reactions have not been studied in these rodents.

Subgenus *Aschizomys* Miller, 1898

Diagnosis: Skull relatively high: height at anterior margin of alveolus of M^1 equal to, or larger than length of upper molar row. Interorbital space of braincase not highly flattened. Enamel thick; apices of triangles of masticatory surface of molars rounded. M^3 not longer than M^1 . Lateral surface of M^3 with three folds; difference in depth of anterolateral and medial fold not large or nil. Anterior unpaired loop of M^3 separated from rest of tooth; width of medial fold not less than width of adjacent triangles.



32 Figure 16. Skull of flat-skulled vole (*Alticola strelzovi* Kastschenko).

Composition of subgenus: One species: A. (*A.*) *macrodis* Radde, 1862. Possible, the southern Japanese "*Clethrionomys*" *smithii* Thomas, 1905, in which molar roots have not been found in adults, also belongs to this subgenus and not to *Eothenomys*, as proposed by Jameson (1961).

Distribution and zonal affinity: This species inhabits rocky areas

of bare mountain peaks, talus in the Japanese stone pine zone, plains and montane tundra, among rocks of river valleys, and occurs from sea level up to more than 2,100 m. It is found in eastern Siberia from lower reaches of the Lena River up to the Chukchi Peninsula, the Altai-Sayan montane area, and mountain ranges in the southern Amur region.

- 134 *Evolution and phylogeny*: It has been described as an independent genus. Most Russian mammalogists, however, have considered it either a subgenus of *Altaicola* (Vinogradov, 1927; Vinogradov and Argiropulo, 1941; Ognev, 1950; Vinogradov and Gromov, 1952; Gromov *et al.*, 1963) or its independent status has not been recognized (Bobrinskii *et al.*, 1965; Heptner and Rossolimo, 1968). Vinogradov (1927) specially examined the question repeatedly raised by mammalogists abroad about the closeness of *Aschizomys* with *Clethrionomys*, and supported their independence. In his opinion, the relationship between *Aschizomys* and the Central Asia genera *Alticola* s. str. and *Anteliomys* requires more study. At present, the affinity between *Aschizomys* and *Clethrionomys* is being re-examined in the light of the taxonomic position of forest voles from the Japanese islands which are close to the true *Clethrionomys*, but they either exhibit late appearance of roots or total loss of roots. However, to consider *Aschizomys* a subgenus of *Clethrionomys*, as suggested by Jameson (1961) based on his erroneous assumption of the presence of roots in adults of *Aschizomys*, turns the problem upside down. Finally, it appears feasible to interpret *Aschizomys* as an independent genus of the subtribe Clethrionomyi.

5. ? *Alticola* (conf. *Aschizomys*) *smithii* Thomas, 1905—
Smith's Vole

Diagnosis (Tokuda, 1941): Size close to *Clethrionomys rutilus*, but tail relatively longer, although shorter than in the *andersoni* group. Body length up to 105 mm, tail up to 47 mm (up to 50% of body length), upper molar row up to 5.3 mm. Dorsal surface darker in color than in Siberian red-backed vole, which contrasts less with grayish-brown color of sides. Tail slightly bichromatic, with sparse hairs. Brain case larger than in *C. rutilus*, and with relatively broad and possibly short interorbital space. Predominant type of M^3 structure is broadly fused anterior pair of triangles. Molars rootless even in old animals; intraorbital alveolar bulges prominent.

Composition of species: Two or three subspecies.

Distribution and zonal affinity: Inhabits montane forests up to 2,500 m and, in the absence of *Microtus montebelloi*, also is found in outcrops of shrubs and meadows at sea level in certain southern Japanese islands: Honshu, Kyushu, Sikoku, and Togo (islands of Oka group). In sympatric areas, it usually occupies higher altitudes than *Clethrionomys*. This is the only species of microtines found on Sikoku and Kyushu.

Evolution and phylogeny: Inclusion of this species under *Eothenomys* or *Anteliomys*, as proposed by some Japanese researchers, is rejected because of the simple structure of M^1-M^2 in the former and M^3 in the latter. Like *Clethrionomys andersoni*, it represents an offshoot of fairly ancient forest voles from the *rufocanus* group or, possibly, *rutilus*, which have lost molar roots. If the latter is true, then this is a case of parallel evolution of *Alticola* in forestless montane areas and *Clethrionomys* on forested islands. Absence of members of both groups of microtines with rootless molars in northeastern China and Korea can be explained by differences in the Pleistocene evolution between the biomes in these regions and those in northeastern Siberia. Should Smith's vole be included under the genus *Clethrionomys*, restoration of the old subgeneric name *Paulomys* given by Thomas would be acceptable.

135 6. *Alticola (Aschizomys) macrotis* Radde, 1861—
Large-eared Vole

Diagnosis: In external features as well as skull structure, closer to members of the subgenus *Alticola* than to *Platycranius*. Length of tail, well-covered with hairs, from one-fifth to one-third trunk length; tail distinctly bichromatic in summer and slightly so in winter. Based on these features and the more intense brownish-gray pelage, *Aschizomys* is well-distinguished from the eastern forms of *Alticola* and the *argentatus* group, whose range is contiguous with the boundary of the Altai-Sayan mountain regions. Differences in skull structure, in addition to those mentioned above, include a weak facial section and a very small auditory bulla in *Aschizomys*.

Composition of species: Two distinctly differentiated subspecies: *A. (Asch.) m. macrotis* Radde, 1861 (eastern Sayan, Yabloneve, Barguzin, and Primor'e ranges) and *A. (Asch.) m. lemminus* G. Miller, 1898 (montane tundra in northeastern Siberia). As for the subspecies *A. (Asch.) m. vicina* Portenko, 1963, which inhabits a large part of Yakutia, according to the opinion of its author, M.V. Popov (*Rodents of Yakutia* edited by V.A. Tavrovskii, 1971) considers it

necessary to look at new material, and to compare animals from the northern and southern parts of the republic.

Such features as color of pelage on dorsal surface and its seasonal variability, tail length, and difference in depth of both anterolateral folds of M^3 , show distinct clinal variability in an eastward direction: *A. m. lemminus* is lightest in color, with a short tail, and turns whitish in winter; it exhibits the least marked differences in depth of anterolateral folds of the last upper molar.

Distribution and zonal affinity: Corresponds to the subgenus.

Taxonomic notes: Several forms of uncertain taxonomic status appear within the limits of the subgenus, but their taxonomic place is not known. These are: *A. olchonensis* Litvinov, 1960 and *A. baicalensis* Litvinov, 1961—insular forms from Baikal; the former probably belongs to the subgenus *Aschizomys*, and not to *Alticola*, as concluded by the author; and also *Aschizomys vinogradovi* Rasurenova, 1933 (= *altaica* Vinogradov, 1933), which is quite close to the type species and possibly does not differ from it. The taxonomic position of *Aschizomys* from the Altai-Sayan montane regions nevertheless needs to be reexamined on the basis of new material and, as suggested for forms of the other two subgenera, new methods of study and new characters particularly incorporating the "soft morphology."

5. Genus *Hyperacrius* Miller, 1896 (Figure 17)

Diagnosis: Voles with rootless molars; cement absent or sparse. Body length up to 116 mm and upper molar row 5.4–7.2 mm. Enamel well-differentiated. Triangles of masticatory surface of molars may be variably fused (often widely fused on all upper as well as lower molars including M_1). Paraconid section of M_1 folded not more than once. Number of folds on each side of M^3 two, its posterior lobe short and broad. Lower incisor extends beyond dental foramen and forms an alveolar knob on lateral surface of base of articular process. Mental foramen slightly shifted toward dorsal margin of incisor section.

Composition of genus: Two species: *H. fertilis* True, 1894 and *H. wynnei* Blanford, 1881 (Phillips, 1969).

Diagnosis: Pelage dense, relatively short and not differentiated as in other rodents adapted to semifossorial life style. Color predominantly dark chocolate-brown to ochre, with metallic sheen. Data on seasonal dimorphism not available. Tail one-fifth to one-third trunk length, densely covered with hairs that are longer at tail tip. Plan-

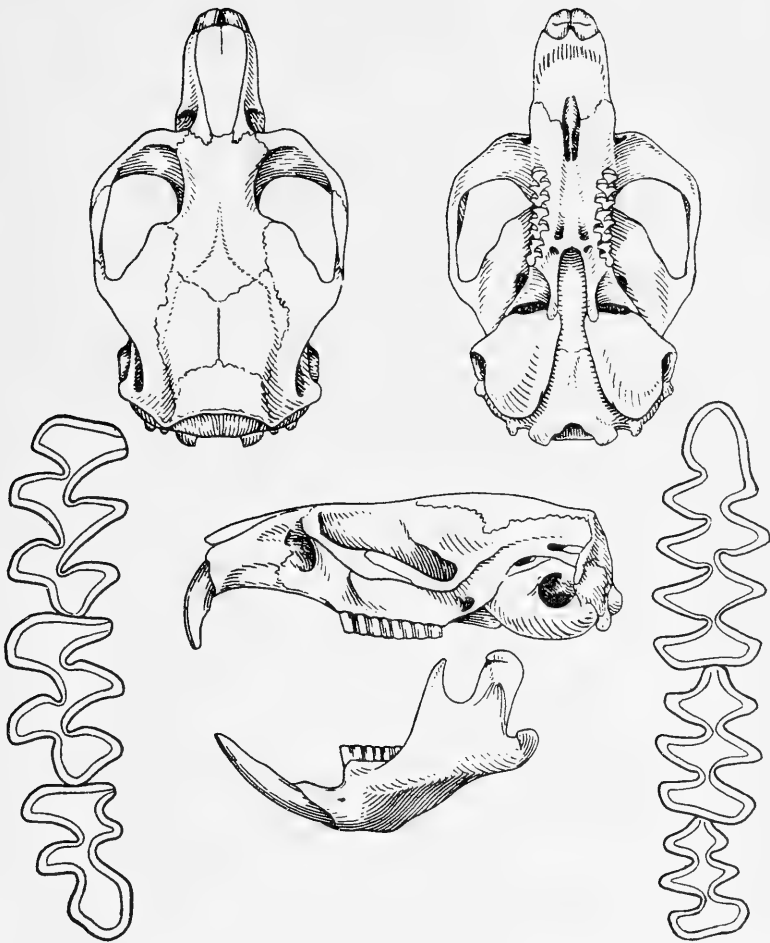


Figure 17. Skull of *Hyperacrius fertilis* True.

tar pads five on both hind feet. Claws long and thin, especially on forelimbs. Eyes small. Pinna small, completely masked by pelage or protrudes only slightly. Structure of upper lips and their diastemic projections and relative length of limbs and their parts not described. Nipples reportedly few: three pairs.

Interorbital space with poorly developed longitudinal ridges, parietal crests barely visible, posterior part of frontals without depressions, and parietals slightly flattened. Symphysis of mandibles

forms large angle with ventral margin of jaw (shorter only in *Prometheomys*) (Figure 17).

137 *Distribution and zonal affinity:* It is found in coniferous forest and alpine meadow zones on southern slopes of the western Himalayas, Indus River valley, Kashmir, and Jhelum, at altitudes of 1,900 to 3,600 m above msl.

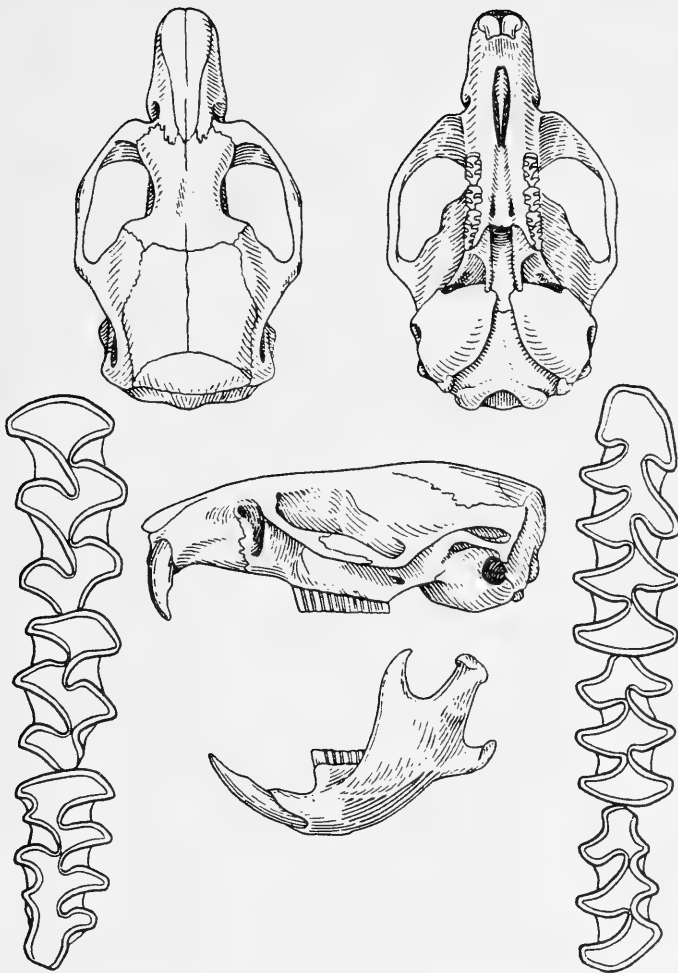
Evolution and phylogeny: Fossil remains are not known. It has been assumed that the present-day range of the genus is a relict area of earlier members that lived in coniferous forests over a much large territory in Central Asia before the Himalayas were elevated. Hinton's conclusion (1926) that *Hyperacrius* is an ancient branch of microtines closely related to *Alticola* appears correct even today. Incidentally, some paleomammalogists (Kretzoi, 1955b) have tried to find forms among members of this genus that are related to lagurides, in particular the genus *Lagurodon* (according to current taxonomic notes, a subgenus).

6. Genus *Antelionomys* Miller, 1896 (Figure 18)

138 *Diagnosis:* Voles with rootless cemented molars. Body length up to 126 mm and upper molar row 5.0–6.5 mm. Enamel not differentiated. Triangles of masticatory surface of molars may be variably fused in both upper and lower molars including M_1 . Number of folds on each side of M^3 at least three, more often four; posterior lobe narrow. Paraconid section of M_1 incompletely folded twice. Lower incisor extends beyond dental foramen and may form an alveolar knob on lateral surface of articular process. Mental foramen not shifted toward dorsal margin of incisor section.

Composition of genus: Three or four present-day species: *A. wardii* Thomas, 1912, considered only a subspecies of the next species by Allen (1940); *A. chinensis* Thomas, 1891; and *A. custos* Thomas, 1912. Two other species, earlier (Hinton, 1926) included under the genus *Eothenomys*—*E. olitor* Thomas, 1911 and *E. proditor* Hinton, 1923—are now included in *Antelionomys*.

Diagnosis: Pelage moderately dense and moderately long (similar to that of montane *Microtus*), but comparatively shorter because of sparse guard hair. Color dark, brown to chocolate-brown. Data on seasonal dimorphism not available. Tail one-third to two-thirds trunk length, poorly covered with hair, dark, monochromatic. Claws not elongated, comparatively sharply curved, slightly longer on hind feet than on forefeet. Eyes medium in size. Pinna large, with well-developed antitragus. Structure of upper labial processes



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Figure 18. Skull of *Antelionomys wardii* Thomas.

not known. Ellerman (1941) indicated that the number of nipples is equal to that of *Eothenomys*: two pairs. Interorbital space dorsally with well-expressed longitudinal depression extending to suture between parietals. Latter slightly flattened. Mandibular rami with steeply sloping ventral margin.

Distribution and zonal affinity: This species inhabits open alpine meadows up to altitude of 4,500–4,800 m in southeastern China

(Sychuan and Yunan); their presence in mountains of northern Vietnam is not excluded. Reliable finds from Japanese islands not known: "A". *smithii* Thomas (Tokuda, 1955) should probably be included under *Alticola* (*Aschizomys*) (p. 204).

Ecologically, these species replace voles of the genus *Neodon*. They occupy an isolated position in the subtribe Alticoli in external appearance, quite similar to that of the high-montane voles of *Neodon*, but have retained the skull and molar structure typical of *Alticola*, with a highly complex M^3 . A few mammalogists (Allen, 1941) consider *Antelionomys* only a subgenus of *Eothenomys* or even its synonym, which clearly emphasizes the inadequate study of these genera.

Subtribe CLETHRIONOMYI nov.

Diagnosis: Posterior sections of hard palate well-differentiated ("Clethrionomys" type). Anterolateral folds of M^3 reduced (rarely unreduced). Anterior unpaired loop of this tooth separated from anterolateral triangle and width of folds on medial side less than, rarely about equal to, width of corresponding triangles.

Composition of subtribe: Two extant genera—*Clethrionomys* Tilesius, 1850 and *Eothenomys* Miller, 1896.

KEY TO SPECIES OF GENUS CLETHRIONOMYS

- 1 (4). Body length more than 120 mm; length of upper and lower molar rows more than 6.3 mm.
- 139 2 (3). Pelage of dorsal surface brownish-gray (similar to voles of *Microtus*), without rusty or reddish tones. Interorbital space broad and flat. Posterior end of lower incisor extends above dental foramen and forms alveolar knob on lateral surface of ascending jaw *C. sikotanensis* Tokuda.
- 3 (2). Pelage of dorsal surface with distinct rusty tones. Interorbital space narrow, with lateral ridges separated by groove-like depression. Posterior part of incisor does not extend above dental foramen and does not form alveolar knob
..... *C. rufocanus* Sundevall.
- 4 (1). Body length less than 120 mm; length of upper and lower molar rows less than 6.3 mm.
- 5 (6). Pelage of dorsal surface brownish-gray, without rusty or reddish-chocolate-brown tones. Tail length up to 62% trunk length *C. frater* Thomas.

- 6 (5). Pelage of dorsal surface with distinct rusty or reddish-chocolate-brown tones, especially in individuals with one coat year-round. Tail length not more than 56% trunk length.
- 7 (8). Color of dorsal surface predominantly rather bright, rusty-chocolate-brown (summer coat) or light, yellowish-chocolate-brown (winter coat). Tail covered with long dense hairs; length not more than 44% trunk length *C. rutilus* Pallas.
- 8 (7). Color of dorsal surface predominantly dull, with rusty-Brown tones, at times with distinct rusty tinge. Tail covered with comparatively short sparse hairs; length usually more than 45% trunk length *C. glareolus* Schreber.

7. Genus *Clethrionomys* Tilesius, 1850

Diagnosis: Voles with rooted molars with sparse cement (ancient forms) on cemented, although in some forms the roots in all or in some individuals (usually belonging to later litters) may appear very late, at the end of the first or even second year of life, and remain undifferentiated for a long time. Masticatory surface of M^1 with four triangles, of M^2 with three triangles, behind anterior unpaired loop. Paraconid section of M_1 with no more than one fold. Auditory bulla comparatively large, dilated, usually protrudes downward beyond level of masticatory surface of upper molars.

Composition of genus: Subgeneric taxonomy has not determined. Separation of the Early Anthropogene subgenus *Acrorizomys* Topačevski, 1965, for forms with posterior root of M_2 not always slipping along margin of the incisor (I did not find the "forked" contact to which the author refers in any of the original material examined by me), or in which the posterior end of M_2 extends beyond the dental foramen, is hardly tenable. A similar and, at times, greater extension of the root is typical of all species of the *rufocanus* groups, and the above primitive relationships between the posterior root of M_2 and the incisor, as correctly noted by Topachevskii (1965), are typical of all the very ancient voles with rooted molars. Such a relationship is also found sometimes as an atavistic feature in the teeth of *Clethrionomys glareolus* in the initial stages of root separation. Separation of these subgenera is presently not accepted by most mammalogists: *Paulomys* Thomas, 1905 for the rootless Japanese "*Clethr.*" (conf. *Aschizomys*) *smithii* Thomas, 1905; *Caryomys* Thomas, 1911 for the southern Chinese *Clethrionomys inez* Thomas, 1909 and *Clethrionomys eva* Thomas,

1911; *Glareomys* Rasorenova, 1933 for *Clethrionomys rutilus* Pallas, 1779; and *Craseomys* Thomas, 1906 for species of the *rufocanus* group. However, all the supraspecific groups of the genus, especially the large-toothed red-backed voles, could with greater claim demand an independent subgeneric status.

Numerous present-day species, which have increased in number through insular and montane forms and most of which have not received independent species status, are quite distinctly grouped into three supraspecific groups. They are related to three major European species—*rufocanus*, *glareolus*, and *rutilus*—whose independent species status is very clearly demonstrated by a sharp disruption of the ontogenesis of sterile hybrids. The known extinct species are related to *glareolus* and *rutilus* or possess intermediate characters between them.

The first group includes *Clethrionomys rufocanus* Sundevall, 1846, *C. andersoni* Thomas, 1905, and *C. sikotanensis* Tokuda, 1935, as well as forms from the Pliocene to the Pleistocene of Siberia, yet to be described. Species of this group are probably not represented in the present-day fauna of the New World. Hinton (1926) included *C. occidentalis* Merriam, 1890 in this group which is not known in extinct fauna.

The second group includes *C. glareolus* Schreber, 1780, *C. frater* Thomas, 1908, and, possibly, the independent species *C. ponticus* Thomas, 1906 and *C. gapperi* Vigors, 1830 in the New World. Cautious authors use open nomenclature in designating the extinct Anthropogene form of this group, terming it *Clethrionomys* (conf.) *glareolus* or *gapperi*. Without taking into account features subject to age and individual variability, one may also include in this group these species, most of which were described on the basis of a small number of isolated teeth: *C. kretzoi* Kowalski, 1958; *C. acrorhiza* Kormos, 1933; *C. hintonianus* Kretzoi, 1968 (= *hintoni* Kormos, 1934); *C. esperi* Heller, 1930; *C. harrisoni* Hinton, 1926; *C. kennardi* Hinton, 1926 (the material for the last two species includes a fairly well-preserved skull), and others. From the fauna of the USSR may be added *C. sokolovi* Topacevski, 1935 and *C. iorensis* Buatschidze, 1968.

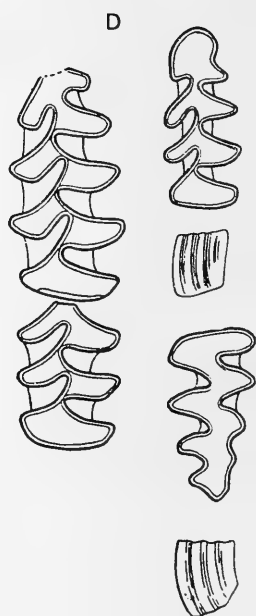
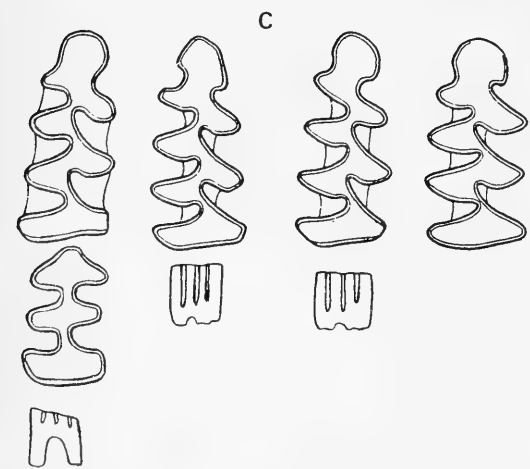
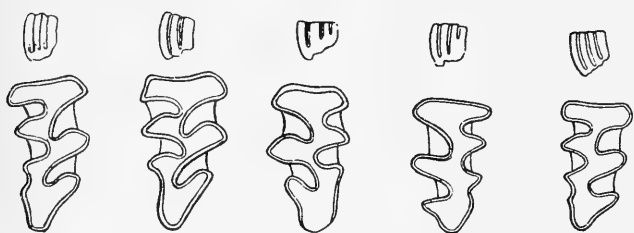
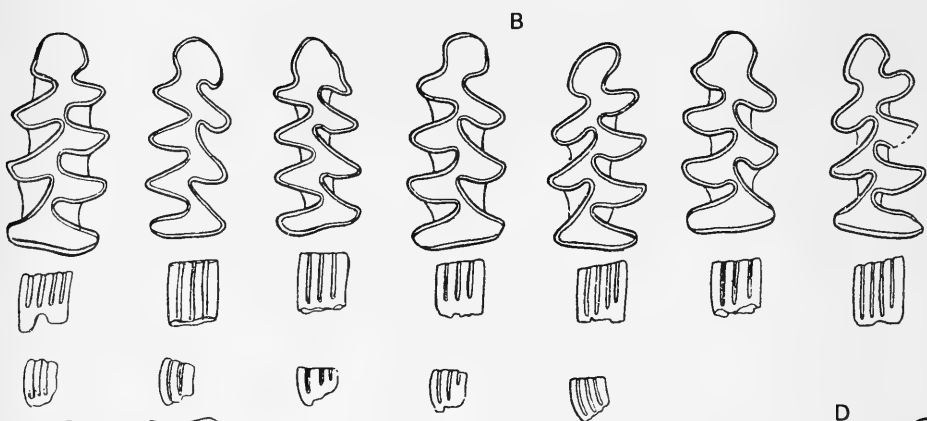
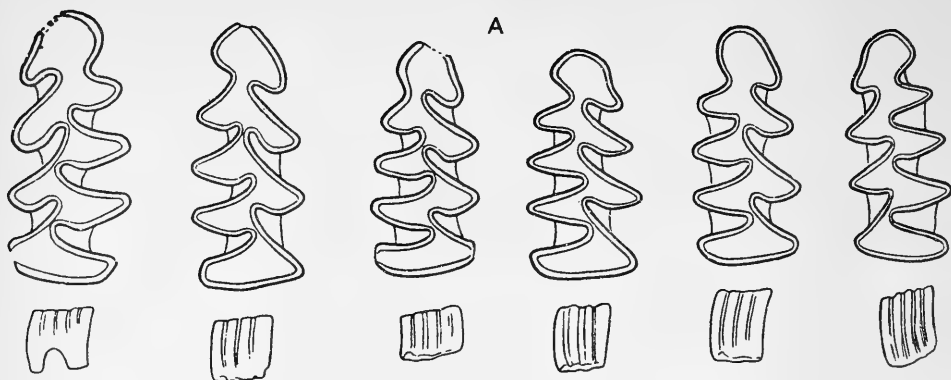
The third group includes *C. rutilus* Pallas, 1779, which, most probably, has no related species in the New World. Several of the Siberian fossil forms of this group have yet to be investigated (Figure 19).

Description: Body length up to 130 mm, rarely up to 150 mm, upper row of molars up to 6.8 mm and 8.0 mm respectively. Color

of dorsal surface dark, reddish-brown, with varying degree of red tones—fairly bright brick-red to almost no red tones, in which case color typical of some members of *Microtus* (for example, *M. Oeconomus Pallas*). In the northern and montane forms seasonal dimorphism is well-expressed: the pelage is lighter in color during winter and redder in some individuals. Tail length from one-fourth to one-half body length, or may be slightly greater. It is variably covered with hairs which are better developed in the short-tailed forms, in which the long terminal hairs may form a brush. Pinna larger than in *Microtus*, but slightly smaller than in *Alticola*; eyes medium in size. First digit (pollex) of forefoot without claw or nail, or with small nail, and rarely with well-developed, small flat nail. Nipples: four pairs. Skull with relatively long narrow facial section and interorbital space. Zygomatic arches low in middle part. Posterior end of lower incisor, if extends beyond dental foramen, forms an alveolar knob on lateral surface of articular process in only a few extant as well as extinct forms.

Distribution and zonal affinity: This species inhabits plains and montane forests up to their northern and altitudinal limits. In the south, it is found in isolated forests and river floodplains, penetrating deep into open biomes; in the north, it occurs in forest-tundra and shrub-covered tundra. In the Pleistocene of Western Europe as well as Siberia including its northeast region, fossil remains are regularly found together with species of mixed fauna of the first (Riss) and second (Vyurmsk) periods of glaciation. It is found in the entire northern hemisphere, south up to Turkey, Trans-Caucasus, mountain ranges of Tien Shan, southern Siberia, and northern Mongolia, mountains of southern China, Japanese and southern Kuril' Islands, Sakhalin, Korea, and Kamchatka. In the New World, it is found up to northern California in the west, Arizona and New Mexico in the central zone, and North Carolina in the east. I obtained specimens from most of the Atlantic Islands (including Ireland) and from the Polar Basin.

Evolution and phylogeny: Judging solely from finds of isolated teeth, and without remains of the skull and hence no knowledge of the structure of the bony palate, forms with less cemented teeth may be included under the ancestors of *Clethrionomys*. These do not differ from the teeth of *Pliomys episcopalis* Mehely, and both are found in the Early Pleistocene of Moldavia (the early Khaprovsk fauna). A large number of simultaneously occurring species of other voles with rooted molars (for example, minute *Villanyia*) makes it possible to identify the M^3 belonging to these forms. The smallest



among such molars has one medial fold and a flattened “*Pliomys*” structure in the anterolateral section with a reduced anterolateral fold as well as a primary simple structure, and is probably most typical for the common ancestors of *Pliomys* from the *episcopalis* group and *Clethrionomys*. It is apparent that the structure of the posterior sections of the bony palate plays a decisive role in the generic identification of such forms.

1. aff. *Clethrionomys kretzoi* Kowalski, 1958 (foss.)

Diagnosis: Size small. Length of M_1 —2.0–2.3–2.4 mm (holotype 2.4 mm; Poland, Kadziel’nya). Similar dimensions also recorded for this molar in this species in the USSR (2.25–2.35–2.50 mm; n = 18). The maximum deposit of cement appears only in fully adult specimens with roots longer than one-fourth crown height and is normally not visible from the masticatory surface. A slight reduction in enamel in the depth of folds may also be seen in such individuals. Major triangles of masticatory surface of M_1 mutually fused to a variable degree but isolated from folds, and the lobes generally shifted relative to each other at the base of the paraconid section; the unpaired anterior loop is fused with the latter, rarely isolated. Lateral folds of M_1 narrow and directed anterodorsally; apices of corresponding triangles rounded, the frontal one narrow and long, but often papillate in structure. Posterior root of M_2 in normal specimens (those of Early Pleistocene) lies lateral to the incisor (Kowalski, 1958a). Triangles of the masticatory surface of this molar opposite, paired.

Age and distribution: Ancient, i.e., first half of Early (?) Pleistocene, common in central and eastern Europe. In the east, up to Altai in western Siberia. Claims (Pokatilov, 1966) of its occurrence in Trans-Baikal region require verification.

Taxonomic notes: The author of the species repeatedly changed his interpretation of its generic affinity, sequentially including it under *Dolomys* (first description), *Pliomys*, and *Clethrionomys*. In Soviet literature, it has mainly been included under the last two genera, often using open nomenclature. Comparison with other

141 Figure 19. Molars of extinct *Clethrionomys* sp. (material from the Geological Institute, Academy of Sciences, USSR, western Siberia, collections of V.S. Zazhigin, 1964–1965).

A—Ulovo; B—Razdol’e; C—Kizikha; D—Anui River, high floodplain.

Clethrionomys species is difficult, since only isolated molars and M_1-M_2 in a skull fragment are known to date for *C. kretzoi*. Chaline (1974), who had an M^1 as well as an M^3 (Villafrancan deposits, France), notes the "Mimomys" structure of the latter, which does not contradict the affinity of this species to *Clethrionomys*. Hence the introduction of a new name, *Mimomys burgondiae*, is not necessary.

The nature of modification with time is also not clear in *C. kretzoi*. It can only be assumed that in the more ancient forms the molar crowns were lower than the typical crown, the posterior root of M_2 "sat" on the incisor, and that the triangles of the masticatory surface were not so narrow and were better formed (Kotlovina location) (Aleksandrova, 1965a, Figure 8).

Among the extinct species of *Clethrionomys* described from *Mimomys* faunas of approximately equal age only *C. solus* Kretzoi, 1958 (= *intrans* Kretzoi, 1958) (location Villan-5, southern Hungary) and *C. sebaldi* Heller, 1963 (north of the French Alps, FRG) have been reported. Regarding the first of these species it is quite probable that, like the only tooth of *Allophaiomys*, the lone M_1 (2.2 mm) of this species was obtained from the much younger, upper layers of the site. With respect to all other features, given the very brief description it is impossible to judge the affinity of *C. solus* to *C. kretzoi*; in fact, their synonymy is not excluded. It is possible that in *C. sebaldi*, also described on the basis of a solitary M_1 (2.2 mm) from a young individual, the sparse cementation, broadly fused triangles, and unique structure of the paraconid section, may likewise prove to be juvenile characters, as the author noted (Heller, 1963).

2. *Clethrionomys acrorhiza* Kormos, 1933 (foss.)

Diagnosis: Size small. Length of upper molar row 4.7, 4.8 mm; M_1 —2.0—2.25 mm. Extent of cementation not indicated. Major triangles of masticatory surface usually isolated but those at base of anterior unpaired loop fused with it as well as among themselves. Loop *per se* poorly isolated laterally but well-separated medially. Nature of slope, size, and shape of triangles most similar to *C. kretzoi*. Lower incisor passes between roots of M_2 . Triangles of masticatory surface of M_2 opposite, and anterolateral triangle in form of a posteriorly directed denticle. Lower incisor thin, width 0.6—0.8 mm.

Age and distribution: Second half of Early Pleistocene, southern Hungary.

Taxonomic notes: Apparently, this species is close to *C. kretzoi*; however, the location of the lower incisor makes it more primitive, despite the fact that remains were obtained from younger deposits than the typical *kretzoi*. But since lower jaws of typical *Clethrionomys* with a lateral position of the roots of M_2^2 are not known, the possibility is not excluded that this character was incompletely formed in *C. acrorhiza*.

Kormos (1933) considered *C. acrorhiza* closer to *C. glareolus*, which exhibits similarity of characters with *C. rutilus* in the structure of the anterior unpaired loop.

3. *Clethrionomys sokolovi* Topačevski, 1965 (foss.)

Diagnosis: Close to the preceding species but larger. Length of lower molar row 5.9 mm; M_1 —2.4, 2.5 mm. Cementation moderate (always visible from masticatory surface). Major triangles of M_1 fused (usually posterior and middle ones). Structure of anterior pair of triangles and nature of slope of folds similar to present-day
144 *C. rutilus*. Lower incisor longer than in any known extinct species of the genus (extends much above dental foramen and forms an alveolar knob on lateral surface of jaw), passing under posterior root of M_2 . M_2 with small, normally developed anterolateral triangle.

Age and distribution: First half of Early Pleistocene (Tamansk faunas). Aside from the type locality (Nogaik), reliable remains have been found nowhere else to date.

Taxonomic notes: This species differs from *C. acrorhiza* in addition to large size, in the relatively longer M_1 (Topachevskii, 1965). As in the preceding species, *C. sokolovi* has been found together with remains of *Clethrionomys* in which the roots of M_2 are lateral in position. It is quite possible that the large number of isolated M_1 with sparse cement belonging to forest voles from the lagurodont—*Allophaiomys* fauna are actually molars of *C. acrorhiza* or *C. sokolovi*, but not *C. kretzoi*, under which they are usually included.

Forest voles of the *acrorhiza*—*sokolovi* group are probably closely related to *C. iorensis* Buatschidze, 1968 from the Early Anthropogene (lagurodont—*Microtus*) fauna of Trans-Caucasus (Shiraksk steppe), which the author (Buachidze, 1968) considered close to *C. acrorhiza*. Actually, the difference I indicated between this small forest vole (M_1 —2.2—2.3 mm) with cementation normal for the genus, and the extinct Hungarian species is not great, namely,

greater isolation of the triangles of the masticatory surface of M_1 . Unfortunately, the position of the lower incisor in relation to the roots of M_2 has not been indicated. The material is interesting since it permits confident identification of the M^3 of this species, since *C. iorensis* is the only vole with rooted molars in the composition of Shiraksk fauna. With a length of 1.7–1.75 mm ($n = 7$), the heel of this tooth has a comparatively simpler structure: a third medial fold and, accordingly, a fourth “tooth” are not present in all specimens and, when present, are poorly developed. Unfortunately, given diagrams based either on poorly processed negatives or imprints, the depth relationship of the two lateral folds cannot be established with sufficient confidence; certain other structural details are also difficult to observe (thickness of enamel, etc.).

We may note that an identical structure of M^3 is found in *Clethrionomys* from the lagurodont—*Allophaiomys* fauna of Ufa region of Ural; a good series of these remains was recently described by Sukhov (1970). The author has included this series with no explanation under *Clethrionomys* ex gr. *glareolus* Schreb. Incidentally, even in this material the position of the posterior root of M_2 could not be established.

4. *Clethrionomys hintonianus* Kretzoi, 1968 (= *hintoni* Kormos, 1934, praeoccup.) (foss.)

Diagnosis: Size small. Length of lower molar row 5.0–5.5 mm, M_1 —2.2–2.4 mm. Cementation, judging from the diagram (Kormos, 1934b, Figure 48), moderately abundant (described as “scant” by the author). Major triangles of masticatory surface of M_1 isolated; those located at base of anterior unpaired loop fused and almost not separate from latter; lateral one narrower, stronger and directed posteriorly. Anterior unpaired loop symmetrical, fungiform, especially in type specimen, and lateral fold bordering loop deep and not smaller than medial fold. Roots of M_2 laterad. Both M_2 and M_3 with three transverse enamel fields (opposite triangles broadly fused); anterolateral denticles of these teeth narrow and shifted backward. Lower incisor comparatively strong.

145 *Age and distribution*: End of Early to Middle Pleistocene, Hungary (Nodkhorshaned).

Taxonomic notes: Forest voles of Western and central Europe from the commencement of the Middle Pleistocene usually belong to present-day species. *C. hintonianus*, which has retained the general plan of structure more than other typical members of *C. glareolus*, displays a certain similarity to the red-backed vole (*C. rufo-*

canus Sund) in the anterior unpaired loop of M_1 and anterolateral sections of M_2 – M_3 . Other features are detailed in the next form.

5. *Clethrionomys esperi* Heller, 1930 (foss.)

Diagnosis: Close to the preceding species and possibly identical. Length of lower molar row about 5.2 mm; M_1 —2.2–2.3 mm ($n = 4$). Differs from *C. hintonianus* in narrower and longer triangles of masticatory surface of M_1 , especially lateral triangles of M_2 and M_3 , more abundant cementation, isolated middle pair of triangles of M_2 , and a tendency toward a similar isolation in M_3 .

Age and distribution: Second half of Early to Middle (?) Pleistocene: Austria, Hungary, western Czechoslovakia.

Taxonomic notes: The author of the first description rightly considered this species close to *C. refocanus*; remains of *Clethrionomys* ex gr. *glareolus* were also found at the same site.

Forms close to the red-backed vole are known in USSR only from later deposits.

6. *Clethrionomys rufocanus* Sundevall, 1846–1847— Red-backed Forest Vole (Figure 20)

Diagnosis: Size large. Body length up to 145 mm, tail up to 57 mm (41% trunk length), upper molar row up to 7.6 mm, lower row up to 7.3 mm; M_1 —2.5–2.8–3.2 mm. Dark, rusty to chocolate-brown tones in pelage of dorsal surface of body are usually distinct, and often form a very narrow field, the so-called mantia, which is distinctly demarcated from the gray sides; lateral surfaces of head also gray. Tail covered with relatively short hairs, monochromatic or slightly bichromatic.

Skull of adult animals angular, with relatively narrow, groove-like, depressed interorbital space; zygomatic arches high in middle part; and postorbital processes relatively large. M^3 often simpler in structure, with three grooves and two folds on both sides. M_1 often with traces of second-order folds in form of depressions on one or both margins of anterior unpaired loop.

Description: The skull rapidly loses juvenile features with age: the brain case becomes angular and flattened on top and the post-orbital processes, occipitals, parietals, and interorbital crest are well-developed. The interorbital space narrows sharply, especially in posterior part, where the width may be 2.6 mm. The lateral margins of the interorbital space are highly contiguous, although not fused into a single crest. The interparietal is comparatively short in transverse direction. The bony palate is comparatively narrow;

both posterior pits are large (larger only in *C. sikotanensis*) and broadly touch each other and the lateral depressions at the base of the hard palate. The horizontal section of lower jaw, including the incisor section, are relatively high, and the angular and articular processes are short and broad.

146 Molars are relatively broad; the triangles of the masticatory surface are narrower than in any other species of this region. The

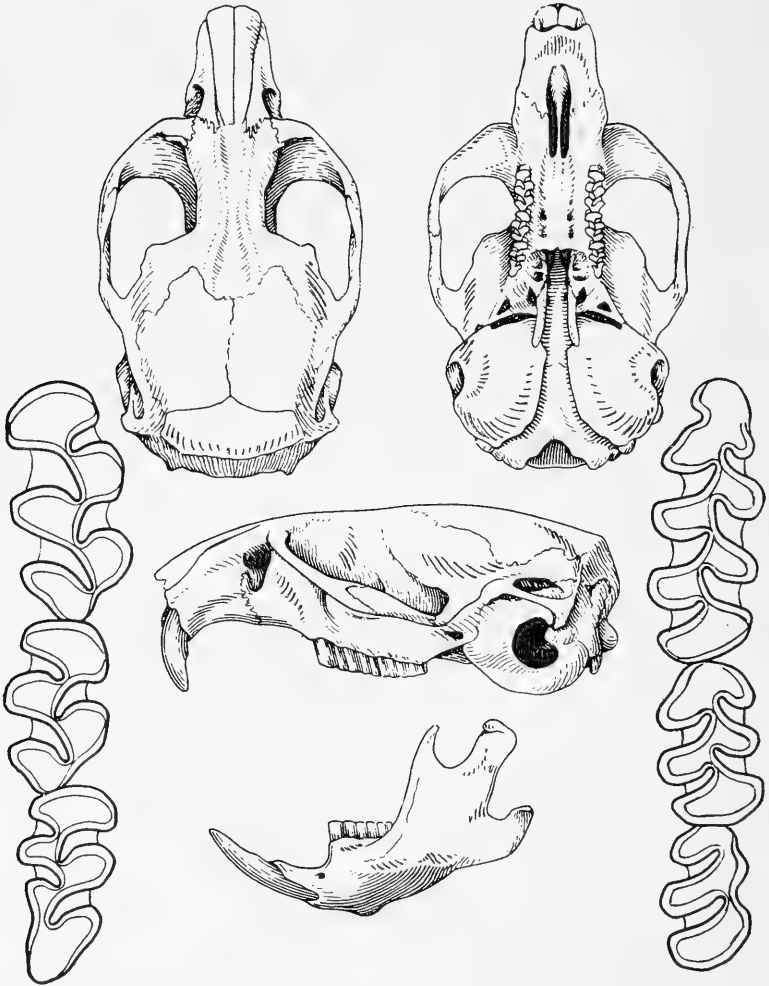


Figure 20. Skull of large-toothed red-backed forest vole (*Clethrionomys rufocanus* Sundevall).

enamel fields on the lower molars tend toward complete isolation not only on M_1 , which is normal, but also on M_2 and sometimes on M_3 (middle pair). The roots form later than in other species of the genus, and in some forms, only toward the end of the first year of life.

Distribution and zonal affinity: This species inhabits primarily montane-taiga regions of northern Eurasia up to upper forest boundary, including the elfin woodland belt from northern Norway, Kola Peninsula and northern Finland to extreme northeastern Siberia, Kamchatka, Sakhalin; Shanter, northern (Paramushir, possibly Onkotan) and southern (Kunashir, Shikotan, Zeleny) Kuril' Islands; northern Japan (Hokkaido); mountain regions of central and southern China; and northern parts of Assam (India) and Burma. Elucidation of the subspecific affinity of forms from 147 northeastern China, northeastern Mongolia, and northwestern Mongolia is required (Bannikov, 1954; Zimmermann, 1964).

Composition of species and nature of geographic variability: The number of subspecies is more than the six listed here: *C. r. rufocanus* Sundevall, 1846–1847 (Europe and Siberia up to Trans-Baikal region); *C. r. irkutensis* Ognev, 1924 (Siberia, east of Baikal); *C. r. wosnessenskii* Poljakov, 1881 (Kamchatka, Karaginsk, and Paramushir Islands); *C. r. bedfordiae* Thomas, 1905 (Sakhalin, southern Kurils, Hokkaido); *C. r. regulus* Thomas, 1907 (Korea); and *C. r. schanseius* Thomas, 1908 [southern China and adjacent montane regions of India (Assam), and Burma].

The characters of subspecific variability are not well-defined. Proceeding eastward, the rusty tone of the dorsal pelage becomes slightly brighter, and in Trans-Lena Siberia some lengthening of the tail is observed. Insular forms have the longest tail and are also the largest in size. Some tendency toward less isolation of the triangles of the masticatory surface of the lower molars is observed in the skull structure of eastern forms compared to western forms.

Evolution and phylogeny: Reliable (not yet described) fossil remains are known to date only from the beginning of the Late Pleistocene from Ural and western Siberia. In Europe, some small Pleistocene forms of *Clethrionomys*, type *C. esperi*, with isolated middle triangles in M_1 and M_2 and a tendency toward bilateral second-order folds of the anterior unpaired loop of M_1 , may be considered possible ancestral forms. It is also possible that the large-sized (length of M_1 —2.5 and 2.6 mm) *C. rufocanoides* Storch, Franzen and Malec, 1973 from the Early Pleistocene deposits in Würm (FRG), is actually closer to present-day species than to others. How-

ever, the holotype is an aged specimen with eroded molar crowns and the other features listed by the authors are undoubtedly age-dependent. The Japanese vole (*C. andersoni* Thomas) from Honshu Island and *C. glareolous* are possibly the closest to present-day species.

Among all the present-day species of the genus, *C. rufocanus* is the most specialized form; it feeds mainly on green leaves (Vorontsov, 1961), as is clearly indicated by the structural features of the skull and molars. The latter, especially in eastern forms of the species, are also distinguished by a significant crown height and late root initiation. At the same time, south Asian continental members are also close to *Eothenomys* and *Antelionomys* on the one hand, and to certain members of *Alticola* on the other. But there is no single opinion regarding the generic relationship of the two south Chinese species—"Eothenomys" *inez* Thomas and "E". *eva* Thomas. Hinton (1926) considers them as sexually mature individuals of *C. rufocanus*, whereas Allen (1940) following Howell (1929) included them under *Eothenomys* with equal emphasis, and combined them into a separate subgenus, *Caryomys* Thomas.

7. *Clethrionomys andersoni* Thomas, 1905—Anderson's Vole

Diagnosis: Body length up to 120 mm, tail up to 68 mm (59.75% trunk length), upper molar row 6.4–6.9 mm (Aimi, 1967). This species is close to *C. rufocanus* but differs in longer tail, which is always greater than half trunk length, and duller color. Skull slightly more juvenile in appearance than in the neighboring large-toothed red-backed vole (subsp. *bedfordiae*, the auditory bullae more inflated and rounded, and M³ with permanent, well-developed, fourth medial groove (Tokuda, 1941).

148 *Distribution and zonal affinity:* Japan: montane (primarily coniferous) forests of Honshu.

Evolution and phylogeny: Two forms—*C. a. niigatae* Anderson, 1909 (central part of Honshu) and *C. a. imaizumii* Jameson, 1961 (southern part of Honshu and tough-leaved subtropical forests of Kii Peninsula)—are sometimes considered synonyms of *C. andersoni* (occasionally only the latter one), sometimes independent subspecies (Aimi, 1967), and sometimes closely related to independent species (Jameson, 1961). In all the specimens of *C. imaizumii* studied, no molar roots were found and therefore its relationship to another species, conf. *Aschizomys smithii* Thomas, is also not excluded. Jameson (1961), using the taxonomic grouping of Japanese *Clethrionomys*, agreed with Imaizumi (1957) that *C. andersoni* al-

though close is well-distinguished from *C. rufocanus*. Hokkaido Island, where the latter species lives, and Honshu were separated before the Pleistocene; thus, *C. andersoni* is an example of formation of an insular species within the limits of the genus *Clethrionomys* during the Pleistocene.

8. *Clethrionomys sikotanensis* Tokuda, 1935—
Shikotan Vole (Figure 21)

Diagnosis: Size larger than in other species of the genus. Body length up to 160 mm, tail up to 65 mm (46% trunk length), upper molar row up to 7.9 mm, lower row up to 7.7 mm; M_1 —3.0—3.1—3.25 mm. Red and rusty-red tones lacking in dorsal surface, replaced by brown to chocolate-brown tones that are typical of many members of *Microtus*. Transition in color of sides gradual. Tail monochromatic or slightly bichromatic, covered with short hairs.

Based on angular profile and major skull proportions, this species resembles the large-toothed red-backed vole, differing in short and broad rostral section, complete absence of interorbital crest in old individuals, long and complex structure of M^3 with four denticles on both lateral and medial sides. Anterior unpaired loop of M_1 similar to *C. rufocanus*, but depressions of second-order folds disappear faster with age, and sometimes develop only from one side. Unlike all other species of the genus, the lower incisor extends above the dental foramen, forming an alveolar knob on the lateral side of the base of the articular process.

Composition of species: The Sakhalin species, *C. microtinus* Kuzjakin, 1963 (nomen nudum!) is probably an independent subspecies of the Shikotan vole.

Description: The skull, even in adult and old individuals, is somewhat more juvenile in appearance than in large-toothed red-backed voles of the same age, due to a broad and uniformly deep interorbital space anterior to the frontoparietal suture. It is much more convex near the dorsal margin of the zygomatic arches than in *C. rufocanus*, and the angle of the frontonasal slope in profile is greater than in this species. Moreover, the bony palate is slightly broader, the postpalatal depressions are much larger than in any species of the genus, the incisor alveoli are longer and generally terminate close to the anterior margin of the alveolus of M^1 , the incisors have a longer crown and the upper incisors are notably broader, and the angular process of the lower jaw is shorter and broader than in the large-toothed red-backed vole. Molar roots form

later in *C. sikotanensis* than in other species of forest voles in Russian fauna and on M_1 most probably are never greater than one-third crown height. As a result, the intraorbital alveolar knob on the root section of the upper molars end on the lateral surface of the mandibular rami (from M_1 – M_2), and the alveolus of M_3 are retained for a longer period; thus the skull of this species resembles that of common voles (*Microtus*).

149 *Distribution and zonal affinity:* This species is known from southwestern Sakhalin and Shikotan Islands and possibly occurs on other southern Kuril' Islands. In Shikotan, sympatric with the large-toothed red-backed vole (*C. rufocanus bedfordiae*). It inhabits meadows and leads a life similar to that of common voles of the "marsh" group.

Evolution and phylogeny: This is a large vole with a relatively long tail, similar in external appearance to voles of *Microtus*, e.g. *M. oeconomus*; however, the structure of the bony palate and the presence of rooted molars provide the basis for including it under *Clethrionomys*. Tokuda (1935) initially separated this species into an independent genus, *Neoaschizomys*; subsequently, he himself admitted (Tokuda, 1941) to exaggeration of structural characters. The Shikotan vole was first included in Russian fauna by Kuzyakan (Bobrinskii *et al.*, 1965), but its affinities are not clear. Possibly, it is more distanced from *C. rufocanus* and *C. andersoni* than other species of the genus, e.g. *C. rutilus*. Thus, the time of its geological separation would probably be earlier than that of Anderson's forest vole. It would be interesting to determine the relationship of the Shikotan vole to the small extinct species, *C. sokolovi*, which also has a long lower incisor that forms a distinct alveolar knob at its posterior end.

9. *Clethrionomys glareolus* Schreber, 1780— European Forest Vole (Figure 22)

Diagnosis: Size medium. Body length up to 120 mm, tail up to 56 mm (56% trunk length), upper molar row up to 6.1 mm, lower row up to 6.0 mm; M_1 —2.1–2.45–2.75 mm. Dark, rusty to chocolate-brown and reddish to chocolate-brown tones dominant in dorsal surface; sides of body and head similarly colored, with change in color gradual. Tail distinctly, rarely slightly, bichromatic with moderately abundant pelage.

Skull roundish, without crest even in old individuals, including the interorbital region. M^3 comparatively complex in structure, with four denticles on medial and, often, lateral side as well. Ante-

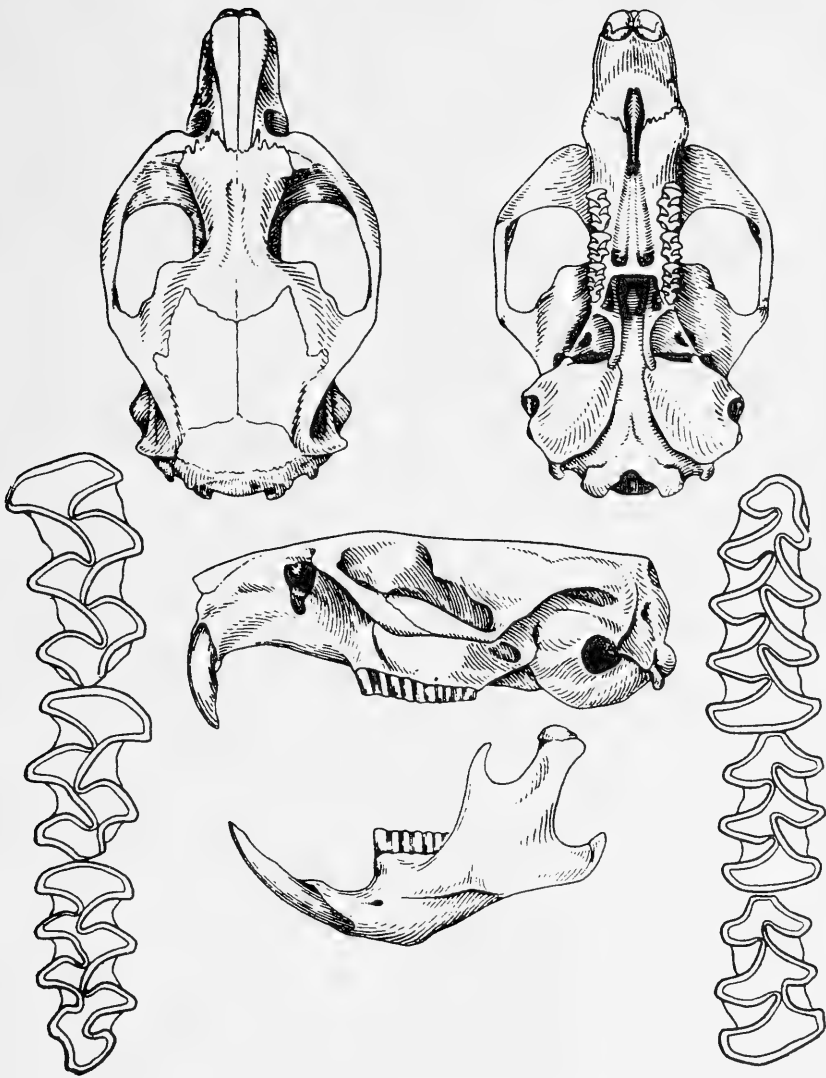
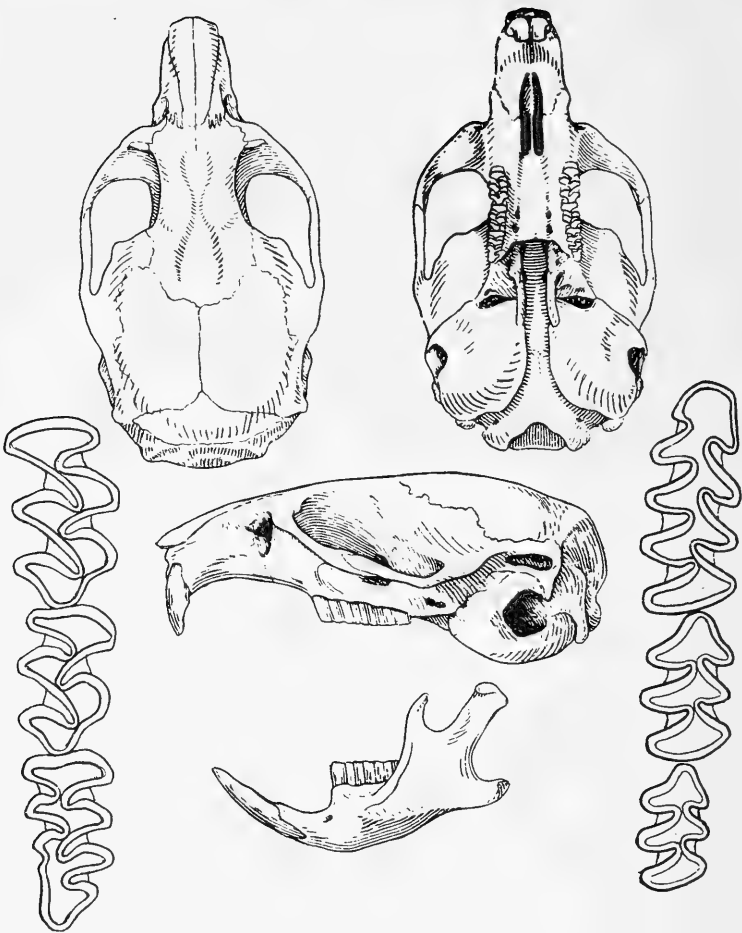


Figure 21. Skull of the Shikotan vole (*Clethrionomys sikotanensis* Tokuda).

151 rior unpaired loop of M_1 , without traces of secondary lobes, rounded, asymmetric, poorly isolated on medial side, the depression here usually smaller than on lateral side and rapidly disappears with age.



150 Figure 22. Skull of the European forest vole (*Clethrionomys glareolus* Schreber).

Composition of species: Chromosomal and hybrid analyses (Steven, 1955; Rauschert, 1963; Orlov, 1968) have finally confirmed the independent species status of some forms (for example, *C. frater* Thomas, 1908) and the subspecies status of others (for example, *C. g. nageri* Schinz, 1845 and *C. g. erica* Barret-Hamilton and Hinton, 1913). However, the taxonomic status of many of them, especially the five forms from the Balkan Peninsula (Mirić, 1970), still remains unclear. This is also true for the Trans-Caucasian and east

Turkish species *C. ponticus* Thomas, 1906, and among the extinct forms, *C. kennardi* Hinton, 1926.

The independent status of the following subspecies may be considered more or less confirmed: *C. g. harrisoni* Hinton, 1926 (foss.) (Late Pleistocene of British Isles); *C. g. nageri* Schinz, 1945 (high altitudes of Alps and Carpathians); *C. g. norvegicus* Miller, 1900 (mountains of northern Norway); *C. g. helveticus* Miller, 1900 (foothills of Western Europe, foothills and partly montane regions of central Europe); *C. g. glareolus* Schreber, 1780 (plains of Western Europe and central and eastern Europe); *C. g. suecicus* Miller, 1909 (southern and central Scandinavia, northern European part of the USSR up to the Middle Urals, the Ural range, and Trans-Ural area); *C. g. britannicus* Miller, 1900 (main islands of British archipelago); *C. g. isticus* Miller, 1900 (plains and foothills of southeastern Europe, Pennon depression); *C. g. saianicus* Thomas, 1911 (Salair range, Altai and Sayans); and *C. g. ponticus* Thomas, 1906 (Southwestern Trans-Caucasus and adjacent regions of Turkey).

Additionally, at least four insular forms are known, mainly from small islands in the British archipelago: *C. g. alstoni* Barret-Hamilton and Hinton, 1913; *C. g. erica* Barret-Hamilton and Hinton, 1913 (near the Hebrides); *C. g. skromerensis* Barret-Hamilton, 1903 (islands near the western coast of Wales); and *C. g. caesarius* Miller, 1908 (Normandy).

Description: The skull, compared to that of large-toothed red-backed vole is juvenile in appearance: crests are absent, the cranium is slightly convex in vertical region, and the postorbital processes are small. The interorbital space has a comparatively weak longitudinal depression in anterior part; the convexity is often notable but with a distinct depression in posterior part, as well as on frontals anterior to frontonasal angle. The interparietal is transversely elongate. The bony palate is relatively broad; postpalatal depressions are small, isolated. The horizontal section of lower jaw is low, angular, and the articular processes long and narrow.

The molars are relatively narrow: the triangles of the masticatory surface are short and broad at base. Division of enamel fields on lower molars is always observed on M_2 and M_3 , and in several cases also on major triangles of M_1 . Roots develop relatively early, i.e., in three- to four-month-old animals (this character is geographic).

Distribution, zonal affinity, and variability: This species is found at present in broad-leaved, coniferous-broad-leaved, and dark coni-

ferous forests in mountains and plains of Europe, western Siberia, and montane area of central Siberia, from northeastern Spain (center to the Pyrenees), France, Scotland, northern and southwestern Italy, and northern parts of Asian Turkey to Altai, northern slopes of western Sayans, coastal area of Middle Yenisey and Baikal regions (new collections have not been made in recent years). The boundary coincides with the upper forest limits (in the east, from the upper boundary of secondary mixed forests) in the mountain and the boundary of forest-tundra in the plains; animals penetrate the tundra through floodplain forests. In the Trans-Ural region, from the Ob' River, the boundary moves southward and is poorly demarcated between the Ob' and the Yenisey. South, up to central Mediterranean, the Carpathians and floodplain forests of the Ukraine, Voronezh district, Saratov and Kuibyshev area of Trans-Volga, floodplain forests of the Ural River in the south up to Uralsk, and the western Siberian forest-steppe. Several island localities are known along the southern border and, most probably, the species strays into northwestern Trans-Caucasus and adjacent regions of Turkey.

This species has been found in Late Pleistocene in Western and partly central Europe in mixed faunas from the Würm glaciation period but is not found in eastern Europe. It penetrated into Crimea and lived in the floodplains of the Middle Don. However, remains have not been found to date in central Caucasus.

Geographic variability reveals a fairly confused picture of size and perhaps color, but to a lesser extent than in *C. rutilus*. Thus, many insular as well as montane forms are generally larger and darker in pigmentation than plain forms, but small (*britannicus*) and light-colored (*skromerensis*) forms appear among the former (Steven, 1953), and some montane forms are smaller than plain forms in the Far East. Reduction in size with altitude as well as with westward movement has been observed in the large central European subspecies *nageri* (Claude, 1970). In the European part of the USSR, some lightening of coloration southward has been noted (Ognev, 1950), and simultaneously some increase in vividness of red tones in broad-leaved forest animals eastward. Variability of skull structure in populations from the European part of the USSR is expressed as follows: in northern forms, molar structure is more typical of *C. rufocanus* with a strong tendency toward isolation of the triangles of the masticatory surface, the major triangles on M_1 , the middle triangles on M_2 and M_3 , and the unpaired anterior loop and its mediobasal triangle. The southern population is character-

ized by a predominantly Early Pleistocene type of structure and isolated triangles which, similar to the type, have not been preserved to a great extent in present-day western populations (west of the Yenisey) of the red-backed Siberian vole (*C. rutilus*). Moreover, the "Pliomys" type structure of the anterior section of M^3 is found more often in southern populations of *C. glareolus* than in northern populations, the M_3 becomes narrower, the enamel thicker, and the folds and denticles of the molars more rounded.

Evolution and phylogeny: Remains identified as those of *C. glareolus* have usually been recovered from deposits not older than the Late Pleistocene. Actually, fragmentation of most of the remains does not permit a more precise identification for material from submontane Crimea (Gromov, 1961) and the Moldavian Carpathians (Lozan, 1971). Only Hinton (1926), with well-preserved material from the Late Pleistocene of England, including two relatively less damaged skulls, could describe two extinct species with confidence. One of them, *C. harrisoni*, can hardly be considered more than a subspecies of *C. glareolus*. As for the second, the author considers *C. kennardi* close to the present-day montane vole *C. g. nageri*, assuming that the relatively large-toothed extinct form with a spongy bony tissue in the cavity of the auditory bullae (a character lacking in all known forms of the genus) or a form close to it, was distributed in Europe at the time of the last (Würm) glaciation, after which it was restricted to the hill regions of Western and central Europe. Strangely enough, Hinton says nothing about the affinity of the extinct species to the comparatively large forms from small islands in the British archipelago mentioned above.

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There is no dependable paleontological record for the evolution of this species in the eastern parts of its range. Nor is the time of its separation from the Tien Shan montane-forest vole (*C. frater* Thomas) clear. Even Kirikov (1935) assumed a break in the distribution of *C. glareolus* between its Trans-Ural and montane southern Siberian areal. True, it was later established that no such discontinuity ever existed. Nevertheless, the European forest vole is distributed here in a relatively narrow belt in the southern Ob' region, where it has adapted to sparse mixed taiga as well as aspen and grassy cut sparse forest, avoiding coniferous forests and marshlands (Laptev, 1958). All this and the comparatively rare occurrence of the species in the eastern range indicate a minor interruption and possible subsequent mergence of these parts of the range.

10. *Clethrionomys frater* Thomas, 1908—
Tien Shan Forest Vole (Figure 23)

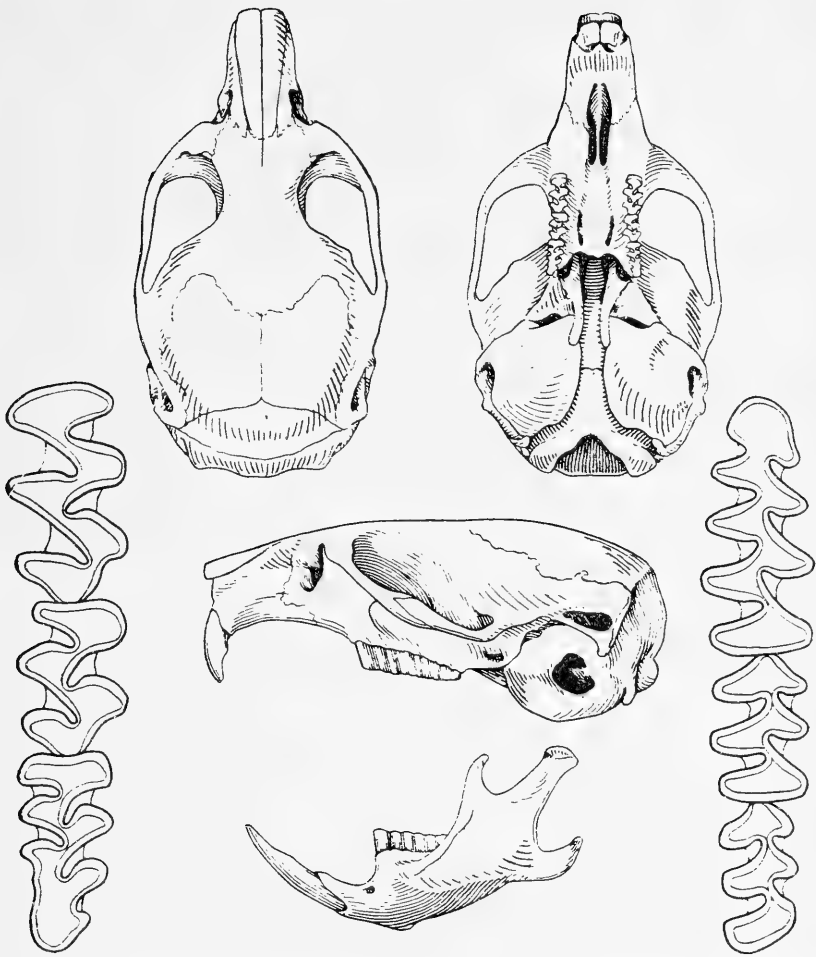
154 *Diagnosis:* Similar in size to *C. glareolus* but with a relatively longer tail. Body length up to 113 mm, tail up to 59 mm (62% trunk length), upper molar row up to 6.0 mm, lower row up to 5.8 mm; M_1 —2.2–2.4–2.65 mm. Rusty and reddish to chocolate-brown tones barely perceptible in color of back and sides; brownish-gray tones dominant. Tail less sharply bichromatic than in the European forest vole, with somewhat denser pelage. Skull, considering the juvenile nature of its general appearance, similar to that of *C. glareolus*, from which it differs in slightly smaller auditory bullae (particularly distinct compared to montane forms of European species) and slightly higher and broader brain case. The character detected by Ognev (1951), namely, a small gap between the posterior end of the upper incisor and the root of M^1 , is valid as a distinguishing character from the European forest vole, but is not valid for all populations of this species. In particular, no differences are found in comparing the large southern and montane forms. The structure of the anterior section of M_1 and the number of denticles on M^3 are essentially identical to *C. glareolus*.

Composition of species: Subspecies not described. Taxonomic position of *C. centralis* Thomas, 1904 from the Chinese part of Tien Shan not known. V.S. Vinogradov, who studied the type specimen in the British Museum collection, has indicated its closeness to voles of the *rutilus* group (Vinogradov and Argiropulo, 1941).

Description: The skull maintains juvenile appearance somewhat longer than in the European forest vole: the brain case of *C. frater* of the same age is somewhat inflated, the lateral parts of the occipital crest are poorly developed, and the depression anterior to frontoparietal suture smaller. Furthermore, in the Tien Shan species, the interorbital space and dorsobasal section of the zygomatic arches are more flattened, the dorsal profile straighter, and both postpalatal pits often located in a common depression. Many of these characters, including the marked juvenile skull structure, bring *C. frater* closer to *C. rutilus*.

Based on the structure of the masticatory surface of M_1 , *C. frater* is closer to the southern populations of *C. glareolus* and the eastern populations of *C. rutilus*; M_2 and M_3 with isolated middle triangles and "Pliomys" type structure of M^3 are rarely found.

Distribution and zonal affinity: This species inhabits montane forests of Tien Shan, but reliable finds from western Talassk Alatau and the Ferghana range are not known.



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Figure 23. Skull of Tien Shan forest vole (*Clethrionomys frater* Thomas).

Evolution and phylogeny: Fossil remains of *Clethrionomys* have not been found to date within the limits of Tien Shan. The Tien Shan relicts are generally considered Pleistocene in age. The independent species status of *C. frater* was finally demonstrated rather recently through hybrid analysis. It was shown (Orlov, 1964, 1974) that the reproductive isolation of this species from *C. glareolus* as well as *C. rutilus* is no less than that between these two

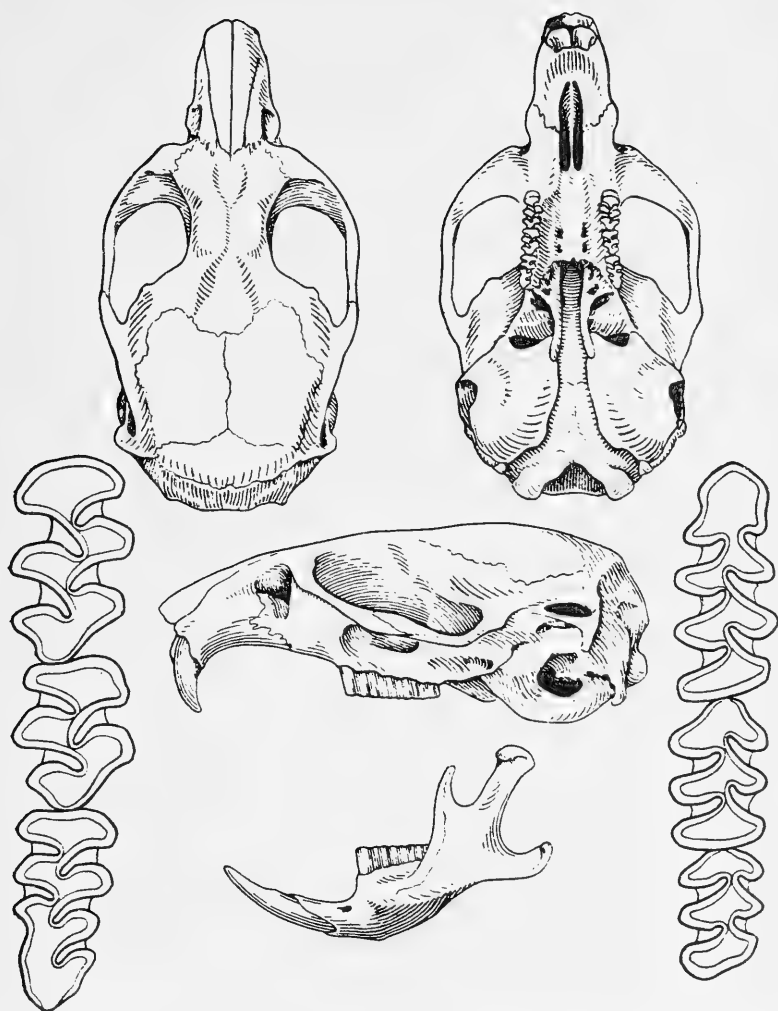
species *per se*. Hybrids were obtained with difficulty, accompanied by distinct ontogenetic disturbances, and the hybrid males sterile.

11. *Clethrionomys rutilus* Pallas, 1779—Siberian Red-backed Vole (Figure 24)

Diagnosis: Size medium but more variable than in other Palearctic species of the genus. Body length up to 117 mm, tail up to 42 mm (45% trunk length), upper molar row up to 5.4 mm, lower row up to 5.2 mm; M_1 —1.95—2.15—2.4 mm. Comparatively light-colored, but rusty to chocolate-brown and reddish tones dominant in color of dorsal surface, especially in winter pelage, often forming
 155 a “mantia”; sides of trunk and head light gray or ochereous-yellow. Tail often distinctly bichromatic, densely pubescent, with long terminal hairs.

Skull maximally similar to that of *C. frater* but even more juvenile in appearance. Unpaired anterior loop of M_1 on medial side less distinctly demarcated than in the European and Tien Shan forest voles; M_3 highly variable, but generally similar in number of folds.

Composition of species: Researchers differ sharply regarding the number of subspecies. For example, Rossolimo (1962), who investigated the absolute dimensions and color of this species throughout its European range, says it does not differentiate into a subspecies. Contrarily, Ognev (1950), and many who share his views, recognize at least ten subspecies. Rausch (1950), who rejected the red-backed voles of North America as a subspecies, has included them here; moreover, two subspecies are indicated for Canada (Hall and Kelson, 1959). Undoubtedly, many of the forms described, for
 156 example, *C. rjabovi* Beljaeva, represent no more than color variation due to mutation (Rossolimo, 1971). K.P. Kuzyakin (Bobrinskii *et al.*, 1965), whose views on the fauna of the USSR are generally endorsed, indicates that six subspecies may be accepted until special examination of the material proves otherwise: *C. r. rutilus* Pallas, 1778 (Siberia between the Ural and Yenisey Rivers); *C. r. rossicus* Dukelsky, 1928 (European part of the USSR); *C. r. vinogradovi* Naumov, 1930 (basin of Lower and Middle Yenisey); *C. r. jacutensis* Vinogradov (northern Siberia, east of Lena, Kamchatka, and western Alaska); *C. r. amurensis* Schrenk, 1858 (southeastern Siberia); and *C. r. lategriseus* Argyropulo, 1939 (Kazakhstan, montane tract). A seventh form may also exist—*C. r. tundrensis* Bolschakov and Schwarz, 1965 (tundra between the Ural and Lena Rivers). In the eight known American subspecies, the most widely distributed are: *C. r. dawsoni* Merriam, 1888 (large part of Alaska and Canada);



155 Figure 24. Skull of the Siberian red-backed vole (*Clethrionomys rutilus* Pallas).

C. r. washburni Hanson, 1952 (north of central Canada); *C. r. platycephalus* Manning, 1957 (area of Mackenzie River); *C. r. albiventer* Hall and Gilmore, 1952 (St. Lawrence Island),³ and up to five subspecies occupying small areas along the northwestern coast

³It is interesting that, based on the structure of the soft parts of the penis, this species is closer to *C. rufocanus* than to *C. rutilus* (Hooper and Hart, 1962).

of North America and adjoining islands. A well-distinguished subspecies is *C. r. micado* Thomas, 1905.

Description: In addition to juvenile characters, possibly more strongly expressed in *C. rutilus* than in any other Palearctic species, the skull is also characterized by a relatively longer, narrower facial section, a broader, more flattened interorbital space, and the interparietal reduced anteroposteriorly. The lower jaw has a low horizontal ramus (lower only in *C. r. gapperi*), long diastema, smoothly curved incisors, and elongate articular process. The molars are relatively narrow, with short, broad triangles on the masticatory surface, and close-set anteroposteriorly; their apices in sexually mature individuals are more rounded than in individuals of the same age in other species. The extent of fusion of the major triangles of M_1 and the middle pair of M_2 and M_3 is variable and also evidences geographic variability. The basal triangles of the paraconid of M_1 are fused or only the medial one has an anterior unpaired lobe. Roots develop later than in *C. glareolus*, at five to six months of age; differences are particularly striking outside the sympatric range of the two species.

Distribution, zonal affinity, and variability: It is found in forest, forest-tundra and forest-steppe zones, and corresponding vertical belts, and in the open biomes of the northern high mountains up to the shrub line. It occurs from central Sweden and north up to the northern coast of Lake Ladoga, upper reaches of the Volga, northern Ilmen region, northern Mordovia, northeastern Tararia, southern Ural, central parts of Kazakhstan hills, Altai-Sayan mountain range including the mountains of northern Mongolia, northeastern China, northern Japan (Hokkaido Island), Sakhalin, Paramushir Island (Kuril' range) and Bering Island (drifted), throughout northeastern Siberia, Kamchatka, Alaska, and adjacent part of Canada up to the Western coast of Hudson Bay.

The variability of external as well as skull characters is not great and describes a mosaic pattern. Specific characters are more distinct in the structure of the masticatory surface of the lower molars in the Siberian populations, which have retained a greater similarity to the extinct Kretzoi vole.

157 Clinical variability is displayed only in the dull coloration of the dorsal surface from north to south in Eurasia (Rossolimo, 1962) and light coloration and yellowing in North America (Rausch, 1950). European populations in the Far East have the darkest color due to higher humidity. The brightest orangish-red tones are typical of voles from Yakutia, northeast of which the animals have a shorter

tail than in the remaining part of the continent. Tails are still shorter in Hokkaido voles. Geographic variability of skull structure has not been studied sufficiently but judging from changes that have taken place in animal populations that drifted about 100 years back from the mainland to Bering Island, these features appear quickly under conditions of isolation (Shaposhnikov, 1961). The most clear-cut differences in molar structure are seen between vole populations of Siberia before and after the Yenisey. A general tendency toward change in an easterly direction is expressed in the greater isolation of the anterior unpaired loop of M_1 , due in particular to the depression caused by the lateral fold, separation of the major triangles of this tooth, and isolation of the medial triangle at the base of the paraconid. The middle triangles of M_2 – M_3 are also isolated. Moreover, M_3 is relatively small in the eastern populations, and has a small lateral fold that anteriorly often resembles a denticle. M_3 is more complex, its anterior section rarely "*Pliomys*" in structure. All the aforelisted changes are reversed in the same direction for *C. rufocanus*.

Evolution and phylogeny: Reliable fossil remains are known only from Siberia and the Far East from Late Pleistocene deposits. The affinities of many extinct forms of Late and Early Pleistocene from territories west of the Ural range cannot be established with sufficient confidence. Many of these forms, however, are characterized by primitive traits of the masticatory surface of the molars, which have been fully retained by present-day populations of *C. rutilus* especially from the eastern parts of its range. Thus Razorenova's opinion (1962) that the red-backed vole is the original species of Siberian forest-tundra and plains of light coniferous taiga that recently spread westward at present lacks sufficient paleontological evidence. As mentioned above, within the Late Pleistocene "cold" mixed faunas, remains of *Clethrionomys* are not known for the USSR; instead, all the typical characters of *C. glareolus* for the forest-steppe faunas of the same periods (as also for the mixed faunas of central and eastern Europe) are seen.

It can be assumed that *C. rutilus* is a relatively late Wisconsin migrant in the New World and has not succeeded in penetrating south and east of the Hudson Bay, but occupying areas of the northern archipelago. Inhabitants of Hokkaido should probably be dated to the Late Pleistocene. Subspecies segregation corresponds in both cases to this epoch.

12. *Clethrionomys gapperi* Vigors, 1830—American Forest Vole

Diagnosis: Size similar to the European species, *C. glareolus*, but tail relatively shorter (although longer than in *C. rutilus*). Body length up to 112 mm, tail up to 56 mm (47% trunk length) (Hall and Cockrum, 1952; based on materials in the Zoological Museum of Moscow State University, tail length up to 45.4%; n = 7). Upper molar row 5.0–5.6–6.1 mm, lower row 4.7–5.1–5.4 mm, M₁—1.95–2.1–2.35 mm (n = 14). Grayish-brown tones dominant in color of dorsal surface, sides of body, and head, as in the Tien Shan forest vole. “Mantia” lacking. Tail distinctly bichromatic, covered with stiff hairs. Skull similar to that of *C. frater*, but appears to be somewhat more juvenile. Structure of M₁ and M₃ generally similar in both species.

Composition of species: Hall and Kelson (1959) have listed 27 subspecies, many of which have been described from southern border ranges.

Distribution and zonal affinity: It is found in the forest zone of North America south and east of the range of *C. rutilus*. The montane forest range extends south in the form of two tongues, one west, one east, up to 34–35° N, and up to the Appalachian Mountains. In the eastern part some changes in the boundary have been noted in a north–south direction as well as vertically (Guilday *et al.*, 1969) during the Late Pleistocene (Wisconsin and Illinois) glaciation.

Evolution and phylogeny: Fossil remains in the central part of the continent are known from the end of the Middle Pleistocene (Hibbard *et al.*, 1965); however, only those from the Late Pleistocene have been included indisputably under this species. Hinton (1926), who compared a series of skulls of the type form of *C. gapperi* and the British forms of *C. glareolus*, indicated the absence of species differences. Affinity with *C. occidentalis* Merriam, 1890 is not clear. Sheppe (1960) has reported that the differences between the two American species in external characters are no less significant than those between other species of the genus.

13. *Clethrionomys occidentalis* Merriam, 1890—Oregon Forest Vole

This species inhabits a small range in the montane forests of the west coast of North America, between the Columbia River and 39° N up to 2,000 m above msl (Hall and Cockrum, 1952). Five subspecies have been described from this area. Hinton (1926) con-

sidered this vole an American counterpart of the European large-toothed red-backed vole. *C. occidentalis* differs from *C. gapperi* in darker dorsal color, with a less distinct border between the dorsum and sides, and a brownish ventral surface (in *C. gapperi*, ventral surface gray). The tail is relatively longer, the auditory bullae larger and more flattened, and the molars, on the average, are relatively broader (Sheppe, 1960). The ranges of these two species are contiguous but probably do not overlap. The independent species status of *C. occidentalis* is quite probable, although not yet proved.

8. Genus *Eothenomys* Miller, 1896 (Figure 25)

Diagnosis: Voles with rootless molars but abundant cement. M^1 with five and M^2 with four triangles on masticatory surface behind anterior unpaired loop; if the posterior pair not isolated, then the medial side is always with four and not three denticles. Paraconid section of M_1 with two folds (second fold not complete); sometimes the primordial lobe of the third fold is also present on lateral side. Auditory bullae comparatively small, not inflated, and do not protrude perceptibly beyond masticatory surface of molars.

Composition of genus: Three present-day species—*Eothenomys melanogaster* Milne-Edwards, 1872; *E. miletus* Thomas, 1914; and *E. elensis* Thomas, 1910. The species *olitor* Thomas, 1911 and *proditor* Hinton, 1923 should be included in the genus *Antelimiomys* (Allen, 1940); and *eva* Thomas, 1911, *inez* Thomas, 1911, and *smithii* Thomas, 1905 under *Clethrionomys*.

159 *Description:* Body length up to 130 mm, rarely 140 mm, upper molar row up to 6.9 mm. Color of the dorsal surface is dark brown. Data on seasonal dimorphism is not available. Tail length is similar to that of *Clethrionomys*, the tail has sparse hairs and a sparse brush at tip. The pelage is well-developed. Size of eyes is not known. The pollex of forelimb has a flat claw. There are two pairs of nipples. Number of chromosomes, $2n = 56$.

The skull has a relatively short facial section and interorbital space. The zygomatic arches high in middle section. The posterior end of lower incisor always extends high beyond mandibular ramus and forms an alveolar knob on lateral surface of articular process.

Distribution and zonal affinity: This species inhabits high montane areas in southeast Asia [1,700–4,200 m above msl in Assam (India), Burma, China (Yunan, Hansu, and Taiwan) and northern

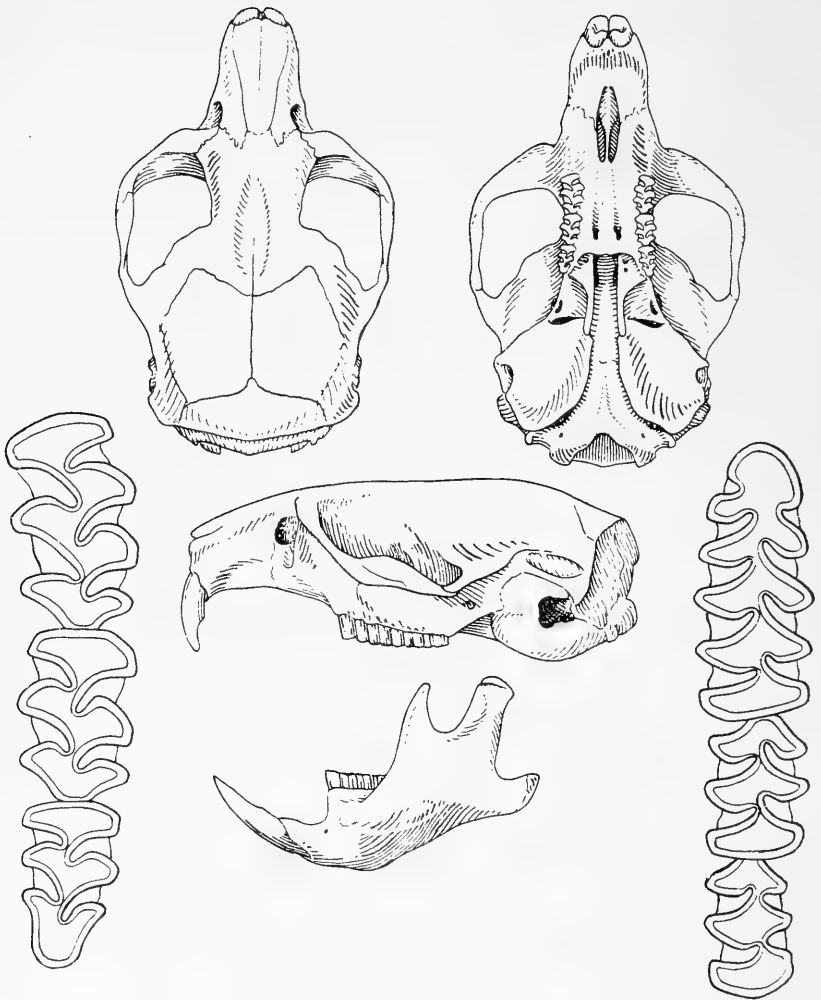


Figure 25. Skull of *Eothenomys melanogaster* Milne-Edwards.

Vietnam]; reports of its occurrence in Japan (Jameson, 1961) have not been confirmed.

Evolution and phylogeny: Confirmed fossil remains are not known. Finds from the Middle Pleistocene of China (Young, 1934) actually belong to another genus of Microtini. The position of *Eothenomys* somewhere above the base of the tribe Clethrionomyini is indisputable, and its considerable affinity to *Clethrionomys* was

even emphasized by Hinton (1926). The last revision of the group was done by Allen (1940); later publications are not known to me.

V. Tribe LAGURINI Kretzoi, 1955

Diagnosis: Bony palate with postpalatal pits of variable size, not interconnected, with width of bony constriction between them variable ("*Microtus*" type structure). Molars rootless and cementless; rarely, cement present. Lateral and medial triangles of masticatory surface of lower molars do not differ in size. Enamel not differentiated or poorly so in ancient forms, but distinctly differs in thickness in present-day genera, especially in *Eolagurus* and late *Lagurus* (Markova, 1974). Paraconid section of M_1 folded once, rarely incompletely twice, without traces of secondary simplification. M^3 moderately long or long, and with or without traces of secondary simplification. M_3 often long, longer than in all other Microtini, with well-isolated alveolus; anterior section of tooth not shifted laterad relative to longitudinal axis of molar row. Posterior end of lower incisor only in rare cases extends beyond level of dental foramen.

Composition of tribe: There are four genera: extinct—*Prolagurus* Kormos, 1938 and *Jordanomys* Haas, 1966; extant—*Lagurus* Gloger, 1841 and *Eolagurus* Eversmann, 1840. Many authors consider *Lagurodon* Kretzoi to be an independent genus, which has been listed here only as a subgenus of *Prolagurus*. On the other hand, *Prolagurus* and *Eolagurus* could be considered subgenera of the widely accepted genus *Lagurus* (Kormos, 1938; Kretzoi in earlier publications; Terzea, 1968, 1970). Recently, Kretzoi (1969) adopted a detailed division and recognized all the above-listed taxa as independent genera, as well as the genus *Laguroopsis* Kretzoi, which he established for *Lagurus pannonicus* (*Lagurodon helleri* Kretzoi, 1956) from Eppelsheim (FRG); *Hyperacrius* was questioned by him.

Like Zazhigin (1969, 1970), I do not approve to excessive fragmentation of the genera of the tribe, at least not until data on the structure of the skull of known species is complete.

Description: Small- and medium-sized voles. Body length up to 120 mm in the former, 240 mm in the latter. Length of upper molar row up to 90 mm, of lower row up to 9.5 mm. Dorsal surface monochromatic, grayish-ocher to sandy-yellow, with black stripe extending along middle of back (at least in young animals), rarely

absent. Seasonal dimorphism of pelage coloration negligible; long hairs and generally lighter color observed only in individuals living in areas of sharp continental climate. Tail, even if longer than hind foot, only slightly so, with rather dense light-colored hairs (sometimes only on lower side); terminal hairs may reach half tail length or exceed it. Eyes large, larger in *Eolagurus* than in any other vole. Pinna small, with reduced ear lobe, without antitragus or with rudimentary one; helix well-developed. Structure of rhinarium distinctly differs in members of the two present-day genera in size, density of hairs on upper alae nasalis, and separation of latter from lower alae nasalis; lower alae nasalis slightly lobate in middle part, with well-developed posterolateral sections, not fused
 161 with those of upper sections; and nares broadly open. Upper lips do not fuse under incisors. Upper labial flaps large, rectangular, touch at midline of palate, comparatively poorly pubescent; lower labial flaps small or moderately developed. Upper labial vibrissae small; genal, mental, and carpal vibrissae long, latter particularly so in *Eolagurus*.

Relative length of limbs not known; paw and foot reduced, their width variable. Palm moderately, sole densely covered with hairs. Digital pads well-developed, either isolated or fused into single pad. Inner palmar pad present, although not large; inner metatarsal pad absent. Digits of forelimb; III, IV, V, II, I; pollex rudimentary, without claw or with small flat obtuse claw; other claws up to half digital length or slightly shorter. Hind limb: III, IV, II, V, I or IV \approx II, with well-developed or moderately developed claws; claw on 5th digit up to half digital length or longer (*Eolagurus*). Seasonal differences in length of claws perceptible but not large.

Dorsal profile of skull (its structure not known for extinct forms) with notable dip at base of zygomatic arches. Crests present on relatively short and narrow interorbital space; well-expressed groove-like depression may form here in old individuals. Crests moderately developed on slightly flattened and angular brain case. Zygomatic arches not high in middle section and narrow slightly or not at all (*Eolagurus*). Orbits small or medium in size (*Lagurus*) and moderately or highly shifted ventrally. Orbital plane either close to horizontal (*Lagurus*) or forms moderate angle. Postorbital processes small, directed towards front and sides. Masseteric [= zygomatic] plate of maxilla high in *Eolagurus* (higher only in *Dicrostonyx*) or, contrarily, low and broad *Eolagurus*, *Prolagurus*). It forms a large anterior dihedral angle (greater than in any other microtines) with the sagittal plane, exceeding 270°. Auditory bullae

vary in size, their cavity variably filled with small-celled spongy bony tissue. Symphysis of mandibles forms moderate posterior angle with dentary. Angle of ventral margin of symphysis moderate to large (in *Lagurus* up to 150°). Ascending section not broad: when mandibular ramus horizontal, its anterior margin overlaps molar row commencing from second prism of M_3 . Length of articular process varies from small in *Lagurus* and *Prolagurus* to large in *Eolagurus*. Apex of coronoid process reaches base of articular section, while that of angular process extends slightly beyond its posterior margin. Mental foramen extends quite far forward.

Upper molars more close-set than in other voles, barely diverge downward. Anterior section of M^1 slightly shifted laterally. Molars rootless, with low crown (*Lagurus*) or moderately high crown. In *Eolagurus*, bases of M^1 – M^2 form strong alveolar bulges inside orbit and bases of M_1 – M_2 along lower crest of masseteric ridge.

M_1 relatively short. At least one pair of triangles present at base of its paraconid section, which are fused in early forms and isolated in later forms; second pair of triangles at base of anterior unpaired loop variably developed. Unpaired anterior loop rounded, rounded-rectangular, or digitate. Anterior island vestigial (juvenile); folds either present on paraconid section or traces absent. Unlike in all other microtines, middle lateral triangle of M^1 and M^2 with small projection on medial wall, and sometimes M^3 also. All triangles of masticatory surface of M^3 completely (in extant members) or almost completely (in extinct forms) isolated. Although this tooth is not shifted lingually in tooth row, its medial wall and lower end are lodged in separate alveoli. When dentary placed in lateral position, alveoli seem to protrude downward in form of projection anterior to base of angular process. M^3 without "islands" or their traces, relatively long, with two to three folds and three to four denticles on lateral side and two folds and two to three denticles on medial side; heel long and narrow, its end sometimes directed laterad. Crowns of upper incisors long or moderately so and curve abruptly. Lower incisors long, curve abruptly (*Lagurus*) or smoothly (*Eolagurus*, *Prolagurus*). Angle of incisor contact large, larger than in other microtines, 1.5 times greater than right angle. Upper incisors moderately broad and, as in the case of the lower ones, also moderately or highly compressed laterally. Anterior surface of upper incisors slightly convex, with weak groove-like longitudinal depression; profile of their combined cutting edge broadly M-shaped. Lower incisor lodged along lingual margin of mandibular ramus; its posterior end passes between the alveoli of M_2 and M_3 , so that the former lies

completely on the lateral side and the latter on the medial. Posterior end of incisor extends to upper posterior margin of dentary and may form small alveolar knob here, or ascends upward into base of articular process, reaching or extending beyond (*Lagurodon*) dental foramen.

Skeletal structure characterized by relatively long iliac in pelvis; short scapula (in *Lagurus*), shorter than in other voles (except *Alticola*); and comparatively short humerus with long inner epicondyle.

Distribution and zonal affinity: These forms are found from forest-steppes up to deserts of western and central parts of the Palearctic, as well as western part of the central Nearctic in plains and mountains; in rocky mountain steppes of Tien Shan up to 2,800 m above msl, in northern Tsaidam up to 3,000 m above msl. They are found in Eurasia from lower reaches of the Dnieper up to northern foothills of Altai, south up to the Black Sea coast, Cis-Caucasus, Caspian, and northern Kazakhstan steppes; and northern deserts and desert-steppes of Mongolia and northern China.

In the Early Pleistocene of the same latitudes, these forms occurred in the savanna fauna of the plains and foothills, from the Carpathians to Trans-Baikal; in the Late Pleistocene found together with the marmot "lemming" and in mixed faunas under conditions of the cold periglacial "steppes," from France and the British Isles and slightly north of the boundaries of the present range.

Evolution and phylogeny: Fossil remains are known from the Early Pleistocene beginning from the Early Tamansk (Late *Mimomys*) faunas, including the first voles with rootless molars, e.g., the genera *Allophaiomys* and *Arvicola*. A somewhat earlier occurrence is possible—at the end of the Villafrancan (Ancient Pleistocene, Khaprovsk faunas). Most probably, these forms originated during the Villafrancan from the cementless *Villanyia* (Zazhigin, 1969; Erbaeva, 1973) and *Eolagurus* and *Prolagurus*—*Lagurus* possibly from different species at different regions, respectively in the eastern and western parts of the present range. This tribe peaked in the first half of the Pleistocene. Soviet mammalogists even at the end of the nineteenth century included all present-day genera in the supraspecific group *Limmi*. Much later, Argiropulo (1946) paid attention to the similarity between *Eolagurus* and *Dicrostonyx* which, in his opinion, "...excludes the possibility of convergent evolution" (p. 45). He left the final solution however, to such time when the genital structure could be analyzed. Such data has since been obtained (Anderson, 1960; Hooper and Hart, 1962) and reveals sharp differences between the

two genera. Here, following the example of Kretzoi, they are treated as members of different tribes.

KEY TO GENERA AND SPECIES OF TRIBE LAGURINI

- 1 (2). Body length less than 115 mm. Dark stripe extends along spine (sometimes absent in young individuals) Genus *Lagurus* Gloger (p. 248)
One species, *L. lagurus* Pallas.
- 2 (1). Body length more than 115 mm. Adults without dark stripe along spine (sometimes present in young individuals) Genus *Eolagurus* Argyropulo (p. 252).
- 3 (4). Pollex of forelimb with large obtuse claw. Auditory bullae enlarged; their ventral margin extends below level of tooth row. Mastoid processes high, beyond level of occipital condyles *E. przewalskii* Büchner.
- 4 (3). Pollex of forelimb with small pointed claw. Auditory bullae not enlarged; their ventral margin does not extend below level of tooth row. Mastoid processes do not protrude beyond level of occipital condyles *E. luteus* Eversmann.

1. Genus *Jordanomys* Haas, 1966 (foss.)

Diagnosis: Size small. Length of M_1 —2.2—2.6 mm. Anterior unpaired loop simple in shape, oval, slightly elongate anteroposteriorly, without traces of secondary lobe, without rostriform posterolateral extension, and broadly fused with triangles at its base. M^3 complex in structure; its masticatory surface with two medial folds and three lateral. Anterolateral fold slightly smaller than successive one ("Pliomys" type of structure). As in the case of early members of the genus *Prolagurus*, enamel thick and undifferentiated.

Composition of genus: Two species—*J. pusillus* Haas, 1966 and *J. haasi* Tchernov, 1968.

Age and distribution: This genus is described from Early Pleistocene, and is also known from the Middle Pleistocene of Palestine. It is identical in structure of M_1 , but much larger forms that are designated Lagurini gen. (?) (Shevchenko, 1965; Aleksandrova, 1965a) have also been indicated for the Early Pleistocene of southern Ukraine and Moldavia. The morphotype of this tooth in the Early Pleistocene of Kryzhanovka (Odessa coast of the Black Sea) prevails in *Prolagurus praepannonicus* Top. (Topachevskii, 1973).

Taxonomic notes: The taxonomic status and independent position of this poorly studied genus presently is not clear. It may be the last branch in the evolution of any one of the lines of the genus *Villanyia*. This genus has lost roots concomitant with evolving an M^3 of complex structure and is convergent with late lagurids or some members of *Alticola*. Either way, the recent discovery of M^3 of a second and larger species of this genus (Tchernov, 1968b), the earlier assumption (Haas, 1966) of generic affinity with *Hyperacrius* is probably invalidated.

2. Genus *Prolagurus* Kormos, 1938 (foss.)

Diagnosis: Size small. Length of M_1 —2.0—2.7 mm. Anterior unpaired loop of this tooth variable in shape—from round to rounded-rectangular and even, in rare cases, triangular—without traces of secondary lobe, sometimes with sharp posterolateral rostriform extension. Loop *per se* either fused with triangles at its base or isolated from them. M^3 always with simplified structure; its masticatory surface with one medial fold and two lateral.

Composition of genus: There are two subgenera—*Lagurodon* Kretzoi, 1956 and *Prolagurus* Kormos, 1938 (Zazhigin, 1969, 1970). Sometimes the latter subgenus is considered a subgenus of the former (Topachevskii, 1973).

Age and distribution: Early Pleistocene (Ancient Tamansk—Tiraspol' faunas). It is found from eastern Europe to the Trans-Baikal region. In the north, it is found up to known limits of distribution of faunas of open biomes of this epoch and in the south, down to Israel, Trans-Caucasus, and Altai-Irtysh.

Taxonomic notes: Origin from voles with rooted molars of the genus *Villanyia* is quite possible (Zazhigin, 1969; Erbaeva, 1973). Although this seems to be contradicted by secondary simplification of the paraconid section of M^3 , in any case one of the proposed ancestral forms is *V. laguroides* Erbaeva. For the second proposed form—*V. fejervaryi* Kormos—the structure of this tooth is not known. Thus, it may be considered that separation of *Villanyia*, an ancestor of *Prolagurus*, must have occurred before simplification of the anterior section of M^3 began in most of its species. Among present-day microtines, an ancient relationship with *Alticola* is possible.

Subgenus *Lagurodon* Kretzoi, 1956

Diagnosis: Anterior unpaired loop of M_1 broadly fused with triangles at its base, and latter also fused with one another. Anterior unpaired loop rounded but longitudinally elongate; posterolateral rostriform extension may be completely isolated from loop *per se* and acquire status of an independent additional triangle.

Composition of subgenus: One species—*P. (L.) arankae* Kretzoi, 1954.

Age and distribution: It is known from the end of Ancient (?)—Early Anthropogene, primarily in western part of range of genus to its extreme southern limits. It is in association with the *Allophaiomys* fauna, and later in lagurid and lagurid—*Microtus* faunas of Early Pleistocene. It is also known in later as well as eastern faunas, which are dominated by members of the next subgenus.

Taxonomic notes: Most West European paleontologists believe that *Lagurodon* is an independent genus; I, also, held this view earlier (Gromov, 1966, 1967). Now, however, I support the later conclusion of Zazhigin (1969, 1970) who, on the basis of indigenous material, revised the taxonomic relationships between groups within the tribe, because this subgenus affords no insight into the evolution of the tribe.

1. *Prolagurus (Lagurodon) arankae* Kretzoi, 1954

Diagnosis: Length of M_1 —2.1–2.3–2.7 mm ($n = 205$); M^3 —1.4–1.5–1.85 mm ($n = 78$). To date, only the structure of broken teeth and a fragment of the anterior section of the dentary is known. The size and structural features of M_1 have remained fairly constant in this species in time as well as in space. Nevertheless, the ratio of individuals in different populations in which the triangles of the masticatory surface are fused to a greater or lesser extent varies, while the anterolateral triangle tends toward isolation from the opposite medial triangle. Isolation of triangles is also observed in M^3 . Unfortunately, structural details of this tooth and its variability are not adequately known since this species is usually found in small numbers at places in which it occurs in “pure” form, i.e., segregated from species of the subgenus *Prolagurus*.

Age and distribution: It may be conjectured that the earliest remains belong to the Late Khaprovsk fauna. Zazhigin (1969) has noted that the relative abundance of remains of this species among other lagurids decreases eastward within the range of this genus,

an indication of its intense mesophilic nature. But Topachevskii (1973), based on the absence of *L. arankae* in the Chertkov fauna (western Ukraine), disagrees.

Taxonomic notes: The species is considered either a "blind end of evolution" (Zazhigin, 1969, 1970), or the initial link in the evolutionary series proceeding through *Prolagurus* to *Lagurus* (Topachevskii, 1965; Terzea, 1970).

Topachevskii (1973) has noted that in the Azov and Black Sea region, the chronocline variability of structure of M_1 during the existence of the Tamansk faunal association involved an increase in relative length of the paraconid, reduction in extent of fusion of its basal triangles and, at the end of this period, reduction also in extent of their fusion with the anterior unpaired loop.

Subgenus *Prolagurus* Kormos, 1938

Diagnosis: Anterior unpaired loop of M_1 either fused with or isolated from triangles at its base, and triangles either fused with or isolated from each other. Shape of loop *per se* variable within the same limits seen in the subgenus *Lagurodon*; but if rounded, lacks rostriform posterolateral angle (although sometimes acute), and if rounded-rectangular, lies at an angle to the longitudinal axis of the tooth.

Composition of subgenus: Three species—*P. (P.) praepannonicus* Topachevskii, 1965; *P. (P.) pannonicus* Kormos, 1930; and *P. (P.) posterius* Zazhigin, 1969.

Taxonomic notes: The taxonomic position of "*Lagurodon helleri*" Kretzoi, 1956 remains unclear. The type species of the doubtful subgenus *Laguroopsis* Kretzoi, separated on the basis of a single specimen of M_1 from Mundesheim (FRG), was described by Heller (1936) as *Lagurus pannonicus*. Based on structure of the masticatory surface, it is closest to the species of this subgenus. However, the basal triangles are more strongly fused in this specimen than in any of the known morphotypes of this tooth from eastern Europe typical of *P. (P.) praepannonicus*. It is also significant that the occurrence of lagurids in the purely *Mimomys* fauna of this locality has never been confirmed.

Age and distribution: Same as in the subgenus *Lagurodon* but only for the eastern part of the range of the genus; in the west, found in the more northern range of *Prolagurus*, and dominates *Lagurodon*.

Taxonomic notes: Many authors have considered *Prolagurus* a subgenus of *Lagurodon* or of *Lagurus*. Judging from the manifestation of some archaic features in the ancient forms typical of *L. arankae*, possibly these subgenera had common ancestors which, through divergent evolution, gave rise to the genus *Lagurus*.

2. *Prolagurus (Prolagurus) praepannonicus* Topačevski, 1965

Diagnosis: Length of M_1 —2.0–2.3–2.5 mm ($n = 40$). Anterior unpaired loop of M_1 usually rounded. Loop fused with its basal triangles, although width of their connecting neck usually not large, narrower than distance between posterior wall of medial triangle and anterior wall of lateral triangle.

Composition of species: While studying the spatial distribution of the predominant morphotypes of structure of M_1 , Topachevskii (1973) separated from Ukrainian material three subspecies for the Early Tamansk period, which differ in degree of isolation of the anterior unpaired loop: *P. (P.) p. praepannonicus*, *P. (P.) p. terropolitanus*, and *P. (P.) p. tauricus*. He also mentions *P. (P.) p. primaesus* for the Early Tamansk period.

Age and distribution: Known from Early Anthropogene from Azov to Irtysh.

Taxonomic notes: In most of the known localities, remains of this species are found together with those of the next species. The relative abundance of remains with a completely separated anterior unpaired loop in M_1 (*pannonicus* type) increases toward the present day. This provided a basis for some specialists to consider the two species one, with a varying ratio of morphotypic variants in different localities. Yet there are biomes in which the two types are found in "pure form." Such are Nogaisk in the Azov region where the *praepannonicus* type is dominant (Topachevskii, 1965) and Betfia V in Rumania where the *pannonicus* type is found exclusively (Terzea, 1968). Thus, sites with a mixed composition can be characterized as hosting both species, which gradually displaced each other in time. Probably, the question will only be resolved when more complete remains, other than isolated M_1 , are found.

The dominant morphotype of M_1 structure in subsp. *primaesus* from the upper levels of Kryzhanovka is very similar to that of the west Asian genus *Jordanomys*.

P. (P.) tschumakovi Kretzoi is a nomen nudum (Chumakov, 1963). On the basis of the only known M_1 from a well at Rudnoi Altai, it cannot be said whether the Altai form warrants independent

status. In any case, the given structure of the anterior unpaired loop of M_1 leads neither to the European nor to the Western Siberian material (Zazhigin, 1970; Topachevskii, 1973).

3. *Prolagurus (Prolagurus) pannonicus* Kormos, 1930

Diagnosis: Dimensions of M_1 as in the preceding species. Anterior unpaired loop usually rounded-rectangular, rarely rounded or rhomboid, and completely isolated from its basal triangles, which are fused with each other.

Age and distribution: Same as in the preceding species; also known from Trans-Baikal region.

Taxonomic notes: Already described in this section for the preceding species. Rudiments of folds of the anterior unpaired loop of M_1 and posterior section of M^3 have been noted in some individuals in later forms from western Siberia. This would indicate that evolution probably occurred in the direction of the genus *Lagurus* (Zazhigin, 1969).

167 4. *Prolagurus (Prolagurus) posterius* Zazhigin, 1969

Diagnosis: Length of M_1 —2.15–2.4–2.7 mm ($n = 17$); M^3 —1.5, 1.7, 1.9 mm. Anterior unpaired loop of M_1 usually rounded-rectangular and lies at an angle to the longitudinal axis of the tooth (*E. luteus* type). Loop completely isolated from its basal triangles, and triangles likewise isolated from each other.

Age and distribution: End of Early Pleistocene (Late Tiraspol' fauna) in European part of the USSR and Western Siberia.

Taxonomic notes: This species represents a blind terminal link in the evolution of the subgenus. It has completely isolated elements of the paraconid section of M_1 , but without traces of secondary simplification. Structure of M^3 not complex.

3. Genus *Lagurus* Gloger, 1841

Diagnosis: Size medium. Length of M_1 —2.65–3.1 mm. Anterior unpaired loop of M_1 rhomboid or triangular and either with traces of secondary lobes, at least on lateral side, or with well-developed secondary pair of opposite triangles. Anterior section in form of asymmetric trifoliate structure or secondary triangles shifted relative to each other, sometimes completely isolated (asymmetric trifoliate structure). Anterior part of paraconid section always isolated from its basal triangles. M^3 with complex structure;

its masticatory surface with two medial folds and up to three lateral folds; anterior folds on either side equal in depth.

Composition of genus: One extinct species—*L. transiens* Janossy, 1962 and one extant species—*L. lagurus* Pallas, 1773. A few marginal forms of the latter species have been designated subspecies (Gladkina, Meyer and Mokeeva, 1963).

Description: Body length up to 120 mm, tail up to 19 mm (15% body length), upper molar row up to 6.8 mm. Eyes are comparatively small, notably shifted backward and upward. Pinna small, without antitragus. Tail always shorter than hind limb. Color grayish-ocher; animals at all ages with distinct black stripe along spine.

Skull is relatively low and slightly convex: its height at anterior margin of alveolus of M^1 is greater than the length of upper molar row by less than half length of this tooth. The masseteric [= zygomatic] plate of maxilla relatively low and broad. The crest on ventral margin of basioccipitals is barely developed. The crowns of upper incisors are comparatively short, their combined width not great. Alveolus of lower incisor is not shifted inward, and extends to the dental foramen or only slightly beyond it; the pit on lingual surface of ascending jaw is small, slightly isolated posteriorly.

Distribution and zonal affinity: This genus inhabits plains, mountains (up to 4,000 m above msl), steppes, especially southern continental forest-steppes, and northern deserts. It is found in Eurasia between the Dnieper and Yenisey Rivers; in the south, up to central Tien Shan, northwest China and northern Mongolia. In the Pleistocene, the western part of the range reached France and Great Britain and the eastern part of Trans-Baikal. At the end of the Pleistocene, during the last (Würm) glaciation, it occurred together with *Stenocranius* in large-scale "mixed vole faunas" throughout eastern Europe and western Siberia. The western part of the present-day geographic range continues to diminish even now.

Evolution and phylogeny: Fossil remains are known from the second half of Early Anthropogene (Tiraspol' fauna); these forms most probably originated from species of the subgenus *Prolagurus*. Specimens with transitional characteristics in structure of M_1 were found among the fossil remains of *P. pannonicus* from western Siberia (Zazhigin, 1969) from the stratotype of the Tiraspol' fauna (Aleksandrova, 1971).

1. *Lagurus transiens* Janossy, 1962 (foss.)

Diagnosis: Slightly smaller than the present-day species. Length

of M_1 —2.25–2.6–2.9 mm (n = 48), M^3 —1.8–2.1–2.3 mm (n = 22). Anterior unpaired loop of M_1 rhomboidal or in form of equilateral triangle with apices directed forward, and with incomplete second-order fold in form of a unilateral depression. Posterior section of M^3 similar in shape but apices directed backward; third lateral and fourth medial denticles not developed.

Age and distribution: End of Early-Middle Pleistocene; from central Europe to western Siberia.

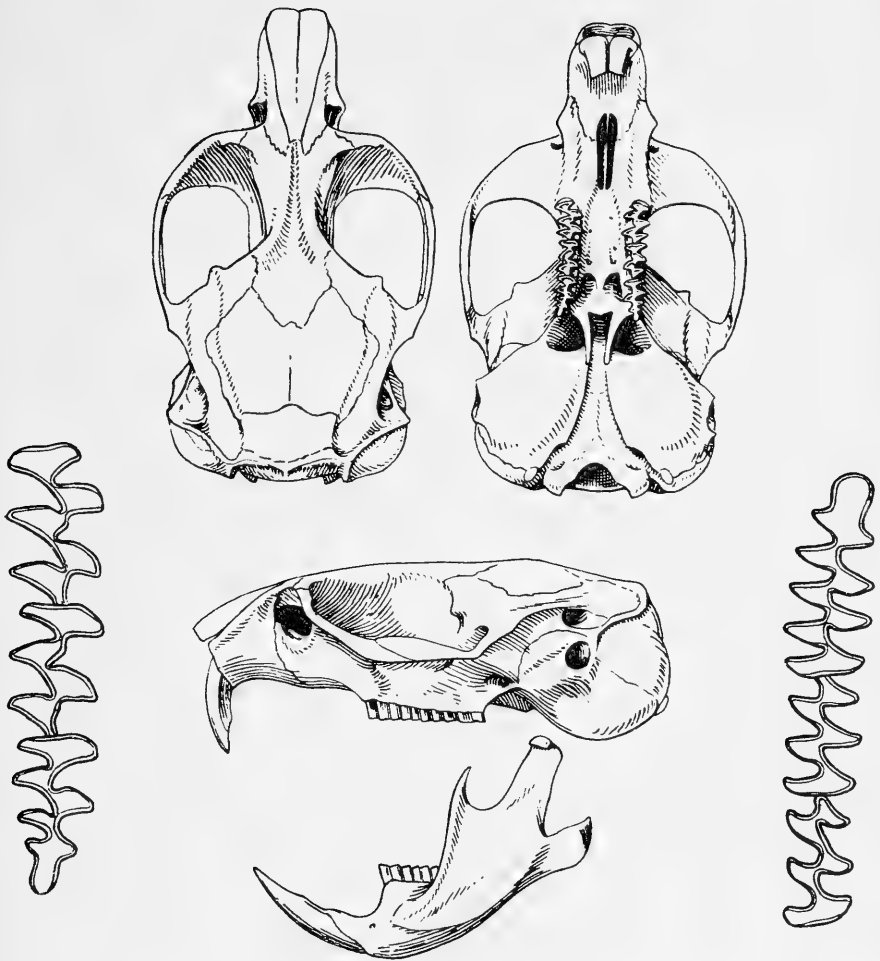
Taxonomic notes: An increase in relative abundance of remains with complete second-order folds in the anterior section of M_1 and posterior section of M^3 is observed in *L. transiens* populations from Middle to Late Pleistocene, indicating a gradual transition toward present-day species. This process was completed at varying rates in different parts of the range (Maleeva, 1971; Aleksandrova, 1971; Maleeva and Vorob'eva, 1973). One such population, living at the beginning of the Middle Pleistocene in Dobrudzhu, was described as subspecies *L. t. casianicus* Radulesco and Samson, 1974.

2. *Lagurus lagurus* Pallas, 1777—Steppe Lemming (Figure 26)

Diagnosis: Anterior unpaired loop of M_1 in form of oval or comparatively short digitate process, with well-developed basal triangles that may be variably shifted relative to each other—from an extreme case of morphotype variability up to total isolation. Posterior section of M^3 highly complex, its masticatory surface with two folds and three denticles on lateral side, and three and four respectively on medial side.

Composition of species and variability: There are present-day species—*L. l. lagurus* Pallas, 1778 (southern European part of the USSR, central regions of Kazakhstan, Altai steppes); *L. l. agressus* Serebrennikov, 1929 (northern European part of the USSR, northern Kazakhstan); *L. l. altorum* Thomas, 1912 (south and southeastern Kazakhstan, northwestern China, and Mongolia); and *L. l. abacanicus* Serebrennikov, 1929 (steppes of Minusinsk basin). The last species, occupying the isolated eastern part of the species range, can be separated into a prespecies (Gladkina, Meyer and Mokeeva, 1963). One extinct subspecies has also been identified: *L. l. major* Zazhigin in litt. (northern Ukraine, Late Pleistocene).

Variability of present-day forms includes an increase in size in the eastward direction and relatively greater abundance of archaic morphotype structures of M_1 (“transitional” and “*posterius*” types) and M^3 . Size of extinct forms decreased toward present times. Color



169 Figure 26. Skull of the steppe lemming (*Lagurus lagurus* Pallas).

becomes lighter and yellower toward the east and south; moreover, narrowing of the black dorsal stripe is observed in an eastward direction.

Distribution and zonal affinity: Same as for genus.

- 169 *Evolution and phylogeny:* Fossil remains have been reliably identified from the Late Pleistocene when differentiation of both denticles of the secondary lobe at the base of the anterior unpaired loop of M_1 was completed, and this morphotype became dominant.

The immediate ancestor was *L. transiens* Janossy.

Taxonomic notes: Aleksandrova (1976) isolated the species *L. pleistocaenicus* from stratotypic deposits with Hozarsk fauna (Lower Volga, Middle Pleistocene). The structural features of the masticatory surface of M_1 , indicated by the author, recently have been described by Markova (1974), based on a large amount of material from the Middle Pleistocene deposits of the Dnieper region. Predominance of the morphotype "*pleistocaenicus*" corresponds to the transitional form between *transiens* and *lagurus*, and can hardly be considered more than a subspecies.

4. Genus *Eolagurus* Eversmann, 1840

Diagnosis: Size large. Length of M_1 —2.9–4.1 mm. Anterior unpaired loop of masticatory surface of M_1 rounded or rounded-
170 rectangular and isolated from fused or isolated from triangles at its base. If completely isolated, then width of cingulum not more than double thickness of enamel at same level. M^3 always simple in structure, with two lateral folds and one to two medial.

Composition of genus: Two extinct species—*E. argyropuloi* I. Gromov and Parfenova, 1951 and *E. simplicidents* Young, 1934; and two extant species—*E. luteus* Eversmann, 1940 and *E. przewalskii* Büchner, 1888.

Description: The body length is up to 240 mm; the upper molar row is up to 9.0 mm. Pinna are small without antitragus. Tail is slightly longer than the hind limb. Color is monochromatic and sandy-yellow; a black dorsal stripe is present only in individuals with juvenile pelage. The skull is relatively high and convex; its height at anterior margin of alveolus of M^1 is greater than the length of upper molar row by more than half length of this tooth. The masseteric [= zygomatic] plate of the maxilla is relatively high and moderately broad. The crest on the ventral surface of the basioccipitals is well-developed. The crowns of upper incisors are relatively long, their combined width is large. The alveolus of the lower incisor is markedly shifted lingually, its posterior end extending beyond dental foramen; the pit on the lingual surface of the ascending jaw is deep, and sharply isolated posteriorly.

Distribution and zonal affinity: This genus inhabits desert steppes of northwestern China and Mongolia, similar to montane meadows of northern fringe of Tibetan plateau; it is found from Zaisan basin and foothills of Altyn-tag in the west to northwestern part of inner Mongolia in the east. It is not found in the Dzhungarian-

Gobi desert belt. The present range forms the eastern part of the vast generic range. It is found in the Late Pleistocene ("mixed" faunas) and Early Holocene, and reaches the eastern part of Rumania, the foothills of Crimea, Ufa and Sverdlovsk areas of the Ural and Trans-Ural regions, and northwestern Altai. During the early period of evolution, it occupied areas west of the Volga and Caspian semideserts and in the seventeenth century depressions in the Ural area and, most probably, several places in northern Kazakhstan. The Trans-Baikal "branch" range of the genus has disappeared, and possibly did so much earlier, at the end of the Early Pleistocene.

Evolution and phylogeny: Fossils are known from the Early Pleistocene, the most ancient of which is somewhat later than the first finds of *Prolagurus*. Probable origin is from voles with cementless rooted molars (*Villanyia*) among which, for example, forms are found in the *fejervaryi-lagurodontoides* group with some similarity in structure of the anterior unpaired loop of M_1 and partially fused triangles of the masticatory surface. Recent information on the history of the genus confirms the earlier opinion (Gromov, 1957a) that the change in structure of teeth of *Eolagurus* (especially M^3) was such slower than in the small lemmings of the *Prolagurus-Lagurus* line, and affirms the general trend of these changes. The characters on which the independent species status of the extinct forms was initially based (specimens few), now with an increase in amount of material, are understood as a series of chronocline morphotypic variability of structure of M_1 and M^3 . Possibly, similar to the case of small lemmings, it is more appropriate to consider these forms as subspecies characterized by a dominance of a single morphotype. However, judged on differences in the two present-day species of *Eolagurus*, one may conclude that the evolution of the skull *per se* was sufficiently rapid, that it compels us to treat with caution concerning both a lower taxonomic rank, and also a unification of known extinct forms, in spite of the slight apparent differences in structure of teeth.

- 171 1. *Eolagurus argyropuloi* I. Gromov and Parfenova, 1951 (foss.)

Diagnosis: Only holotype known—an isolated M_1 of an old individual with enamel that is distinctly differentiated in thickness. Length of masticatory surface 2.7 mm—a size close to the uppermost limits for *Lagurus* but smallest in *Eolagurus*. Tooth relatively broad—broader than in other extant and extinct forms. Anterior

unpaired loop not completely isolated from broadly fused triangles at its base, although width of cingulum only slightly greater than double thickness of enamel. Basal triangles of tooth partially fused, but not so markedly as to warrant depiction in the schematic pattern accompanying the description (Gromov and Parfenova, 1951).

Age and distribution: More precisely undated; Early Anthropogene of eastern Azov region (between Postov and Tagaurog).

Taxonomic notes: If the dimensions proposed for M_1 are not considered, individuals of *E. simplicidents* as well as the ancient *E. luteus* are found readily which exhibit a similar stage of isolation of the triangles of the masticatory surface. However, as rightly pointed out by Zazhigin (1969), variability in the material from the type locality is not known, and later differences cannot be established more precisely. The two M_1 of *Eolagurus* from Kairy (Kherson district of Ukraine) from the composition of Ancient Tamansk fauna, are also characterized by similar primitive traits (Topachevskii, 1973), whereas a more "advanced" morphotype of M_1 structure prevails among remains from western Siberia (Zazhigin, 1970). Thus, it is possible that the species named *argyropuloi* can be retained for the most ancient Eastern European members of the genus in which an archaic morphotype structure of M_1 and M^3 is dominant, i.e., triangles of masticatory surface broadly fused (more than double thickness of enamel).

2. *Eolagurus simplicidents* Young, 1934 (foss.)

Diagnosis: Based on size, close to *E. luteus* Eversmann. Length of lower molar row 6.2–7.1–8.0 mm; M_1 —2.85–3.1–3.5 mm. Differs in short facial section of skull, and relatively short upper diastema and nasals. Bony palate and incisor alveoli relatively longer and interorbital space broader than in present-day species. Dentary weak, with lower and thinner horizontal section. Articular process and angular process longer and narrower. Molars relatively broader. Lower incisor broader, shorter, with longer prealveolar and alveolar parts. Triangles at base of anterior unpaired loop of M_1 broadly fused, may be opposite or shifted relatively to each other. Remaining triangles of masticatory surface of M_1 , including anterior unpaired loop, variably fused and in different combinations, but in the dominant morphotype fusion no more than twice enamel thickness. M^3 relatively shorter than in present-day *E. luteus* because of shorter heel, which is broadly fused with the posterolateral triangle.

Composition of species: The more ancient, somewhat larger (length of lower molar row 6.2–7.1–8.0 versus 6.3–6.9–7.3 mm), and somewhat longer-snouted form, with more archaic traits of structure of M_1 and M^3 , has been separated into the subspecies *E. s. sibiricus* Erbaeva, 1966.

Age and distribution: Early Pleistocene of Trans-Baikal region and China (Chovkoudyan I).

172 *Taxonomic notes:* Relating the large Trans-Baikal lemmings from the *luteus* group to "*Pitymys*" *simplicidents* Young, known from a single M_1 of a young individual (length according to author's measurements 2.7 mm; restored, based on impression, about 2.9 mm), is highly tentative, more so because the text mentions the presence of an insignificant cement deposition in the folds of the tooth. But the abundant and comparatively complete collections from Trans-Baikal region permit us to determine fairly reliably differences from the present-day species *E. luteus* Eversmann (Erbaeva, 1970). Some archaic features of the skull are common to those of the second present-day species, *E. przewalskii* Büchner. The affinity of *E. simplicidents* with the large lemmings from eastern Europe of the same geological age is less clear; the teeth of the latter are at a similar level of evolution, but the structure of the skull is not known. These forms include *E. gromovi* Topačevski, 1963; *E. praeluteus* Schevtschenko, 1965; and *E. volgensis* Alexandrova, 1976. They are considered extinct subspecies of *E. luteus* in this book.

3. *Eolagurus luteus* Eversmann, 1840—Yellow Steppe Lemming (Figures 27 and 28)

Diagnosis: Dimensions: length of lower molar row 6.3–7.1–7.7 mm; M_1 —2.8–3.2–3.4 mm. Facial section of skull long, as a result of which, upper diastema and nasals also relatively long. Interorbital space narrow. Dentary strong, with higher and broader horizontal section. Articular process and angular process shorter than in the Early Pleistocene species. Molars relatively narrow. Triangles of masticatory surface of M_1 , in most individuals, isolated from each other and from the anterior unpaired loop. Fusion of basal triangles of anterior unpaired loop mainly seen in extinct forms; however, only in a small number of individuals (not more than one-third) does this fusion attain the level typical of the preceding species. Such an archaic type of M_1 structure is observed in a few members of extant species. Heel of M^3 relatively long and, in most cases, isolated from contiguous anterior section of tooth.

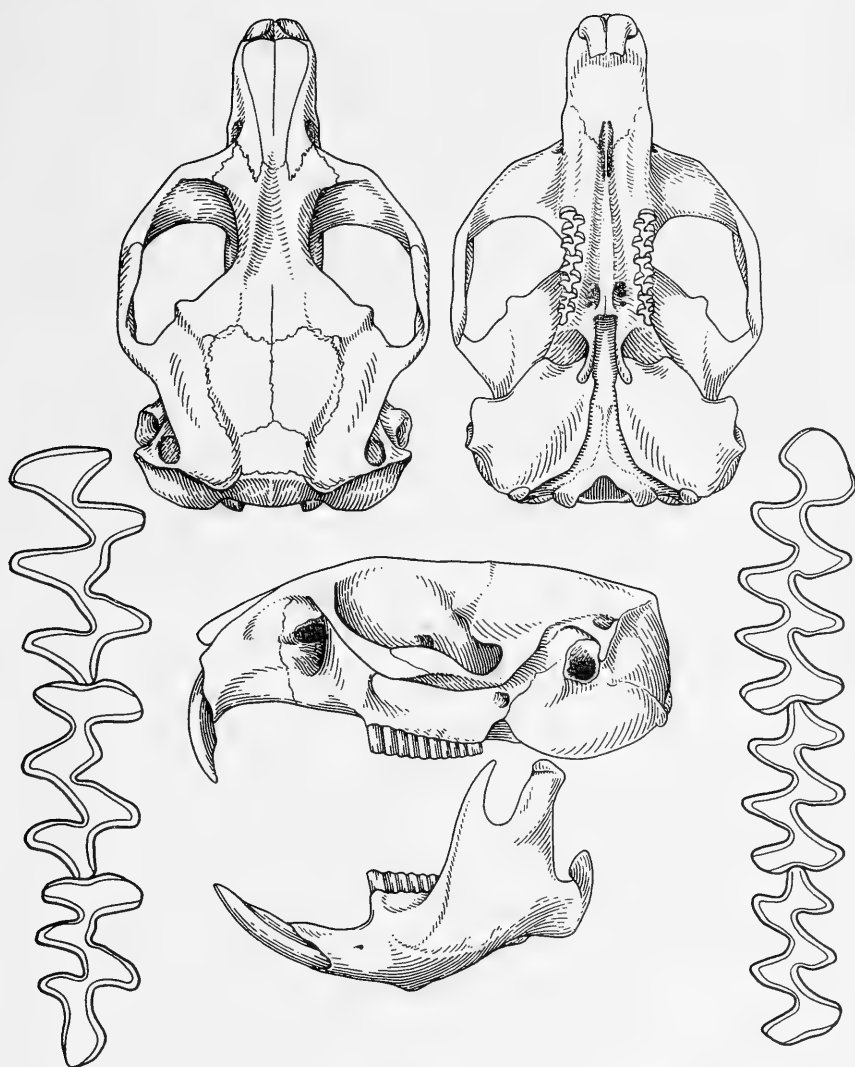
Composition of species: Intraspecific taxonomy of the present-day forms was not analyzed. Extinct subspecies are: *E. l. gromovi* Topačevski, 1963 (Early Pleistocene); *E. l. praeluteus* Schevtschenko, 1965; and *E. l. volgensis* Alexandrova, 1976 (Middle Pleistocene). New collections have shown (Erbaeva, 1970) that at least the two former subspecies, earlier considered independent species, are not above subspecific level, and together with the third are characterized by a shift in the dominant morphotype of M_1 and M^3 structure, from more archaic to the one dominant in the present-day species.

Description: Body length is up to 165 mm. Color is grayish-yellow. Pollex of forelimb has a small pointed claw. Dorsal profile of skull has a sharp dip at bases of zygomatic arches. The pupil is comparatively large. Parietal crests are not wide-set. The auditory bullae are barely enlarged, and do not extend below masticatory surface of upper molars. The mastoid processes do not project beyond occipital condyles. Upper incisors are broad and curve abruptly. The angular projection at apex of anteromedial fold of M^3 is absent or poorly developed—a character also pointed out by Bikhner (1888).

Distribution and zonal affinity: This species inhabits the zone of dry (Mongolian) steppes and partial wormwood/saltwort-covered semideserts and stable sands. In the USSR it was found relatively recently on the left bank of the lower reaches of the Cherny-Irtysh (eastern part of the Zaisan Basin) and it appeared possibly, as a result of en masse reproduction in the adjacent region of Mongolia (Magilov and Vekenov, 1969*), where, as in the adjoining parts of the Sintszyan-Uigur region of China, they are widely distributed north of the Dzhungarian-Gobi desert.

Evolution and phylogeny: The majority of individuals from most populations, even from the Middle Pleistocene, probably possessed the type of molar structure typical of the present-day yellow steppe lemming, with completely isolated elements of the masticatory surface of the molars and a relatively long “heel” on M^3 . However, as mentioned above, and rightly pointed out by Bikhner, this genus exhibits similarity in features of molar structure, while differences in skull structure may be considerable. The characters of the latter are little known for extinct forms of the *luteus* group. Available data permits us, however, to consider *E. simplicidentis* the possible ancestor of *E. luteus*. Of particular

* Not listed in bibliography—Eds.



173 Figure 27. Skull of the yellow steppe lemming (*Eolagurus luteus* Eversmann).

174 interest is the taxonomic position of the large Middle Pleistocene animals from the Crimea which, judging from the dimensions of the lower row of molars, have attained the size of the present-day Tibetan lemming.



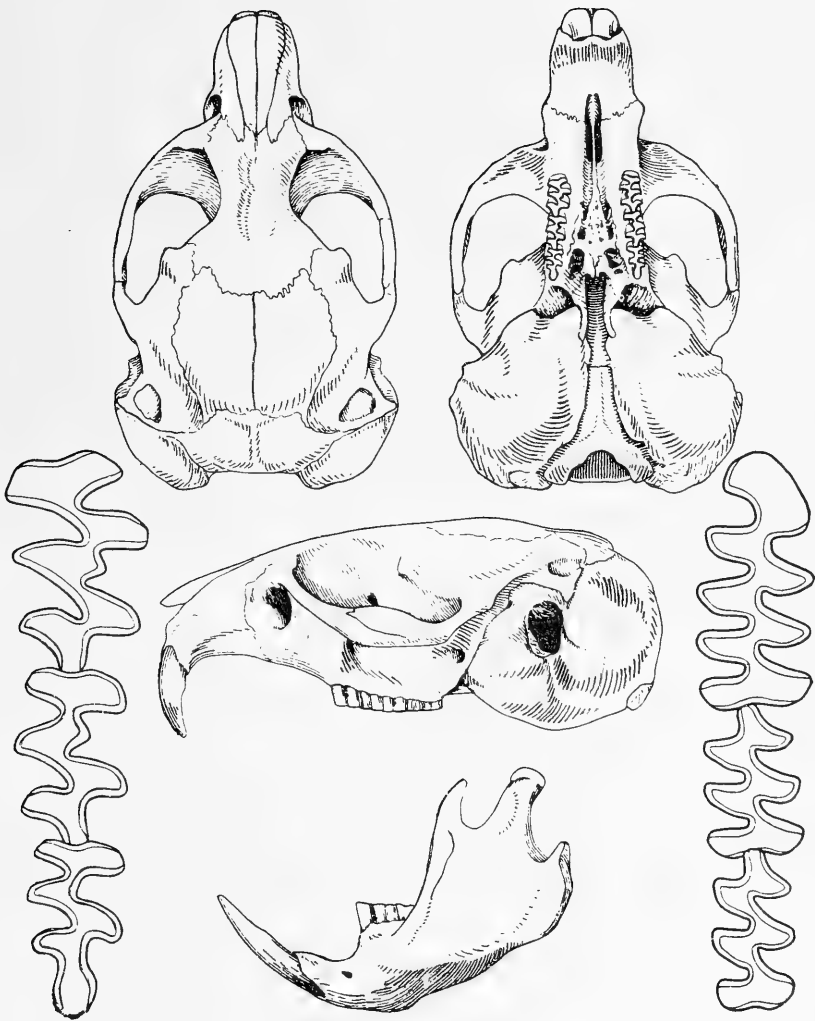
Figure 28. Yellow steppe lemming (*Eolagurus luteus* Eversmann)
(photo by M.N. Meyer).

4. *Eolagurus przewalskii* Büchner, 1888—Tibetan
Yellow Steppe Lemming (Figure 29)

Diagnosis: Dimensions: Length of lower molar row 7.4–8.1–9.3 mm; M_1 —3.15–3.5–3.8 mm. Facial section of skull comparatively short; upper diastema and nasals also enlarged. Interorbital space broad. Dentary weak, with relatively low and narrow horizontal section. Articular process and angular process long. Molars relatively broad. Degree of isolation of triangles of masticatory surface of molars as in *E. luteus*, except for “heel” of M^3 , which is partially fused with contiguous anterior section of tooth.

Composition of species: Intraspecific forms not separated; northwestern population possibly represents a unique form.

Description: Body length (in dry hides) up to 195 mm. Color is without a significant admixture of grayish tones: light, sandy-yellow, often dominated by reddish tones (summer pelage). The pollex of forelimb has a large obtuse claw. The dorsal profile of skull is without a sharp dip at the bases of the zygomatic arches. Pupils are comparatively small. Vertical crests are wide-set. Audi-



175 Figure 29. Skull of the Tibetan yellow steppe lemming (*Eolagurus przewalskii* Buchner).

tory bullae are highly enlarged and extend below the masticatory surface of the upper molars; the mastoids project beyond the occipital condyles. The upper incisors are relatively narrow and curve

smoothly. The angular projection is often present at apex of anteromedial fold of M^3 .

Distribution and zonal affinity: This species inhabits montane zone of northern Tibet where it was collected in meadows near lakes (Tsaydan) and along river banks (region south of Lobnor). New data on this species had not appeared since the end of the nineteenth century up to August, 1968, when F.B. Chernyavskii sent a specimen of *Eolagurus* from the northern area of Bol'shie lakes in western Mongolia (Lake Khirgis-Nur) to the Zoological Institute, Academy of Sciences, USSR. This species is similar in external features to *E. luteus*, but exhibits skull traits characteristic of *E. przewalskii*. This unexpected discovery compels us to shift the boundary of distribution of the species significantly northward and conclude that the two species live together in western Mongolia.

Evolution and phylogeny: Fossil remains are not known. If the new material shows that the subfossil pieces from Pamir (Gromov and Egrov, 1953) (Lake Rang-kul) also belonged to this species, it must be concluded that the range of this predominantly montane form was much wider even recently. The Tibetan yellow lemming is a well-differentiated species (Vinogradov, 1922) and not a subspecies of *E. luteus*, as is usually assumed. It is characterized by several of the archaic traits mentioned above, some of which are common to Early Anthropogene members of *Eolagurus* belonging to the *simplicidents* group.

? LAGURINI Incertae Sedis

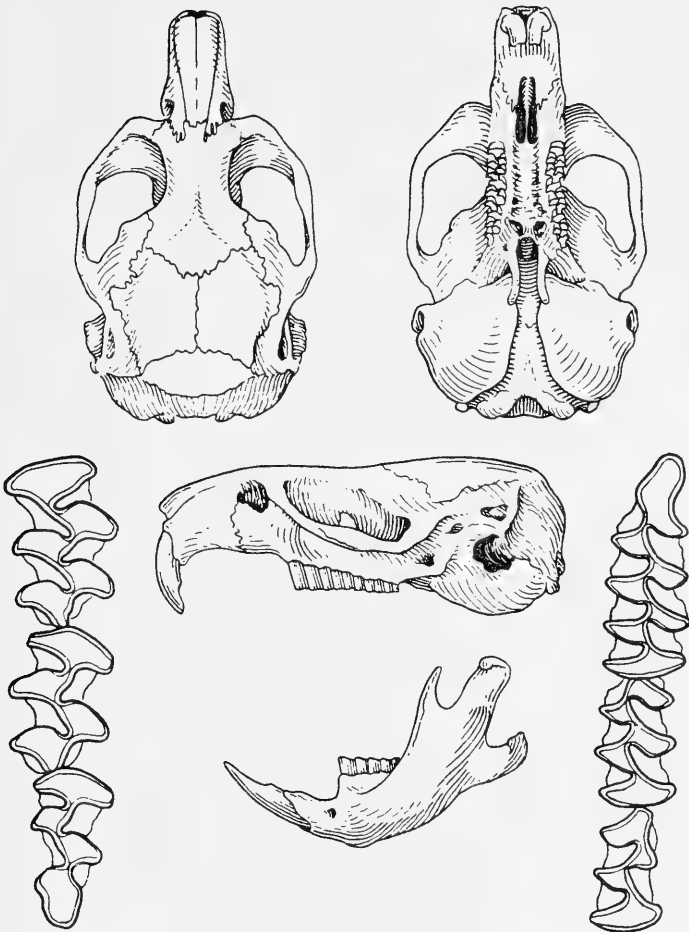
5. Genus *Lemmiscus* Merriam, 1912—American Lemmings (Figure 30)

Diagnosis: Size medium. Length of M_1 —2.35–2.85 mm ($n = 8$). Anterior unpaired loop of M_1 in form of laterally directed rectangle with rounded apex; fuses with large and well-isolated lateral triangle of secondary lobe of paraconid section; no traces of this lobe evident on medial side. All remaining triangles of masticatory surface of M_1 completely isolated, as is the case for all other molars, upper as well as lower. M^3 simple in structure, with two folds on both sides; anterolateral fold may be smaller than second one in young individuals. Heel of M^3 digitate, with three vestigial denticles on one or both sides. Unlike all other lagurids, folds of the molars lack cement.

Composition of genus: One species—*L. curtatus* Cope, 1868, is divided into six subspecies, of which *L. c. levidensis* Goldmann,

1941 is sharply distinguished by features of genital morphology (Dearden, 1958).

Description: Body length up to 107 mm (according to Hall and Kelson, 1959, up to 113 mm), upper molar row up to 6.6 mm ($n = 8$). Size and position of eyes not known. It differs from *Lagurus* in pinna with small antitragus, a longer tail (always much longer than hind limb), a light ochreous-gray color of dorsal surface, and an absence of longitudinal dorsal stripe, even in young individuals.



176 Figure 30. Skull of the American lemming (*Lemmiscus curtatus* Cope).

The skull is flattened only slightly less than in *Lagurus* (brain case more inflated). Auditory bullae are smaller, a groove-like depression in interorbital region is absent, and folding of the frontoparietal crest into a small longitudinal crest observed in posterior section in old individuals. The bony bridge between postpalatal pits is more isolated, particularly its posterior section. The masseteric [= zygomatic] plate of maxilla is lower and broader than in the European steppe lemming. The crest on ventral surface of basioccipital is just barely perceptible. Crowns of upper incisors are longer, their combined width is moderate for Microtini. The alveolus of the lower incisor is not shifted lingually, but its posterior part extends much beyond dental foramen, and its tip forms a small but distinct knob on lateral side of base of articular process. Pit on lingual side of ascending jaw is smaller but deeper than in *Lagurus*.

Distribution and zonal affinity: Mountains (up to 3,300 m above msl) and foothills, forest-steppes, and partly light coniferous forests in western North America, east from ocean ranges, approximately between 34 and 51°, and up to the Great Plains.

Evolution and phylogeny: Data on discovery of fossil remains were not reported until 1965 (Hibbard *et al.*, 1965). This species is a member of the unique line of development of lagurids with distinct archaic ("arankoid") features of the masticatory surface of M_1 and M^3 . Their evolution proceeded not along the line of structural complexity of their anterior and posterior sections respectively, but along the line of isolation of triangles, the strong differentiation of enamel, and the appearance of cement with retention of a low crown. Affinity within the limits of the early microtine fauna is not clear. Data on the baculum structure (Dearden, 1958) and soft parts of the male genitalia (Hooper and Hart, 1962) indicate a greater similarity with *Clethrionomys* and *Phenacomys* than with any other Microtini. It therefore cannot be ruled out that the features of similarity with Old World lagurids appeared convergently. At the same time, the nature and degree of differences indicated above leave no doubt regarding the generic status of these voles. As in the case of *Prolagurus*, affinity with the ancestors of *Alticola* is also possible and thereby with the Pleistocene faunas of Central Asia.

VI. Tribe DICROSTONYXINI Kretzoi, 1965

Diagnosis: As in *Lemmus*, bony palate with deep interconnected postpalatal pits covered by cowl-like posterior margin of palate. Molars rootless and devoid of cement. Differences in size

of lateral and medial triangles of masticatory surface of lower molars insignificant. Enamel thinner (or absent) on anterior walls of triangles of upper molars and on posterior walls and apices of triangles of lower molars. Enamel always absent on secondary loops, at least along their perimeter. Paraconid section of M_1 folded 2.0 to 2.5 times. M^3 moderately long, without traces of secondary simplification. M_3 without lateral alveolar bulge. Lower incisor short; posterior end extends only up to posterior margin of alveolus of M_3 .

Composition of tribe: One extant genus—*Dicrostonyx* Gloger, 1841 and one extinct genus—*Praedicrostonyx* Guthrie and Matthews, 1971 known to date only from isolated teeth.

Description: Medium-sized voles with body length up to 160 mm. Length of upper molar row is up to 9.0 mm, lower row up to 8.0 mm. Color of dorsal surface is brown or brownish-gray, with black dorsal stripe particularly distinct in summer pelage and also in young individuals. Seasonal dimorphism is well-defined; the pelage is very light to completely white in winter. The tail is shorter than hind limb, densely covered with hair, the terminal hairs, longer than hind legs. Eyes are medium in size. The pinna are small, with barely developed lobe and reduced helix, without anti-tragus, and densely covered with hairs. The rhinarium is small. The upper alae nasalis is covered with hairs, the lower ones are glabrous, freely lobate in middle part. The narial pit is closed. The upper labial flaps are well-developed though less so than in true lemmings; lower labial flaps are small and do not encircle incisors. Mental and labial vibrissae (except corner ones) are short, the carpal vibrissae absent. Forelimbs as well as hind limbs are reduced; brush of hair is relatively long, the feet short; all feet are broad. Palm and sole are densely covered with hairs. Metatarsal pads are reduced and perceptible only in very young individuals. Interdigital pads present only on 3rd and 4th digits of forefeet; interdigital pads of hind feet are fused; the calcaneal pad is absent. Digits on forelimbs are III, IV, II, V, I; the pollex is obtusely conical without claw; the remaining claws are long and greater than length of digits, and the claw on 3rd digit in particular is highly compressed laterally. Claws on middle digits enlarge markedly toward winter due to overgrowth of claw itself and hardening of the palmar and interdigital pads during growth. Since the palm *per se* grows slowly, the claws are apically bifurcate. Digits of hind limbs are II, II = IV, V, I; claws are long; the claw of the hallux reaches

the base of the claw of the 2nd digit, and enlarges slightly during winter.

The skull has a more or less uniform convex profile and only a slight dip in the basal region of the zygomatic arches. Crests are relatively narrow and long. Interorbitals are well-developed, not fused, with a groove-like depression between them; the crest on the broad and somewhat angular brain case is moderately developed. The zygomatic arches are comparatively high in the middle section; although lower than in Lemmini, their plane forms only a small angle with horizontal plane. Postorbital processes are in form of two large obtuse projections. The masseteric [= zygomatic] plate of maxilla are higher than in any other vole, are moderately wide, forming angle not more than 25° greater than a right angle with sagittal plane. Angular protuberances of palatals are comparatively long and narrow, especially in middle part, and their bases wide-set. The auditory bullae are small; their inner cavity are filled considerably with large-celled spongy bony tissue. The symphysis of the mandibles has a well-developed posterior angle. The angle of ventral margin of symphysis, as in true lemmings, are on the average about 140° . The ascending jaw is relatively broad; when mandibular ramus is horizontal, it covers molars commencing from second prism of M_2 . Articular process is relatively short, shorter than in Lemmini; the ratio between length of coronoid and angular processes as in this tribe. The coronoid process falls far short of reaching apex of articular process; the angular process extends notably beyond its posterior margin. Location of mental foramen is usual for most Microtini.

In upper tooth row, the anterior sections are moderately wide and the posterior sections are notably divergent. Anterior section of M_1 deviate distinctly downward. Molars are rootless with relatively low crowns. Root tips of M^1 – M^2 form small alveolar bulges inside orbit; roots of lower molars usually do not form such bulges along lower crest of masseteric ridge. M_1 is relatively long (longer only in *Clethrionomys*). Unlike all other extant microtines and the majority of ancient microtines (except for some members of *Pliomys*), the paraconid section of M_1 has two loops forming two pairs of completely isolated triangles anterior to basal triangles (in fossil remains they are almost completely isolated). Triangles at base of the short and broad anterior unpaired loop are usually strongly shifted relative to each other and may also be isolated. Neither anterior "islands" nor vestigial (juvenile) folds occur on the paraconid section. Unlike in other microtines (including fossil forms known to

date), in present-day species of voles M^1 and M^2 has one normally developed additional medial triangle and one underdeveloped lateral triangle, which may also have a small lingually directed lobe. Additional folds and their corresponding cingula may also be developed on the anterior section of M_2 – M_3 , which pass along the entire tooth height. M_3 does not project lingually. M^3 is moderate in length, without traces of "islands". In extant forms, three folds and four denticles occur on each side and a short round-rectangular heel is present.

The crowns of the upper incisors are reduced, but in the lower incisors they are moderately long; in both they are sharply curved, but their facing angle is comparatively small. The upper incisors are moderately broad; the upper incisors are moderately and lower ones are relatively strongly compressed laterally. The anterior surface of the upper incisors have a longitudinal groove forming a rounded angle with the lateral surface; the posterior surface of each upper incisor have a moderately developed depression; the profile of their combined cutting edge is in the form of a obtuse angle and the apex directed labially; sometimes the profile is slightly M-shaped. The lower incisors, as in Lemmini, lie along lingual margin of jaw; the roots of all molars lie on lateral side of incisors.

The skeletons of the extant genus is characterized by a reduced iliac of the pelvis, short neck of femur (which is shorter than in any other microtines) a short fused segment of the fibula, the high crest of the greater trochanter of the humerus, and a much broader diaphysis of the ulna and radius than seen in any other known vole. Such broadening is already distinctly evident in Late Pleistocene forms. Distal phalanges are long and the basal phalanges of the metapodia reduced.

Distribution and zonal affinity: Tundras (including Arctic tundra) and northern part of forest zones (forest-tundra of the Holarctic). It is found from lower reaches of northern Dvina and Kanin peninsula up to northeastern Siberia, including greater part of adjoining islands of the Polar Basin, Alaska (except central belt) and Canada, including larger part of islands in the Canadian archipelago. It is not found in tundra along southern coast of Hudson Bay, but lives in northern Labrador and Greenland. In the Aleutians, it is found west up to Umnak Island. It is absent in Iceland and Spitzbergen. In mountains of the tundra zone (Polar Ural, Byrrang, Alaska) it is found up to 1,700 m above msl.

Like Recent lemmings, in the Early and Middle Pleistocene of Western Europe, members of this tribe occurred in the faunas

of foothill forest-steppes. In the Late Pleistocene (Würm) glaciation, they were common species of the foothills and low montane areas of middle latitudes of the Holarctic and of the tundra-steppes (periglacial steppes) with their characteristic lemming (marmot) fauna, from France in the west to some mountains in Altai, Aldanya region, and northwestern (Alaska) and northern parts of North America in the east.

Evolution and phylogeny: Fossil remains up to the Early Pleistocene (Kromer-Huntz in the Old World and Kansas-Yarmuth in the New World) are not known. For this period they have been reported from Western and southeastern Europe (France, Czechoslovakia) together with true lemmings and late members of (*Mimomys*) and *Pliomys* (Fejfar, 1966) as well as for northeastern Siberia (Zazhigin, 1976) and Alaska (Guthrie and Matthews, 1971), together with *Lemmus*, *Clethrionomys* and unique common voles possibly from the *Allophaiomys* group. Later, they were rarely found in Eurasia, which is possibly explained by their migrations during the glacial periods. They became common only in the Late Pleistocene; their remains from this epoch have also been found in North America (Guilday and Dautt, 1961).

As in the case of Lemmini, ancestors of forms with rooted molars are not known and thus their affinity with extant members of the subfamily poses a problem. Argyropulo (1946) has indicated their closeness to Arctic lemmings and yellow steppe lemmings (*Eolagurus*); their affinity to *Dicrostonyxini* and *Lagurini*, which I proposed earlier (Gromov, 1966), should be considered not well-founded. The dissimilarity in structure of teeth is too great, and the likeness in several features of skull structure is no more than a result of convergence. Much more probable is the affinity of *Dicrostonyxini* with the subtribe *Pliomyi* through the genus *Praedicrostonyx*. They possibly share common ancestors with some forms which had early started on the path of complexity of M_1 , without secondary simplification of the anterior section of M^3 , as is typical of voles of the *Pliomys* line of evolution. Either way, separation of Lemmini by earlier researchers into the two tribes Lemmini and *Dicrostonyxini*, as proposed by Kretzoi (1955b), completely accords with our present understanding of the division of the subfamily of microtines into large taxa and the probable considerable antiquity of Arctic lemmings. Resemblance to *Dicrostonyx* voles of the extinct North American Plio- to Pleistocene genus *Pliolemmus*, as proposed by Pidoplichko (1951) and by me (Vinogradov and Gro-

mov, 1952) on the basis of M_1 structure, has not been confirmed by the new material presented by Hibbard (1956a).

1. Genus *Praedicrostonyx* Guthrie and Matthews, 1971 (foss.)

Diagnosis: Posterior ends of M^1-M^3 and anterior ends of M_2-M_3 are without additional, or with small, longitudinally elongate-oval additional lobes. Only small falcate processes may be developed here, especially on the lateral side of molars, but not necessarily all along crown height. M^3 with two pairs of lobes behind anterior unpaired loop; posterior ones broadly fused. Enamel weakly differentiated in thickness.

Composition of genus: One to two species—*P. hopkinsi* Guthrie and Matthews, 1971 (? = *P. antiquitatis* Chaline, 1972) and conf. *P. compitalis* Zazhigin, 1974.

181 *Age and distribution*: Ancient (?) to Early Pleistocene of Western Europe, northeastern Siberia and Alaska. Judging from finds, range of genus possibly circum-Holarctic.

Taxonomic notes: For a long time nothing was known about the ancestors of Arctic lemmings. The recent simultaneous discovery of remains of primitive ancestral forms in the Chukchi Peninsula, Alaska, and France established that they are ancient inhabitants of the Holarctic. *P. compitalis* has been tentatively included under this genus. Morphotypic variability of teeth of the type species is not sufficiently known. Molar structure appears quite uniform in published reports. One would assume that a segment of the population, at least among later forms, would have already developed elements of complexity in the structure of the occlusal surface. However, these forms are not characterized by additional lobes. From the time that such emerge, the corresponding forms should be considered members of the genus *Dicrostonyx*. It is understandable that when dealing with a continuous series of variability in time, the boundary between taxa necessarily becomes subjective to some extent.

1. *Praedicrostonyx hopkinsi* Guthrie and Matthews, 1972

Diagnosis: Size large. Length of M_1 —3.8–5.7 mm ($n = 29$), M^3 —2.0–2.65 mm ($n = 19$). Falcate processes absent on posterior ends of M^1-M^2 and anterior ends of M_2-M_3 . Posterior end of M^3 in form of elongate-rounded heel.

Age and distribution: Early (?) Pleistocene of Alaska.

Taxonomic notes: The identity of the Alaskan *P. hopkinsi* and the French *P. antiquitatis* Chaline is based solely on similarity in molar structure and can only be confirmed with more abundant and complete material (remains of the lemming from Valero, France are represented by a single mandibular ramus with an incomplete row of teeth). Temporal and geographic gaps are also conspicuous.

2. conf. *Praedicrostonyx compitalis* Zazhigin, 1974

Diagnosis: On average, probably smaller than the preceding species (length of M_1 —3.8 mm). Posterior ends of M^1 — M^3 and anterior ends of M_2 — M_3 with falcate processes exhibiting stronger development on lateral side of molar. Heel of M^3 broad, rounded, with vestigial fourth lateral denticle.

Age and distribution: Early Pleistocene of Chuckchi Peninsula.

Taxonomic notes: The possibility is not excluded that a study of larger material will significantly change our opinion regarding the independent species status of this form.

2. Genus *Dicrostonyx* Gloger, 1841—Arctic Lemmings

Diagnosis: Posterior ends of M^1 — M^3 with at least one additional medial lobe and a fused underdeveloped lateral one that is transversely elongate; corresponding structures evident throughout crown height. M_2 — M_3 also with bilobate transverse processes on anterior tooth end. M^3 with isolated second pair of triangles and a third pair evidencing initial stages of isolation. Enamel distinctly differentiated.

Composition of genus: Two to three extinct species—*D. renidens* Zazhigin, 1974; *D. simplicior* Fejfar, 1966; *D. guilielmi* Sanford, 1870 (? = *D. henseli* Hinton, 1910). Based on macromorphological characters, at least two extant species are distinguishable: *D. torquatus* Pallas, 1779 and *D. hudsonicus* Pallas, 1779.

Age and distribution: End of Early Pleistocene to the present. The Early Pleistocene form is possibly related through several transitions with species of the preceding genus, at least in relation to molar structure. Past and present range coincides with that of the tribe.

Evolution of the genus in the New World is possibly more complex than in the Old World. If the data on sufficiently notable differentiation is confirmed, then Macpherson's (1965) assumptions will have to be accepted, that is some form of *Dicrostonyx*, (possibly at the stage of molar evolution corresponding to that

of *D. hudsonicus*), was widely distributed in the northern part of the continent up to the last (Wisconsin) glaciation. In the last period it underwent relatively rapid evolution in areas free of glaciation (inner parts of Alaska and some islands) as well as in different periglacial regions with differing ecological conditions. After the recession of glaciation, a more complex mosaic of forms evolved which, in the opinion of Rausch and Rausch (1972), may be considered a supraspecies.

Taxonomic notes: Composition of the genus cannot be considered final even in relation to present-day species. Studies in recent years have shown that several subspecies, primarily those from islands, are "chromosomal species." Corresponding differences also characterize Arctic lemmings of the Old and New World (Gileva, 1973; Gileva and Nobanova, 1974; Kozlovskii, 1974; Rausch, 1974). This compels us to be cautious in assessing the taxonomic status of extinct forms. These have shown rapid complexity in molar structure in chrono-clinical morphotypic variability at least from the Middle Pleistocene [Agadzhanian (1971, 1973) and Zazhigin (1976)]. Based on changes in time of the dominant morphotype in this continuous series, to date I have separated only three forms and tentatively assigned them the status of species.

Establishment of the genus *Praedicrostonyx* has not clarified the ancient ancestral affinity of Arctic lemmings. We have already mentioned the possible existence of common ancestors of *Dicrostonyxini* and *Clethrionomyini* through the subtribe *Pliomyi*.

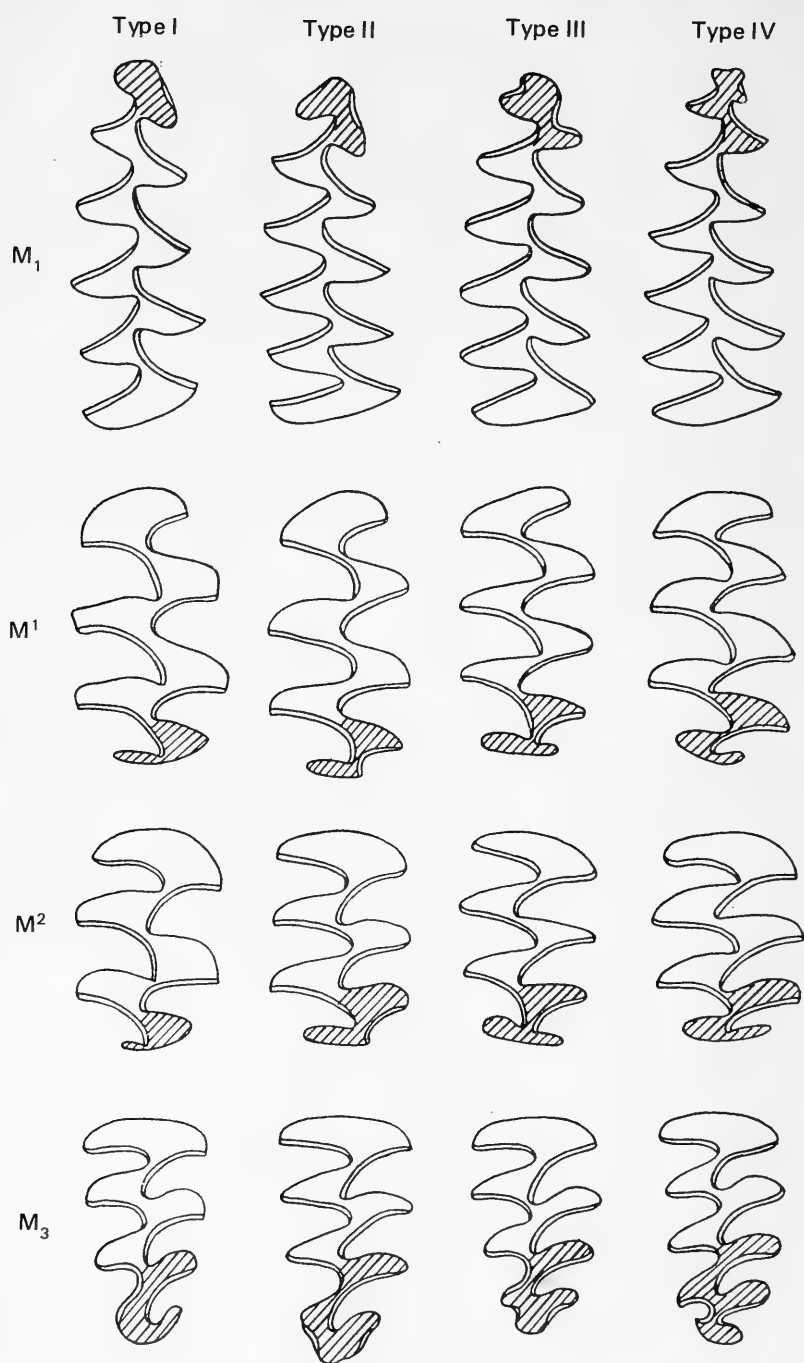
1. *Dicrostonyx renidens* Zazhigin, 1974 (foss.)

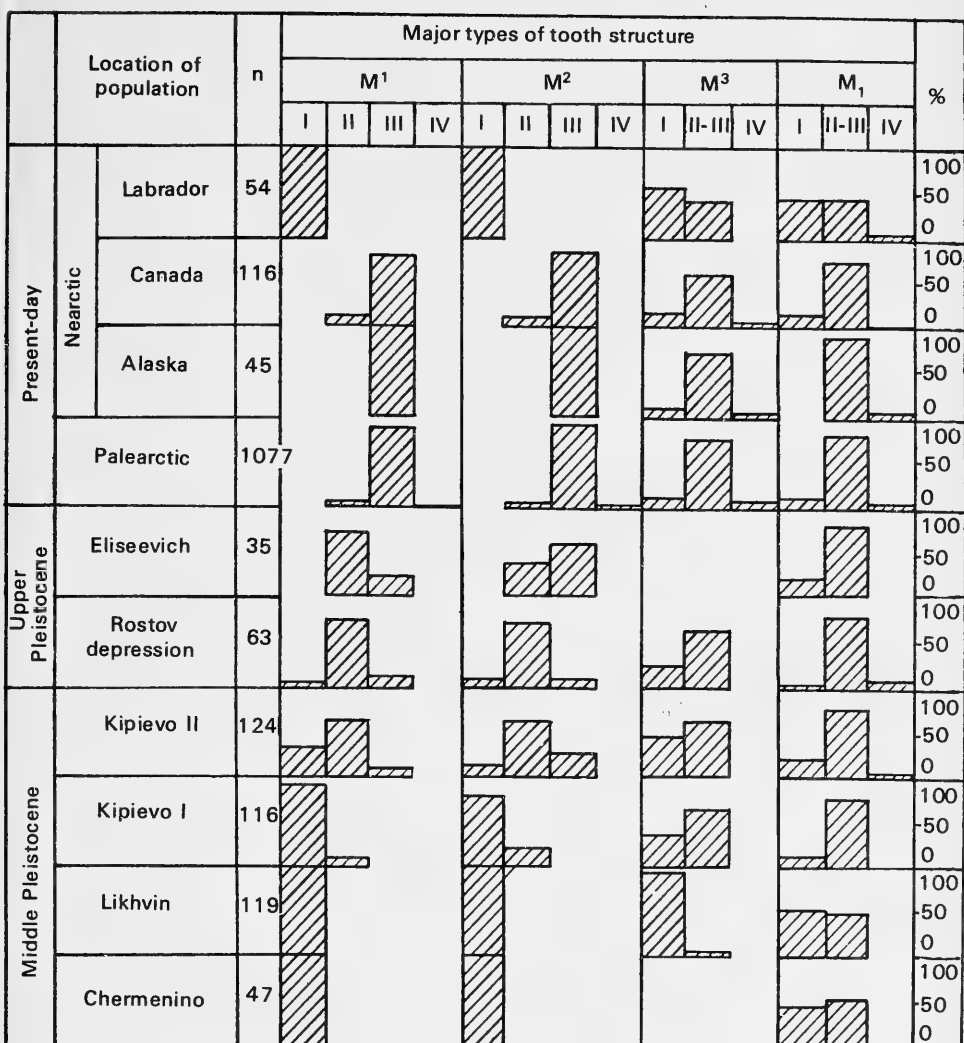
Diagnosis: Dimensions: length of M_1 —3.7 mm, M^3 —2.6 mm (Zazhigin, 1976). Based on the small sample available, the dominant type of structure of the upper molars is characterized by the occurrence of a small additional medial lobe on the posterior end of M^1 — M^2 (sixth and fifth respectively), which is not triangular but rounded and fused with a smaller lateral lobe. Rounded common perimeter of these two lobes without enamel. Additional (third) pair of lobes in form of triangles isolated in posterior section of M^3 , with which broad massive heel of tooth fused. Triangles of occlusal surface comparatively poorly compressed anteroposteriorly.

183 *Age and distribution:* Early Pleistocene of Chukchi Peninsula (Bol'shaya Chukoch'ya River).

2. *Dicrostonyx simplicior* Fejfar, 1966 (foss.)

Diagnosis: Size comparatively small. Length of M_1 —2.9—3.4—





184 Figure 31. Morphotypic molar variability of Arctic lemming (*Dicrostonyx*) in second half of the Pleistocene.

4.0 mm, M^3 —2.0—2.5—2.8 mm (Likhvin; Agadzhanyan, 1971) and 2.95—3.49—4.3 mm ($n = 29$) and 1.8—2.24—2.65 mm respectively (Kipievo; Agadzhanyan and Isaichev, 1976). Sixth and fifth additional medial lobes of M^1 and M^2 larger than in preceding species and triangular in shape, not rounded. Small lateral process associated with them often present but medial one absent. M^3 with falcate heel that may be directed either medially or laterally. Proportions of triangles of occlusal surface as in *D. renidens*.

Age and distribution: End of Early (Tiraspol' fauna)—beginning of Middle (Persian, Early Hazara faunas) Pleistocene of Western Europe (Czechoslovakia, FRG), European part of the USSR (Upper Volga near Rybinsk, Oka of Inner Chokalin, and Kipievo on Pechora), and Siberia (mouth of Aldan River).

Taxonomic notes: The last two species were separated on the basis of structure of dominant morphotype of upper molars and are related to each other through intermediate forms (Figure 31).

3. *Dicrostonyx guilielmi* Sanford, 1870 (? = *henseli* Hinton, 1910) (foss.)

Diagnosis: Size variable. Length of M_1 —2.2—2.8—3.2 mm ($n = 17$) in small forms and 3.2—3.5—4.0 mm ($n = 15$) in large forms; length of M^3 —2.1—2.3—2.7 mm (European part of the USSR; Agadzhanyan, 1973). Dominant type of molar structure more complex than in preceding species. Behind the additional posteromedial lobes of M^1 — M^2 (sixth and fifth respectively) occurs a large lateral lobe (future seventh) and a small medial process in the form of a transversely elongate lobe with oval formations that are fused with each other; posterior margin with thin enamel coat. Third pair of triangles in posterior section of M^3 better differentiated than in preceding species. Isolation of lateral lobe of fifth pair terminates on anterior section of M_1 , and fold of lobe of sixth pair located on medial side. Triangles of occlusal surface of all molars comparatively notably compressed anteroposteriorly.

Age and distribution: Late Pleistocene (Würm) lemming (marmot) and mixed faunas of western and eastern Europe and western Siberia.

Taxonomic notes: The ratio of archaic types of molar structure shifts significantly in different populations of Late Pleistocene lemmings—characters dominant in more ancient species, as well as progressive characters typical of the extant species *D. torquatus*. This mosaic of characters provided the particular basis on which Janossy (1954) denied an independent species status to the Late

Pleistocene members of *Dicrostonyx*. Nevertheless, as rightly noted by Agadzhanyan (1973), this mosaic of characters, in which traces of the type described above are dominant, is a special characteristic of the species.

Affinities between *D. guilielmi* and *D. henseli* are presented below, with a description of the extant species *D. torquatus*.

4. *Dicrostonyx hudsonicus* Pallas, 1779—Hudson's Lemming

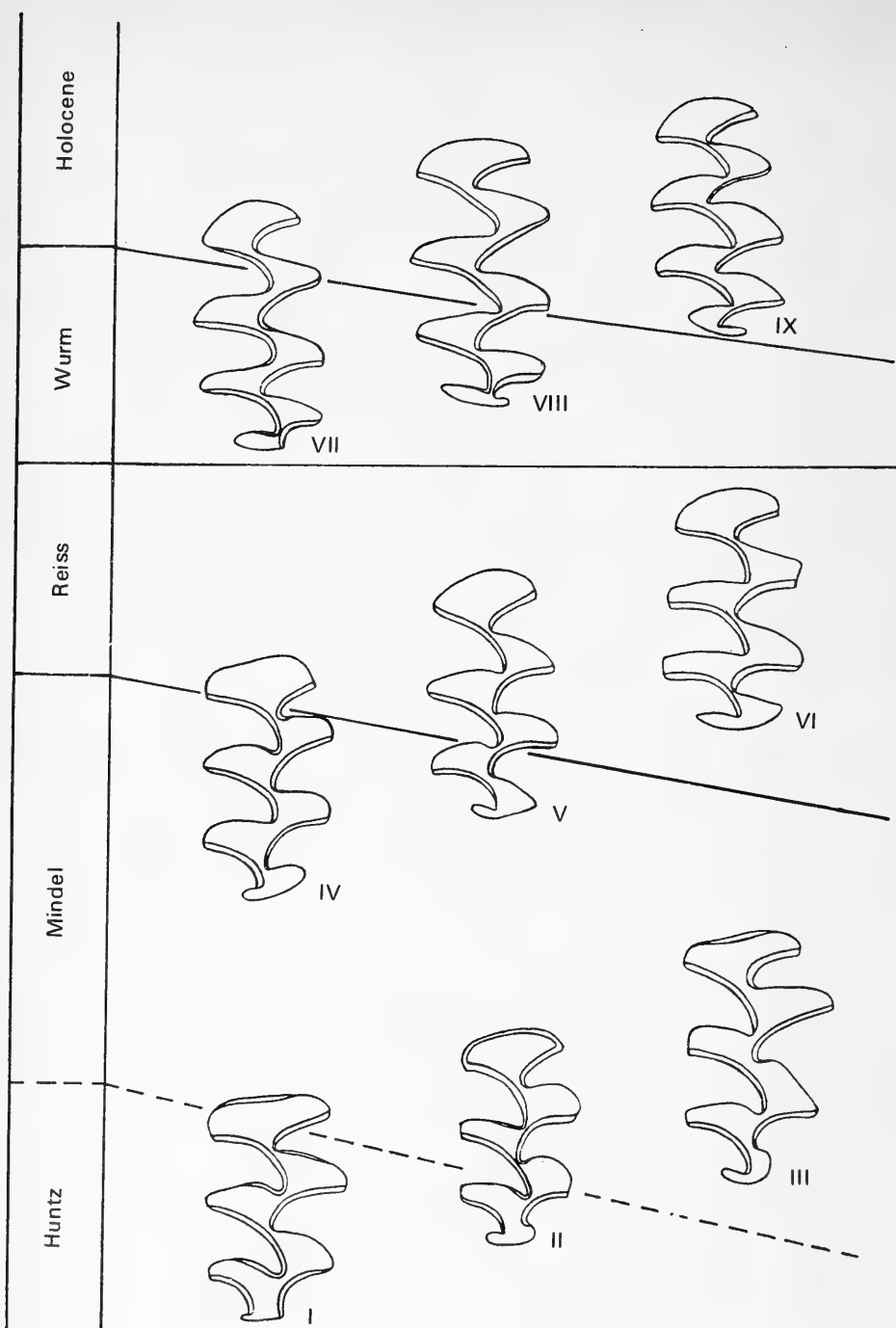
Diagnosis: Size comparatively large. Body length up to 158 mm, 185 condylobasal length of skull up to 30 mm; M_1 —3.25–3.57–3.9 mm, M^3 —2.1–2.34–2.6 mm ($n = 16$; data from Agadzhanyan). Summer pelage less dense and longer than in the next species, dull gray, with rusty tones on sides of trunk and head barely perceptible. Interparietals usually paired. Nasals comparatively narrow and long, pterygoid process short and massive. Incisor alveoli broader and longer than in the next species; prognathism of upper incisors negligible. Structure of posterior section of M^1 – M^2 as in *D. simplicior*. Anterior section of M^3 without additional medial lobe, or latter barely perceptible (Figure 32).

Distribution and zonal affinity: Tundra of Labrador and some islands near its western coast.

187 *Evolution and phylogeny:* Fossil remains are known from the Late Pleistocene for the region south of the Great Lakes (Guilday, 1963). It is believed that from the end of this period this species (a local relict or eastern Riss migrant) was isolated from the remaining American part of the range of the genus by the forest along the southern coast of Hudson Bay. It is similar to *D. simplicior* in underdeveloped additional elements of the posterior section of the upper molars. The relationship of other characters requires further analysis.

5. *Dicrostonyx torquatus* Pallas, 1779—Arctic Lemming (Figure 33)

Diagnosis: Size: comparatively small, and only in some larger forms reaches dimensions of preceding species. Body length usually up to 140 mm, condylobasal length of skull less than 30 mm. Length of M_1 —2.75–3.3–3.87 mm ($n = 75$), in larger forms of the New World—3.33–3.65–5.00 mm ($n = 42$; data from Agadzhanyan). 188 Summer pelage denser and longer than in Hudson lemming, fairly bright, ash-gray with distinct rusty tones on sides of trunk and head. Interparietal, generally unpaired; nasals comparatively broad and alae nasalis long and narrow. Incisor alveoli narrow, reduced;



186 Figure 32. Diagrammatic representation of variability in structure of anterior upper molar in Arctic lemmings (*Dicrostonyx*) in the Pleistocene. I to III—types in *D. renidens* Zazhigin; IV to VI—types in *D. simplicior* Fejfar-hudsonicus Pallas; VII to IX—types in *D. guilielmi* Sanf.-torquatus Pallas.

prognathism of upper incisors comparatively well-defined. Of the additional elements on posterior end of M^1 – M^2 , lateral one in most morphotypes isolated into a seventh and sixth triangle respectively. Third (posterior) pair of lobes on M^3 well-differentiated. Structure of anterior of M_1 somewhat more “shifted” than in the phyletically close *D. guilielmi*.

Chromosome number of *D. torquatus* varies mainly from $2n = 45$ in males and 44 in females to 50 or even 51, but females always with one chromosome less (Gileva, 1973).

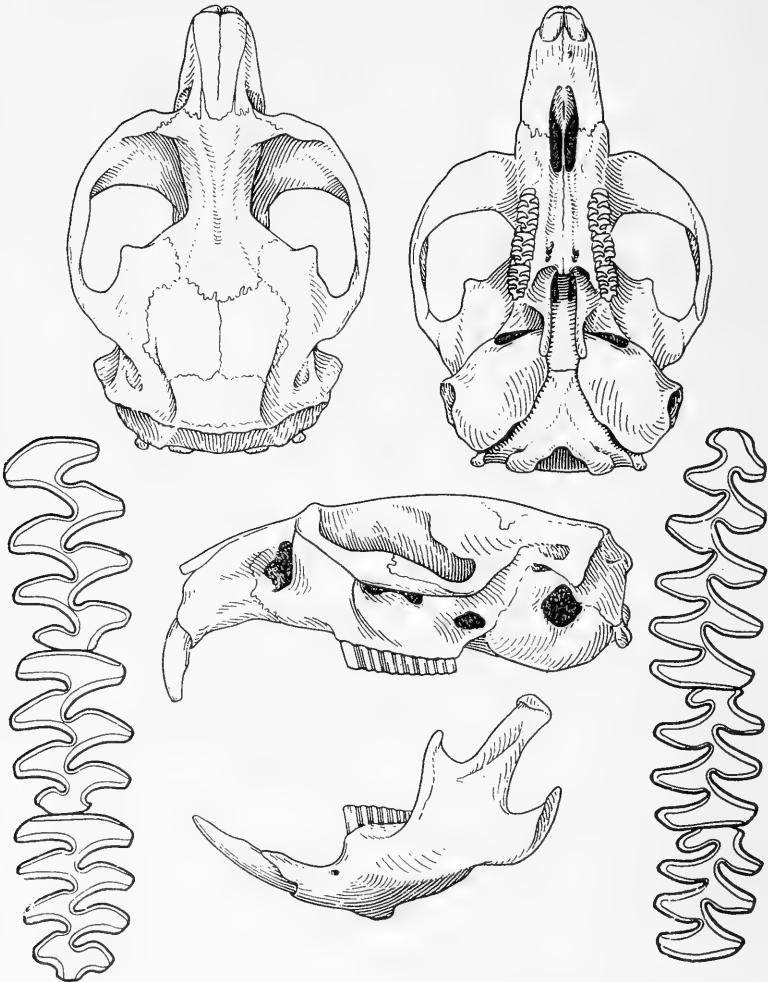
Composition of species: The intraspecific variability of present-day as well as extinct forms has not been adequately described, nor have the affinities of the Arctic lemming of the Old and New World. The recently discovered “chromosomal species” of North America (30 to 35 and 42 to 44 chromosomes in diploid set) should throw light on further morphological and hybrid investigations. It may be mentioned here, however, that even without chromosomal analysis, many American researchers consider such forms as *D. groenlandicus* Traill, 1823 or *D. rubricatus* Richardson, 1839 as warranting independent species status.

Chernyavskii (1972) believes that there are no more than five subspecies in the tundras of the Old World. Two are continental—*D. t. torquatus* Pallas, 1779 (tundras west of the Yenisey) and *D. t. chionopaes* G. L. Allen, 1914 (tundras east of the Yenisey)—and three insular—*D. t. unguatus* Baer, 1841 (Novaya Zemlya); *D. t. vinogradovi* Ognev, 1948 (Wrangel Island; close to American forms; Kozlovskii, 1974); and *D. t. torquatus* subsp. ? (Novaya Zalya). Rausch (1953), who initially refused to accept subspecies other than the nominal one, later listed six. F.B. Chernyavskii has noted the clinal nature of variation in color of *D. torquatus*: eastward, rusty tones in the dorsal surface are replaced by chestnut, mottling enhanced, and the sharp longitudinal black stripe lost; moreover, isolated forms occur more north than the mainland form.

The taxonomic status of the extinct Late Pleistocene species from Western Europe—*D. guilielmi* Sanford and *D. henseli* Hinton—is also not clear. Differences in skull structure, pointed out by Hinton (1926), could be assessed as vagaries of comparison, at least for the majority of present-day forms of *Dicrostonyx*. The dominant morphotype structure of the upper molars of extinct species recovered from various localities, should also be determined and evaluated.

Extreme variants of M_1 (presence of elongate lateral lobe and a third fold) were attributed to an independent subspecies: *D. t. altaicus* Vinogradov, 1922. The name was also given to tentatively designate the remains of Early to Middle Pleistocene forms from Hungary (Janossy, 1965). Incidentally, isolated teeth of the dentary, especially M_1 , are less suitable for taxonomic evaluation.

Distribution and zonal affinity: The species (broadly speaking) is characterized by an almost continuous circumpolar distribution



187 Figure 33. Skull of the Arctic lemming (*Dicrostonyx torquatus* Pallas).

in the tundra and northern forest tundra zone, in the plains, and partly in montane regions (in Alaska up to 1,700 m above msl), with the exception of northern Scandinavia, Iceland, Spitzbergen, greater part of Greenland, and some smaller islands of the Polar Basin, as well as the Komandor Islands west of Umnak Island. Earlier range coincides with that of the genus (except for data available for *D. hudsonicus*). In the New World, fossil remains have been recovered south of the modern boundaries in Fairbanks region (Alaska).

VII. Tribe LEMMINI Gray, 1825, stat. nov.

Diagnosis: Bony palate with interconnected postpalatal pits covered by cowl-like posterior margin of palate. Rarely, pits only partially interconnected or separated by bony bridge. Molars rootless, usually devoid of cement. Differences in size of lateral and medial triangles of masticatory surface of lower molars significant. Enamel poorly differentiated (except at deepest point of folds); differentiation occasionally notable (extinct forms of *Synaptomys*). Paraconid section of M_1 complex, sometimes incompletely, without traces of secondary simplification. M^3 moderately long, also without traces of secondary simplification. Its posterior section in form of simple small loop, and anterior section, similar to anterior section of M^2 , unlike structure in all other microtines, formed by two transverse lobes connected to medial side of tooth. Lower incisor short; posterior end does not extend beyond posterior margin of alveolus of M_3 . Latter lacks separate bony socket (alveolus).

Composition of tribe: Three present-day genera—*Synaptomys* Baird, 1857; *Myopus* G. Miller, 1910; and *Lemmus* Link, 1795.

Description: Small to medium-sized voles, with body length up to 100 mm in former and 160 mm in latter. The length of the upper molar row is up to 10.5 mm, the lower row is up to 10 mm. Color of body monochromatic or with alternating light- and dark-colored regions (stripe and spots); brown and reddish tones dominant. Seasonal dimorphism of pelage is either negligible or distinct (*Lemmus*). The tail is shorter than the hind limb, or only slightly longer, with fairly dense light- or dark-colored hairs; the terminal hairs may be longer than half tail length. The eyes are small or medium in size. Pinna are very small to normal, covered with dense hairs completely or only toward front. The antitragus is poorly developed or absent. Rhinarium is small. The upper alae nasalis is barely isolated, densely covered with short hairs, and glabrous only

along outer margin. The lower alae nasalis are slightly lobate in the middle section, with well-developed outer parts that are fused or almost fused on outer tips of upper alae nasalis and isolated narial pit. The upper labial flaps are small and free. Among vibrissae, those of the upper lip and corner ones of lower lip and longer. Carpal vibrissae may be absent. Hind limbs are relatively long, fore- and hind feet reduced. All feet are either densely pubescent with less well-developed pads or poorly pubescent with well-developed pads. Digits of forelimbs are: III, IV, II, V, I or IV = II; the pollex has short obtuse claw flattened laterally; other claws are long, not shorter than half length of digits, and sometimes much longer. Digits of hind limbs are III, IV, II, V, I or III = IV; claws are the same length as on forelimbs: the claw of hallux may not reach pad of 2nd digit.

190 The skull has a steep dip in profile at bases of zygomatic arches, there is a moderately (*Synaptomys*) or strongly developed crest in narrow interorbital space and broad flattened brain case. The facial section is reduced. Zygomatic arches are high in the middle section, relatively higher than in any other microtines, are anteriorly wide-set and markedly converge posteriorly. The orbits are medium in size and lie closer to anterior end of skull than in other voles. The orbital plane forms a comparatively small angle with the horizontal plane. The postorbital processes are in the form of plates. The meseteric [= zygomatic] plate of maxilla is relatively broad and forms angle of not more than 25° with sagittal plane. The pterygoid processes are comparatively short and broad, especially in middle part, with wide-set bases (a distinction from *Dicrostonyxini*). The auditory bullae are comparatively large, the cavity is completely or mostly filled with small-celled spongy bony tissue. The mandibular symphysis is in the form of a broad arc; the angle of the ventral margin of the arc is moderate (about 140°). The ascending jaw is narrow; when mandibular ramus is horizontal, it overlaps molars from about the posterior prism of M_2 . The articular process is long; the coronoid process is distinctly short of reaching its tip; the apex of the angular process, extends beyond its posterior margin. Mental foramen very close to anterior part of masseteric ridge.

The upper molar row is relatively narrow anteriorly and diverges posteriorly more than in other microtines. The molars have a relatively high crown. The root ends of the upper molars do not form tubercles or bulges inside orbit or, if they do, they are small; the lower molars, lateral to incisor, may form notable alveolar bulges along lower crest of masseteric ridge. M_1 is short and has a primarily simple structure of paraconid section; in extant forms,

it often has a long, narrow, digitate anterior unpaired loop above incompletely isolated triangles at its base. Anterior "island" or vestigial (juvenile) lateral folds are absent on paraconid section. The posterior section of the upper molars is without additional lobes. M^3 is without "islands" or their traces in anterior or posterior sections of tooth. The medial denticles of M^1 – M^2 are acute but truncate parallel to the alveolar margin of jaw. M^3 is not shifted inward of the tooth row. The crowns of the incisors are shorter than in other microtines, moderately to very (*Synaptomys*) broad. The extent of incisor curvature, size of facing angle in both upper and lower ones, as well as shape of cross section are variable. The anterior surface of the upper incisors has a distinct, rarely shallow longitudinal groove; the edge of the incisor lateral to groove describes a distinct dihedral angle to medial edge. The posterior surface of each incisor also has a deep longitudinal, rarely moderately deep (in some members of *Synaptomys*), groove-like depression. Profile of combined cutting edge of incisors M-shaped. Lower incisor short, situated on lingual margin of jaw, the molar sections of the teeth lie on its labial side.

The skeleton is characterized by a relatively short pelvis, long neck of femur, short crest of tibia, long and narrow scapula, and comparatively short ulnar process. Distal phalanges long, basal phalanges of metapodia may be greatly reduced.

Distribution and zonal affinity: Tundras and forest zones of plains of northern Holarctic and their high-altitude analogues up to 2,000 m msl (Alaska). It is found from northern Sweden and Norway up to middle part of Russia in the west, and from the sea coast and some islands of the western part of the Polar Basin up to the mountain ranges of central and eastern Siberia and Kamchatka in the east; in North America spreads southward almost to 50° N in the east and 40° W.

191 In the Early Pleistocene of the Carpathian region, it is found together with species of submontane forest-steppes. In the Late (Würm) Pleistocene, it is included in the composition of the unique extinct mammal complexes of the so-called periglacial steppes, which today are covered with broad-leaved forests, and forest-steppes over large areas from western (France) and central Europe up to the Alps, Chukchi Peninsula, and central part of the Great Plains of the New World.

Evolution and phylogeny: Fossil remains are known from the Early Pleistocene (Kromer) in the Old World, and in the composition of Late (Tamansk and Tiraspol') *Mimomys* faunas of the southern part of Western and eastern Europe and northeastern

Mongolia. In North America, it probably is found somewhat earlier than in the composition of Blancan (Late Khaprovsk or Tamansk) faunas encompassing extinct genera of voles with rooted molars. Thus, rooted and cementless ancestral forms of true lemmings among the primitive members of microtines must have undergone a fairly long evolutionary trend in the Pleistocene. However, neither the affinities nor the individual stages of this evolution are confirmed by factual paleontological material and are based to date only on indirect evidence. Either way, present-day members of Lemmini exhibit a tendency toward a mixture of archaic and highly specialized features. Among the former group particularly characteristic are the reduced incisors and I believe, contrary to Hinton (1926), primarily simplified anterior lower radical teeth. Among the highly specialized characters are the structure of the upper incisors described above, M_3^3 , high crowned molars, presence of cement in folds of the latter, as well as a series of structural features of the skull associated with well-developed masseter muscles. Some morphological features, for example, structural details of M^3 , permit us to conjecture a possible close affinity with the vole-toothed European hamsters of *Baranomys* and the American *Prosomys*, as well as an evolution that proceeded for a long time under the conditions of open bogs in the forest zone somewhere in the central part of the Holarctic.

True lemmings are a distinctly segregated group of microtines which, even during the initial separation of the family (subfamily), were given an independent suprageneric status that has been contradicted by no one subsequently.

KEY TO SPECIES AND GENERA OF TRIBE LEMMINI

- 1 (2). Claws of fore- and hind limbs do not differ in size. Pads glabrous in anterior section and with well-developed calluses Genus *Myopus* G. Miller (p. 288).
One species, *M. schisticolor* Lilljeborg.
- 2 (1). Claws of forelimbs significantly larger than those of hind limbs. Pads densely covered with hairs that extend over calluses Genus *Lemmus* Link (p. 281).
- 3 (4). Dorsal surface of head and anterior part of back black. Light-colored, yellowish to chocolate-brown spots very distinct above eyes and behind pinnae *L. lemmus* L.

- 4 (3). Dorsal surface of head and anterior part of back brownish-ocher. Light-colored spots absent above eyes and behind pinnae.
- 5 (6). Body length less than 120 mm. Ventral surface of head and neck bright, rusty-brown *L. amurensis* Vinogradov.
- 6 (5). Body length more than 120 mm. Ventral surface of head and neck at least in lower part, grayish or yellowish
..... *L. sibiricus* Kerr.

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1. Genus *Lemmus* Link, 1795—True Lemmings

Diagnosis: Body length up to 150 mm. Bright ochereous-brown tones dominant in color of dorsal surface, at least in posterior half of back. Anterior part of back may exhibit one black spot, one longitudinal black stripe along spine, and extension of black- and light-colored regions onto head. Ash-gray tones absent in color of ventral and lateral sides. Seasonal dimorphism of peltage, at least in relation to length and density, well-defined. Tail shorter than foot, densely covered with hairs, with terminal hairs longer than half tail length. Pads densely pubescent up to base of digits; only one to two highly reduced, flat calluses retained. Claws on forelimb longer than digits. Eyes medium in size. Pinna small, with long helix that is completely covered with hairs. Length of fused section of upper lips less than width of incisor. Distance between tip of anterior unpaired tubercle of soft palate and middle of frontal transverse ridge not more than between anterior tubercle and posterior ridge. Posterior ridge entire, without middle transverse fold. Chromosome number, $2n = 50$.

Forelimbs relatively long, with long and broad manus.

Length of facial section of skull more than 25% axial length. Position of orbit median; angle formed by its plane with horizontal plane small. Upper diastema longer than molar row. Postpalatal pits fused; posterior margin of bony palate often with small backwardly directed dentoid process. Auditory bullae notably laterally compressed. Pterygoid pit on inner surface of angular process of mandible isolated. Width of ventral margin of mandible at anterior angle of masseteric ridge not smaller than length of M_1 , and width of base of angular process much smaller than its length along dorsal margin. Facing angle of incisors small. Indistinct longitudinal groove on anterior surface of upper incisor shifted toward inner margin. Lower incisor extends posteriorly almost to middle of M_3 . M^3 notably broader than M^2 ; its second (counted from front) lat-

eral fold does not reach half width of tooth; and third fold does not reach half depth of second. Folds of M_3^3 much narrower than those of other molars.

Humerus with relatively high head, greater trochanter with well-developed crest, and lower epiphyses well-developed. Olecranon process of ulna comparatively short; facet for insertion of radius broader than in *Myopus*. Distal phalanges of forelimbs longer than, rarely equal in length to, both basal phalanges; metacarpals shorter than basal phalanges.

Composition of genus: Probably not more than three to four species: *L. lemmus* L., 1758; *L. sibiricus* Kerr, 1792 (= *obensis* Brants, 1827 and most probably, = *trimucronatus* Richardson, 1825); and *L. amurensis* Vinogradov, 1924. Further study, including hybrid analysis, should finally solve the taxonomic status and relationship of the Kamchatka, eastern Siberia, and North American yellow-bellied lemmings of the *chrysogaster-trimucronatus* group, as well as the Palearctic, forest and high-montane *L. amurensis*. Species affinities of extinct forms have not been established to date. Usually, they are designated as *Lemmus* conf. *lemmus* or *Lemmus* conf. *obensis* (= *sibiricus*). However, the possibility is not excluded that some of the remains belong to ancient forms of *Synaptomys*.

Distribution and zonal affinity: This genus inhabits plains, montane-tundra, and forest-tundra of the Holarctic, several islands of the Polar Basin and, at places, also open biomes of the northern part of the forest zone. Found from northern Scandinavia to the west coast of Hudson Bay and Baffin Land. It is found in mountains up to 800 m above msl in the northern Urals, 1,200 m in eastern Siberia, and 2,000 m in the Rocky Mountains. In the eastern part of the range extend farther southward (central Kamchatka, Amur district, northern Columbia) than in the west (lowlands of North Dvina and Polar part of northern Urals). In the Pleistocene it is found up to the central region of France and the British Isles, but no remains have been found to date south of the Alps, and they are rare in the central Carpathians. In the east, they are found all along the northern range and, at places, even southward.

Evolution and phylogeny: Fossil remains are known from the Early Pleistocene but are slightly more ancient in Western Europe and Alaska (Late Khaprovsk faunas) than in the USSR (Late Tamansk and Tiraspol' faunas of western Ukraine). In the Early Pleistocene, common lemmings constituted the forest-steppe faunas of the foothill regions of Western Europe, particularly the Carpathians. Late Pleistocene finds are common for lemmings and

“mixed” faunas of the cold tundra-like and forest-steppe environment of preglacial areas throughout the plains of western and central Eurasia, especially north of the south European mountain system as well as in the Alps region. Strangely, fossil remains have not been found to date beyond the limits of the present-day range in North America, although *Synaptomys*, *Dicrostonyx*, and several northern species of *Microtus* are found here. Only one locality is known to me from literature in the now forest-covered part of the Yukon valley (Repenning *et al.*, 1964), attesting to local shifts in range boundaries during the Pleistocene.

This genus comprises more specialized species than the other two genera; their affinities are not described.

1. *Lemmus lemmus* L., 1758—Norwegian Lemmings

Diagnosis: Body length up to 150 mm, tail up to 15.5 mm (average 12.5% trunk length). Length of upper molar row 7.3–8.3–8.8 mm, lower row 7.8–8.2–8.8 mm; M_1 —3.1–3.3–3.5 mm.

Color of dorsal surface bright, contrasting, especially in full-grown winter pelage of individuals still retaining young coat in posterior part of back. Entire anterior part of trunk covered by distinct black spot; posterior part of trunk light-colored, yellow to chocolate-brown, with black stripe along spine variably developed (and barely perceptible in winter pelage). Two yellow to chocolate-brown stripes extend above eye and ear, terminating separately on upper surface of neck. Ventral surface light-colored, creamy-yellow. Sharp seasonal dimorphism absent.

Skull structure, exhibiting sharp age-dependent changes (finally formed in animals older than five months; Koshkina and Khalanskii, 1961), may differ from next species only in series and in medium size. A large number of skull characters were studied by Vinogradov (1925) and subsequently listed by investigators with slight modifications (Ognev, 1948; Gromov *et al.*, 1963). Compared to the skull of the Ob' lemming, that of the Norwegian lemming is characterized by smaller dimensions, narrower facial section, including posterior part of nasals, less-developed processes at base of zygomatic arches on upper side, higher sagittoccipital crest (between occipital foramen and lambdoid crest), anterior sections of upper molars more wide-set, weaker (narrower) incisors, especially lower ones, reduced M^1 , and smaller folds on all upper molars (triangles of occlusal surface correspondingly less transversely elongate).

Composition of species: Intraspecific differences have not been established.

Distribution and zonal affinity: Montane tundra of Scandinavia and the Kola Peninsula. It is not found south of Kandlaksha.

Evolution and phylogeny: The possibility is not excluded that at least some of the Late Pleistocene material from Western Europe belongs to these species. An attempt to establish identity with *L. lemmus* and *L. obensis* by Sidorowicz (1960) cannot be considered well-founded; it is not accompanied by an analysis of degree of reliability of earlier established differences and, hence, lacks scientific validation.

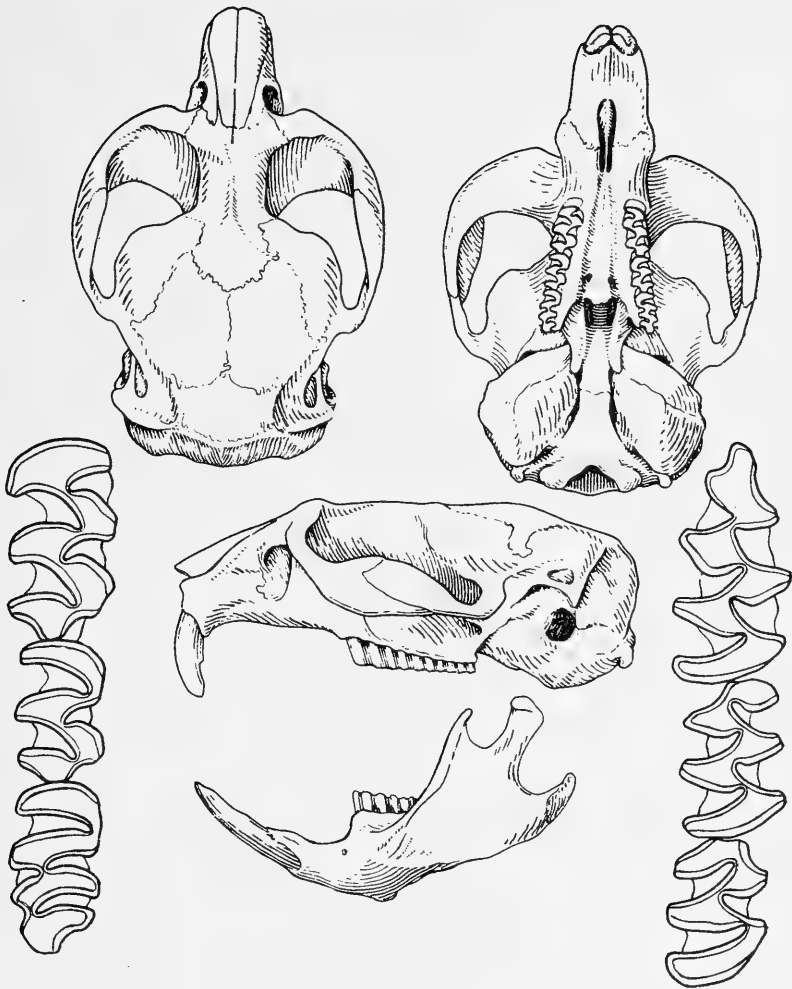
2. *Lemmus sibiricus* Kerr, 1792—Ob' or Siberian Lemming (Figure 34)

Diagnosis: Body length up to 160 mm in large forms and 140 mm in small forms. Differences in body length are no less distinct in medium-sized forms which, according to Krivosheev and Rossolimo (1966) and Chernyavskii (1967) are 134 and 105 mm respectively. The length of the tail ranges up to 20 and 14 mm (average 12.2% body length in long-tailed forms and 9.2% in short-tailed forms). Length of upper molar row 7.3–8.3–8.8 mm, lower row 7.8–8.2–8.8 mm; M_1 —3.1–3.3–3.5 mm.

Large black spot in anterior part of back absent. General color of dorsal surface yellowish-ocher, often with distinct bright rusty tones, which are more vivid in posterior part of back; anterior part of head gray. Most animals in the western populations have a black (brown during winter) anterodorsal longitudinal stripe, varying in intensity, beginning from dark-colored forehead, and sometimes even lateral stripes from the snout extending toward the pinnae through the eyes; in the latter case, one light-colored spot may occur above each stripe. Ventral surface light, yellowish in animals from the western part of the range, gray or brown to rusty-brown in animals from the eastern part. In the former case, border between color of dorsal and ventral surfaces on sides of head and neck particularly sharp; in the latter case, marked solely by splash of gray color from lower surface. Winter tail pelage highly pigmented in eastern part of range; summer pelage almost completely white.

Distinctive structural features of the skull are apparent from the comparative study presented under the preceding species.

Composition of species and variability: If the specific status of the eastern Siberian and North American lemmings is recognized, but the latter not considered distinct from *L. sibiricus* (which is



195 Figure 34. Skull of the Siberian lemming (*Lemmus sibiricus* Kerr).

hardly true), then the number of subspecies recognized by different authors ranges from two (Krivosheev and Rossolimo, 1966) to four (Chernyavskii, 1967, 1972) for the Palearctic; five (Rausch, 1953) to eight (Hall and Kelson, 1959) for the Nearctic, with six listed only for Alaska! The actual total number of subspecies can hardly be more than 10. The well-established subspecies are: *L. s. sibiricus* Kerr, 1792 (from the lower reaches of the North

Dvina to the lower reaches of Kolyma; Novaya Zemlya ?); *L. s. novosibiricus* Vinogradov, 1925 (islands of Novosibirsk); *L. s. chrysogaster* J. Allen, 1903 (= *s. paulus* Gl. Allen) (Chukchi, Kamchatka ?); *L. s. portenkoi* Tschernyavsky, 1967 (Wrangel Island); *L. s. trimucronatus* Richardson, 1825 (? = *chrysogaster* J. Allen, 1903) (Canada excluding its southwestern region); *L. s. helvolus* Richardson, 1928 (Rocky Mountains, opposite Alberta, Canada); *L. s. harroldi* Swarth, 1931 (Nunivak Island); and *L. s. nigripes* True, 1894 (Pribilof Islands). Subspecies from continental Alaska include: *L. s. alascensis* Merriam, 1900 (Cape Barrow); *L. s. minusculus* Osgood, 1914 (southwestern Alaska); *L. s. subarcticus* Bee and Hall, 1956 (Brooks Range); and *L. s. jiconensis* Merriam, 1900 (upper reaches of Yukon River). The taxonomic position of the Kamchatka lemming is not clear; it has been designated *L. flavescens* Brandt, 1845 and also *L. kittlitzii* Middendorf, 1853 (according to Vinogradov, 1925, both names are nomina nuda!): new material has not been described from Kamchatka since the end of the last century. The validity of the subspecies identified for populations inhabiting a part of the range occupied by the type subspecies is also not clear, from where *L. s. bungei* Vinogradov, 1925 has been reported for the Lena delta.

Most researchers have reported unanimously the absence of geographic variability in skull structure, an aspect usually remarked on in Palearctic lemmings. However, it is possible that the small samples of different populations preserved in museum collections do not suffice to identify such variability. A low variability has been reported for summer coloration but, contrarily, a distinct geographic variability reported for winter coloration: eastward the color becomes light and dull, and the black dorsal stripe disappears. An indistinct size gradation has been established by Krivosheev and Rossolimo (1966) i.e., an increase in size northward in the eastern part of the range. Most probably, size variation also exists from west to east, and insular forms are larger than mainland ones. In the Palearctic, the most distinct "limit of variability" is observed in eastern Siberia, in the lower reaches of Kolyma and in the spurs of the northern Anyuiskii range (Chernyavskii, 1972), east of which yellow-bellied forms occur, which also inhabit North America.

Distribution and zonal affinity: Same as for genus, except that these animals are not found in montane-tundra west of the White Sea. Most probably, a related form lived in the Pleistocene in the preglacial biomes of central Siberia within the limits of the present forest zone, south of the central Trans-Ural region in the west, and

the Lower Pri-Aldan in the east. The taxonomic position of the analogous east European form is not clear.

Evolution and phylogeny: This is already discussed in the description of the genus and the preceding species. We may note here that the molars of *Lemmus* from the Ancient Pleistocene deposits of Alaska are not distinguishable from those of the present-day American *L. sibiricus* (Guthrie and Matthews, 1971). Material from deposits of the same age from the far northeastern part of Siberia (Chukchi River) have still to be analyzed. Possibly, at least a part of the remains of *Lemmus* from the composition of Late *Mimomys* fauna here belong to *Synaptomys*.

3. *Lemmus amurensis* Vinogradov, 1924—Amur Lemming

Diagnosis: Size: smaller than other species of the genus. Body length up to 120 mm, tail up to 14.5 mm, its relative length (single specimen) about 20%. Length of upper molar row 7.5, 7.6 mm, lower row 7.2, 7.2 mm; M_1 —2.7, 2.9 mm.

Color of dorsal surface in animals with summer pelage monochromatic, grayish-chocolate-brown; longitudinal black stripe may broaden significantly in anterior part of back and on head, forming there an oblong spot. Dark stripe also present on sides of head, extending through eyes toward pinnae. Ventral surface light-colored, yellowish-ocher. Bright rusty spots present above pinnae and in region of vibrissal bases (based on an August specimen from southeastern part of Verkhoyansk range). Winter pelage dark, reddish-chocolate-brown on dorsal surface and rather bright, reddish-chocolate-brown on ventral surface, without sharp boundary between them. Dark brown spot present on head and along middle of anterior third of trunk (based on an April specimen; holotype from village Pikan on Zeya River).

Several features of juvenile nature have been noted by Vinogradov (1924, 1925) in the skull structure, in addition to small size: relatively large and round brain case; low and narrow zygomatic arches; and relatively larger auditory bullae than in the other two species; claws less well-developed and claw-bearing phalanges shorter (their length not more than total length of other two) and narrower forefeet.

Composition of species: Two subspecies—*L. a. amurensis* Vinogradov, 1924 (Trans-Baikal and Amur region) and *L. a. ognevi* Vinogradov, 1933 (Verkhoyansk range).

Distribution and zonal affinity: This species inhabits bogs of forest zone and bald peaks and high mountains in Trans-Baikal re-

- 197 gion (Chita district), Amur region (village Pikanon, Zeya River) and southeastern part of Verkhoyansk range (upper reaches of Nel'gekhe River in Aldan basin).

Evolution and phylogeny: Fossil remains are not known and can hardly be identified from material of usual preservation. This is one of the least studied species of rodents in Russian fauna, known to date only from a small number of specimens. The sites of recovery are distributed over a vast area, from the Aldan region to the border areas of the Trans-Baikal region. Vinogradov (1925) pointed out the relict nature of this species. Krivosheev and Rossolimo (1966) proposed that *L. amurensis* is a possible forest counterpart of *L. sibiricus*. I noted earlier the similarity of *L. sibiricus* to the Chukchi-American form (Gromov *et al.*, 1963). Let me mention here that the features of the black pattern in the anterior section of the trunk somewhat resemble the pattern in *L. lemmus*, and may prove to be an archaic aspect of the species.

2. Genus *Myopus* G. Miller, 1940—Forest Lemmings

Description: Body length up to 100 mm. The color of the dorsal surface, at least in posterior part of back is dominant bright rusty-red tones (similar to forest voles of *Clethrionomys*). Black dots or hairs are absent on back and head. Dark and ash-gray tones are present in the color of the ventral surface and body sides, which sometimes continue onto back also. Seasonal dimorphism of pelage is not significant, no more than in the tribe Microtini. Tail is longer than the hind foot and is moderately covered with hairs, the terminal hairs are shorter than half tail length. Feet covered with hairs only up to pads; there are five pads (one metatarsal) and are normally developed. Claws on forelimbs are not longer than digits. Eyes are small. Pinna are not reduced, have a long helix, and the outer side has a tuft of hairs. Length of the fused segment of the upper lips is greater than the width of the incisor. Distance between apex of the anterior tubercle of the soft palate and middle of the frontal transverse ridge is much greater than between these and the posterior tubercle. The posterior tubercle has a deep transverse fold in the middle.

Forelimbs are relatively shorter than in *Lemmus*, carpals are shorter and narrower.

The length of the facial section of skull is more than 25% axial length. Position of orbit is median, as also the angle formed by

its plane with horizontal plane. Upper diastema is longer than the molar series. The structure of the postpalatal pits is similar to that of *Lemmus*. The auditory bullae are rounded. The pterygoid pit on the inner surface of angular process of mandible is isolated. The width of ventral margin of mandible at anterior angle of the masseteric ridge is much smaller than length of M_1 , and width of base of angular process notably smaller than its length along dorsal margin. Facing angle of incisors is moderate. There is an indistinct longitudinal groove on the anterior surface of the upper incisor is shifted toward inner margin. The lower incisor extends posteriorly almost to the posterior margin of M_2 . M^3 distinctly broader than M^2 ; its second (counted from front) lateral fold does not reach half width of tooth; third fold absent or barely perceptible. Folds of M_3^3 much narrower than those of other molars.

Humerus has a relatively lower head than in *Lemmus*, a less well-developed crest of the greater trochanter, and a weaker lower epiphysis. The olecranon process of the ulna is longer than in *Lemmus*; facet for insertion of the radius is narrower. Distal phalanges of forelimb are shorter than both basal phalanges; metacarpals are longer than basal phalanges.

198 *Composition of genus*: One extant species—*M. schisticolor* Lilljeborg, 1884. The extinct form described (*M. brandti* Tschersky, 1879) can hardly be considered a subspecies of this species.

Distribution and zonal affinity: Forest zone, especially taiga plains, and montane forest belt from southern Sweden and Norway, Kaliningrad district, northern and central Russia to Kolyma, Kamchatka and Sakhalin. In the south, it is found up to central parts of Finland, northern Urals, southern periphery of taiga plains in Tans-Ural and western Siberia, montane-forest regions of northern Mongolia (Kentai, southeastern Hangai), northeastern China and Japan. It penetrates forest-steppes (Trans-Baikal region) and river valleys into tundras (northern part of Ob' region, Khromo-Alazeisk interfluve).

Evolution and phylogeny: Fossil remains are known from the Late Pleistocene cave deposits of the Ural region, Sayans, and Primor'e. It is less specialized than *Lemmus*, more specialized than *Synaptomys*. Affinities are not known.

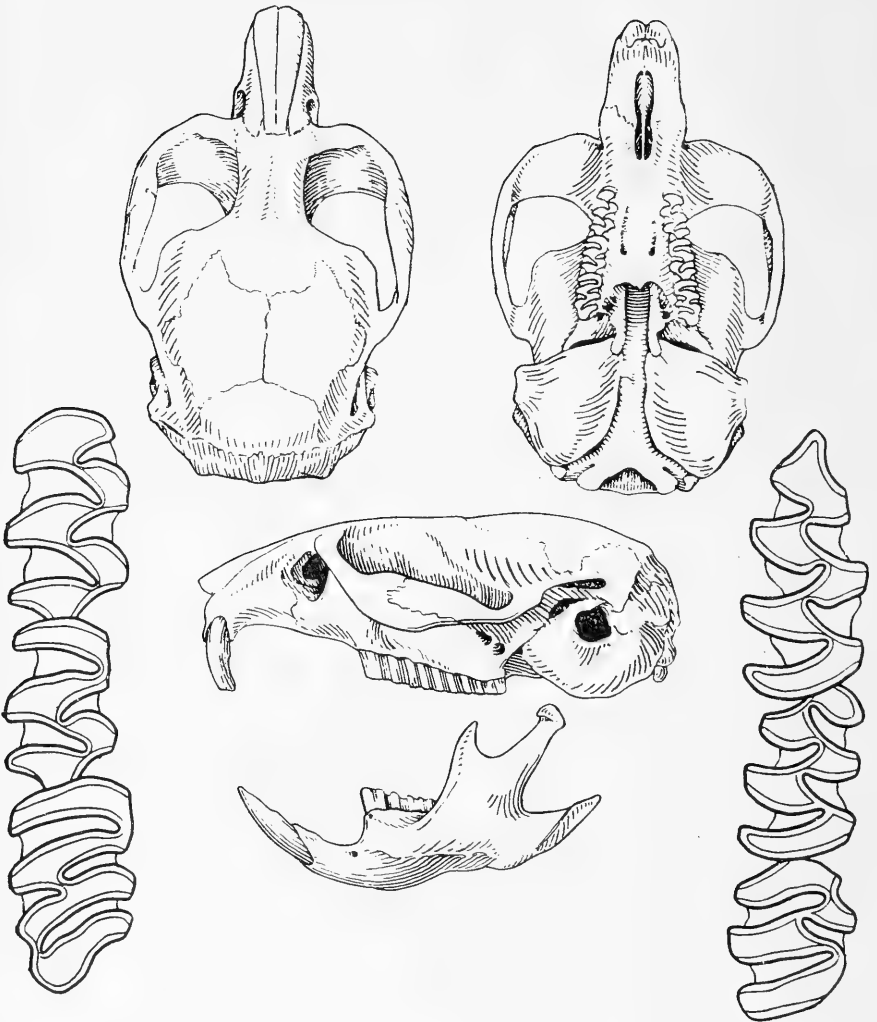
1. *Myopus schisticolor* Lilljeborg, 1884—Forest

199 Lemming (Figures 35 and 36)

Diagnosis: Body length up to 111 mm in northern Finland (n = 60; Artimo, 1969) and up to 130 mm in east European and Siberian

animals; tail up to 16 and 19.7 mm for the two latter forms respectively (average about 15% and not more than 20% body length). Length of upper molar row up to 8.3 mm, lower row up to 8.2 mm; M_1 —2.9—3.05—3.2 mm (n = 14).

In addition to the small size and skull features listed above,



198 Figure 35. Skull of forest lemming (*Myopus schisticolor* Lilljeborg).

which distinguish the forest lemming from *Lemmus*, these may be noted: less flattened dorsal surface of brain case, shorter facial section, narrower nasals, broader interorbital space, shorter M_3 , and greater curvature of upper incisors.

Composition of species: The number of extant subspecies (mainly distinguished by color) is hardly more than five: *M. s. schisticolor* Lilljeborg, 1884 (Scandinavia, Finland, European part of the USSR); *M. s. vinogradovi* Scalon and Rajevski, 1940 (northern and central Urals, northern part of Trans-Ural region); *M. s. taylori* Gl. Allen, 1914 (extreme northeastern part of range ?, Kamchatka); and *M. s. sajanicus* Hinton, 1914 (? = *morulus* Hollister, 1912) (from Podkamennaya Tunguska to Okhotsk coast, Amur district, Trans-Baikal region, Sayan ?, Altai; northwestern China and northern Mongolia). The affinity of subspecies from Sakhalin still remains uncertain (*M. s. vinogradovi* Joschimura, 1944—nomen praeocc.). One extinct form is known—*M. s. brandti* Tschersky, 1879 (Late Pleistocene, Sayans).

Distribution and zonal affinity: Same as for the genus. A rare species, especially in southern parts of the forest zone where new finds gradually enable us to determine the boundaries of distribution more precisely (Glotov, Telegin and Yudin, 1970).



199 Figure 36. Forest lemming (*Myopus schisticolor* Lilljeborg); photo by O.I. Semenov-Tyan-Shanskii.

Evolution and phylogeny: Fossil remains are known from the Late Pleistocene caves of the Sayans (Cherskii, 1879) and Primor'e (Ovodov, 1970). Data on phylogeny are given in description of genus.

200

3. Genus *Synaptomys* Baird, 1857—Marsh Lemmings

Description: Body length up to 100 mm or slightly more. Dull, grayish-brown tones dominant in color of dorsal surface, at least in posterior part of back (as in *Microtus*). Black dots or stripes not present on head or back. Color of anterior part may be more grayish than in posterior part. Color of ventral and lateral surfaces fairly light, brownish-gray. Seasonal dimorphism of pelage coloration as in *Microtus*. Tail slightly longer than foot; terminal hairs shorter than half tail length. Extent of hair cover on foot same as in *Microtus*. Pads six (two metatarsal). Claws of forelimbs, apparently, not longer than digits. Size of eyes, structure and size of pinna (latter, apparently, not smaller than in *Myopus*), as well as anatomy of lips, rhinarium, and palate have not been described.

Proportions of limbs and their components not studied.

Length of facial section of skull not more than 25% axial length. Orbit shifted more forward than in other members of Lemmini; angle formed by orbit with horizontal plane small. Upper diastema not longer than molar series. Postpalatal pits isolated by bony bridge; unlike in other members of Lemmini, basisphenoid with longitudinal groove-like depression. Auditory bullae rounded. Pterygoid pit on inner surface of angular process of mandible not isolated. Width of ventral margin of mandible at anterior angle of masseteric ridge much greater than length of M_1 , and width of base of angular process about equal to length along its dorsal margin. Angle of incisor contact moderate. Well-developed longitudinal groove on anterior surface of upper incisor shifted toward its lateral margin. Lower incisor does not extend posteriorly beyond posterior margin of alveolus of M_3 (except in one extinct species). M^3 not broader, or only slightly broader than M^2 ; its second fold (counted from front) reaches or almost reaches (in extinct forms) opposite side of tooth; third fold barely developed or absent. Folds of M_3^3 not narrower, or slightly narrower than those of other molars.

Characteristics of limb bones and their girdles not studied.

Composition of genus: Two extant subgenera—*Synaptomys* Baird, 1857 and *Mictomys* True, 1894, and two extinct subgenera—*Metaxyomys* Zaczewski, 1972 and *Pliotomys* Suchov, 1976. There is fairly unanimous acceptance of the subgeneric

classification of present-day forms among American authors, although the difference in species of these subgenera is no greater than, for example, between "good" species in the tribe Microtini.

Distribution and zonal affinity: North America, from tundra zone (except Arctic subzone) up to northern parts of range in open biomes of the Great Plains, where they are often found in bogs, including sphagnum-covered marshes. During the second half of Pleistocene glaciation, the range boundary extended to Florida and northwestern Mexico; later, when glaciation receded northward, extensions were retained along the southern boundary up to the northern parts of Washington, Kansas, Georgia and North Carolina.

Evolution and phylogeny: Fossil remains are known from Ancient to Early Peistocene: Blancan fauna of North America and Khaprovsk (*Mimomys*) faunas of western Ural (Sukhov, 1976) and northeastern Mongolia (lower reaches of Orkhon River) (Devyatkin and Zazhigin, 1974). The genus, apparently flourished during the Pleistocene. There is reason to believe that its unique forms, earlier accepted as species of *Lemmus*, were widely distributed at this time in Eurasia also. Extinction of *Synaptomys* in the Old World and reduction of its range and variability of species in the New World, are possibly related to preponderance of voles of the genus *Microtus*.

Synaptomys are the least specialized members of the tribe. Unlike the forest lemmings of the Old World coexisting with *Clethrionomys*, *Synaptomys* adapted to a life in open marshes side by side with *Microtus*. Phylogeny not clear. In the New World, marsh lemmings together with *Pliolemmus* were the first rootless forms of microtines to appear.

Subgenus *Metaxyomys* Zaczewski, 1972 (foss.)

Diagnosis: Paraconid section of M_1 typical of voles with rounded anterior unpaired loop. Lateral triangles of lower molars isolated, their apices, if truncate, only slightly so. Middle pair of triangles of M_{1-3} fused; separation of middle triangles of M^3 incomplete. Cementation present or absent in posterolateral fold of M_1 . Lower incisor does not extend beyond anterior margin of M_3 .

Composition of subgenus: Three species—*S. (M.) vetus* Wilson, 1933 (Early Pleistocene of northwestern North America); *S. (M.) landesi* Hibbard, 1954 (Early Pleistocene of central parts of North America); and *S. (M.) anzaensis* Zaczewski, 1972 (? Middle Pleistocene of California).

Age and distribution: Early to Middle Pleistocene of North America.

Taxonomic notes: Zakrzewski (1972) reported that the characters of the subgenus are intermediate between those of present-day subgenera.

Subgenus *Pliotomys* Suchov, 1977 (foss.)

Diagnosis: Paraconid section of M_1 of vole type; all triangles of lower molars isolated, and apices of their lateral angles poorly truncate. Anterolateral fold of M_1 with abundant cement deposition. Middle pair of lobes in the only known M^3 broadly fused.

Composition of subgenus and geological age: One species—*P. mimomiformis* Suchov, 1976 (Ancient Pleistocene of Ufa region in Ural area).

Taxonomic notes: The subgenus probably characterizes an independent line of development of the most western members of the genus *Synaptomys* known to date. It combines features of the extinct American subgenus *Metaxyomys* (shape of anterior unpaired loop of M_1 and fusion of middle lobes of M^3) and the present-day subgenus *Synaptomys* (separation of triangles of lower molars). The establishment of an independent subgenus based on the small sample of material available thus far is largely dictated by the wide geographic separation of the closely related finds of remains of marsh lemmings.

1. *Synaptomys (Pliotomys) mimomiformis* Suchov, 1977

Diagnosis: Size: length of M_1 —3.0–3.05–3.0 mm; M^3 —0.95 mm. Reconstructed length of lower molar row about 6.2 mm. Lateral folds cemented up to approximately two-thirds their length. Enamel poorly differentiated; absent at apices of triangles and on medial surface of anterior unpaired loop of M_1 .

202 *Taxonomic notes:* Isolated lobes on lower molars indicate that this species represents a relatively late stage in evolution.

Subgenus *Synaptomys* Baird, 1857 (Figure 37)

Diagnosis: Pelage of pinnae does not differ in color from surrounding pelage. Postpalatal pits separated by bony bridge, which is as broad as in *Microtus*. Incisors relatively broad; upper incisors without sharply expressed structure in form of tubular wearing along lingual surface and with M-shaped common cutting edge typ-

ical of *Lemmus*. Paraconid section of M_1 similar to that of *Lemmus* but with small angular anterior unpaired loop. Degree of differentiation of lateral triangles of lower molars as in preceding subgenus. Middle pair of lobes of M_1 – M_3 isolated as on M^3 . Cement present in posterolateral fold of M_1 . Lower incisor may extend beyond anterior margin of M_3 .

203 *Composition of subgenus*: One extant species—*S. (S.) cooperi* Baird, 1857. Based on small differences in size and tooth structure commencing from the Early Pleistocene, a series of extinct forms has been described. Among these, *S. (S.) rinkerii* Hibbard, 1956 is one of the first voles with rootless molars known in the New World (Hibbard, 1970b). Remains from Mongolia also belong to this subgenus.

Distribution and zonal affinity: Inhabit forest and forest-steppes in western part of range, spreading southward along marshy and deforested areas.

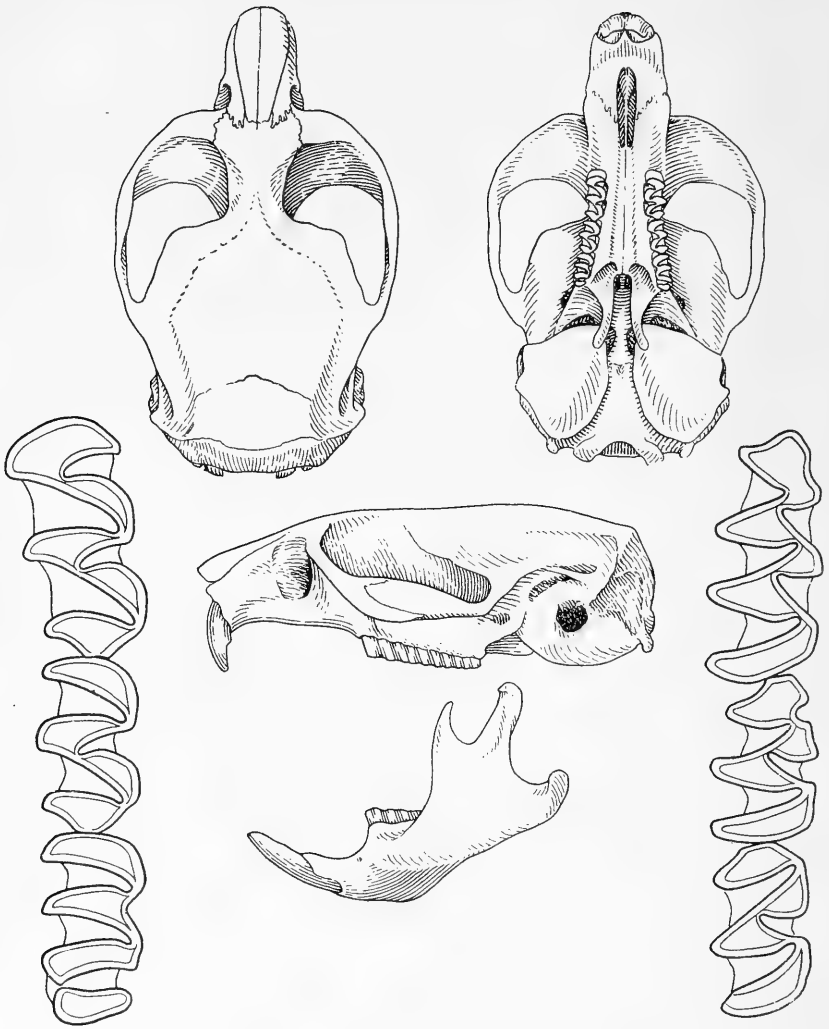
Subgenus *Mictomys* True, 1894

Diagnosis: Pelage of pinnae differs from surrounding pelage in brighter color. Postpalatal pits separated by narrow bony bridge. Incisors comparatively narrow; upper incisors with well-developed tubular wearing along lingual surface and distinct M-shaped cutting edge (as in *Lemmus*). Paraconid section of M_1 similar to species of preceding subgenus. Lower molars with smaller lateral triangles. Middle pair of lobes on M_1 – M_3 similar to those on M^3 , fused. Cement absent in lateral folds of M_1 , at least in posterolateral one. Lower incisor extends to posterior margin of M_2 in present-day members but continues beyond M_3 in extinct forms.

Composition of subgenus: One extant species—*S. (M.) borealis* Richardson, 1928; three to four extinct forms have also been described.

Distribution and zonal affinity: They are found in tundra, forest-tundra and taiga zone of North America, from Alaska to Labrador. In the west, species of the subgenus *Mictomys* form the southern boundary of the range of the genus; their area in the east covers only a narrow strip of forest-tundra in southeastern Canada and overlaps area of the subgenus *Synaptomys*. But in the Late Pleistocene (post-Wisconsin), this overlap was more significant, covering part of Pennsylvania and Virginia.

Evolution and phylogeny: Fossil remains are known from Middle Pleistocene—*S. (M.) kansasensis* Hibbard, 1958 and *S. (M.)*



202 Figure 37. Skull of the marsh lemming (*Synaptomys cooperi* Baird).

meltoni Paulson, 1961 (Kansas). Later, as in the case of the preceding subgenus, the southern part of the range underwent significant reduction. It includes more specialized forms than the subgenus *Synaptomys*.

VIII. Tribe MICROTINI Miller, 1896 (Simpson, 1945, partim!)

Diagnosis: Posterior sections of bony palate with two large, well-isolated posterior palatal pits with bony bridge between them. Bridge either rises sharply toward margin of interpterygoid groove (*Microtus* type) or, rarely, primarily in extinct forms, postpalatal pits small and bony bridge flatter, thicker, and gradually merges into margin of groove (*Pliomys*–*Phenacomys* type).

Molars rooted in extinct forms and with or without cement, but in almost all present-day species rootless and cementless. Size of lateral and medial triangles of masticatory surface of lower molars differs, rarely equal. Enamel undifferentiated in some extinct forms, but well-differentiated in other extinct forms and almost all extant members. Paraconid section of M_1 with one or two folds; in either case, fold incomplete and in latter case often on just one side. In some evolutionary lineages secondary simplification observed. Length of M^3 variable in large number of rooted forms and tooth exhibits traces of secondary simplification in anterior and posterior sections, but no difference in depth of either anterolateral folds. Alveolus of M_3 in rootless forms usually well-developed, and anterior section of tooth may be markedly shifted lingually. Lower incisor variable in length, extends to dental foramen or beyond it.

Composition of tribe: Suprageneric classification has not been determined. At present, some genera have been tentatively (and to a possible extent artificially) included under Arvicolini and Microtini (without description). Some other genera have an equal right to the same status, for example, the present-day American genus *Neofiber* True, 1884 with its ancestral genus *Proneofiber* Hibbard and Dalquest, 1973 (see p. 478).

The total number of genera is at least 18 to 20. Extinct genera: *Promimomys* Kretzoi, 1955; *Mimomys* F. Major, 1902; *Villanyia* Kretzoi, 1956; *Ischymomys* Zazhigin, 1977; *Aratomys* Zazhigin, 1977; *Ogmodontomys* Hibbard, 1941; *Cosomys* Wilson, 1932; ? *Ophiomys* Hibbard and Zakrzewski, 1967; *Proneofiber* Hibbard and Dalquest, 1973; *Allophaiomys* Kormos, 1931; *Cromeromys* Zazhigin (in litt.), 1976; extant genera: *Arvicola* Lacépède, 1799; *Microtus* Schrank, 1798; *Lasiopodomys* Lataste, 1887; *Chionomys* Miller, 1908; *Proedromys* Thomas, 1911; *Phenacomys* Merriam, 1889; and *Neofiber* True, 1884.

Description: Size: mostly small and medium. The body length is from 85 to 170 mm, only in rare cases (*Arvicola*) up to 250 mm. The length of the upper molar row is up to 6.6 mm in small and

10 mm in large forms, and of the lower row from 6.4 to 10.5 mm. The color of the dorsal surface is monochromatic, dark, grayish-brown, with varying degrees of dominance of brown or gray tones; rarely, it is sandy-yellow, sometimes much lighter (some species of subgenus *Phaiomys*). The border with the ventral surface is diffuse. Seasonal variation in the pelage is indistinct, but it is better defined in northern forms of *Microtus* and montane dwellers (*Phaiomys*). Tail is one-fifth to one-third of the trunk length; however, it may only slightly exceed length of hind foot (tarsus) (*Lasiopodomys*) or reach two-thirds trunk length (*Chionomys*). Usually, it is distinctly or poorly bichromatic, and rarely monochromatic—light (*Lasiopodomys*) or dark (*Arvicola*)—and covered with short hairs; the latter species slightly longer at tail tip but does not form a brush, at least not in individuals with summer pelage. Eyes are medium to large, and largest in *Lasiopodomys* (but not as large as in *Eolagurus*). Pinna are small, hidden in pelage (*Pitymys*, *Arvicola*) or readily visible (*Lasiopodomys*, *Blanfordimys*), to fairly large (*Chionomys*, some members of *Phaiomys*). Anititragus is large, especially in the subgenus *Microtus* and in *Chionomys*, and rarely small (*Blanfordimys*). Sometimes large tragus (*Arvicola*) or small (*Lasiopodomys*) is present. Rhinarium medium in size. Separation of both alae nasalis into right and left halves distinct, rarely weak (*Pitymys*), and also upper from lower. Further lobation in lower alae nasalis variable—from almost none in *Lasiopodomys* to well-expressed in middle and additional lobes in *Arvicola* and some members of *Microtus*. Lateral section of right and left lobes of lower alae nasalis particularly well-developed in *Arvicola*, and fuse with lateral sections of upper alae nasalis to completely closed narial pit. In most members of other genera, the outer section of the lower alae nasalis is also divided to some extent into separate lobes. However, in this case the enlarged and downcurved outer ends of the upper alae nasalis play the role of closing the narial pit. Upper labial flaps large, rectangular, often fleshy; they are either closely contiguous long midline of bony palate (*Lasiopodomys*, *Pitymys*) or only by their anterior section, ahead of the postincisorial papilla (longitudinal palatal ridge absent here). As indicated above, in the latter case closing of both flaps becomes automatic with opening of the mouth and stretching of the mucous membrane of the oral cavity, with which the flaps are fused. Lower labial processes small. Vibrissae small; upper labial and carpal vibrissae longest in *Chionomys*, *Phaiomys*, and *Pitymys*; mental vibrissae longest in

Microtus and *Arvicola*; genal vibrissae, as in most microtines, weak (thin and short) and may be absent.

Fore- as well as hind limbs relatively long *Arvicola*; only hind limbs lengthened in *Chionomys* and *Phaiomys*. Fore- and hind feet moderately long in most members; forefoot narrow in *Arvicola*, and hind foot narrow in *Chionomys* (relatively narrower only in *Myopus*). Palm and sole, except for metatarsal section, glabrous. Metatarsal more densely covered with hairs in *Lasiopodomys* and *Blanfordimys* than in other tribe members. *Arvicola* with dense lateral fringe of stiff hairs. Plantar pads well-developed (except for three posterior plantar calluses in *Lasiopodomys*); however, lateral metatarsal pad may be absent (*Arvicola* and many members of *Microtus*). Inner palmar pad may also be absent. Palmar pads largest in *Lasiopodomys*. Digits of forelimbs: III, IV, II, V, I or III \approx IV; pollex reduced, often with small blunt claw. Last digit longest in *Lasiopodomys*, but absent in some members of *Chionomys*. Digit of hind limb: besides same length ratios as on forelimb, also III, IV \approx II, V, I (*Arvicola*, *Lasiopodomys*) and IV, III, II, V, I (*Chionomys*). Claws small, except in *Lasiopodomys* and *Stenocranius*. Claw on 5th digit usually reaches half length of 4th digit or slightly longer. In some northern forms, claw elongation toward winter has been noted.

Dorsal profile of skull straight, rarely with distinct dip at bases of zygomatic arches (in *Arvicola*, *Stenocranius*), or uniformly convex (in some species of *Phaiomys*). Interorbital space usually short, narrow in middle part or throughout its length (*Lasiopodomys*, *Stenocranius*), and rarely flattened. In first case, short ridges at different stages of convergence present, from fairly wide-set with groove-like longitudinal depression between them to close-set or forming short crest. *Stenocranius* and some forms of *Arvicola* have a well-developed crest. Brain case uniformly round, dorsally flattened (*Pitymys*), or convex (*Blanfordimys* and some members of *Phaiomys*); it is angular in forms with developed crests in interorbital space and correspondingly on parietals. Shape of zygomatic arches variable; however, they are not particularly high in middle section (highest in *Chionomys*).

Orbit medium in size, slightly shifted backward, rarely large (*Arvicola*, *Lasiopodomys*). Angle formed by orbital plane with horizontal plane moderate, 40–45°. Postorbital processes small or absent. They are best developed in *Arvicola* and *Stenocranius* in which they are small rectangular processes. Masseteric [= zygomatic] plate of maxilla low and broad or moderately high and

broad. Angle of its plane to sagittal about 140° in most forms; it is smallest in *Arvicola* (125°). Auditory bullae small, rarely large (*Chionomys*, *Blanfordimys*, and *Phaiomys*) due to overgrowth of mastoids. Auditory cavity filled with large-celled bony tissue.

206 Medial junction of mandibular symphysis not well-defined. Angle of symphysis with ventral margin of dentary varies from large (symphysis small) in extinct forms with rooted and rootless molars (except for *Thyrrennicola*) and among extant members of *Pitymys* and *Stenocranius*, to comparatively small (symphysis large) in *Arvicola* and *Phaiomys*. Ascending jaw broad in those forms in which anterior margin of mandibular ramus covers molar row commencing from second prism of M_2 , and the posterior notch is small (*Arvicola*, *Allophaiomys*, *Phaiomys*); ascending jaw narrow in forms with deep notch (*Chionomys*, *Stenocranius*). Articular process short or moderately long. Tip of coronoid process reaches, almost reaches, or extends beyond (*Arvicola*) tip of articular process. Apex of angular process slightly, rarely appreciably (*Chionomys*) extends beyond posterior margin of articular process. Mental foramen almost removed from anterior angle of masseteric ridge, and more highly shifted dorsally in *Arvicola* than in other genera.

Upper tooth row posteriorly not wide-set, except in *Pitymys* (relatively wider-set) and in *Stenocranius* (relatively close-set). In latter case, posterior divergence of teeth greater and posterior section of M^3 more laterad. Molars rooted only in extinct forms of *Villanyia*, *Mimomys*, *Ogmodontomys*, and others. Crown in rooted forms low or moderately high; in rootless forms, lowest in *Pitymys* and highest in *Arvicola*. Molar sections of M^1 from small alveolar bulges inside orbit in *Arvicola* and *Pitymys* (also noted in young individuals of some late forms of *Mimomys*), and only M^2 in some forms of *Microtus*. Alveolar bulges absent or barely perceptible in *Lasiopodomys*, *Chionomys*, and some members of *Stenocranius* and *Microtus*.

Molar sections of M_1 — M_2 do not form bulges along lower crest of masseteric ridge or such barely perceptible (in any case in M_1) in *Pitymys*, *Chionomys*, and some members of *Microtus*; in all other cases such bulges are present. Difference in size of lateral and medial triangles of occlusal surface of lower molars very distinct in some late cemented forms of *Mimomys*, extinct *Microtus*, and extant members of *Chionomys*. There is no difference in this respect in upper molars. Enamel either uniformly thick throughout lateral surface of molars (Pliocene and pre-Pliocene genera as well as

Early Anthropogene *Villanyia* and *Mimomys*), or in most extinct and almost all extant members of tribe, thinner on anterior margin of anterior unpaired loop of M_1 , apices of denticles of folds and on one of the walls of the triangles. Dentine areas often found on lateral surface of tooth at places of enamel thinning; other conditions remaining the same, the higher the crown the higher the dentine tracts and the more complex the profile of the lower enamel margin. The highest extension of these dentine tracts occurs in the anterior part of the paraconid of M_1 , and along the ridges of the prisms. Differentiated enamel on the masticatory surface of molars produced two types of structure (see above p. 33): (a) the primary, typical of more ancient members of the tribe, in which the posterior margin of the triangles is thicker than the anterior margin on the lower molars (vice versa on the upper molars); and (b) the secondary type, observed in geologically younger forms, in which the pattern is reversed. In the process of transition to rootless molars in the genera *Arvicola* and *Allophaiomys*, the type of enamel differentiation changes from primary to secondary, passing through some transitional stage wherein enamelization is again almost identical on both sides of the triangles.

M_1 is moderately long, being shortest in *Lasiopodomys* and longest in *Blanfordimys*, where it constitutes slightly more than half length of molar row. From 1.0 to 1.5 triangles occur at base of paraconid in M_1 . In the simplest case, these triangles are incompletely isolated from the anterior unpaired loop and broadly fused with each other. One pair is present when the lobe ahead of the paraconid part is completely isolated from it, and another pair at different stages of formation at the base of the unpaired loop. Lobes of the second pair of triangles may differ in size on the right and left sides of the tooth, or be completely absent on one or the other side. It should be kept in mind that, within the limits of the tribe such morphological features were brought about by different ways. Thus, in one phyletic line, an apparently simple tooth has appeared partly as a result of secondary simplification of an initially more complex tooth in ancestral forms, as already described (p. 33). In another case, the initially and primarily simple tooth underwent continuous complexity, as in the case of the *Arvicola* and *Allophaiomys* lines. Accordingly, a true outer "island" and prismatic fold formed in the first of these lines of evolution of the paraconid section, which may disappear in different species during ontogeny or phylogeny. In the second lines, a false "island" (prismatic fold) may appear at the same place, which happens more often in more ancient and extinct

forms than in extant ones, giving the tooth an atavistic appearance (Figure 6).

M^3 is moderately long; among members of the tribe it is shortest in *Arvicola* and longest in *Microtus* s. str. An "island" occurs in its posterior section and sometimes also in the anterior section in many rooted forms. The posterior "island," which disappears with age, is also, but rarely, observed in the posterior section of M^1 and M^2 . In some phyletic lines of rooted forms, as well as in young individuals of some species without roots (often up to the commencement of grinding of teeth or in its initial stages), false "islands" may appear (also see p. 34). The molar has three to four lateral denticles and from two (sometimes incomplete in some members of *Arvicola*) to four medial denticles. The heel of M^3 is often reduced.

The crowns of the lower incisors are moderately long or long, especially in the genus *Microtus*; in the upper incisors, the crowns are long, especially in *Ondatra*. The curvature of the upper incisors is moderate, rarely sharp (*Stenocranium*) or weak (*Lasiopodomys* and some members of *Phaiomys*). The lower incisors are moderately or smoothly concave (*Stenocranium*, *Lasiopodomys*). The cutting edge is very small (prognathic incisors) in *Blanfordimys*, some members of *Phaiomys*, and *Arvicola*, to moderate in most forms. The upper incisors are relatively broad; in *Arvicola* and *Lasiopodomys*, the corresponding values are within the limits of their maximum values in microtines. Their anterior surface is flattened or slightly angular, and the angle formed with the lateral surface slightly rounded. A weak groove-like depression is sometimes present on the anterior surface; it may be more distinct in early members (strongest in *Ogmodontomys*). In profile, the combined cutting edge of the upper molars is slightly or distinctly M-shaped (*Pitymys* and many members of *Microtus* s. str.); in the latter case the posterior surface is deeply pitted. The lower incisor terminates below the dental foramen only in some *Chionomys*, in most forms not below its upper margin, while in many others its extension is much greater (especially in ancient forms with rooted molars as well as in *Arvicola*). In this case, its posterior end may form an alveolar knob not only on the lateral surface of the articular process, but many also protrude beyond its posterior margin (*Lasiopodomys*, *Phaiomys*, *Allophaiomys*, some members of *Microtus*). The incisor in rooted forms passes under the margin of M_2 (different stages of transition from the ridges of the incisor are observed), between the molar sections of M_2 and M_3 , and rarely under the molar section of M_3 or even between its roots

(*Aratomys*). The alveolus of M_3 is usually well-developed (but less so in most *Pitymys*); in some members (*Stenocranius*) it extends downward beyond the lower margin of the angular notch; the tooth *per se* is often shifted lingually by its anterior section relative to the longitudinal axis of the molar row.

Postcranial skeletal features are not known for extinct species. In present-day species, significant differences have been noted for earlier members; in comparing such extreme types of adaptation as *Microtus*, *Arvicola*, and *Chionomys*, only a few characters, mainly in structure of forelimb bones and shoulder, can be termed common. These are the comparatively short scapula, relatively short humerus, with a more rounded head than in members of other taxonomic groups of the subfamily, and relatively long forearm with narrow (low) ulna in its middle section, and other such features.

Distribution and zonal affinity: Being the central (main) tribe of the subfamily, and most abundant in composition and diversity of adaptations, Microtini includes zonal forms from all environments—from the tundra to the subnival zone. However, since the forest-steppe *per se* became extinct before the advent of the Recent epoch, forms inhabiting the forest zone living among its open biotopes—marshes of different types, floodplains, and upland meadows (except some species of *Pitymys*). At the same time, in the Plio-Pleistocene, judging from the composition of associate fauna, forest forms were present among Microtini, particularly of the genera *Villanyia* and *Promimomys*. The boundaries of distribution of the tribe coincide with those of the subfamily (Figure 2) except for some areas of its northern border where Microtini do not penetrate as far north as Lemmini and Dicrostonyxini.

Evolution and phylogeny: Fossil remains are known in both hemispheres, at least from the Middle Pliocene. In the Old World, they have been found still earlier in the east, in the Late Miocene to Early Pliocene faunas (*Ischymomys*); in the New World (*Ogmodontomys*), they possibly occurred from the end of the Middle Pliocene. Actual finds point to the probable origin of both types from some unknown vole-toothed hamsters. The presence of baranomiid (more precisely, hesperomiid) characters in many extinct migrants of the Old and New World, and also in some extant members (for example, in Lemmini), offers good indirect evidence in support of such an origin.

Based on material collected to date, separation of the subtribe Microtini can be dated to the Mio-Pliocene boundary. In Eurasia, this subtribe was associated with the large species of the genus

Promimomys, and through *Mimomys* s. str., or through the subgenus *Microtomys* continued to the rootless *Allophaiomys*, and further to *Microtus*. The subtribe Arvicolini is associated with another group of *Mimomys* voles, the so-called *intermedius* group; recently, Zazhigin (1975) proposed that they be considered members of a special genus, *Cromeromys*. Inclusion of *Villanyia* in the evolution of the present-day genera of the tribe is not so clear. At the same time, for some of its species the ancestral status relative to the tribe Lagurini is absolutely clear and, as mentioned above (p. 242) *Villanyia* probably should be excluded from the tribe Microtini. Ancestral forms of the genus *Microtus* probably evolved in the Eurasian continent; during the course of evolution, some members migrated to America where they gave rise to distinct vicarious species. Possibly, differentiation at the generic level was achieved in the New World by the two southernmost high-montane subgenera of *Microtus*—*Orthriomys* and *Herpetomys*—and by *Chilotus*, which differ markedly from other members in number of diploid chromosomes (Matthey, 1957).

KEY TO GENERA, SUBGENERA, AND SPECIES OF TRIBE MICROTINI

- 1 (2). Body length more than 150 mm. Pinna with antihelix. Masticatory surface of M_1 with only one lateral triangle Genus *Arvicola* Lacépède (p. 341).
One species, *A. terrestris* L.
- 209 2 (1). Body length less than 150 mm. Pinna without antihelix. Masticatory surface of M_1 with at least two lateral triangles.
- 3 (4). Pinna length almost equal to half head length. Longest vibrissae extend far beyond posterior margin of head Genus *Chionomys* Miller (p. 466).
- 4 (3). Pinna length significantly less than head length. Longest vibrissae do not reach or barely extend to posterior margin of head.
- 5 (6). Claw of middle digit of forelimb about two-thirds digital length. Tail length about one-fifth trunk length. M^3 with three denticles on medial side. Auditory bullae do not protrude downward beyond molar row Genus *Lasiopodomys* Lataste (p. 400).
- 6 (5). Claw of middle digit of forelimb much less than two-thirds digital length. M^3 with more than three denticles on medial

side; if with three, then either tail length greater than one-fifth trunk length, or auditory bullae protrude downward beyond molar row

Genus *Microtus* Schrank (p. 358).

- 7 (10). Masticatory surface of M_1 ahead of the posterior unpaired loop and pair of triangles, with pair of opposite fused lobes isolated from anterior section of tooth.
- 8 (9). Tail uniformly light-colored, about one-fourth trunk length. Auditory bullae enlarged; mastoid section protrudes beyond occipital condyle, and lower section beyond molar row Subgenus *Blanfordimys* Argyropulo (p. 408).
One species, *M. (B.) afghanus* Thomas.
- 9 (8). Tail dark, or bichromatic—light on ventral side and dark on dorsal; length more than one-fourth trunk length. Auditory bullae not enlarged, do not protrude either beyond occipital condyle or beyond molar row
- Subgenus *Pitymys* McMurtrie (p. 372).
- 10 (7). Masticatory surface of M_1 in front of the three posterior mutually isolated triangles, if with pair of fused lobes, then also fused with anterior section of tooth (usually only by medial lobe).
- 11 (12). Condylbasal length of skull almost 10 times its least interorbital width and 2.5 times its width above external auditory meatus
- Subgenus *Stenocranius* Kastschenko (p. 394).
One species, *M. (S.) gregalis* Pallas.
- 12 (11). Condylbasal length of skull less than 10 times its least interorbital width and less than 2.5 times its width above external auditory meatus.
- 13 (14). Large digit of forelimb with well-developed, acute claw ..
..... Subgenus *Neodon* Hodgson (p. 363).
- 14 (13). Large digit of forelimb with short, obtuse claw.
- 15 (16). Brain case and interorbital space broad, flattened. Auditory bullae highly enlarged, protrude downward markedly beyond molar row and posteriorly beyond occipital condyle
- Subgenus *Sumeriomys* Argyropulo (p. 403).
One species, *M. (S.) socialis* Pallas.
- 210 16 (15). Brain case and interorbital space comparatively narrow, uniformly convex. Auditory bullae not enlarged and only in rare cases slightly extend beyond molar row and occipital, sometimes not reaching occipital condyle
- Subgenus *Microtus* Schrank (p. 358).

1. Genus *Ischymomys* Zazhigin, gen. nov. (foss.)

Diagnosis: Voles with cementless molars. Length of M_1 —2.8—3.25 mm, M^1 with three roots and M^2 — M^3 with four. Posterior “island” may be present on all upper molars, rapidly disappears on anterior molars, but always present on M^3 . Anterior “island” absent on M^3 . Paraconid section of M_1 with an “island” that forms during closure of first medial fold and disappears before roots reach half crown height. True prismatic fold absent; false (juvenile) fold often observed instead. Enamel equally thick throughout periphery of tooth. Position of roots of posterior lower molars relative to incisor not known.

Composition of genus: Only one species is known: *I. quadriradicatus* Zazhigin sp. nov.

Age and distribution: Late Miocene—Early Pliocene of Middle Ishim.

Taxonomic notes: The most ancient among the known microtines belongs to this genus; discovery of its remains compels us to consider the time of origin of voles as Early Miocene in Asia. It may be noted that in spite of the comparatively well-studied fauna of rodents from the European Miocene, to date remains of microtines have not been found there. In *Ischymomys*, together with features reflecting unique molar specialization, there are also several archaic features, viz., full number of roots on posterior upper molars, as seen in hamsters, and undivided posterior lobe of M^1 (similar to *Microscoptini*). Other archaic characters are also found together with advanced traits, viz., tendency for full separation from anterior unpaired loop of first pair of triangles at base of paraconid section; presence of two medial folds on M^3 . Together with *Promimomys*, this genus should be placed near the base of the line giving rise to ancient Pliomyini on the one hand, and Microtini with cementless molars on the other, thus becoming the ancestral form for *Mimiomys*—*Villanyia* of the Old World and *Ogmodontomys*—*Cosomys* of the New World.

1. *Ischymomys quadriradicatus* Zazhigin sp. nov.

Holotype: Right M_1 of adult with roots slightly more than half crown height. No. 952/51 in collection of Geological Institute, Academy of Sciences, USSR; collectors, I.G. Zal'tsman and V.A. Martynov.

In addition to this tooth, there are more than 60 isolated molars in the collection of the Geological Institute, Academy of Sciences, USSR.

Dimensions: Holotype: length of M_1 —3.0 mm. Paratypes: length of M_1 —2.8–3.0–3.25 mm (n = 10), M_2 —1.8–2.05–2.15 mm (n = 8), M_3 —1.85–2.2–2.55 mm (n = 9), M^1 —2.1–2.4–2.6 mm (n = 10), M^2 —2.0–2.2–2.3 mm (n = 4), M^3 —1.25–1.4–1.5 mm (n = 5).

Description: Roots commence growth very early and are completely formed (one-fifth to one-fourth crown height) by beginning of wear of occlusal surface of molars. Anterior roots of M^2 – M^3 usually fused in upper part; completely free in only 2 of 12 M^2 , and one of 5 M^3 . Triangles at base of paraconid section opposite and at later stages of wear may be isolated from anterior unpaired loop.

211 On the teeth of young individuals a longitudinally elongate “island” is formed from the constriction of the medial part of the anteromedial fold, and forms a backward-directed bend before its isolation. Anterior unpaired loop with long-persisting juvenile folds, posterolateral parts of which may form false prismatic fold. Major anterior triangles of M_1 are fused in animals of all ages. Unlike other microtines, M_2 and M_3 are similar not only in shape, but also in size, length, and width. Their middle lobes are almost completely formed while the anterior ones are less so. Anterolateral fold of M_3 only slightly smaller than next fold.

In M^1 posterior lobe does not divide to form two triangles; three pairs of rhomboidal lobes present on its masticatory surface, as in *Microscoptini*. Middle pair of rhomboidal lobes on all upper molars fused but isolated from anterior and posterior pairs; however, unlike members of *Microscoptini*, they are slightly shifted in relation to each other. Two opposite triangles lie beyond anterior unpaired loop of M^3 , which are separated from rounded heel by fold of about equal depth. Posterior “island” of this tooth formed through simultaneous fusion of heel with both margins of tooth.

The associated mammal fauna form a mastodont faunal complex of early hypparionid faunas typical of savanna-like biomes of the Mio-Pliocene.

Age and distribution: Ishim strata, in which these forms were preserved, often of the Late Miocene (Ermak formations, according to division recently proposed by Biryukov *et al.*, 1968). The site is situated on the right bank of Ishim River, in the environs of Petropavlovsk. Teeth were collected by washing sandy layers in green clay. Remains clearly redeposited (possibly several times) from a few more ancient layers. Dentine and enamel of teeth with almost similar light-colored tone.

2. Genus *Aratomys* Zazhigin, gen. nov. (foss.)

Diagnosis: Voles with rooted cementless molars. Length of M_1 —2.5–3.2 mm. M^1 – M^3 with three roots which, at least on two posterior molars, are separated throughout their length only rarely. M^3 always with early formed posterior “island” but no anterior one. Paraconid section of M_1 with “island” within anterior unpaired loop, which is not formed through closure of any folds; “island” disappears when roots reach half crown height. True prismatic fold absent; often replaced by false (juvenile) fold. Enamel layer equally thick throughout periphery of tooth. Lower incisor passes under anterior root of M_3 , whose posterior root remains on its labial side.

Composition of genus: Only a single species known—*A. multifidus* Zazhigin sp. nov.

Age and distribution: Middle Pliocene of western Mongolia.

Taxonomic notes: *Aratomys* displays several characters common to the North American Pliocene *Ogmodontomys*, such as nature of “island” on M_1 , position of roots of lower molar teeth relative to incisor, and so on. At the same time, it is also close to *Ischymomys* through characters such as early commencement of root formation, long retention of juvenile fold on margin of anterior unpaired loop of M_1 , absence of true prismatic fold, incomplete division of posterior lobe of M^1 into two triangles, and so forth. Further study of the Pliocene microtine fauna of Central Asia will enable us to better determine the phylogeny of *Aratomys*.

1. *Aratomys multifidus* Zazhigin sp. nov.

Holotype: Right half of mandible of adult with complete set of molars in middle stage of wear, with articular process intact. No. 957/81 in collection of Geological Institute, Academy of Sciences, USSR; collector, V.Z. Zazhigin, 1967. Isolated teeth have also been recovered.

Dimensions: Holotype: length of M_1 – M_3 —7.0 mm; M_1 —3.0 mm, M_2 —2.05 mm, M_3 —1.85 mm. Paratypes: M^1 —2.4–2.63–2.85 mm, M^2 —1.95–2.13–2.3 mm, M^3 —1.55–1.79–2.1 mm.

Description: As in *Ischymomys*, roots commence growth early and by beginning of wear of occlusal surface of M_1 , are one-fifth crown height. Anterior roots of M^2 – M^3 often used in upper part. Triangles at base of paraconid section opposite, poorly isolated from anterior unpaired loop, and in middle-late stages of wear completely fused with it. “Island” present on anterior unpaired loop but for relatively shorter period; disappears when roots attain half

crown height. Lateral margin of anterior unpaired loop with long-persisting juvenile folds, posterior one replacing true prismatic fold found in *Promimomys* and *Mimomys*; during wear, false prismatic fold somewhat displaced forward. Posterior pair of triangles of M_1 and middle ones of M_2 – M_3 fused in animals of all ages. Anterior lobe of M_3 simple in structure, i.e., either barely divided or division rapidly disappears with age. Anterolateral fold of M_3 much smaller than next one.

Posterior lobe of M^1 incompletely divided into two. Anterior pair of lobes of this tooth and middle ones of M^2 almost completely isolated. Behind anterior unpaired loop of M^3 , as in *Promimomys*, one lateral triangle isolated from the first pair and slightly fused with heel. Posterior "island", as in *Ischymomys*, formed through simultaneous fusion of heel with both margins of tooth.

Age and distribution: Western Mongolia, Chono-Khariakh demarcated area, beds of transitional Middle to Late Pliocene age. Material was collected during scanning of contents of sandy-pebbled clay lenses embedded in a thick argillaceous stratum. Judging from state of preservation of remains, redeposition was insignificant. Teeth and bony matter have retained close to natural color.

Paleo-ecological data: Associate fauna not extensive. Contained hares (two species of *Ochotona*, *Alilepus*) and from rodents, small primitive mice of *Parapodemus* sp. (?). Probably biomes of not very dry Mio-Pliocene savanna.

3. Genus *Ogmodontomys* Hibbard, 1941 (foss.)

Diagnosis: Similar to the genus *Aratomys*, but differs in: (1) early disappearance of "island" in paraconid section of M_1 and, possibly, different manner of its formation (similar to *Ischymomys* ?); (2) larger size of both known species (length of M_1 —3.0—3.3—3.5 mm); and (3) complex structure of M^3 : two triangles, lateral and medial, present behind anterior unpaired loop; and posterior "island" absent; if "island" present, differs in initial stages of wear. Anterior surface of upper incisors with longitudinal groove-like depression.

Composition of genus: Two species—*O. poaphagus* Hibbard, 1941 (type species) and *O. sawrockensis* Hibbard, 1957.

213 *Age and distribution:* The age by which roots have formed is not indicated (Hibbard, 1941); they are probably isolated on upper molars for most of their length. Triangles at base of paraconid section of M_1 are shifted relative to each other and broadly fused with

anterior unpaired loop. The lateral one fuses with it in later stages of wear, then completely disappears. Time of appearance and disappearance of "island" in *O. sawrockensis* not known; probably, formed by closure of medial fold, as in *Ischymomys*.

Lateral margin of anterior unpaired loop has many juvenile folds. That fold in some individuals is located at place of true prismatic fold of some European genera, but disappears sometimes during middle stage of wear; it is not clear whether this fold is displaced forward during wear. Posterior pair of basal triangles on M_1 and middle pair on M_2 – M_3 fused in animals of all ages (*O. paophagus*) or not fused (*O. sawrockensis*). Anterior lobes of M_2 – M_3 with slightly demarcated lateral and medial triangles, but this separation rapidly disappears with age. Anterolateral fold of M_3 notably smaller than next one.

Posterior lobe of M^1 with incompletely separated lateral and medial triangles. Anterior pair of lobes of this tooth and middle ones of M^2 almost completely divided. Medial lobe of M^3 fused with rounded heel, on which small third triangle may be distinguished on lateral side.

Taxonomic notes: *Ogmodontomys* is probably a Pliocene endemic of North America. It is either closely related to the more primitive Mongolian *Aratomys*, or represents an example of a similar level of development of a unique branch of microtines. The question may be answered by more detailed scrutiny of the structure of the paraconid section of M_1 , viz., aspects of formation of "island" and prismatic fold. At present, it is indicated that the major difference between the two genera pertains to structural features of M^3 : in *Ogmodontomys*—absence, at least in larger percent of adult individuals of "island," and presence of an "extra" triangle on occlusal surface. We may note that Zakrzewski (1967), who revised the genus *Ogmodontomys*, found a posterior "island" on only one of 75 posterior upper molars of *O. paophagus*. The author proposed that *Ogmodontomys* possibly has European ancestors which evolved here later into *Cheria* (*Promimomys* according to my scheme). If the former of these assumptions has now found some paleontological support, this is not yet true for the latter. A large time gap exists between *Villanyia* and *Promimomys* on the one hand, and *Aratomys*–*Ogmodontomys* on the other. American paleontologists derived the genus *Cosomys* directly from *Ogmodontomys*.

4. Genus *Cosomys* Wilson, 1932 (foss.)

Diagnosis: Voles with rooted cementless (sparsely cemented ?) molars. Length of M_1 —3.0—3.3 mm. M^1 — M^2 with three roots, and M^3 usually with two. M^3 with neither anterior nor posterior “island”. Paraconid section of M_1 in some individuals with an “island” that disappears in early stages of wear (probably, at commencement of root initiation); “island” formed through closure of anterolateral (medial ?) fold. Apparently, true prismatic fold absent and juvenile fold replaces it in some individuals. Enamel layer on lower molars thinner at bottom of folds and, possibly, on anterior walls of triangles; enamelization of upper molars not known. Position of roots of posterior lower molars relative to alveolus of incisor not indicated.

214 *Composition of genus:* One species is known—*C. primus* Wilson, 1932. Possibly, “*Mimomys*” *monahani* Martin, 1972, from the *Microtus* fauna of Nebraska will also be included under this genus. The remains from Saw Rock Canyon in Kansas included under the former species by Hibbard (1949), possibly belong to *Ogmodontomys* (*O. sawrockensis* ?).

Description: Time of root initiation and details of their structure not indicated in description. Triangles at base of paraconid sections of M_1 slightly shifted in relation to each other and broadly fused with anterior unpaired loop; lateral triangle fuses rapidly and completely with it during wear. Juvenile folds on margin of anterior unpaired loop few in number and shallow. False prismatic fold shallow, short, and disappears earlier than “island” during wear; it is not displaced forward during wear. Posterior pair of triangles of M_1 and middle ones of M_2 only slightly fused, and that, too, not in all individuals. Anterior lobe of M_2 consists of two more or less isolated triangles. Similar structures not found on M_3 , where anterolateral fold much smaller than next one.

Posterior lobe of M^1 completely divided into lateral and medial triangles. Anterior pair of lobes of this tooth and the middle ones of M^2 almost completely divided. Behind anterior unpaired loop of M^3 , two distinct triangles present, one lateral and one medial, fused with loop as well as with each other. Smaller triangular denticle may also be separated on medial margin of heel.

Age and distribution: End of Pliocene; central region of North America, from northern California in the west.

Taxonomic notes: Earlier ideas about the identity of *Cosomys* and *Mimomys* or the subgeneric status of the former (Wilson, 1932;

Kretzoi, 1955b; Hibbard, 1959) are not shared now by most researchers, including the latter author himself, who studied the collection of European voles with rooted molars. The idea of a single line of evolution of the American microtines with rooted molars of the Plio-Pleistocene in the *Ogmodontomys*-*Cosomys*-*Ophiomys* series is not well-accepted at present. The material has not been sufficiently analyzed by our American colleagues and it is difficult to formulate an unequivocal opinion based on existing reports in literature. The following features in particular require elucidation: position of the alveolar parts of the incisor relative to the roots of M_2 and M_3 , nature of formation of the "island" on the anterior section of M_1 , and presence or absence of cement.

Judging from the brief description and diagrams, it cannot be ruled out that the Chinese (Shansi, Pinglu, Ancient ? Pleistocene) *M. orientalis* Young, 1935 belongs to this genus. In any case, the structural features of the paraconid section of M_1 precludes the possibility of this species belonging to *Mimomys* from the *intermedius* group, as was thought by the author of the species, or to the *Promimomys* group in our interpretation (another possibility is that *M. orientalis* belongs to the *pliocaenicus* group).

5. Genus *Villanyia* Kretzoi, 1956 (foss.)

Diagnosis: Voles with rooted cementless molars. Length of M_1 —2.1, 2.9 mm. M^1 - M^2 with three roots. Anterior "island" present on M^3 only in more ancient forms; posterior "island" forms early and often disappears early. Paraconid section of M_1 , without "island", but with low false prismatic fold displaced forward. Latter not observed in all species, and in those in which it is present, not always in all individuals. Depending on ancient nature of forms, enamel varies from equally thick throughout periphery of tooth to variations thereof. Posterior root of M_2 in ancient forms "sits" on incisor, at least on its lingual margin; in later forms, located on labial side of incisor. Anterior root of M_3 usually located on lingual side of incisor and only posterior root, situated in bony alveolus, on its lingual side.

Composition of genus: Recently, V.S. Zazhigin (in litt.) stressed the separation of the subgenus *Kulundomys*, under which in addition to *V. fejevaryi* Kormos, he also included his recently described species *V. betekensis* and *V. prolaguroides*, thus combining these Villanyian species with the most archaic characters. Furthermore, the new material collected by the author in Mongolia has enabled

him to propose that the less-known species, *V. chinensis* Korm., is also a member of a unique line of evolution of the subgeneric status. Incidentally, it is hardly possible to reliably identify some remains from the description and diagram of teeth given by Kormos (1934a) for his species. It is essential to reexamine the original material.

More than 10 species have been described (some merely named), of which some are hardly more than subspecies of a few sparsely distributed forms: *V. exilis* Kretzoi, 1956 (type species); *V. praehungarica* Schevtschenko, 1965 (? = *V. petenyii* Mehely, 1914); *V. fejervaryi* Kormos, 1934 (? = *lagurodontoides* Schevtschenko, 1965); *V. hungarica* Kormos, 1938; *V. eleonorae* Erbajeva, 1975; *V. laguriformes* Erbajeva, 1973; *V. gromovi* Erbajeva, 1976; *V. arankoides* Alexandrova, 1976; *V. steklovi* Zazhigin (in litt.); *V. betekensis* Zazhigin (in litt.); *V. chinensis* Kormos, 1934; *V. sokolovi* Schevtschenko, 1968; *V. prolaguroides* Zazhigin (in litt.); and *V. heshuicus* Zheng, 1976.

Description: Roots (except in ancient species) formed relatively late: M_1 simultaneous with commencement of wear of occlusal surface, but in geologically younger forms much later (transition to rootless). Tendency for reduction of roots in the same direction well-expressed. Triangles at base of paraconid section of M_2 distinctly shifted in relation to each other, especially in later forms, and apex of third (counting from back) medial fold lies above opposite one. Fusion of triangles with anterior unpaired loop complete. Juvenile folds on anterior margin of latter small, short, and disappear rapidly during wear. Prismatic fold commences as an independent one, unrelated to juvenile fold or (in young individuals) associated with relict juvenile folds; its ridge either does not reach occlusal surface or is greatly lowered on lateral side, due to which folds barely perceptible at early stages of wear of masticatory surface. During process of wear, prismatic fold may be markedly displaced forward due to similar slope of formed ridge. Groove bordering fold anteriorly may also be formed simultaneously, in which case fold becomes a triangular projection on posterolateral margin of anterior unpaired loop ("Lagurodon"-type structure). Basal triangles of M_1 isolated; if insignificant fusion present, mostly occurs between posterior pair or middle pair. Anterior section of M_2 - M_3 usually well-differentiated into two triangles, although partially fused; even middle pair of triangles on these teeth partly, rarely completely, fused. Anterolateral fold of M_3 not smaller than next one.

Posterior lobe of M^1 completely divided into two triangles and thus with five triangles on its masticatory surface. Partial fusion of

lobes may be observed in M^2 . One lateral triangle present behind anterior unpaired loop of M^3 , broadly fused with it, but usually isolated from posterior section of tooth; primordium of second lobe, if present, in form of small denticle. Anterolateral fold always smaller than next one (“*Pliomys*-type structure”). Heal of this tooth laterally with anteromedial triangle, that is variably differentiated but never completely isolated. Heel, during course of formation of posterior “island,” merges with posterior section of tooth simultaneously from both sides. “Island” disappears in many forms before teeth are functional, and not later than root length equal to one-third crown height.

Age and distribution: From commencement of Ancient Pleistocene to commencement of Early Pleistocene (Ancient Tamansk faunas) from southwestern Europe to Trans-Baikal region, Tadzhikistan, Mongolia, and northern China.

Taxonomic notes: The genus was separated by Kretzoi on the basis of two M_1 belonging to the smallest of its species, *V. exilis*. The author, however, with no justification indicated its proximity to *Prometheomys*. These two M_1 lack a prismatic fold and were the dimensions not small, could readily be identified as extreme variants of one of the five other cementless species found in the same area. Four years later, Kowalski (1960a) described this species in detail from larger material recovered in southern Poland, and considered *Villanyia* a subgenus of *Mimomys*. Five years later Topachevskii (1965) restored the generic status of *Villaynia*, combining in it two subgenera—*Villanyia* proper and *Cheria* (*Promimomys* in our scheme)—and placed it in contrast to the genus *Mimomys*. These were my views as also those of A.F. Skorik later on (Skorik, 1972; Topachevskii and Skorik, 1975). These authors attach great importance to the absence of cement in the folds of the molars. Most probably, for this group, as also many of the more archaic genera of voles with rooted molars, this character can still be considered significant. Incidentally, even here the possibility is not excluded that somewhere in the terminal branches we shall find if not cemented, at least sparsely cemented forms.

In either case, the general direction of morphotypic evolution of the molars of *Villanyia* is sufficiently distinct, and coincides in many ways with that of other rooted molar forms. Significant characters include: increase in height of crown and associated with it, the later initiation of roots and increase in height of dentine tracts; reduction and forward displacement of false prismatic fold simultaneous with its poor isolation from the anterior unpaired loop;

tendency toward elongation of the latter; reduction in anterior "island" on M^3 ; change in position of posterior root of M_2 in relation to the incisor; and several others.

A unique feature of *Villanyia* is the nature of formation of the prismatic fold in most species. This character distinguishes *Villanyia* from *Mimomys*, where the juvenile fold appears to persist for a long time, and also from *Promimomys*, where the ridge forming this fold is the result of longitudinal separation of the edge of the anterolateral prism. Moreover, unlike members of other genera of the tribe, *Villanyia* exhibit secondary simplification of the anterolateral section of M^3 (structure known only for some species), combines with a primarily simple paraconid structure in M_1 , which is probably more typical of genera of the tribe Clethrionomyini. But none of this provides a basis yet for including *Villanyia* in the taxonomy of microtines in accordance with the strict requirements of "vertical classification." In any case, it is beyond doubt that the offsprings of some *Villanyia* with rootless molars gave rise to lagurids in a wider sense (including even *Alticola*). We lack justification for accepting their participation in the formation of present-day *Microtus* and species close to this genus.

1. *Villanyia praeungarica* Schevtschenko, 1965

(? = *M. petenyii* Mehely, 1914)

Diagnosis: Size relatively large. M_1 —2.8–1.1 mm (holotype, southern Ukraine), 2.55–2.9 mm (n = 5, paratypes), M^3 —1.6, 217 1.7 mm. Maximum width of paraconid section of M_1 equal to or slightly less than its medial length. Prismatic fold present on M_1 in most individuals; it is long, distinctly isolated from anterior unpaired loop, and exhibits no tendency for notable forward displacement during wear. Enamel varies from undifferentiated in more ancient members of the species to completely differentiated in later forms (in depth of folds and on walls of prisms). Major triangle of masticatory surface of M_1 , if fused, are not more than twice thickness of enamel (in later forms). Middle pair on M_3 opposite, rarely fused only partially, as on M_2 . M^3 with three isolated fields and comparatively long-persisting posterior "island".

Composition of species: Subspecies are not recognized, although geographic as well as chronocline variability is sufficiently manifested.

Description: Many other features of the tooth and skull structure not known or not described. Earlier fossil remains from Ancient Anthropogene of southwestern Ukraine (Kotlovina) are

possibly somewhat smaller (M_1 —2.3—2.5—2.9 mm; $n = 17$), with still undifferentiated enamel. However, from one fragment of a mandibular ramus of an adult animal it is clear that the posterior root of M_2 is already entirely located on the labial side of the incisor, whereas in *V. petenyii* it “sits” on it.

Age and distribution: End of Late Pleistocene to Ancient Anthropogene, from eastern parts of central Europe to eastern borders of western Siberia. A characteristic form of *Mimomys* (Khaprovsk) faunas of the European part of the USSR.

Taxonomic notes: Mehely (1914) described *Mimomys petenyii* from remains recovered in Hungary (Beremend). The published description and diagrams (Plate IV, Figures 5—8) indicate that this form is very close to *V. praeungarica* and, possibly, identical. The dentary teeth shown in Figures 6 and 7 could be considered as belonging to two forms. The former (a young animal with rootless teeth) is not distinguishable from *V. tanaïtica* Schevtschenko, and the latter from the typical *V. praeungarica*. If the differences between these species are confirmed, then as proposed by Erbaeva (1970), *V. tanaïtica* may be considered a synonym of *V. petenyii*, simultaneously retaining the second name.

The lower molars of *V. tanaïtica* Schevtschenko, 1965 exhibit these characters: M_1 — M_2 —4.15 mm and M_1 —2.55×1.0 mm long (holotype, Rostov area of Azov territory, Liventsovka); narrow, with elongate paraconid section of M_1 , the width of which is much less than its medial length, lying far ahead of prismatic fold; and undifferentiated enamel. However, Aleksandrova (1971), who investigated *Villanyia* from the *praeungarica* group obtained from Liventsovka in large quantity (environs of Rostov-on-Don), discovered a continuous series of variability of M_1 , in which the structure typical for *V. tanaïtica* is primarily that of young individuals and some adults at early stages of root development. Incidentally, I am not entirely confident that no mix-up of the two species occurred in this case, more so because a similar relationship can be found in certain localities for *V. praeungarica* and *V. fejervaryi* Mehely (? = *lagurodontoides* Schevtschenko)—which indisputably are two independent species.

2. *Villanyia fejervaryi* Kormos, 1934 (? = *lagurodontoides*) Shevtschenko, 1965

Diagnosis: Dimensions similar to preceding species: M_1 — M_3 —
218 6.65 mm, M_1 —2.9 mm (holotype, Hungary, Nodhorshanhed);
 M_1 —2.45—2.75 mm ($n = 12$; southern Ukraine). Differs in weak

development and shorter prismatic fold of paraconid of M_1 (in large percent of individuals with roots, over one-fourth of crown height absent), that is displaced forward during wear, the anterior corner disappearing, and lateral margin of paraconid acquiring structure typical of extinct lemmings (*Lagurodon*). Molars with much higher crown; roots initiated late in ontogenesis. Incomplete fusion of the basal triangles of masticatory surface of M_1 observed in some animals. In holotype, these triangles are completely isolated on M_2 ; middle pair on M_3 rarely broadly fused and anterior pair isolated. Other characters have not been described; upper molars not found.

Composition of species: *V. f. fejevaryi* Kormos, 1934 (Early Pleistocene, Hungary); *V. f. lagurodontoides* Schevt-schenko (second half of Ancient Pleistocene, Azov and Don regions); *V. f. arankoides* Alexandrova, 1976 (first half of Pleistocene, Don area of Azov region); and *V. f. betekensis* Zazhigin (in litt.), 1976 (first half of Pleistocene, western Siberia).

Among the subspecies listed, probably the last one has the maximum claim for independent species status. It is characterized by a series of archaic features in molar structure, which gave the author a basis for considering it the ancestral form in the subgenus *Kulundomys* established by him.

Description: Enamel in specimen from western Ukraine (Kotlovina) undifferentiated or only slightly thinner in depth of folds. It can be seen from the two fragments of the mandibular ramus that the posterior root of M_2 is located on the labial side of the incisor.

Age and distribution: Ancient-initial phase of Early Pleistocene. Dominant in younger *Mimomys* faunas—Late Khaprovsk and Ancient Tamansk faunas in southern European part of the USSR. From Hungary to southern Kulunda; comparatively rare in the Urals.

Taxonomic notes: I examined the holotype of *Mimomys fejevaryi* in the collection of Kormos (Natural History Museum, Budapest). It differs in no way from some species from the series of the southern Ukrainian *M. lagurodontoides*; the closeness of these species has also been noted by Shevchenko (1965). He also pointed out the decrease with time in relative abundance of *praeungarica*-type teeth and increase in abundance of *lagurodontoides*-type teeth within the limits of the Kuyal'nisa deposits on the Odessa coast of the Black Sea. A similar picture was seen in a comparison of fauna from Kotlovina I and Kotlovina II (southwestern Ukraine).

3. *Villanyia hungarica* Kormos, 1938

Diagnosis: Close to *V. praeungarica*. Dimensions possibly slightly smaller: length of M^1-M^3 —5.85, 6.2 mm, M_1-M_3 —5.75—5.9—6.25 mm ($n = 6$); M_1 —2.25—2.4—2.6 mm ($n = 12$; Hungary, Villany Beremend). Maximum width of paraconid section of M_1 often slightly more than its medial length. Prismatic fold usually absent, but poorly developed in some specimens. Enamel, if thinned, then present only in depth of folds. Partial fusion of triangles of masticatory surface observed in middle pair of M_3 . Other features common to *V. praeungarica* not described.

Composition of species: Subspecies not described.

Description: In the large volume of material from Villany ("Villany-Kalkber," on original labels of Kormos) there is a fragment of the anterior section of the skull of a young animal with a short and broad rostrum (length of diastema 6.45 mm, width 4.85 mm) and intact tooth rows. M^3 has two separate fields; anterolateral fold smaller than successive ones ("Pliomys"-type structure); and well-isolated lateral and barely perceptible posteromedial denticles present on heel. Although fossil remains of *Pliomys episcopalis* have been found at this location, it is more likely that this skull fragment belongs to one of the three species of *Villanyia* found here.

Age and distribution: Ancient Pleistocene, Hungary.

Taxonomic notes: The historical separation of this species has been briefly described by Shevchenko (1965). To date, sequential remains of *Villanyia* from the *praeungarica* group are not known in Russian fauna, among which animals without a prismatic fold on M_1 would definitely predominate.

4. *Villanyia eleonora* Erbajeva, 1975

Diagnosis: Central Siberian member of the group close to *V. praeungarica*. Length of M_1-M_3 —5.2 mm (holotype, Trans-Baikal, Chikoi River, Beregovaya form), M_1 —2.0—2.5—2.8 mm (paratype, $n=180$). In the paraconid section of M_1 in 80% of the specimens, prismatic fold well-developed, absent or poorly developed in 20%. Enamel undifferentiated. Triangles of masticatory surface of M_2 and M_3 broadly fused. M^3 with only two isolated fields and only very rarely a transitory "island"; extent of development of denticles on posterior field of M^3 variable.

Composition of species: Subspecies not identified.

Description: All M^1 and about 10% of M^2 with three roots. Posterior root of M_2 "sits" on incisor. Bony palate with slightly devel-

oped middle ridges. Incisor alveolus terminates at anterior margin of M_1 .

Age and distribution: Ancient Pleistocene of Trans-Baikal region.

Taxonomic notes: The comparatively complete material available for these species from Trans-Baikal, at present cannot be compared with European forms since these fossil remains are far less complete and, moreover, not fully described.

5. *Villanyia laguriformes* Erbajeva, 1973

Diagnosis: Size medium. Length of M_1 — M_3 —5.8 mm, M_1 —2.65 × 1.1 mm (holotype; Trans-Baikal, Uda River, Ulus Dodogol); 5.6, 5.7, and 2.5—2.6—2.7 mm (n = 16, paratypes respectively). Width of paraconid section of M_1 small, rarely equal to its medial length; prismatic fold absent. Enamel distinctly differentiated. Anteromedial fold of M_1 deep and anterior unpaired loop with very narrow cingulum that tends toward elongation. Anterior pair of lobes of M_2 and M_3 broadly fused, middle pair isolated. M^3 without "island", with long narrow "heel"; lateral denticle on heel barely developed or absent. Uncharacteristic of *Villanyia*, but typical of lagurids, projection ("protoconulid") always present on medial wall of middle prism of M^1 and M^2 .

Composition of species: *V. gromovi* Erbajeva, 1976 (second half of Ancient Pleistocene, Trans-Baikal region) is probably not more than a subspecies of this species.

Description: Teeth with high crown: height of crown of M_1 —4.00—4.22—4.70 versus 3.00—3.37—3.70 mm in *V. eleonorae*. Roots initiated late, their shape clearly indicating tendency toward rootless structure. All upper molars with two roots. Roots of M_2 lie on labial side of incisor.

Age and distribution: Ancient Pleistocene (first Half), Trans-Baikal region.

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Taxonomic notes: Structural features of the upper molars are typical of lagurids, as noted by Erbajeva (1973), and confirms a possible close phyletic link with them. However, to date, such features have not been explained for such forms as *V. fejervaryi*; the structure of its M_1 is closer to that of ancient members of Lagurini. In any case, in the geologically younger form—*V. gromovi*—the "protoconulid" on M^1 — M^2 has a tendency to disappear, and typical changes in the structure of the paraconid section of M_1 as well as M^3 are not seen. Thus, there is no basis to place *V. laguriformes* in the series of direct ancestors of ancient lagurids, albeit its structural

features, like those of *V. prolaguroides*, separated by V.S. Zazhigin, clearly emphasize the presence of phyletic links of *Villanyia* with the tribe Lagurini as a whole.

6. *Villanyia exilis* Kretzoi, 1956

Diagnosis: Smaller than other known members of the genus. Length of M_1 in two isolated specimens from the type locality (Hungary, Villany V)—2.0, 2.1 mm; M_1 — M_3 —4.7 mm, M_1 —2.1—2.2—2.3 mm ($n = 15$), M^3 —1.3, 1.4 mm (Poland, Rembelitsy Krulevskie). Maximum width of paraconid section of M_1 almost equal to its medial length. Prismatic fold absent or present on this molar (percentage of individuals not indicated). When present, unlike in other members of *Villanyia*, located close to apex of anterolateral triangle (*Promimomys*-type structure), but well-separated from it and also from the anterior unpaired loop. Roots initiated early. Enamel probably undifferentiated. Anterior pair of triangles of masticatory surface of M_2 and M_3 not isolated. Middle pair isolated on M_2 , fused on M_3 . Root of M_2 located on labial side of upper surface of incisor. Structure of M^3 not reliably known. Smaller cementless rooted molar of voles from Polish locality near Rembelitsy Krulevskie probably belongs to this species (Kowalski, 1960). In this tooth there are three fused fields, the "heel" well-expressed, anterior denticles developed, and posterior "island" present. Unlike other species of *Villanyia*, two folds of M^3 equal in depth; anterior one not smaller than posterior.

Composition of species: Subspecies not described. Fossil remains of this species in Russian fauna are much larger than the type form (M_1 —2.3—2.6 mm; $n = 8$).

Age and distribution: Ancient Pleistocene, Hungary and Poland; possibly wider distribution in the Villafranc of Western Europe. In the USSR, found in the composition of Ancient Pleistocene (Khaprovsk) faunas from Moldavia to the Azov region; reliable finds either not present eastward or belong to the next species.

Taxonomic notes: Kowalski (1960a), who compared the dentition of the type specimen of M_1 with specimens from Rembelitsy Krulevskie (Poland), found no differences between them. Moreover, the tooth from Perrie (France) in the Natural History Museum in Basel, likewise does not differ in size and structure from the tooth of *V. exilis*. In the fossil remains of the USSR, the teeth of other small *Villanyia* without a prismatic fold could easily be confused with the teeth of this species.

7. *Villanyia steklovi* Zazhigin (in litt.)

Diagnosis: Close to the preceding species but probably somewhat larger. Length of M_1 —2.2–2.37–2.6 mm ($n = 25$). Enamel poorly differentiated and slightly thinned only in apices of folds. Prismatic fold longer than in *V. exilis*, dentine areas lower. Posterior root of M_2 lies on upper surface of incisor. M^3 most probably with two “islands”.

Age and distribution: First half of Ancient Pleistocene, southwestern Siberia.

Taxonomic notes: Poorly studied species; possibly ancestral to *V. exilis*.

6. Genus *Ophiomys* Hibbard and Zakrzewski, 1967 (foss.)

Diagnosis: Voles with rooted cementless molars. Length of M_1 —2.3–2.8 mm. M^1 with three roots; M^2 generally and M^3 always with two roots. M^3 without “islands”. Paraconid section of M_1 with “island” formed through closure of apex of anterolateral fold that disappears during wear much before roots reach half crown height. Prismatic fold, probably, juvenile; not present in all specimens. Enamel layer equally thick along periphery of tooth. Position of roots of M_2 – M_3 relative to alveolus of incisor not described.

Composition of genus: Probably there is only one species—*O. taylori* Hibbard, 1959. As for *O. parvus* Wilson, 1933 and *O. meadensis* Hibbard, 1956 (the former considered the type species of the genus), both could probably be included under the subgenus *Pliophenacomys* of the present-day genus *Phenacomys*.

Description: Time of root initiation not indicated (Hibbard and Zakrzewski, 1967). Relative abundance of animals with third root of M^2 varies in different populations from 20 to 80%. Triangles at base of paraconid section of M_1 almost not displaced relative to each other; degree of their fusion with anterior unpaired loop variable. Data for geologically younger forms indicate an increase in number of individuals with elongate anterior unpaired loop (closeness to *Pliophenacomys*). Time of appearance and disappearance of “island” on M_1 not indicated. Lateral margin of anterior unpaired loop with poorly developed juvenile folds, but with fairly constantly expressed angular projections on posterolateral margin. Prismatic fold poorly developed or totally absent in 10 to 15% specimens. Details of its structure and formation not described. Lateral triangle of basal pair of M_1 almost completely fused with antero-medial triangle, rarely with posterior one. Middle pair of triangles

of M_2 barely fused or isolated, but fused on M_3 . Anterior lobes of these teeth barely divided into lateral and medial triangles; division rapidly disappears with age. Anterolateral fold of M_3 not smaller than next one.

Posterior lobe of M^1 almost completely divided into two triangles; preceding pair may be rather broadly fused, as also middle pair on M^2 . Two triangles present behind anterior unpaired loop of M^3 —lateral and medial—which are almost totally isolated from each other and also from the heel. Small triangular denticle may be isolated on lateral margin of heel.

Age and distribution: Late Pliocene, North America.

Taxonomic notes: Several details in the generic description are rather imprecise. Sufficiently clear differences from *Cosomys* have not been reported, which is regrettable because the two genera have been found together in some sites. Information on many important structural details of the teeth is lacking and, in some cases, no mention made of their change with age. Such deficiencies do not permit an unequivocal solution regarding the direct relationship between *Cosomys*—*Ophiomys* as indicated by the authors. Also, there are several gaps in the description of the genus *Cosomys*. In terms of development, *Ophiomys* is close only to *Villanyia* from the Old World; however, it is slightly more archaic.

It may be noted that the insufficiently studied American genus *Nebrascomys* Hibbard, 1957 (? = *Atopomys* Patton, 1965) might possibly belong to another tribe of microtines (? Prometheomyini) or even to some vole-toothed hamsters. It was described (Hibbard, 1957, 1970) from the Early Anthropogene deposits of Nebraska from a fragment of the anterior section of the mandible of an old individual with a single defective M_1 . This is a small vole with rooted molars in which, possibly, the structure of M_1 is simple. As indicated later (Hibbard and Zakrzewski, 1967), the triangles of M_1 — M_3 are broadly fused. Both authors consider this genus ancestral to *Atopomys*.

7. Genus *Promimomys* Kretzoi, 1955 (foss.) (= *Cheria* Kretzoi, 1959)

Diagnosis: Voles with rooted cementless, rarely sparsely cemented, molars. Length of M_1 —2.4—3.8 mm, M^3 —1.4—2.5 mm. M^1 with three roots; M^2 with three, rarely two; M^3 with three, but often with two that tend to fuse in later forms. M^3 always with early formed posterior “island” and, in some ancient forms,

also with an anterolateral "island" that forms during later stages of development. M_1 with true "island" formed through closure of apex of anterolateral fold. In ancient forms, this "island" is retained throughout the animal's life; in later forms, it disappears at various stages right up to commencement of root formation. True prismatic fold also present which, in ancient forms, has formed even before root initiation and extends entire height of crown; in later forms, this fold is reduced, depending on degree of tooth hypsodonty. Posterior root of M_2 either "lies" on incisor, encircling it from sides like a prong in more ancient forms, or moves down from upper margin of incisor in later forms. Both roots of M_3 located on lingual side of incisor. Enamel rarely equally thick throughout perimeter of tooth, more often thins at apices of folds. Degree of development of dentine tracts, as in other genera, increases with crown height; in M_1 primarily in the paraconid and entoconid sections.

Composition of genus: P. moldavicus Kormos, 1932 (= *Cheria gracilis* Kretzoi, 1959) (type species); *P. stehlini* Kormos, 1931; *P. occitanus* Thaler, 1955; *P. baschkirica* Suchov, 1970; and *P. antiquus* Zazhigin (in litt.), constituting two main lines of development: "cheria" line (small forms) and *stehlini* line (large forms).

Description: Roots form early. On M_1 commencement of root separation ("squeezing" stage) coincides with time of commencement of wear of the masticatory surface. Third (lateral) root of M^1 free in most species throughout its length and not displaced forward; in M^2 anterior pair of roots often fused in upper section; in M^3 with two roots, usually trace of fusion of both in form of longitudinal groove. Triangles at base of paraconid of M_1 often notably shifted mutually and apex of third (counted from back) medial fold extends above opposite one. There is no tendency toward elongation of the anterior unpaired loop. "Island" on latter formed due to apex of third medial fold initially being horseshoe-shaped or at least in form of forwardly directed projection; subsequently, it becomes uniformly rounded. Elongation of "island" takes place when roots reach one-third, one-half, or even three-fourths crown height in ancient forms; and from moment of root formation up to one-fourth crown height in later forms. Juvenile folds on anterior margin of unpaired loop of M_1 long-retained in larger forms, especially on anterolateral margin and, sometimes, one of them may occur inside "island". Prismatic fold looks like well-separated ridge that extends parallel to edge of third lateral prism (counting from back). In ancient forms, this fold extends almost entire height of crown and does not disappear until roots attain about four-fifths

crown height. Lateral and anteromedial triangles of M_1 not fused or extent of fusion not greater than double thickness of enamel (often in young individuals); lateral and posteromedial triangles often fused. Anterior lobes of M_2 and M_3 isolated; in middle pair of triangles, isolation may be slight and more strongly expressed in the last pair of molars. Anterolateral fold of M_3 not smaller, or just barely smaller than next one.

Posterior lobe of M^1 divided and thus its masticatory surface, as in *Villanyia*, with five triangles. Middle pair of triangles on M^1 – M^2 almost completely isolated; their partial fusion observed, however, in some individuals, mostly at a young age. One medial and one to three lateral triangles present behind anterior unpaired loop of M^3 , which are isolated in young individuals from the loop and also from the rounded heel. Fusion, when, observed, not more than double thickness of enamel. Medial lobe and small posterolateral lobes fused. Structure of M^3 simplified during process of formation of "islands". Heel increases in direction of posterior section of tooth, first from the lateral and then from the medial side; until this happens, a deep fold exists here. Apex of anterolateral fold also closed in old individuals of some forms, giving rise to an "island". After disappearance of "island", M^3 acquires the secondarily simplified structure typical of most members of *Pliomyini*.

Age and distribution: From end of Middle Pliocene (Kuchurgan faunas of western Ukraine and Moldavia, Late Russi faunas of Western Europe) to end of Ancient Pleistocene (Late Khaprovsk faunas). From France and Italy to Trans-Baikal region. Some forms, most probably of this genus, have been found in Late Pliocene faunal associations of Turkey east of Erzurum (Tobien, 1972).

Taxonomic notes and affinity: The generic status of *Promiomys* is not accepted by those paleomammalogists who consider the presence or absence of cement an absolute character. Thus, Skorik (1972) and Topachevskii and Skorik (1977) consider it only a subgenus of the broadly interpreted genus *Villanyia*. However, it is already well-known that sparsely cemented species appear at the end of both lines of development of the genus (Sukhov, 1970; Agadzhanyan, 1976).

Kretzoi established the genus in 1955 for the new species *Promiomys cor*. However, in 1958, after studying the holotype as well as other extinct microtines from the same localities housed in the collections of the Geological Institute in Budapest, I concluded that the author had described under this name a specimen of a very old individual, which was later identified by him as *Cheria gra-*

cilis Kretzoi, 1959, having roots possibly already four-fifths crown height and without prismatic fold. A similar error was later committed by Topachevskii (1965) regarding a related fossil form from the Kuchurgan gravel in the Odessa district,⁴ who considered *Cheria* a synonym of *Promimomys*.

224 Of the general features of microtine evolution toward hypsodonty in both lines, reduction in number of roots of the upper molars, shift in time of root and fold formation, disappearance of the "island" on M_1 , increase in height of dentine tracts, and appearance of less-cemented forms have already been described.

The larger ancient forms of this genus relate it to the tribe Ondatrini through the European genus *Dolomys* and the American genus *Pliopotamys*. On the other hand, the smaller ancient forms of the "*cheria* line", with late isolation of the "island", are difficult to distinguish from the small pliomyins with which, possibly, they have a common origin. At the same time, the later forms directly link *Promimomys* with the cemented species of the genus *Mimomys*, and thereby with the majority of the extinct and extant arvicolins.

1. *Promimomys stehlini* Kormos, 1931

Diagnosis: Size large. Length of lower molars 8.7 mm; M_1 —2.8–3.0–3.8 mm. "Island" on paraconid section of M_1 in more ancient forms develops late and fold often remains open even up to root length more than half crown height, whereas in later forms the "island" is already closed by the time of root initiation (western Ukraine, Kotlovina). Dentine tracts absent on lateral surfaces of tooth. Juvenile folds on margin of anterior unpaired loop long-retained. M^3 with three isolated roots in ancient forms, of which anterior one fused in later forms. Anterior "island" on this tooth formed only in old individuals of more ancient forms and, in later forms, as in the case of old individuals among more ancient forms, lateral cement appears (at times on one side, but normally throughout tooth height).

Composition of species: *P. s. occitanus* Thaler, 1955 [end of Middle to commencement of Late Pliocene, Western Europe (Moldavia)]; *P. s. stehlini* Kormos, 1931 (first half of Late Pliocene, same locality); and *P. s. polonicus* Kowalski, 1960 (= *hainackensis* Fejfar, 1961) (Late Pliocene, Western and eastern Europe).

⁴V.S. Zazhigin considers it possible to include the Kuchurgan jaw not under microtines, but in the genus *Baranomys*. *Promimomys*, as interpreted by Repenning (1968), is also close to *Baranomys*.

Age and distribution: End of Middle Pliocene to commencement of Ancient Pleistocene [in the USSR—Kuchurgan (?), Moldavian, and Early Khaprovsk faunas]. It is predominantly a Western European species, which is very common in the Late Pliocene faunas from southern France, Italy, and the Asian part of Turkey up to Moldavia and possibly western Ukraine (Kuchurgan gravel).

Taxonomic notes: This is one of the most primitive species of the European rooted microtines with structural features reflecting affinities with pliomyins, to which attention was first drawn by Kowalski (1960b, 1970). A very early root initiation and late “island” formation on the paraconid section of M_1 , leads to a long retention of the “*Dolomys*”-type structure of this tooth throughout the animal’s life and, as in the next species, leads to a description of forms belonging to *Dolomys* (Aleksandrova, 1966), or to separation of forms intermediate between *Mimomys* and the present genus (Kowalski, 1960b; Sulimski, 1964). Recent studies (Chaline, 1974; Agadzhanian, 1976) have shown that several closely related forms exist in the Pliocene faunas of Europe, which have been described as independent species, revealing distinct chronoclinal and geographic variability within the limits of the widely understood species *P. stehlini*. Incidentally, at present it is not possible to determine with confidence to which of its types one or the other form belongs, nor to assess the transition of later
225 less-cemented forms to *Mimomys pliocaenicus*. Here, the boundary between *Promimomys* and *Mimomys*, as in other cases of phyletic evolution, is tentative. I include the species *pliocaenicus* under *Mimomys*, and the closely related species as subspecies, following one of Chaline’s (1974) hypotheses.

2. *Promimomys moldavicus* Kormos, 1932

(= *Cheria gracilis* Kretzoi, 1959)

Diagnosis: Size medium and small. Length of lower molar row up to 6.0 mm; M_1 —2.25–2.5–2.6 mm (Hungary, Charnota; n = 14); in larger forms, M_1 —2.6–2.8–3.0 mm (Moldavia, Ufa, Ural region). “Island” on paraconid section of M_1 forms comparatively early; in more ancient forms, formed by time roots attain one-third crown height; in younger forms, at alveolar stage and rootless condition of molars; it rapidly disappears with age (in more ancient forms, when the roots reach half crown height). Dentine tracts distinct on lateral surfaces of this tooth. Juvenile folds on margin of anterior unpaired loop of M_1 disappear comparatively rapidly with age. Structure of M^3 as in preceding species. Masticatory surface with

two "islands"; however, anterior "island" forms earlier than in *P. stehlini*. Enamel, in later forms, thins in depth of folds, insignificant cement deposition appears laterally, and posterior root of M_2 slides from incisor.

Composition of species: At least five to six subspecies: *P. m. moldavicus* Kormos, 1932 (Late Pliocene, southwestern Moldavia); *P. m. gracilis* Kretzoi (Late Pliocene, southern Hungary); *P. m. acculaewae* Suchov, 1970 (Ancient Pleistocene, eastern European part of the USSR) *P. m. jachimovitcii* Suchov, 1970 (Ancient to Early Pleistocene, Ufa area of Ural region); *P. m. septimanus* Michaux, 1971 (Ancient Pleistocene, France); and *P. m. silasensis* Janossy, 1974 (Late Pliocene, Hungary). Subspecies status highly probable for *P. m. issikkulensis* Kretzoi, 1961 ("*Katamys issikkulensis*" Kretzoi, nomen in collection!), which needs to be described (Ancient Pleistocene, Issyk-Kul and Irtysh Basin) as well as for *P. m. praeglacialis* Kretzoi, 1969 (Early Pleistocene, Hungary).

Age and distribution: From Middle Pliocene to end of Ancient Pleistocene (Khaprovsk faunas) from France, Czechoslovakia, Hungary, and Turkey to Issyk-Kul and Irtysh regions. Unlike preceding species, this is predominantly an Asian species.

Taxonomic notes: *P. moldavicus* is more widely known under the name *Cheria gracilis*, and is close to the preceding species but represents an independent line of development. The most archaic forms are associated with the central regions of the Palearctic but not yet sufficiently known. It widely replaces *P. stehlini* in the Pliocene east of the Dnester. In the case of mixed occurrence of their fossils (narrow belt east and northeast of the Carpathians), they are readily differentiated by dimensions. As in the case of *P. stehlini*, later closure of the "island" on the paraconid section of M_1 was one reason for the confusion of some young individuals with pliomysins, as happened for example, with *Pliomys kowalskii* Schevtschenko, 1965. On the other hand, specimens of old individuals with an "eroded" "island" and prismatic fold, were described as ancient brachiodont forms with primarily simple structure of the paraconid section of M_1 (Kormos, 1932a; Kretzoi, 1955a). The species is typical of the Khaprovsk faunas of our country. Sukhov (1970) demonstrated the well-expressed variability in time of such characters as size, time of root formation, formation and disappearance of the "island" on the paraconid section of M_1 , and others; size also changes in space. The relationship of *P. moldavicus* to similar forms from Siberia, and Central and Middle Asia is least clear, for example, *Mimomys antis* Savinov, 1974 from the Late Pliocene of Dzhun-

garian Alatau or *Promimomys antiquus* Zazhigin (in litt.) from the Middle (?) Pliocene from the left bank of the Ob' River. The latter species, known from a single M_1 , does not permit assessment of the taxonomic importance of the archaic characters indicated by the author.

Most probably, *Mimomys proseki* Fejfar, 1961; *M. franconicus* Heller, 1937; and *M. konstantinovae* Alexandrova, 1966 are also synonyms—all of which were described from an M_1 .

3. *Promimomys baschkirica* Suchov, 1970

Diagnosis: Dimensions similar to small forms of the preceding species: Length of M_1 —2.3 mm (holotype), 2.15–2.4–2.65 mm ($n = 40$). Differs from these forms in “island” on paraconid section of M_1 appears at stage of rootless molars, i.e., in very young animals, and disappears before roots reach one-fourth crown height. Also, enamel in teeth of fully mature individuals somewhat differentiated on lateral sides of triangular prisms.

Composition of species: Subspecies not described.

Age and distribution: Early Pleistocene, Ufa area of Ural region (Tamansk fauna).

Taxonomic notes: Only isolated lower molars and fragment of a mandibular ramus with M_1 and M_2 are known, in which it is evident that the posterior root of the second tooth “slides” from the incisor. The author of the species rightly considers it close to later forms of *P. moldavicus* [*Mimomys (Cheria) gracilis* in his terminology]; however, he is hardly right in considering *Villanyia praeungarica* as one of its later descendants. It is possible that *Promimomys baschkirica* may eventually prove to be no more than a subspecies of *Promimomys moldavicus*.

8. Genus *Mimomys* F. Major, 1902 (foss.)

Diagnosis: Voles with rooted molars, with cement deposition along outside of folds; cementation insignificant in ancient forms and abundant in later forms. Length of M_1 —2.7–4.5 mm. M^1 with three roots (rarely M^2 and M^3) only in more ancient forms. If “island” present on M^3 , only posterior one, which disappears early; “island” often absent. Paraconid section of M_1 with or without “island,” which forms through closure of apex of anterolateral fold and usually disappears before roots reach half crown height (in later forms, up to moment of root initiation or earlier). True prismatic fold present, though reduced, and often not in all individuals

or only in young ones. Position of posterior root of M_2 and roots of M_3 as in *Promimomys*. Enamel worn in depth of folds and on posterior walls of triangular prisms on lower molars and anterior walls on upper molars. Dentine tracts always well-formed.

Composition of genus: Subgeneric taxonomy has not been fully determined, although a serious attempt was made in this direction (Zazhigin, 1975). Three subgenera are quite acceptable: *Mimomys* F. Major (type subgenus), *Microtomys* Mehely, and *Kislangia* Kormos. Separation of the subgenus *Tianshanomys*, recently described by Lychev and Savinov (1974), does not seem well-founded (confirmation of subgeneric status for isolated species showing mixed structural features). Subgeneric status should probably be assigned to the genus *Cromeromys* Zazhigin, 1975 (for the *intermedius* group). Here the nontaxonomic meaning of "species group" is used for closely related groups.

Description: Roots form relatively late, especially in later forms (transition to rootless molars), and in more ancient forms as well as in *Villanyia*, up to commencement of wear of masticatory surface. Distinct tendency for reduction of third root of upper molars. Triangles at base of paraconid section of M_1 may be notably shifted relative to each other, up to complete isolation of medial one, with lateral always remaining widely fused with anterior unpaired loop. "Island" on paraconid section of M_1 and prismatic fold not necessarily present together; some forms and individuals characterized by presence of "island" and absence of prismatic fold. Rarely, this fold forms only in upper section, but even then ridge extends to masticatory surface even in young individuals retaining juvenile folds. Forward displacement of prismatic fold with wear negligible since lower end of ridge slightly deflected forward; modification of fold into angular projection does not occur at edge of anterior unpaired loop. Juvenile folds of latter narrow, short, disappear at very commencement of wear. Lateral basal triangle of M_1 may be partially fused with either medial ones or with both; fusion more often seen in ancient forms and in young individuals. In most forms, anterior and middle lobes of M_2 and M_3 variably isolated, especially on M_2 ; middle pair of M_3 sometimes widely fused. Anterolateral fold of M_3 not smaller than next one.

Posterior lobe of M^1 always completely separated and thus masticatory surface of tooth with five triangles. Partial fusion of middle triangles may be seen in M^2 . Two complete triangles lie behind anterior unpaired loop of M^3 , of which medial one may be fused with posterior lobe, but more often separated from lateral triangle.

Moreover, a third small lobe may also be incompletely separated behind the posterior one; rarely, small third denticle also present on opposite side. During formation of transitory posterior "island," heel fuses with posterior section of tooth first along lateral side and only much later with medial side.

Age and distribution: From Late Pliocene to second half of Middle Pleistocene throughout central part of the Palearctic up to Kolyma basin; south up to western Asian part of Turkey.

Taxonomic notes and evolution: Appearance of cementation on lateral surfaces, reduction and loss of prismatic fold, late root initiation, and gradual "sliding" of posterior root of M_2 from labial side of incisor, are evolutionary tendencies distinctly manifested even in the distant past in the genus *Promimomys*. A rapid loss of archaic features and dominance of the genus *Mimomys* coincided in time with the appearance of the first microtines with rootless molars, together with which *Promimomys* survived up to the end of the Middle Pleistocene.

Subgeneric divisions reflect several evolutionary lines, starting with early species of the genus *Promimomys*, possibly even in the Late Pliocene, in core deposits of the *Dolomys*-*Promimomys* faunas. The large form of this genus, type *P. stehlini*, gave rise to the evolutionary series of forms belonging to the group *pliocaenica* (subgenus *Mimomys* s. str. and through *M. cappettai* Michaux, 1971, possibly subgenus *Kislangia*), which probably terminated in a blind branch that did not give rise to species with rootless molars. The small forms of *Promimomys*, or those of the *P. moldavicus*-type, gave rise to two, perhaps three series, some terminal species of which serve as the evolutionary basis for the rootless-molar forms of the tribe, including *Allophaiomys* as well as *Microtus* itself, and genera closer to the latter. Species of the *intermedius* group led to the appearance of the present-day genus *Arvicola*. In this case, it is quite probable that the eastern part of the Palearctic had its own parallel lines of development, for example, those related to the genus *Aratomys*.

Resurrection of the phyletic sequence of species in these lines, given our present knowledge of extinct microtines with rooted molars, looks more like a morphological series of changes in the structure of M_1 and M^3 . It may happen that forms now included in a single series will in the future be assigned to different branches of the main or lateral stems. Simulation of a natural system will only be achieved with an increase in number and variability of characters studied and a general completeness of material.

Subgenus *Mimomys* F. Major, 1902

Diagnosis: Length of M_1 in largest forms—2.1–3.4–3.7 mm. M^1 – M^2 with three roots; sometimes M^3 also with three roots. Anterior “island” on M_1 and posterior “island” on M^3 present, initiated toward commencement of root formation, and often retained in animals with rooted molars that reach half crown height or more. Prismatic fold present. Posterior root in most cases “sits” on incisor.*

Composition of subgenus: Two to three species: *M. pliocaenicus* F. Major, 1902 (type species); *M. minor* Fejfar, 1961; sometimes *M. coelodus* Kretzoi and even *M. reidi* Hinton are included here (*M. newtoni* F. Major, according to the classification adopted here).

Age and distribution: Same as for genus, but not found later than the beginning of Early Pleistocene.

Taxonomic notes: Diagnostic features given here are based on the description given by Topachevskii (1965). It combines species distinguished by maximum number of archaic structural features, and closer to ancestral forms of the genus *Promimomys*.

1. *Mimomys (M.) pliocaenicus* F. Major, 1902

Diagnosis: Size large. Length of upper molar row 7.0–8.0 mm, lower row 7.7–8.5 mm (Poland, Kadzielnya); M_1 —3.4–3.8 mm (up to 4.1 mm), M^3 —1.9–2.4 mm (same place). Cement deposition abundant; commences before root initiation. “Island” on paraconid section of M_1 formed by time of root separation and persists at least until roots reach half crown height; same true of prismatic fold. Enamel distinctly differentiated. Triangles on masticatory surface of M_1 completely isolated in mature individuals, slightly fused on M_2 , and broadly fused on M_3 . Hind root “sits” on incisor.* M^2 in most individuals with three roots, M^3 with two.

Composition of species: The only subspecies described is *M. (M.) p. minor* Fejfar which, probably, should be more properly considered an independent species (Bazarov, Erbaeva and Rezanov, 1976). On the other hand, several closely related species (see below) can hardly be considered more than subspecies.

Description: A fragment of skull from collection of T. Kormos (Beremend, No. 3802/1), he examined in the Natural History Museum in Budapest is characterized as follows: length of tooth row

* Which molar not given; however, as in *M. (M.) minor*, should probably read M_2 —Eds.

8.35 mm; interorbital space comparatively narrow with deep groove-like depression in middle; diastema notably larger than length of tooth row (9.55 mm); incisor alveoli short (5.2 mm), acute at ends, the posterior one not extending to anterior margin of alveoli of molars. Structure of bony palate, more complete than specimen from same locality described by Mehely (1914, Plate III, Figure 2), of typical "*Microtus*"-type; comparatively shallow postpalatal pits nevertheless distinct and bony bridge between them almost half maximum width of each pit.

Posterior end of lower incisor "slides" along lateral side of mandibular ramus, below the dental foramen, and forms a distinct alveolar knob on it.

Age and distribution: End of Late Pliocene to first half of Early Pleistocene, from southern France to Irtysh region.

Taxonomic notes: The most probable ancestral form is *Promimomys stehlini polonicus*—a late sparsely cemented form very close to the species described here.

Kretzoi (1955b) separated the Ancient Pleistocene species *M. pliocaenicus* from the inner carpathians into an independent species, *M. mehelyi*. However, the differences pointed out by him in the structure of the anterior section of M_1 , as rightly pointed out by Kowalski (1958), may be considered subspecific in importance. *M. kretzoi*, described by Fejfar (1961) from the Late Pliocene of Czechoslovakia (Khainachka I), is hardly more than one of the age stages of *M. pliocaenicus* (Bazarov, Erbaeva and Rezanov, 1976). The distinctly small forms of *M. pliocaenicus* from the USSR, which are of the same age as those of the West European species, with M_1 about 3.0 mm long, are designated either as *M. conf. pliocaenicus*, or considered close to *M. minor*. Undoubtedly, the first species forms a series of forms, here replacing each other in time as well as in space. Thus, for example, northern forms of the same age were probably larger than southern ones (Sukhov, 1970).

2. *Mimomys (M.) minor* Fejfar, 1961

Diagnosis: Size small. Length of M_1 —2.6, 2.8, 2.8 mm (holotype and cotypes), 2.3–2.5–2.8 mm (Trans-Baikal region); M^3 —2.0 mm (cotypes), 1.6–1.7–1.8 mm (Trans-Baikal region). Cementation may be slightly less abundant compared to *M. pliocaenicus*; time of commencement of deposition not known. "Island" and prismatic fold on anterior section of M_1 disappear by time roots reach half crown height. Enamel slightly less differentiated than in *M. pliocaenicus*. Triangles of masticatory surface of M_1 completely isolated; on re-

maining lower molars (known only for Trans-Baikal specimens), middle ones fused, and sometimes also anterior ones of M_2 , and anterior ones on M_3 . Posterior root of M_2 lies on labial side of incisor in mature individuals and "slides" from its surface in young individuals. M^2 and M^3 with two roots.

Composition of species: Subspecies not separated.

Age and distribution: Ancient Pleistocene of Czechoslovakia and Trans-Baikal region (?).

Taxonomic notes: Combining the small Trans-Baikal forms of *Mimomys* with the *pliocaenicus* group into a single species together with the Czechoslovakian *M. minor* (Bazarov, Erbaeva and Rezanov, 1976) is somewhat risky, especially since it has been done mainly on the basis of similarity in size of M_1 . Comparison of the remaining features of the Trans-Baikal form is not possible due to the absence of comparable material for *M. minor*.

It is possible that in the future the Trans-Baikal form will be considered identical to the Ancient Pleistocene species *M. orientalis* Young, 1935. This form has a cemented M_1 that is 2.8 mm long (only holotype known; tooth of young individual at initial stage of root formation from sands of southern Shansi, Pinglu, locality no. 34) and the masticatory surface not differing in structure from typical species of the *pliocaenicus* group.

Subgenus *Kislangia* Kretzoi, 1954

Diagnosis: Length of M_1 —3.8–4.2 mm. M^2 and M^3 with two roots (their number not indicated for M^1). Anterior "island" present on M_1 or absent; posterior "island" present on M^3 . Prismatic fold not present on paraconid section of M_1 . Position of posterior root of M_2 relative to incisor not known.

Composition of subgenus: Three species described—*Mimomys* (*K.*) *rex* Kormos, 1934 (type species); and *M. (K.) ondatrina* Kretzoi, 1958 and *M. (K.) kadici* Kretzoi, 1958 (doubtful species).

Age and distribution: Ancient Pleistocene, Hungary and Moldavia (?), Early Pleistocene, Azov region (?).

Taxonomic notes: The initial separation of the species by Kormos (1934b) was based primarily on large dimensions and absence of prismatic fold on paraconid section of M_1 . Possibly, as the author himself considered, such forms are a unique link in the evolutionary series of *pliocaenicus* in the subgenus *Mimomys*. This is also supposed to be indicated by the structural features of the anterior section of the skull described by Kormos. However, the

combination of these structural features in the paraconid section of M_1 should be viewed with caution: reduced and anteroposteriorly flattened anterior unpaired loop, absence of prismatic fold, and position of "island" so close to apex of anteromedial fold as to appear "stretching" from it and not from tip of anterolateral angle. Perhaps Michaux (1971) is right, that the *M. cappettai* described by him is a link in the unique line of development from *Promimomys stehlini* to *Mimomys rex*.

3. *Mimomys (Kislangia) rex* Kormos, 1934

Diagnosis: Size large. Length of lower molar row more than 8.0 mm, viz., 9.8 mm (holotype), 8.6–10.05 mm; M_1 —4.1 mm (holotype), 3.8–4.2 mm. Cementation abundant in folds of molars and probably appears much before initiation of roots. Unlike in other members of the genus *Mimomys*, the "island" in the paraconid section is very small and lies near the apex of the anteromedial fold; time of its formation and appearance not known. Triangles of masticatory surface of all lower molars completely isolated. Heel of M^3 reduced and extends toward lateral side.

Composition of species: Subspecies not identified.

Age and distribution: Villan mountains in southern Hungary. Fauna from Villan-3 locality, from where the species was described, belongs to end of the Ancient Pleistocene.

Taxonomic notes: It may be considered probable that the youngest members of the subgenus from Kishlang fauna differ from *M. rex* in specific status. However, both the above species described from here need to be redescribed since right now they are no more than "nomen dubius." Remains of large voles with rooted molars, included by the above authors under *Kislangia*, have been reported in the Ancient and Early Pleistocene faunal association of the USSR (Khaprovsk and Tamansk faunas) by Topachevskii (1965) and Aleksandrova (1965a). However, they may belong to the large form of the *pliocaenicus* group as well as to late members of *Promimomys stehlini polonicus*.

Diagnosis: Length of M_1 in largest forms not more than 3.5 mm. All upper molars with two roots, but M^1 in a few individuals of some species may have three; traces of fusion of anterior of two roots often observed. Anterior "island" on M_1 and posterior "island" on M^3 , if present, disappear by root initiation, and in many

species these "islands" are totally absent because the prismatic fold is also absent. Posterior root of M_2 located in most forms on labial side of incisor, and only in more ancient forms on its upper ridge.

Composition of subgenus: Five to six species—*M. (M.) intermedius* Newton, 1881 (= *savini* Hinton, = *majori* Hinton) (type species); *M. (M.) newtoni* F. Major, 1902 (? = *pusillus* Mehely, 1914); *M. (M.) dehmi* Brunner, 1958; *M. (M.) cantianus* Hinton, 1910; and *M. (M.) pseudintermedius* Erbajeva, 1976.

Possibly, these species also belong here: *M. coelodus* Kretzoi, 1954; *M. antis* Savinov and Lytshev, 1970; *M. irtysheensis* Zazhigin (in litt.); and *M. gansunicus* Zheng, 1976.

Age and distribution: Same as for genus.

Taxonomic notes: Diagnostic features are presented mainly on the basis of Topachevskii's (1965) description. It combines most of the progressive members of the genus, fossil remains for which are known from the late section of its geochronology. A sharp increase in root height and transition to a rootless tooth state are particularly evident in this subgenus (Gromov, 1967). Based on structural features of the bony palate, Zazhigin (1975) has proposed that this subgenus should include only one species—*M. pusillus* Mehely (the *newtoni-reidi* group in the system accepted here), and has suggested a new generic name for the group *intermedius*, namely, *Cromeromys*.

4. *Mimomys* (? *Microtomys*) conf. *coelodus* Kretzoi, 1954

This name was given to voles with less-cemented lower molars with dimensions equal to large members of *Promimomys moldavicus* (M_1 —2.4—2.7—3.0 mm). The two species are always found together in the Late Khaprovsk and Early Tamansk faunas throughout the western part of this species' range. The earlier and later forms of *Mimomys* conf. *coelodus* differ from each other in time of disappearance of the "island" and prismatic fold on M_1 . The fold disappears in much later forms by the time of root initiation, and the tooth then resembles that of *M. coelodus* Kretzoi, known from a single M_1 from the Early Pleistocene fauna of Kishlang (Hungary).

V.P. Sukhov has emphasized that differences from *Promimomys moldavicus* [*M. (Cheria) gracilis* in his terminology] are very small. These differences are: constant presence of a small amount of cement and different periods of formation and disappearance of the "island" on M_1 (which is later in initiation and earlier in disappearance than in *P. moldavicus*, which coexists with the species under discussion). However, Sukhov's observations require

confirmation in a larger amount of material. Thus, though affinity with *P. moldavicus* is quite probable, the subsequent history is not clear. Possibly, *M. medasensis* Michaux, 1971 (Ancient Pleistocene, France) may prove the connecting link.

Under the less-cemented forms (cement may not be visible from upper side), like the most ancient *M. conf. coelodus*, the Khaprovsk (Liventsovka) species *M. livenzovicus* Alexandrova, 1973 (M_1 —2.35—2.75—3.5 mm; $n = 22$) is included with enamel fields that tend to wear out quickly and with prismatic fold placed high on M_1 . Structure of remaining teeth not known. Besides this similarity, the author has also noted closeness to *M. p. minor* (*M. minor* in my understanding). Here, differences consist only in lesser cementation and lesser length of paraconid section of M_1 in the Liventsovka form.

Group *newtoni-reidi*

5. *Mimomys (Microtomys) newtoni* F. Major, 1902
(? = *pusillus* Mehely, 1914)

232 *Diagnosis*: Size small. Length of lower molar row less than 7.0 mm (5.3—6.1 mm in Rumanian form); M_1 —2.3 mm (holotype, in which roots not formed), 2.5—2.7—2.9 mm (Rumanian form). Size of former measurement in greater number of specimens reaches 6.85 mm, of latter measurement up to 3.05 mm. Cement moderate or abundant; deposited before pulp closes. At the same time, anterior section of M_1 may have early disappearing “island” in some individuals. Prismatic fold variably expressed, often present only in young individuals, but in some populations in almost 50%, and retained until roots reach half crown height. Enamel distinctly differentiated. Triangles of masticatory surface divided or partly fused on M_1 (basal triangles); middle pair fused on M_2 and M_3 , rarely isolated. Incisor passes between roots of M_2 and M_3 ; rarely posterior root of former “slides” on labial side from upper margin of incisor.

Composition of species: Intraspecific classification was not analyzed due to lack of clarity in taxonomic status of closely related forms described as independent species from isolated samples of M_1 . These are mostly of animals from deposits of about the same age in Western Europe and not redescribed yet from new material obtained from the type locality: *M. reidi* Hinton, 1910; *M. pusillus* Mehely, 1914; *M. dehmi* Brunner, 1958; and *M. simplex* Kretzoi, 1954.

Age and distribution: Fossil remains known from within limits of entire range of subgenus; in the west from end of Pliocene to Middle Pleistocene (Riss Interglacial period); in Western Europe, they possibly survived up to Late Pleistocene ("*Clethrionomys*" *erli* Brunner, 1936 from "mixed" faunas of the Franconian Elbe, FRG).

Taxonomic notes: Besides *M. newtoni*, Western European paleomammalogists are inclined to separate *M. pusillus* described by Mehely (1914) as an independent species. This species exhibits more abundant cementation, a poorly developed prismatic fold, and better isolated triangles of the masticatory surface of the lower molars. Actually, this form has been described in greater detail and from a more complete sample than *M. newtoni* and *M. reidi*; its upper limit of size borders that of small forms belonging to the *intermedius* group. The subspecific status of this form was also recognized by Hinton.

The relationship between *M. newtoni* and *M. reidi* also remains unclear. The latter species was described from somewhat more ancient deposits than the former, and until 1926 was known only from a single M_1 at the stage of root formation, with a small quantity of cement, well-differentiated enamel, and lacking an "island," and posterior root of M_2 "sitting" on the incisor. Until recently, this form [*M. reidi*] was also frequently given specific status, although it is probably only a subspecies of *M. newtoni*, if not its synonym. In the Early and Ancient Anthropogene faunas of the USSR, usually a series of comparatively small M_1 are included under *M. conf. reidi*. The maximum length of which is only slightly more than 3.0 mm, less cemented and has a poorly developed and early disappearing prismatic fold, an early disappearing "island" that is not always present, and a relatively broader crown than in the similar West European forms. Usually, such teeth are separated from the teeth of *M. pusillus*, which is known only from a small number of localities of Khaprovsk fauna, especially on the basis of molar proportions. Probably, the other difference between the two species lies in structural features of the posterior section of the bony palate
 233 (based on diagrams and isolated remains), which is not suitable for identification of the usual abundant material. It is clear from the foregoing that to resolve the question of affinity between these forms, new material consisting of well-preserved fossils, must be collected and described, primarily from the type locality of *M. reidi* and *M. newtoni* (southern England).

As for *M. dehmi* Brunner, this is the smallest (length of M_1 —2.2–2.3 mm; $n = 3$) and most hypsodont form of the group, like the latest members of *M. intermedius per se*, and is still found in the composition of microtine faunas from the end of the Early Pleistocene. An independent species status cannot be excluded. At the same time, it hardly differs from “*Clethrionomys*” *erli* Brunner (1936)—length of M_1 —2.0–2.45 mm, roots of M_3 on labial side of incisor—from the Late Würm (pre-Riss ?) mixed faunas of the FRG. If its identity is confirmed in the future, then this discovery should be considered the latest find of fossil remains of *Mimomys* known to the present time. *M. simplex* Kretzoi, 1954 from the Late Pleistocene fauna of Kishlang (Hungary) can hardly be considered an independent species; the only known M_1 barely differs from a similar tooth of an old individual of *M. pusillus*.

It should be kept in mind, however, that the discovery and study of fossils of the skull of the forms presented above, may compel us to alter our view regarding their taxonomic status and to differently assess the nature of change of various characters in time and space. Presently, the known type of variability appears to correspond most to chronocline variability of a single, widely understood species.

Group *intermedius*

6. *Mimomys* (? *Microtomys*) *pseudintermedius*

Erbajeva, 1976

Diagnosis: Dimensions close to those of preceding species. Length of lower molar row less than 7.0 mm (5.5, 5.9, 6.2 mm); M_1 —not more than 3.0 mm; 2.2–2.6–2.8 ($n = 8$). Cementation in fold of molars minimal; time of commencement of deposition not known. “Island” on paraconid section of M_1 not detected in material available. Prismatic fold wedges out approximately at one-third crown height and absent in old individuals. Enamel thins only in folds of molars. Triangles of masticatory surface of lower molars isolated on M_1 and broadly fused on M_2 and M_3 . Incisor passes under posterior root of M_2 . Structure of upper molars not reliably known.

Composition of species: Subspecies not described. It is quite possible that *M. antis* Savinov and Lytshev, 1970; *M. irtyschensis* Zazhigin, in litt.; and *M. gansunicus* Zheng, 1976 are no more than Asian Late Pleistocene subspecies of this species. If this is so, the name *antis* has priority over the other two.

Age and distribution: Late Pliocene to Ancient Pleistocene (Khaprovsk *Mimomys* fauna) from western Siberia up to Kolyma depression. Some archaic forms of the *intermedius* group are also present in the Late Pliocene of Moldavia; however, to date they have not been reported from the comparatively well-studied Pliocene theriofaunas of Western Europe.

Taxonomic notes: The species is probably ancestral to the later species, *M. intermedius*. The most archaic features are reported for the sparsely cemented species, *M. antis* and *M. irtyshenis*. There is a *Mimomys*-like fold which extends to base of crown (isolated M_1 of latter species known), a presence of three roots on at least some upper molars, comparatively short dentine tracts, and a presence of posterior "island" on M^3 (*M. antis*). Like *M. intermedius* and later faunas of Western Europe, *M. pseudintermedius* is found at least in the Trans-Baikal region together with *M. reidi* (*newtoni*, according to the classification here). However, M.A. Erbaeva (Bazarov, Erbaeva and Rezanov, 1976) has reliably identified a large number of M_1 of this species in this area: they have a well-differentiated enamel, are roughly equal in depth on lateral and medial folds of M_1 ; there is a correspondingly longer prismatic fold, retained in older individuals and cement is deposited at much later stage. Voles from the *intermedius* group likewise are found in the late vole faunas of the *newtoni*–*reidi* group and the probable offspring of *M. pseudintermedius*, but are readily separated in the series.

7. *Mimomys (Microtomys) intermedius* Newton, 1881
(= *savini* Hinton, 1910; = *milleri* Kretzoi, 1958)

Diagnosis: Size variable; medium and large animals dominant. In larger animals, length of lower molar row at least 7.0 mm (7.4–8.0 mm); M_1 at least 3.0 mm (3.05–3.7 mm). In smaller forms, lower molar row may not reach 6.0 mm, and M_1 —3.0 mm and not greater than size of species of the *newtoni*–*pusillus* group (2.4–2.7–3.1 mm in *M. i. parvus* Suchov). Cement abundant in folds of molars, appears thick before root initiation. "Island" on paraconid section of M_1 absent and, possibly, its structure primarily simple. Prismatic fold absent (morphotype *intermedius*) or reduced and barely formed in most individuals (morphotype *savini*), disappearing rapidly with wear. Enamel always distinctly differentiated. Triangles of masticatory surface of M_1 either completely isolated (typical structure, or just barely fused); anterior pair may be fused on M_2 , and always fused on M_3 . Incisor passes between roots of M_2

and M_3 . Traces of third root sometimes also observed on M^1 , but it has no independent socket in alveolus.

Composition of species: *M. i. intermedius* Newton, 1881 (Early Pleistocene, Western and eastern Europe and southwestern Ukraine); *M. i. kislansensis* Kretzoi, 1958 (second half of Early Pleistocene, southeastern Europe, western Ukraine, and Black Sea region); *M. i. meridionalis* Topačevskii, 1973 (end of Early Pleistocene, southern Ukraine; Topačevskii, 1973); and *M. i. parvus* Suchov, 1970 (Early Pleistocene, Ufa area of Ural region).

Age and distribution: Late Pliocene to Early Pleistocene. From France and southwestern England, mountains of Kuznetsk Alatau and between 42 and 52° W and 42 and 52° E (Trans-Ural region).

In the USSR, it is the typical form of the Tamansk and Tiraspol' faunas; however, in Western Europe, it hardly survived to the extinction of analogues of the latter [Tiraspol' fauna]. Janossy (1969) proposed the demarcation of boundaries between the Early and Middle Pleistocene in which fossils of species from the *intermedius* group are already present.

Taxonomic notes: Several paleomammalogists, including those who in recent years have reexamined the original material of Hinton in the British Museum, propose that the species *M. savini*, *M. intermedius*, and *M. majori* are no more than forms representing the range of variability of a single species—individual variability for the first two and also age-dependent variability for the latter. This point of view is clearly stated by Kretzoi (1965b) and Thaler (1966). Following the example of Topačevskii (1965) and Zazhigin (1975), most Soviet paleomammalogists are of the same opinion. Such a broadly understood species would exhibit regular
235 chronoclinical variability, in particular, of such characters as size and extent of development of prismatic fold. This is partly reflected in subspecies classification presented here. However, the question remains unsolved about the primary or secondary simplified structure of the paraconid of M_1 . The former is possible if the prismatic fold of *M. intermedius* is a pseudofold (juvenile) and not a shortened and reduced true fold. If the latter is correct, we have to accept that the paraconid of this species underwent simplification for the second time, and the "island" had disappeared here already at the later stages of embryogenesis. This question acquires fundamental importance since, based on characters of a primarily simple structure of the paraconid, some authors (Zazhigin, 1975) include microtines of the *intermedius* group under the independent genus *Cromeromys*. Moreover, as rightly pointed out by Kretzoi (1965b),

recognizing all three species as variants of a single species is correct only if in the future it is found that they do not differ in skull structure.

The question of the affinities of the group is likewise unresolved. They are related either to the *newtoni-pusillus* group through some form of *M. irtyshensis* Zazhigin (in litt.) or with *M. pseudintermedius* Erbajeva, 1976, or with the *pliocaenicus* group, as was earlier proposed by Hinton (1926) also.

8. *Mimomys* (? *Microtomys*) *cantianus* Hinton, 1910

An insufficiently studied form, and later member than other species of the *intermedius* group. It is known from a small number of fossils from deposits of the upper terrace of the Thames (second half of the Early to Middle Pleistocene). It is identical with *M. majori* in structure of the paraconid section; however, roots are initiated later: in the specimens available, closure of the grooves of folds in the molar section of M_1 is just barely perceptible. The question of the taxonomic status of this species is resolvable only with additional study of new material from the type locality (Kretzoi, 1965b). To avoid creating redundant (nomen nudem) names for fossils from the USSR, under *M. cantianus* we may also include the Late Tiraspol' *Cromeromys*, which are transitional to the rooted-molar forms of the genus. Incidentally, some authors have already named this species *Arvicola contiana* (Sutcliffe and Kowalski, 1976).

9. Genus *Arvicola* Lacépède, 1799—Water Voles

Description: Body length up to 250 mm. Color dark brown to almost black, slightly lighter on ventral side. Tail up to two-thirds trunk length, covered with short, stiff, sparse hairs, at times with sparse, brush-like terminal cluster. Eyes medium in size. Pinna small, with poorly pubescent lobe, completely covered toward front with dense bundle of hairs. Helix poorly developed; antitragus well-developed, rectangular or triangular in shape and, unlike in most other microtines, tragus definitely covers opening of auditory meatus. Upper alae nasalis sharply isolated from middle lobe of lower alae nasalis; maximum distance between lateral ends of former at least twice combined width of middle lobe of latter. Narial pit almost closed; exterior opening in form of narrow deep slit. Length of fused region of upper lips reduced, not more than width of upper incisor. Upper labial flaps rectangular, with short region of con-

236 tact, densely covered with hairs. Among the transverse ridges of soft palate, only anterior one entire, second one almost completely interrupted, third one always interrupted. Postpalatal folds four. Head with complete set of vibrissae; mental and corner vibrissae of lower lip particularly well-developed. Carpal vibrissae reduced.

Forelimbs relatively longer than in any other microtines (up to 95% trunk length); size of hind limbs only slightly greater than mean length for subfamily. Foot, unlike ankle, relatively long, although not wider than in species of *Microtus*. Palm and sole glabrous. Metatarsal calluses well-developed, especially on forelimbs: two carpal pads present, one metatarsal. Dense lateral fringe present on hind foot, thinner fringe on forefoot (besides *Arvicola*, found only in *Ondatra*). Third digit of both feet longest, 4th digit longer than 2nd on forefeet but equal on hind. Highly reduced pollex of forelimb with small flat claw; claws on 2nd and 4th digits longest, reaching half digital length. Claws on hind limbs not longer than on forelimbs, much shorter than half digital length, and slightly curved.

Profile and general proportions of skull similar to those of larger species of the subgenus *Microtus*. Dorsal profile with slight dip at bases of zygomatic arches and with barely perceptible depression in interorbital region. Length of brain case much greater than width, its upper surface flattened. Vertical crests well-defined and form distinct border on upper and lateral surfaces of brain case. Interorbital crests distinct. Profile of skull in region of zygomatic arches more or less rounded, without perceptible posterior widening or narrowing.

Orbit large; its plane forms angle of about 30° with horizontal plane—an index close to mean value for microtines, as are height and proportions of masseteric plate of maxilla and magnitude of dihedral angle formed by it with sagittal plane. Auditory bullae small; spongy bony tissue present only along their walls and does not fill cavity.

Relative size of molar row within limits of mean values for the subfamily. M_1 and M^3 not elongate. Molars rootless, with high crowns (higher only in *Neofiber* and *Ondatra*). Enamel differs in thickness in ancient forms, possibly in direct late descendants of *Mimomys*—since in the latter and in geologically younger descendants belonging to *Arvicola* s. str., the ratio is reversed: enamel on lower molars thicker on posterior side of triangles and thinner on anterior. This species was first described by Heller (1969). There is no difference in size of lateral and medial triangles of the masti-

catory surface. Neither formation of additional elements on upper molars nor reduction in lateral triangles on lower molars observed. Opposite triangles fused only in anterior sections of M_2 and M_3 . M_3 not shifted inward and aligned with M_1 – M_2 ; alveolus of M_3 isolated only in lower section and does not protrude downward beyond margin of jaw. Crowns of incisors long, their proportions medium. Lower incisor forms well-developed knob at half length of articular process. Facing angle of incisors small. Steepness of curvature of lower incisors moderate for subfamily, for upper, close to minimum in tribe (less only in *Blanfordimys* and *Pitymys* from the *ibericus* group).

237 Skeleton of forelimbs characterized by relatively long humerus with broad head and high crest on inner side. Ulna narrow, diaphysis lower. Pelvis long (longer only in *Ondatra*). Femur slightly reduced, tarsus markedly so. Femur and tibia with broad lower sections; former also with long collar (relatively longer than in other microtines).

Variability: Size increases in a southerly direction, Pleistocene to Recent. The degree of expression of a fossorial morphotype skull structure also reduces in a southerly direction in present-day populations. In mountains (e.g., Caucasus), size decreases with altitude, and the importance of a fossorial morphotype increases.

During the Pleistocene, besides an increase in dimensions, a general reduction in number of morphotypes of M_1 and M^3 also took place, the relative abundance of typical Pleistocene morphotypes decreased or disappeared, and a new morphotype appeared. This restructuring, reflecting changes in the nature of the trophic relationship of the species, took place more intensely in the western than eastern part of the range (Maleeva and Popova, 1975).

Some characteristics of change with time and in structure of other parts of the skull are likewise notable. They were described by me (Gromov, 1957b, 1961) and by Tropin (1975) for water voles of the present steppe and desert-steppe environments for the southern European part of the USSR in the Middle Pleistocene to Early Holocene. Juvenile structural features disappeared during this time; the facial section, judging from increased relative length of the diastema, elongated; the relative length of the lower molar row decreased; M_1 increased; and the lower incisor became stronger and more smoothly curved. Taxonomic assessment of the various combinations of the characters mentioned above, as in the case of others not displaying a unidirectional change, but indicating suffi-

ciently convincing differences in individual chronopopulations, is a subject for future study.

Composition of genus: Two present-day species—*A. terrestris* L., 1758 and *A. sapidus* Miller, 1908 (Reichstein, 1963). From Western Europe, several extinct species have also been described: *A. bactonensis* Hinton, 1926; *A. abbotti* Hinton, 1910; *A. mosbachensis* Schmidtgen, 1911; *A. antiquus* Pomel, 1853; *A. greenii* Hinton, 1926; *A. praeceptor* Hinton, 1926; *A. gracilis* Heller, 1955; *A. weiheimensis* Heller, 1962; *A. moenana* Heller, 1969; *A. chosaricus* Alexandrova, 1976; and *A. kalmanckensis* Zazhigin (in litt.). However, after the work of Hinton (1926), the taxonomy of extinct water voles was reexamined only in part (Heller, 1969; Koenigswald, 1973) and that of Russian fauna not analyzed at all except to separate some tentative forms on the basis of Late Pleistocene material from the southern European part of the USSR, Trans-Ural region, and a recent description of the Hazari form. One difficulty is that the small-sized *Arvicola* and the large *Allophaiomys* with an M_1 slightly longer than 3.0 mm, are probably not distinguishable on the basis of isolated teeth, if we exclude the often poorly detectable difference in nature of enamel differentiation. Extinct *Arvicola* are thus described here based on the above-mentioned publications and on new data compiled by Maleeva and Popova (1975).

The independent generic status of *Arvicola* is presently undisputed by mammalogists. It was earlier rejected by Heptner (1952) but his arguments were not convincing, as pointed out by Zimmermann (1955a).

Distribution and zonal affinity: Voles of this genus are inhabitants of meadows, bogs, and various marshy biotopes (including shrubs) in the floodplains of large rivers, along banks of lakes, small rivers, and rivulets as well as marshland forests in all vertical environments except deserts of the southern type, Arctic tundra, and the subnival zone. It is found in mountains up to 3,200 m above msl, from the Pyrenees to western Trans-Baikal, central and southern parts of Verkhoyansk range, and eastern Aldan region. Southward, found up to northern coast of the Mediterranean and Black Sea, northwestern Asia east to northwestern Iran, northern and eastern Kazakhstan, northwestern China, and Mongolia. It is absent in the Far Eastern Palearctic as well as in North America, where large species of *Microtus* lead a similar life style. It is also interesting to note that the eastern boundary of the water vole's range coincides in the extreme southeastern region with that of the western bandicoot rat (*Nesokia*), studied by Lay (1967).

It has been observed that fluctuations in the coastline and desiccation of inland reservoirs due to climatic changes and transgressions, somewhat altered the southern boundary of the water vole's range in the Caspian and northern Kazakhstan region in the second half of the Pleistocene and in the Holocene (Tropin, 1969). It is quite likely that similar changes occurred in other parts of the range during the Pleistocene.

Evolution and phylogeny: Fossil remains are known from the beginning of the Early Pleistocene (Western Europe) and from its second half (the Tiraspol' fauna in the USSR), together with the first finds of voles with rooted molars of the genera *Allophaiomys* and *Microtus* and the later rooted-molar *Mimomys*. The direct origin of species of *Arvicola* from latter forms of the latter genus belonging to the *intermedius* group, as a result of loss of roots is well-known; the initiation of roots dates back in geological time to later phases of individual development. According to one extreme opinion (Heller, 1969), each form in this group—*intermedius*, *majori*, and *savini*—as understood by Hinton, corresponds to its own form [species of *Arvicola*: *bactonensis* (= *mosbachensis*), *greenii*, and *moenana*, respectively]. If all the aforementioned forms of *Mimomys* are considered morphotypes of a single species, one species of *Arvicola* ought to correspond to it which, on the basis of the Law of Priority, should be named *A. mosbachensis* Schmidtgen, 1911. Chaline (1972) reached this same conclusion through biometric studies of material from France. Yet, as correctly noted by Heller (1969), true water voles are characterized by differentiation of enamel, which is not true of late *Mimomys*, early species of *Arvicola*, nor closely related ancient forms.

If we consider the time of the first discovery of the fossils of the genus, it may be that the process of root loss took place earlier in the east than in the west, and that the water vole appeared later in the forest biomes of the north than in the south. Probably the totality of adaptations to an amphibious life style was more effective in *Arvicola* than in the probably extinct amphibious *Allophaiomys*; thus the former rapidly pushed the latter initially westward and then eastward within its range. There is no doubt that the totality of characters not repeated in other species of the tribe, together with features typical of this genus alone (structure of the pinna, soft palate, features of venous circulation, and so forth), were decisive in complete utilization of the natural possibilities of bog and coastal biotopes in a highly variable environment, even though *Arvicola* have not reached the level of specialization found in *Ondatra*.

1. conf. *Arvicola mosbachensis* Schmidtgen, 1911 (foss.)

Size smaller than in small present-day forms of the genus: length of upper molar row 6.0 to 7.0 mm (at masticatory surface); 239 M_1 —3.0 to 3.4–3.7 mm (Heller, 1969; number of specimens measured not indicated, more than 70 lower molars studied).

In structure of M_1 , this species does not differ from *Mimomys intermedius*, except in absence of roots. According to Hinton (1926), like the ancestral species, it shows secondary simplification of the paraconid section of M_1 with the “island” having disappeared and total absence of the prismatic fold, thereby differing from all known present-day and extinct members of *Arvicola*. Hinton has also pointed out the similarity in structure of the limb bones with those of *Mimomys intermedius* and the weakly expressed features of *Arvicola*.

Fossils found in the Ancient to Early Pleistocene deposits of eastern England and Mosbach (FRG), sands of continental Europe, and analogues of Tiraspol’ gravel (Early Pleistocene). Chaline (1972) also included under this species the Middle Pleistocene water voles of France. *A. weinheimsis* Heller, 1969, described from a single M_1 from the Early Pleistocene sands of Weinheim (FRG), is possibly no more than an old specimen of *A. mosbachensis*. The characters of *A. moenana* Heller, 1969, under which the author included a single M_1 from the middle level of the Mosbach sands, with a poorly developed prismatic fold, especially in the anterior section, are hardly more than indices of morphotypic variability of *A. mosbachensis*.

2. conf. *Arvicola greenii* Hinton, 1926 (? = *bactonensis* Hinton, 1926) (foss.)

Described on the basis of isolated molars from the Mosbach sands and considered a direct descendant of *M. majori*. Heller’s (1969) dimensions for M_1 (3.0–3.3–3.6 mm) are similar to those of the preceding species. In the opinion of the author of the species, the anterolateral fold of M_1 , as in the case of its rooted-molar ancestor, is deep, closing to form an “island,” and in the majority of individuals, the anterior margin of the anterolateral prism has a prismatic fold. Thus, Hinton recognized two lines of evolution among large rootless-molar microtines from rooted-molar forms of the *intermedius* group, from which the *majori*–*greenii* line gave rise to the true *Arvicola*. However, we must mention that Topachevskii (1965) has pointed out that he detected the prismatic fold on the paraconid section of M_1 , an archaic feature of the teeth of *Arvicola* from the Middle Pleistocene deposit of the Dnieper.

A somewhat larger form, similar to *A. greenii*, with long upper and lower molars, about 7.5 mm, and M_1 —3.7—4.0 mm from Late to Early Pleistocene deposits of England (middle terrace of the Thames) and continental Europe (northern Italy), are included under a separate species—*A. bactonensis* Hinton, 1926. Some authors consider the undifferentiated enamel of this species an index of transition from the *Mimomys*-type differentiation to the reverse differentiation that is typical of *Arvicola*.

3. *Arvicola chosaricus* Alexandrova, 1976 (foss.)

Diagnosis: Dimensions smaller than in the present-day species of *Arvicola* from the Lower Volga region: length of M_1 —3.5—3.9 mm ($n = 5$), almost similar to *A. bactonensis* from the close of the Early Pleistocene. Paraconid section relatively shorter: 39—42% molar length versus 45—48% in present-day species, and height of crown much smaller. Similarly, in water voles of the *greenii* group, the anterolateral fold is deep, but the prismatic fold absent, and the enamel poorly differentiated.

240 *Age and distribution:* From Middle Pleistocene, southeastern Europe (lower reaches of Volga); described from Chernoyarsk sands, stratotype of Hazari faunas.

Taxonomic notes: I consider this species a descendant of *Mimomys majori* and an ancestor of *Arvicola terrestris*. It is closest to *A. bactonensis*, as well as to water voles from the predominantly Middle Pleistocene deposits of the Urals and Don; among these remains the dominant type of structure is characterized by strong isolation of the anterior unpaired loop of M_1 from the lateral side (Gromov, 1957c).

4. *Arvicola abbotti* Hinton, 1910 (foss.)

Described from the Late Pleistocene deposits, forming karst holes in the limestone in Kent (England): its remains are known from several places in the British Isles. In skull structure, combines characters of present-day amphibious (morphotype *amphibius*) and fossorial (morphotype *scherman*) members of the species *A. terrestris*. Length of upper molar row 9.5 mm (holotype), 9.5, 9.4, 9.4 mm; length of lower row 9.4, 10.3 mm. Judging from skull structural features, characterized by smaller eyes than in *A. terrestris*, smaller pinna, as well as forwardly directed upper incisors, barely perceptible alveolar knob on the mandible, and a small angular process.

In continental Europe (France, FRG), the Late Pleistocene water vole is similar to *A. abbotti*, and was designated *A. antiquus* Pomel, 1853. Thus, Storch (1971) proposed that this form be used to designate Late Pleistocene water voles of mixed and lemming faunas of England and continental Western Europe, which became extinct during Holocene reforestation, and were subsequently replaced by *A. terrestris*. The different values for width of nasals given by Hinton and Storch prevent me from considering *A. abbotti* and *A. antiquus* identical, in which case the former would be synonym of the latter (the taxonomic importance of this character was noted by Reichstein, 1963). Hinton, who studied the regional material of *A. antiquus* from France, wrote about the narrow nasals while Storch reports that they are broad (remains from upper reaches of the Danube).

5. *Arvicola gracilis* Heller, 1955 (foss.)

A small *Arvicola* (length of lower molar row 7.1 mm) from the Late Pleistocene (Würm) deposits of the Weinberg mountains in the Franconian, Elbe (FRG), was separated as an independent species by Heller (1955). Enamel less well-differentiated than in the present-day species, lower incisor shorter and posterior end does not form such a distinct alveolar knob, and articular process correspondingly incurved. The author considers this species close to *A. scherman*; however, from the features presented, it is not clear whether the juvenile characters mentioned by him are due to age or are of taxonomic importance. With only a single mandibular ramus known, the question remains unsolved.

6. *Arvicola sapidus* Miller, 1908

Diagnosis: Size large. Body length 187–220 mm, tail 112–127 mm, lower molar row 10.0–10.7 mm. Skull with relatively long brain case, absolutely and relatively long tooth row and incisor alveoli, and broad nasals. Only the latter of these characters does not overlap in numerical values with those of the next species (Reichstein, 1963). Diploid number of chromosomes, 60.

241 *Composition of species*: Two subspecies are described—*A. s. sapidus* Miller, 1910 and *A. s. tenebricus* Miller, 1910.

Distribution and zonal affinity: Inhabits banks of various kinds of flowing and stagnant water bodies throughout Spain and France, except western regions of the latter (Giban and Spitz, 1967).

Evolution and phylogeny: Fossil remains are not known. It is probable that it represents a relict form which was not subjected

to Pleistocene glaciation from the Iberian peninsula and, possibly, in southern France, and later all of France. In overlapping areas of the range of the next species, this species is ecologically isolated since *A. terrestris* is a "fossorial" form. Chaline (1972) assumes that isolation of the two present-day species took place in the Middle Pleistocene.

7. *Arvicola terrestris* L., 1758 (Figure 38)

Diagnosis: Size variable. In large forms body length 108–205 mm, tail 106–131 mm, lower molar row most often 9–10 mm; in small forms, these values are respectively 130–190 mm, 75–125 mm, 9.0 mm; M_1 —3.6–4.1 mm in small forms and up to 4.5 mm in large ones. Skull with relatively short brain case, absolutely and relatively short tooth row, narrow incisor alveoli, and barely broadened nasals (anterior end). Diploid number of chromosomes, 36.

Composition of species and variability: The subspecies listed by various authors are manifold. Ellerman (1941) indicated 25 subspecies, of which, based on an older work of Ognev (1933), 20 are reported for the USSR; *A. amphibius* and *A. scherman* with three subspecies each are recognized as independent species. Ognev (1950) listed 15 subspecies; only *A. scherman* is considered an independent species.

The same number of subspecies, including *A. scherman*, was given in the monograph *Mammals in the Fauna of the USSR* (Gromov *et al.*, 1963). Bobrinskii, Kuznetsov and Kuzyakin (1965) have listed seven subspecies, including *A. scherman*. Analysis of the West European forms of *A. terrestris* was done by Reichstein (1963) but the actual number of subspecies is not yet clear; there may be no more than ten. Either way, the question requires special study, primarily of the already large collection of material. Resolution of the problem is complicated by the fact that the species exhibits an exclusively wide age-dependent and population variability in characters used in taxonomy. These variabilities often overlap geographic variability (Panteleev and Terekhina, 1976). This is particularly true of the degree of expression of juvenile features in adult individuals as well as of characters typical of "swimming" and "digging" morphotypes and the ratio of corresponding individuals in a population of the subspecies. Both these facts are intimately linked with the solution to the question of the independent species status of *A. scherman*.

In the western part of the range, one more difficulty arises: here several features of the southern forms undergo changes similar to

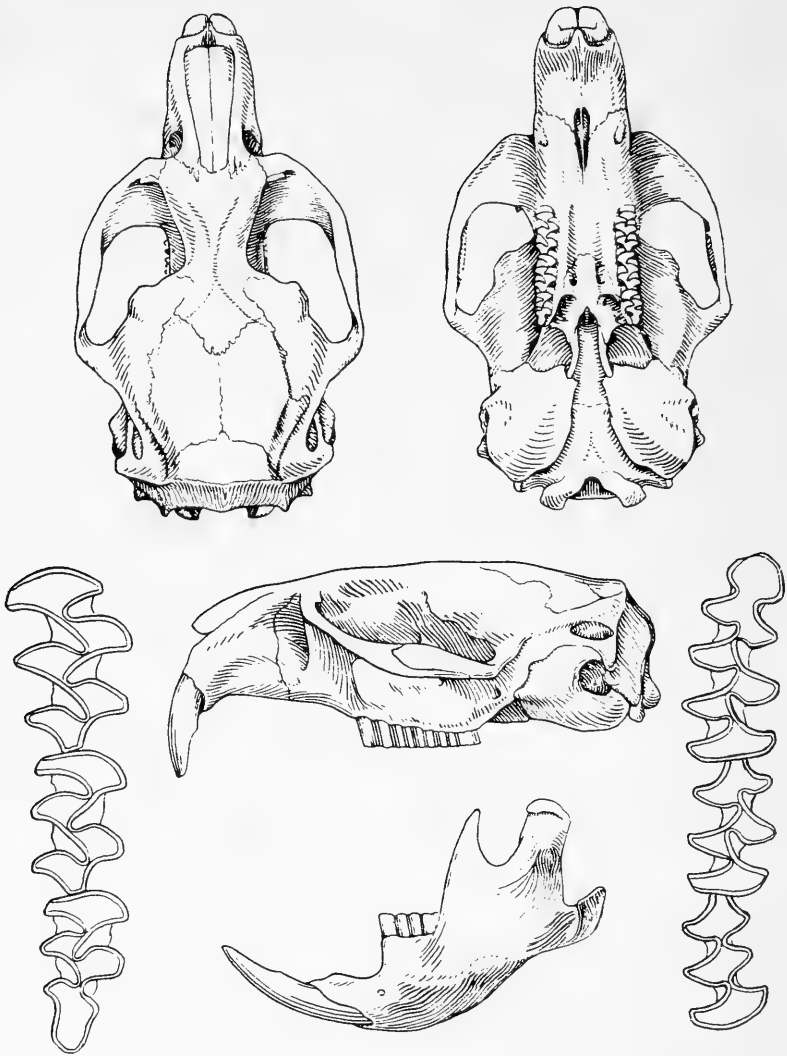


Figure 38. Water vole (*Arvicola terrestris* L.).

those in *A. sapidus*.

Subspecies of *A. terrestris* have been grouped here following B.A. Kuznetsov. In my opinion, it presently takes into account—better than any other grouping—the environmental and geographic aspects of populations of the species in the USSR: *A. t. terrestris* L., 1758 (forest zone of European part of the

USSR and northern part of Western Europe); *A. t. meridionalis* Ognev, 1923 (forest-steppe and steppe of European part of the USSR, western Siberia, and western Kazakhstan); *A. t. pallasii* Ognev, 1913 (northern Siberia and the Urals up to Yakutia); *A. t. variabilis* Ognev, 1928 (southern Siberia, northeastern Kazakhstan, and rarely, northern Mongolia); *A. t. scyntheticus* Thomas, 1914 (southern Kazakhstan, Kirgizia); *A. t. persicus* de Filippi, 1866 (Trans-Caucasus, northern Iran; each of the five subspecies described for the northern part of the Caucasian Isthmus and the main Caucasian range requires special study to ascertain its subspecific status); *A. t. hintoni* Aharoni, 1932 (northern Syria); and *A. t. scherman* Shaw, 1801 (western Ukraine, Moldavia, possibly southern Belorussia, montane region of Western Europe). In Western Europe, *A. t. amphibius* L., 1858 (England); *A. t. reta* Miller, 1910 (Ireland); *A. t. italicus* Savi, 1839 (Italy); and *A. t. exitus* Miller, 1910 (Switzerland) are separated. The taxonomic status of *A. t. corabensis* V. and E. Martino, 1937 (Macedonia) and several other forms, including those from the Balkan Peninsula, require special investigation.

Distribution and zonal affinity: Same as for genus.

Evolution and phylogeny: In spite of the abundance of fossils of water voles in all deposits, beginning from the Late Pleistocene, the time of probable separation of the species has yet to be established, and the main reasons for this have been indicated above. I feel that the independent species status of the small water vole *A. scherman* still remains an enigma. Most Western European mammalogists consider it a subspecies of *A. terrestris*. One important reason for such an opinion is the similarity of diploid number of chromosomes and free crossing of forms. Actually (usually) if rodents within the limits of a genus exhibit a species differentiation for this parameter, then the similarity of the two forms reliably determines their intraspecific status. However, exceptions to this rule are also known. Either way, the central European water voles must have passed through a complex Pleistocene evolution, being compressed in the periods of glaciation between the boundaries of the Scandinavian and Alpine glaciers. As rightly stated by Stein (1962), the diminutive glacial form (*A. antiquus* Pomel ?) from the "Snowy Alps" (in Darwin's sense), which occupied montane terrain during the postglacial period, including the northern slopes of the Alps, was pushed there by a larger form spreading from the east. However, Stein does not consider *A. scherman* even a subspecies, but simply a mixed montane middle European population of two

subspecies of *A. terrestris*, the smaller one of which he named *A. t. exitus* Miller. However, it should be kept in mind that the author worked only with dimensions and Reichstein (1963) only with a few craniometric parameters. The differences may be much finer and may reflect the initial stage of species differentiation of a prespecies nature (species "*in statu nascendi*"). The problem is further compounded because the large-sized *A. terrestris* also forms small and large races in time as well as in space over its present-day range. The larger race might possibly and more rightly be considered a morphotype of the two biotopic populations.

10. Genus *Proedromys* Thomas, 1911

Description: Voles not distinguishable in external features from the short-tailed and short-eared forms of the genus *Microtus*. In skull structure, the following features have been noted (Thomas, 1911a): (1) presence of groove-like depressions along the anterior surface of strongly curved upper incisors; (2) short lower incisors that do not extend very far into the articular process of the jaw; and (3) M^3 with simplified structure: medial side with only one fold and two denticles. Other features of the skull are not distinctive. Skull massive, frontotemporal crests probably fuse with age with interorbital space into longitudinal crest. Auditory bullae not enlarged, their walls formed by a loose large-celled bony tissue. Molars rootless, cement present, enamel well-differentiated. Paracoid section of M_1 with one fold, its lateral triangle isolated from anterior unpaired loop, and latter fused with medial triangle. M_3 without anterolateral denticle.

Composition of genus: One present-day species: *P. bedfordi* Thomas, 1911.

Distribution and zonal affinity: Known from a single specimen from China (Hanshu Province). Life style not described.

Evolution and phylogeny: Fossil remains not found. Judging from the structural features mentioned above, this might possibly constitute a relict group of microtines, the affinities of which are not known.

11. Genus *Allophaiomys* Kormos, 1932 (foss.)

Diagnosis: Voles with rootless molars, with abundant cement on lateral surfaces. Size comparable to medium-sized *Microtus* (length of M_1-M_3 —5.2–6.3 mm; M^1-M^3 —5.4–6.4 mm). Incisor

alveoli comparatively long (more than 60% diastemal length), barely narrowed posteriorly, and almost extend to anterior margin of alveolus of M^1 . Deep groove present between lower surface of alveolar sockets of M_3 and margin of angular process commencing from its anterior margin. Postpalatal pits large, widely open posteriorly. Enamel in ancient forms undifferentiated, in later forms thins only in upper folds; thinning just barely perceptible in inner part of posterior walls of prisms on lower molars and anterior part of upper molars. In later members of the genus, differentiation of enamel complete.⁵ Lobes of masticatory surface, except those of middle pair of M_3 isolated. Fusion, if occurs (more often on M_2), not greater than thickness of enamel. M_1 with incomplete primary fold of paraconid section; in some populations cingulum of anterior unpaired loop tends to elongate; shape of loop variable. M^3 with three denticles on both lateral and medial sides. Alveolus of lower incisor, in a typical case, forms a common margin posteriorly with posterior margin of articular process over more than half its length and, sometimes, also a distinct bulge.

Composition of genus: Four species have been described: *A. pliocaenicus* Kormos, 1932 and *A. laguroides* Kormos, 1932 (first half of Early Pleistocene, Hungary); *A. ruffosi* Pasa, 1947 (Early Pleistocene, Italy); and *A. deucalion* Kretzoi, 1969 (end of Early Pleistocene, Hungary). Probably, "*Arvicola*" *terrae-rubrae* Teilhard, 1940 should also be included (end of Ancient Pleistocene, China) under this genus. The independent status of the first two species was not confirmed on the basis of new material (Terzea and Juresak, 1967). It is not certain whether the distinguishing features of the other two European forms are no more than an index of individual and often partly chronoclinal variability.

Age and distribution: End of Ancient (?), Early (Tamansk as well as ancient and developed Tiraspol' faunas) Pleistocene. In the west, possibly up to beginning of Middle Pleistocene. From France and Holland (Meulen and Zagwijn, 1974) and Italy to Trans-Baikal and China.

Taxonomic notes and evolution: This genus comprises the first voles with rootless molars known from Eurasia to date. Based on

⁵Zazhigin (1975), working with material from western Siberia, paid attention to the fact that the enamel in most ancient members of *Allophaiomys* is differentiated as in "*Mimomys*", i.e., thinner on anterior walls of lower molars and posterior walls of upper molars. Thereafter, as in the case of evolution of *Arvicola*, differentiation in a reverse direction takes place, passing through the stage of undifferentiated enamel.

isolated molars, the diminutive forms, in which the length of M_1 is less than 3.0 mm, may be indistinguishable from *Phaiomys*, and the larger forms from diminutive *Arvicola*. Chaline's proposal (1972) that *Allophaiomys* be considered a subgenus of *Microtus* has not been pursued by the author himself.

245 More than ten years ago Topachevskii (1965) had already clearly indicated the probable relationship between *Allophaiomys* and *Microtus*. European paleomammalogists, in particular Chaline (1966, 1972), and earlier Kowalski (1960b), as well as Terzea (1970) and others expressed the same view. The most "universal" understanding about *Allophaiomys* as the progenitor of most rootless-molar microtines of the tribe Arvicolini (except genus *Arvicola*) has been provided by Chaline. Actually the intra- and interpopulation variability in structure of M_1 of *Allophaiomys* is such that with changes in time of the dominant morphotype in the case of direct (phyletic) evolution, or in the case of population segregation, selection of any of these tooth types in various members of *Microtus*, *Pitymys*, *Stenocranius*, *Neodon* (*Phaiomys*), *Chionomys*, and members of other supraspecific taxa is readily derived, and an apparent diphyletic origin of *Microtus* s. str. and *Pitymys* can likewise be illustrated, in accordance with Chaline's theory. However, equating the evolution of teeth with the evolution of taxa is rather risky, especially since the parallel variability may be quite significant.

As for the probable closest rooted-molar ancestor of the genus, so far we have had no clear idea of where to begin the search among ancient microtines. Chaline (1972) has proposed some *Vilanya* of the *lagurodontoides* group (*fejervaryi* according to our nomenclature here). Among present-day arvicolins, the closest to *Allophaiomys* in level of molar evolution are the Central Asian *Phaiomys* and *Lasiopodomys*; *Pitymys* from the *ibericus* group are also at this stage.

1. *Allophaiomys pliocaenicus* Kormos, 1932

Description of holotype: Based on fragment of bony palate of immature individual (No. 3816/1 in Kormos' collection, Natural History Museum, Budapest). Incisor section possibly fitted after diagram prepared (Kormos, 1932b, p. 327, Figure 1). Dimensions of holotype: length of M^1-M^3 —6.1 mm, M^1-M^2 —4.25 mm, diastema—7.1 mm, incisor alveoli—7.65 mm, width of bony palate between inner margins of alveoli of M^1 —1.75 mm. Paratypes (according to Kormos): length of M^1-M^3 —5.8–6.4 mm, M_1-M_3 —6.0–6.3 mm.

Based on data on the evolution of chromosomal sets in microtines, an attempt was made to determine the probable chromosome number in species of this genus (Chaline and Matthey, 1971). It is proposed that $2n = 56$.

Composition of species: Up to four subspecies have been mentioned: *A. p. pliocaenicus* Kormos, 1932 and *A. p. laguroides* Kormos, 1932 (first half of Early Pleistocene, Hungary); *A. p. nutriensis* Chaline, 1972; and *A. p. pitymioides* Chaline, 1972 [beginning of Middle (?) Pleistocene, France].

Description: Structure of bony palate similar to specialized microtines (*Arvicola*, *Stenocranius*); anterior margin of postpalatal pit slightly short of posterior margin of M^2 ; palatomaxillary suture almost at level of its anterior margin. Paired longitudinal depression of bony palate shallow but distinct; median crest poorly developed. Kormos indicated smoothly curved incisors, with crowns of lower ones shorter than in *Phaiomys* and *Arvicola*. Alveolar knob of lower incisors small, located on posterior margin of articular process above dental foramen. Posterior notch of lower jaw small; coronoid directed more smoothly downward than in the aforementioned microtines. Comparatively thin enamel noted in molars. Broad but sharp triangles, apically rounded, with broad folds between them; hence tooth appears "elongate" as in lagurids; similar to latter, posterior ends of M^1 – M^2 backwardly elongate. Furthermore, in these teeth the anterior margin of the medial triangles slopes backward and bears additional rounded processes, in which the corresponding ridges are separated along the walls of the prisms.

Age and distribution: The age is same as for genus. Species are described from caves in Betfia X (Pushpekfurd) in western Rumania (Episkopia). The distribution is the same as for genus. In 246 the USSR, north up to Ufa latitude, eastern European part, and southern Kulunda, Yubinsk, area of Irtysh and Trans-Baikal in Asian part; remains are known almost exclusively from these localities in river alluvia.

Taxonomic notes: Soviet paleomammalogists usually refrain from taxonomic designations of individual populations of this fairly widely distributed species and instead describe aspects of morphotypic variability of their molars (Topachevskii, 1973) and preferring to use open nomenclature in naming the populations. This is quite justified since to date remains of the skull are known only from the type locality.

The unusually broad interpretation of this genus erodes the morphological and temporal boundaries between it and *Microtus*, at least in relation to molar structure; later Mid-Pleistocene *Allophaiomys* with completely differentiated enamel of the "Microtus-type" are hardly distinguishable from members of some other genera of arvicolins.

Variability: Among the remains from the European part of the USSR, which are similar in dimensions to the Hungarian remains (Nagornoe, Nogaisk, Sennya, Akkulaevo), the average length of M_1 is always about 2.5 mm. A large number of specimens have an elongate anterior unpaired loop, especially those from east European and west Siberian populations, and fewer specimens a nivaloid and symmetrical (arvaloid) anterior part of the paraconid section. Instead, specimens with a rounded or rounded-angular anterior unpaired loop are dominant. Thus, some specimens have a paraconid section that is structurally close to ancient *Pitymys*, for example, *P. hintoni* Kretzoi, or some more primitive members among present-day species. In this case, the most dependable differential characters are the shape of the triangles and the nature of enamel differentiation.

Among the remains of animals that are generally larger than specimens from the type series (Kryzhanovka, Moroz, Morozovka and, most probably, Kamik in Poland), the mean length of M_1 —2.7—2.8 mm prevails and, like the preceding group, individuals with an arvaloid- and nivaloid-shaped anterior part of the paraconid and an unpaired loop broadly fused with its basal triangles are represented. Hence differences from *Phaiomys*, based on isolated M_1 , especially for nivaloid variants, are less reliable than in the previous case for *Pitymys*, and involve the same features of enamel differentiation and secondary folding of the anterior unpaired loop, although expressed to a lesser extent in most cases than in the Asian high-montane voles.

Since the evolution of *Allophaiomys*, as in other groups of microtines, should have proceeded along the line of folding of the paraconid section, forms in the first group with an elongate anterior unpaired loop fused with its basal triangles, ought to be considered more progressive and an increase in their relative predominance in later times should be expected. Kretzoi (1965b) paid particular attention to this condition and considered it, as did the author of *A. ruffosi* Pasa, an indication of a more progressive form. At the same time, against this common evolutionary background, there was undoubtedly some geographic variability. Thus the predominance of

animals with an M_1 structure typical for the first group, most probably increased eastward, and the population of large animals with a dominant arvaloid structure of M_1 ought, possibly, to be considered a local geographic race (Shevchenko, 1965). Incidentally, the relationship between geological and geographic variability in this genus in the USSR, as pointed out by Sukhov (1970), is not yet clear.

2. ? *Allophaiomys terrae-rubrae* Teilhard, 1940

Diagnosis: Dimensions as in the European *Allophaiomys*. Length of upper molar row 6.5 mm, lower row 6.0 mm; M_1 —2.7 mm (holotype; all dimensions based on diagram); structure of posterior sections of bony palate similar. Interorbital region with well-developed crest; posterior margin of alveolus of lower incisor extends up to anterior margin of alveolus of M^1 . Anterior section of M^1 with ancient *Allophaiomys* appearance; M_3 not elongate, shows tendency for middle pair of triangles to be markedly shifted lingually relative to both anterior teeth.

Age and distribution: Ancient Pleistocene deposits near Beijing (locality No. 18). The author of the description indicated a wide distribution of this species in the "Late Pleistocene" (Villafranc) of China (Nikhevan, Yashe basin in Shansi Province), i.e., in deposits which are, probably, more ancient than those in which the first fossils of *Allophaiomys* in the western part of the generic range were embedded.

Taxonomic notes: Judging from published date, "*Arvicola*" *terrae-rubrae* differs from present-day members of the closely related genera *Neodon* (*Phaiomys*) and *Lasiopodomys* as follows: from the former in length of incisor alveoli, reaching margin of alveoli of M^1 ; poorer development of interorbital crest (possibly an age-dependent difference); absence of constriction in middle part of nasals; better developed heel of M^3 ; and absence of "oeconomus beak" on paraconid of M_1 . Structural features of the skull *per se* bring the Chinese forms close to *Lasiopodomys*; differences in the material described thus far are less significant and relate mainly to structure of the anterior section of M_1 and middle section of M_3 .

Thus, it is quite possible that *A. terrae-rubrae* is a primitive rootless-molar member of the extinct group of Central Asian voles with differentiated M_1 , which corresponds to the dominant morphotype of the more ancient populations of the European *Allophaiomys*, but already displaying several specific structural skull features of

present-day forms in particular, as in Brandt's vole, a species recently also noted by Chaline (1972).

12. Genus *Microtus* Schrank, 1978—Common Voles

Description: Body length up to 100 mm in small forms and up to 175 mm in larger ones. Color varies from dark, chocolate-brown on dorsal surface and ash-gray on ventral, to fairly light, ocher or pale yellow on dorsal surface and whitish on ventral. In rare cases, diffuse dark stripe present along spine in anterior part of back, which is more vivid in young animals. Relative length of tail about one-fifth trunk length in short-tailed species and slightly more than half trunk length in long-tailed ones. Pubescence of tail insignificant; terminal brush usually absent; exception—some northern short-tailed species in winter pelage. Eyes relatively large; however, size does not reach maximum typical of tribe, and varies slightly—from 12% in *Pitymys* to 16% in *Microtus* s. str. Pinna from relatively very short with dense pubescent lobe partly hidden in pelage of dorsal surface of head, to long, reaching half head length, poorly pubescent, protrudes markedly from pelage. Helix comparatively short, tragus absent. Antitragus well-developed, in form of large rectangle or broadly triangular fold; rarely, in fossorial forms, small but compactly covers small external part of auditory meatus. Upper alae nasalis always distinctly separated from middle lobe of lower by deep groove. Maximum distance between ends of former not more than 1.5 times combined width of latter at middle lobe. Narial pit open. Length of fused part of upper lips not more than 2.0 width of upper incisor (usually not more than 1.5 times). Diastemal processes of upper lip rectangular or rounded-rectangular. Region of contact moderately long and degree of pubescence variable. Transverse ridges of soft palate entire, although posterior one with deep transverse fold in middle. Postpalatal folds five, rarely four (second one reduced posteriorly). Head with complete set of vibrissae; carpal vibrissae either present or absent.

Relative length of limbs close to average size for the subfamily—slightly more than four-fifths trunk length in forelimbs and equal to full in hind limbs, their individual segments average for tribe. Only foot shorter and broader than in any other present-day members of the tribe. Palm glabrous, sparsely pubescent only in posterior part, up to metatarsal pads. Sole, except for interdigital calluses, with only one medial and, sometimes, one small lateral metatarsal pad. Palm with only one medial carpal pad, located at base of large callus

near pollex. Third digit of both limbs longest, 4th longer than 2nd, especially on forelimbs, rarely equal. Reduced pollex of forelimb with small blunt unguis claw. Other claws moderately long, often longer on hind limbs than on forelimbs (greater than half length of digits), and variable in shape: from very short and sharply bent (some members of *Neodon*) to long and straight (*Stenocranius*).

Profile and proportions of skull and its sections variable. If features typical of *Microtus arvalis* Pall. are taken as the average type, then forms of the *Pitymys*-type lie farthest on the one hand, and those of the *Stenocranius*-type on the other. In this case, the latter are related to the average type through *Microtus fortis* Büchn. and *M. oeconomus* Pall., and the former, to some extent, through species of the subgenera *Sumeriomys* and *Blanfordimys*. Dorsal profile of skull straight, usually without steep slope in basal region of zygomatic arches (except in *Stenocranius*-type) and often without perceptible slope in interorbital region (except in *Pitymys*-type). Length of brain case slightly greater than width, rarely difference significant; dorsal surface barely convex, vertical crests less perceptible and do not form sharp border between upper and lateral surfaces of brain case. In forms approaching the *Pitymys* group, these features are less distinct while in forms closer to *Stenocranius*, they are highly developed. Extent of development of longitudinal crest of interorbital region also variable: from totally absent in first group to well-developed in second. In profile, zygomatic arches more or less uniformly rounded, broadening slightly toward the back. Rarely, broadening absent (*Pitymys*-type), or distinct constriction present (*Stenocranius*-type). Orbit size average for tribe, rarely large (*Neodon*). Orbital plane forms angle of 45° with horizontal, rarely less (in both group types), and not notably shifted backward. Masseteric [= zygomatic] plate varies from relatively low and broad (*Pitymys*-type) to narrow and high (*Stenocranius*-type). In forms closer to latter, its plane forms very small dihedral angle with sagittal plane. Bony bridge between postpalatal pits broad within limits of *Pitymys*-type and narrow in *Stenocranius*-type. Auditory bullae only rarely markedly enlarged; inner cavity more or less filled with spongy bony tissue.

Relative length of dental row within limits of average size for subfamily; M_1 and M^3 tend toward elongation. Molars rootless, crown height moderate (in *Pitymys*, crown lower), and width less (except in *Stenocranius* and some species of *Microtus* s. str.). Enamel well-differentiated. Difference in size of lateral and medial triangles of masticatory surface least expressed on lower molars

and on M^3 . Tendency toward formation of additional elements observed in posterior section of M^1-M^2 and toward reduction (underdevelopment) of anterolateral loop of M_1-M_3 . Fused opposite triangles often present on M_3^3 , rarely on M_2 , in many subgenera as well as in individual species. The most common feature is fusion of basal triangles of paraconid section of M_1 . Posterior lower molar often distinctly shifted lingually (especially in *Phaiomys* and *Stenocranius*), its alveolus well-developed and isolated, often protruding downward beyond margin of jaw.

Crowns of incisors long or moderately long, rarely relatively longer (in *Pitymys* on upper incisors, and in *Microtus* s. str. on lower ones). Anteroposterior cross section of lower incisors larger than lateral in most members of the subfamily. Posterior end of lower incisor terminates above dental foramen and forms a moderately, barely (*Sumeriomys*), or well-developed alveolar knob on lateral surface of articular process. Steepness of curvature of incisors and magnitude of facing angle highly variable.

Skeleton of forelimbs characterized by relatively short clavicle, long acromion process of scapula, short and narrow humerus, its diaphyses with reduced inner epicondyle. Olecranon process of ulna relatively longer than in other members of the tribe. Diaphyses of femur as well as tibia in hind limbs also relatively thin. Hind limbs characterized by shortest fused fibula within limits of tribe.

Composition of genus: More than 10 subgenera, mostly extant: *Microtus* Schrank, 1798; *Sumeriomys* Argyropulo, 1933; *Neodon* Hodgson, 1849 (? = *Phaiomys* Blyth, 1863); *Pitymys* McMurtrie, 1831 (? = *Pedomys* Baird, 1857); *Stenocranius* Kastschenko, 1901; *Blanfordimys* Argyropulo, 1933; *Iberomys* Chaline, 1972; *Orthriomys* Merriam, 1898; *Herpetomys* Merriam, 1898; *Aulacomys* Roads, 1894; and *Chilotus* Baird, 1897; and *Suranomys* Chaline, 1972 (foss.). The number of present-day species constitutes up to 50 in world fauna and up to 20 in Russian. Extinct species number 8 to 10.

Researches vary widely in their understanding of the subgeneric composition of this genus. Thus, in Hinton's (1926) classification, there are no subgeneric divisions whatsoever; present-day subgenera are considered genera. Argyropulo (1933), Ognev (1950), Bovrinskii, Kuznetsov, and Kuz'yakin (1965) recognized seven subgenera in Palearctic fauna while Vinogradov and Gromov (1952) and Gromov and colleagues (1963) recognized eight. Ellerman (1941) has listed only four subgenera, with two Palearctic. In this book, six Palearctic subgenera are described; two of those recognized

earlier—*Chionomys* Miller and *Lasiopodomys* Lataste—are treated here as independent genera. Opinion is far from unanimous regarding the Nearctic subgenera of *Microtus*. The taxonomic status for two of the last four subgenera listed above is not well-founded due to the absence of essential material. As for the subgenus *Aulacomys*, some authors erroneously consider it a subgenus of *Arvicola*, (Hooper and Hart, 1962).

Distribution and zonal affinity: Same as for tribe. The largest number of species, including those of the central subgenus *Microtus* s. str., are meadow and meadow-marsh forms in mountains and plains, and in many natural zones inhabit interzonal biotopes. Only a few forms have adapted to living in steppe and desert-steppe conditions.

Evolution and phylogeny: Fossil remains of microtines reveal teeth at evolutionary stages that characterize present-day forms from the subgenera *Pitymys*, *Stenocranius*, and *Microtus* s. str., known from the Early Pleistocene (the Tiraspol' faunas) remains recovered from open biomes in the European part of the USSR, Irtysh region, as well as Western Europe (Bihar faunas?). However, since a similar type of tooth development is repeated in time in different phyletic lines of the subfamily, we cannot be certain that the extinct forms really belong to the foregoing subgenera. Remains of the probable ancestors of rooted-molar voles of the genus have yet to be found, mainly for taxonomic reasons. Remains of ancient microtines are absent from the temperate zone occupied in the past by forests where, most probably, this type of evolution of the group took place (Gromov, 1967). Either way, in the Old World, the origin of this genus from the late, cemented *Mimomys*, possibly from the *newtoni-reidi* group and further through *Allophaiomys*, as proposed by Topachevskii (1965, 1973), Zazhigin (1975), Chaline (1966, 1972), and other authors, can hardly be refuted. Hinton (1926) considered some Central Asian *Phaiomys* with simplified M^3 , similar to *Mimomys* s. str., one of the closest present-day rootless-molar descendants of extinct rooted forms. The same may also be said for some forms of *Pitymys*, in particular, the large species from the *duodecimcostatus* group or the *Blanfordimys*, which are considered by Chaline (1972) the closest descendants of the extinct *Allophaiomys*. These two authors agree about the presence of ancient elements of the subfamily in the present-day montane fauna of Asia.

The nature of the relationship and taxonomic status of these species as ecological analogues of the faunas of the Old World in

the faunas of the New, constitutes a debatable topic, especially for the southern forms. If the absence of independent subgeneric separation of the North American voles from the Eurasian subgenera of *Stenocranius*, *Pitymys*, and *Microtus* s. str., raises no doubts for most mammalogists, then to include *M. longicaudus* under the European genus *Chionomys* hardly requires justification! The presence of independent substituting genera in the form of pairs such as *Pitymys*—*Pedomys*, *Aulacomys*—*Arvicola*, *Sumeriomys*—*Chilotus* is also not acceptable to everyone. It is usually believed that the extent of isolation of the corresponding American forms is greater than subgeneric, although it is undoubtedly stronger in the southern forms than in the northern. Incidentally, I know of no author who has specially investigated the tribe as a whole in this respect, using sufficient material from both continents.

1. *Microtus* (subgen. ?) *deceitus* Guthrie and Matthews, 1972 (foss.)

Diagnosis: Length of lower molar row 8.4 mm; M_1 —3.7 mm (holotypes). Length of M_1 —2.9—3.9 mm ($n = 30$), M^2 —2.1—2.6 mm ($n = 18$) (paratypes) (Guthrie and Matthews, 1971).

Anterior section of M_1 with two normally developed and isolated triangles of the paraconid; anteromedial triangle may be widely fused with the unpaired loop. Latter of the "*Pliomys*"-type, with rounded anteromedial margin and posterolateral rostriform, extending downward and backward in form of a "beak". Anterior pair of triangles isolated in M_2 . Anterolateral denticle of M_3 small, middle pair of lobes incompletely yet distinctly separated. Structure of M^1 — M^2 without distinctive features. M^3 with simple, *Allophaiomys*-type structure, with narrow medial denticles extending far behind and posterolateral triangle fused with "heel". A less-cemented form.

Age and distribution: Known only from type locality—Early Pleistocene deposits of Cape Deceit in Alaska.

Taxonomic notes: A poorly studied and insufficiently described species. Its authors consider it an initial form for the European *Microtus*, which simultaneously brings it closer to *M. paraoperarius* Hibbard, although the M_1 in the known members of this species is at an earlier stage of development (structure of M^3 not known; Hibbard, 1944; Paulson, 1961). At the same time, if we consider only the diagrams presented by the above authors, doubt arises as to whether some members of this species might belong to the genus *Pliomys*—the young specimens to *P. deeringi*, a species described

from the same locality. On the other hand, the authors themselves point out that the teeth of *M. deceitus* are not always distinguishable from those of *Praedicrostonyx* collected from the same place. If the inclusion of this species under the genus *Microtus* is correct, the simplified structure of M^3 compels us to place the species under the most primitive forms, barely deviating from the initial *Allophaiomys*-like ancestors.

Subgenus *Neodon* Hodgson, 1849 (? = *Phaiomys* Blyth, 1863)

Diagnosis: Size medium, rarely small. Close to members of *Pitymys* but less adapted to semifossorial life style in their external morphology. Pelage dense and long, guard hairs small. Unlike species of the other subgenera, pollex of forelimb with well-developed obtuse claw (as in *Lasiopodomys*). Number of genal and lower lip vibrissae reduced. Eyes small. Pinnal lobes not reduced, with thin tuft of hairs toward front; antitragus broadly triangular, well-isolated.

Skull retains juvenile appearance and is proportionate for a longer time than in *Microtus* s. str. Brain case comparatively high and convex. Interorbital space often relatively narrow, with low crests in contact with each other or fused into well-developed longitudinal crest. Articular process of dentary not reduced, alveolar bulges on it well-developed, rarely moderately developed. Anterior section of M_1 varies from a primarily simple structure (*Arvicola*-*Allophaiomys*-type) to 1.5 folds, rarely (in one species) 2.0 folds. In complex tooth, basal triangles of paraconid section, although mutually shifted more than in *Pitymys*, nevertheless exhibit "*Pitymys*" fusion. Anterolateral denticle on M_3 may be completely absent.

Composition of subgenus: Of the more than 10 species described for the montane regions of Central and Middle Asia, the supraspecific group *leucurus* is distinct. This group in more elaborate classifications of microtines is often given the status of an independent subgenus under *Phaiomys* or within the limits of the genus *Microtus* or *Pitymys*. Some species form another two groups: the *juldaschi* group and the *irene* group. Two poorly studied species have a unique position: *millecens* Thomas, 1911 and *sikimensis* Hodgson, 1849. Possibly, four species of the American subgenus *Pedomys* Baird (Hall and Kelson, 1959) should be considered an independent group in this same subgenus. However, some later American authors have decisively included them under *Pitymys* (Hooper and Hart, 1962). Like Ellerman (1941), I, too, recognize

three groups of species within the composition of the subgenus *Neodon* but, in my assessment, they differ in composition and volume. Their further cytotaxonomic and genetic study may also induce many changes in classification.

One to two species occur in Russian fauna—*M. (N.) juldaschi* Severtzov, 1879 and, possibly, *M. (N.) carruthersi* Thomas, 1909.

Age and distribution: Reliable fossil remains of the extinct forms of the *juldaschi* group are known only from the end of the Middle Pleistocene in the USSR (Tashkent region). Present-day forms live in the montane-forest belt and open environments at high altitudes in Tien Shan and the Pamir-Alai range, commencing from their periphery, as well as the Himalayas and mountains of Tibet and southwestern China in the eastern part of their range. Distribution of western Pamir of Tibet is not explained. Discovery of fossil remains on the northern border of the present range in submontane zones points to a probable shift in boundaries of vertical distribution in relation to glaciation of mountain peaks.

Taxonomic notes and evolution: Sometimes considered a subgenus of *Microtus*, sometimes of *Pitymys*; combined with the subgenus *Phaiomys* (and together with it sometimes included under the genus *Lasiopodomys*) or considered independent. The totality of differences from true *Microtus* is generally greater than from *Pitymys*, so the latter opinion also is not groundless. Actually, the subgenus is represented by species that in terms of evolution are close to *Pitymys*, but live in the inner part of the Asian continent and, possibly, North America. Forms of the subgenus which are more primitive in terms of tooth structure (the *leucurus* group) live in the eastern part of the range of the subgenus, whereas *Pitymys* lives in the western (the group *ibericus*). Ancestral phyletic links are not known. We have already mentioned two probable links: with the late, cemented forms of *Mimomys* or with the ancient known molar forms of *Allophaiomys*.

2. *Microtus (Neodon) leucurus* Blyth, 1863 (Figure 39)

Diagnosis: Size large. Body length up to 130 mm, tail up to 35 mm, upper molar row probably up to 7.1 mm, lower row up to 7.0 mm; M_1 —3.0—3.2—3.5 mm ($n = 10$). Dorsal surface light, sandy-gray; brownish darkening prominent around snout. Tail comparatively thick, monochromatic, often lighter in color than dorsal surface of body, and covered with comparatively sparse long hairs.

Skull relatively broad: zygomatic width in adult animals up to 80% of condylobasal length. Length of brain case almost equal to its

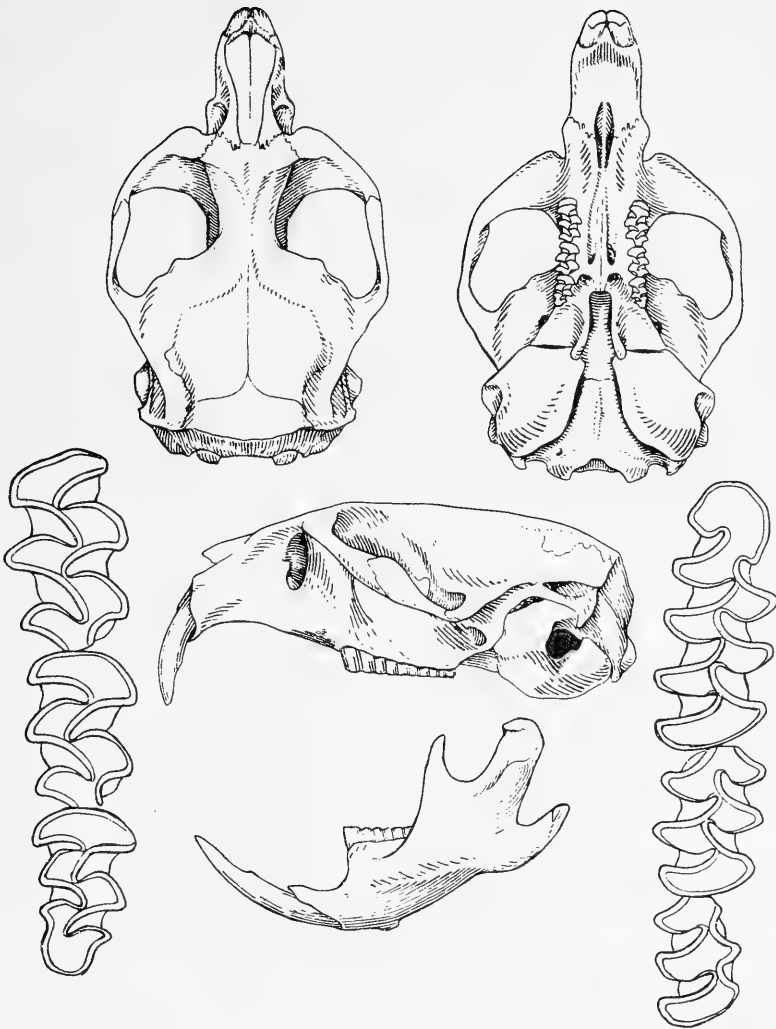


Figure 39. Skull of *Microtus (Neodon) leucurus* Blyth.

width, longitudinal crest in interorbital space well-developed over at least posterior two-thirds. Auditory bullae highly dilated, especially anterior section. Anterior margin forms almost a right angle with longitudinal axis of skull. Bony wall of auditory meatus with well-isolated anterior section. M^3 with isolated triangles and short heel,

and shorter, rarely equal in length to M^2 . M_1 simple in structure; usually with poorly developed pointed projection of second-order fold and five (like *M. oeconomus*), rarely six, if anterior unpaired loop isolated, closed fields. Anterolateral denticle of M_3 absent.

Composition of species: The following forms are probably independent subspecies; however, their taxonomic status requires further study: *M. (N.) leucurus* Blyth, 1863 (western Tibet) (= *blythi* Blanford, 1875); *M. (N.) strauchi* Büchner, 1888 (northern Tibet); *M. (N.) fuscus* Büchner, 1888 (eastern Tibet, Zaidam) (= *tsaidamensis* Satunin, 1903); *M. (N.) everesti* Thomas and Hinton, 1922 (northern Nepal); and *M. (N.) walton* Bonhote, 1902 (central Tibet, Lhasa).

Distribution and zonal affinity: High mountains of Middle Asia (Tibet, Himalayas). Western boundary not defined, nor its existence in peripheral ranges along northern and eastern borders of Tibetan plateau where, apparently, it is replaced by forms of the next groups described below. If the species identification of a subfossil piece of skull from a large vole (length of upper molar series 6.3 mm) from a cave in the environs of Kalgan (northern China) belonging to "*Arvicola strauchi*" (Young, 1927) is correct, then it would appear that even relatively recently the boundary of its range extended far eastward.

Taxonomic notes: After the receipt of original material from Middle Asia by the Zoological Institute, Academy of Sciences, USSR, no further collections were made here. Only one skin with skull of "*Phaiomys blythi*" was obtained from Ladakh, providing a basis for Vinogradov to confirm the "label" identities of *M. blythi*, *M. leucurus*, and *M. strauchi*. A comparison of the description of *M. tsaidamensis* given by K.A. Satunin with the series (up to 20 specimens) collected in Zaidam by N.N. Prazeval'skii ("*Microtus strauchi* var. *fuscus*"), revealed that the differences in structure of M^3 and M_1 do not suffice for recognizing its species status. It is quite possible that this is not even a subspecies but rather an extreme variant in the variability spectrum of the basic species. Incidentally, it may be noted that the *fuscus* form was described from a series comprising mainly summer animals in which the color is darker and more matte. This is particularly true of younger individuals.

Evolution and phylogeny: If judged from tooth structure, then the group of forms included in this species represents the least-changed offspring of their probable extinct *Allophaiomys* ancestors. Changes are better defined in related groups of the same ancestry. *Pitymys*, *Neodon* s. str. and its possible lateral branch, *Proedromys*.

The independent subgeneric status of *Phaiomys* s. str. is possible; however, inclusion of species of *Lasiopodomys* under it is erroneous (Allen, 1940).

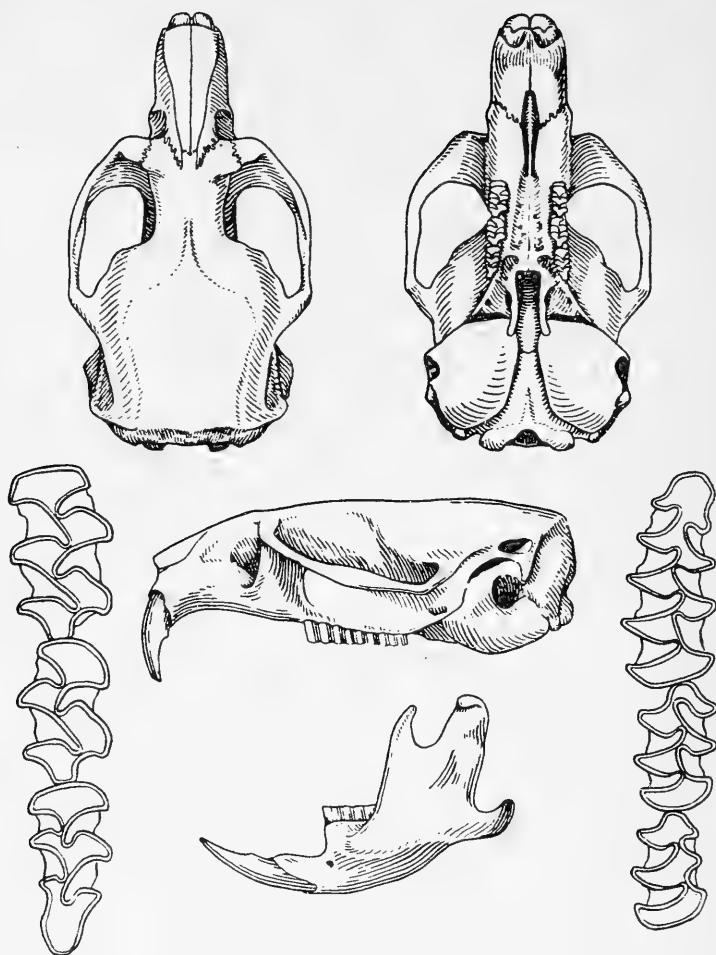
3. *Microtus (Neodon) juldaschi* Severtzov, 1879 (? = *carruthersi* Thomas)—Pamir-Alai or Carruther's Vole (Figure 40)

Diagnosis: Size medium. Body length up to 120 mm, tail up to 38 mm, upper molar row up to 6.7 mm, lower row up to 6.5 mm; M_1 —2.5–2.8–3.0 mm (n=12). Dorsal surface fairly light, sandy, close to color of preceding species, but sometimes darker, grayish, without sharp seasonal dimorphism. Brownish color near snout faint even in light-colored forms. Tail comparatively thin, grayish, slightly bichromatic or monochromatic, and covered with fairly short hairs.

Skull comparatively narrow: zygomatic width in adult individuals only rarely exceeds 60% of condylobasal length. Length of brain case notably greater than its width, longitudinal ridge of interorbital space barely developed. Two frontoparietal crests only close-set, in contact in posterior third. Auditory bullae barely inflated; anterior section similar to lateral, flattened and anterior margin forms acute angle with longitudinal axis of skull. Bony wall of auditory meatus with barely isolated anterior section. M^3 often with fused lobes on masticatory surface (middle pair and posterolateral with heel); heel elongate. M^3 longer than, or equal in length to M^2 . M_1 with two lateral denticles on paraconid section (unilateral secondary complexity) and generally with six to seven closed enamel fields. Posterolateral denticles of M_3 present.

Distribution and zonal affinity: Forest (mainly juniper) and alpine belts of the Pamir-Alai range, western and northwestern Tien Shan (400–4,500 m above msl).

Composition of species and taxonomic notes: Number of infraspecific forms not known. The juniper form—*M. carruthersi* Thomas, 1909—is considered a subspecies here since the differences between it and the Pamir vole are not large and, in spite of karyological differences (Gileva and Pokrovskii, 1970), results have been published regarding the free hybridization of Pamir and Gissar populations and hybrid fertility (Bolshakov and Pokrovskii, 1969). Unfortunately, the material for this experiment was taken not from the type locality of the juniper vole (Gissar range) but from Matcha River on the northern slope of the Zeravshan range. It is quite possible, therefore, that we are confronted with two independent species. Karyological analysis of voles



255 Figure 40. Skull of Carruther's vole [*Microtus (Neodon) carruthersi* Thomas].

from the two regions (Lyapunova and Fisher, 1969), though not confirmed by hybrid analysis, indicate fairly significant differences in chromosome sets of different populations (taxonomic position of the juniper vole from Kirgizia remains unclear). Additional experiments are presently underway (M.N. Meyer) in the Zoological Institute, Academy of Sciences, USSR, to explain aspects of reproductive isolation between animals of the topotypic populations of both forms.

In comparing the Pamir (Kara-Kul), and Gissar forms, the juniper vole is distinguished by smaller size, darker dorsal surface, notably more juvenile profile and proportions of skull and, on the average, a less-differentiated paraconid section of M_1 . The population from the Alai valley shows intermediate structure (Bol'shakov, Rossolimo and Pokrovskii, 1969).

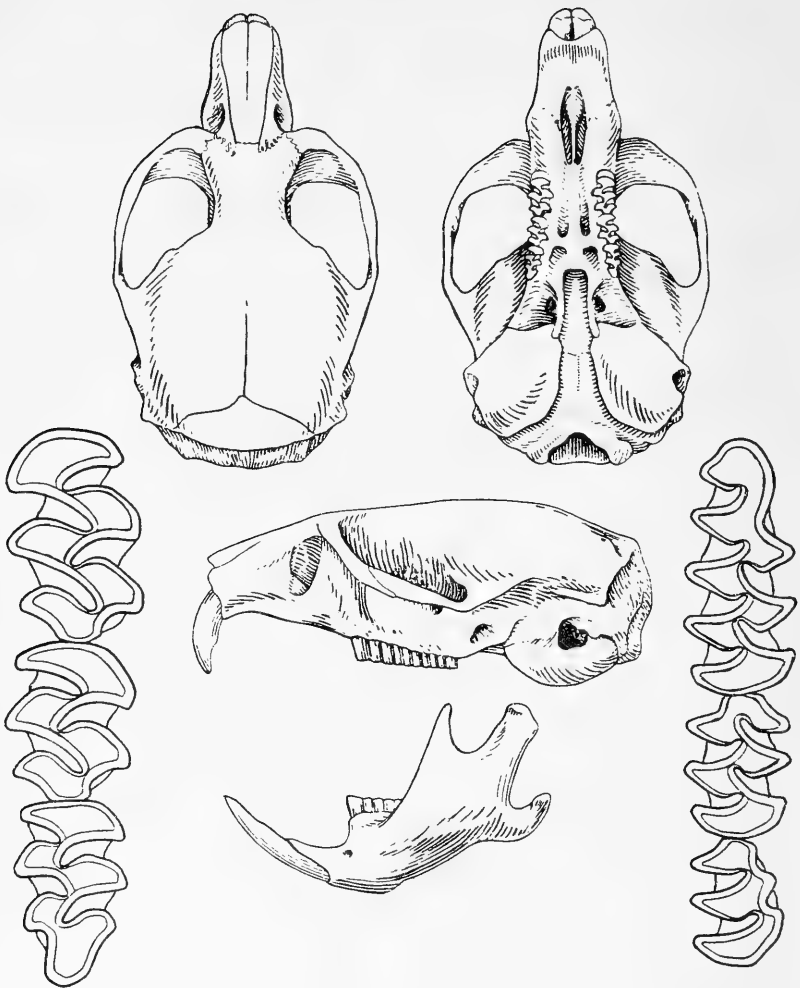
256 *Evolution and phylogeny:* The discovery of fossil remains has already been mentioned. Within the limits of this broadly understood species, all the forms are clearly close to *M. (N.) irene* Thomas, and not to *M. (N.) leucurus*, although the Pamir animals are close to them in coloration. Possibly, a more distinct intermediate character will be expressed in specimens from the Kuen-Lun-Kara-Korum hill complex, where, to date, no material has been collected.

4. *Microtus (Neodon) irene* Thomas, 1911 (Figure 41)

Diagnosis: Size variable. Body length up to 134 mm in large southern forms and up to 107 mm in smaller northern ones; tail up to 43 and 40 mm (probably, relatively longer than in either of the two preceding species); upper molar row up to 7.0 and 5.9 mm respectively, lower row up to 6.8 and 5.9 mm. Length of M_1 in smallest form (*oniscus*)—2.4 mm. Dorsal surface dark, from grayish to vivid chocolate-brown. Tail comparatively thin, distinctly bichromatic, its pelage (summer coat) sparse (Allen, 1940).

257 Skull, in proportions of brain case, resembles that of *M. leucurus* (except for the subspecies *forresti* in which it is more elongate) and in width of space between zygomatic arches resembles *M. juldaschi*. Differs from both these species in uniformly inflated auditory bullae, without a perceptible lateral flattening, longer nasals without narrowing at base of anterior third, weaker and less prognathous upper incisors, and shorter lower incisors, forming comparatively weak alveolar knob on lateral surface of articular process (differences greater in smaller forms than in larger ones). Structure of molars similar to *M. leucurus*, but anterior unpaired loop of M_1 isolated from fused triangles at its base, and heel of M^3 slightly longer. Allen (1940) pointed out that cement is not always present in folds; since it is present in adult individuals, one may assume that it appears relatively late.

Composition of species: Allen (1940) is inclined to recognize the following subspecies: *M. (N.) i. irene* Thomas, 1911 (Sychuan); *M. (N.) i. oniscus* Thomas, 1911 (Hanshu); and *M. (N.) i. forresti* Hinton, 1923 (northern Yunan). This division is also maintained by Ellerman and Morrison-Scott (1951). Later publications not known.



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Figure 41. Skull of *Microtus (Neodon) irene* Thomas.

Distribution and zonal affinity: Open, mainly meadow-like, environments in alpine ranges along eastern-southeastern fringes of the Tibetan plateau within the limits of the Chinese Provinces Yunan (northern part), Sychuan (central part), and Hanshu.

5. *Microtus* (conf. *Neodon*) *millecens* Thomas, 1911

Diagnosis: Dimensions (holotype): body length 90 mm, tail

53 mm (more than half body length), upper molar row 5.7 mm, lower molar row 5.6 mm (maximum size 5.8 mm; $n = 6$) (Thomas, 1911b; Allen, 1940).

Dorsal surface dark, chocolate-brown. Pinnae protrude slightly from pelage. Tail bichromatic and comparatively densely covered with hairs.

Skull with flat brain case and straight dorsal profile, without crests, including those of interorbital space. M^2 with large additional posteromedial triangle, M^1 with tendency toward such. M^3 variable in structure: from simple (simplex type) to complex, with three lateral and four medial denticles; in both cases, anterior pair of triangles fused. M_1 similar to *M. juldaschi*, but anterolateral triangle at base of paraconid section isolated from anteromedial; latter fused with anterior trifoliate structure. M_2 with fused anterior and middle pairs of lobes.

Distribution and zonal affinity: Known only from type locality: northern Sychuan, montane-forests, about 3,000 m above msl.

Taxonomic notes: After the type series, possibly new collections were not made; described with varying degree of details after Thomas (1911b, 1912a) by Allen (1940) and Ellerman (1941), both of whom expressed an opinion regarding the taxonomic position and relationship of the species. Its highly flattened skull prompted Allen to conclude that this vole lives among rocks or taluses (long and abundant pelage excludes subterranean life style, in which case, also, other adaptations arise), and the totality of its distinctive features led him to believe that it would eventually be separated into an independent subgenus. I have included it tentatively under the subgenus *Neodon* which, at present, appears the most natural.

258 6. *Microtus* (conf. *Neodon*) *sikimensis* Hodgson, 1849
(Figure 42)

Diagnosis: Body length up to 100 mm, tail 43 mm, upper molar row 6.2 mm and lower 6.4 mm (Biswas and Khajuria, 1957).

Dark-colored vole with relatively long tail [longer only in *M. (N.) millecens*]. Based on size and proportion of skull, probably closest to the Pamir vole (*M. juldaschi*). But upper incisors much less prognathous and lower incisors, judging from extent of development and position of alveolus, shorter. M^1 and M^2 with distinct tendency toward isolation of additional lobes in posterior part. M^3 with three lateral and four medial denticles. M_1 with two complete folds in paraconid section, well-expressed "*Pitymys*" fusion of basal

pair of triangles, and second pair almost isolated from anterior loop (Hinton, 1926, Figures 25 and 29).

259 *Distribution and zonal affinity: Eastern Himalayas: Sikkim and*

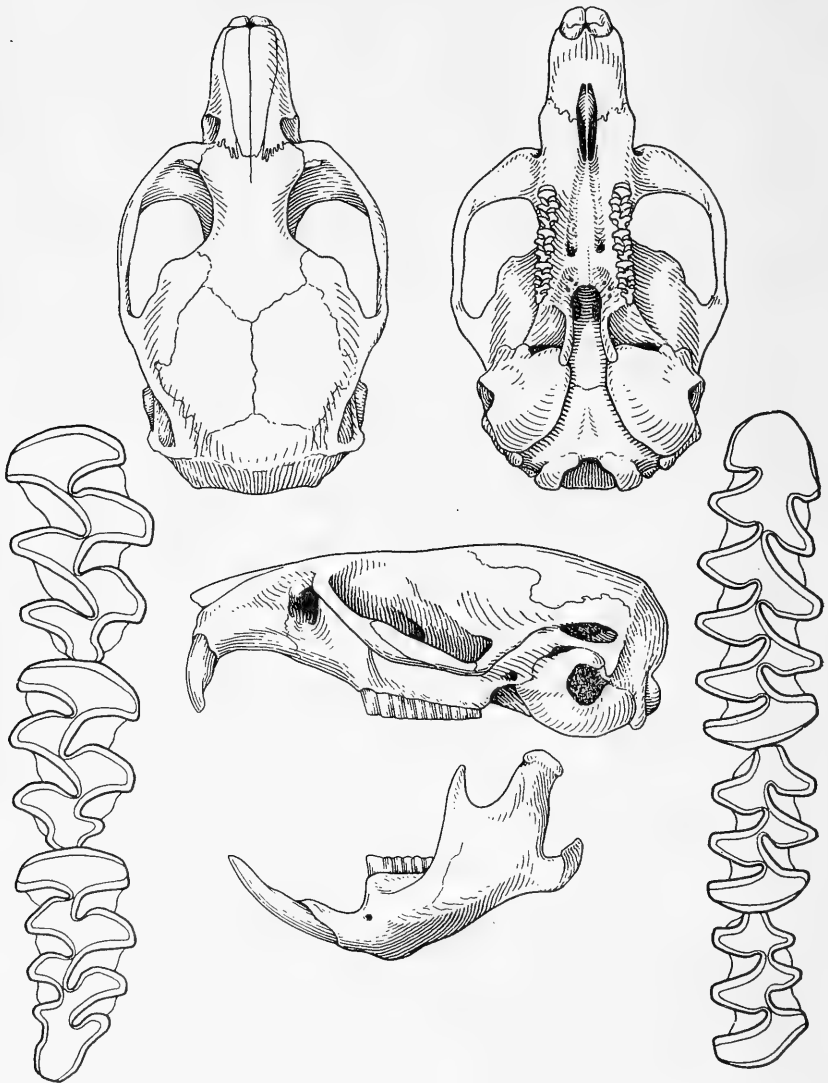


Figure 42. Skull of *Microtus* (conf. *Neodon*) *sikimensis* Hodgson.

adjoining regions of Bengal where it lives in forest belt, in glades near its upper boundary, and between rocks at height of up to 3,600 m above msl (Khajuria, 1962).

Taxonomic notes: Poorly studied and poorly described. Based on structure of complex M_1 , resembles the Talysh species (*Pitymys schelkownikovi*) and in tendency toward simplification of posterior part of M^1-M^2 , other members of *Pitymys* and *Eothenomys*. Sometimes considered an extreme eastern member of *Pitymys* s. str.

6. Subgenus *Pitymys* McMurtrie, 1831—Pine Voles

Diagnosis: Small, rarely medium-sized voles with short tail, better adapted to semifossorial life style than other members of the genus. Pelage dense, comparatively short, slightly differentiated into underfur and guard hair. Eyes relatively small. Pinna slightly reduced, covered with hair; antitragus small, rectangular, relatively poorly developed.

Skull with relatively broad, low, flattened brain case. Interorbital space without longitudinal crest, sometimes with distinct groove-like depression. Articular process of dentary reduced. Molars with low crown (within limits of subfamily; lower only in *Lemmiscus*). Paraconid section of M_1 with 1.5 folds, rarely with two complete folds. At least one of the opposite pairs of triangles at base of paraconid fused (“*Pitymys*” fusion). Anterolateral denticles on M_1 and M_3 not completely reduced, at least not in present-day Palearctic species.

Composition of subgenus: Up to 60 species described, mostly from Western Europe, their actual number at least three times less. Their merger into three supraspecific groups, as proposed even by Miller (1912), has not lost its validity (Ellerman, 1941). These groups are *subterraneous*, *ibericus*, and *savii*. Even a subgeneric name, *Micrurus* F. Major, was proposed for the latter (Hinton, 1921) (within the limits of the genus *Pitymys*) based on its lesser adaptation to a semifossorial life style and difference in number of teats. The American species *P. pinetorum* Le Conte, 1829 and two closely related forms are closer to the *ibericus* and *savii* groups: *parvulus* Howell, 1916 and *quasiater* Coues, 1874, for which various supraspecies names have been proposed (*Psammomys*, *Ammomys* and so on).

Kratochvil (1970) and Kratochvil and Kral (1974) have recently presented a more detailed group classification for Old World species. Thus, in addition to the separation of *P. schelkownikovi* into a sep-

arate group (the independent status of this species was also emphasized by Shidlovskii, 1962), Kratochvil has divided the *subterraneus* group into three subgroups, separating besides *subterraneus per se*, the Pontic-Caucasian group *majori* and, following König (1961), the alpine-Caucasian group of *multiplex-tatricus*. The *ibericus* group of Miller has likewise been divided by him into three subgroups: the Aegean subgroup *thomasi*, the Apennine subgroup *savii*, and the gallo-iberian subgroup *duodecimcostatus*. The last two subgroups were already considered independent by Balsac and Beaufort (1967). The changes proposed to date are based largely on the results of historical zoogeography rather than sufficiently convincing morphological data. Of the new features, Kratochvil has employed mainly one: the degree of deviation of plane of coronoid process of the mandible from plane of the articular process—a feature that is difficult to ascertain and subject to great variability, including biotopic. He has ignored the structure of the lower molars, incisors, bony palate, and upper diastema. Finally, Chaline (1974b) has similarly separated the supraspecific group *Meridiopitymys* (a subgenus of *Pitymys*) on the basis of a single character—fusion of the middle pair of triangles of M^3 —combining under it *duodecimcostatus*, *thomasi*, *atticus*, and *henseli* (foss.).

The taxonomic status of the European forms of *Pitymys* at the species/subspecies level is presently under scrutiny by several Western European researchers, based mainly on chromosomal analysis. It suffices to say that at the last theriological symposium in Brno (1971), dedicated to the problems of species and zoogeography of European mammals, almost 25% of the papers presented pertained to problems of classification of *Pitymys*. The new data—true, not supported by hybrid analysis, which Kowalski (1960c) has emphasized as essential—revealed sufficiently sharp differences between Palearctic forms in a single group, which differ only slightly in external and skull features. Hence it is obvious that we are still far from finalizing the true species composition of this subgenus.

Clarity regarding the extinct forms is also lacking. Without doubt, the subgenus *Pitymys* includes the Early Pleistocene *M. (P.) hintoni* Kretzoi, 1941 (central and eastern Europe); the Middle Pleistocene *M. (P.) pauli* Bate, 1935 (Island of Malta); *M. (P.) apscheronicus* Argyropulo, 1941 (Apsheron Peninsula, Binagada); and the Late Pleistocene *M. (P.) (melitensis)* Bate, 1920 (Island of Malta). As for "*Pitymys*" *arvaloides* Hinton, 1923 and *P. gregaloides* Hinton, 1923 (Early Pleistocene of central and eastern

Europe), it seems to me more appropriate to consider them, at present, ancestral forms corresponding to the present-day species *Microtus arvalis* and *M. gregalis*, which are at the "Pitymys"-stage of evolution of M_1 , similar to the modern American *Pedomys*. This conclusion is indirectly supported by the partial fusion of the "Pitymys" triangles in the young *M. arvalis*, as well as manifestation of this character as an atavistic trait in adult individuals of this species (Janossy and Schmidt, 1960, 1975).

Age and distribution: Fossil remains of microtines with rootless molars and "Pitymys" fusion of the triangles of the paraconid section of M_1 , have been found in Early Pleistocene deposits together with similar remains of species of most of the other subgenera of *Microtus*.

This group inhabits the zone of broad-leaved forests, southern part of subzone of mixed forests, forest-steppes and their corresponding vertical belts, as well as alpine meadows, above the forest boundaries, primarily in the southern part of the range of the genus. It is found from the Kursk and Voronezh districts of RS-FSR up to the Iberian Peninsula; southwest North America; south up to the Caucasian Isthmus, northwestern Iran, northern Turkey, and southern Europe (including some Mediterranean islands). In the New World, it is found up to central Mexico.

Paleontological data confirming the movement of pine voles associated with Würm glaciation into the shelter of eastern Europe, Samara Luka, or southern Ural, are not available to date. It may be thought that members of the subgenus spread eastward later than other forest fauna and unlike, for example, dormice, did not succeed in reaching the Volga. Yet, the existence of isolated areas north in the present range (Belovezhsk Pushcha, eastern part of Leningrad
261 district, and Prionezh'e) point to their deeper penetration in this direction in the period of the last postglacial climatic optimum. A different picture is characteristic of Western Europe and probably for the Caucasian Isthmus. The sufficiently complex Anthropogenic evolution of montane environments during the Alpine phase of orogenesis, particularly along the southern border of the Mediterranean, caused a distinct manifestation of speciation of varying intensity here, wherein some forms could have evolved at places retaining favorable slope orientation, while others secondarily inhabited territories that became unfavorable during the period of Pleistocene cooling. As rightly pointed out by Kratochvil (1970), this species is particularly evident in the composition and nature

of distribution of species of *subterraneus* and did not push out the *ibericus* group.

Taxonomic notes and evolution: Ancient members at the stage of evolution of molars, close to the high-montane forms of the genera *Neodon-Phaiomys*, and occupying the base of the phylogenetic tree of rootless, cemented-molar microtines, are the probable ancestors of *Microtus* s. str. The semifossorial life style of some forms living in comparatively stable natural conditions of the extraglacial region of Western Europe (the Iberian Peninsula, southern France, and Italy), similar to the interior regions of Asia, helped retain primitive structural features. However, the diphyletic origin of *Pitymys* from *Allophaiomys*, based on a comparison of primitive species (the *ibericus* group) and the more progressive species of this form, as proposed by Chaline (1972), is not acceptable. The proposition is based on insufficient knowledge of the entire variability of present-day species of the subgenus on the one hand, and synonymization of teeth evolution with species evolution on the other. The general direction of evolutionary changes in molars of *Pitymys* is similar in many other groups of microtines, which involves complexity of structure of M^3 and M_1 . For the former, complexity is seen in restructuring of the simple tooth with three denticles and two folds on each side (simplex type), which is also typical for the Central Asian *Phaiomys*, *Arvicola*, and late *Mimomys*, up to the highly complex type with three to four folds in the *subterraneus* group and others. For M_1 , complexity includes tooth elongation, tendency toward elongation of the anterior unpaired loop, and fusion of the second opposite pair of triangles at its base—features that are maximally seen in the four northern and southern forms in the eastern part of the range of the subgenus.

Various stages of adaptation to a fossorial life style are discernible in the extent of development and varying combinations of such characters as size of eyes, length of claws, length and degree of prognathism of upper incisors, size of auditory bullae, and so forth.

KEY TO SPECIES OF SUBGENUS *PITYMYS*

- 1 (4). Tail length more than 30% body length. Nipples, two to three pairs. M^3 with three lateral denticles. Denticles at base of anterior unpaired loop of M_1 do not form additional pair of triangles; instead, fused with each other, underdeveloped, and widely fused with loop.

- 2 (3). Dorsal surface dark gray; ventral surface ash-gray. Tail distinctly bichromatic. Nipples, two pairs. Dorsal profile of skull without discernible dip near base of rostral section
 *M. (P.) subterraneus* Selys-Longchamps.
- 3 (2). Dorsal surface gray with distinct brownish tinge, ventral brownish-gray. Tail monochromatic, rarely slightly bichromatic. Nipples, three pairs. Dorsal profile of skull with distinct dip near base of rostral section
 *M. (P.) majori* Thomas.
- 4 (1). Tail length less than 30% body length. Nipples, four pairs. M^3 with four lateral denticles. Denticles at base of anterior unpaired loop of M_1 form additional pair of triangles that are fused between themselves but isolated from other triangles.
 *M. (P.) schelkovnikovi* Satunin.

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7. *Microtus* (? *Pitymys*) *henseli* F. Major, 1882 (foss.)
 (Figure 43)

Diagnosis: Comparatively large vole: "basic" length of skull, according to author, 27 mm; length of upper molar row 6.3–6.7–7.4 mm, lower row 7.2–7.4–8.0 mm; M_1 —2.7–3.3–4.0 mm ($n = 30$; Chaline, 1972). Anterior unpaired loop of M_1 broad and short with tendency toward isolation from opposite, or at least widely fused, first pair of triangles of paraconid. Second pair of triangles distinct.

Description: Major (1882) reported several traits typical of *Arvicola*, under which the species was initially included. He emphasized in particular the length of the narrow facial section of the skull. Accordingly, the diastema, incisor alveoli, and nasals that extend far forward, are also long. Sagittal crest well-developed, interorbital space narrow, auditory bullae small, postpalatal pits deep, and teeth—molars as well as incisors—weak in relation to size of skull. Hinton (1926) added to these the well-developed postorbital processes and the highly specialized bony palate, similar to *Stenocranius*.

Two fragments of the bony palate and two mandibular rami preserved in the Zoological Institute, Academy of Sciences, USSR were given to me for analysis, and together exhibited complete dentition (Western Sardinia, region of Iglezias). The following structural features were seen: (1) posterior end of incisor alveolus significantly short of margin of alveoli of M_1 ; (2) width of bony palate between anterolateral angles of alveoli of M^1 small: 2.7 and 2.7 mm; (3) palatal grooves and postpalatal pits deep, bony bridge between

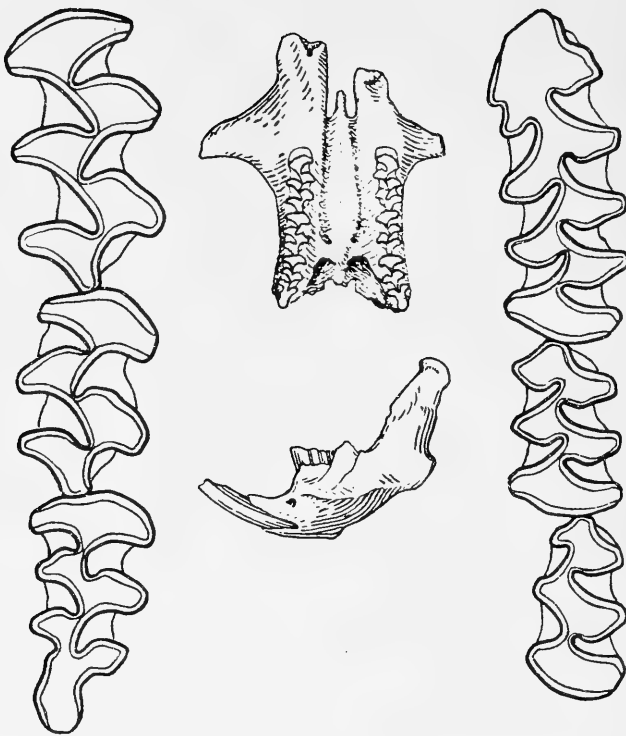


Figure 43. Skull of *Microtus* (? *Pitymys*) *henseli* F. Major.

263 them rather narrow; (4) intraorbital alveolar bulge of M^2 moderate; (5) ventral margin of mandibular ramus rises upward abruptly, much more sharply than in *Arvicola*; and (6) posterior end of lower incisor extends beyond dental foramen and forms knob on lateral surface of articular process.

Molars similar to those of large forms of present-day European *Pitymys*. Posterior end of M^1 – M^2 without additional structures; M^3 with three lateral and three medial denticles, fused middle pair of lobes, and posterior pair touch heel. Isolation of opposite triangles on M_2 incomplete, same triangles widely fused on M_3 . Alveolus of M_3 poorly developed and molar distinctly shifted lingually in tooth row. Enamel well-differentiated; cement abundant.

Age and distribution: Middle to Late Pleistocene, islands of Corsica and Sardinia.

Taxonomic notes: The generic name *Tyrrenicola* was proposed

for this insular form. It was considered either an independent genus (even by me; Gromov, 1972), or was accepted as an insular form of *Allophaiomys* surviving to the end of the Pleistocene (Kowalski, 1966; Kretzoi, 1969) or, finally, as a species of the genus (subgenus) *Pitymys* (Chaline, 1972). After examination of the original material, I consider the last assessment the most correct. Even Hinton pointed out the similarity in molar structure of *Tyrrhenicola* and *Pitymys*. Probably, the skull of this species rarely retained the structural properties of *Allophaiomys*, which is the probable ancestor of all voles of the "*Pitymys*" line.

8. *Microtus (Pitymys) hintoni* Kretzoi, 1941 (foss.)

Diagnosis: Size medium. Length of M_1 —2.3–2.5 mm (south-western European part of the USSR). Anterior unpaired loop isolated from opposite triangles and broadly fused with basal triangles. It is reduced—length slightly more than width. Traces of secondary lobe, if present, only in form of shallow notch and small "beak" on medial side; lateral margin entire, without "gregaloid" lobes.

Age and distribution: End of Ancient to Early Pleistocene of central Europe, southern parts of eastern Europe. Found for the first time in Rumania in Late Tamansk faunas (Morozovka, Betfiya X); earliest member of the genus *Microtus*, possibly surviving to Khozara faunas (Cherny Yar of Lower Volga; Aleksandrova, 1965b; Terzea and Jurcsák, 1968).

Taxonomic notes: The author (Kretzoi, 1941) rightly compared this species with *Pitymys ibericus* Gerbe (in the present sense), a more archaic eastern form of *P. duodecimcostatus* Selys-Longchamps, considering it more primitive. It has an even greater affinity with the American *P. pinetorum* Le Conte. The decisive criterion for including *P. hintoni* not only under the *ibericus* group, but under the subgenus *Pitymys* as such, should be the structure of M^3 , described below for this group, but not known to date for the extinct species. Kretzoi emphasized the differences between *P. hintoni* and (*P.*) *gregaloides* Hinton. However, based on considerable material, where the two forms are sympatric it is difficult to distinguish them on the basis of M_1 structure (almost not known or not studied), and hence many paleomammalogists prefer to speak of a collective group—*P. ex gr. hintoni-gregaloides* (Shevchenko, 1965; Kowalski, 1958a). It has already been stated that these forms are more appropriately considered members of different evolutionary lineages—subgenus *Pitymys* and subgenus *Microtus* respectively—which even by the beginning of the Early

Pleistocene had branched off from a common *Allophaiomys* ancestor.

In my opinion, the central European Early Pleistocene *Pitymys* 264 *schmidtgeni* Heller, 1933 (middle horizon of Mosbakh sands) and *P. dehmi* Heller, 1958 (Erpfingen), described from isolated individuals and later reported also in isolated remains together with ancient forms of the subgenus *Microtus*, should more correctly be considered extreme variants of the morphotypic variation series of "*P.* *gregaloides* (the first species), and *P. gregaloides* proper, or "*P.* *arvaloides* Hinton (second).

9. *Microtus (Pitymys) duodecimcostatus* Selys-Longchamps, 1839 (= *P. ibericus* Gerbe, 1854)

Diagnosis: Size variable. In smaller type form (König, 1961), body length up to 95 mm, tail up to 26 mm (25–27% body length), upper molar row 5.5–6.0 mm, lower row 5.5–6.4 mm; length of M_1 not reported. In larger western form, body length up to 107 mm, and tail length up to 29 mm (Miller, 1912).

Dorsal surface lighter than in other species of the subgenus, with sandy-gray tones, but brownish pelage in western form; ventral surface grayish, sometimes with yellowish tones. Tail whitish, from monochromatic to distinctly bichromatic. Nipples, two pairs. Chromosome number, $2n = 62$.

Dorsal profile of skull from slightly to markedly convex, ventral more convex in rostral section than in occipital. M_1 – M_2 without additional lobe in posterior section, terminate in short and fairly broad rectangular "beak". M^3 shorter, rarely equal to M^2 , with three medial and three lateral denticles; middle lateral denticle significantly smaller than both marginal ones and faces middle lateral [sic]* one; corresponding triangular fields broadly fused. Second-order folds of anterior section of paraconid of M_1 usually vary in depth: lateral one much smaller than medial and may be almost absent.

Composition of species: Most forms of subspecies status, only differing slightly in size and color, and described from Spain. Their range overlaps in many cases and their independent nature, therefore, is doubtful. *M. (P.) d. duodecimcostatus* Selys-Longchamps, 1839 (= *P. provincialis* Miller, 1909) (southeastern France); *M. (P.) d. ibericus* Gerbe, 1854 (Spain, Murica**); *M. (P.) d. flavescens* Cabrera, 1924 (Spain, Catalonia); *M. (P.) d. pescuus* Miller, 1911

* So given in Russian original; should read "medial"—Eds.

** Place name could not be confirmed—Eds.

(Spain, Grenada); *M. (P.) d. regulus* Miller, 1908 (Spain, Valencia); and *M. (P.) d. centralis* Miller, 1910 (central Spain).

Description: Comparatively broadly conical skull characterized by reduced facial section and significant height in middle part (higher only in *Pitymys thomasi*). Auditory bullae comparatively small, inflated; mastoids also distinctly inflated. Anterolateral denticles of M^3 reduced. Upper incisors long, highly prognathous. Posterior end of lower incisor extends to base of upper third of short, broad articular process, forming well-developed alveolar knob on its lateral surface, above which process sharply deflected inward. Chromosome number, $2n = 62$ (type form).

Distribution and zonal affinity: Plains and low alpine meadows (up to 1,000 m above msl) throughout southeastern half of Iberian Peninsula, from where it extends along a narrow coastal belt in southern France up to Provence, spreading northward along the Rhone valley to lower reaches of Isere. In Spain, sympatric with *M. (P.) lusitanicus* Gerbe; in Provence, replaced by *M. (P.) multiplex* Fatio in montane regions. Presence in Balkan Peninsula not proven.

Taxonomic notes: *M. (P.) duodecimcostatus* (= *ibericus*) is a typical member of the *ibericus* group according to Miller and *galloibericus* as understood by Kratochvil. Closer to it (also distinguishable by diploid chromosome number) is the smaller *M. (P.) lusitanicus* Gerbe, 1879 (= *mariae* F. Major, 1905) from the northern Pyrenees (including those in France) and northern Portugal with three subspecies: *M. (P.) l. pelandimius* Miller, 1906; *M. (P.) l. depressus* Miller, 1908; and *M. (P.) l. hurdanensis* Agancino, 1938. The independent species status of *M. (P.) lusitanicus* has recently been detailed by Balsac and Beaufort (1967).

Evolution and phylogeny: Voles with rootless molars, with poorly differentiated anterior section of M_1 in which basal triangles are fused (type *P. hintoni*); most probably, belongs to *ibericus* and can be considered the ancestral form of present-day species. First appearance in time slightly earlier than probable ancestors of the subgenus *Microtus*; toward the middle of the Early Pleistocene these forms were found together over much of central and eastern Europe.

10. *Microtus (Pitymys) thomasi* Barret-Hamilton, 1903

Diagnosis: Larger than other species of the subgenus. Body length up to 140 mm, tail up to 24 mm (less than 30% body

length; 20.2% in fully mature specimen preserved in collection of the Zoological Institute, Academy of Sciences, USSR; Mirić, 1970). Length of upper molar row 6.4–6.5 mm, lower row 6.2–6.4 mm ($n = 5$); M_1 —3.0 mm ($n = 3$).

Dorsal surface dark gray (similar to *Pitymys subterraneus*), ventral light gray. Tail distinctly bichromatic. Nipples, two pairs. Chromosome number, $2n = 44$ (Petrov and Živcović, 1972).

Dorsal profile of skull slightly convex (similar to western form of preceding species), slightly more so in rostral section than in occipital. Skull in middle part higher than in any other species of the subgenus; not only plane of tooth row but also alveolar margin of jaw lie below auditory bullae. Structure of posterior section of M^1 — M^2 similar to *P. duodecimcostatus* and *P. savii*. M^3 equal to, or shorter than M^2 , with three lateral and three medial denticles. Middle pair of triangles of M^3 completely isolated or barely fused. Difference in size of middle medial denticle and both marginal denticles, if detected, never so conspicuous as in *P. duodecimcostatus*. Anterior section of M_1 similar to type species of latter.

Description: Skull massive and rounded, with broad zygomatic arches, and least juvenile in appearance compared to skull of other species of the subgenus. Auditory bullae small. Anterolateral denticle of M_3 not reduced. Size and degree of prognathism of upper incisors maximum within limits of the subgenus; likewise length of lower incisors and corresponding structure of articular process. Comparatively long, narrow angular process characteristic, which is directed more upward than backward.

Distribution and zonal affinity: Plains and foothill meadows in southwestern Yugoslavia, north up to Neretva River and watershed of rivers falling into the Adriatic and Black Seas; Albania (?) and, most probably, Greece, where this is the only species over greater part of subgenus' range (Ondrias, 1966).

Composition of species and taxonomic notes: Subspecies have not been described. Possibly, we will have to consider *P. atticus* Miller, 1910 (= *bryoni* Bolkay, 1926) as a southern subspecies. Petrov and Zhivkovich (1974), who had material from the "terra typica" of the Greek form for comparison, have recently come to the same conclusion. In any case, if the independent species status of this form is not recognized (the only real differences so far among those indicated are three pairs of nipples in *P. atticus* and number of chromosomes in NF twice greater), inclusion here appears more justified than under *P. duodecimcostatus*, as its extreme western form (Ondrias, 1966), or under *P. savii*. This fact

was recently noted in particular by Niethammer (1971) and Wik-ing (1971), who believe that based on number of nipples, *P. atticus* is closer to the *majori* group, and based on karyotype closer to *P. taticus*. It can be separated from the karyotype of the Carpathian species through Robertsonian rearrangement. The only skull from Greece in the collection of the Zoological Institute, Academy of Sciences, USSR, has all the characteristic features of *P. thomasi*. The independent status of this species appears warranted even on the basis of morphological features, as well as its affinity with the *ibericus* group (the Aegean subgroup of Kratochvil).

11. *Microtus (Pitymys) savii* Selys-Longchamps, 1838

Diagnosis: Size medium and small. Body length up to 105 mm, tail up to 28 mm (23.5–29.2% body length), upper molar row 5.4–5.8 mm, lower row 5.4–6.0 mm ($n = 12$; Italy; Miller, 1912); M_1 —2.4–2.6–2.8 mm ($n = 10$; Sicily; Maleč and Storch, 1970).

Dorsal surface dark, with prominent gray tones, often with pale or brownish pelage; tail indistinctly bichromatic. Chromosome number, $2n = 54$. Nipples, two pairs.

Dorsal profile of skull not uniformly convex, slopes gradually in rostral and occipital sections. Structure of posterior section of M^1 and M^2 similar to preceding species. M^3 almost equal to, or longer than M^2 , with three medial and three lateral denticles. Middle lateral denticle not much smaller than marginal ones and its triangular field totally isolated from the facing field, and rarely slightly fused. Structure of anterior section of M_1 similar to preceding species.

Description: Skull with comparatively broad zygomatic arches. Auditory bullae small, inflated, but as in preceding species, because of comparatively high middle part of skull only slightly protrude downward beyond plane of tooth row. Prognathism of upper incisors moderate, their length comparatively great. Anterolateral denticle of M_3 reduced, at least in Sicilian population (Maleč and Storch, 1970). Lower incisor in southern Swiss population (Kratochvil, 1970) extends to about half height of comparatively narrow articular process, without forming well-developed alveolar knob on its lateral surface, above which process not deflected inward. In southern Swiss and Italian populations chromosome number, $2n = 54$.

Distribution and zonal affinity: Meadows of plains, lower and middle ranges of southern Alps, Apennine Peninsula, some Mediterranean islands (Sardinia, Malta; Late Pleistocene), and central and

southern regions of western France. Reliable finds from Yugoslavia not known to date (Petrov and Zhivkovich, 1974). Sympatric with *P. multiplex*; in France with *P. lusitanicus* and *P. subterraneus*.

Composition of species and taxonomic notes: Several forms have been indicated as subspecies, whose taxonomic status may alter with future more detailed studies. *M. (P.) s. savii* Selys-Longchamps, 1838 (Italy); *M. (P.) s. pyrenaicus* Selys-Longchamps, 1847 (French Pyrenees); *M. (P.) s. brunneus* Miller, 1908 (southern France); *M. (P.) s. planiceps* Miller, 1908 (southern France); *M. (P.) s. felteni* Maleč and Storch, 1963 (Macedonia); *M. (P.) s. nebracensis* Mina-Palumba, 1868 (Sicily); and the extinct Late Pleistocene *M. (P.) melitensis* Maleč and Storch, 1970 (Island of Malta). The relationship of the two French forms to the Apennine form is not clear. The subspecies *M. (P.) s. pyrenaicus*, based on details of chromosomal structure, is sometimes considered an independent species (Wiking, 1971), as are voles from Macedonia, which have been described as a well-differentiated independent species, *M. (P.) felteni* (Petrov, Živković and Rimsa, 1976).

Evolution and phylogeny: Fossil remains are known from northern Italy (environs of Verona) from the Early Pleistocene (Pasa, 1949). Judging from the Malta discovery, the range even during the Late Pleistocene was wider. However, many details are not clear in the evolution of this species, in particular the time of formation of the French-Italian division of the range, evolution of the species in the Balkans where it is possibly represented by a relict population (Kratochvil, 1970), and so forth. The archaic structure of M^3 and the comparatively high skull are features distinctly relating *P. savii* to the *ibericus* group, in which, according to Kratochvil, it is a member of a unique Apennine subgroup.

12. *Microtus (Pitymys) tatricus* Kratochvil, 1952—Tatry Vole

Diagnosis: Size medium and large (larger in neighboring montane population of *P. subterraneus*). Body length up to 117 mm, tail up to 49 mm (35.6–41.1% body length), length of upper molar row up to 5.6–6.7 mm, lower row 5.4–6.4 mm (Kratochvil, 1970); information on length of M_1 not available.

Dorsal surface dark gray, sometimes with faint admixture of brown tones; ventral side ash-gray. Tail distinctly bichromatic. Guard hairs comparatively well-developed, such that general nature of pelage more closely resembles *Microtus* than *Pitymys*. Nipples, two pairs. Chromosome number, $2n = 32$.

Dorsal profile of skull similar to preceding species. Small additional medial lobes present in posterior section of M^1 and M^2 in some individuals, which are better developed on M^2 . M^3 with three lateral and four medial denticles in large number of individuals. Middle pair of triangles on this tooth usually isolated, lateral one with tendency toward reduction. Structure of M_1 not described.

Description: Height of skull and its temporal width not significant. Auditory bullae comparatively large and inflated; mastoids likewise notably enlarged. Structure of anterior denticle of M_3 not described. Incidentally, Kowalski (1960c) provided a diagram of the lower dental row in which the anterolateral denticle of M_3 is distinctly reduced. Upper incisors far less prognathous and shorter than in the *ibericus* group, but both characters better expressed than in species of the *subterraneus* group. Posterior end of lower incisor extends to half length of articular process, does not form alveolar knob on its lateral surface, above which process not deflected inward. The significant features of this species are the lowest number of diploid chromosomes among all the known species in the subgenus and the unique structure of the baculum (Hrabe and Polach, 1971).

Distribution and zonal affinity: High alpine meadows and sparse forests (often lives in taluses) of the western Carpathians (Tatry) at height up to 2,300 m above msl and Beskids (1,300–1,550 m msl). Its occurrence in alpine meadows in the eastern Carpathians and in the USSR is quite possible, where, to date, only *P. subterraneus* has been recorded (Sokar, 1960).

Taxonomic notes: Kratochvil (1970) has recently published a detailed description of the species and emphasized that a reliable differentiation from *P. subterraneus* is possible only for overwintered animals and only in the totality of characters, among which the author attaches importance to the position and structure of the posterior sutures of the nasals, position of the plane of the coronoid process relative to the plane of the articular process, structure of M^3 , and extent of development of the auditory bullae. However, even these features are only valid for distinguishing this species from the Carpathian populations of *P. subterraneus*. Their use in distinguishing it from other members of the Alps–Carpathian group of forms, such as *P. multiplex* Fatio, 1905, *P. lichtensteini* Wettstein, 1927, *P. bavaricus* König, 1962, and *P. druentius* Miller, 1911—the taxonomic position of which has not been sufficiently studied to date—is less reliable; of these species, at least the first

has a known diploid number of $2n = 48$, and the second species has 46 (Petrov and Živković, 1971).

Evolution and phylogeny: The closeness of *M. (P.) tatricus* to the species listed above, with which it forms a single (probably genetic) group, is beyond doubt. Kratochvil correctly pointed out that the species forming this group must have undergone a complex Pleistocene evolution. It is quite possible that individual populations of some ancient form of the *subterraneus* group survived glaciation in favorable parts of the Alps-Carpathian region, occupying open high montane environments, at the foot of which *P. subterraneus* spread through a belt of deciduous forests and meadows. The possible affinity with *P. atticus* through chromosomal structure has already been noted (p. 383).

13. *Microtus (Pitymys) subterraneus* Selys-Longchamps, 1838
—European Underground Vole

Diagnosis: Size medium. Body length in larger forms up to 105 mm, rarely reaching 100 mm in smaller ones; tail length up to 44 and 40 mm (32–38% body length) respectively (Mirić, 1970). Length of upper molar row up to 5.6 mm, lower row up to 5.5 mm; M_1 —2.45–2.6–2.8 mm (European part of the USSR) and 5.0–6.7 and 5.0–6.0 mm in the large montane forms (Kratochvil, 1970).

Dorsal surface, ventral surface, and tail similar to *P. tatricus*. Nipples, two pairs. Diploid number polymorphic: $2n = 52, 53$ and 54 (Meylan, 1971).

Dorsal profile of skull flattened or slightly convex. In former case, slopes insignificantly in rostral section and more so in interorbital constriction. Structure of posterior section of M^1 – M^2 as in *P. tatricus*. M_1 with two incomplete to complete pairs of triangles; anterior unpaired loop often rounded, asymmetric. Dimensions and structure of M^3 in most individuals similar to *P. tatricus*; in some populations, a tendency toward separation is seen in middle pair of triangles of this tooth, right up to complete isolation, and also in basal pair of triangles of paraconid of M_1 .

Composition of species: The *subterraneus* group includes more than 20 species and 10 subspecies (Ellerman, 1941) or, according to another claim (Ellerman and Morrison-Scott, 1951) up to 25 subspecies. In the latter case, the taxonomic rank of several forms is clearly degraded. This relates not only to *P. majori* Thomas, 1905 and *P. schelkovnikovi* Satunin, 1907, but also to several species from the “Alps-Carpathian group” of Kratochvil (see above), many of which are sympatric with *P. subterraneus*. These are mainly *P.*

multiplex Fatio, 1905 (Switzerland) and *P. lichtensteini* Wettstein, 1927 (western and central Yugoslavia); the latter is only a subspecies of the former. Petrov and Zhivkovich (1974) consider them undisputable independent species.

There are two subspecies in Russian fauna: *M. (P.) s. ucrainicus* Vinogradov, 1922 (Ukraine, Moldavia) and *M. (P.) s. transvolgensis* Schanev and Schaposchnikov, 1958 (Kalinin district). The taxonomic position is not clear for pine voles from the extreme northwestern (Belovezhsk Pushcha), northern (eastern part of Leningrad district, Prionezh'e), and southeastern (Voronezh National Park) areas of discovery; voles from Poland are also included under the type form (Belgium) (Haitlinger, 1970).

Description: Height of skull and width at zygomatic arches moderate for subgenus. Auditory bullae comparatively large but flat; mastoids notably inflated. Anterior denticle of M_3 variably reduced. Upper incisors small, moderately prognathous. Structure of lower incisor and ascending mandible similar to *P. taticus*.

Distribution and zonal affinity: Broad-leaved forests and forest-steppes of plains and mountains from northern and central France to central and southern regions of the European part of the USSR. In the south found up to southern slopes of Alps, central parts of Balkan Peninsula (Macedonia, northeastern Greece), Bulgaria, European part of Turkey, and up to about 48° N in the Ukraine. Found in mountains up to subalpine and alpine belts—1,700 m above msl in the High Tatra and 1,800 m in Macedonia. Northern boundary coincides with that of subgenus. In the Late Pleistocene within the composition of the "cold" mixed faunas, their remains have been found only in Western Europe and to date not reported from the USSR.

Evolution and phylogeny: Fossil remains of this species or closely related ancestral species from the European part of the USSR are known from the Late Pleistocene, and in Western Europe from the Middle Pleistocene. A numerical predominance of remains of *Microtus* over *Pitymys* has been recorded for the middle Middle Pleistocene of central Europe. The closest ancestors of *Microtus (P.) subterraneus* are not known. In any case, as rightly pointed out by Janossy (1969), these could not be the extinct forms of "*P.*" *arvaloides* Hinton and *Microtus arvalinus* Hinton types. The closest affinity established to date is with *P. multiplex*, which produced hybrids in an experiment (Meylan, 1972), in spite of a difference in chromosome number; true, the litter size was not large, but the hybrids were partly fertile in backcrossing.

14. *Microtus (Pitymys) majori* Thomas, 1905—
Caucasian Pine Vole

Diagnosis: Size medium. Body length up to 105 mm in large forms and up to 100 mm in small; tail up to 44 and 40 mm (38–40% body length) respectively. Length of upper molar row up to 6.1 mm, lower row up to 5.8 mm; M_1 —2.6–2.7–2.9 mm in large forms and 2.4–2.6–2.8 mm in small.

Dorsal surface brownish-gray, without reddish tinge; ventral surface grayish, rarely slightly brown. Tail monochromatic or slightly bichromatic. Nipples, three pairs. Diploid number polymorphic: $2n = 54$ and 52 (Daghestan).

Dorsal profile of skull distinctly slopes at base of rostral section, and often also in interorbital and at beginning of postorbital. Structure of posterior section of M^1 – M^2 as in the *subterraneus* group; tooth length and number of denticles on M^3 same. M_1 in most individuals of a population with two incomplete pairs of triangles; anterior unpaired loop partly fused with basal triangles, its shape variable, not low, but broad and symmetrically fungiform.

Composition of species: It is quite possible that the infraspecific structure is more complex than presently understood. Only four subspecies have been reported: *M. (P.) m. majori* Thomas, 1905 (western Trans-Caucasus and eastern Black Sea regions); *M. (P.) m. ciscaucasicus* Ognev, 1924 (northern Cis-Caucasus, western and central parts of the Great Caucasian range); *M. (P.) m. suramensis* Heptner, 1948 (? = *intermedius* Schidlowski, 1919) (southern regions of the Great Caucasian range except eastern part); and *M. (P.) m. dagestanicus* Schidlowski, 1919 (Daghestan, high mountains of Lesser Caucasian range).

Description: Skull with comparatively narrow temples and rarely low in middle part. Auditory bullae, on the average, as in *Pitymys subterraneus*. In individual animals of any population, middle pair of lobes on M^2 may be fused. Middle pair of lobes on M^3 fused, with no tendency toward isolation. Anterolateral denticle of M_3 not reduced. Upper incisors larger than those of *P. subterraneus*, notably protrude forward (especially in animals from population of open high montane biomes). Posterior end of lower incisors extends slightly beyond half length of articular process, does not form knob on its lateral surface, and root itself bends sharply here.

Distribution and zonal affinity: Belt of deciduous forests of mountain ranges of Caucasian Isthmus in northern Turkey from sea level up to upper forest boundary; alpine meadows and meadow-steppes up to subnival zone. In the Palearctic, relict colonies, at

present separated from continuous range (Stavropol upland, Pyatigor'e, etc.) attest to Holocene (?) changes in northern boundaries related to evolution of forests of this territory (Vereshchagin and Gromov, 1953). This relationship is also found in Trans-Caucasus (Vereshchagin, 1959) where voles live at sites of former deciduous forests.

Taxonomic notes: Probably, in nature there is only the supra-species *majori*, or the *majori* group as understood by Kratochvil (1970), consisting of no more than one species. Here the taxonomic status of the high-montane (alpine and mountain meadow) forms should be explained first, and the position of forest forms secondly (especially the western and Black Sea archaic forms on the basis of tooth structure). Their morphological differences extend beyond the limits typical of differences in biotopic populations of other microtines. Such, in particular, are the differences of the Dagestan form, the species status for which was long insisted upon by the author (Shidlovskii, 1938) who, possibly unnecessarily, ultimately changed his view (Shidlovskii, 1962, 1976). Steiner (1971), who studied the alpine and forest populations of *Pitymys* biometrically in the Artvin Province of Turkey, believes that they became included in different "semi-species"—*dagestanicus* and *majori*. Recently, Ivanov and Tembotov (1974) demonstrated the presence of 52 chromosomes in the diploid set of *Pitymys* from Dagestan. As in several other cases, the results of hybrid analysis would play a deciding role in determining the taxonomic status. *P. dagestanicus* is characterized by a more flattened skull than in other forms (especially compared to the type form), small eyes (cross section less than 2.2 mm), and long, markedly oblong upper incisors, indicating a greater adaptation to a fossorial life style. A similar morphotype is typical of pine voles from the high altitudes of western Caucasus.

Evolution and phylogeny: Fossil remains from the beginning of the Middle to Late Pleistocene belonging to a somewhat larger form than the present-day vole (length of M_1 —2.5–2.6–2.8 mm versus 2.2–2.4–2.6 mm), with a broader lower incisor, and relatively shorter diastema and mandible, are known from the caves of western Georgia in the mammalian faunas of alpine-meadow and montane-steppe types. In eastern Trans-Caucasus, the following larger species, possibly from the same group (see below), existed in recent geological times.

271 15. *Microtus (Pitymys) apscheronicus* Argyropulo, 1941 (foss.)

Diagnosis: Size large. Length of lower molar row 6.3 mm; M_1

—3.15 (holotype), 6.5 and 3.15 mm (paratype) (both mandibular rami possibly belong to a single individual). Anterior loop of M_1 not completely separated from basal triangles, apically directed backward, and with rounded anterior angles. Posterior end of lower incisor extends beyond half length of articular process, forming a distinct knob on its lateral surface. Width of articular process not large, and no inward deflection observable. Anterolateral denticle of M_3 completely reduced.

Age and distribution: End of Middle Pleistocene, Binagady (Apsheron Peninsula, eastern Trans-Caucasus). Known only from the type locality among rodent fauna dominated by desert-steppe species (jerboas and gerbils, among which pine voles constitute less than 1.0%).

Taxonomic notes: Even Argyropulo (1941) emphasized the greater similarity of the extinct Apsheron species to *Pitymys majori* than to voles of the *ibericus* group, which are closer in dimensions. In particular, the mandibular ramus is characterized by an angular process with a posterior notch and a relatively broad ascending section (Gromov, 1952). The likeness of this form to the eastern Caucasian form of present-day *P. majori*, appears to be more than that of the type form. New material, especially of the upper molars, is required for a detailed analysis.

16. *Microtus (Pitymys) pauli* Bate, 1935 (foss.)

Diagnosis: Size large. Condylbasal length of skull 22.6 mm; length of upper molar row 6.4 mm, lower row 6.2 mm (holotype; Bate, 1935). Length of M_1 about 3.3 mm (restored by me from a diagram).

Dorsal profile of skull straight, slopes slightly in interorbital region, and slightly more so in rostral section than in occipital. M^1 – M^2 with well-developed additional medial triangles (similar to *Pitymys schelkovnikovi*). M^3 longer than M^2 , with four medial and three lateral denticles and a rudimentary fourth denticle (often found in *P. majori* and *P. subterraneus*); middle pair of denticles fused. M_1 with two pairs of complete triangles; anterior unpaired loop not fungiform, but irregularly trifoliate with folds of second lobe shifted relative to each other and broadly contacting corresponding fields of triangles.

Description: Skull comparatively high in middle part (almost identical to *P. schelkovnikovi*). Auditory bullae large, uniformly inflated, significantly flattened laterally in anterior section. Anterolateral denticle of M_3 well-developed. Upper incisors,

probably, rather markedly prognathous; length not known (often broken in front of alveoli). The author noted the similarity of structure of the lower incisors in *P. majori*.

Age and distribution: Pleistocene (not dated precisely) of Island of Malta.

Taxonomic notes: Among present-day species, closest to *P. schelkovnikovi* or to some forms of *P. majori*, which was also mentioned by Bate (1935); among extinct species, close to *P. 272 apscheronicus*. A more complete comparison with the latter species will be possible when the skull structure of the Apsheron form becomes known and new dentaries are collected for both species. At present, the locality of *P. pauli* is the extreme southwestern range for species of the *subterraneus* and *major* groups, with complex structure of M^3 . It is interesting that in Malta this species during the Pleistocene was sympatric with the extinct form of *P. savii*, i.e., species of the *ibericus* group. At present, there are no microtines on Malta.

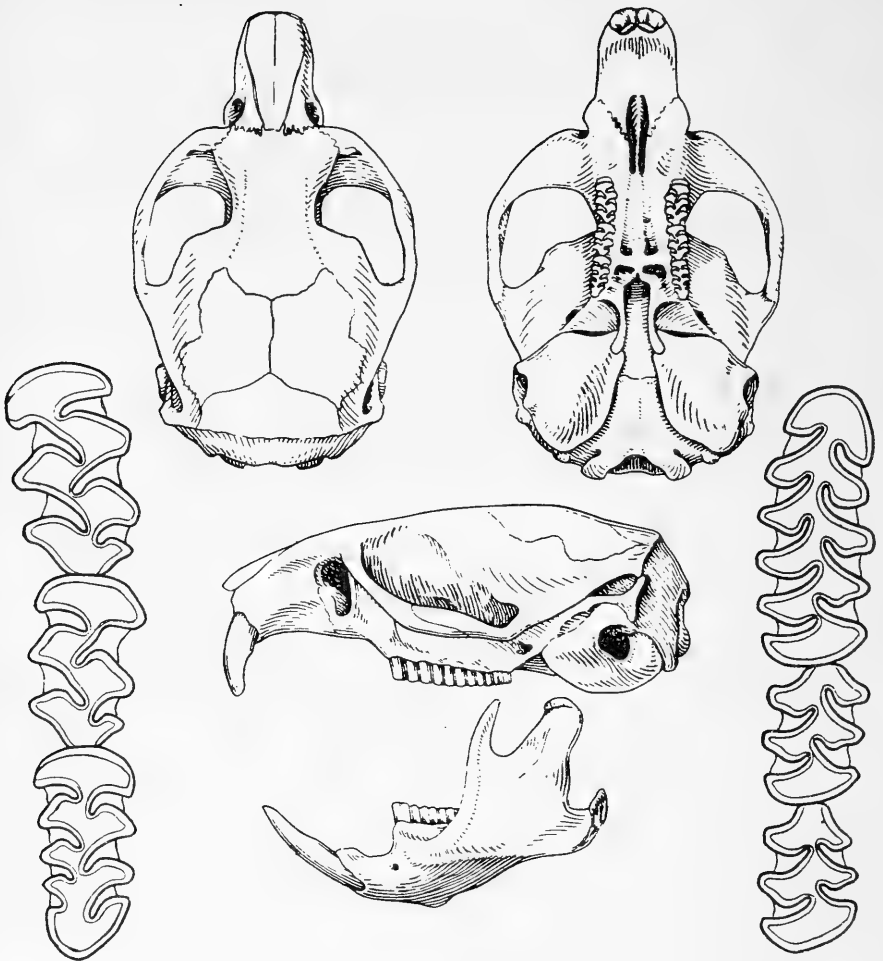
17. *Microtus (Pitymys) schelkovnikovi* Satunin, 1907—
Shelkovnikov's Pine Vole (Figure 44)

Diagnosis: Size medium. Body length up to 107 mm, tail up to 24 mm (19–23% body length), upper molar row up to 6.4 mm, lower row up to 6.7 mm (Aleksperov, 1959); M_1 —2.8–3.0–3.1 mm ($n = 5$).

Dorsal surface dark, brownish-red; ventral surface grayish-brown; transition between two surfaces gradual. Tail faintly bichromatic. Nipples, four pairs. Diploid number, $2n = 54$.

Dorsal profile of skull smoothly convex. M^1 – M^2 as in the 273 extinct species *Pitymys pauli*, with well-developed additional medial triangles in posterior part, fused with posterolateral ones. M^3 longer than M^2 ; most individuals with four medial and four lateral denticles. M_1 with two complete pairs of triangles at base of anterior unpaired loop, and latter broad, low, and symmetrically fungiform.

Description: Skull with comparatively high, broad temples (as in species from the *ibericus* group). Auditory bullae small, placed only slightly below plane of tooth row. Number of denticles on M^3 on both sides may reach five, and thus this tooth attains maximum complexity of structure within limits of the subgenus; second pair of lobes fused. Anterolateral denticle of M_3 well-developed. Upper incisors small, orthodont. Posterior end of lower incisor does not extend beyond half length of articular process, and latter without sharp deflection inward.



272 Figure 44. Skull of Shelkovnikov's pine vole [*Microtus (Pitymys) schelkovnikovi* Saturnin].

Distribution and zonal affinity: Humid forests in foothills of Talysh and, probably, the Elbrus mountains of Iran.

Taxonomic notes: The slightly smaller *M. (P.) dorothea* Ellerman, 1949 from northern slopes of the Elbrus may possibly be a subspecies of Shelkovnikov's vole.

Evolution and phylogeny: Reliable fossil remains not known.

Differences from the extinct Binagadian *Pitymys apscheronicus*, which is similar in dimensions, are not less than those of large Western European forms from the *ibericus* group. Maximum similarity is seen with the Pleistocene Maltese species *P. pauli*, and through it with *P. majori*, although *P. schelkovnikovi* is clearly distinguished from this eastern member of the *subterraneus* group in Miller's interpretation (1912), which was also mentioned by Shidlovskii (1962) even before Kratochvil (1970).

18. *Microtus (Pitymys) pinetorum* Le Conte, 1830 (Figure 45)

Diagnosis: Size large. Body length up to 120 mm, tail up to 25 mm (Hall and Kelson, 1959). Relative size of tail not mentioned; in specimen in collection of the Zoological Institute, Academy of Sciences, USSR, 21.9% and in specimen of the Geological Museum, Moscow State University, 23%. Length of upper molar row 5.8–6.5 mm, lower row 5.5–6.2 mm; M_1 —2.7–2.9–3.0 mm ($n = 5$). Smaller size reported for the Late Pleistocene species *Pitymys pinetorum* from Pennsylvania: 2.4–2.65–2.9 mm ($n = 110$) (Guilday, Martin and McGrady, 1964).

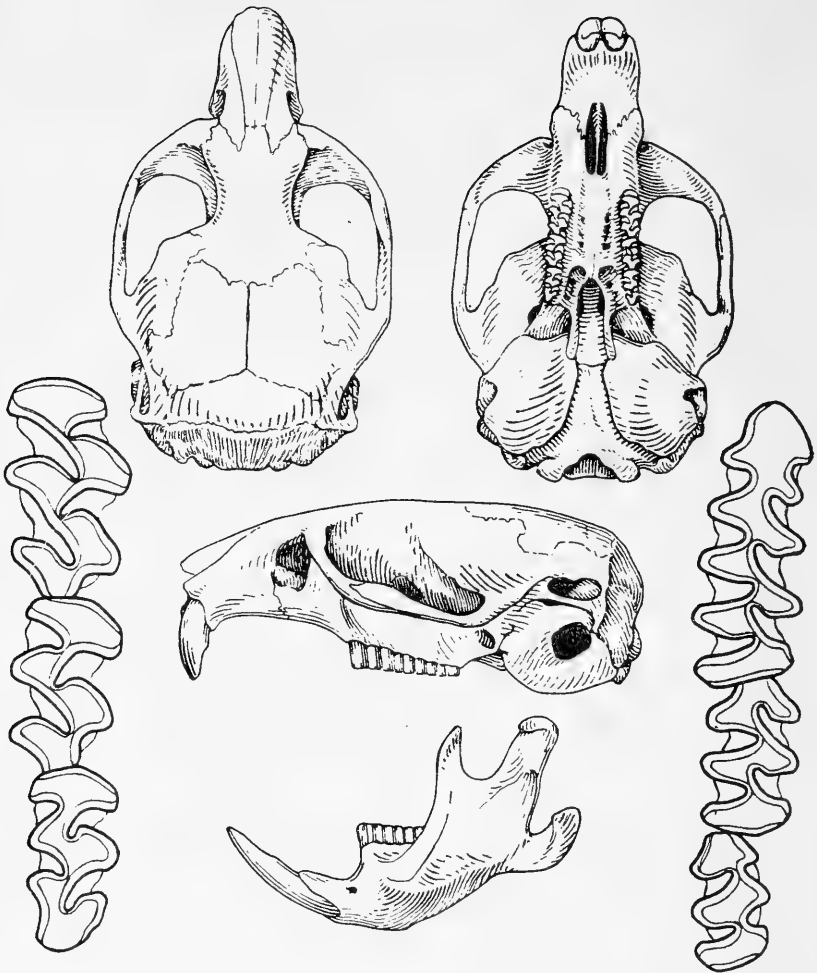
Dorsal surface ocher to chocolate-brown; ventral surface silver-gray. Tail monochromatic, rarely faintly bichromatic. Nipples, two pairs. Chromosome number, $2n = 62$ (Matthey, 1955).

Dorsal profile of skull slightly convex, almost does not slope in occipital section but slopes steeply in rostral. Structure of posterior part of M^1 — M^2 as in *P. savii*; M^3 generally similar. This tooth is equal to, or shorter than M^2 , with three denticles on each side; middle pair of triangles slightly fused or isolated; middle lateral denticle slightly smaller (shorter) than both marginal ones, but this difference far less than in *P. duodecimcostatus*. Anterior part of M_1 generally with low, broad anterior unpaired loop and poorly developed depressions of secondary lobes of paraconid, especially lateral one, which rapidly disappears.

Description: Skull with moderately broad zygomatic arches, high in middle part, almost identical to the European species *M. (P.) duodecimcostatus* and *M. (P.) savii*. Auditory bullae as in former species. Anterolateral denticle of M_3 reduced. Upper incisors short, orthodont. Length of lower incisors and middle part of articular process similar to the *ibericus* group.

274 *Distribution and zonal affinity:* Alpine meadows in southeastern part of North America, up to 1,500 m above msl.

Composition of species and taxonomic notes: Hall and Kelson (1959) list six subspecies and two closely related species: *M. (P.)*



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Figure 45. Skull of *Microtus (Pitymys) pinetorum* Le Conte.

parvulus Howell, 1906 (northwestern Florida) and *M. (P.) quasiater* Coues, 1874 (isolated belt in north-central Mexico).

Evolution and phylogeny: Fossil remains known from the Late Pleistocene. The more ancient Mid-Pleistocene species (Irvingtonian* faunas) *Pitymys meadensis* Hibbard, 1944 probably belongs to the subgenus *Micortus*, which is at the "Pitymys" stage of evolution

*[sic], Irvingtonian—Eds.

but in a somewhat different direction than the present-day North American members of *Pedomys* included under it. The taxonomic position of such Pleistocene species as *Pitymys* (vel *Pedomys*) *dideltus* Cope, 1871, *Pitymys* (vel *Pedomys*) *involutus* Cope, 1881, and *Pitymys* (vel *Pedomys*) *aratei* Webb, 1974, is not clear (Hibbard, 1955).

275 *P. pinetorum* belongs to the extant European group *ibericus* with a simplified structure of M^3 and high skull; differences are not greater than those of the European species of this group. Such a range is a good index of the past Trans-Atlantic connection between the two continents, and the discontinuous range of the American species is a result of the complex Pleistocene history of alpine-forest biomes in the New World.

Subgenus *Stenocranium* Kastschenko, 1901—
Narrow-skulled Voles

Diagnosis: Size medium, rarely large, with short and moderately long tail, and adapted to semifossorial life style that is somewhat better evolved than in species of the subgenus *Microtus*, but less than in *Pitymys*. Pelage dense, variable in length, distinctly differentiated into guard hair and underfur. Eyes small; ear lobes reduced, with dense tuft of hairs in front. Antitragus large, rectangular, well-isolated.

Skull structure, as in all other subgenera, with high, narrow brain case, interorbital space narrow along longitudinal axis, and with well-developed high longitudinal crest. Articular process of dentary moderately long. Molars with moderately high crown. Paraconid section of M_1 with 1.5 lobes, rarely two (often incomplete); anterolateral denticle absent but, if present, usually less distinct than anteromedial, which is reduced on M_3 and may be completely absent. Opposite triangles at base of paraconid isolated, at least in all present-day forms.

Composition of subgenus: One Palearctic species: *Microtus* (*S.*) *gregalis* Pall., 1778. One Nearctic species is also closer to it—*M.* (*S.*) *miurus* Osgood, 1901, and to a lesser extent—*M.* (conf. *S.*) *abbreviatus* Miller, 1899. The Late Pleistocene species *M. anglicus* Hinton, 1910 is considered a subspecies here, although its independent species status is not excluded.

Age and distribution: Fossil remains of known microtines with cemented molars are similar to those of the present-day narrow-skulled vole based on structure of anterior part of paraconid of M_1 ,

known since the Early Pleistocene (Tiraspol' faunas), and usually designated *Pitymys gregaloides* Hinton. Remains of skull have been discovered only from the Late Pleistocene (mixed and lemming faunas), and mummified bodies have been found in Siberia, which permit us to believe that as of the Late Würm in the Palearctic the "gregaloid"-type of adaptation had evolved. Inhabitants of open environments from desert steppes to plains, montane tundra, and alpine meadows. Absent in Recent epoch in steppes and bald mountain peaks west of the Ural range. Live in tundra and forest-tundra of Arkhangel'sk region to eastern Siberia where distribution is disrupted (in river valleys); absent in Chukchi, Kamchatka, Chukchi islands, and eastern Siberian seas, as well as montane tundras of western North America, east up to the Mackenzie River. Common in steppes of southern Ural region, western Siberia, greater part of Kazakhstan, central Yakutia, middle Amur region, Trans-Baikal region, northern and central Mongolia (high peaks of Gobi Altai), and northern China, as well as montane-steppes and open biomes of high mountains of Pamir-Alai (up to 3,500 m above msl), Tien Shan, and Altai-Sayan.

276 During the Late Pleistocene the western part of the range of the subgenus reduced sharply concomitant with a diminution of mixed lemming fauna, which continued from the Ural range up to central France and southern England and covered a large part of southeastern Europe. Simultaneously, segregation of the forest zone took place in the remaining part of the range into the northern (tundra) and southern parts (steppe), desert-steppe and montane-steppe, as well as lower and upper montane reaches. Probably, the boundaries of the range remained more or less constant only in northeastern Siberia and southwestern America, although distribution was largely mosaic.

Taxonomic notes and evolution: Group with highly specialized characters that in skull structure became apparent recently and, possibly, convergently in the Old and New World; such characters are considered an adaptation to life in narrow burrows and cracks in frozen ground. A comparatively later appearance in time of such an adaptive type is underlined by the complex structure of M^3 , as well as by the fact that throughout its wide Palearctic range, this was the only species in spite of its fairly complex evolution. As mentioned above (p. 360), at the base of the evolutionary branch of the subgenus are located the closely related Early Pleistocene microtines of *Allophaiomys*, with a "gregaloid" structure of the anterior section of M_1 , but also with a "*Pitymys*" division of triangles

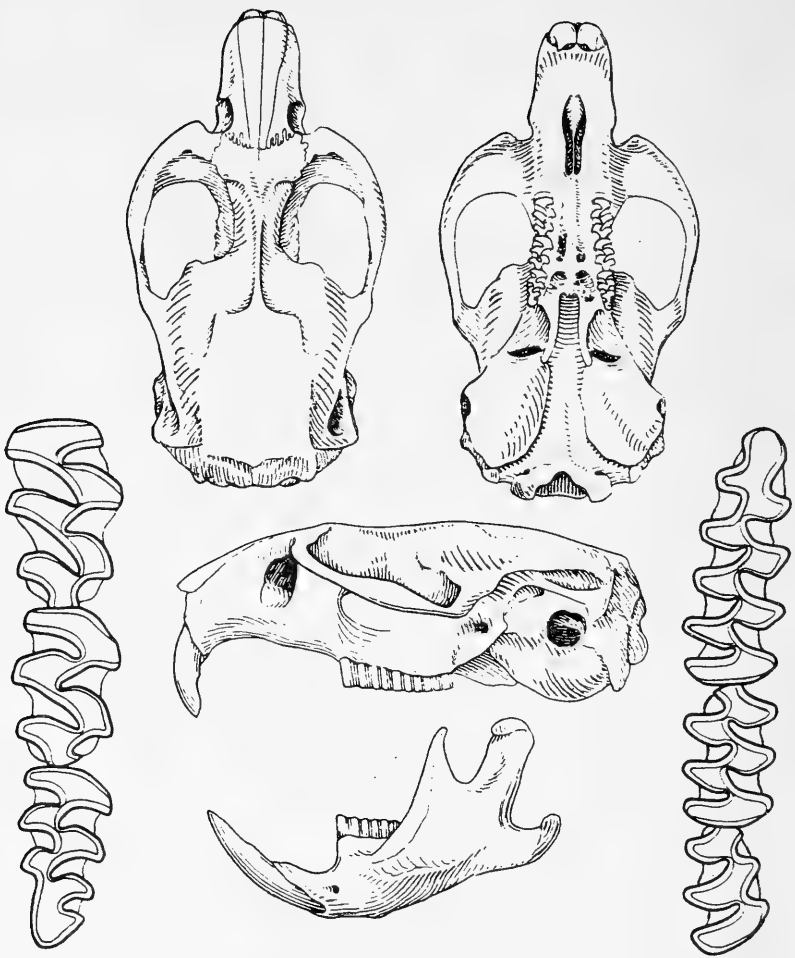
at the paraconid base, which here are considered members of the genus *Microtus* with an indistinct subgeneric differentiation. A certain number of molars with almost completely divided triangles appear in the later faunas of this time together with similar remains and, in some of the latest forms, the "gregaloid"-type completely replaces the "*Pitymys*" (Platovo and other localities). Unfortunately, skull remains of this form have not been recovered to date.

19. *Microtus (Stenocranius) gregalis* Pallas, 1778—
Narrow-skulled Vole (Figure 46)

Diagnosis: Body length up to 140 mm in large forms and 115 mm in small ones; tail up to 43 and 24 mm respectively. Relative length of latter varies from 21.5–33.3% in long-tailed forms, and up to 24–28% in short-tailed ones. Length of upper molar row 6.1–6.8 and 5.6–6.1 mm, lower row 5.7–6.6 and 5.0–5.7 mm; M_1 —2.4–2.8–3.1 mm ($n = 36$) and 2.2–2.5–2.9 mm ($n = 38$) in large tundra and smaller steppe forms respectively.

Dorsal surface varies from chocolate-brown to gray, distinctly speckled, with light tips on guard hairs, to brownish-ocher, at times up to fairly light-colored, with less prominent speckling. Ventral surface from dark gray to yellowish-ocher. Diffuse black stripe present on occiput and along anterior part of spine (especially in young individuals). Tail distinctly bichromatic. Chromosome number, $2n = 36$ (Lyapunova and Mirokhanov, 1969a).

Dorsal profile of skull irregular: straight in region of brain case, slopes at interorbital space, steeply so toward rostrum from base of zygomatic arches, and forms close to a right angle in occipital region. Narrow bony palate barely broadens posteriorly, terminates with two deep postpalatal pits separated by narrow bony bridge; palatal grooves deep. Articular fossa of zygomatic squamosa narrow and long, and correspondingly, articular condyle of pr. articularis shifted forward and laterally flattened (more so on outer than inner side). Upper incisors long, sharply curved, cutting edge M-shaped, lingual surface distinctly tubular, "nibbling" surface high; lateral surfaces flattened, and slight groove-like depression may extend along anterior surface. Posterior end of lower incisor, even if it extends beyond upper margin of dental foramen, does so only slightly and does not form an alveolar knob on lateral surface of articular process. Alveolar bulges of roots of upper molars do not extend into orbit. M^1 – M^2 in individuals of some populations tend toward formation of additional lobes at posterior end and on M_1 toward isolation of complete triangles from second lobe of paraconid



277 Figure 46. Skull of narrow-skulled vole (*Stenocranius gregalis* Pallas).

section.

Composition of species: Actual number of extant subspecies probably less than listed here: *Microtus* (S.) *g. gregalis* Pallas, 1778 (= *g. dukelskiae* Ognev) (from Ural region to Irkutsk, Minusinsk steppes, Sayans, and Tuva); *M.* (S.) *g. eversmanni* Poljakov, 1881 (= *tarbagataicus* Ognev, 1944) (Altai, Tarbagatai, Tien Shan, south of Issyk-Kul); *M.* (S.) *g. montosus* Argyropulo, 1932 (Altai valley, Zaalaik range); *M.* (S.) *g. castaneus* Kastschenko, 1923 (Talassk,

278 Zailiisk, Kirgizian ranges, central Tien Shan, south of Issyk-Kul); *M. (S.) g. raddei* Poljakov, 1881 (= *angustus* Thomas, 1808) (Chuya steppe in Altai, Trans-Baikal region, Mongolia, northern China); *M. (S.) g. dolguschini* Afanasjev, 1938 (lower reaches of Ili, Zaisan basin); *M. (S.) g. major* Ognev, 1918 (Yunan, northern Ural); *M. (S.) g. tundrae* Ognev, 1944 (tundras in northern Europe); *M. (S.) g. nordenskiöldii* Poljakov, 1881 [Taimyr, probably identical with *M. (S.) g. major*]; *M. (S.) g. buturlini* Ognev, 1922 (from lower reaches of Lena to Kolyma and Anadyr); *M. (S.) g. brevicauda* Kastschenko, 1901 (central Yakutia, Trans-Baikal region except southern part, central Amur region; and *M. (S.) g. zachvatkini* Heptner, 1922 (northeastern Aral region, ? central Kazakhstan; a beautiful subspecies). Extinct forms to which subspecies has been attributed to date: *M. (S.) g. anglicus* Hinton, 1910 (steppe and mixed faunas of Late Pleistocene, central and eastern Europe); *M. (S.) g. egorovi* Feigin, 1972, in litt. (Late Pleistocene, northeastern Siberia; described from dead voles found permafrost); and *M. (S.) g. martelensis* Chaline, 1972 (end of Late Pleistocene, France).

Distribution and zonal affinity: Same as for subgenus in Palearctic part of range.

Taxonomic notes: The independent species status of *M. miurus* Osgood, repeatedly included under *S. gregalis* as a subspecies, can finally be considered proven (see below). As for the infraspecific forms, hybridization tests conducted by Feigin in the Laboratory of Mammals of the Zoological Institute, Academy of Sciences, USSR confirmed that at least for half the subspecies listed above, morphological differences between tundra, steppe, and montane forms are not more than subspecific; all major forms intercrossed freely and produced fertile progeny, although they always displayed some differences in postembryonic development as well as in structure. Among the latter, as I mentioned earlier (Gromov *et al.*, 1963), tundra populations are characterized by a larger size, more prominent rusty tones in coloration, dense pelage, longer claws of forelimbs (Vinogradov, 1946), skull with broader temples and interorbital space, and more complex structure of paraconid section of M_1 . Some morphophysiological differences have also been indicated (Shverts, 1969).

Evolution and phylogeny: The common evolutionary path of this species is reconstructed only on the basis of changes in time of formation of the masticatory surface of M_1 , from the *Allophaiomys*–*Pitymys* ancestors through the *Pitymys*, i.e., gregaloid to gregaloid ancestors *per se* (Chaline, 1972). This may appear to be hypotheti-

cal, because it is based only on data on structure of M_1 . The evolution of the species in the Late Pleistocene, however, is more convincingly documented, including fossil skull remains (Tiede and Westerheln in the FRG, Aihem in southern England, Novgorod-Seversk in Chernigovshchine, caves in Altai, and so on). Based on a comparison of size and dominant structure of M_1 taken from a very large number of remains from different localities between Desna and Aldan, it is possible to separate this species into Würm steppe, mixed, and lemming faunas of two forms: the ancestors of the present-day tundra forms, which are absent in the middle latitudes of the northern European part of the USSR as well as western Siberia, and the probable ancestors of the modern steppe forms. The latter became extinct in central and eastern Europe, but east of Ural were the ancestral forms of the present-day steppe populations of western Siberia and Kazakhstan (Maleeva, 1971). At the eastern end of the range, interesting facts came to light in a study at the Zoological Institute, Academy of Sciences, USSR of the mummified bodies of
 279 narrow-skulled voles from Indigirka basin, whose absolute age has been estimated at 35,000 to 37,000 years, which corresponds to the beginning of the last glaciation. It was found that the morphological adaptations of this subgenus were not completely formed in this form: brain case has not acquired the typical proportions, facial section was not reduced, and features of the postcranial skeleton indicate that adaptation for digging was less well-developed than in its ancestors now occupying the same territory. Furthermore, the totality of differences (the most important the larger size and greater width of skull) is greater than in some present-day forms. This fact may serve as a basis for deciding the highly probable species status of the Late Pleistocene form [*M. (S.) anglicus*] which, like the extant species, has a Trans-Palearctic range and may likewise be divided into a series of subspecies (Figure 47).

20. *Microtus* (conf. *Stenocranius*) *miurus* Osgood, 1901

Diagnosis: Body length up to 120 mm, tail up to 41 mm (20–25% body length), in two specimens studied 21 and 27%; upper molar row 5.6–6.7 mm in large forms (Rausch, 1964) and 5.2–6.3 mm ($n = 10$) in small forms, lower row 5.6 mm; M_1 —2.7 mm.

Dorsal surface similar to eastern *M. (S.) gregalis* in coloration. Dark stripe on occiput and in anterior part of back absent. Tail distinctly bichromatic and densely covered with hairs. Chromosome number, $2n = 54$ (for northern subspecies).

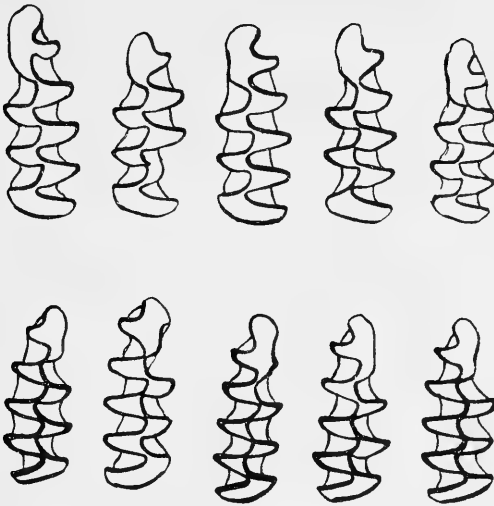


Figure 47. Anterior lower molars of extinct narrow-skulled vole (*Stenocranius anglicus* Hinton) (from Chaline, 1972).

A significant similarity in skull structure with *M. (S.) gregalis* has been noted by all researchers. However, the structure of the posterior part of the bony palate in *M. (S.) miurus* is actually less complex (Rausch, 1953; Repenning, Hopkins and Rubin, 1964): postpalatal pits smaller and bony bridge separating them broader. However, these differences reduce with age. More significant are differences in molar structure, whereby, *M. (S.) miurus* is considered close to *M. abbreviatus* Miller, an observation made by the author of the species himself (Osgood, 1901). Actually, in the two sexually mature specimens of *M. (S.) miurus* studied by him, the structure of the anterior part of M_1 is complex: second lobe of paraconid complete and, in one case, its lateral triangle completely isolated from anterior lobes, which are fused with each other and with anteromedial triangle; additional (fifth) fold also present on medial side of both teeth.

Distribution and zonal affinity: Arctic alpine and subalpine tundra of Alaskan ranges (Brooks, Mackenzie, and Alaskan); along ocean coast southward up to about 60° N (Rausch, 1964). In the Late Pleistocene, it also covered the Yukon depression where it is now absent, and also east of the Mackenzie River.

been described. The present-day forms are larger but, unlike *M. (S.) gregalis*, darker in color than the southern forms. The taxonomic position of *M. miurus* has been variously discussed by mammalogists, some including the American form *M. gregalis* as a subspecies, others recognizing its species status. The ultimate solution was arrived at when chromosomal analysis was done for both species: five subspecies of *M. (S.) gregalis* (Lyapunova and Mirokhanov, 1969a; Fedyk, 1970) and one subspecies of *M. (S.) miurus* (Rausch and Rausch, 1968). The differences were so significant that the reproductive isolation of both forms appears highly probable. Nevertheless, this does not exclude the need for conducting corresponding experiments.

Evolution and phylogeny: Fossil remains from earlier part of the Late Pleistocene not known. Structure of M_1 more complex than in *M. (S.) gregalis*, and also some aspects of their biology (hiding in haystacks for winter and a unique squeak), permit us to assume the possibility of evolution of the gregaloid type independent of the Palearctic type from some progressive ancestral form of the *Microtus* group. The closest present-day form is considered to be the isolated species *M. abbreviatus* Miller.

21. *Microtus* (conf. *Stenocranius*) *abbreviatus* Miller, 1899

Diagnosis: Body length up to 140 mm, tail up to 22 mm (15.0–18.8% body length); length of upper molar row 5.8–7.5 mm ($n = 69$; Rausch and Rausch, 1968). Dorsal surface as in *M. (S.) miurus*, but with distinct ochereous tinge on sides, and ventral surface grayer. Tail same color as in *M. (S.) miurus* but much shorter. Chromosome number, $2n = 54$.

Distribution and zonal affinity: Hall and St. Matthew Islands in the Bering Sea, where they inhabit meadow-type areas, avoiding dry as well as bog land.

Composition of species and taxonomic notes: Each island has its own subspecies. The above researchers undertook a detailed comparison of the skull of this species with those of *M. (S.) miurus* and *M. oeconomus*, one of the insular species included under *M. abbreviatus*. They found that the skull of *M. abbreviatus* is highly similar to that of *M. (S.) miurus* (structure of bony palate, maseteric [= zygomatic] plate, etc.) and has retained a number of characters of the subgenus *Microtus*: facial section not so markedly reduced; crests, including intraorbital, poorly developed; dorsal profile of brain case highly convex. The authors also confirm the structural similarity of M_1 in *M. (S.) miurus* and *M. abbreviatus*. In

my opinion, it resembles some of the eastern voles from the *fortis* group, and the West European Pleistocene species *M. malei* Hinton among extinct ones.

Evolution and phylogeny: Based on the geology of the amphiberian dryland, which partially covers both islands, the above authors concluded that these insular subspecies were isolated from the mainland 30,000 to 35,000 years ago, at the time of the last (Würm–Wisconsin) glaciation. As indicated above, forms similar to the gregaloid-type existed by this time in northeastern Siberia. All this makes probable the independent nature of parallel lines of evolution of voles in the New World. The degree of affinity between *M. (S.) miurus* and *M. abbreviatus* should be decided through experiments on hybridization, conducted without success to date and providing no definitive answer. Fedyk (1970) has recently reexamined the question of the possible relationship between *M. abbreviatus* not only with *M. (S.) miurus* and *M. (S.) gregalis*, but also with *M. (M.) middendorffii* Poljakov, 1881, the results of which are presented in the discussion of the latter species (p. 451).

Subgenus *Sumeriomys* Argyropulo, 1933—Social or Steppe Voles

Diagnosis: Voles of medium size with short tail; general adaptation to semiaquatic life style better developed than in *Microtus* and *Stenocranius*, but less compared *Pitymys*. Pelage dense, short, poorly differentiated into guard hair and underfur. Eyes small (smaller only in *Pitymys*). Pinna reduced, with very small tuft of hair in front. Antitragus in form of a small, barely isolated, and broadly triangular fold, smaller than in species of other subgenera.

Skull with broad, moderately high, and barely inflated brain case, a broad interorbital space, and flat or with a longitudinal groove. Auditory bullae larger than in other subgenera of common voles, mastoids often distinctly dilated. Articular process of dentary moderately long and broad. Molars with relatively high crown. Paraconid section of M_1 with two (incompletely divided) lobes; opposite triangles of basal pair completely isolated (at least in present-day forms). Anterolateral denticle on M_1 with two normally developed folds, and latter also present on M_3 .

Composition of subgenus: Two extant species: *M. (S.) socialis* Pallas, 1770 and *M. (S.) guentheri* Danford and Alston, 1880. It is quite possible that chromosomal and hybrid will reveal that at

least some forms from the periphery of the range (*M. irani* Thomas, *M. musteri* Hinton) and possibly mountain isolates, for example *M. schidlowskii* Argyropulo and *M. betae* Kretzoi, are independent species. The extinct forms described can hardly be considered more than subspecies of extant forms.

Age and distribution: Fossil remains known from the Middle Pleistocene; in the USSR, from the Late Kazara faunas and up to the present time only from the limits of the present-day range. Older skull remains have not been found and, based on isolated teeth, I could detect no significant difference from *M. (M.) arvalis* Pall. (Gromov, 1952). Inhabitants of steppes of plains, foothills, and mountains (predominantly dry meadows) as well as semideserts where, however, they are not zonal species. Also inhabit deforested areas of these zones, including cultivated ones. From the southwestern parts of the Balkan Peninsula, left bank of the Dnieper, northern Caucasus, northern Caspian region, Aral area of Alakul basin south of Kirenaika, northwestern Asia and western parts of Asia Minor, northern and western Iran (not found east of Khukhrud range), and northeastern China. In mountains up to 2,100 above msl. Within range limits, distribution discontinuous, especially along southern boundary.

Taxonomic notes and evolution: Adaptation to semifossorial life style, unlike in *Pitymys*, took place under conditions of dry biomes. Affinities not known, even with the North American high-montane subgenus *Chilotus*. Incidentally, neither group, as assumed by Ognev (1948), is presently recognized by Soviet mammalogists. There is no paleontological support for the evolution of the subgenus. However, its fairly early isolation and predominant evolution concomitant with xerophytic environments of the Mediterranean (Vereshchagin, 1959) are quite probable. It spread to northern Africa possibly not earlier than the Late Pleistocene (Tchernov, 1968b). The nature of changes in several skull features in both species occurred from this time and attest to an increase in adaptation for digging by means of the incisors and feeding upon coarser food (Gromov, 1952; Tchernov, 1968b).

22. *Microtus (Sumeriomys) socialis* Pallas, 1770—Steppe Vole

Diagnosis: Body length up to 105 mm, tail up to 24 mm in small forms and 122 mm and 31 mm respectively in larger forms. Corresponding relative length of tail 23.8–26.8% in short-tailed forms and 25–31% in long-tailed forms. Length of upper molar row 5.5–6.5 mm, lower row 5.4–6.4 mm; M_1 —2.7–2.8–3.0 mm.

Dorsal surface varies from light, sandy to fairly dark, ochreous gray; ventral surface from light silvery to ash-gray. Tail light-colored, mono- or slightly bichromatic. Chromosome number, $2n = 62$ (Matthey, 1957).

Brain case flattened on dorsal side. Auditory bullae large, their length, on the average, 12.5–13.0% greater than alveolar length of upper molar row. Mastoids inflated. Maseterric [= zygomatic] plate low or broad, postpalatal pits deep. Posterior end of lower incisor extends to base of final third of articular process and in fully mature individuals forms well-defined alveolar knob on its lateral surface.

Composition of species: Six to eight subspecies: *M. (S.) s. socialis* Pallas, 1770 (northern Caspian region); *M. (S.) s. parvus* Satunin, 1901 (northeastern Cis-Caucasus); *M. (S.) s. nikolajevi* Ognev, 1960 (southern Ukraine, Crimea); *M. (S.) s. gravesi* Goodwin, 1934 (central and southeastern Kazakhstan, northwestern China); *M. (S.) s. binominatus* Ellerman, 1941 (eastern Trans-Baikal region); *M. (S.) s. paradoxus* Ognev and Heptner, 1928 (Kopetdag, Elbrus range) [? = *M. (S.) s. irani* Thomas, 1921]; *M. (? S.) s. schidlovskii* Argyropulo, 1933 (western America); *M. (? S.) s. betae* Kretzoi, 1962 (Lebanon); and *M. (? S.) s. hyrcania* Goodwin, 1940 (northeastern Iran).

Distribution and zonal affinity: Inhabit steppes of plains as well as foothills and low mountains, which have become desertified xerophytic steppes, up to 1,400 m above msl in the Caucasus (plateau vole of America lives still higher) and 2,000 m in Kazakhstan (western Tien Shan) from left bank of lower Dneiper to Alakul basin and foothills of Tarabagatai; in the present epoch three apparently isolated areas: southern Ukraine, Caspian–Caucasus, and Kazakhstan. The first two areas are not in contact, by and large, from steppes of right banks of the Donets and Don Rivers up to eastern Cis-Caucasus. Second and third areas occur from the Volga–Ural steppes to the northern Aral region and Arysksums (Lobachev, 1968). However, even within the limits of the areas inhabited, distribution is mosaic and significantly discontinuous in places. It is possible that they were not filled after a notable reduction in population strength associated with the Holocenic xerothermic period. Traces of extinct foci of distribution are well-recorded by subfossil paleontological material from montane Mangyshlak (Gromov and Fokanov, 1961) and northeastern Ustyurt, in the Volga–Ural steppes where these animals lived even in the Eversmann period, and in the Apsheron Peninsula where, even in the

283 Late Pleistocene, their distribution was continuous. The present-day "range" in Trans-Caucasus has been detailed by Vereshchagin (1959) and Shidlovskii (1962). Incidentally, the southern boundary of the range cannot be defined precisely, since the taxonomic position of the border forms has not been explained.

Taxonomic notes: The relationship of *M. (S.) s. paradoxus* to the southern Iranian species (Isfahan and Faras Provinces), *M. irani*, should not be considered finally decided. It is possible that *M. irani* and *M. paradoxus* form one independent species and are not subspecies of *M. socialis*, as believed for example, by Ellerman and Morrison-Scott (1951) and Lay (1967); nor is its type form identical to *M. paradoxus*, as I believed earlier (Gromov *et al.*, 1963). Significantly, Matthey (1956) reported a different number of chromosomes for *M. socialis* and *M. irani*— $2n = 54$ and 62 respectively. The latter figure was recently obtained for the Kopetdag vole also (personal communication from G.G. Feigin). Unfortunately, it is not known from where Matthey obtained his material of the two forms.

Probably, the question of the taxonomic status and affinity of the Armenian plateau vole, *M. (S.) s. schidlovskii*, also cannot be solved without complete cytogenetic data. Its real differences from the Trans-Caucasian type, *M. socialis*, were described by the author of the species. It is quite likely that, as proposed by some Soviet mammalogists, this is a small form belonging to the *guentheri* group, or even an independent species related to the very small high-montane *socialis* of Syria and Lebanon, which live here together with Guenther's vole but in a different altitudinal zone (Kowalski, 1958b).

Evolution and phylogeny: Reliable fossil remains are known from the end of the Middle Pleistocene (Binagada, Apsheron Peninsula), as well as from the Late Pleistocene (Crimea, Moldavia; Gromov, 1961; Lozan, 1971). The closeness of the present-day species to *M. guentheri* appears indisputable; however, paleontological material does not suffice for dogmatic judgment.

23. *Microtus (Sumeriomys) guentheri* Danford and Alston, 1880—Guenther's Vole

Diagnosis: Body length up to 137 mm, tail up to 36 mm in large forms and up to 27 and 28 mm in small forms (Ondrias, 1966); relative length of tail small, about one-fourth body length (in specimens housed in the Zoological Institute, Academy of Sciences, USSR—22.3, 22.6, 22.8%). Length of upper molar row 5.2–8.4 mm,

lower row 5.4–8.6 mm (in smaller forms 5.2–7.1 and 5.4–7.0 respectively; $n = 187$; Ondrias, 1966). Length of M_1 —3.3 and 3.3 [sic] mm; in the Palestine population—2.7–3.0–3.3 mm ($n = 24$; Tchernov, 1968b) or 2.8–2.94–3.2 mm ($n = 15$; Kretzoi, 1962).

Dorsal surface ochreous to chocolate-brown, ventral surface grayish, sides with distinct yellowish tone. Tail similar in color to *M. socialis* but relatively shorter. Number of chromosomes, $2n = 54$, $NF = 56$ (Matthey, 1954, from Vorontsov, 1958).

Brain case distinctly convex in dorsal profile. Auditory bullae comparatively small, their average length only 11–12% greater than length of upper molar row. Mastoids slightly enlarged. Masseteric [= zygomatic] plate of maxilla comparatively high and narrow; post-palatal pits minute. Posterior end of lower incisor extends only to half length of articular process and does not form distinct alveolar knob on its lateral surface in adult individuals.

Composition of species: Six to seven subspecies have been listed: *M. (S.) g. guentheri* Danford and Alston, 1880 (= *philistinus* Thomas, 1917) (Asia Minor, Lebanon, Syria, Palestine); *M. (S.) g. hartingi* Barret-Hamilton, 1903 (Greece and European part of Turkey); *M. (S.) g. martinoi* Petrov, 1939 (Macedonia and Siberia; poorly distinguishable form); *M. (S.) g. stranzensis* Markov, 1960 (Bulgaria); *M. (S.) g. lydicus* Blacler, 1916 (Izmir, western part of Asiatic Turkey); *M. (S.) g. shevketi* Neuhauser, 1936 (Adana, southwestern Asiatic Turkey); and *M. (S.) g. musteri* Hinton, 1926 (Cyrenaica).

Distribution and zonal affinity: Inhabits steppes of plains and foothills in western part of range of subgenus: northeastern Greece, Macedonia, southeastern Serbia and Bulgaria, European part of Turkey as well as Asia Minor, and northwestern Asia where, at places, found together with some smaller form of the subgenus but, probably, isolated from it vertically. This is the only microtine to penetrate northern Africa (Cyrenaica) for which remains are known from the Late Pleistocene.

Evolution and phylogeny: Some mammalogists even now include this vole under the *arvalis* group as “a marginal species” (Kratochvil, 1955). In identical number of diploid chromosomes, *M. guentheri* is closer to *M. irani* than to *M. socialis*. Affinity with *M. (S.) s. schidlovskii* has already been discussed. A large series of remains of *M. guentheri* from Palestine from cave deposits of Mid- to Late Pleistocene provided Tchernov (1968b) a basis for describing the nature and direction of chronoclinal variability and to conclude that the earlier extinct forms described here, like *M. mac-*

covni Bate, *Chionomys mochintoni* Bate, *M. agrestis*, and *Pitymys* sp. ?—are mere morphotypic variants of a single species that does not differ from the extant *M. guentheri* in these features: archiac “*Pitymys*” fusion of triangles at base of paraconid of M_1 and additional denticles at posterior end of M^1 and M^2 . The author found no basis for separating members of the Pleistocene form, which, however, would have been the only form since the dominant type of structure differs absolutely from the one typical of present-day species.

Subgenus *Blanfordimys* Argyropulo, 1933—Afghan Voles

Diagnosis: Medium-sized, comparatively short-tailed voles. Adaptation to semifossorial life style not greater than in the subgenus *Microtus*. Pelage dense and long, comparatively poorly differentiated into guard hair and underfur. Eyes relatively large. Pinna not reduced, sparsely covered with hair. Antitragus small, broadly triangular, and comparatively less isolated.

Skull with broad, flattened brain case, high because of markedly enlarged auditory bullae and stronger mastoids than in any other microtine, extending backward beyond occipital condyles. Interorbital space smooth or with groove. Articular process of dentary not reduced. Molar crowns medium in height (not more than in the subgenus *Microtus*). Paraconid of M_1 with 1.5 lobes. Anterior unpaired loop of this tooth isolated from its basal lobes, rarely fused them; latter usually broadly fused (“*Pitymys*” fusion). Anterolateral denticle of second fold of M_1 absent, of M_3 small, but not completely reduced. Chromosome number, $2n = 54$.

Composition of subgenus: One present-day species—*M. (B.) afghanus* Thomas, 1912. Possibly, the subspecies *bucharicus* is an independent species; it was initially described as such by Vinogradov (1928).

Age and distribution: Fossil remains earlier than Mid-Pleistocene not found to date. Inhabits semideserts and desert-steppes in foothills and lower mountain zones up to 2,200 m above msl from the Great Balkans and Kopetdag in the west to the Muratau, Gissar, and Zeravshan ranges in the east. In the south extends up to central part of Afghanistan and southern foothills of the Darvaz range; north up to Kugitang and Babatag. Judging from paleontological data, its range during periods of Pleistocene glaciation and mountain saturation covered the lower and, possibly, foothill regions in the northeast.

Taxonomic notes and evolution: Unique voles with simplified (archaic) M^3 or at earliest stages of folding (simplex type), related to the Middle Asian species of *Neodon* (*Phaiomys*) and *Lasiopodomys*, and among European species—*Pitymys*. Interestingly, some structural details of this tooth, in particular, the small middle lateral denticle, whose apex does not extend up to apices of adjacent ones, greatly resemble those in more primitive members of *Pitymys* from the *ibericus* group. Vinogradov (1928) also pointed out some, probably convergent features of similarity in skull structure with voles of the subgenus *Sumeriomys*, in particular the nature of the auditory bullae.

24. *Microtus* (*Blanfordimys*) *afghanus* Thomas, 1912—
Afghan Vole (Figure 48)

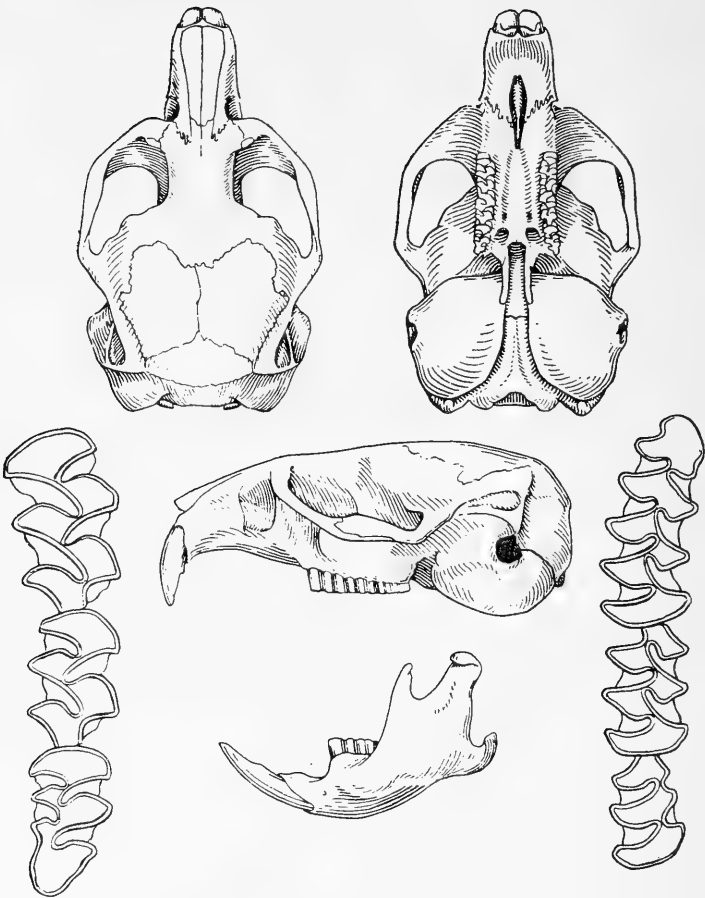
286 *Diagnosis:* Body length up to 117 mm, tail length up to 30 mm (up to 30% body length in long-tailed forms and 28% in short-tailed forms). Length of upper molar row 6.0–6.4–6.8 mm in larger forms, 5.7–6.1–6.3 mm in smaller; length of lower row 6.1–6.3–6.6 mm and 5.8–6.1–6.6 mm respectively. M_1 —2.6–2.9–3.2 mm ($n = 20$). Colour comparatively light, from pale to grayish-ocher. Tail light-colored and mono- or slightly biochromatic.

Composition of species: Three extant subspecies: *M. (B.) a. afghanus* Thomas, 1912 (southeastern Turkmenia, northern Afghanistan); *M. (B.) a. bucharicus* Vinogradov, 1928 (peripheral ranges of Pamir-Alai, mountains of eastern Afghanistan); and *M. (B.) a. balchanensis* Heptner and Shukurov, 1950 (western Turkmenia, Kopetdag, Great Balkans).

Distribution and zonal affinity: Same as that of subgenus.

Taxonomic notes: As mentioned above, the taxonomic status of *M. bucharicus* Vinogradov cannot be considered finally decided. Its morphologically distinguishing characters from desert-steppe members of the species (Badkhyz, Karabil') are quite significant: larger size, relatively longer tail, grayer dorsal coloration, larger (broader and more enlarged) auditory bullae, more complex structure of M^3 (rudimentary fourth denticle present in some specimens), as well as M_1 with these features: anterior unpaired loop with comparatively well-developed fold and second lobe long-retained on medial margin, and fusion of basal triangles less complete. Chromosomal and hybrid analysis of these forms has yet to be done.

Structure of interorbital space still not described for the typical Afghan vole from Afghanistan (Gulran, extreme northwestern part of country). If, as may be assumed from the description given by



285 Figure 48. Skull of Afghan vole [*Microtus (Blanfordimys) afghanus* Thomas].

O. Thomas, it has at least a small crest (never present in representatives of Russian fauna), then the question of the possible affinity of the type to another subgenus must be considered.

Subgenus *Microtus* Schrank, 1798—Common Voles

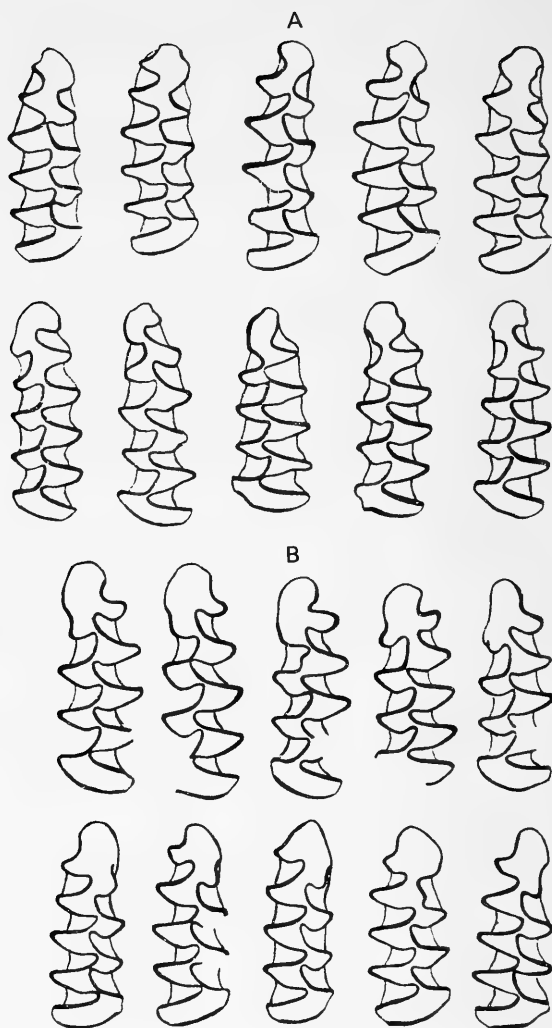
Diagnosis: Size medium and large, with moderately long or long tail. General adaptation to semifossorial life style evolved less distinctly than in species of other subgenera. Pelage variable

in length and density, well-differentiated into guard hairs and underfur. Eyes comparatively large. Pinna well-developed, with dense tuft of hair toward front. Antitragus large, rectangular, well-isolated. Skull with comparatively narrow (narrower only in *Stenocranius*), high, and slightly convex (angular) brain case. Interorbital space narrow in middle part. Vertical crests in adult individuals almost convergent, or touch, or with well-developed longitudinal crest along midline. Articular process of dentary short (shorter only in *Pitymys*). Molars with higher crown than in species of other subgenera. Paraconid section with two incomplete lobes, at times only on one side; basal triangles opposite and isolated. Lateral lobe of second pair variable—from barely perceptible to large, at times completely isolated from anterior unpaired loop.

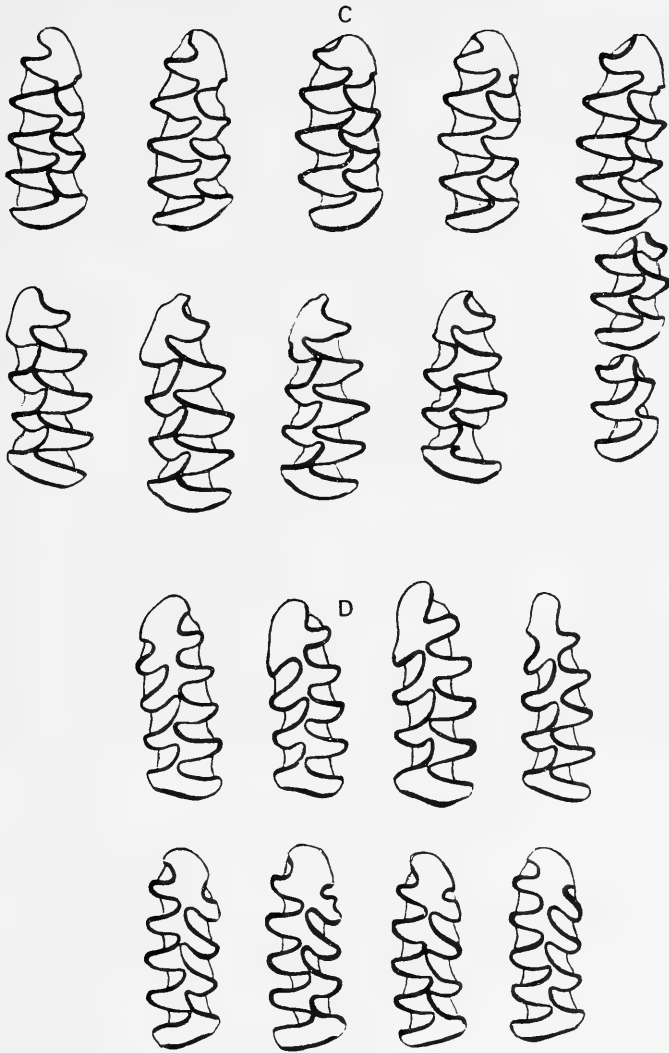
Composition of subgenus: More than 20 present-day species, all large, and more than 10 found in Russian fauna: *M. arvalis* Pallas, 1778; *M. subarvalis* Meyer, Orlov and Scholl, 1972; *M. agrestis* Pallas, 1758; *M. oconomus* Pallas, 1778; *M. fortis* Büchner, 1889; 287 *M. maximoviczii* Schrenk, 1858; *M. sachalinensis* Vassin, 1955; *M. transcaspicus* Satunin, 1905; *M. ilaeus* Thomas, 1902; *M. mongolicus* Radde, 1862; *M. middendorffii* Poljakov, 1886; *M. hyperboreus* Vinogradov, 1933; and *M. montebelli* Milne-Edwards, 1871. Additionally, in the Old World—*M. cabreræ* Thomas, 1906; *M. kikuchii* Kuroda, 1923; and *M. calamorum*. In the New World, at least eight species are listed: *M. pennsylvanicus* Ord, 1815; *M. montanus* Peale, 1848; *M. californicus* Peale, 1848; *M. towsendii* Bachman, 1839; *M. longicaudatus* Merriam, 1888; *M. chrotorrhinus* Miller, 1894; *M. mexicanus* Saussure, 1861; and *M. xanthognatus* Leach, 1815. Without doubt, as in the case of the Old World forms, detailed information on chromosomal and hybrid analysis will confirm, in addition to the foregoing species, at least another five distributed mainly peripherally in the range of several of the aforementioned forms, including insular ones.

Several extinct forms have been described: *M. ratticipoides* Hinton, 1923; *M. agrestoides* Hinton, 1923; *M. arvalinus* Hinton, 1923; *M. corneri* Hinton, 1910; *M. malei* Hinton, 1907, *M. brandi* Brunner, 1940; *M. brecciansis* Giebel, 1847; *M. paraoperarius* Hibbard, 1944; *M. spehuton* Cope, 1871; and others. Many were distinguished on the basis of small differences in structure of M_1 (Figure 49).

Separation of subspecific groups without attributing taxonomic status to them has been attempted repeatedly by various authors. A critical analysis (for Palearctic forms) worth noting was done by Ellerman (1941). Given our present knowledge, these subspecific



groups can be divided into five: (1) *fortis* (*fortis*—?*cabrerae*) group, for which S.I. Ognev, in one of his early publications on the taxonomy of rodents (1914), even proposed a unique subgeneric name—*Alexandromys*, and recently Chaline (1972) has proposed the name *Iberomys* for *M. cabrerae* as well as *M. malei* and *M. oeconomus*; (2) *maximoviczii* (*maximoviczii*, *montebelli*, *sachalinensis*, *kikuchii*)



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Figure 49. Molars of extinct members of *Microtus*.

A—*Microtus agrestis* Pallas; B—*M. malei* Hinton; C—*M. brecciensis* Chaline; D—*M. (Pitymys) lusitanicus* Bonzu* ; × 15 (from Chaline, 1972).

* Given earlier as *M. lusitanicus* Gerbe, 1879 (p. 264 of the original)—Eds.

group; (3) *arvalis* (*arvalis*, *subarvalis*, *mongolicus*, *transcaspicus*, *ilaeus*, *hyperboreus*, *middendorffii*) group; (4) *oeconomus* group; and (5) *agrestis* group, with a single species. The number of similar groups for the New World genera corresponds to the seven Nearctic species listed above plus the *oeconomus* group (Bailey, 1900). However, one may not assume that in all these cases the principle of affinity has been upheld while combining species into groups. Incidentally, the term "supraspecies" was recently used, with some justification, in relation to *arvalis* (Malygin and Orlov, 1974).

Age and distribution: Fossil remains known from the Early Pleistocene (Tiraspol' fauna); appeared soon after the first microtines with rootless molars. Inhabit entire Palearctic and Nearctic, extending southward beyond these limits (China, northern Mexico), where they form the southern boundary of distribution of the subfamily. In the north live in the subzone tundra, in the south continue into semideserts where, however, they are not zonal species. In mountains, found up to 3,000 m above msl. Occurrence of many insular forms typical.

Taxonomic notes and evolution: This is the least specialized group of species, adapted to life in humid biotopes of meadow and meadow-marsh type, in which it also evolved. Probably, many species, at least in Eurasia, moved into the "*Pitymys*" stage of molar development during the Pleistocene. This subgenus is closest to *Stenocranius*; many species, especially along the periphery of the range, also have an underdeveloped (reduced ?) anterolateral denticle on the paraconid of M_1 .

KEY TO SPECIES OF SUBGENUS *MICROTUS*

- 1 (2). Medial margin of M^2 with two denticles; additional posterior denticle and corresponding fold not detected *M. (M.) agrestis* L.
- 288 2 (1). Medial margin of M^2 with two denticles; additional posterior denticle and corresponding fold absent.
- 3 (4). Lateral margin of M_1 with three denticles; six closed dentine-enamel fields present on masticatory surface *M. (M.) oeconomus* Pall.
- 4 (3). Lateral margin of M_1 with four denticles; masticatory surface with more than six closed dentine-enamel fields.
- 5 (12). Tail length, on the average, at least 35% body length; body length, on the average, more than 130 mm.

- 6 (7). Dorsal surface with predominance of comparatively light and grayish to chocolate-brown tones. Triangles at base of anterior unpaired loop of M_1 well-developed, isolated or almost isolated from it, and broadly fused between themselves *M. (M.) transcaspicus* Satunin and *M. (M.) ilaeus* Thomas.
- 289 7 (6). Dorsal surface with predominance of dark chocolate-brown to brown tones. Triangles at base of anterior unpaired loop of M_1 not well-developed, not isolated from it, and not broadly fused between themselves.
- 8 (9). M^3 in most individuals with five lateral and five medial denticles. If lateral ones four, width of anterior (paraconid) section of M_1 not less than 1.35 mm. Small perpendicular lobe of M_3 distinct and often almost isolated from antero-medial lobe *M. (M.) sachalinensis* Vassin.
- 9 (8). M^3 in most individuals with three, rarely four lateral and four medial denticles. Width of anterior (paraconid) section of M_1 less than 1.35 mm. Anterolateral lobe of M_3 not developed, and one broad field present in lateral section of tooth.
- 290 10 (11). Dimensions comparatively large: body length up to 175 mm (average 128 mm), hind foot up to 25 mm (average 22.8 mm). Width of anterior (paraconid) section of M_1 not less than 1.25 mm. Posterior section ("heels") of M^3 more than 7.4 mm. Lateral side of anterior unpaired loop of M_1 usually without denticle *M. (M.) fortis* Büchner.
- 11 (10). Dimensions comparatively small: body length up to 152 mm (average 125.6 mm), hind foot up to 22 mm (average 19.8 mm). Width of anterior (paraconid) section of M_1 less than 1.24 mm. Posterior section ("heels") of M^3 less than 7.4 mm. Lateral side of anterior unpaired loop of M_1 usually with notch *M. (M.) maximoviczii* Schrenk.
- 12 (5). Tail length, on the average, less than 35% body length; body length, on the average, less than 130 mm (usually less than 120 mm).
- 13 (14). Tail length not more than 25% body length. Width of auditory bullae at anterior margin of auditory meatus more than length of upper molar row; mastoids distinctly inflated *M. (M.) hyperboreus* Vinogradov.
- 14 (13). Tail length more than 25% body length. Width of auditory bullae at anterior margin of auditory meatus less than

length of upper molar row; mastoids flattened.

- 15 (16). Tail distinctly bichromatic. Dorsal surface with bright rusty tones; ventral surface light-colored, with color extending onto lower part of cheek
 *M. (M.) middendorffii* Poljakov.
- 16 (15). Tail slightly trichromatic. Dorsal surface without bright rusty tones; light coloration of ventral surface does not extend onto lower part of cheek.
- 17 (18). Plantar of hind foot with six-calluses. Anterolateral denticle of M_1 with acute apex and well-isolated from anterior unpaired loop *M. (M.) arvalis* Pallas
 and *M. (M.) subarvalis* Meyer, Orlov and Scholl.
- 18 (17). Plantar of hind foot with five calluses. Anterolateral denticle of M_1 with rounded apex, comparatively poorly isolated from anterior unpaired loop
 *M. (M.) mongolicus* Radde.

25. *Microtus (Microtus) fortis* Büchner, 1889—Reed Vole

Diagnosis: Body length up to 150 mm in small forms and 170 mm in large, southeastern forms. Tail up to 60 mm (up to 64% body length, average about 40%). Length of upper molar row up to 8.2 mm in small forms and 8.5 mm in large; length of lower row up to 7.5 and 8.5 mm respectively. Length of M_1 —3.3—3.5—4.0 mm.

Dorsal surface comparatively light, without predominance of brownish-gray tones (in lighter forms with "Norway rat" tinge, according to a fairly precise identification by E. Büchner); ventral surface light-colored, ash-gray. Tail distinctly or slightly bichromatic in most individuals. Forefeet on dorsal surface comparatively light-colored. Plantar of hind feet usually with five calluses, but in some populations more often with six. Chromosome number, $2n = 52$ (Meyer, Jordan, and Walknowska, 1967).

Skull, compared to those of related species in Russian fauna, juvenile in appearance; crests poorly developed; interorbital crest forms late, is low, and barely protrudes downward beyond level of interorbital space; vertical crest barely perceptible; middle occipital crest absent, as a result of which posterior margin of interparietal straight. Rhinarium comparatively short and broad. Teeth relatively large. M_1 may have distinct anterolateral denticle, more often absent, in which case, anterior unpaired loop rounded-rectangular.

Composition of species and variability: Six to seven poorly studied present-day subspecies: *M. (M.) f. fortis* Büchner, 1889 (Ordo re-

gion of China); *M. (M.) f. calamorum* Thomas, 1902 (southern part of Great Chinese Plains); *M. (M.) f. uliginosus* James and Johnson, 1955 (central part of Korea); *M. (M.) f. dolichocephalus* Mori, 1930 (central part of northeastern China); the last two forms possibly belong to the next species—*M. (M.) f. michnoi* Kastschenko, 1910 (southwestern Trans-Baikal region, Amur area, Ussuri basin, Putyatin Island, Lesser Hingan).

Southern forms (in western part of range) and eastern forms (in north) are larger than northern and western forms and appear to be longer tailed. Light brownish-ocher tones better expressed in southern forms than in northern ones.

Distribution and zonal affinity: Inhabit marsh-meadow and floodplain-meadow areas of forest and forest-steppe zones of southwestern Trans-Baikal region, Vitim hills (north up to mouth of Selenga, Chita, and Nerchinsk), Amur region, northeastern Mongolia, eastern China, as well as Korea. In southeastern China, spread south almost up to 20° N (Zimmermann, 1964).

Evolution and phylogeny: Fossils of large voles with structure of M_1 typical for species are known from the Late Pleistocene in Trans-Baikal and the Early Pleistocene of northern China (Erbaeva, 1970). Affinities not known. Based on structure of anterior section of M_1 and M^3 , *M. fortis* is closest to the large Iberian species, *M. cabreræ* Thomas, and its probable ancestral form, *M. breccien-sis* Giebel. It is tempting to propose that this is an index of relative closeness, known for several species of mammals and birds living in the Pyrenees and the Far East; however, special studies are required to confirm this. As for the affinity to *M. maximoviczii*, frequently discussed in literature, this is probably better explained by similarity in conditions of survival than by common phylogeny.

26. *Microtus (Microtus) maximoviczii* Schrenk, 1858
(= *ungurensis* Kastschenko, 1913)—Ungur Vole or
Maximovich's Vole

Diagnosis: Dimensions similar to small forms of preceding species: body length up to 155 mm, tail up to 50 mm in Upper Amur populations and up to 58 mm in those from northeastern China (Shaw, 1958) (up to 40% body length, average about 35%; Heptner and Shvetsov, 1960). Length of upper molar row up to 7.3 mm, lower molar row 7.2 mm; M_1 —2.6–2.9–3.2 mm.

Dorsal surface dark, with predominance of chocolate-brown tones; ventral surface dark gray. Tail usually mono- or slightly bichromatic, often in basal half. Forefeet dark-colored on dorsal

side. Hind feet usually with six plantar calluses. Chromosome number, $2n = 42$ (Meyer, Jordan and Walknowska, 1967).

Skull with more senile appearance than in preceding species. Crests relatively well-developed, including interorbital, which continues onto parietals when fully developed. Parietal crests and middle occipital crest also well-developed, as a result of which posterior margin of interparietal forms angle in middle with apex directed downward. Rhinarium comparatively long and narrow. Teeth small. M_1 often with small but well-formed anterolateral denticle, rarely denticle reduced and then in most individuals of the same population; profile of posterolateral section of anterior unpaired loop of M_1 acquires shape typical of this molar in preceding species.

Composition of species: Subspecies not described; however, the possibility is not excluded that a part of *M. fortis* (Korea, northeastern China) belongs to the Ungur vole.

Distribution and zonal affinity: Inhabits marsh-meadow and meadow-shrub biotopes in forest zone of Upper Lena area of Baikal region, Trans-Baikal, and Amur region; north almost up to Zhigalovo village of Lena, Barguzim, central parts of the Vilyui plateau, Chita, Nerchinsk, and upper reaches of Amur; northeastern Mongolia and China; northern part of Greater Hingan, lower reaches of Sungar and Ussuri.

Taxonomic notes: The independent species status of *M. maximoviczii* was finally proved through chromosomal and hybrid analysis. At the same time, a detailed comparative analysis of characters differentiating the two species, from those mentioned even by Vinogradov and Obolensky (1927) as well as some proportions of the skull, recorded in considerable material by Meyer (1977), showed that in contrast to the results obtained by Heptner and Shvetsov (1960), there is a complete possibility of identification (using these measurements) with the necessary reliability for each individual, including also young ones. The name *maximoviczii*, as the older synonym, has priority over the later name, *ungurensis*, given by F. Kashchenko. The holotype of the Maximovich vole was studied by B. S. Vinogradov and S.I. Obolensky, who included it under *M. fortis*, and also by Ognev (1950). I can only confirm the correctness of the opinion of the latter regarding the affinity of the holotype to the young Ungur vole.

27. *Microtus (Microtus) sachalinensis* Vassin, 1955—
Sakhalin Vole (Figure 50)

Diagnosis: Body length up to 175 mm, tail up to 65 mm (average about 36% body length and no more than 43%) (n = 15). Length of upper molar row up to 8.6 mm, lower row up to 8.3 mm; M_1 —3.4—3.6—3.8 mm (n = 10).

Dorsal surface brown with distinct admixture of rusty tones and darkening on upper surface of head. Ventral surface light-colored, pale gray. Tail distinctly bichromatic. Forefeet light chocolate on dorsal surface. Hind feet usually with five plantar calluses. Chromosome number, $2n = 50$ (Meyer and Volobuev, 1974).

Skull similar to that of *M. fortis*, from which it differs in: (1) more complex structure of M^3 , with five denticles on medial side in most individuals and four denticles on lateral side, and without closed dentine-enamel fields; (2) skull broader at squamosa and less convex in region of bases of zygomatic arches, as a result of which dorsal profile less sharply sloped toward rostral section than in *fortis*; (3) weaker longitudinal depression in front of place of convergence of crests of interorbital space; (4) narrower masseteric [= zygomatic] plate of maxilla; (5) stronger incisors, especially upper ones, which have a more distinct longitudinal groove on anterior surface; (6) normal (“*arvalis*”) structure of anterior section of M_1 , although anterior unpaired loop broader and shorter than in *M. maximoviczii*; and (7) stronger development of anterolateral denticle of M_3 .

Distribution and zonal affinity: Inhabits open and sparse forest-covered marshy areas in central Sakhalin depressions (Poranai region). It is not clear whether it also lives in Sakhalin or another species of *fortis* (recorded occasionally in middle and northern parts of island).

Taxonomic notes: Until recently, poorly studied. New material from the type locality and cytogenetic studies conducted by the Zoological Institute, Academy of Sciences, USSR, have confirmed its independent status, contrary to the categorical opposite opinion of Reimers and his colleagues (1968). A high degree of complexity in molar structure, maximum in the group, is a characteristic feature. As the lectotype (holotype not identified by the author), Meyer (1977) proposed specimen No. 371184, a female in the collection of the Zoological Institute, Academy of Sciences, USSR (Sakhalin, left bank of Olene' River near mouth), October 1, 1954, B. Vasin.

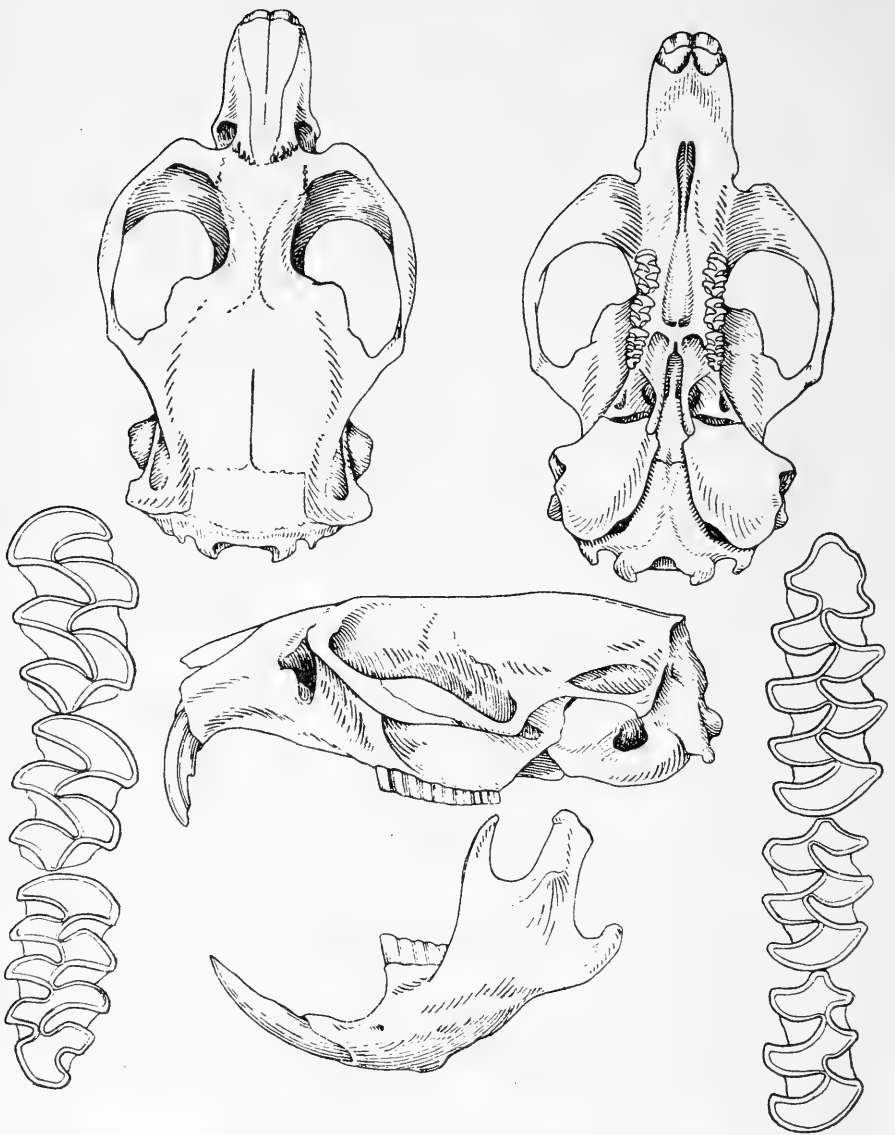


Figure 50. Skull of Sakhalin vole (*Microtus sachalinensis* Vassin).

294 28. *Microtus (Microtus) kikuchii* Kuroda, 1920—Taiwan
Vole

Diagnosis: Body length up to 140 mm, tail up to 98 mm (average

70% body length, up to 73%), length of upper molar row up to 7.2 mm ($n = 4$; Tokuda, 1941), lower molar row up to 6.9 mm; M_1 about 3.0 mm.

Dorsal surface monochromatic, yellowish-chocolate-brown; ventral surface light bluish-gray. Tail distinctly bichromatic. Forefeet dorsally white. Hind feet with six plantar calluses. Unlike in other species of the group, only two pairs of nipples present (based on one specimen only!). Chromosome number, $2n = 28-30$ (Tateishi, 1937a, 1937b; Makino, 1950).

Like in *M. fortis*, skull juvenile in appearance, but crests even more poorly developed. Auditory bullae larger than in other species of subgenus. Large-toothed species. M^3 with tendency toward complexity as seen in *M. sachalinensis* (Aoki and Tanaka, 1941). M_1 with well-developed anterolateral lobe of paraconid, highly reduced anterior unpaired loop, and more sharply shifted anterior pair of folds than in *M. fortis*, which are shifted relative to each other. Middle pair of lobes divided not only on M_2 but often also on M_3 ; anterior pair divided only on M_2 .

Distribution and zonal affinity: Mountain regions of Taiwan (China); holotype captured from Morrison mountain at height of 3,000 m.

Taxonomic notes: A unique isolated form, differing sharply from other species of the subgenus in long tail, large auditory bullae and, possibly, in number of nipples.

29. *Microtus (Microtus) malei* Hinton, 1907 (foss.) and *M. (Microtus) paraoperarius* Hibbard, 1944 (? = *spheoton* Cope, 1871) (foss.) (Figure 49, B)

Diagnosis: Size of first species: length of M_1 (alveolus) —2.9–3.1–3.22 mm ($n = 5$; Hinton, 1907); second species: lower molar row 5.4–6.0–6.5 mm; M_1-M_2 —4.1–4.5–4.7 mm ($n = 20$); M_1 —2.6–3.0–3.4 mm ($n = 20$; Paulson, 1961).

Structure of paraconid section of M_1 in both species resembles that of some voles from the *fortis* group, or *M. oeconomus*, or certain specialized forms of *Chionomys* (the *gud* group); anterolateral denticle of paraconid section of M_1 small, its triangle incompletely formed, fused variably (usually widely), rarely isolated from normally developed anteromedial triangle, and broadly fused with anterior unpaired loop. Apices of anterior folds usually markedly shifted relative to each other. Degree of isolation of anteromedial denticle in forward direction changes from slight (“*oeconomus*” beak) to great, with deep fold present.

Composition of species: *M. (M.) m. malei* Hinton, 1907 (end of Ancient to beginning of Early Pleistocene, England); *M. (M.) m. burgondiae* Chaline, 1972 (Middle Pleistocene, southern France); *M. (M.) m. noaillensis* Chaline, 1972 (end of Middle Pleistocene, France); and *M. (M.) m. gennii* Chaline, 1972 (Late Pleistocene, France).

Age and distribution: The first species was described from the Cleveland cave deposits of southern England, comparable to the late deposits of the high Thames terrace or early deposits of its middle terrace, i.e., from end of the Ancient or beginning of Early Pleistocene. Ancient genera of rooted-molar voles have not been found in the composition of this fauna. The second species, from the Early to Middle Pleistocene fauna of southeastern Kansas, was recovered from layers under the known marker horizons of volcanic ash. There are no ancient genera of microtines here, and the existing genera belong to forms with a broad *Pitymys*-type fusion of the basal triangles of the paraconid of M_1 (*Pitymys*–*Pedomys*).

295 *Taxonomic notes:* In both species, M_1 is at the same stage of evolution. However, the absence of data on other skull structures, including teeth, does not permit a more precise determination of their taxonomic position. Incidentally, Hinton (1907) noted the absence of M^3 with a simplified structure among remains of voles from the type locality of *M. malei*. This M^3 has a simple structure typical of present-day *Chionomys nivalis*, the remains of which are also identified from here by the author. Thus, we can only speak of the presence of *Chionomys* of the *gud-roberti* type. As for the structural features of M_1 reported by the author as distinguishing the tooth of *Microtus malei* from the tooth of *Chionomys* (special reference to *C. nivalis*), such as better developed anterolateral denticle, anterolateral depression on anterior unpaired loop, and larger width of tooth—these are not sufficiently clear in the diagrams (Hinton, 1926, Figure 66). Therefore, the entire fossil material from this locality included under *malei* and *nivalis* should more appropriately be considered as belonging to a single species of the genus (probably subgenus), *Microtus*.

Three years after describing this species, the author (Hinton, 1910a), after repeated study of the original and new material, came to the same conclusion reached by me, emphasizing that *M. malei* is a species which can be considered ancestral in relation to *M. oeconomus* and *C. nivalis*. Therefore, it is not understandable why, 16 years later, he reverted to his prior opinion and separated two forms in the material studied. It should also be noted that among

the remains included by Hinton under "*M.*" *nivalinus* (Figure 65 in his work of 1910), some of the material could well have been considered *M. malei*. If there is a shift in morphotypic variability of M_1 structure in this species in time as well as in space, it is easy to understand it in the direction of *M. oeconomus* as well as *Chionomys gud-roberti*. This latter type of structure in *M. malei* can readily be seen in the teeth of *Allophaiomys*. All this was recently repeated by Chaline (1972), who reexamined Hinton's material and even proposed a new subgeneric name, *Suranomys*, for the species *malei*, *oeconomus*, and all three species of the genus *Chionomys* (in my understanding). This is a clear example of reluctance to follow the law of priority, since Kretzoi (1964) had proposed the name *Pallasiimus* much earlier for the present-day species mentioned here.

A similar opinion is valid for *M. paraoperarius* in which variants of M_1 structure in the direction of *M. oeconomus* (*M. operarius* in the earlier interpretation of American mammalogists) are fairly distinct (Hibbard, 1944, Figure IIg; Paulson, 1961, Figure 7f, g). However, in the New World, these differences were hardly fully realized: *M. oeconomus*, a later, probably Late Pleistocene migrant from the east into the fauna of North America, judging from paleontological data never reached the middle latitudes. Therefore, I see no reason to include *M. paraoperarius* under the group *oeconomus* (*operarius* group) as was done by the author of the species. The proposed relationship of this species to *M. deceitus*, from the Early Pleistocene deposits of Alaska (Guthrie and Matthews, 1971) does not appear convincing to me.

30. *Microtus (Microtus) oeconomus* Pallas, 1778—Root Vole

Diagnosis: Size highly variable among Palearctic members. Body length in large forms (Kamchatka) up to 150 mm, in medium-sized animals (Western Europe) up to 137 mm (Zimmermann, 1942), and in small voles (Mongolia, northern China) up to 118 mm (Allen, 1940). Tail length up to 60 mm in large forms and up to 50 mm in small forms, on the average (up to 36% body length and not more than 42% in short-tailed forms, and 44 and 54% in long-tailed). Length of upper molar row up to 7.6 mm, lower row up to 7.7 mm (in mounted forms up to 6.3 and 6.4 mm). M_1 —3.1–3.3–3.6 mm in large forms and 2.7–2.9–3.2 mm in small ($n = 15$).

Dorsal surface from fairly thick dark and matte, chocolate-brown or grayish-brown, to comparatively light and bright, ochre to chocolate-brown. Ventral surface from ash-gray to silvery-gray.

Tail slightly or distinctly bichromatic, rarely monochromatic. Hind feet with six plantar calluses, Chromosome number, $2n = 30-32$.

Skull similar to that of other species of the subgenus, with well-developed crests, including interorbital ones. Paraconid of M_1 in typical case without secondary lateral lobe and lateral margin of tooth with three denticles and two isolated triangles. Anterior section of paraconid fused with basal anteromedial lobe and masticatory surface of tooth with six closed fields. However, in some individuals, and in some populations in most individuals, there is an incompletely developed fourth lateral denticle, anterior part of paraconid section is isolated from both its basal lobes, and masticatory surface has seven closed fields, as a result of which tooth becomes identical to that of species close to *M. fortis*.

Composition of species: Up to 15 Nearctic and up to 20 Palearctic subspecies have been described, whose validity is impossible to assess at present. A few extinct forms of infraspecific status have also been reported. The following extant subspecies are well-known: *M. (M.) o. arenicola* Selys-Longchamps, 1841 (isolated section of range in Holland; independent subspecies status requires confirmation); *M. (M.) o. mehelyi* Ehinson, 1929 (isolated section in range in Hungary; ditto); *M. (M.) o. medius* Nilson, 1844 (Scandinavia, Kola Peninsula); *M. (M.) o. ratticeps* Keyserling and Blasius, 1841 (northern part of central Europe and northern part of forest zone of eastern Europe); *M. (M.) o. stimmingi* Nehring, 1899 (southern part of forest zone from western Ukraine and Belorussia up to northern Volga region); *M. (M.) o. petschorae* Ognev, 1944 (tundras of northern Europe); the last three subspecies are, probably, only size variants; *M. (M.) o. oeconomus* Pallas, 1778 (from southern Ural and Ural region up to Kustanai, Omsk, and Barnaul); *M. (M.) o. altaicus* Ognev, 1944 (Altai-Sayan mountain region); *M. (M.) o. montium-caelestium* Ognev, 1941 (Tien Shan mountain region); *M. (M.) o. dauricus* Kastschenko, 1910 (Baikal and Trans-Baikal areas); *M. (M.) o. kjusjerensis* Koljushev, 1965 (tundra and taiga in northern Siberia east of Taz River; middle Siberian plateau); *M. (M.) o. suntaricus* Dukelsky, 1928 (central Yakutia); *M. (M.) o. koreni* Gl. Allen, 1914 (Kolyma basin and Kolyma hills); *M. (M.) o. kamtschaticus* Pallas, 1776 (Kamchatka, Karaginsk Island); *M. (M.) o. tshuktschorum* G. Miller, 1899 (Chukchi, Anadyr territory, Koryaksk hills); *M. (M.) o. schantaricus* Ognev, 1929 (Zhan-tar Island); *M. (M.) o. ushidae* Kuroda, 1924 (northern Kurils; in central Kurils found south up to Simushir, possibly endemic); *M. (M.) o. limophilus* Büchner, 1889 (Zaisan basin, western Mongolia,

western Gobi); and *M. (M.) o. flaviventris* Satunin, 1912 (montane forest of Hanshu and Shansi). In Alaska and western Canada, there are at least four to five subspecies on the continent and up to ten on the islands. The best-known are: *M. (M.) o. endoecus* Osgood, 1909 (northern Alaska); *M. (M.) o. operarius* Nelson, 1893 (central Alaska); *M. (M.) o. kadiakensis* Merriam, 1897 (Kodiak Island, southern Alaska); *M. (M.) o. makferlani* Merriam, 1897 (western Canada, eastern part of central Alaska); and *M. (M.) o. yakatanensis* Merriam, 1900 (eastern coast of Gulf of Alaska).

297 Among extinct forms, the Early Pleistocene *M. o. ratticipoides* Hinton, 1923 (Europe, western Siberia), similar to the Middle Pleistocene *M. o. epiratticeps* Young, 1934 (northern China) can hardly be considered more than a subspecies based on evolutionary level of the lower molars.

Variability: Insular forms are larger than continental ones and have a relatively longer tail (Zimmermann, 1942). Over the most of the range, northern forms are larger with shorter tails than southern forms. However, in eastern parts of the Palearctic, where forms are still larger than in the western parts (difference particularly significant for the Cis- and Trans-Lena, Siberia), the picture might possibly be reversed (Chernyavskii, 1972). However, the large size of the Kamchatka form can be explained in that it behaves as an insular form. The color becomes light in open environments, acquires yellowish tones in the tundra zone, and grayish tones in forest-steppes. The extent of differentiation of the paraconid section of M_1 and posterior section of M^3 increases in an eastward direction. Increase in frequency of occurrence of individuals with a second lateral denticle on the paraconid of M^1 is particularly notable at the boundary of Trans-Yenisey, Siberia, and with a divided paraconid section from Trans-Ural region. Size has increased from the Late Pleistocene to the present time, and likewise the extent of differentiation of the anterior section of M_1 and posterior of M^3 . In particular, the anterolateral denticle of the second fold of the paraconid of M_1 in extinct forms ("oeconomus beak") is less well-developed, and the paraconid *per se* longer and narrower (Young, 1934; Maleeva, 1971).

Distribution and zonal affinity: Inhabitants of marsh-meadow and meadow-forest parts of tundra, forest zone, and forest-steppes. Do not avoid saline lakes, river meadows of semideserts, and marshy banks of streams in the alpine belt up to a height of 2,500 m above msl (Tien Shan). Found from northern central Europe to Alaska and western Canada, including most of the islands in the Bering

and Okhotsk seas; Aleutian Islands west up to Unalaska, Kuril' Islands in the south up to Simushir Islands (in central Kuril', possibly endemic); Sakhalin (?) (at least excluding southern part). Isolated pockets of distribution in the western region known in Holland and Hungary. In Western Europe, continuous range passes almost along line connecting Schleswig, Lubeck, Brandenburg, Negleca, Opole (Zimmermann, 1942) and farther up to Drogobych, Vinnits, Cherkasy, Sumi, northern part of Voronezh district, Volsk, Buzulukh, Orenburg, encircling southern tip of Ural range (along floodplains of Ural River up to Yanvartsev). Several isolated areas in present-day range located in southeastern and western Siberia, Kokchetav and Pavlodarsk districts of Kazakhstan and southeastern part of the republic in the lower reaches of Il, Dzhungarian range, and Alakul and Zaisan basins. Region of continuous distribution further covers Altai (including part of Mongolian Altai), Sayans, Barguzinsk, and Yablonevo ranges, and entire southeastern part of Siberia north of range of species belonging to *fortis* group and partly sympatric with them. Probably, an isolated section is also located in montane forests of northwestern China (Hanshu and Shansi Provinces) and, possibly, in turn, not connected to the more northern Zaidan and western Mongolian forests. In North America, the eastern continental boundary extends from western Coronation Gulf through the Great Slave Lake and upper reaches of the Mackenzie River to Sitka city (Novo-Arkhangel'sk) on the Pacific coast (Hall and Kelson, 1959).

In the Pleistocene, together with the steppe species (in its earlier sections), mixed, and lemming faunas (later sections), distributed much more south and west of present-day boundaries, up to southern France, Poland, Transylvania and Dobruj, central parts of Moldavia, Crimea, and Lower Don and Lower Ural Rivers. In the plains of the European part of the USSR, during Late Pleistocene glaciation, the southern boundary was probably quite sharply extended northeast together with the boundary of the "cold" faunas from Kanev region of the Dnieper up to Samara Luka. In the beginning of the Holocene, together with the formation of a continuous forest belt, the range was broken into tundra and forest-steppe parts, and was accompanied by fairly distinct speciation, which is fully evidenced in the paleontological material for the Sverdlov area of the Trans-Ural region (Maleeva, 1971).

Reliable fossil remains in North America have not been found beyond the limits of the present range.

Evolution and phylogeny: Fossil remains of voles with a structure of M_1 typical for the western forms of present-day species are known from the beginning of the Early Pleistocene (late Cromer of England). The species, on the whole, is represented by forms which are more highly differentiated than, for example, the narrow-skulled vole with a similar range. Moreover, even such extreme forms as the semidesert subspecies *M. o. limnophilus* and the neighboring montane-forest subspecies *M. o. altaicus*, which differ quite sharply morphologically, produce completely viable progeny (Mare *et al.*, 1973*). Phyletic links with the large Early Pleistocene *M. (Microtus) malei*-type voles on the one hand, and (through it ?) with present-day species from the *fortis* group on the other, are probable.

298 31. *Microtus* (conf. *Microtus*) *cabreræ* Thomas, 1906—Pyrenees Vole

Diagnosis: Body length up to 125 mm, tail up to 44 mm (average 35% and not more than 37% body length). Length of upper molar row up to 8.0 mm ($n = 9$; Niethammer, Niethammer and Abs, 1964).

Dorsal surface dark, chocolate-brown to gray, similar to *M. agrestis*; ventral surface gray with yellowish tinge. Tail slightly bichromatic. Hind feet with six plantar calluses. Chromosome number not known.

Dorsal profile of skull highly and uniformly convex, without rostral dip. Crests in interorbital space of known specimens not convergent, but separated by broad groove. Broad incisor alveoli and low masseteric [= zygomatic] plate of maxilla characteristic in structure (compared to *M. arvalis*). Lower incisor reduced, extends only to angle of posterior mandibular notch. Dental foramen situated higher than in common and field voles, on narrower and longer bony shaft than in these species, and forms posteromedial margin of the articular process. In most individuals, M^3 with simplified structure—three lateral and three medial denticles and a reduced heel; a fourth denticle, if present, poorly developed. In M_1 , lateral denticle of second fold of paraconid absent and anterior unpaired loop rounded-rectangular (similar to *M. fortis*); medial denticle well-developed and isolated, even apically. Posterolateral denticle of M_3 absent, middle pair of lobes divided.

Composition of species: Two poorly differentiated subspecies

*Not listed in bibliography—Eds.

known: *M.* (cf. *M.*) *c. cabreræ* Thomas, 1906 (central and northern Spain) and *M.* (cf. *M.*) *c. dentatus* Miller, 1910 (southeastern Spain).

Distribution and zonal affinity: Eastern half of Iberian Peninsula, from Wesk in the north to Sierra Seguera in the south. Holocene remains have been found in southern France (Montpelier) (Balsac, 1939), which attest to the recent contraction of the eastern part of the range of this species. Reportedly, the region of its distribution slightly overlaps that of *M. arvalis*.

299 *Evolution and phylogeny:* Fossil remains from Early Holocene not known. A rare species, which should be considered the most archaic member of the common vole. In short incisors and simplified structure of M^3 , it is close to forerunners of the subgenus; in degree of differentiation of the anterior section of M_1 , it corresponds to the present-day species *M. fortis* and is identical to extinct forms from the *malei-paraoperarius* group. The closest related species is the Middle Pleistocene *M. brecciensis*.

32. *Microtus (Microtus) brecciensis* Giebel, 1847

(? = *coronensis* Kormos, 1933) (foss.) (Figure 49, C)

Diagnosis: Size large. Length of M_1 —2.5–2.9–3.5 mm ($n < 100$; southern France), 2.7, 3.0 mm (Hungary). The highly differentiated medial side of the paraconid section is the most characteristic feature of this tooth, which has a large and sharply isolated triangle on the second fold. The two folds bordering it are deep and in extreme variants of morphotypic variability may be completely isolated from the anterior unpaired loop. Lateral triangle, contrarily, small, its anterior fold disappearing rapidly during wear, and other folds fused with anterior unpaired loop; long lateral margin of paraconid thus acquires a uniform convex or rectangular outline. Enamel distinctly differentiated. Major triangles, similar to those at base of paraconid section, isolated among themselves, and basal ones isolated from anterior part of paraconid. All lobes of M_2 divided, middle pair of M_3 fused, and anterolateral denticle absent. All medial lobes of lower molars distinctly larger than lateral ones. Cement absent. Structure of upper molars and skull not described.

Age and distribution: Early to Late Pleistocene of southern Europe, from Spain to Italy and Hungary where, probably, this species was described under the name *M. coronensis* from the *Microtus-Pliomys* fauna of Brasho (Early Pleistocene).

Taxonomic notes: Chaline (1972) restores the old name given by Giebel after reexamining all the material available, and rightly included as a synonym of this species, the one described earlier by

him—*M. mediterraneus*. The author notes affinity primarily with *M. cabreræ*, assuming that *M. brecciensis* is its ancestral form. Kormos (1933) had earlier indicated the closeness of this species to voles from the *calamorum* group, i.e., to *M. fortis*, which does not contradict the view held by Chaline (see above). Either way, the dimensions, proportions, and structural features of the M_1 of *M. brecciensis* differentiate it well from associated species of microtines. Remains of the type specimen of *M. brecciensis* have not been found to date in the USSR.

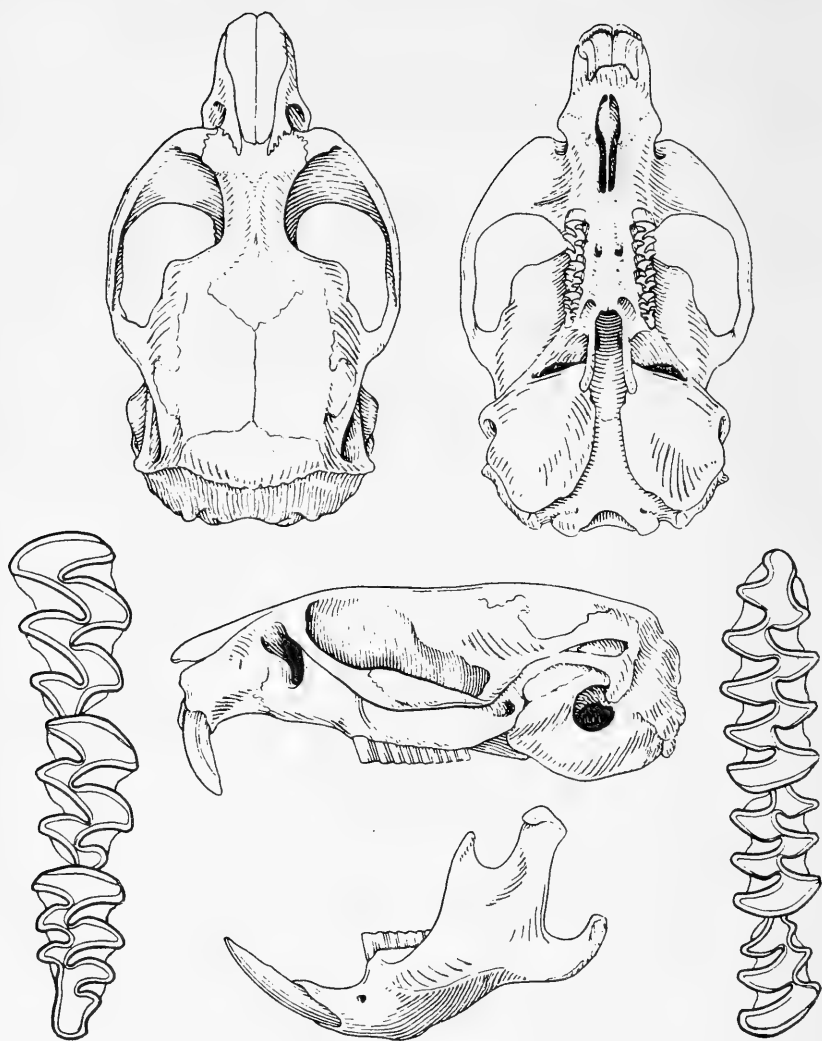
33. *Microtus (Microtus) agrestis* L., 1961—Field Vole
(Figure 51)

Diagnosis: Body length up to 140 mm in large forms and up to 130 mm in small forms, tail up to 51 mm in long-tailed forms and up to 36 mm in short-tailed ones (average about 40% and not more than 45% in former and 25.7 and 29% in latter). Length of upper molar row up to 7.0 mm, lower row up to 6.8 mm; M_1 —2.6—2.9—3.1 mm.

The comparatively long pelage creates the impression of slightly ruffled hair (in live animals). Dorsal surface dark, with predominance of gray or brown tones; ventral surface dark gray. Tail bi-
300 monochromatic. Forefeet light-colored on dorsal surface. Hind feet usually with six plantar calluses. Chromosome number, $2n = 50$ (two giant sex chromosomes are a characteristic feature).

Skull differs from similar-sized members of the subgenus in crest of interorbital space; larger, broader, and laterally less flattened auditory bullae; short lower incisor does not extend beyond dental foramen, weakly curved, and does not form alveolar knob on lateral surface of mandibular ramus. M^2 , and often also M^1 , with additional medial triangles on posterior end. Anterior unpaired loop of M_1 in a typical case narrow, isolated from second pair of lobes of paraconid by equal depth of folds on lateral as well as medial side, exhibiting tendency toward complete isolation.

301 *Composition of species*: Somewhat more than 20 extant subspecies have been described, a large number (15) from Western and central Europe, including four subspecies from the islands north of Great Britain. The actual number of subspecies is probably less, at least on the continent. Usually the following continental forms are recognized: *M. (M.) a. agrestis* L., 1961 (= *estiae*, Reinwaldt, 1924) (northern European part of the USSR, Scandinavia, Finland); *M. (M.) a. gregarius* L., 1766 (Baltic region, middle and southern European part of the USSR); *M. (M.) a. argyropuloi* Ognev, 1944



300

Figure 51. Skull of field vole (*Microtus agrestis* L.).

(southern and central Ural); *M. (M.) a. ognevi* Scalon, 1935 (from northern Ural to Turukhansk and the Lower Yenisey basin); *M. (M.) a. mongol* Thomas, 1911 (from southern and Kalbinsk Altai to Baikal); *M. (M.) a. arcturus* Thomas, 1911 (Dzhungaria, Chinese Turkestan); *M. (M.) a. rozianus* Bocage, 1865 (Portugal, north-

ern Spain); *M. (M.) a. leverniedii* Crespon, 1884 (southern France, southern FRG, Switzerland, northern Italy, Rumania, Transylvania); *M. (M.) a. orioecus* Cabrera, 1924 (Spain, Catalonia); *M. (M.) a. bailloni* Selys-Longchamps, 1841 (France, except southeastern area, northern FRG and GDR, Poland); *M. (M.) a. tridentinus* Del Riaz, 1924 (northern Italy); *M. (M.) a. pannonicus* Ehik, 1924 (Hungary); *M. (M.) a. wettsteini* Ehik, 1928 (southern Austria—Karintia, Hungary; a beautiful form); and *M. (M.) a. punotus* Montegu, 1923 (Slovenia, Yugoslavia). The subspecies status of the Carpathian voles in the USSR has yet to be explained. The taxonomic position of *M. clarkiei* Thomas, 1923 from Yunan (China) and *M. agrestoides* Hinton, 1923 from the Early Pleistocene of England among the extinct forms is not clear. The former species, in the opinion of Allen (1940), belongs to the *agrestis* group, while the latter requires redescription (see below). Recently, Chaline (1972) separated a large Middle Pleistocene and a smaller Late Pleistocene field vole from France into separate subspecies: *M. (M.) a. jansoni* Chaline, 1972 and *M. (M.) a. aubinensis* Chaline, 1972.

Variability: Size increases in mountains and toward periphery of the range (Zimmermann, 1950; Gromov *et al.*, 1963). The frequency of occurrence of individuals with additional lobes on M^1 and complex structure of M^3 increases east and north. Zimmermann (1956) showed that the absence of such additional lobes on M^2 , together with the simple structure of M^3 (simplex form) is found in Europe only in some individuals from one Dutch insular population. Such a structure was assessed as an index of the process of reduction whereas, in fact, a reverse phenomenon takes place: an archaic structure is retained in one of the populations under insular conditions. Data for the east European and Asiatic members of this species are not available.

Distribution and zonal affinity: Inhabits open and shrub biotopes in montane and plain forests; continues into tundra along floodplains of rivers and open biomes south of the present-day forest boundary. Found in mountains up to 1,850 m above msl (Carpathians). All of Europe except southern parts of Spain and Italy, greater part of Rumania, Bulgaria, European part of Turkey, and southern Balkan Peninsula, where the relict localities are known. In the USSR, found south up to Ivano-Frankovsk, Vinnits, Kiev, and Chernigov districts, and northern part of Voronezh district; along insular forests up to Mordavia, Chuvashia, Tataria, and Udmurtia; along Ural range up to its southern tip (Zalaire). Boundaries in forest-steppes of western Siberia not known and

finds south of 60° N between the Ural and Ob' Rivers also not known. Known from the western Ob' region and northern part of the Barbinsk forest-steppe, widely distributed in the Altai-Sayan mountain chain up to Baikal region, and spreads into northeastern China as well as Aldania. In Siberia, boundary of continuous range passes somewhere in the watershed between the Yenisey and Lena Rivers in the region of 110–115° E.

- 302 Range in the Late Pleistocene, confirmed by a few reliably identified remains, passed much more southward, reaching Dobruza, northern Moldavia (Lozan, 1971), Zhiguli, and Chistopole region of Kama, i.e., more northward than boundary of *M. oeconomus* which, however, may simply indicate a lack of information.

Evolution and phylogeny: Pasa (1949) described from the Ancient Pleistocene of northern Italy (Verona) a fragment of the upper jaw with an M^2 with an additional medial denticle, as well as a few isolated M_1 , which he included under *M. agrestis*. However, one cannot be totally confident about the correctness of his identification since remains of other microtines were also found at the same place, in which the upper molars exhibit a tendency toward formation of additional lobes (*Pitymys*, *Chionomys*), and also the structure of the anterior section of his M_1 is not typical for the species. Among the later deposits of England (early layers of the middle Thames terrace—Middle Pleistocene), *M. agrestoides* has been described on the basis of isolated molars: "... early member of the group of *M. agrestis*, mainly characterized by persistent development of a fourth lateral fold in the last upper molar (*M. agrestoides* sp. n.)" (Hinton, 1923, p. 93). Diagrams and dimensions of this tooth are not given. The solitary M_1 of this form, illustrated by the author (Hinton, 1926, Figures 1, 5), was earlier (Hinton, 1907) included by him under *M. nivalis*! Since a complex structure of M^3 is always found not only in present-day northern forms of *M. agrestis*, but also in other species of the subgenus *Microtus*, the taxonomic position of *M. agrestoides* remains unclear and requires redescription based on new material. Thus, the early evolution of *M. agrestis* has not been analyzed based on paleontological data. The probable ancestors of the species should be searched among the *arvalis* group, including forms attaining a high degree of differentiation in structure of the paraconid section of M_1 .

Remains have also been found in the composition of lemming and mixed faunas of central and eastern Europe, which can be included with considerable confidence under *M. agrestis*, even

though they are often indicated as belonging to *Microtus* ex gr. *arvalis-agrestis*.

34. *Microtus (Microtus) pennsylvanicus* Ord, 1815—
Pennsylvania or Meadow Vole

Diagnosis: Body length up to 148 mm in large forms and up to 128 mm in small forms, tail up to 56 mm (on the average, about 39% and not more than 45% body length) ($n = 20$). Length of upper and lower molar rows up to 7.2 mm; M_1 —2.8–3.1–3.5 mm ($n = 13$), M^3 —2.4–3.53 ($n = 54$; Oppenheimer, 1965).

Dorsal surface dark, as in *agrestis*, and with predominance of chocolate-brown tones; ventral surface dark gray. Tail dark, mono- or slightly bichromatic. Forefeet dark on dorsal surface. Hind feet with six plantar calluses. Chromosome number, $2n = 46$.

Skull in general plan of structure very similar to that of *M. agrestis*. Differences include the somewhat shallower dip in dorsal profile in rostral section and somewhat more inflated parietals (compared to individuals from similar topographic conditions in the European part of the USSR and North America). Auditory bullae of the Pennsylvania vole are smaller, their width on frontal side of auditory meatus always significantly smaller than length of upper molar row. Crowns of incisors longer, especially upper ones, which are also more abruptly curved. Posterior end of lower incisor, though not forming an alveolar knob on lateral surface of jaw, extends beyond dental foramen. Additional medial lobe on posterior end of M^1 probably less-developed, and found less often than in *M. agrestis* (comparison of individuals from northern part of range), and anterior unpaired loop of M_1 shorter, less laterally compressed, and rarely differentiated from lobes at its base (forma *maskii*). Moreover, in *M. pennsylvanicus* one often observes a tendency, less typical of Palearctic species, toward isolation of the lateral of these lobes, the medial one thereby widely fused with the anterior unpaired loop (in 17% specimens of typical American form; Oppenheimer, 1965). In Eurasia, such a structure is more common among the extinct Microtinae from the *arvalis-agrestis* group.

Composition of species: Hall and Kelson (1959) have listed 24 subspecies, primarily from the peripheral parts of the range, a major part of which is occupied by four or six subspecies, including the nominal one (southeastern part) and *M. (M.) p. drummondii* Audubon and Bachman, 1853 (large part of Canada). Geographic variability and extinct forms have not been described.

Distribution and zonal affinity: One of the very common and abundant species of voles of the New World; inhabits mainly meadows, partly bog-like areas, and clearances in forests and forest-steppe zones of North America. Continuous boundary of range extends to the Canadian border and southwest and northern parts of Georgia in the southeast. An isolated region at the end of the Pleistocene or beginning of the Holocene has been identified in Colorado and New Mexico. Found in mountains up to 1,700 m above msl (Hall and Kelson, 1959).

Evolution and phylogeny: Fossil remains known from beginning of the Late Pleistocene (Illinois period; Hibbard, 1956b, 1970c) from area of present range and near its boundary in the Great Plains, and slightly more southward.

Frank (1959), who conducted hybridization experiments with the type form *M. pennsylvanicus* and *M. agrestis* from central Europe, has finally confirmed the independent status of both species, accepted on the basis of differences in structure of baculum (Anderson, 1960) and chromosome number.

35. *Microtus (Microtus) arvalis* Pallas, 1778—Common Vole

Diagnosis: Body length of small forms up to 100 mm, in large continental forms up to 135 mm, and in stray cases up to 200 mm (Stein, 1958). Tail length up to 34 mm in small forms and 51 mm in larger (average about 33% body length in short-tailed and 37% in long-tailed forms). Length of upper molar row respectively 4.1–4.6 and 6.2–7.0 mm (7.5 mm), lower row 4.2–4.8 and 6.1–7.2 mm. Length of M_1 —2.6–2.8–2.9 and 2.7–3.0–3.2 mm ($n = 12$).

Body predominantly gray with varying intensity of chocolate-brown and reddish tones dorsally, ochreous tones on sides, and light gray on ventral surface. Tail mono- or slightly bichromatic. Forefeet dorsally similar in color to body surface. Hind feet usually with six plantar calluses, but in several subspecies some individuals only have five. Chromosome number, $2n = 46$.

Dorsal profile of skull from poorly smoothly convex to flat and even slightly compressed in interorbital region, with well-expressed slope in rostral section. Longitudinal crest present in interorbital space in fully mature individuals. Crowns of incisors moderately long, comparatively poorly curved, especially upper ones. Auditory bullae small, their width in front of auditory meatus less than length of upper molar row. Posterior end of anterior upper molars without additional medial lobes. M^3 in typical case with three lateral and four medial denticles (forma typica; Rörig and Börner,

1905). Paraconid section of M_1 very often in form of symmetrical triangle isolated from lobes at its base. Anterior unpaired loop comparatively broad, with less-distinct tendency toward isolation and formation of forma *maskii* than in *M. agrestis*.

Composition of species: Various authors have listed from 20 subspecies (Bashenina, 1966) up to 30 subspecies (Stein, 1958) (excluding *M. mongolicus* and *M. transcaspicus*), but the former number is closer to reality. From nine (Bobrinskii, Kuznetsov and Kuzyakin, 1965) to twelve (Gromov *et al.*, 1963) subspecies have been reported for Russian fauna. Like many other species of the genus, subspecies from the peripheral range are less well-studied than others. A large number of forms described from the Balkan Peninsula, mostly from isolated specimens, have recently been considered members of differentiated montane populations with no taxonomic status and belonging to the northern European subspecies *levis* (Kratochvil, 1954; Ondrias, 1966; Mirić, 1970). This subspecies, together with the nominal form and subspecies *duplicatus* and *rossiae-meridionalis*, occupies a large part of the species' range. The following subspecies are the most reliable: *M. (M.) a. asturianus* Miller, 1908 (mountain regions of northwestern Spain); *M. (M.) a. meridianus* Miller, 1908 (mountain regions of southeastern France); *M. (M.) a. meldensis* Delost, 1955 (plains of northwestern France); *M. (M.) a. yoensis* de Balsac, 1940 (Yo Island, Biscay coast of France); *M. (M.) a. sarnius* Miller, 1909 (Jersey Island); *M. (M.) a. orcadensis* Miller, 1904 (Orkney Island; including *ronaldshaiensis* Hinton, 1913; *rousaiensis* Hinton, 1913; *westrae* Miller, 1908; and *sandayensis* Miller, 1905); *M. (M.) a. arvalis* Pallas, 1778 [plains of southwestern central Europe from far northeastern France up to Hartz in the south, Sosnovy mountains in western Czechoslovakia (Bohemia)]; *M. (M.) a. duplicatus* Rörig and Börner, 1905 [plains of northern central and eastern Europe from Oder River and northern part of Czechoslovakia (northern Slovakia) up to Ural range; south up to southern boundary of forest-steppes in European part of the USSR; including *incognitus* Stein, 1931; *cimbricus* Stein, 1931; and *ruthenus* Ognev, 1950]; *M. (M.) a. levis* Miller, 1908 (foothills and mountain regions of southern part of central and eastern Europe, south up to Bulgaria, northern Greece; including *brauneri* Martino, 1926; *calypsus* Montegu, 1923; *igmanensis* Bolkay, 1920; *hewelkae* Bolkay, 1925; and probably *angularis* Miller, 1908; *grandis* V. and E. Martino, 1948; *epiroticus* Ondrias, 1966; *rhodopensis* Heinrich, 1936; and *heptneri* Hamar, 1963); *M. (M.) a. incertus* Selys-Longchamps, 1841 (Switzerland,

montane northern Italy); *M. (M.) a. rossiae-meridionalis* Ognev, 1924 (southern European part of the USSR, east up to Don River and south up to northern boundary of desert-steppes); *M. (M.) a. iphigeniae* Heptner, 1946 (Crimean Peninsula); *M. (M.) a. machlisi* Neuhauser, 1936 (northern Black Sea coast of Turkey); *M. (M.) a. relictus* Neuhauser, 1936 (central Turkey, region of Lake Tuz); *M. (M.) a. macrocranius* Ognev, 1924 (Cis-Caucasus, northern slope of Great Caucasus; including *brevirostris* Ognev, 1924); *M. (M.) a. gudauricus* Ognev, 1924 (eastern part of Great Caucasus); *M. (M.) a. transcaucasicus* Ognev, 1924 (Trans-Caucasus; possibly not distinguishable from *mystacinus*); *M. (M.) a. mystacinus* de Filippi, 1865 (western part of Elbrus range in northwestern Iran); *M. (M.) a. transuralensis* Serebrennikov, 1929 (middle and southern plains of Trans-Ural area); *M. (M.) a. caspicus* Ognev, 1950 (plains of Azov region, Caspian region, western Kazakhstan); *M. (M.) a. kirgisorum* Ognev, 1950 (plains and foothills of northern Kirgizia, adjacent parts of Kazakhstan, Ferghana); *M. (M.) a. innae* Ognev, 1950 (peripheral ranges of northwestern Tien Shan—Dzhungarian and Trans-Ilian); *M. (M.) a. obscurus* Eversmann, 1841 (Altai and adjacent areas; including *baikalensis* Fetissoff, 1941); and *M. (M.) ? a. khorkontensis* Goodwin, 1940 (mountains of northeastern Iran).

It should be noted that in the central part of the range of this species, where the twin species—46-chromosome *M. arvalis* and 54-chromosome *M. subarvalis*—are sympatric, the species affinity of subspecific forms is not clear and, in this case, could not be established even with special studies. At the same time, results of chromosomal analysis of a large percentage of the western and central European *M. arvalis* did not reveal the presence of the 54-chromosome species in this part of the range.

It was recently established that two groups of subspecies exist within the limits of *M. arvalis*, which are distinguished by minute structural differences in autosomes: the Western and central European forms, as well as the northern forms from eastern Europe on the one hand, and the southern and eastern forms on the other (Meyer, Orlov and Skholl, 1972b). However, these differences, observed within the range, like some other chromosome arrangements (Kral and Lyapunova, 1975), do not prevent fully fertile hybrids.

Distribution and zonal affinity: Open meadows and meadow-steppes as well as cultivated areas, including crops, fallow areas, and deforested parts of mountains and plains of Europe; absent in greater part of the Pyrenees, Normandy, and plains of south-

eastern France, greater part of the Apennine Peninsula, and all Mediterranean islands, Great Britain, Ireland and adjacent islands (except Orkney and Jersey), in Scandinavia, Jutland, and Finland (except southern parts), and southern Balkan Peninsula (including greater part of Greece). In the European part of the USSR, found north up to the Karelian Isthmus, east up to 63–64° N (Obozersk in Arkhangel'sk district, Severo-Uralsk in central Ural; Marvin, 1968, 1970), Condo-Sis'yina watershed, Tobol'sk Novosi, Altai and nearby areas, and southwestern Baikal. South up to Trans-Caucasus, northern Turkey, northern Iran, lower reaches of Volga and Ural Rivers, northern and northern central Kazakhstan, almost up to line between Aktyubinsk and Tamir on Lake Chelkar, Karsakpai, Kizylrai, and Chingstau mountains in Semipalatinsk. Areas of inhabitation even farther south include Tarbagatai, Zaisan, and Alakul basin as well as foothills and lower hills of peripheral ranges of Tien Shan (Dzhungarian, Zailiisk, Kirgizian, Talass, Chatkal as well as Turkestan). However, this vole does not penetrate deeper into its montane range, although found up to 3,000 m above msl. The only "deep" isolated locale known is in Kulyaba region. Incidentally, the entire southeastern boundary needs to be verified, and the corresponding forms reinvestigated relative to the independent species status of *M. transcaspicus*, *M. ilaeus*, and *M. mongolicus*, which live sympatrically with *M. arvalis* at some places.

Variability: Insular forms are larger than continental forms; on the continent, northern forms larger than southern ones, while the difference is greater in the central part of the range than along its periphery where differences disappear in mountain regions; however, montane forms are somewhat larger than plain forms. Disturbances in size variability are observed even in the forest-steppe zone of eastern Europe (Bashenina, 1966). Color variability is seen in darkening of pelage in montane form in an eastward direction; rusty tones are more typical in southern and central forms. Structure of M^3 becomes more complex in southward direction (reduction in relative abundance of "simplex type"), and more prominent in western than central part of range, and in the east probably not at all manifested. Geographic variability of M_1 morphotype has not been studied in this species. In extinct forms, it involves reduction in tooth size (at least in southeastern Europe) as well as loss of "Pitymys" fusion of triangles on masticatory surface. Similar morphotypes have been described as extinct forms—"Pitymys" *arvaloides* Hinton, 1923 and *Microtus arvalinus* Hinton, 1923—but

as archaic manifestations are even found occasionally in teeth of extant *M. arvalis* (Janossy and Schmidt, 1960, 1975).

It should be kept in mind that the geographic variability of many morphological characters of present-day species overlaps seasonal biotopic variability as well as numerical, and hence population samples from similar conditions of life and comparable cyclic fluctuations should be compared for characterization of taxonomic status.

Evolution and phylogeny: Fossil remains of the Pleistocene comprise the two species discussed above. Early Pleistocene forms (upper freshwater layers, England)—“*Pitymys*” *arvaloides*—have also been found in central and eastern Europe together with those not differing from the present-day *M. arvalis* in structure of M_1 . These should probably be considered representatives of the *Microtus* and not the *Pitymys* line of development, as concluded by the author (Hinton, 1923), and should thus be included under the single species *Microtus (Microtus) arvaloides*, in which most members also have fused triangles at the base of the paraconid of M_1 (see also, p. 380). Up in the geochronological scale, the relative abundance of animals with such molars decreases sharply, and the molars of the Würm species, *M. arvalinus* Hinton, 1923, according to the evidence of the author himself, are distinguished from those of present-day species only by smaller size and juvenile folds of the posterolateral margins of the anterior unpaired loop of M_1 , which has been retained in the initial stages of wear. Such Middle to Late Pleistocene remains are often designated as *Microtus* ex gr. *arvalis-agrestis*, and in eastern Europe also as *Microtus* ex gr. *arvalis-socialis*.

The Late Pleistocene large-sized species *M. corneri* Hinton, 1910, mainly from the British Isles, soon after its description was, and even today still is, considered the ancestral form of the extant insular species *M. (M.) a. orcadensis*. Remains of the smaller *M. arvalis* have been found in the fauna of the same locality but, as rightly pointed out by Zimmermann (1959), a maximum number of fossils of different ages appear in the Arthem crevices and the latter form was included in the later lemming fauna. Its affinity with other Pleistocene subspecies described from France—*M. (M.) a. dommensis* Chaline, 1972 and *M. (M.) a. santenayensis* Chaline, 1972; and also *M. (M.) a. lazaretiensis* Chaline, 1972 from end of the Middle Pleistocene—is neither clear nor was it investigated by the author. Mention should be made here of Bashenina's proposal (1966) that *M. (M.) a. orcadensis* Miller could be considered

a species (in my opinion, it should be assigned a prespecies status), in spite of the fact that on crossing with continental forms, *M. arvalis* readily produced fertile progeny (Zimmermann, 1959). This conclusion is not without biological significance, although if the question is examined from the point of view of the genetic concept of species, it may appear senseless. There are no voles of the *arvalis* group on the main island of Great Britain and the latest discovery of their fossil remains is at least 10,000–12,000 years old. The age of *M. a. orcadensis*, obtained from Orkney, is probably about the same.

Current views on the affinity of *M. arvalis* are reflected in the concepts "supraspecies *arvalis*" or "the *arvalis* group," which have recently undergone significant simplification. The most voluminous scheme was presented by Kratochvil (1959), who included *Microtus cabreræ* and even *M. guentheri* under a supraspecies *arvalis*, for which he was rightly criticized by Bashenina (1966). The former species is considered here an archaic form of the genus *Microtus*, with a molar structure still closer to that of some extinct forms (p. 427); the second species, according to most mammalogists, is interpreted as a species of the subgenus *Sumeriomys*. Among the prespecies indicated by Kratochvil, *M. mongolicus*, *M. transcasicus* as well as *M. ilaeus* are independent species, and *M. a. orcadensis* with its closely related forms (see above) as well as *M. a. sarnius* may be considered corresponding stages of free species.

Given our present knowledge, probably it is more correct to consider the *arvalis* group as primarily consisting of the twin species *M. arvalis* Pallas and *M. subarvalis* Meyer, Orlov and Scholl. The latter species, judged in terms of karyotype, is more ancient than the former (Meyer, Orlov and Scholl, 1972c), and *M. transcasicus* Satunin and *M. mongolicus* Radde are close to it. The position of the Japanese species *M. montebelli* M.-Edwards, remains unclear, but possibly ought also to be included in this group as an extreme eastern form. Among the extinct forms, most probably *M. corneri*, *M. arvaloides*, and *M. arvalinus* should be included in this group, although their actual taxonomic status needs further verification (see above). The more distant ancestors of the group should be searched among forms with a molar structure typical of *M. cabreræ* among extant species, and *malei*, *brecciensis*, and *paraoperarius*-type microtines among extinct ones, though definite relationships in this case are still not clear.

The common vole has no present-day morphoecological analogue in the New World. Conclusions regarding the last stages of Anthropogene evolution of its range in the Old World should be reexamined in the light of the discovery of *M. subarvalis*. If we consider that *M. arvalis* in origin is a western form and *M. subarvalis* an eastern one, the views of Kratochvil (1959) correspond more with the evolution of *M. arvalis*, and those of Bashenina (1966) with the evolution of *M. subarvalis*. Unfortunately, paleontological material is not available. We know that remains of voles with lower molars of the *arvalis*-*agrestis*-type are reported for most "fixed faunas" of the Würm period in western and central Europe including montane regions. In this case, the occurrence of skull remains in many caves attests to the abundance of *M. arvalis* here. Most probably, this light-loving form of open biotopes survived the early glacial period interacting with the forest vole (*Clethrionomys*) and lemming. At the same time, an insignificant number of fossils of voles with an M_1 of similar structure have been found among remains of species belonging to "mixed faunas" of the last glaciation, which also cannot be separated with sufficient confidence from extreme variants of structure of this tooth, which are typical of *Stenocranius*, the massive voles of mixed faunas. The situation is reversed in the south, for example in Crimea. It may be thought that the 46-chromosome *M. arvalis* evolved as a species in the western part of the European continent relatively late. We can think about this with reference to the nature of the range of the present-day species, which was absent at places never exposed to glaciation (greater part of the Iberian and Apennine Peninsulas), because they had separated from the mainland in the Late Pleistocene (Mediterranean islands) or joined it at this time (Normandy and Jutland Peninsula). Only in the post-Würm period did this species spread eastward together with meadow biotopes of broad-leaved forests, where the sympatric part of its range evolved together with the 54-chromosome *M. subarvalis*. This latter species could have survived the Würm glaciation in the southeastern European part of the USSR and in the mountains of southeastern Europe (Yugoslavia) in so-called "refuges," after which it, too, spread northward. A similar opinion with regard to *M. arvalis* (old interpretation) is held by Kratochvil (1959).

36. *Microtus (Microtus) subarvalis* Meyer, Orlov and Scholl, 1972⁶

This recently described twin species of the common vole was isolated on the basis of a distinct number of chromosomes ($2n = 54$) as well as results of hybrid analysis showing that its hybrids with *M. arvalis* s. str. are heterozygotic and with $2n = 50$, and sterile in both cross combinations. *M. subarvalis* is currently under intensive and comprehensive study. Features which distinguish it from *M. arvalis*—shape of sperm head, heat conduction of muscular tissue and different tolerance to cohabitation, and possibly also size (in average values)—have been established. Differences in characters normally used in classification, however, have not yet been found, but additional verification is needed.

Distribution and zonal affinity: *M. subarvalis* occupies the central, partly eastern, and southwestern part of the range of *M. arvalis* described above. To date, it has not been found west of the Balkan Peninsula (Zivković *et al.*, 1974) and mixed populations of the two species have not been found beyond the northeastern part of western Siberia.

Evolution and phylogeny: The possible appearance and distribution of the species have been described above. Its closely related species are eastern members of the *arvalis* group, such as *M. transcaspicus*, *M. ilaeus*, and *M. mongolicus* (Meyer, Orlov and Skholl, 1972b).

37. *Microtus (Microtus) transcaspicus* Satunin, 1905—
Trans-Caspian Vole

Diagnosis: Size large. Body length up to 147 mm, tail up to 42 mm (average about 33% and up to 43% trunk length). Length of upper molar row 7.3–8.2 mm, lower row 7.1–8.2 mm ($n = 7$; Zeravshan floodplain; Davydov, 1962); M_1 —3.1–3.28–3.6 mm ($n = 20$; lower reaches of Amu-Darya).

Color variable: dorsal surface from rusty-brown of various intensity to ash-gray and light ochreous-sandy (Murgab and Kushka floodplains); ventral surface from light to dark gray with ochre-

⁶ The species name *subarvalis* is preoccupied: *M. subarvalis* Heller, 1930—the extinct form from Mosbach sands, FRG. But the recent proposal (Zivković *et al.*, 1974), as expounded by its authors, to replace the name *M. subarvalis* with *M. epiroticus* Ondrias, 1966 for the 54-chromosome vole described from Greece (Ondrias, 1966), cannot be considered the final solution to the problem. According to the rules of nomenclature, name substitution can only be done after the subspecies of *M. arvalis* described prior to 1966 have been investigated cytogenetically, and it has been demonstrated that there are no 54-chromosome forms among them.

ous or brown tones. Tail mono- or slightly bichromatic. Forefeet light-colored on dorsal surface. Chromosome number, $2n = 52$ (Köpetdag).

Skull similar to that of *M. arvalis*, but larger, with poorly developed crests, including the late-formed short and low sagittal crest, located in comparatively broad interorbital space, giving the skull a juvenile appearance. Brain case comparatively long and narrow, as is facial section of skull (latter in comparison with *M. ilaeus*). Auditory bullae small, flattened laterally. Articular process of dentary shorter and broader than in other species of the group. Posterior end of lower incisor extends above dental foramen and in not fully mature individuals forms alveolar knob on lateral surface of jaw. Predominant structure of molar complex. Posterior end of M_1 and M^2 with tendency toward formation of additional medial folds (more often on M^2); however, even in case of maximum development, these folds have more the form of *Dicrostonyx*-type plates than *agrestis*-type columns, and do not extend entire height of crown. M^3 often with fourth lateral denticle. M_1 with tendency toward two complete folds in paraconid section; anterior unpaired loop in most animals rounded, almost completely removed from widely fused triangles at its base.

Composition of species: Since *M. ilaeus* Thomas, until recently considered a subspecies of the Trans-Caspian vole, has been recognized as an independent species (see below), the question of subspecific differentiation of *M. transcaspicus* remains open, and the general nature of variability remains unstudied. Specimens from the Kushka and Murgab floodplains differ in color, which was also noted by Ognev (1950).

Distribution and zonal affinity: Inhabits floodplains of rivers and adjoining flooded areas in Soviet Central Asia and partly in Kazakhstan from the Atrek basin in the west up to the middle and lower course of the Syr-Darya in the east. Boundary with the next species needs to be verified; *M. ilaeus* probably lives in the Tashkent region and upper reaches of Syr-Darya. Range discontinuous and species found sporadically at places as relict colonies beyond the limits of floodplains of large water courses, indicating a stronger hydrographic network development in the recent prehistoric as well as early historic past. Does not extend into mountains and is replaced by the common vole in the high-montane meadow belt of the peripheral ranges of Tien Shan.

Evolution and phylogeny: Fossil remains of M_1 of similar size and structure are known from deposits at end of the Middle Pleis-

tocene of Tashkent region; however, it is not excluded that they belong to the next species.

Results of cytological analysis (Lyapunova and Mirokhanov, 1969; Meyer and Orlov, 1969; Malygin, 1973) have conclusively demonstrated the correctness of Vinogradov's views held since 1936 (Vinogradov, Argiropulo and Heptner, 1936) about the independent species status of this form. It became isolated at the southeastern boundary of the range of the *arvalis* group in the river valleys of Soviet Central Asia living under conditions of an arid climate. The opinion that *M. transcaspicus* also includes the northern Iranian species *M. mystacinus*, *M. khorkontensis*, and even voles of this group living in the northern part of Asiatic Turkey (Bashenina, 1966), can hardly be considered justified. New data have been obtained for the first of these species based on a study of the original material by Lay (1967). The second species still remains too insufficiently studied to warrant such a conclusion and, in this respect, we have to agree with Ognev (1950) that *M. arvalis* and *M. subarvalis* are undoubtedly voles of Asiatic Turkey.

It is more tempting to think of phyletic links between the large Late Pleistocene *M. corneri*, mainly from the British Isles, and the large present-day forms of the *transcaspicus-ilaeus* type. However, no data can be cited in favor of such an approach, except to mention
 310 the general trend in faunal evolution, in accordance with which extinct forms of rodents from the western region of their range are more similar to present-day forms from its eastern part than to their local descendants. Details of skull and tooth structure of *M. corneri* are not yet reliably known.

38. *Microtus (Microtus) ilaeus* Thomas, 1905—Ilian Vole

The need for raising this form, which until recently, was considered a subspecies of the Trans-Caspian vole, to the status of independent species appeared after determination of the karyotype of the typical *M. transcaspicus* from Kopetdag, which distinctly differs from *M. ilaeus* in $2n = 54$ (Tashkent region; Meyer and Orlov, 1969; Meyer *et al.*, 1971). Hybrid analysis by the former two authors displayed distinct reproductive isolation from the 54-chromosome *M. subarvalis*. Experiments on hybridization with the Trans-Caspian vole are underway. However, the probability of obtaining fertile hybrids is less than in the former case, if we consider that karyologically both forms are quite distinct from each other (Lyapunova and Mirokhanov, 1969).

M. ilaeus is probably smaller than the Trans-Caspian vole (body length up to 135 mm; $n = 9$, Talass valley), color duller, and rostral section of the skull shorter and broader.

Distribution and zonal affinity: Inhabits floodplain biotopes of basins in the upper reaches of Syr-Darya, Talass, and Chu Rivers. Probably, only *M. subarvalis* or *M. arvalis* lives in similar conditions north of, and in the Dhuliisk mountains, and *M. transcaspicus* in the middle and lower courses of the Syr-Darya. The range boundaries of *M. ilaeus*, *M. transcaspicus*, and *M. arvalis*-*subarvalis* need to be precised.

Evolution and phylogeny: The possible affinity of fossil remains from Tashkent region to this species was mentioned earlier. Based on chromosome number, *M. ilaeus* will have to be considered a more archaic form than *M. transcaspicus*.

39. *Microtus (Microtus) mongolicus* Radde, 1862— Mongolian Vole

Diagnosis: Size medium. Body length up to 123 mm, tail up to 39 mm (average about 29% and not more than 32% body length). Length of upper molar row up to 6.3 mm, lower row up to 6.6 mm; M_1 —2.45–2.6–2.9 mm.

Dorsal surface dark, chocolate-brown; ventral surface also dark, ash-gray. Tail sharply bichromatic: dorsal surface often darker than ventral (as distinguished from *M. maximoviczii*). Plantar calluses five, rarely six. Unlike most species of the *arvalis* group, the winter pelage is much denser and longer than the summer. Chromosome number, $2n = 50$ (Meyer, Jordan and Walknowska, 1967).

Skull similar to such small forms as *M. arvalis*-*subarvalis* but more juvenile in appearance and lighter in structure. Rostral section far less massive, most probably due mainly to weaker (narrower) incisors, which are slightly prognathous and not orthodont as in members of the preceding species (Leningrad district). Nasals narrow. Lower incisor longer and extends far upward onto articular process. Auditory bullae lower and distinct, notably not reaching masticatory surface of upper molars. Masseteric ridge of mandibular ramus higher and broader in frontal section. Molars with higher crown than in northern forms of *M. arvalis*-*subarvalis*. Anterior lower molar with second underdeveloped, lower lateral fold on paraconid that rapidly disappears during wear. As a result, anterior section of tooth acquires "gregaloid" shape typical of western population of *M. gregalis*, with short anterior unpaired

- 311 loop. Anterolateral denticle of paraconid of M_1 also always less well-developed than in the common vole.

Composition of species: Subspecies not described. Possible differences between the Trans-Baikal and Mongolian populations in relative length of tail has been indicated (Gromov *et al.*, 1963).

Distribution and zonal affinity: Inhabits steppes of Trans-Baikal, northern and northeastern Mongolia, from southern Tuva steppes in the west up to northern Khingan steppes in the east. Boundaries of range need to be precised everywhere because the Maximovich vole and subadult individuals of the narrow-skulled vole, which are similar in size and color, have repeatedly been included under this species.

Evolution and phylogeny: Mandibular rami of Early Pleistocene age with structure of M_1 similar to that of the extant species have been found in Trans-Baikal, somewhat more northward of the boundary of the northern range (Erbaeva, 1970).

The Mongolian vole is the Far Eastern member of the *arvalis* group. Its independent species status was recently confirmed cytogenetically as well as by hybrid analysis, which concludes discussion of its taxonomic status. The phenomenon of "opposing variability" of *M. mongolicus* and *M. gregalis* with regard to structure of M_1 is interesting: the predominant morphotype of its structure acquires a gregaloid form in the former species and an arvaloid form in the latter.

40. *Microtus (Microtus) montebelli* Milne-Edwards, 1868—1874

Diagnosis: Body length up to 121 mm, tail up to 48 mm (average 37% and not more than 41% trunk length; $n = 12$; Tokuda, 1941). Length of upper molar row up to 6.8 mm, lower row up to 6.5 mm; length of M_1 not known.

Dorsal surface comparatively light, chocolate-brown to ocher, sometimes fairly vivid; ventral surface gray, often with ocherous tones. Tail slightly bichromatic. Forefeet light-colored on dorsal surface. Plantar calluses five. Chromosome number, $2n = 30$.

Skull similar to that of *M. arvalis*, but as in other species from the eastern part of the range of this group, more juvenile in appearance due to extent of development of crests and proportions of the skull: interorbital space and brain case comparatively broad and latter also low. Rostral section less massive. Moreover, auditory bullae smaller than in *M. arvalis* (including *subarvalis*) and bony meatus of auditory passage less isolated; lower incisor much longer, extends beyond half length of articular process, and forms

well-expressed alveolar knob on its lateral surface. Molars similar to those of *arvalis*, possibly with somewhat higher crown; anterior lobes of paraconid of M_1 not reduced; M^2 with complex structure (medial denticles four; lateral three, sometimes four).

Composition of species: Two subspecies: *M. (M.) m. montebelli* M.-Edwards, 1868–1874 (Honshu and Kyushu Islands) and *M. (M.) m. brevicorpus* Tokuda, 1938 (Sado Island near west coast of Honshu).

Distribution and zonal affinity: Inhabits open terrain, including areas under cultivation, plains and lower hills of Honshu and Kyushu Islands as well as Sado Island (Japanese archipelago). Reports published in Soviet literature about finds of this species in Sakhalin and Kuril' Islands are not yet confirmed.

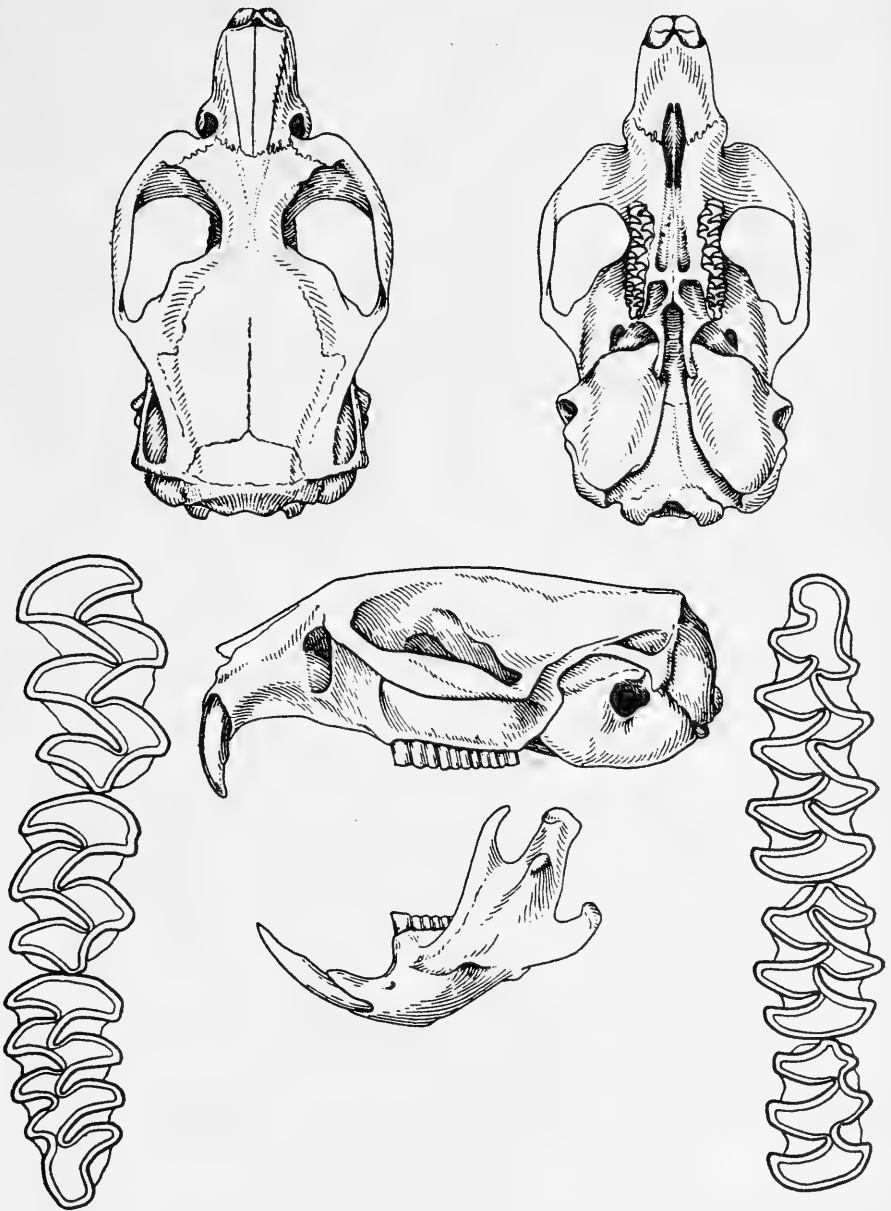
- 312 *Evolution and phylogeny:* Fossil remains known from the Late Pleistocene. It is probably more correct to consider *M. montebelli* a Far East member of the *arvalis* group in a broader sense.

41. *Microtus (Microtus) hyperboreus* Vinogradov, 1933—
North Siberian Vole (Figure 52)

Diagnosis: Body length up to 140 mm, tail up to 32 mm ($n = 29$; Krivosheev, 1963, 1971) (average about 20% up to 28% body length). Length of upper molar row up to 7.6 mm, lower row up to 7.2 mm. Length of M_1 —2.9–2.97–3.05 mm ($n = 8$).

- 313 Dorsal surface dark, of two types—brownish-black or chocolate-brown to gray; ventral surface monochromatic ash-gray. Seasonal dimorphism of pelage more prominent than in other microtines: winter pelage blacker, longer, and denser than summer. Tail thick with sharply demarcated dark dorsal surface, densely hairy, and terminal hairs long. Forefeet dark on dorsal surface, only slightly lighter-colored than back. Hind feet with five calluses on plantar; in western part of range, occasionally individuals with six plantar calluses found. Chromosome number cannot be considered conclusive; $2n = 50$ has been reported (Lyapunova and Krivosheev, 1969).

Dorsal profile of skull with strong rostral dip. Zygomatic arches in middle part relatively poorly separated and more or less parallel. Interorbital space reduced, longitudinal crest poorly developed and, as indicated by Krivosheev (1971), formed only in overwintered animals. Auditory bullae large, with pneumatic space; maximum internal length (together with mastoids) exceeds the coronoid length of upper row of molars at least by combined length of the first two molars. Anterodorsal parts of bullae completely fill the



312 Figure 52. Skull of the North Siberian vole (*Microtus hyperboreus* Vinogradov).

pre- and postarticular fossae. Mastoids inflated and markedly extend backward beyond occipital base. M_1 similar to *M. mongolicus*, with barely developed anterolateral denticle and fold bordering it from back side, as a result of which its paraconid section acquires a gregaloid form during wear. M^3 with complex structure; number of denticles on each side usually four, rarely five. Posterior end of lower incisor extends far upward on articular process and forms a distinct knob on its lateral surface.

Composition of species: The subspecies *swerevi* Scalon, 1935, described from Taimyr, was later identified as simply one of the color forms found in other parts of the range as well (Ognev, 1950; Krivosheev, 1963, 1971). However, this color form might actually be dominant in the western part of the range.

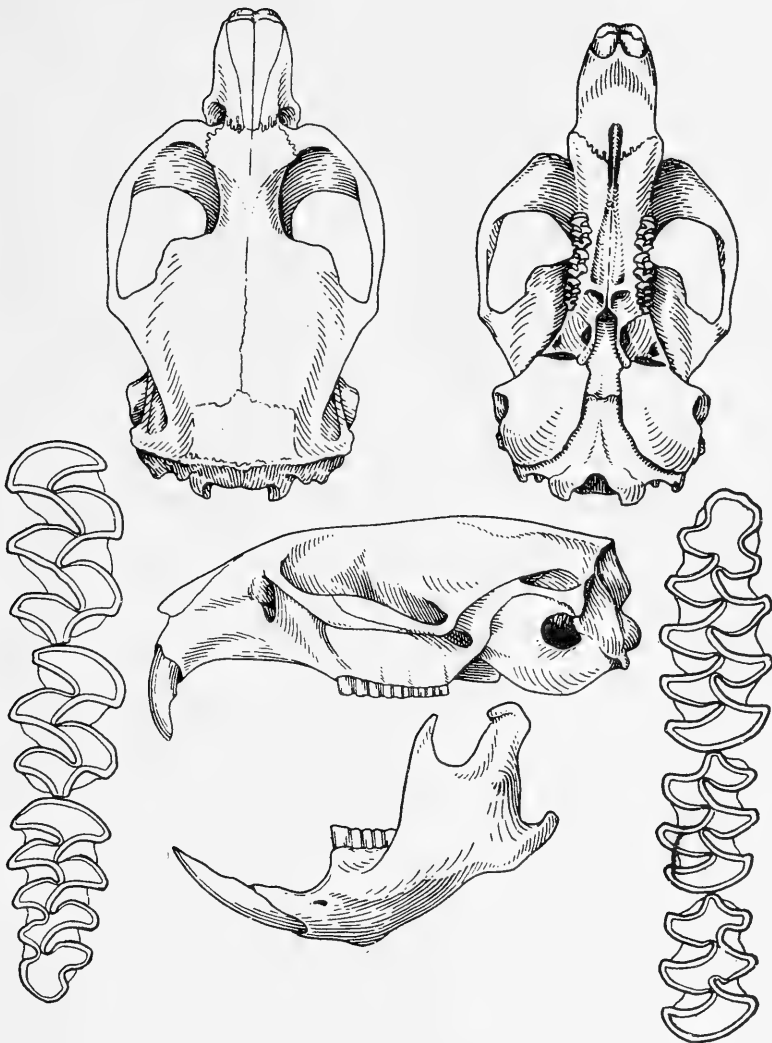
Distribution and zonal affinity: Inhabits meadows, including steppe-like regions along river valleys, and forest-tundra in foothills and mountain regions of central and eastern Siberia, from Taimyr Peninsula in the west up to upper reaches of Indigirka and Kolyma in the east; sightings south of 65° N not known to date.

Evolution and phylogeny: Fossil remains not known and can hardly be identified without a well-preserved skull. Affinities not known. Species first listed by Vinogradov (1933) in identification keys without diagnosis and reference to holotype. Ognev (1950) proposed as the holotype, specimen No. 15722 from southern Verkhoyansk in the collection of the Zoological Institute, Academy of Sciences, USSR, which was probably presented by the author (Vinogradov, 1933). To date, the North Siberian vole has not been properly differentiated from Middendorff's vole. In their sympatric areas the two species are separated according to habitats. The chromosome characterization of *M. hyperboreus* also needs to be precised. The geographic variability of some skull features in this species is such (see below) that its eastern members are actually closer to the North Siberian vole than to their own western members. However, there can be no doubt about the independent species status of this form.

314 42. *Microtus (Microtus) middendorffii* Poljakov, 1881—
Middendorff's Vole (Figure 53)

Diagnosis: Body length up to 145 mm, tail up to 32 mm (in laboratory animals up to 150 and 42 mm respectively). Relative length of tail not more than 22% in short-tailed forms and 34% in long-tailed forms (average 18.3 and 28.5 mm; $n = 10$; material of M.N. Meyer). Length of upper molar row up to 7.3 mm ($n =$

85; Krivosheev, 1971), lower row 7.2 mm; M_1 —2.8—2.97—3.2 mm (n = 22).



314 Figure 53. Skull of Middendorff's vole (*Microtus middendorffii* Poljakov).

Dorsal surface rather bright, chocolate-brown to ochre; ventral surface light, ash-gray. Seasonal dimorphism of pelage well-expressed, though less so than in preceding species. Tail thickness normal for species of the genus *Microtus*, sharply bichromatic, comparatively sparsely pubescent, with long terminal hairs. Forefeet grayish on dorsal surface, lighter in color than back. Plantar cal-
 315 luses five, rarely six (in some animals from eastern populations). Chromosome number, $2n = 50$ (Matthey and Zimmermann, 1961; Lyapunova and Krivosheev, 1969).

Based on skull structure, close to the preceding species, but rostral dip somewhat fainter, zygomatic arches wide-set in middle part, and profile of skull more or less rounded. Maximum differences are seen in dimensions of auditory bullae. These are smaller, less inflated than in the North Siberian vole, and their maximum internal length exceeds length of upper molar row by slightly more than length of M^1 . Upper part of bullae does not reach articular fossa. Mastoids flattened, do not protude downward beyond occipital base. M_1 with comparatively well-developed anteromedial denticle and restricting fold on back side. M^3 with simpler structure than in *M. hyperboreus*, and therefore shorter; medial denticles usually four and lateral three; a more complex variant, respectively with five and four denticles, is often found in the eastern part of the range. Alveolar knob of lower incisor less prominent than in *M. hyperboreus* of equal age.

Composition of species and variability: Two subspecies—*M. (M.) m. middendorffii* Poljakov, 1881 (from basin of Taz River up to eastern limits of range) and *M. (M.) m. ryphaeus* Heptner, 1948 (northern Ural and Yamal).

Size increases in eastward direction, while relative length of tail decreases, and auditory bullae become larger and more inflated. Size of M^3 increases due to complexity in structure of its posterior section; in eastern populations a fifth medial denticle is present in at least one-third of the animals, and the posterolateral denticle is not reduced. In M_1 the anterior pair of lobes of the paraconid are shifted more strongly relative to each other in animals from the western part of the range than in eastern populations.

Distribution and zonal affinity: Inhabits plains of tundras from northern Ural and lower reaches of Kolyma River.

Evolution and phylogeny: Fossil remains are not known. Phyletic links with voles close to *M. arvalis* s. str. have been reported, and Middendorff's vole is considered a derivative of a Late Pleistocene form that became separated in the northern Eurasian

mainland by forests dividing the open terrain of northern and temperate latitudes. Actually, remains (stray molars) similar to the molars of *M. arvalis* have been found in "mixed faunas" of the Late Pleistocene of the European part of the USSR. Kratochvil (1960) reported significant differences in structure of male genitalia of Middendorff's vole and of closely related microtine species; he proposed its elevation to an independent genus, an opinion no longer shared by others. Finally, some researchers have related this vole to the North American insular species *M. abbreviatus* (p. 403) (Matthey and Zimmermann, 1961; Lyapunova and Krivosheev, 1969). A phyletic link between these species is quite possible.

43. *Microtus (Microtus) chrotorrhinus* Miller, 1894—
Rock Vole

Diagnosis: Size medium. Body length up to 125 mm, upper molar row up to 7.2 mm ($n = 52$; Guilday *et al.*, 1964), lower row 6.2 mm; M_1 —2.9 mm.

Dorsal surface dark, brownish-gray; distinctly yellow or yellowish-orange tones predominant on sides of head, particularly between eyes and snout. Ventral body surface ash-gray. Tail slightly bichromatic. Forefeet light-colored on dorsal surface. Hind feet with five (?) calluses on plantar. Chromosome number, $2n = 60$ (Meylan, 1967).

316 Skull elongate, with narrow zygomatic arches, narrow interorbital space, and short wide-set longitudinal crests. Dorsal profile of skull with slight rostral slope that is distinctly steeper in interorbital region. Mandibles weak, with long articular and long, narrow angular processes. M^3 with complex structure—four (rarely five) lateral and five medial denticles, and fused anterior pair of triangles. Predominant type of structure of anterior section of M_1 asymmetric or slightly asymmetric trifoliate and anteromedial fold smaller than anterolateral ones. Anterior pair of lobes fused on M_2 , all three lobes broadly fused on M_3 . Posterior end of lower incisor extends just slightly beyond dental foramen and does not form knob on lateral surface of articular process.

Composition of species: Hall and Kelson (1959) have reported three subspecies.

Distribution and zonal affinity: A rare species, inhabiting montane forests with rock outcrops and taluses, up to 1,800 m above msl; in eastern part of North America spreads eastward up to 95° E

and along the Appalachian mountains southwest up to northern Alabama and Georgia.

Evolution and phylogeny: Reliable remains known from the Late Pleistocene [not distinguishable from *M. (M.) pennsylvanicus* on basis of dentary]. The next species is considered closest phylogenetically and some authors consider the rock vole its subspecies. However, even in the Late Pleistocene when they were sympatric, their remains were differentiated in size and structural details of the masticatory surface of the molars. Resembles *M. agrestis* in presence of fused sex chromosomes.

44. *Microtus (Microtus) xanthognatus* Leach, 1815—
Yellow-snouted Vole

Diagnosis: Size large (it and *Aulacomys* are the largest members of the tribe in the New World). Body length up to 180 mm, upper molar row up to 9.1 mm, lower row up to 8.4 mm; M_1 —3.3–3.6–3.9 mm ($n = 14$; Guilday and Bender, 1960).

Dorsal surface dark, ochreous-brown, with fairly vivid rusty-yellowish tones on sides of anterior part of snout; ventral surface dark, rusty-gray. Tail barely bichromatic, more distinctly so in winter pelage, relatively shorter than in preceding species. Forefeet dark on dorsal surface. Data not available on number of plantar calluses nor chromosome number.

Skull similar to that of preceding species, but larger and with better developed crests, including that of the interorbital space. Anterior to this crest, in older individuals, a groove develops which disappears in a forward direction. Dentary strong, with normally developed processes. M^3 somewhat less complex than in preceding species, with three lateral and four (rarely three) medial denticles and invariably divided anterior pair of triangles. Predominant type of structure of anterior section of M_1 asymmetric trifoliate, with poorly developed anteromedial fold (poorer than lateral ones) and deep fold behind that tends to isolate anterolateral triangle of paraconid; anterior unpaired loop distinctly deviates laterad. Middle pair of lobes of M_2 divided, fused on M_3 , sometimes fusion negligible. Structure of incisors similar to *M. chrotorrhinus*.

Composition of species: Subspecies not reported.

Distribution and zonal affinity: Northern part of forest zone of 317 plains and foothill regions of North America, from central Alaska up to southwestern corner of Hudson Bay; south up to 52° N, west up to central region of Canada (Alberta).

Evolution and phylogeny: Fossil remains known from Pleistocene of Alaska (mummy from permafrost grounds); found together with remains of preceding species in southern Appalachian mountains, i.e., almost 16° S and 1.5 km west of present limits of its range. Here, in one cave, remains of this species constituted more than 40% of total rodent remains (Guilday and Bender, 1960; Guilday *et al.*, 1964).

45. *Microtus (Microtus) longicaudatus* Merriam, 1888—
Long-tailed Vole (Figure 54)

Diagnosis: Body length up to 136 mm, tail up to 73 mm (up to 65% body length). Length of upper molar row up to 6.6 mm, lower molar row up to 6.4 mm; M_1 —3.05–3.1–3.2 mm.

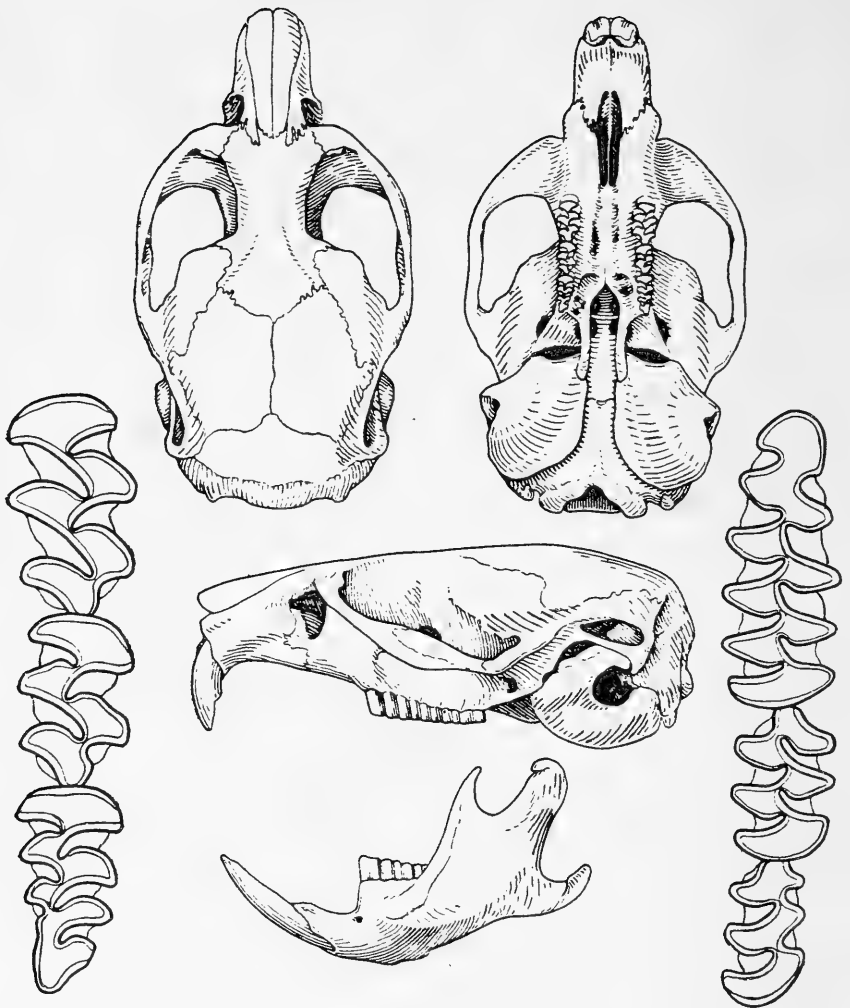
318 Dorsal surface dark, chocolate-brown to gray; ventral surface dark gray. Tail barely to distinctly bichromatic. Forefeet light-colored on dorsal surface. Hind feet with six plantar calluses. Chromosome number, $2n = 56$.

Skull relatively low compared to long brain case, without crests, with distinct groove-like depression along interorbital space. Dorsal profile slightly convex, uniformly slopes forward from posterior section of parietals. Auditory bullae uniformly rounded, almost without lateral flattening; mastoids slightly inflated. M^3 with three (both higher ones small) lateral denticles (sometimes rudiment of fourth also present) and four much larger medial ones. Structure of anterior section M_1 variable: from slightly to totally asymmetric trifoliate to highly elongate-rounded anterior unpaired loop. All lobes isolated on M_2 , fused in pairs on M_3 . Posterior end of lower incisor does not extend above dental foramen.

Composition of species: Hall and Kelson (1959) have listed 14 subspecies and one closely related insular species (?)—*M. (M.) coronarius* Swarth, 1911.

Distribution and zonal affinity: Inhabits foothills and mountain regions of western North America, from semidesert to alpine meadows at 3,000 m above msl, and from northern tip of the Cordilleras to latitude of California, west up to Monitor range and Sacramento hills.

Evolution and phylogeny: Fossil remains not known and, in absence of skull, these can hardly be conjectured. Affinities not known; relative small convergence with *Chionomys* discussed earlier.



317 Figure 54. Skull of American long-tailed vole (*Microtus longicaudatus* Merriam).

46. *Microtus (Microtus) californicus* Peale, 1848—
California Vole

Diagnosis: Body length up to 142 mm, tail up to 68 mm (up to 52% body length), length of upper molar row up to 7.7 mm, lower row up to 6.8 mm; M_1 —3.0, 3.3, 3.4 mm.

Dorsal surface dark, grayish-chocolate-brown; ventral surface dark gray. Tail indistinctly bichromatic. Forefeet light-colored on dorsal surface. Hind feet with five to six plantar pads. Chromosome number, $2n = 54$.

Skull similar to that of preceding species, slightly larger than skull of *M. agrestis*, and slightly higher than in *M. longicaudatus*, with a more sloping rostral section, and auditory bullae larger, distinctly flattened. M^1 , and especially M^2 , with additional lobes on posterior end. M^3 with three lateral denticles (some individuals with primordial fourth) and four medial. M_1 with tendency towards two folds (*M. transcaspicus* type), its anterior unpaired loop isolated from fused lobes by only narrow constriction, and latter shifted relative to each other at base. All lobes of M_2 isolated, fused on M_3 . Posterior end of lower incisor does not form alveolar knob on lower margin of dental foramen.

Composition of species: Hall and Kelson (1959) have listed 14 subspecies.

Distribution and zonal affinity: Montane forests of the Pacific coast of North America, approximately from 45° N up to latitude of California and height of 2,700 m above msl.

47. *Microtus (Microtus) montanus* Peale, 1848—
High-montane Vole

Diagnosis: Body length up to 145 mm, tail up to 69 mm (less than half body length), upper row of molars up to 7.5 mm, lower row—5.8–6.6–6.8 mm ($n = 6$); M_1 —2.8, 3.1, 3.2, 3.2, 3.3 mm.

319 Dorsal surface similar in coloration to that of preceding species; tail slightly more distinctly bichromatic. Forefeet darker on dorsal surface. Hind feet with six planter pads. Chromosome number, $2n = 24$.

Skull structure characterized by comparatively narrow rostrum in its anterior section, incisor alveoli narrow ventrally, distinctly prognathous upper incisors, and long lower incisors, which extend beyond upper margin of dental foramen and form alveolar knob on lateral surface of articular process. M_1 – M_2 without additional structures on posterior end. M^3 with three lateral and four (rarely three) medial denticles. M_1 with tendency toward isolation of anterolateral lobe of paraconid; anteromedial lobe broadly fused with unpaired loop. Triangles of M_2 isolated, of M_3 fused.

Composition of species: Hall and Kelson (1959) have listed 18 subspecies.

Distribution and zonal affinity: Open terrain of foothills and mountain regions of North America, from British Columbia up to California, and almost up to 110° E eastward, at 900 to 3,000 m above msl.

48. *Microtus (Microtus) mexicanus* Saussure, 1861

Comparatively small (body length up to 150 mm) and short-tailed (tail length less than double foot length). Range limited; mountains of northern Mexico and adjoining parts of Arizona and New Mexico in the USA. Eleven subspecies have been listed; *M. fulviventer* Merriam, 1898 is considered a closely related species.

49. *Microtus (Microtus) towsendii* Bachman, 1839

A rare species from the western parts of America; range limited to northern part of the Cascade mountains, from Vancouver Island up to northern part of California. Six subspecies have been recorded (Hall and Kelson, 1959). Chromosome number, $2n = 50$.

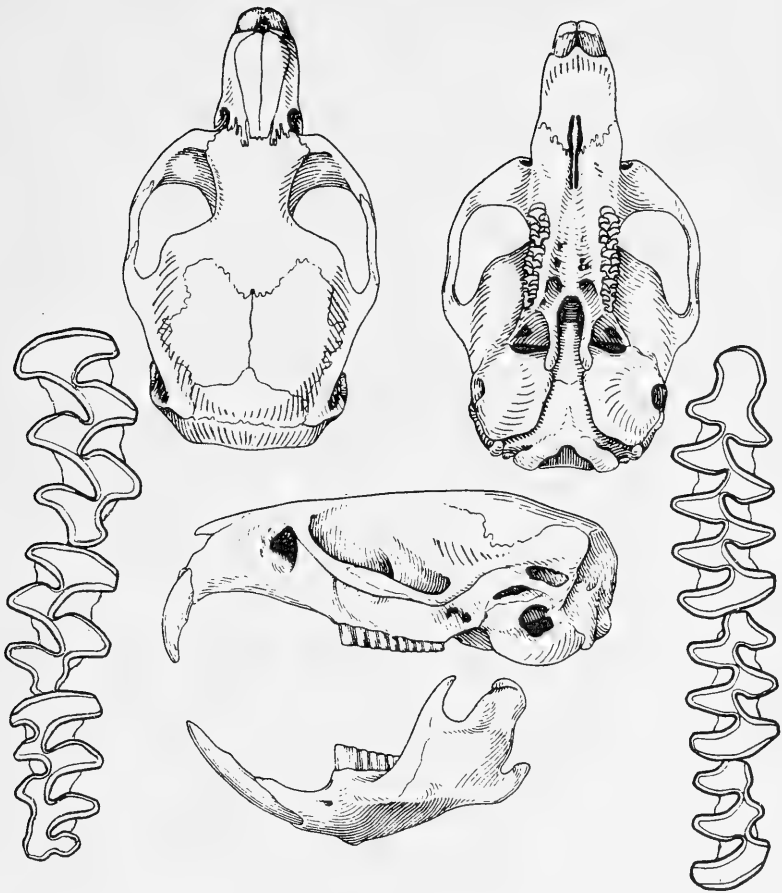
Subgenus *Aulacomys* Roads, 1894—Medium-sized
Long-tailed Voles (Figure 55)

Diagnosis: Medium-sized, long-tailed voles, adapted to a semi-aquatic life style. Pelage long, dense, and soft; guard hair not less developed than in some large species of the subgenus *Microtus* that inhabit marshy biotopes. Relative size of eyes not known. Pinna reduced and hidden in pelage; antitragus large.

Skull with relatively broad, somewhat flattened, and slightly angular brain case; interorbital space relatively broad, its longitudinal crest absent or poorly developed. Incisor alveoli characteristically reduce sharply (not gradually as in *Arvicola*) in posterior direction. Articular process of dentary reduced, molars with long roots, only slightly shorter than in *Microtus*. Paraconid section of M_1 with two incomplete lobes, opposite triangles at its base isolated. Anterolateral denticle (lobe of second pair) may be almost isolated from anterior unpaired loop. Anterolateral denticle absent on M_3 .

This subgenus differs from other American microtines in small auditory bullae, elongate diastema (especially upper one), reduced incisors of dentary, and fully curved upper incisors directed forward (prognathous). Chromosome number, $2n = 56$.

Composition of subgenus: One species—*M. (A.) richardsonii* De Kay.



320 Figure 55. Skull of American water vole [*Microtus (Aulacomys) richardsonii* De Kay].

320 *Age and distribution:* Fossil remains not known. Primarily a montane-forest form living in coniferous forests in northern part of the Rocky Mountains in southwestern Canada and northwestern USA, south up to the central part of Utah, and usually not below 1,500 m above msl, spreading into alpine belts.

Taxonomic notes and evolution: The inclusion of *Aulacomys* by most contemporary American mammalogists in *Arvicola* as a subgenus reflects the original idea of the author of the species. Researchers have recently found adequate confirmation of similarity

of structure of male genitalia (Hooper and Hart, 1962). Incidentally, most American investigators usually indicate that they lacked comparative material for the European genus. Zimmermann (1956a) was in the opposite camp, but shared this view. In any event, contrary to Zimmermann's interpretation, the combination of adaptive features of *Aulacomys* for a semiaquatic life style comprises a different set of features than found in *Arvicola*, and identical but not perfected specializations only slightly exceeding the limits of adaptation to life in biotopes with high humidity, as seen in many species
 321 of the subgenus *Microtus*. At the same time, these do not contradict opinions regarding the subgeneric independent status of the American species (Hall and Kelson, 1959). Inclusion of Palearctic voles from the *fortis* group under the subgenus *Aulacomys*, as was done by Ellerman (1941), following the example of Thomas, cannot be considered reasonable.

Subgenus *Chilotus* Baird, 1858—Oregon Voles

Diagnosis: Medium-sized, with short or moderately long tail. Degree of adaptation to semifossorial life similar to that of Palearctic members of *Sumeriomys*. Pelage short and soft; guard hair thin and sparse. Size of eyes not reported. Pinna short, slightly isolated, and covered with hair; structure of lobes not known. Chromosome number, $2n = 17$ (females) and 18 (males).

Skull with broad, flattened but rounded brain case. Interorbital space comparatively broad, often with a groove-like depression; longitudinal crest not developed in all forms. Relative length of articular process and height of molar crowns not known. Paraconid section of M_1 with two incomplete lobes; lobes at base isolated. Lateral lobe of second (anterior) pair may be isolated from fused medial one and anterior unpaired loop. Anterolateral denticle of M_3 small or absent.

Composition of subgenus: One present-day species—*M. (C.) oregoni* Bachman, 1839.

Age and distribution: Fossil remains not known. Inhabits open meadows and meadow-steppe regions of foothills and mountains in western North America between 40 and 49° N.

Taxonomic notes and evolution: Subgeneric status is almost universally accepted by American mammalogists. Among Russian mammalogists, this view is held by Ognev (1950) who, however, while enlarging on the not fully convincing opinion of Hinton (1926), also included under it Palearctic voles of the subgenus

Sumeriomys. Extreme views are held by Matthey (1957) on the one hand, and by Hooper and Hart (1962) on the other. The former notes $2n = 17$ in males of *M. oregoni* XO heterochromosomes; such a number has never been confirmed in any of the existing members of microtines. This compelled Matthey to consider the Oregon vole a member of a different genus. The other two authors have proposed that there is no basis for considering this species a member of even an independent subgenus. On the contrary, they propose that *Microtus arvalis* and *M. agrestis* should be included under independent subgenera. Most probably, in the present case, as in the case of several other Nearctic microtines, only ecological parallelism is observed among the high-montane forms of Palearctic members of *Sumeriomys*. However, a different set of skull characters—presence of an interorbital crest, flattening of auditory bullae, simple structure of M^3 —like the unique structure of the chromosome apparatus, make a subgeneric separation of this group fully valid.

Subgenus *Herpetomys* Merriam, 1898—Guatemala Voles

Diagnosis: Medium-sized, with moderately long tail. General adaptation to semifossorial life style probably developed to a greater degree than in *Microtus*. Pelage long and soft. Pinna large, hidden in pelage. Relative size of eyes and details of structure of ear lobe not described. Unlike in all other microtines, inguinal pair of nipples absent.

Proportions of brain case similar to *Microtus* but, probably, less angular. Width of interorbital space moderate, its vertical crests fused to form longitudinal one, albeit over short distance. Relative length of articular process and crown height of molars not known. Paraconid section of M_1 with one lobe; other lobes fused or incompletely isolated; second fold barely perceptible. Anterolateral denticle of M_3 absent.

Composition of subgenus: One extant species—*M. (H.) guatemalensis* Merriam, 1898.

Age and distribution: Fossil remains not known. Occupies isolated, probably relict, areas of the range in mountains of western Guatemala about 3,000 m above msl, and thus the southernmost member of this subfamily.

Taxonomic notes and evolution: The surraspecific taxonomic status of this subgenus is under debate elsewhere. Most American authors, including those who studied the genitalia (Anderson,

1960; Hooper and Hart, 1962), find no basis for separating it as an independent genus. Hinton (1926), as in the case of the next genus, proposes its possible origin from the American rooted-molar voles *Phenacomys*; moreover, *Herpetomys* is considered a vole that evolved more in the direction of *Microtus*. We may note that some American species of the subgenus *Pitymys* as well as *Pedomys* (including extinct ones) have lower molars at a similar stage of differentiation.

Subgenus *Orthriomys* Merriam, 1892—Mexican Voles

Diagnosis: Large voles, with long tail. General adaptations in external characters to a semifossorial life style probably no less than in *Microtus*. Pelage soft. Pinna long, slightly hidden in pelage. Other comparative features of external anatomy not described.

Brain case comparatively low and broad, its crests comparatively poorly developed, including interorbital. Relative length of articular process and crown height not known. Paraconid section of M_1 with one fold and that, too, incomplete; anterior unpaired loop fused at least on medial side. Anterolateral lobe of M_3 barely perceptible.

Composition of subgenus: One present-day species—*M. (O.) umbrosus* Merriam, 1893.

Age and distribution: Fossil remains not known. Isolated and, probably, relict, in mountain area of central Mexico (known only from Mount Zempoala at 2,500 m above msl).

Taxonomic notes and evolution: As with *Herpetomys*, most authors consider this a subgenus, although compared with *Herpetomys*, it appears more an independent genus (simplification of "Arvicola" structure of M^3 , small auditory bullae, and so forth). Its possible affinity with *Phenacomys* was discussed under the preceding subgenus.

13. Genus *Lasiopodomys* Lataste, 1887—Brandt's Voles

Description: Body length up to 150 mm. Color from light, sandy-gray, to dark, brown. Average length of tail about one-fifth trunk, and not longer than 30%. Pelage fairly dense, hairs variable in length; loose tuft of long terminal hairs may be present.

Eyes large, larger than in other genera of the tribe, and within the subfamily larger only in *Eolagurus*. Pinna small, with reduced but rather densely pubescent lobe, covered toward front with rather

sparse tuft of long hairs. Helix well-developed, antitragus reduced, not covering outer meatus of auditory passage, or absent. Upper alae nasalis barely isolated from middle lobe of lower alae nasalis; distance between outer ends of former about equal to combined width of middle lobes. Marginal lobes of lower alae nasalis poorly expressed. Narial pit half-closed; external opening in form of fairly deep, narrow slit. Length of fused part of upper lips about equal to double width of upper incisors. Upper labial (diastemic) flaps rectangular, with long region of contact, with not very dense, comparatively short hairs. Two anterior ridges of bony palate entire, posterior one interrupted. Postpalatal folds four to five. Maxillary and mental vibrissae reduced, genal vibrissae absent. Carpal vibrissae present.

In relative length, limbs, as in *Microtus*, reduced but relatively broad, broader than in other members of the tribe (except for lemmings). Hind feet elongate. Palms glabrous, soles may be covered with sparse hairs almost up to base of digits. Digital pads large, especially on forelimbs. Carpal calluses two, metatarsal also two, inner one distinctly smaller than outer. Forelimbs with almost equal-sized 3rd and 4th digits, both longer than 2nd. Third digit of hind limbs longer than others, 4th digit about equal to 2nd. Forelimbs with small acute claw on reduced pollex (similar to *Neodon*); length of claws on remaining digits much greater than half digital length. Claws on hind limbs also elongate but do not reach half digital length. Claws of all limbs sharp, slightly curved.

Skull in general outline resembles that of *Microtus*. Dorsal profile with a distinct dip at base of zygomatic arches, without depression in interorbital region. Length of brain case about equal to its width or slightly greater, with flat or slightly convex dorsal surface and distinctly demarcated lateral surfaces. Frontoparietal crests form well-developed longitudinal crest in interorbital space, or such absent. Skull profile in zygomatic section more or less rounded, slightly convergent posteriorly. Orbit markedly shifted posteriorly, its plane forming an angle of about 40° with horizontal plane. Masseteric [= zygomatic] plate of maxilla relatively high and quite wide, its plane with sagittal forming angle that is slightly larger than mean for tribe and close to mean value for subfamily. Auditory bullae not enlarged, their walls consisting of rather thick, loose spongy bone. Mastoids slightly convex. Short and broad articular process of dentary very characteristic.

Molar row moderate in length. M_1 relatively short (shorter only in *Myopus*), M^3 moderately long. Molars rootless, with relatively

high crowns. Enamel well-differentiated in thickness. Difference in size of lateral and medial triangles of masticatory surface seen only in lower molars. Posterior section of M^1 – M^2 with elongate “heel,” but without additional structures. Posteromedial lobes of these teeth have lost triangular shape typical of majority of voles and look like narrow segmentoid fields (archaic and correspondingly juvenile character of many microtines). Fused lobes opposite, persistent only in M_3 . Unlike most other voles, all lateral triangles reduced on this tooth and lobes narrow, elongate. Tooth only slightly shifted in tooth row (more often only anterior section), but its radical section is highly deflected posteriorly. Posterior section of M_3 alveolus well-isolated and lateral section may protrude slightly beyond margin of jaw. Crowns of upper incisors long, those of lower incisors moderately long. Posterior end of lower incisor does not form distinct alveolar knob on lateral surface of articular process, but may protrude slightly beyond its posterior margin. Both pairs of incisors abruptly curved, their facing angle moderate.

Characteristic features of limb bones not studied.

Composition of genus: Two extant species—*L. brandti* Radde, 1852 and *L. mandarinus* Milne—Edwards, 1871. An extinct species has also been described from Choukoudyan I: *L. brandtioides* Young, 1934; however, its independent species status was not confirmed in studies by Erbaeva (1970).

Distribution and zonal affinity: Feather-grass steppes and meadows in mountains and plains of southern Trans-Baikal region, northern Mongolia, from southwestern Hangai to western foothills of Great Hingan, western and northwestern China, and Korea. Fossil remains with identical structure of M_1 have been found in the Late Pleistocene in Irtysh, which possibly indicates that earlier distribution of species of this genus north of the Zaisan gateway as part of the erstwhile species-rich Mongolian faunal “tongue”. In Trans-Baikal, the range boundary shifted slightly south and east during the Holocene (Erbaeva, 1970).

Evolution and phylogeny: Fossil remains are known from the Early Pleistocene in Trans-Baikal and the Middle Pleistocene in China (fauna of synantropic layers). Independent generic status is not recognized by all authors. Some, including all Soviet mammalogists, consider Brandt’s voles only a subgenus of *Microtus*, while others include them under *Phaiomys* (= *Neodon*). Nevertheless, it may be concluded from a comparative assessment of their distinguishing features that *Lasiopodomys* includes two

rather sharply differentiated species representing the remnants of an ancient group, possibly abundant in the past. In toto, these characteristics form an evolutionary aspect no less significant than in other genera of Microtini. The undoubted affinities of *Neodon* with the *blythi* group have not been confirmed by paleontological data thus far. Separation of *L. mandarinus* into an independent genus, *Lemmimicrotus* Tokuda (Tokuda, 1941), lacks sufficient evidence.

KEY TO SPECIES OF GENUS *LASIPODOMYS*

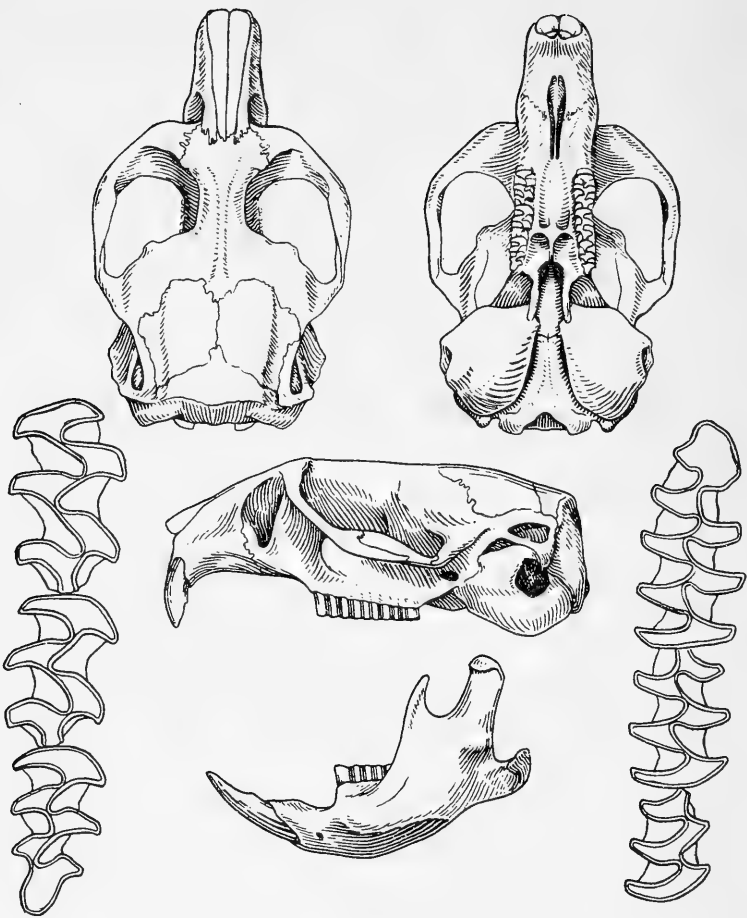
- 1 (2). Color of dorsal surface with predominance of light, ochreous-sandy tones. Longitudinal crest present in interorbital space in fully mature animals. Incisor alveolus much longer than combined length of M^1-M^2 *L. brandti* Radde.
- 2 (1). Color of dorsal surface with predominance of dark, grayish-brown tones. Interorbital space without longitudinal crest even in older animals. Incisor alveolus, even if longer than total length of M^1-M^2 , only slightly so
 *L. mandarinus* Milne-Edwards.

1. *Lasiopodomys brandti* Radde, 1852— Brandt's Vole (Figure 56)

Diagnosis: Body length up to 150 mm in large forms and up to 130 mm in small forms; tail up to 35 mm in long-tailed forms and up to 26 mm in short-tailed forms (on the average, 15 and 25% respectively, and not more than 29%). Length of upper row of molars 6.1–6.6–7.1 mm, lower row 6.1–6.5–7.1 mm; M_1 —2.7–3.0–3.1 mm.

Color light, with sandy-yellow tones of varying intensity dominant. Tail mono- or slightly bichromatic. Posterior part of feet rather densely covered with hairs. Chromosome number, $2n = 34$.

Dorsal profile of skull slightly convex, brain case slightly inflated. Longitudinal crest forms in interorbital space with age. Post-orbital processes small but distinctly isolated. Incisor alveolus comparatively long, auditory bullae small, mastoids not inflated. Anterior unpaired loop of M_1 with poorly developed and disappearing anteromedial depressions. M_3 comparatively long, also heel of M^3 , its medial and lateral lobes often isolated. Upper incisors distinctly opisthodont. Posterior end of lower incisor comparatively slightly shifted laterad, and its alveolar knob slightly raised if it extends to notch of articular process.



324 Figure 56. Skull of Brandt's vole (*Lasiopodomys brandti* Radde).

Composition of species: Two present-day subspecies—*L. b. brandti* Radde, 1852 (Trans-Baikal region, western part of northeastern China and Mongolia west up to about 102° E) and *L. b. hangaicus* Bannikov, 1948 (western Mongolia, southern and western Hangai).

326 *Distribution and zonal affinity:* Correspond to that in northern part of range of genus.

Evolution and phylogeny: Same as for genus. Dentition typical for extant species, without significant change since the Middle

Pleistocene, although it is possible that variability of structure in the anterior section of M_1 in extinct forms was more than in present ones (Erbaeva, 1970, 1976).

**2. *Lasiopodomys mandarinus* Milne-Edwards, 1871—
Chinese Vole**

Diagnosis: Smaller than preceding species. Body length up to 115 mm, tail up to 28 mm (on the average, about 20% and not more than 30% body length). Length of upper molar row 5.6–6.0–6.8 mm, lower row 5.7–6.0–6.04 mm, M_1 —2.6–2.8–3.0 mm.

Color dark, grayish-chocolate-brown. Tail slightly or distinctly bichromatic. Posterior part of feet semiglabrous. Chromosome number, $2n = 47-48$.

Dorsal profile of skull straight, brain case flattened. Interorbital space without crest. Postorbital process slightly isolated. Incisor alveoli reduced. Auditory bullae larger than in preceding species, mastoids enlarged. Anteromedial depression on anterior unpaired loop of M_1 better developed and more persistent. M_3 reduced, also heel of M^3 , its lateral and medial triangles often fused. Upper incisors distinctly prognathous. Posterior end of lower incisor distinctly directed laterad and alveolar knob extends to notch of articular process.

Composition of species: Four to five poorly studied and barely distinguishable extant subspecies: *L. m. mandarinus* Milne-Edwards, 1871 (China: Nansi Province, except northwestern part, northern part of Hanshu and Shansi Provinces); *L. m. johannes* Thomas, 1910 (northwestern part of Shansi Province; possibly, a weaker variant); *L. m. faecius* Gl. Allen, 1924 (northern part of Gehe Province; possibly, not differing from type); *L. m. kischidae* Mori, 1930 (central and southern part of Korea); and *L. m. vinogradovi* Fetissov, 1936 (Trans-Baikal region, northeastern Mongolia).

Distribution and zonal affinity: Steppe and meadow-steppes near mountains and plains, up to 1,300 m above msl in Mongolia and 3,000 m in northwestern China. It is not clear whether the Trans-Baikal–Mongolian and Chinese–Korean parts of the range are not contiguous. The species is sufficiently well-known only from southwestern parts of northwestern China (*Microtus jecholensis* Mori, 1939 = *Lasiopodomys m. mandarinus* Tokuda, 1941). Under the name of *Microtus dolichocephalus* Mori, 1930 from the central part of northeastern China, probably a young specimen of *Microtus fortis* Büchner has been described.

Evolution and phylogeny: Fossil remains are not known, and known isolated teeth and skull fragments bearing them cannot be reliably distinguished from those of *Lasiopodomys brandti*. The Chinese vole differs significantly from Brandt's vole; these differences are no less than, for example, between *Chionomys gud* and *C. roberti* or between some species of the subgenus *Pitymys*. This species compelled mammalogists to suggest the desirability of its separation from the genus *Lasiopodomys* (Allen, 1940), which was ventured rather unsuccessfully by Tokuda (1941). I suggest that such differences are largely due to the fact that in the composition of the genus only its extreme ecological or, accordingly, morphological variants were retained, which are not related to each other through transitional forms today.

14. Genus *Chionomys* Miller, 1908—Snow Voles

Description: Body length up to 160 mm. Color from gray, pale and brownish-gray, to dark brown. Tail, on the average, at least half trunk length, covered with stiff, short, and rather sparse hairs, and without terminal brush. Eyes small. Pinna very small, covered with hair, to large and distinctly visible, with moderately pubescent lobe. Entire pinna or only its base with dense tuft of hairs toward front. Helix well-developed, antitragus large, broadly triangular in shape. Upper alae nasalis isolated from middle lobes of lower alae nasalis by distinct and narrow groove. Maximum distance between outer ends of former not more than 1.5 times greater than combined width of latter at middle lobe. Narial pit half-closed, external skin ridge low. Length of fused part of upper lips about 1.5 times combined width of upper incisors. Upper labial (diastemic) flaps rectangular, with rather long region of contact, densely covered with hairs. All three palatal ridges of bony palate entire, although posterior one strongly constricted in middle. Postpalatal folds five. Maxillary vibrissae very long, the longest reaching scapular region, and form tactile field that is larger than in other members of the tribe (Kratohvil, 1956). Genal and mental vibrissae reduced. Carpal vibrissae present.

Forelimbs moderately long, hind limbs notably elongate (up to 56% trunk length). Fore- and hind feet long but narrow, relatively narrower than in other mocketines. Palm and sole glabrous or sparsely pubescent only in posterior part. Calluses on plantar large, papillate. Carpal calluses two, metatarsal also two, inner one smaller than outer. Third digit of all limbs longest, 4th digit longer than

2nd. Forelimbs with highly reduced pollex with small flat claw. Claws of other digits shorter than half digital length. Structure same on hind limbs, claws only slightly longer than those of forelimbs. Claws of all limbs sharp, slightly curved.

Skull, unlike that of other members of tribe, broader and flatter. Dorsal profile at base of zygomatic arches forms variable dip; small depression present in interorbital region. Length of brain case about equal to its width or greater, its dorsal surface flattened or poorly convex, lateral surfaces rounded. Frontoparietal crests weak, usually only close-set in interocular space, and only in old individuals may form low, short crest. Skull profile in zygomatic section more or less uniformly rounded, rarely somewhat divergent posteriorly. Orbit medium in size, its plane forms angle of about 35° with horizontal; size close to average for subfamily, but slightly smaller than in other genera of tribe. Masseteric [= zygomatic] plate of maxilla relatively low (lower only in *Pitymys*), medium in width. Dihedral angle formed by it with sagittal plane of skull within average limits of subfamily, but lowest limits of tribe. Auditory bullae medium in size or enlarged; mastoids bulge slightly; bulla cavity mostly filled with large-celled spongy bone.

Relative size of teeth small, smaller than in other genera of tribe. M_1 relatively short, M^3 long or moderately so. Molars rootless, with moderately high crowns. Enamel poorly differentiated in thickness (thinner only in depth of folds). Difference in size of lateral and medial triangles of masticatory surface, if present, seen only on lower molars and on M^3 . Tendency toward additional structures on posterior end of anterior upper molars observed; however, they rarely assume the shape of small denticles. Fused opposite triangles present on M_3 , rarely in anterior section of M_2 . M_3 not shifted lingually and aligned with M_1 – M_2 ; its alveolus isolated only in lower section and does not protrude beyond margin of jaw. Crowns of upper incisors relatively large, of lower incisors moderate. Posterior end of lower incisor does not form alveolar knob on lateral surface of articular process. Facing angle of incisors moderate; upper incisors rather abruptly and lower incisors moderately curved.

Skeleton of limbs characterized by relatively narrow diaphyses of tubular bones. Possibly because of this, height of humerus relatively low at level of large trochanter, and that of femur at level of third trochanter. Length of inner epicondyle of humerus smaller than in other microtines, that of ulnar process smallest in tribe.

Composition of genus: Three extant species—*C. nivalis* Martins, 1842; *C. gud* Satunin, 1900; and *C. roberti* Thomas, 1906. Ellerman (1941) divided them into two supraspecific groups. One group comprises only *C. nivalis*, with a simple structure of M^3 , and the second group the other two species.

Extinct forms—*Microtus nivalinus* Hinton, 1923; *M. nivaloides* F. Major, 1902; and *M. subnivalis* Pasa, 1949. The first two are most probably “aggregate species” and the last one, as well as Late Pleistocene remains, undoubtedly belongs to *Chionomys*.

Inclusion of the North American high-montane vole *Microtus* (*M.*) *longicaudatus* Merriam, 1888 (Anderson, 1960) under the genus *Chionomys*, appears at first glance, sufficiently justified. However, several differences, for example, a much weaker development of upper labial vibrissae, larger molar crown height, and differences in structure of mandibular rami, are conspicuous, pointing to a common plan of structure typical of *Microtus* species.

Distribution and zonal affinity: Inhabit mountain regions, both rocky outcrops and taluses, as well as coastal biotopes and marshy forest meadows, mountain steppes, subalpine and alpine belts from 125 m (France, valley of southern Rhone) up to 3,500 m above msl. Mountains of the so-called Alpine folds in southern and southeastern Europe from central part of the Pyrenees Peninsula (Castel mountains) up to the Caucasian Isthmus, Kopetdag, and western Iran (central part of Zagros mountains). South up to western and central Turkey, Syria, and Libya. In the Pleistocene, during periods of glaciation and humid climates, boundaries of range changed. During periods of natural Alpine snowy conditions, snow voles were included in Late Pleistocene (Würm) lemming and mixed faunas of Western and central Europe, spreading north up to the British Isles, where they later became extinct. Traces of shift in range boundaries were retained in the form of isolated areas in the mountains of central Spain, Talysh, and Kopetdag, including other small areas, for example, in southeastern France, northern Italy (Malec and Storch, 1964), and in the USSR in Pyatigorye and several places in the lower part of the forest belt of the Great Caucasus range, where isolated populations were found from the subalpine and alpine populations in the Recent epoch.

Evolution and phylogeny: Fossil remains of voles with structure of M_1 similar to that of present-day *Chionomys* are known from the 329 Early Pleistocene of many European localities (the Late Tamansk and Early Tiraspol' faunas). However, the same type of M_1 structure is also found sometimes in the series of fossils of *Allophaiomys*

and *Microtus ex gr. oeconomus* of the same geological age, and the latter also in *M. guentheri* (Tchernov, 1968b). In the USSR, such discoveries are known from the western part of the Russian plains as well as from Trans-Ural region. As indicated above, Topachevskii (1965) in the USSR and Chaline (1966) in France simultaneously and independently concluded that the ancestors of the genus *Microtus* in a wider sense (including also *Chionomys*) should be searched within the limits of the genus *Allophaiomys*; the last author continued to develop his ideas later also (Chaline, 1972).

Neither the generic nor the subgeneric independent status of *Chionomys* is recognized by all mammalogists (Ellerman and Morrison-Scott, 1951). Moreover, some claim there is not sufficient basis for combining species with simple (*C. nivalis*) and with complex structure of M^3 (other two species) in a single group. In my opinion, such a view reflects formal classification, without considering the variability of this character in the first species, nor the total features that characterize the genus as a whole. The latter results from insufficient knowledge of scientists in other countries about the material available in Russian fauna. In my view, *Chionomys* is a quite distinct group of high-montane species of the tribe Microtini, forming a unique rock "life form" analogous to *Alticola* (tribe Lagurini) and *Dolomys* (tribe Pliomyini). One of its species from the *gud-roboti* group had probably secondarily occupied the ecological niche of the water vole and adapted to life among marshy meadows adjoining taluses saturated with meltwater and intersected by alpine rivulets. Later, it descended together with the water vole even into river valleys of forest belts, where it remains confined near water, more often in large areas of poorly grass-covered alluvial deposits.

KEY TO SPECIES OF GENUS *CHIONOMYS*

- 1 (4). Soft, silky pelage on dorsal surface predominantly light-colored, with brownish-gray tones. Tail mono- or slightly bichromatic, with comparatively dense hairs covering horny scales.
- 2 (3). Body length up to 160 mm. Tail slightly bichromatic, with diffuse stripe along dorsal surface. M^3 longer than M^1 , with more than three denticles on each side. Anterior unpaired loop of M_1 fused with anteromedial lobe . . . *C. gud* Satunin.
- 3 (2). Body length up to 130 mm. Tail light-colored, monochromatic. M^3 shorter than M^1 , with no more than three denti-

- cles on each side. Anterior unpaired loop of M_1 isolated from part of tooth located behind it *C. nivalis* Martins.
- 4 (1). Comparatively rough pelage on dorsal surface predominantly dark, with brown or brown to chocolate-brown tones. Tail sharply bichromatic, covered with comparatively sparse hairs, through which horny scales are distinctly visible
 *C. roberti* Thomas.

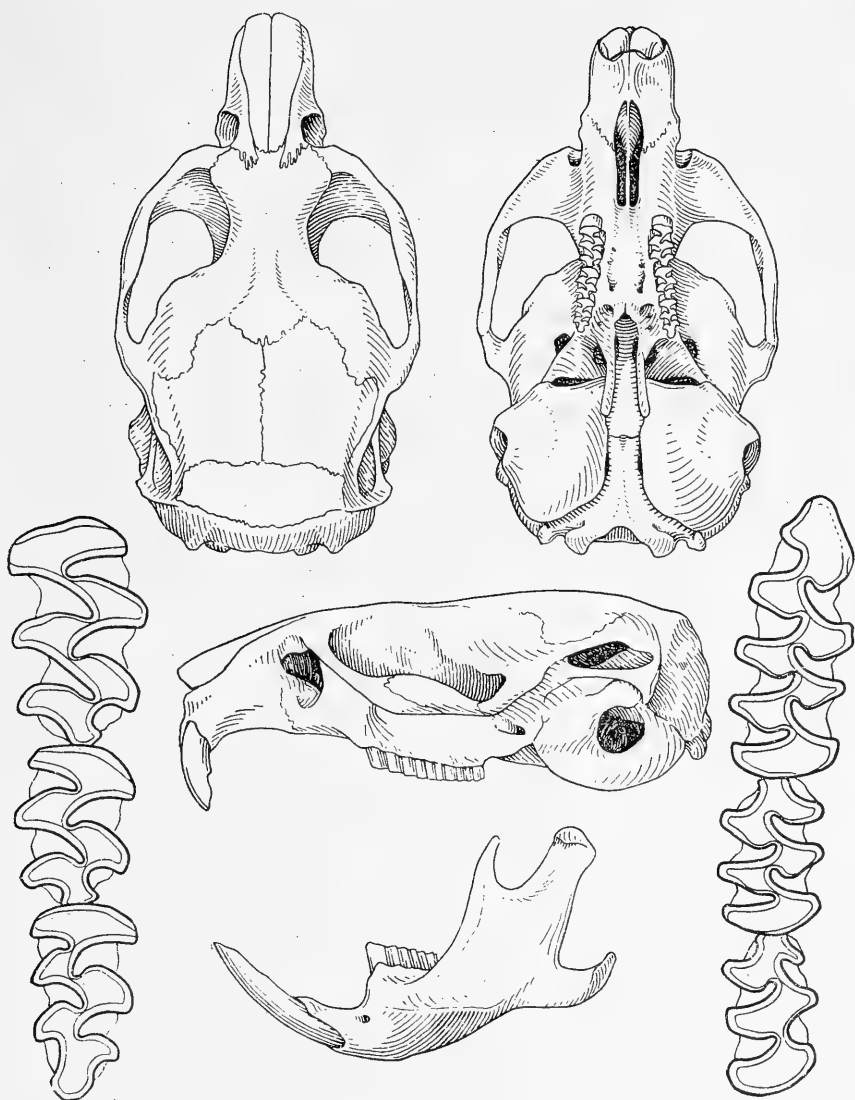
1. *Chionomys nivalis* Martins, 1842—European Snow Vole (Figure 57)

Diagnosis: Body length up to 150 mm in large forms and up to 130 mm in small forms, tail up to 70 and 60 mm respectively (up to 65% in long-tailed forms and 55% in short-tailed forms, average
 330 about 50%). Length of upper molar row 5.5–7.6 mm, lower row 5.6–7.6 mm; M_1 —2.5–3.05–3.4 mm.

Pelage varies from ash-gray to lighter, pale grayish. Tail usually with light-colored dorsal surface, mono- or slightly bichromatic, with comparatively dense hairs through which scales are barely visible, or not visible. Chromosome number, $2n = 56$ (Western Europe).

Dorsal profile of skull with comparatively weak depression in interorbital region, brain case dorsally flattened, and “rostral slope” well-expressed. Zygomatic arches comparatively poorly isolated posteriorly, their profile angular. Auditory bullae enlarged; lower ends distinctly extend beyond plane of masticatory surface of molars;
 331 skull width in auditory region comparatively large. Incisor alveoli just barely narrows in posterior third. Angular process of dentary comparatively long, narrows at base. Upper incisors narrow, short, and straight. M^3 reduced, its relative length in middle not more than 30% length of molar row; in most geographic populations, the greater majority of individuals have three lateral and three medial denticles and, correspondingly, two medial folds. M_1 relatively long, its middle length about 45% length of molar row. It lacks an isolated anterior (4th) lateral denticle; anterior unpaired loop rounded-rectangular; barely perceptible depression present on its anterolateral margin, that rapidly disappears with wear. Both anterior folds often markedly shifted at apices relative to each other.

Composition of species and variability: Ellerman (1941) included 17 forms under the *nivalis* group, and Kratochvil (1956) 15. *C. n. abulescens* Agacino, 1936 has been reported from Russian fauna (Gromov *et al.*, 1963). The following forms are best known: *C. n. abulescens* Agacino, 1936 (central Spain); *C. n. aquitanicus*



330 Figure 57. Skull of European snow vole (*Chionomys nivalis* Martins).

Miller, 1908 (French Pyrenees); *C. n. lebrunii* Crespon, 1844 (= *leucurus* Gerbe, 1852) (southwestern French Alps); *C. n. nivalis* Martins, 1842 (Swiss Alps); *C. n. wagneri* V. and E. Martino,

1940 (Slovakia; form poorly distinguishable from type); *C. n. mirchanreini* Schäfer, 1935 (western Carpathians); *C. n. malvi* Bolkay, 1925 (Yugoslavia, except Slovenia; possibly, only form living in the Balkans) (Ondrias, 1966); *C. n. radnensis* Ehik, 1942 (Radnae mountains in Hungary); *C. n. aleco* Martino and Paspalev, 1952 (Bulgaria, Vitosha mountains); *C. n. ulpius* Miller, 1908 (southern and eastern Carpathians, including western Ukraine); *C. n. olympus* Neuhäuser, 1936 (northwestern Turkey); *C. n. syriacus* Brands, 1827 (= *hermonis* Miller, 1908) (Syria, Lebanon; the former, possibly not *Chionomys*); *C. n. loginovi* Ognev, 1950 (northwestern part of Great Caucasus range); *C. n. trialeticus* Shidlovsky, 1919 (western Trans-Caucasus); and *C. n. dementievi* Heptner, 1939 (Kopetdag, possibly northwestern Iran).

The subspecific affinities of *C. nivalis* from eastern Trans-Caucasus and western Iran (Zerd' nukh Massif in Zagross range) are not known, nor the affinities of *C. n. ponticus* Miller with the Trans-Caucasian *Chionomys*. There is absolutely no doubt that the actual number of subspecies is less than listed. However, the species does form local populations that are variably isolated. A study of the morphological and other features of members of these populations is possible only on large material, using a single method, and with necessary consideration of differences in age groups. This group also requires separation of characters of vertical (zonal) and horizontal variability, as was rightly pointed out by Vereshchagin (1959), who doubted his own results regarding the direction of variability of this and the next species in the Caucasus. Study of the isolated, presently low density populations would be of particular interest.

Anyhow, within the limits of the main range, we can indicate some clinal variability for size or relative length of tail, M^3 or M_1 , and structural details of the latter. Thus, the largest size is found in snow voles of the southern and eastern Carpathians; animals from the Great Caucasus range and from Kopetdag are smaller than others. Caucasian and western Carpathian animals have the longest tail, and those from southwestern Turkey (Felten, Spitzenberger and Storch, 1971), and from Kopetdag are lightest in color. A tendency toward structural complexity of M^3 has been noted for different populations. Thus, it has been indicated from the Bulgarian subspecies (Peshev, 1969) as well as for the subspecies *loginovi*; the frequency of such animals probably increases eastward in the European part of the range. The situation in the Caucasus-Kopetdag part is probably reversed: structural complexity is observed in areas where *C. nivalis* is sympatric with *C. gud.*

Distribution and zonal affinity: Same as for genus.

Evolution and phylogeny: The most ancient reliable discovery of remains of *Chionomys* of the *nivalis* group is from the Early Pleistocene deposits of northern Italy (environs of Verona) from where *Chionomys subnivalis* Pasa, 1949 has been described in the composition of *Microtus-Allophaiomys* fauna containing late *Mimomys*. The well-preserved skull leaves no doubt about the correctness of identification of the genus (Pasa, 1949, Plate VIII, Figures 1–4; condylobasal length of skull 25.5 mm, length of upper molar row 6.2 mm). However it is not clear whether the discovery from a separate site of a mandibular ramus and isolated M_1 from two other localities belong to the same species, especially the former (*loc. cit.*, Figure 5). The independent species status of the form described is also not sufficiently convincing.

Remains from the upper freshwater strata of western Runton, England (Late Kromer—end of Ancient Pleistocene) are closer than others in geological age to the northern Italian find. *Microtus nivaloides* F. Major, 1902 was described from an isolated M_1 . The author's diagram of M_1 (Major, 1902, Figure 18) contains the following legend: "*M. nivaloides* sp. nov. resembles *M. nivalis*, but smaller, and anterior loop more developed; left side and roots not present. . . ." Length of holotype, judging from dimensions, about 2.7 mm, i.e., within the limits of the present-day species. The anterolateral denticle of the paraconid is actually more developed than in the M_1 of *M. nivalis*, at least in adult individuals; however, such a structure is also found in young specimens and therefore can be considered an archaic trait subject to reduction in time. The series of teeth from the same locality for which diagrams were later provided by Hinton (1926, Figure 65, 15–21), are generally quite similar to the diagram of the holotype given by Major, but reveal no differences from *M. nivalinus* Hinton, 1923 described from the same deposits (*loc. cit.*, 22–28). According to Hinton, these species differ from the present-day species only in smaller size. It is noteworthy that the affinity of both forms from this locality is exactly the same as that of *M. nivalis* and *M. malei* Hinton (foss.) from the Middle Pleistocene deposits of England; the absence of differences between them was recognized even by the author himself (Hinton, 1910b).

The considerable difference in structure of the anterior section of M_1 , displaying transitions in fossil material from variants typical not only of *C. nivalis*, but also of *Microtus oeconomus*, and among extinct forms, *M. malei* and *Allophaiomys*, does not permit

us to determine with confidence the species status of these fossils. Therefore, Russian as well as many foreign mammalogists often use "open" nomenclature, designating the Early to Middle Pleistocene forms *Chionomys* ex gr. *nivalinus*—*nivaloides*, while the large number of Late Pleistocene finds from Western Europe are included under *C. nivalis* itself. Chaline (1966, 1971) has repeatedly emphasized the probable affinities between *Allophaiomys* and voles from the *nivalis*—*oeconomus*-type structure of paraconid of M_1 .

2. *Chionomys gud* Satunin, 1909—Caucasian Snow Vole

Diagnosis: Body length up to 150 mm in large forms and up to 126 mm in small, length of tail up to 80 and 75 mm respectively. Relative length of tail more than in the preceding species and, on the average, 63% in long-tailed and 57% in short-tailed forms. 333 Length of upper molar row 1.6–7.8 mm, lower row 6.6–7.8 mm; M_1 —2.1–2.7–3.3 mm, i.e., this tooth is not only relatively but also absolutely smaller than in *C. nivalis*.

Dorsal surface similar in color to preceding species. There are no populations with predominant light ash-gray color typical of *C. nivalis dementievi*. Tail usually slightly or distinctly bichromatic, more densely covered with hairs; in adult individuals, with complete pelage, ring scales not visible.

Skull structure and shape similar to preceding species, but generally juvenile in appearance. In adult individuals from both species, with equal-sized skulls, that of *C. gud* is distinguished by longer brain case, weaker slope of dorsal profile in rostral section, and less inflated auditory bullae, which reach or only slightly extend beyond plane of masticatory surface of molars. Moreover, in many populations of *C. gud*, in most individuals, M^3 complex in structure: four or even five denticles at least on medial side, and its middle line more than 35% length of molar row. Paraconid section of M_1 usually with well-expressed denticles on second fold (fourth lateral and medial). Anterior unpaired loop in this case, depending on degree of mutual shifting of both folds, in greater majority of the population resembles variable asymmetric inverted bell. Moreover, the upper incisors in the Caucasian snow vole are more highly curved than in the European vole.

Composition of species and variability: These four subspecies certainly exist: *C. g. gud* Satunin, 1909 (central part of Great Caucasus range); *C. g. nenjukovi* Formosov, 1931 (western part of Great Caucasus range); *C. g. lghesicus* Shidlovsky, 1919 (eastern part of Great Caucasus range); and *C. g. lasistanicus* Neuhäuser,

1936 (northern Turkey). The subspecific affinities of animals from the Trans-Caucasian population are not known. Reduction in size and lighter coloration in an eastward direction in the Great Caucasus range was not established (Gromov *et al.*, 1963).

Distribution and zonal affinity: Taluses of alpine, subalpine, and even sometimes forest belts of the Great Caucasus range, including some isolated areas (in Pyatigorye and in Terek valley); scattered finds in western Trans-Caucasus and northwestern Turkey.

Evolution and phylogeny: Fossil remains of voles from the *gud-roberti* group (more precise identification based on teeth not possible) earlier than the Middle Pleistocene are not known (Trans-Caucasus, upper reaches of the Rioni). The Caucasian snow vole is closer to the next species in structural complexity of molars, and also to *C. nivalis* in most of its external features. Time of separation of this new Caucasian endemic from the *Allophaiomys* line of development of microtines is not known.

3. *Chionomys roberti* Thomas, 1906—Robert's Snow Vole

Diagnosis: Body length up to 155 mm, tail up to 105 mm (up to 77% trunk length; average more than 65%; unlike in both preceding species, always more than 50%). Length of upper molar row 7.0–8.0 mm, lower row 7.0–8.2 mm; M_1 —3.0–3.16–3.5 mm.

Dorsal surface dark, from brownish to chocolate-brown to dark chocolate-brown. Pelage much rougher than in the two preceding species. Tail dark, mono- or slightly bichromatic, semiglabrous, with well-visible ring scales.

Dorsal profile of skull with well-developed depression in region of interorbital space, a more convex brain case, and barely perceptible nares. Zygomatic arches comparatively wide-set posteriorly and rounded in profile here. Auditory bullae small, usually do not reach plane of masticatory surface of molars. Incisor alveoli narrow sharply in posterior third. Angular process of dentary comparatively short and broad at base. Upper incisors broad, long, and straight. Structure and relative size of M^3 as in *C. gud*. M_1 also similar in structure, but relatively shorter (average less than 45% length of molar row); anterior part of its paraconid section not elongate, since the anterolateral and medial denticles slightly shifted relative to each other, and former with less tendency toward isolation than in *C. gud*.

Composition of species: The following subspecies have been reported, which mainly differ in coloration: *C. r. roberti* Thomas,

1906 (northeastern Turkey); *C. r. occidentalis* Turov, 1928 (western part of Great Caucasus range); *C. r. personatus* Ognev, 1924 (Ordzhonikidze region); and *C. r. pshavus* Shidlovsky, 1919 (southern slopes in middle part of Great Caucasus range).

Distribution and zonal affinity: Riverine biotopes of alpine, subalpine, and forest belts from northeastern Turkey and maritime belts of southwestern Trans-Caucasus (north up to Sochi) to Adzhar-Imeretinsk ranges; Great Caucasus range up to Zakataly and western Dagestan in the east where, most probably, range partly isolated in upper reaches of Andiian Koisu (Vereshchagin, 1959). From sea level to 3,200 m above msl.

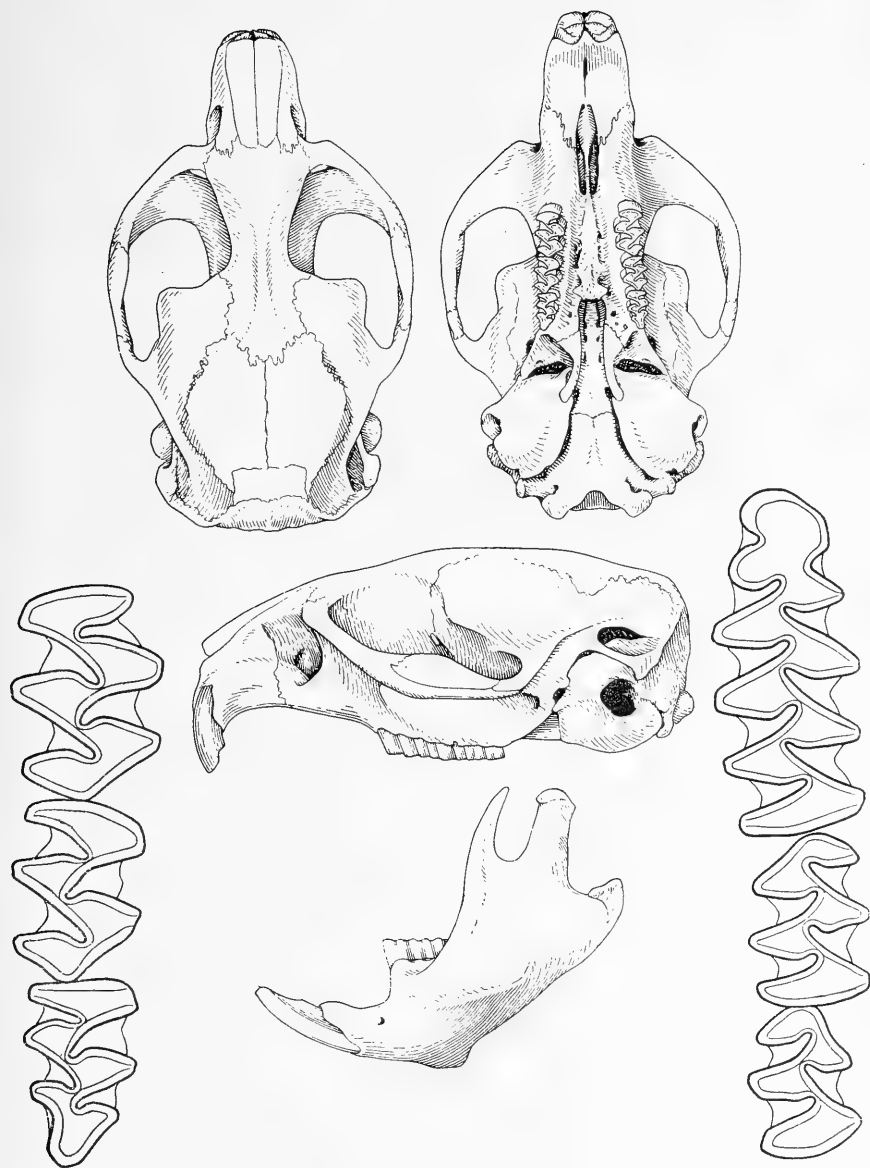
Evolution and phylogeny: Fossil remains are reported from the Late Pleistocene of western Trans-Caucasus; however, precise dating is not reliable.

15. Genus *Neofiber* True, 1884—Florida Water Voles (Figure 58)

Description: Body length up to 220 mm. Color from dark brown to almost black. Tail up to three-fourths trunk length, covered with sparse hairs, without terminal tuft. Eyes probably relatively small. Pinna small, covered with hairs, its structure not described; large rectangular antitragus discernible in dried skin. Structure of rhinarium and adjacent parts not described. Upper labial flaps large, rectangular, with long region of contact, covered with dense hairs. Lower labial vibrissae reduced, genal vibrissae absent. Carpal vibrissae present.

Proportions of limbs and their parts not described. Palm and sole glabrous. Plantar pads well-developed, especially on forelimbs. Carpal pads two, metatarsal one. Third digit of forelimbs slightly longer than 2nd; 4th and 1st digits almost equal. Highly reduced pollex with well-developed claw. Third digit of hind limbs only slightly longer than 2nd and 4th, which are almost equal; claws only slightly longer than on forelimbs where, unlike in hind limbs, they are much longer than half digital length. Claws on all limbs smoothly curved.

Profile and general proportions of skull similar to those of *Arvicola*; however, brain case much higher, and auditory bullae larger. Dorsal profile uniformly raised, without depression in interorbital region, but with slight slope at posterior margin of orbits. Length of brain case much greater than width, its surface flattened. Vertical crests well-defined and form distinct border along dorsal and lateral surface of skull. Interorbital crest well-developed; skull pro-



file along zygomatic arches uniformly rounded. Orbits large; orbital plane forms angle of about 45° with horizontal, an index well within the limits of the average values for microtines, as are the height and proportions of the masseteric [= zygomatic] plate of the maxilla. However, the masseteric surface describes a much greater dihedral angle with the sagittal plane (up to 135°). Auditory bullae large, thin-walled.

336 Relative size of molar row large (larger only in lemmings), M_1 and M^3 small. Molars rootless, crowns large (smaller only than in *Ondatra*). Enamel poorly differentiated in thickness, thinning observed only in depth of folds. No difference in size of lateral and medial triangles of masticatory surface. Formation of additional elements in posterior section of M^1 and M^2 not observed. Opposite triangles of all teeth isolated. Anterolateral denticles of M_3 poorly developed and present only in young individuals; tooth itself only slightly shifted lingually in tooth row and its alveolus only slightly isolated, not reaching lower margin of jaw. Posterior section of lower incisor barely extends to lower margin of mandibular ramus, terminating opposite apex of dental foramen. Relative length of incisor crowns not known, their proportions average for the subfamily. Upper incisors smoothly and lower ones sharply curved, their facing angle moderate.

Structural characteristics of limb bones not known.

Composition of genus: One extant species—*N. alleni* True, 1884; two extinct species have also been described—*N. diluvianus* Cope, 1899 and *N. leonardi* Hibbard, 1943.

Distribution and zonal affinity: Inhabits only tropical marshes in Florida. However, remains found much farther west (Texas) and north (Pennsylvania) even in the Late Pleistocene.

Adaptation to semiaquatic life style, typical of the present-day species, developed almost to the same degree as in *Arvicola*; however, pelage differentiation much better, almost as in *Ondatra*.

Evolution and phylogeny: Fossil remains known from the Middle Pleistocene (Irvington faunas). As in the case of other endemic genera of present-day microtines, the position of *Neofiber* in the tribe Microtini cannot be considered finally decided. In the opinion of Hibbard and Dalquest (1973), it is related to *Pliophenacomys* through the genus *Proneofiber*, i.e., its ancient relationship should be searched within the limits of primitive members of the tribe Clethrionomyini according to the classification accepted here. Strictly speaking, *Neofiber*, as well as *Phenacomys*, would have been more correctly placed under incertae sedis.

16. Genus *Proneofiber* Hibbard and Dalquest, 1973 (foss.)

Diagnosis: Size and general structural plan of molars (fossils of skull and postcranial skeleton not described) as in present-day *Neofiber*. However, all molars with two roots (total alveolar length of upper molars 9.21 mm, lower molars 11.1 mm), broader folds, and abundant cementation. M_1 with more isolated anterolateral fold, bony cover of M_3 not developed, including its posterolateral section. Unlike in *Neofiber*, enamel very well-differentiated; thins not only in upper folds but also in large part of adjoining walls of enamel prisms, anterior on lower molars and posterior on upper molars.

Composition of genus: One species—*P. guildayi* Hibbard and Dalquest, 1973.

Age and distribution: Early Pleistocene of North America (Texas).

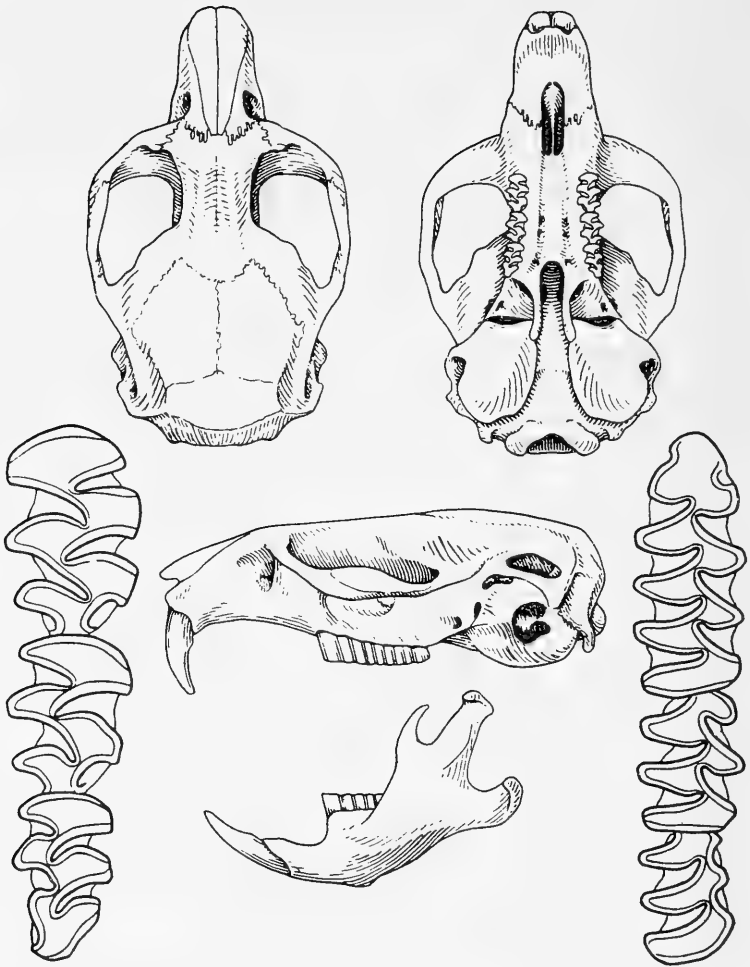
Taxonomic notes: The genus is considered by the author as a probable ancestor of present-day *Neofiber*, although this is more likely only a progressive side branch.

337 7. Genus *Phenacomys* Merriam, 1889—American
Forest Voles (Figure 59)

Description: Body length up to 110 mm. Color grayish-brown, sometimes with distinct reddish tinge or yellowish spots in rostral region. Tail length from one-fourth to three-fourths trunk length. Tail of long-tailed forms rather densely covered with hairs. Size of eyes not reported. Pinna medium in size, covered with rather dense tuft of hairs. Structural details of pinna, rhinarium, and adjoining labial processes not described. Upper labial (diastemic) flaps rectangular, with long region of contact with anterior unpaired lobe, diverging from it by longitudinal postincisor ridge. Flaps densely covered with short hairs. Anterior unpaired ridge of bony palate entire, medium in size, deeply bilobate; posterior ridge (predental) bifurcate, its outer angles probably connected with those of middle ridge (Quay, 1954). Number of postpalatal folds not indicated. Lower labial and mental vibrissae reduced, genal vibrissae absent. Carpal vibrissae present.⁷

Data on proportions of limbs and their parts not given in the literature available to me. Palm and sole covered with sparse hairs,

⁷All further description is based on the study of skins and skulls of a single species—*P. intermedius* Merriam.



338 Figure 59. Skull of American forest vole (*Phenacomys intermedius* Merriam).

and with five and six calluses respectively. Digital pads not enlarged. Carpal and metatarsal pads two each, inner of latter pads smaller than outer. Third digit of forelimbs longer than 4th and both longer than 2nd. Third digit of hind limbs slightly longer than 2nd and 4th, which are equal in length. Highly reduced pollex of forelimbs with small flat claw; claws of other digits more than half

digital length. Length of claws of hind limbs, if greater than this value, still less than in forelimbs. Claws of all limbs sharp and slightly curved.

Skull, in general features, resembles that of large species of *Clethrionomys*, for example *C. rufocanus* Sund.; however, it differs sharply in zygomatic arches unusually high in middle part. Dorsal profile with small and barely perceptible dip at base of zygomatic arches and almost without depression in interorbital region. Length of brain case slightly greater than its width, its dorsal surface slightly convex, lateral surfaces not sharply demarcated from dorsal. Interorbital space with well-expressed groove-like depression. Skull profile along zygomatic arches fairly uniformly rounded; latter distinctly convergent posteriorly. Orbit slightly shifted posteriorly, its plane forming small angle (about 30°) with horizontal plane (smaller angle seen only in some members of Lagurini and *Platycranius*). Masseteric [=zygomatic] plate of maxilla moderately high, relatively broad, its angle with sagittal plane slightly more than 100°, which is less than in other members of this tribe. Auditory bullae small, their walls consisting of dense bone. Mastoids not enlarged.

Relative length of molar row large, M_1 medium, and M^3 greater in size than mean value for tribe. Molars rooted, with low crowns, and enamel at initial stage of differentiation; folds without cement deposits. Difference in size of lateral and medial triangles of masticatory surface of lower molars considerable but less on upper molars (except for M^3). Tendency toward formation of additional lobe in posterior section of M^1 — M^2 not found. Fused opposite triangles present only in lower molars. They may appear on M_1 (in different combinations), in anterior section of M_2 , and on M_3 may consist of three transversely elongate enamel fields. Lower incisor passes under posterior root of M_2 , its posterior end far from reaching dental foramen. Both incisor pairs sharply curved, their facing angle (about 140° larger than in other genera of the tribe (in the subfamily, larger only in *Eolagurus*).

Structural features of limb bones not known.

Composition of genus: Four extant species—*P. intermedius* Merriam, 1889; *P. longicaudus* True, 1890; *P. albipes* Merriam, 1901; and *P. silvicola* Howell, 1921. Differences between long-tailed and short-tailed forms can hardly be less than subgeneric. Three extinct species are described: *P. primaevus* Hibbard, 1925 (Later Pliocene to Middle Pleistocene); *P. finneyi* Hibbard and Zakrzewski, 1972 (Late Pleistocene); and *P. osborni* Martin, 1972 (Early

339 Pleistocene), included under the Indian subgenus *Pliophenacomys* Hibbard, 1938; and also "*Pliomys*" *deeringi* Guthrie and Matthews, 1972 (Ancient Pleistocene of Alaska). The second of these species [i.e., *P. finneyi*—Eds.] is the probable ancestor of the first [i.e., *P. primaevus*—Eds.] (Hibbard and Zakrzewski, 1972).

Distribution and zonal affinity: Coniferous forests of North American in mountains up to above 3,000 m above msl, and in plains. In mountain regions spread south to northern part of New Mexico. Live in open biotopes—dry meadows and marshes, as well as the forest *per se*, where they build nests on trees (longer-tailed forms in western part of range).

Evolution and phylogeny: Fossil remains known from the Late Pliocene.⁸ In the second half of Middle Pleistocene (Late Caucasian fauna) they have been found slightly more east of the present western boundary of the range on the continent. In the eastern part of the range, a significant shift northward has taken place since the Late Pleistocene.

Phenacomys is the only extant group of the tribe which has retained molar roots, as well as such archaic traits as bony palate poorly differentiated in posterior part, short lower incisors, absence of cement on lateral surfaces, enamel poorly differentiated in thickness, and simplified structure of M^3 , together with features of high specialization (marked difference in size of triangles of lower molars, complex paraconid section of M_1 , etc.). In the Old World ecological analogues of *Phenacomys*—the Asian forest voles of *Clethrionomys*—have further evolved from their extinct rooted-molar ancestors.

The affinities of *Phenacomys* with extinct rooted-molar forms, among those which have not undergone secondary simplification in structure of M_1 and M^3 , are beyond doubt. American paleomammalogists consider them primarily members of *Pliomys*—*Pliophenacomys*; however, the phyletic gap between them has not been filled to date, if we exclude the abovementioned, poorly studied species "*Pliomys*" *deeringi*, the relationship of which is not known.

The probable offspring of *Phenacomys*, according to Hinton (1926), are members of the genus *Microtus* in a broader sense. This confirmation may now be extended only to the supraspecific groups endemic to the New World.

⁸There are indications of fossil remains (isolated teeth) in the Ancient Pleistocene of northeastern Siberia.

Ecology and Economic Importance of Microtinae in the Fauna of the USSR¹

CHARACTERISTICS OF THE SUBFAMILY AND SEPARATION INTO BIOLOGICAL GROUPS

340 The ecology and physiology of the species comprising the vole subfamily have not been uniformly studied. While voles are characterized by more or less general ecophysiological features, nevertheless there are differences which if not considered prevent a correct assessment of their position in natural complexes.

The specificity of voles as a definite taxonomic and biologically distinct group of animals is manifested in their highly labile response to conditions of food resources and climatic factors. This response is related to the nature of their thermoregulation, the direction of evolution of the mechanisms ensuring temperature homeostasis, and the rhythm of temperature changes on the earth in time and space (Polyakov, 1950, 1964). Consequently, voles are characterized by unique biological properties: manner of feeding, reproduction, behavior (especially in the building of shelters), formation of daily rhythms of activity, and so on.

Plant parts containing considerable cellulose of comparatively low calorific value, and which are difficult to digest, play a significant role in the feeding of Microtinae. Voles feed very little on seeds and mainly during the cold period of the year, the intensity of digestion is very high in voles, despite their relatively short intestines, which are approximately the same length as in carnivorous mammals (Naumov, 1948; Mokeeva, 1949; Polyakov, 1950; Pegel'man 1951; and others).

One index of intensity of digestion, related to the peristalsis of the stomach and intestines, is the rapidity with which food passes through the digestive tract. In voles, the first portions of food pass through the intestinal tract within 0.5–1.5 hrs (Pravdina, 1961), in

¹ Section contributed by I.Ya. Polyakov.

horses between 72–96 hrs (*Handbook*, 1937*), and in ruminants after an even longer period. Nevertheless, voles assimilate a very high percentage of the organic substances in their food. Thus, according to Drozd (1967, 1968), assimilation of concentrated foods reaches 87.69–92.96% or 84.3–93.5%, and of course foods containing high quantities of cellulose, 73.9%. The general level of energy
341 assimilated from food is high—65.2 to 90.9%.² This is probably related not only to the intense peristalsis of the digestive tract and higher activity of the digestive enzymes of voles, but to the very thorough mastication of food in the oral cavity. It must be noted that despite an apparent omnivorous habit—each vole species consumes food plants belonging to hundreds of species, and several genera, and families—every member of Microtinae has a different requirement for moist (succulent) food.

For most rodents the moisture content of food is their main source of water. Therefore, the water requirement is met by selection of a food plant or its parts and through seasonal changes in food preferences. Vole species comparatively similar in food habits, for example the social vole (*Microtus socialis* Pall.) and the common vole (*M. arvalis* Pall.), differ in water intake through food at the same ambient temperature. This is related to the fact that in the process of thermoregulation, these animals manage with different quantities of water, especially at high temperatures. Species consuming less water are capable of utilizing it economically (Mokeyeva, 1952). The differential food preference based on water content is associated with a different consumption of cellulose and products containing readily digestible substances.

It is important to note that despite intensive digestion, all voles consume a very large quantity of food compared to their weight. In small forms the daily ration is 100–120% of body weight and in young animals up to 300–320% (Mokeyeva, 1949; Polyakov, 1950). Even in such comparatively large forms as the water vole and *Ondatra*, the daily ration may constitute 50% of body weight (Sludskii, 1948, 1962; Panteleev, 1968).

The exceptionally high food requirements of Microtinae is related to the nature of their thermoregulation, the very high expenditure of energy for heat generation, and the high expenditure of body reserves for reproduction. Their thermoregulation is primarily attained through a change in heat production. Even when the ani-

*Not listed in the bibliography—Eds.

²It may be noted for comparison that milch cows receiving specially prepared rations, assimilate 74.2% of the organic substances (Denisov, 1960).

mal is resting, groups of muscles responsible for thermoregulation participate in work (shivering) at a comparatively small fluctuation in ambient temperature from the narrow optimal range (Slonim, 1952, 1961, 1962, 1966). According to Ćorecki (1968), the bank vole (*Clethrionomys glareolus* Schreber) in summer at 20°C consumes 4.29 cc oxygen per hr per gram body weight, and in winter (at the same temperature) 3.65 cc. This corresponds to 0.494 and 0.420 kcal/g of body weight per day. An animal weighing 20 g thus expends about 10 kcal per day. Characteristically, in an active state (running in a drum, exceeding in duration the possible stress in nature), the energy expenditure increases 2.0–2.1 times in the bank vole, 1.5 times in the northern red-backed vole (*C. rutilus* Pall.), and 1.6 times in the tundra vole (*Microtus oeconomus* Pall.) and the European fossorial vole (*M. subterraneus* Se.-Long.) (Grodzinski and Ćorecki, 1967). According to Pearson (1947), the difference between intensity of metabolism at rest and in an active state in the American species of *Pitymys*, *Clethrionomys*, *Peromyscus*, and *Microtus* varies in the range of 1.5–2.1 times.

For comparison, it may be noted that a man weighing 80 kg expends 2,500 kcal/day and a horse with a body weight of 441 kg, 5,000 kcal (Slonim, 1952). The intensity of metabolism in man increases 3–10 times while walking or running and 20 times in sprinting (Jansky, 1965). If these indices are compared with the nature of metabolism in voles, it may be concluded that at rest they expend 43-fold more energy on thermoregulation than the horse and 16 times more than man. During intensive work this difference decreases and does not exceed 3.0–4.0 times. This confirms that voles expend much more energy for thermoregulation than for work related to locomotion, food collection, and burrow construction.

The body losses for reproduction in voles are also several-fold higher than in large mammals. A female common vole completes pregnancy and lactation within one month. If a female (with a body weight of 30 g) feeds 10 neonates over this period, their weight (at the age of 10 days) will be 60 g, which is 200% higher than the weight of the mother. All these resources are obtained by the female from food and transferred to the progeny during pregnancy through the placenta, and after birth through milk. To this we should add the expenditure of energy by the young on thermoregulation and movement, which is also met from the resources of the nursing mother. If a female vole were to reproduce and feed the neonates at the same intensity for nine months, their weight (up to changeover to independent feeding) would exceed her weight by

18 times. We may note, for comparison, that a newborn calf (with a 9-month pregnancy) is not more than 8.0% of the mother's weight. Therefore, in a 9-month period, utilization of resources for breeding by a female vole is roughly 250 times greater than a cow's.

These calculations are confirmed by results characterizing the expenditure of energy in female voles during pregnancy and lactation. The daily assimilation (digestion) of food in barren females of the bank vole with a body weight of 25 g was 17.5 kcal, and in pregnant females 28.7 kcal toward the end of pregnancy. The daily assimilation of food during maximum intensity of lactation was estimated at 38.9 kcal. The requirement for energy resources increased 24% during pregnancy and 92% during lactation. To deliver five young and rear four of them to the age of changeover to independent feeding, a bank vole must additionally assimilate 364 kcal: 75 kcal during pregnancy and 289 kcal during lactation. With the coefficient of assimilation at 88.5%, the additionally expended food resources are estimated at 406 kcal (Kaczmarek, 1966).

In the common vole, the energy requirements of pregnant females weighing 28.5 g is 13.9 kcal per day (average), which is 32% higher than in barren females. Daily assimilation of food by a female weighing 25.2 g at the time of lactation is 26.6 kcal, which is 133% higher than in nonlactating females. Throughout the entire period of pregnancy and lactation, a female additionally assimilates 304 kcal (60.5 kcal during pregnancy and 243.5 kcal during lactation). On average, the intensity of expenditure of energy resources over this period increases 82.5%. To give birth to one vole and feed it to the stage of independent feeding (10 days), the female common vole expends 75.9 kcal. The energy utilization of food of a common vole may reach 82.72% (Migula, 1969).

It is interesting to note that the calorificity of rodents is comparatively lower than the intensity of their energy exchange (Gorecki, 1965). Thus, each gram of vole holds 1.301–1.963 kcal and the body as a whole, not more than 30–40 kcal. Yet the daily energy budget is very high and, on the average, constitutes about 33–35% of the calorificity of the animal. Thus, on the average, in the field vole it was 11 kcal in autumn, 10.6 kcal in winter, and 12.3 kcal during summer in a single animal; the average weight, respectively, was 21, 20.4, and 23.8 g (Hansson and Grodzinski, 1970).

These data show that the major part of the energy assimilated by voles is expended by them for thermoregulation. Therefore, the efficiency of accumulating energy resources is very low in voles. In a special experiment (Spitz, 1968), the consumption of

alfalfa by a common vole population over a four-month period was studied. Results showed that the actual energy "assimilated" in the population was only 3.71% of the energy consumed. According to Drozd (1974), 1.5–8.0% energy was "assimilated" in a population of *Microtus arvalis*.

The large expenditure of energy resources for thermoregulation and breeding, which necessitates a very high food consumption in voles, had led to their exclusive dependence on conditions of the food base. Feeding on growing plant parts, the most readily available food in nature, became an essential adaptation for rodents toward reduction of dependence on quantity of available food. However, this did not lessen their dependence on the qualitative conditions of food, in particular, its moisture content, to which they distinctly respond relative to conditions of heat exchange (Polyakov, 1937–1950; Vereshchagin, 1946). The condition of each vole population is ultimately determined, therefore, by food resources and climatic factors; the latter largely decide the state of vegetation in each biotope and the food requirement of rodents.

The high reproductive potential typical of voles can be considered a compensatory adaptation in view of the extremely unstable requirements of heat exchange and feeding (Polyakov, 1964). At the same time, the high reproductive potential, which demands large energy resources, makes the existence of voles even more intimately dependent on conditions of heat exchange and feeding. This cycle of interdependence determines the general direction of evolution of Microtinae, their infraspecific and specific differentiation (Gladkina, Meyer and Mokeeva, 1962–1966; Polyakov, 1967, 1969; and others).

In this context, it is essential to note one more important characteristic of voles—all of them are not only born blind, but produce morphologically distinct, underdeveloped offspring. Such features also characterize some other animals that expend large energy resources on breeding (Sciuridae, Muridae). Thermoregulation is stabilized in neonates by the time they open their eyes (Polyakov and Pegel'man, 1950, 1953; Golenishchev, 1954; and others). Until a neonate is capable of ensuring its own homiothermy, the temperature required for normal development is created in the nest through the heat discharged by its parents. This is the most economical method and essential for the given direction of evolution of adaptation in voles. If unweaned rodents were to have an independent thermoregulation, this would require energy resources beyond the nursing mother's ability to provide.

A young vole that has changed over to independent feeding but is still sexually immature differs markedly from a sexually mature adult in nature of thermoregulation and food consumption (Polyakov, 1950–1964; Kagantsova, 1953; Golenishchev, 1958; and others). Its response to the environment is not only more labile than that of the adult vole, but the consequences of such interaction also leave a deeper imprint on the formation of the phenotype. On the whole, the nature and development of voles, associated with their born-blind nature, predetermine the wide range of their phenotypic variability. A particularly strong influence on the formation of the phenotype of voles is exerted by environmental influences during the period from birth to eye-opening, when brain development is relatively more than that of the body, i.e., maturation and formation of reflexes (Orbeli, 1961; Himwich, 1962; Polyakov, 1968b; Kuznetsova, 1969; Polyakov and Kuznetsova, 1971). In some species
 344 of voles a mechanism has been discovered that ensures adequate phenotypic variability in nature of environmental influence in the early stages of postnatal growth (Polyakov, 1967, 1969). However, this mechanism has only a relative adaptive significance within the limits of a better adaptation to individual seasons of the year (“spring” and “winter” populations), and not to the entire range of environmental variation throughout the year. The above facts predetermine a quicker formation of biotopic variability in a vole colony, their numerical dynamics, and habitat distribution. Biotopic populations of smaller forms of voles differ in such important indices as phenology and intensity of reproduction, rate of development and morphophysiological aspects of individual age groups, age composition, and resistance to unfavorable factors (Polyakov, 1967, 1979).

All members of a vole family live in the burrow. Burrow-making and use of other shelters can be considered an adaptation that makes thermoregulation easier. The role of shelters in protecting rodents from predators is a secondary phenomenon. This is attested to by seasonal variability in depth of nests, which is associated with changes in soil temperature (Strel'nikov, 1932a, 1932b, 1940; Polyakov, 1950, 1968b). Furthermore, the burrow saves rodents from only a small number of dangerous predators, namely, those that cannot enter or dig into it.

The need for living in burrows or on the surface has led to several specific morphophysiological adaptations in voles. Entry into the burrow after being on the surface is accompanied by a sharp reduction in blood circulation and respiration, leading to a decrease

in pulse rate, and a decrease in frequency and depth of respiration. These reactions are triggered by a sharp reduction in heat supply in the burrow and nest, accompanied by a fall in intensity of oxidative processes in the organism. To accommodate such drastic changes in intensity of blood circulation, venous enlargement has occurred in burrow dwellers. As the heartbeat decreases, the blood is held back; when intensity of blood circulation increases, blood is again taken into general circulation. Such blood receptacles (depots) in voles are represented by the external jugular and subclavian veins. Their diameter in a common vole weighing 20–35 g is 1.5 times greater than in the squirrel, a nonfossorial animal weighing 240–330 g (Tumanov, 1968).

A decline in intensity of blood circulation and respiration inside the burrow and nest is not only dictated by a reduction in energy losses or heat production, but is also vitally important given the limited ventilation and rapid accumulation of carbon dioxide in the burrow. It is noteworthy that in voles adapted to a semiaquatic life style, blood circulation decreases sharply on diving in water. The blood is held back in venous enlargements during diving and during transit from soil surface to the burrow (Galantsev, 1965a, b).

The daily rhythm of activity of voles is associated with ambient temperature conditions. They may be active at any time of day if their presence on the surface is not accompanied by overheating or overcooling. These aspects determine the duration of continuous stay outside the burrows and also in the burrows and nests.

This description of the ecological and physiological characteristics of voles permits us to include them under the category of unique life forms. The term "life form" has long been used in ecology, but different meanings attributed to it. In particular, it is used to describe properties of some large taxa as well as for separating a composite group of species exhibiting similar adaptive characters that ensure their survival in the natural biomes occupied by them. Krivolutskii (1971) has proposed that the term "life form" should only be used for species belonging to a single taxonomic group, if
345 convergent similarities appear in them due to life in a similar environment. The above description of *Microtinae* permits us to give a somewhat more precise interpretation of the concept "life form". All members of the vole subfamily belong to a single life form because the nature of response to environment in all species of this subfamily is associated with their aeromorphosis. Among the vole fauna of the USSR, however, there are groups of species which are well-adapted to different zones—tundra, forests, steppes, high

mountains, associated with water bodies, or lead predominantly a fossorial life. With identical general response to the environment, these groups of species have also developed additional adaptations that enable them to utilize energy resources more rationally in the zone of habitation, depending on distribution in time and space, and quality of these resources. Therefore, the life form characterizes taxa of a higher rank which display distinct aeromorphic differences in reaction to changes in energy resources and climatic factors. Biological groups should be identified within the limits of the life form, reflecting idioadaptive (allomorphic) variability associated with the spread of a given life form in certain definite zones or corresponding ecological formations. Therefore, I am inclined to consider the life form as interpreted by Krivolutskii (1971) as a biological group. In this context, there is hardly any reason to include under a life form animals from any one zone belonging to different large taxa simply because they display a capacity for survival under conditions developing in a given zone (Kashkarov, 1945) through, it would appear, similar adaptations. In reality, the mechanisms of adaptation to similar environmental conditions are unique in various large taxa, which *per se* precludes their inclusion under the same life form. Accordingly, six biological groups can be identified in the vole fauna of the USSR, which together constitute a unique life form.

The first group includes dwellers of forest-steppes, steppes, and semideserts. Along the intrazonal elements of the terrain, these forms may penetrate mountains, deserts, or even forests. This group includes most species of common voles (*Microtus*) and steppe lemmings (*Lagurus*), which occupy major agricultural regions and are characterized by maximum numerical dynamics. These voles are serious pests of agricultural crops and pastoral land.

Hydrophilous forms belong to the second group—inhabitants of wet meadows, marshes, river floodplains, and banks of freshwater reservoirs. These are mainly forest-marsh forms that may penetrate steppes, deserts, and tundra along the intrazonal elements of the relief. The water vole (*Arvicola terrestris* L.) and muskrat (*Ondatra zibethica* L.)—introduced and widespread species—may be considered the most typical members of this group in Russian fauna. We might also include here the tundra vole (*Microtus oeconomus* Pall.), reed vole (*M. fortis* Büchner), and Sakhalin vole (*M. sachalinensis* Vassin), which vary in economic importance. The muskrat is a valuable component of the fur industry, while the water vole has become a pest of agricultural crops and plantations over most

of its range and is a source of infectious diseases. True, the water vole is also a component of the fur industry, but the value of its skin can never justify the damage it causes. Tundra and reed voles play a significant role in the spread of diseases and sometimes cause local damage to crops. Concomitantly, they serve as a food base for carnivorous fur-bearing animals.

The third group includes forest inhabitants—the bank vole or forest vole (*Clethrionomys*)—as well as some species of the common 346 vole which have adapted to life in forests and meadows. The field vole (*Microtus agrestis* L.), European pine vole (*M. subterraneus* Selys-Longchamps), and shrub voles (*M. majori* Thomas and *M. schelkownikovi* Satunin) belong to this group. These forms live in fields and haystacks in some areas and may cause slight damage. Their twin influence (favorable and adverse) is of great importance in the natural rejuvenation of forests, but they always have a harmful effect on forest plantations. At the same time, members of this group have become the major food base for valuable fur-bearing animals, primarily those of the marten family (*Mustelidae*). On the whole, the role of this group of voles in human economic activity should probably be assessed as generally beneficial.

The fourth group contains inhabitants of tundra and forest-tundra—the lemmings (*Lemmus*, *Myopus*, *Dicrostonyx*). Its members also penetrate taiga. They constitute a primary dietary item for carnivores that are valuable objects of commerce, and thus play a positive role in the economy of the northern region.

Under the fifth group are included forms that have adapted to specific mountain and alpine conditions, living among rock outcrops and taluses. They have a limited role to play and are of little interest to man. This group includes the Asian high-montane voles (*Alticola*) and the European snow voles (*Chionomys*).

The unique, sixth biological group comprises species that always live in the upper soil layers (fossorial forms), dwelling in dry steppes, semideserts, plains, and alpine meadows. Some (*Ellobius*, *Myospalax*) have now been excluded from the vole subfamily, while others (*Prometheomys*) are of little economic importance and hence their ecology has hardly been studied.

Only after considering the unique aspects of voles as a definite life form, can the characteristic features of the ecology of each identified biological group be understood, rational control of the harmful species developed, and survival conditions for beneficial species optimized.

COMMON VOLES AND LEMMINGS

General Characteristics

In Soviet fauna, the typical members of this group are the common vole (*Microtus arvalis* Pall.), social vole (*M. socialis* Pall.), Afghan vole (*M. afghanus* Thom.), narrow-skulled vole (*M. gregalis* Pall.), Trans-Caspian vole (*M. transcaspicus* Satun.), Brandt's vole (*M. brandti* Radde), and the steppe lemming (*Lagurus lagurus* Pall.). Middendorff's vole (*Microtus middendorffii* Poljak) and the yellow steppe lemming (*Lagurus luteus* Eversm.) are also close to this group. Naturally, the new species, *Microtus subarvalis* Meyer, Orlov and Skholl, also belongs to this group. This species was recently separated from the composition of *M. arvalis* as a twin species (Meyer, Orlov and Skholl, 1969, 1972). It differs from the main species ($2N = 46$) with the presence of 54 chromosomes, the shape of spermatozoan head, and reproductive isolation. Other morphological and physiological differences between these species, which share an extensive and mostly sympatric range, have not been found to date (Meyer *et al.*, 1972; Gladkina, 1972). Thus, in data referring to this group of voles, hereafter I shall not indicate specific features because they are still not known. Moreover, it is presently difficult to judge which species is implied in data available on ecology and physiology. Some justification can be found in the fact that attempts to find differences between them based on ecological and physiological indices have so far not proved successful. Therefore, when I refer to the common vole, it may be understood that both species are implied.

A similar ecological feature uniting this group of voles is that they exist predominantly in open steppe or meadow areas in plains or mountain regions. Being very sensitive to conditions of feeding and heat exchange, these voles, with a relatively settled way of life, live in different habitats according to seasonal or climatic variations during the year. This is associated not only with migration to new places, but also the varying degree of survival in different habitats. During favorable seasons a rapid increase in numbers and dispersal to form well-defined biological populations in different habitats take place. This process continues until optimal conditions are maintained. Thereafter, with a general deterioration in conditions of survival, the populations die wherever the environment becomes particularly unfavorable, but survive wherever at least minimal requirements are met.

Depending on favorability and variability in time, the voles in each region of the range can be subdivided according to conservation habitats, which ensure survival of the population even during critical periods of the year or for several years in a row, and dispersal habitats where survival of only a few generations is possible (Polyakov, 1950, 1954, 1964).³ In the dry region of the range, places for conservation of voles of this group during summer are shrub thickets, forest boundaries, glades, forest belts, and other similar areas with higher natural or artificial moisture (gullies, banks of reservoirs, irrigated gardens and fields, banks of irrigation canals, etc.). In the northern regions of the range of each species, where a particularly critical situation develops during the cold part of the year, areas not flooded during spring and autumn but having a high snow cover, become conservation habitats. These are the forest fringes, slopes on hillocks, and coastal slopes raised above the general territorial level, as well as various manmade constructions (haystacks, haycocks, buildings, etc.). In areas of cultivated lands, agronomic and management measures play a decisive role (Polyakov, 1937–1968; Sakhno, 1957, 1958a, b, 1959).

The rule of change in habitat noted by Bei-Bienko (1959, 1962) is manifested in the formation of places for conservation of voles and lemmings in individual regions of their range. Thus, conservation habitats of the common vole in the northern part of the range (Leningrad district) are located in the driest places, but with a good snow and hay cover. In optimal conditions of the range (Vinits district), this species survives over a large part of the territory, excluding only the most humid. In the southern part of the range (Kherson district), conservation habitats are found in the most humid places—gullies, irrigated crops, and along irrigation networks.

³The term “survival habitats,” proposed by Naumov (1937), is often used in the literature. This term implies areas where, under a temporarily unfavorable combination of conditions, part of the population can survive. The major distinction between “survival habitats” and “conservation habitats” was analyzed earlier (Polyakov, 1954). Essentially, “conservation habitats” are relatively constant biotopes in which the species can be preserved under extreme conditions. A specific population is created in them. Each zone (region) of the range has its own typical biotope where the species is conserved. Their qualitative features and volume (territory) determine the numerical level of the species in a given zone (region), population dynamics, and morphophysiological characteristics (Polyakov, 1969). “Survival habitats” can be identified within the limits of “conservation habitats” as well as “dispersal habitats”. For example, during torrential rains voles living in elevated areas of any biotope escape death. Such areas are termed “places of survival”.

348 In the eastern part of the range, with a relatively dry continental climate (Kustanai district), forest belts, irrigated gardens, banks of rivers and lakes, and edges of felled forests serve as places for conservation.

Among the common characteristics of voles and lemmings are their preferential feeding on steppe herbs, similar burrow construction, high energy loss to thermoregulation, maximal reproductive potential, high population dynamics, and phenotypic variability under environmental influences.

Individual species of voles are differentiated in this group by their reaction to environmental temperature and affinity to food of variable moisture content. These properties determine the specificity of their range, distribution of habitats, behavior, and other aspects of life.

The entire ecology of voles and lemmings—distribution, behavior, rhythm of activity, numerical dynamics, intrapopulation, interpopulation and interspecific relationships—revolves around the direct influences of conditions of heat exchange and feeding (Strel'nikov, 1932b, 1940, 1950, 1955; Polyakov, 1937–1967).

Thermoregulation and Food Requirements

The body temperature of small voles and lemmings undergoes marked change under environmental influences, a fact demonstrated by numerous experiments (Polyakov and Pegel'man, 1950, 1953; Kagantsova, 1952, 1953; Bashenina, 1962, 1966). Only small changes from normal body temperature (in the range of 32–38°C) are tolerated without consequence. Characteristically, high ambient temperatures are more difficult to tolerate than low temperatures. The social vole at an ambient temperature (in a thermostat) of 40°C becomes overheated within 20 min; its body temperature reaches 44.0–44.5°C and the vole dies (Polyakov, 1938). This was subsequently confirmed for all small voles, the common vole, the narrow-skulled vole and the steppe lemming (Kagantsova, 1953; Bashenina, 1962; Gladkina and Meyer, 1963; and others). Cooling up to lethal consequences in a dry environment (without wetting of pelage), even at temperatures of –20 to –30°C, can continue for a longer time. In this case, cold resistance is significantly influenced by the temperature conditions in which the rodents are maintained (Chentsova, 1963, 1970). The rapidity of change in body temperature in the steppe lemming (*Lagurus lagurus* Pall.) and the narrow-skulled vole (*Microtus gregalis* Pall.) reared in nests with

ambient temperatures of 15–18°C (control) and –2°C (experimental) is shown in Table 1. The rodents were cooled in a thermostat, given no food, and prevented from moving about (kept in small chambers). After maintaining the body temperature for some time, eventually the animal can no longer cope with cooling, and the body temperature begins to fall rapidly. The time of maintenance of stable temperature differed significantly in the various species and groups compared, but the duration of fall of body temperature (up to loss of standing capability) was generally similar. Characteristically, the minimum body temperature at which adult voles and lemmings were able to survive, ranged from 9.0 to 28.5°C. In this experiment, 22% steppe lemmings survived with a drop in body temperature to 9°C, but all the narrow-skulled voles died; 24% of these animals survived when the temperature was lowered to 12°C (Chentsova, 1963).

349 A comparison of results of the influence of high and low temperatures on voles shows that the mechanisms determining heat production (chemical thermoregulation) play a decisive role in the thermoregulation of these animals, but the mechanisms of active heat exchange are not so well-developed (physical thermoregulation). For this reason, they are capable of tolerating cooling, by increasing heat generation. Overheating of voles and lemmings begins as soon as the ambient temperature reaches the level of their body temperature, since they have a poor mechanism of active heat exchange; under these conditions both metabolism and heat production increase. This situation was demonstrated by Slonim (1952) during his comparative study of thermoregulation of mammals.

Species differences in thermoregulation of voles and lemmings are characterized by: (a) indices of intensity of metabolism at low temperatures (usually at 0°C) and temperature of critical point of metabolism; (b) a general change in intensity of metabolism with an increase in ambient temperature; and (c) capacity to withstand overheating after rise in ambient temperature above critical point of metabolism. Probably, species differences in resistance to overcooling should also be considered (Chentsova, 1963, 1970). Only a combination of these data allows us to characterize the thermoregulation of a species. However, it should be kept in view that the temperature optimum in young, sexually immature, but independently feeding voles is shifted toward a higher temperature (by 4–5°C) compared to adults (Polyakov, 1950–1967; Kagantsova, 1953; and others); neonates of all voles, before eye-opening, respond

Table 1. Duration (in minutes) of stable body temperature (T, °C) and its sharp fall (t) without food (from Chentsova, 1963)

Ambient temperature (°C)	Steppe lemming				Narrow-skulled vole			
	Control		Experimental		Control		Experimental	
	T	t	T	t	T	t	T	t
- 2	546	95	717	98	621	99	1,520	81
-10	412	76	128*	82*	385	89	570	80
-15	100	69	186*	85*	147	56	376	55
-20	78	64	130	63	60	50	170	53
-30	42	47	78	41	29	40	120	43

*So given in the Russian original, but one suspects an error has occurred here—Eds.

almost identically to ambient temperature. Thus species-dependent differences in thermoregulation can be considered more reliable only in adults. The thermoregulation of young common voles is much more similar to that of adult social voles and differs little from that of adult and young common [sic] voles* (Table 2).

Moreover, thermoregulation in different populations of a given species can differ significantly depending on the conditions in which these populations grew up (Polyakov, 1950–1967; Kagantsova, 1953; Gladkina, Meyer and Mokeeva, 1962–1966; Chentsova, 1970). Thermoregulation in a subspecies or geographic population can differ either for the entire set of indices or in characteristics determining higher or lower adaptation to rise or fall of temperature. The latter situation is observed in the case of a shift in temperature optimum. In this context, it is important to consider that thermoregulation of individual species can also differ in extent of variability in various populations under the influence of environmental conditions in which they have grown up. Thus, in the steppe lemming and narrow-skulled vole, similar indices of total change in intensity of gas exchange are seen, but various populations of the steppe lemming are characterized by a lesser phenotypic variability in thermoregulation. Thermoregulation, however, differs more markedly in subspecies of steppe lemmings

*An obvious misprint in the Russian original; should read “narrow-skulled voles”—Eds.

350 than in subspecies of narrow-skulled voles living in similar conditions (Gladkina, 1968a, b; Gladkina and Mokeeva, 1970a, b).

Some of the significant changes in thermoregulation of different species, subspecies, and age groups of voles and steppe lemmings are shown in Table 2. They are evident from changes in indices of metabolic intensity as well as from changes in body temperature. These indices are inadequate, of course, and at best provide a broad platform for discussing how thermoregulation can vary depending on species, subspecies, or age.

It may be noted that common and social voles were kept in chambers during the study of gas exchange for 1.5 hr and steppe lemmings and narrow-skulled voles for 0.5 hr. Cages housing the adult and young narrow-skulled voles and steppe lemmings were of the same size. This permitted young animals of smaller body size a certain degree of mobility. Therefore, their metabolism increased at low temperatures and a lesser fall in body temperature was noted than in adult animals.

351 It follows from the foregoing data that the temperature optimum for common voles is lower than for social voles. The same index for steppe lemmings is higher than narrow-skulled voles. Subspecies of steppe lemmings differ in thermoregulation. For example, the subspecies *Lagurus l. abacanicus*, compared to the other (*L. l. agressus*) and the subspecies of narrow-skulled vole displayed no significant differences, while the subspecies *L. l. abacanicus* and *Microtus g. dukelskiae*, from southern Krasnoyarsk, and *L. l. agressus* and *M. g. gregalis* from northern Kazakhstan—territories differing in climate—are characterized by unique responses. In the steppe lemming, these climatic differences caused hereditary fixation of subspecific characters of thermoregulation (statistically significant). The narrow-skulled vole, being endowed with a higher phenotypic variability for thermoregulation, was capable of surviving in these different climatic conditions without significant hereditarily fixed changes in thermoregulation (Gladkina and Mokeeva, 1970a, b, c). This higher phenotypic lability of thermoregulation in the narrow-skulled vole enabled it to survive in more diverse climatic conditions and to exhibit a wider range than the steppe lemming. Ultimately, this may make it a more potentially dangerous pest of agricultural crops (Gladkina, 1968a, b).

It should also be noted that the above aspects of thermoregulation do not offer a direct possibility for the existence of a species or a population in a temperature range typical for near-ground

Table 2. Species, subspecies and age-dependent gas exchange in voles and steppe lemmings (from published data of T.S. Gladkina and R.M. Kagantsova)

Species, subspecies and age groups	Temperature at critical metabolic point, °C	Consumption of O ₂ per min per g body weight in cc	Change in metabolism			Change in body temperature over period of existence in chamber, °C			
			In range of 0° to critical metabolic point	By 1° from 0°C to critical metabolic point	% with increase in temperature from				
							at critical point	at 0°	at 35°
Common vole									
<i>M. arvalis duplicatus</i>									
Adult animals	30	0.056	0.131	235	1.8	1.1	2.9	- 4.0	+2.5
Sexually maturing	35	0.067	0.225	337	2.05	2.3	2.6	- 9.5	+1.1
Social vole									
<i>M. socialis binominatus</i>									
Adult animals	35	0.046	0.145	315	1.9	1.7	3.8	- 6.7	+1.5
Sexually maturing	37	0.052	0.251	482	2.1	3.8	3.1	-17.8	+0.2
Steppe lemming									
<i>L. l. abacanicus</i>									
Adult (3 months)	32	0.054	0.134	248	3.7	3.0	1.5	- 3.2	+0.8

Young (1 month)	32-35	0.062	0.195	316	2.8	4.0	4.1	-2.0	+0.1
<i>L. agressus</i>									
Adult	30-32	0.065	0.167	257	3.1	3.1	4.3	-3.8	+1.2
Young	35	0.060	0.205	341	2.9	3.6	4.0	-3.3	+0.7
Narrow-skulled vole									
<i>M. g. dukelskiae</i>									
Adult (3 months)	35	0.071	0.174	245	3.0	3.5	1.9	-2.8	+0.8
Young (1 month)	35	0.063	0.191	303	2.9	3.0	6.4	-1.2	+1.2
<i>M. g. gregalis</i>									
Adult	32	0.079	0.180	227	3.7	4.6	3.4	-3.5	+1.4
Young	35	0.079	0.210	266	2.8	2.3	1.5	-1.9	+1.2

or ground level at any point in the range. Voles and steppe lemmings cannot survive even for a day outside their burrows or some substitute cover since fluctuations in temperature at soil surface, especially in combination with solar radiation or precipitation, are markedly beyond the limits of temperature range tolerated by these rodents. Only prolonged existence in burrows, nests, or some other cover, with periodic activity on the soil surface, and the type of thermoregulation they have developed, ensure the life of voles and lemmings within the limits of their range. Thus their behavior as well as thermoregulation is subject to substantial, rational adaptive variability (Polyakov, 1964, 1967, 1969).

Differences in thermoregulation and energy exchange in different seasons in voles, like variability of other physiological parameters, have been reported by many researchers (Slonim, 1952–1966; Bashenina, 1962, 1966; Drozd, 1967, 1968; Rauch and Hayward, 1969; Lynch and Folk, 1970; Pasanen, 1971; Zolotukhina, 1974; and others). Shvarts (1965, 1966, 1968) considers these changes linked with heredity, assuming that only those individuals survive that belong to genotypes in which the physiological characteristics are compatible with environmental conditions in the given season. I assume that the seasonal variability for thermoregulation and several other properties of voles are not only genetic, but arise as definite phenotypic attributes in response to the environment (Polyakov, 1964, 1967, 1969).

I propose that the spring and winter populations of voles are formed in nature depending upon the conditions in which neonates are reared. Young voles growing up at the end of spring and beginning of summer, when the temperatures around their nests are not low, are not exposed to periodic cooling when their parents leave the nest. This creates preconditions in which, when they lead an independent life and even in adulthood, they become more resistant to higher temperatures but less tolerant to low. Neonates growing up in the autumn, when low temperatures may prevail
352 around the nest, are exposed to periodic cooling when their parents leave the burrow. This promotes cold resistance. Such animals, when adult, possess a temperature optimum shifted toward lower temperatures.

An experimental study of the development of resistance to low temperatures in rodents was conducted by Chentsova (1963, 1970). Some of her results are briefly presented in Tables 3 and 4. As can be seen from Table 3, populations with different degrees of cold resistance are found in nature depending on the conditions in

which they grew up. Lemmings growing up in spring and at the beginning of summer, when favorable temperatures prevail near the nest, were less tolerant to cold than those growing up at the end of summer and during autumn, when the temperatures around the nest were lower.

Under experimental conditions (Table 4), a significant increase in cold tolerance of steppe lemmings was achieved when low temperature conditions were created near the nest in which the young animals grew up. Chentsova's observations showed that in this case the young animals are chilled when their parents leave the nest, which is accompanied by a periodic reduction in the body temperature of the neonates. The data available permits us to conclude that the shift in temperature optimum toward higher cold tolerance of a population (the winter habit) or heat tolerance (the spring habit) develops depending on temperature conditions in which the young animals grow. In this case, the higher the ambient temperature in the period of development of a neonate, the higher its optimum temperature.

353 As shown by Chentsova's experiments, just a few cooling periods experienced by young rodents suffice to sharply increase their cold resistance when they become adults. If the reproduction of voles and lemmings stops during summer under natural conditions, then the population that develops is of the spring type and not attuned for winter. In this case, they survive only in preservation places where reproduction did not terminate before autumn and where conditions were available for the development of cold resistance in the young animals. Such animals not only tolerate winter better, but also reproduce under then snow if sufficient food is available. Rodents surviving the winter are less adapted to withstand the summer heat. Summer conditions are tolerated by animals which grow up in spring. Cold tolerance in young voles is related to the formation of brown fat reserves in them (Rauch and Hayward, 1969; Pasanen, 1971). In the case of cooling at different ages, the whole metabolic process is directed toward fat synthesis, which increases cold resistance of animals in the adult stage. When reared under high temperatures, this property does not manifest itself in young rodents or is suppressed.

In adult rodents, as demonstrated by Chentsova's experiments (1963–1970), cold tolerance develops less well and is achieved by that cooling of the body which in nature could end in mortality. Therefore, adaptive changes involving temperature response develop fully only in young animals, mainly before the period of eye-

**Table 3. Cold tolerance of seasonal populations of steppe lemmings
(Krasnoyarsk territory)**

Season in which rodents grew up in nature	Age of rodents (months)	Number studied	Weight of animals before experi- mentation	At -20°	
				Average weight loss per hour (%)	Duration of survival (min) Average Maximum
Spring—beginning of summer	1.5—2.0	17	24.7	2.1	408 870
End of summer—autumn	1.0—2.5	27	24.2	1.4	1,077 1,880

Table 4. Cold tolerance of steppe lemmings reared in laboratory under different temperatures

Temperature near nest while rodents were growing up, °C	Age of lemmings studied (months)	Number studied	Weight before experiment (g)	At -20°		
				Average weight loss per hour (%)	Duration of survival (min)	
				Average	Maximum	
15	2	27	23.5	2.2	106	260
-2	2	19	24.8	2.0	335	900

opening. These circumstances in particular may be considered the main reason for an annual complete rejuvenation of the population of voles or lemmings, as well as for variations in composition of age groups of populations in different seasons and years.

Spring and winter populations of rodents differ not only in their cold or heat tolerance, but in their reproductive vigor under similar conditions of temperature and feeding. The reproductive vigor of lemmings reared at different constant temperatures as well as in varied temperatures, is shown in Table 5.

In conditions of a spring population, the reproductive vigor of a winter population was reduced to half, while that of a spring population in conditions of a winter population was 5.5 times less. Therefore, a shift in temperature also affects several other important adaptive responses of rodents, which ultimately find expression in variable reproductive vigor under identical environmental conditions. This determines all the characteristics of a population—its structure, survival, and number.

Thermoregulation is closely associated with the response of voles and lemmings to food. Forms with a temperature optimum shifted toward the higher side consume food with less moisture content. At an optimum ambient temperature (15–20°C), the social vole needs food containing about 55% moisture, while the common vole requires food with 60% moisture (Mokeyeva, 1949). The steppe lemming can manage with food of lower moisture content than the narrow-skulled vole (Gladkina and Meyer, 1963; Gladkina and Mokeyeva, 1970b, c). Young animals before sexual maturity better tolerate a moisture deficit in food than adults.

Table 5. Reproductive vigor of steppe lemmings reared in different temperature conditions and with subsequent change in ambient temperature (data of Chentsova, 1970)

Conditions of rearing	Progeny of 10 females for 10 months	Mean interval between broods (days)	Number of young per litter
Reared at 15°C	368	27	4.6
Same, shifted to -2°C	67	56	4.6
Reared at -2°C	267	35	4.0
Same, shifted to 15°C	198	45	6.0

Behind the differences in relation to food of varying moisture content lies the actual variable consumption of difficult-to-digest plant parts, since they in particular contain the maximum quantity of water. Forms exhibiting a higher moisture requirement have to consume more cellulose. This calls for some differences in feeding of individual species, which become most conspicuous in seasons of the year when conditions of heat exchange become extreme.

Seasonal variability in the feeding of voles is also observed for this reason. More complete information on seasonal feeding is available for the common vole (Bashenina, 1962; Straka, 1966), but it is also generally true for other species of this group. According to Straka (data collected in Bulgaria), in the warmest period of the year (April–September) green food is abundant. In June–August, seeds constitute a large percentage of the ration. This can be explained not only by a higher frequency of occurrence of seeds in this period (particularly seeds at the ripening stage), but also by the lower calorific value of green plant parts. In the colder period (December–January), the consumption of seeds increases. According to Bashenina (1962), in Moscow district green plant parts serve as the major food; during winter (February–March) such are the only food available (together with green shoots). Seeds constitute a large part of the ration in July–September. In the southern part of the range (Volgograd district), the importance of seeds in the feeding of voles increases significantly. However, the role of seeds in the feeding of voles during summer should not be overemphasized. Probably, these are still unripe seeds, which are difficult to identify in the stomach contents. As shown by numerous experiments, under natural conditions, voles consume almost no grain during summer; hence control of these rodents using poisoned grain bait cannot be effective (Polyakov, 1961a, 1968b).

In individual parts of their range, voles select a unique set of food plant species (Table 6). This is primarily due to affinity of habitats of different species in individual regions of the range to specific relief elements. Predominant microclimate, soil composition, and water regime help form the corresponding plant groups and their phenology which, in turn, decide the set of food plants.

Differences in feeding of individual species of voles, as probably also subspecies, are most strongly manifest during the hot period of the year, when the water requirement of rodents increases and the moisture content of food decreases. This permits us to consider that extreme summer conditions are the most difficult period in the life of voles and lemmings, when high temperatures occur to-

Table 6. Importance of individual families of plants (number of species given in parentheses) in feeding of common vole (from N.V. Bashenina).

Moscow district	Vologoda district	Bashkirian district	Dnepropetrovsk district
Compositae (35)	Compositae (18)	Compositae (14)	Poaceae (4)
Poaceae (17)	Poaceae (16)	Leguminosae and Umbelliferae (6)	Compositae (13)
Rosaceae (11)	Rosaceae (10)	Laviatae and Poaceae (4)	Leguminosae (11)
Leguminosae (12)	Umbelliferae, Asteraceae, Laviatae (7)		
Asteraceae (9)			

gether with drought. Particularly during this period, differentiation of places of survival occurs in sympatric individual vole and lemming species. Winter conditions demand higher energy losses to thermoregulation. With sufficient food supply, this problem is successfully tackled by rodents. The quality of food limits their survival to a far lesser extent than in summer.

355 Perhaps it was these conditions that determined the absence in common voles and lemmings of a characteristic typical of other rodents, i.e., storage of food for winter. Small daily reserves of green food are found during summer and autumn periods, which are meant for current use, especially in habitats rich in green vegetation. Usually, the plants are dragged only up to the opening of the burrow and are visible from outside. Such reserves make it possible for the voles not to move out of the burrow during the hot period of the day.

Individual reports are available in Soviet literature on reserves of concentrated food in the burrows of the common vole, meant for the winter period (Bashenina, 1962). True, as rightly pointed out by Bashenina, these reports cannot always be considered indisputable. I also happened to see, particularly in Crimea, reserves of wheat spikes reaching in weight up to 300–500 carefully laid in a chamber of a social vole burrow, similar to reserves of the common vole described by Rossikov (1915). However, they actually belonged not to the social vole, but to a gray hamster (*Cricetulus migrato-*

rius Pall.) which had occupied this burrow after chasing the hosts out.

Among foreign authors, information on the presence of comparatively small winter food reserves of the common vole has been reported by Regnier and Pussard (1926), Hammer and Sutova (1963), and Straka (1966). In 1968 in Kaliningrad district, T.S. Gladkina during extensive digging in October of burrows of the common vole in timothy grass and clover fields, found large food reserves stored in the underground chambers consisting of rhizomes and fleshy lower parts of stems. Individual colonies of voles had four chambers. The maximum quantity of reserves in a single chamber was 1.6 kg, and the total reserves of a colony reached 4.0 kg. In November, 1968, N. Yu. Chentsova noted similar reserves in the burrows of common voles near Pushkin in Leningrad district. Similar reserves have also been found in subsequent years. In discussing these facts, all of us were unanimous that the storage of food by the common vole became possible under conditions created by agricultural productivity. The habit of food storage can significantly increase survival of the common vole during the critical cold period of the year, which would increase its numbers (Gladkina and Chentsova, 1971; Gladkina, 1972). Storage of succulent food has been noted for Brandt's vole. It stores for the winter green (not yellow) juicy leaves, stems, and flowers of dicots, arranging them compactly so that during storage they sour and convert into a dense mass (Khrustselevskii *et al.*, 1952). These authors also report storage of dry plants by this vole, which are later used in spring for making nests. Overwintering of the population and its number the following year depend on the abundance of food reserves. This species is numerically maximum in Mongolia toward the end of the vegetative season. During this period control measures against Brandt's vole are implemented over large areas. However, ultimately, as a result of elimination of part of the population, survival of individual animals is ensured by the reserves stored by the entire population. Voles begin intensive reproduction in spring of the following year. The consequence of such a system of control of Brandt's vole in Mongolia was the appearance of large numbers over a wide area almost every year.

The aspects of thermoregulation noted above and their relation to food ultimately determine the range and habitat distribution of each species included in this group. With the ranges of several species overlapping, these aspects determine their habitat isolation. In the optimum season of the year, every species can be found

in the same place, even occupying the same burrows. However, with the onset of extreme seasons, the natural survival habitats become specific for each species. Only the hayrack and some other structures built by man as well as cultivation of perennial grasses, providing a favorable microclimate and food base, become places for conservation of several species. This does not contradict but confirms that the microclimate and food base in particular have become the decisive factors for conservation habitats of voles and lemmings.

Digging Activity

Significant changes are observed in the building of burrows by all species of voles and lemmings of this group, depending upon the conditions of vegetation and microclimate of a habitat as also seasons of the year. The need to provide optimum temperature and normal composition of air directs the digging activity of rodents and building of burrows and nests. In this context, study of the temperature preference of voles (Kalavukhov, 1950, 1951, 1957; Straka, 1967a, b) enables us to understand the reflex mechanism involved in digging activity that ultimately determines burrow construction. As shown by F. Straka, the temperature preferred by the adult common vole is in the range of 16–22°C. In other species under comparison, it was slightly higher or lower, corresponding to their optimum temperature requirement. On this basis it may be assumed that voles and lemmings create or try to create this temperature in the nest and burrow by changing the depth of passages in different seasons, or the disposition and construction of the nests.

Depending on the compactness of the ground, voles and lemmings dig burrows using their teeth and limbs; on a soft ground digging is done by the forelimbs. Soil is also thrown out by the forelimbs in swift movements, passing under the belly and between the widely placed hind limbs. When a sufficiently large heap of soil has accumulated at the entrance, the animal throws it away using the hind limbs or, turning around, pushes it with the entire body and head while standing on its hind legs. In this case, a typical groove is visible where soil has been thrown.

357 If the ground is hard, the voles dig tunnels using their incisors and the soil is thrown out in the manner described above. Some openings are dug from inside. There are no soil heaps around since

the soil is thrown out through the previously prepared entrance, or a small heap of soil may form through subsequent passage cleaning.

A description of burrows built by voles and lemmings has been provided by many researchers studying their ecology (Zarudnyi, 1897; Silant'ev, 1898; Nikolaevskii, 1918; Rodionov, 1924, 1936; Novikov, 1929; Formozov and Kiris, 1937; Naumov, 1937, 1948; Formozov and Veronov, 1939; Pogosyan, 1948; Bashenina, 1962; Straka, 1966; Popov *et al.*, 1968; and others). I have dug up the burrows of the social vole in Crimea, Trans-Caucasus, and northern Caucasus; of the common vole in the mountains of Crimea and Trans-Caucasus, in Vinnits, Aktyubinsk, Kustanai, and Leningrad districts; of the steppe lemmings in Aktyubinsk, Uralsk, Kustanai, and Pavlodarsk districts; of the Afghan vole in Tadzhikistan; and of the Trans-Caspian vole in Karakalpak and Tashauzsk district of Turkmenian SSR.

Burrow construction is similar in this group of voles and lemmings. The permanent burrows have a larger or smaller number of openings leading to the underground nest. Abandoned nests may be found in a colony together with inhabited ones. Sometimes additional burrows are connected with the main or underground tunnels. Such structures are termed colonies.⁴

In comparing the digging activity of different vole species, our attention is drawn to the number of entrance holes in each colony, depth of nest, and its construction. It may be considered a rule that the colonies of the species living in a hot and dry climate have a larger number of entrance holes and occupy larger areas than boreal species and those that confine their settlement to the moist part of the relief. Thus, colonies of the common vole, on the average, have a smaller number of entrance holes than the colonies of the

⁴It should be noted that there is no clear universal terminology for designating the elements of burrow construction, nor for the entire structure. It is more correct to call the shelters built in soil by rodents as burrows. However, a burrow is usually associated with a single passage leading to the underground nest. In reality, up to 100 and more entrance holes to a single shelter are sometimes found in the burrows of voles. Therefore, such shelters are sometimes termed a "township" (Heptner, 1956) or "khoton" which, in Buryatian, also means a township (Khrustselevskii *et al.*, 1952). A group of shelters forming a larger or smaller settlement of voles is called a colony (Heptner, 1956). However, in some scientific literature and handbooks published in the USSR as well as in field practice, a different terminology is used. Individual shelters are called colonies and entrance holes termed burrows. This is because the organizations conducting observations on voles, estimate their number counting all animals and living holes (opened by digging) (Kosov and Polyakov, 1958; *General Instructions*). A group of colonies is called a settlement (Polyakov, 1968b).

social vole; colonies of the Afghan vole have a larger number of entrance holes than those of the Trans-Caspian and social vole as well as the steppe lemmings; and colonies of the steppe lemming have more entrance holes than those of the narrow-skulled and Trans-Caspian voles. Colonies of Brandt's vole also have a higher number of entrance holes than those of the narrow-skulled vole. It may likewise be considered a rule that each species at places of low food availability and relatively dry conditions will have, on the average, a larger number of entrance holes and occupy more area than in habitats with dense vegetation. For this reason, variation in number of entrance holes in vole colonies has a regular seasonal nature—in periods with maximum food availability (spring), the number of entrances is minimum and increases by summer and autumn. In this context, species-dependent differences in colony structure of the common vole and the lemming decrease, compared to the type of habitats occupied by each species, climate of the region, and seasonal weather conditions.

358 In spring or at the beginning of summer, in habitats rich in food base (in turfy meadows, clover and lucerne crops, tillered winter crops), an occupied burrow (colony) may have a total of two to three entrance holes. I have dug burrows of the social vole, narrow-skulled vole, and steppe lemming in which a female with young or a pair with progeny lived. Under these conditions, communicating paths are laid in the form of tunnels in the root zone of the grass cover. These paths are often cut but when the plant cover begins to thin, they are simply trampled.

In summer and autumn, in habitats with a sparse, dry grass stand, all species of voles and steppe lemmings dig a large number of entrance holes to their colonies. If the number of rodents is high, by autumn the entire area appears riddled.

The number of entrance holes per hectare has reached 50,000–60,000 but more often is 10,000–15,000. Even the common vole, which digs burrows less actively than other species, when its numbers were large, averaged 58 entrances per rodent (Bashenina, 1962). In Azerbaidzhan in wheat stubble fields, up to 120–150 entries per social vole were counted at times of peak numbers and start of numerical decline. However, even at a relatively low numerical level of social voles, by autumn there are areas in which several thousand entrance holes per hectare can be seen.

Characteristics of the digging activity of the social vole in different seasons are shown in Figure 60. It should be noted that usually the number of entrance holes increases mainly at the beginning

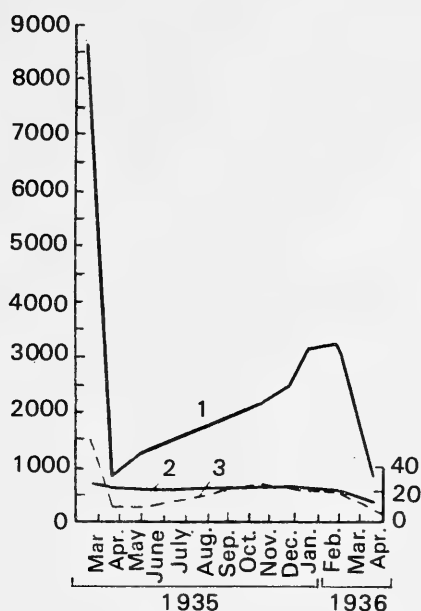


Figure 60. Dynamics of number of entrance holes (1), colonies (2), and "living" holes (3) of the social vole in a virgin pasture in Crimea (Svedlov Collective Farm).

Abscissa—time (months); left ordinate—number of burrows per hectare; right ordinate—number of colonies per hectare.

of reduction in total rodent population. Enhanced digging activity and increase in number of entrance holes can thus be considered an index of deteriorating conditions of survival. But this should not be mistaken for active burrow cleaning, usually observed after rains and in the morning.

Several researchers have concluded that new entrance holes into colonies are dug when runways are laid in the soil toward unexplored food areas (Rodionov, 1924, 1936; Khrustslevskii *et al.*, 1852; Heptner, 1956). With the thinning of vegetation within the limits of a colony, the latter rapidly increases. The area occupied by each colony and the number of entrances increase in the summer when plants cease vegetative growth because of high temperatures and thus their food value declines sharply. The number of inhabitants may thereby decrease. Even in comparatively optimum regions and habitats with a good food supply, an increase in entrances to a colony is observed with a general decrease in number

of rodents living in it (Table 7). During en masse digging of colonies in June, 2.5 entrance holes were the share of one common vole, in August only 0.6, but in October, 10. Bashenina (1962) has reported that 0.88 to 11.3 entrances per individual can be estimated for a lesser number of the common vole, and for a minimum number may vary from 2.55 to 0.60. Such comparisons without indicating the season and general direction of numerical density do not reveal the changing trends in these values.

The number of entrances opened after digging burrows provides only a very general idea of the actual number of voles and lemmings, since the same entrances may be used by several rodents. Furthermore, the higher the total number of entrance holes, the lower the percentage of "living" holes, and still lower the number of animals that can use one and the same entry to the burrow. With a good food base, up to 50% "occupied burrows" may be found in a densely populated habitat under intensive reproduction, although their total number may not increase over 1,000 per hectare. In low-food habitats, where the total number of entrance holes to the burrows may exceed 10,000 per hectare, those "occupied" may not constitute more than 1.0–2.0%.

The depth at which common voles and lemmings build their nests depends significantly on the season, vegetation, nature of relief and objects found on the soil surface (stones, ricks, embankments/bunds, etc.). In the presence of dense vegetation during spring and autumn, in periods of relatively optimal temperature for voles, the nests are built near the soil surface. Sometimes the roof of the nest chamber in turfy meadows lies at a depth of only 5–10 cm, but more often at 20–30 cm. In alpine meadows, nests are often built under stones weighing 20–100 kg, their larger part rising above the soil surface. In May–August, it suffices to shift such a stone to uncover an occupied nest of a vole in the soil underneath. Given the continued presence of ricks and embankments/bunds in fields, voles build nests directly under or even in them. In marshy land and other wet areas, nests of the common and narrow-skulled voles were found in hummocks.

Nests prepared in spring and autumn, the comparatively warmer period of the year, are fairly voluminous and rounded in shape. In wet places, their diameter may reach 18–20 cm and in dry places 14–16 cm. They are made of thin cereal stems split lengthwise, which are very dry, offer good insulation against heat, and are nonhygroscopic. In wet places, the periphery of an occupied nest may be dampened but its interior is always dry. Rodents

Table 7. Change in average number of entry holes to a colony and number of common voles per colony in different periods, 1938 (Vinnits district, Pogreishchanskii region, wheat field)

Indices	Periods							
	June	July	End July	August	End August	September	End September	October
Average number of entry holes per colony	7.0	6.0	5.0	5.0	6.0	12.0	14.0	35.0
Average number of voles per colony	1.5	2.0	3.0	4.0	4.0	6.0	2.0	3.0
Average number of voles weighing less than 10 g in one colony	0.5	1.0	1.0	3.0	2.0	3.0	0.5	0.5

are found in the center of such nests. Furthermore, their interior is lined with particularly soft thin hairs, offering maximum heat insulation.

In the hot period of the year the nest is built much deeper. At this time, occupied nests in Crimea, Trans-Caucasus, and Kazakhstan are often found at a depth of 35–80 cm. During this period common voles and lemmings, unable to dig deep in highly hardened soil, enter it through cracks or occupy the deeper burrows of susliks (*Citellus*) and mole rats (*Spalax*), building their own nests in them. They are forced to do this more often in eastern Siberia, Trans-Baikal, the Lower Volga, western Kazakhstan, and eastern Cis-Caucasus, where summer nests have been found at depths greater than 100 cm.

The summer nesting chamber is floored with grass stems split lengthwise, which do not obstruct heat discharge.

With the onset of cold and in the absence of a snow cover, nests are built at an even greater depth than during summer, but are similar in construction to spring and autumn nests, i.e., large and spherical.

The snow cover plays an exceptional role in the life of voles, a fact convincingly demonstrated by Formozov (1946). As the snow cover reaches a depth of more than 15–25 cm, voles and lemmings build nests directly on the soil surface and lay communication paths under the snow in the form of tunnels (Polyakov, 1881; Zarudnyi, 1897; Gorbachev, 1915; Formozov, 1946, 1957; Chentsova, 1947; Bashenina, 1962; and others). Such nests are spherical and reach 25 or even 30 cm in diameter.

Voles can create an optimum microclimate in nests under the snow. In the absence of warming up and with sufficient food available, voles and lemmings can reproduce under the snow. Formozov reported reproduction of the common vole under snow in the Gorky district; I noted it in Leningrad (1943) and Uralsk (steppe lemming). Chentsova has reported reproduction of the steppe lemming under snow in Krasnoyarsk (Minu-Cinskii region, personal communication), and Kryl'tsov (1955) observed winter reproduction of the steppe lemming in Tselinograd and Kokchetav districts.

Voles do not survive in the snowless areas of eastern Siberia during the very cold winter and therefore large areas are free of them (Formozov, 1946). With a small snow cover and deep frost, voles can overwinter only in places where snowdrifts form—embankments, forest borders, and parts of fields with dense vegetation. Chentsova (1949) believes that the habitat distribution

of the narrow-skulled vole in the Kulunkinskaya steppe of Altai, characterized by very severe winters, is determined not by the food base but by probable survival during winter. Therefore, this vole is found only where the snow cover is at least 30 cm deep in winter.

Crowding is observed among the narrow-skulled vole during winter—up to 10 rodents in a single nest (Chentsova, 1949), which reduces depletion of energy resources for thermoregulation since the heat discharge decreases (Slonin, 1952).

During spring, after snowmelt, the subsnow winter nests made and abandoned by voles and lemmings remain on the soil surface for a long time. Winter paths are discernible at the time of snowmelt in the form of iced channels and tubes up to 5.0 cm in diameter.

361 Voles and lemmings in their underground residences live in temperature conditions differing significantly not only from those at the soil surface, but also from temperatures of the same horizon in which the nest is built. Burrow temperature depends on temperature of the surrounding soil, atmospheric temperature entering the burrow, and the heat discharged by the rodents. It should be kept in mind that during the warm period the soil temperature during the day is much lower at a depth of 20–50 cm than on the surface. Therefore, the air in burrows is cooler than the air outside. This prevents the entry of the warmer outside air in burrows. Only after sunset, when the outside air has cooled, and the air in the burrows has warmed somewhat (at this time the soil temperature at a depth of 20–50 cm is maximum), does the denser and colder outside air flow into the burrow. This daily ventilation is of great significance for voles not only for maintaining a more favorable nest temperature, but also for maintaining a favorable air composition. The possibility is not excluded that the increase in number of entrances in colonies during summer is prompted particularly by the need to ensure the best nighttime burrow ventilation. In vole burrows, as demonstrated experimentally by Nekipelov (1958), a higher concentration of carbon dioxide gas (about 2.0%) forms rather readily with a simultaneous reduction in oxygen content (19%). As noted above, voles are particularly adapted to such a gas regime in the burrow. However, digging activity probably enables them to avoid a lethal concentration of carbon dioxide and oxygen starvation.

Table 8 presents original data characterizing the microclimate of burrows of the social vole in different habitats (Crimean steppe) during the warm period of the year, compared to temperatures at the soil surface. Similar results were obtained in the Karabakh

Table 8. Daily temperature fluctuations ($^{\circ}\text{C}$) in burrows (at depth of 30–50 cm from entry hole) and at soil surface in habitats of the social vole (Crimean steppe, 1936)

Habitat	Date	Place temperature recorded	Time of observation			
			7:00 a.m.	1:00 p.m.	7:00 p.m.	1:00 a.m.
Fallow	June 8	Soil surface	25	50	10	11
		Burrow	18	21	21	20
Wheat crop	June 11	Soil surface	28	60	22	18
		Burrow	17	19	20.5	20
Wheat crop	June 21	Soil surface	35	60	21	19
		Burrow	18	21	28	28
Fallow	July 31	Soil surface	30	49	31	28
		Burrow	27.5	27	31	31
Pasture	Aug. 24	Soil surface	34	61	34	18
		burrow	24	25	30	31
Barley stubble	Sept. 14	Soil surface	12	31	14	7
		Burrow	15	16	16	17
Pasture	Sept. 17	Soil surface	7	25	10	9
		Burrow	14	15	18	18
Barley stubble	Oct. 27	Soil surface	4	20	2	-2
		Burrow	5	6	8	6

362 foothills, Vinnits district, and other regions. Voles can create a microclimate in their burrows close to their optimal physiological requirement, albeit not entirely. The highest temperature in tunnels to the burrows and even in nests recorded in the hot period in Crimea and the Karabakh foothills, were extreme for the social vole, and even in the zone of optimal conditions of its range (Vinnits district), close to extreme for the common vole (Table 9). If the average temperatures in the tunnels to the burrows of different vole species are compared, it can be seen (Figure 61) that the maximum differences occur during the warm period of the year. This confirms the earlier assumption that the distribution of each species is significantly restricted by its ability to survive summer conditions, no less than winter conditions.

The need of voles and lemmings to ensure optimum temperature in the nest leads to significant deviation from "standard" nest construction. Thus, in Aktyubinsk district in the summer of 1937, I found a burrow of a common vole in the vertical wall of a trench, about 2.5 cm from the bottom. The passage was horizontal. The nest was 65 cm away from the single entrance and at a depth of about 2.0 m from the soil surface. During summer trenches laid

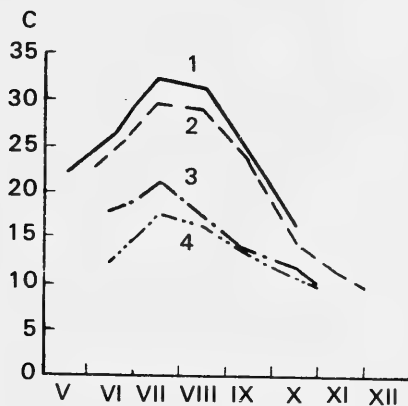


Figure 61. Seasonal change of temperature in vole burrows at depth of 20-25 cm from soil surface.

1—social vole in Karabakh foothills; 2—social vole in Crimean steppes; 3—common vole in Vinnits district; 4—bank vole in Vinnits district (deciduous forests); abscissa—months.

Table 9. Maximum temperatures in tunnels to burrows at a depth of 20–25 cm from soil surface (vertical) and in occupied nests of social, common, and bank voles in July

Species and location	Temperature, °C	
	Burrow	Nest
Social vole (steppe Crimea, Karabakh foothills)	32.5	25.0
Common vole (Vinnits district)	26.5	23.0
Bank vole (Vinnits district)	21.0	21.0

along roads and highways, if not cleared of grass, become conservation places for voles in many regions of their distribution. Burrows are dug in the slopes, which permits placement of the nest at a greater depth from the soil surface. When there is flowing water in such trenches, they become particularly suitable for this species.

Large-scale excavation of burrows has shown that each old colony has one or two abandoned nests in addition to occupied ones. Excavation in spring revealed that abandoned nests are deeper, in summer shallower. The location of an occupied nest always depends on the topography of the area occupied by the vole (Formozov, 1947;

Table 10. Temperature (°C) in nests of the common vole at different depths (habitat—grain crops; Vinnits district, 1939)

Dates of digging	No. of living colonies dug	Depthwise distribution of nests				
		Up to 15 cm	15–20 cm	21–30 cm	31–40 cm	50 cm and more
April 10–20	45	—	5	21	15	4
May 3–28	30	5	12	13	—	—
June 5–30	59	8	14	25	7	5
July 5–30	122	9	18	41	45	9
Aug. 5–30	210	58	122	28	2	—
Sept. 5–30	220	72	123	13	2	—
Oct. 1–15	151	12	32	35	20	2

Naumov, 1948; Bashenina, 1962). Table 10 presents original data on depth of nest placement by the common vole in different seasons and the temperature in such nests.

At the end of summer, voles are happy to occupy ricks, stacks and piles of hay as well as bunds located nearby. Nests are usually built directly in the uppermost soil layer under such covers and also in bunds when they are wet on the lower side. Nests are often located in the lower part of ricks and haystacks (Maksimov, 1964), because here voles can create a microclimate closer to optimum. Combined with an abundant food base, such nest locations enable the animals to reproduce vigorously during winter even in the northern regions of the range (Kuncheruk and Ryumin, 1938; Strel'nikov, 1940; Maksimov, 1964; and others).

There is sufficient evidence to believe that the reproduction of voles in haystacks in autumn, winter, and early spring largely determines range extension north and northeast in some species, especially the common vole. In regions of relatively optimal climate, their conservation is ensured by a higher numerical strength. In this respect, an interesting study was conducted in western Slovakia (Gaisler, Zapletal and Holisova, 1967). The authors found that the common vole is better adapted than other rodents to living in haystacks. This vole reproduces intensely throughout autumn, winter, and spring. Requiring less mobility in terms of food acquisition, it can expend more energy on reproduction.

Temperature in nests according to depth

Average up to 15 cm	15-20 cm			21-30 cm			31-40 cm	50 cm and more
	Max.	Average	Min.	Max.	Average	Min.	Average	Average
—	13.4	8.9	4.6	10.4	9.3	7.2	10.4	10.0
14.8	14.6	12.0	11.1	14.2	12.0	11.0	—	—
19.8	20.5	19.5	16.2	—	16.8	—	17.7	17.8
22.0	22.0	21.7	20.4	21.4	21.3	21.2	22.0	22.0
19.2	16.8	16.7	16.0	—	19.8	—	17.2	—
16.8	18.9	17.3	12.4	17.4	15.8	14.0	14.4	—
10.7	14.8	13.2	12.0	14.6	12.3	10.4	13.2	13.4

The activity of common voles and lemmings on the soil surface is intimately related to digging and its variability. During the hot period all of them are active in the evening, night, and early morning. They are more active during the day in the colder period. In general, they come to the soil surface when temperature conditions are close to optimum or conditions are least extreme. Only with en masse reproduction and a very scant food base, are these animals active on the soil surface even under an unfavorable temperature regime, which accentuates the stressed conditions of a population.

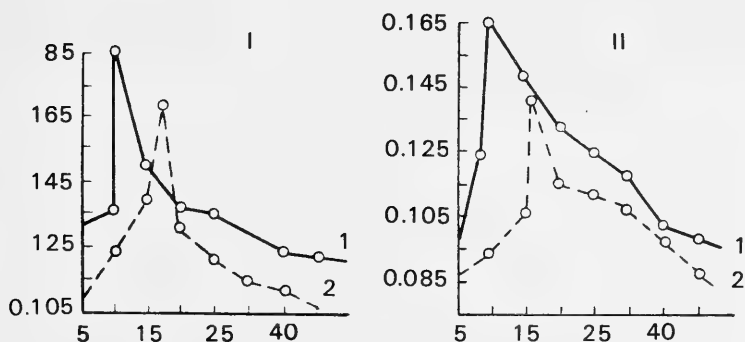
There are reports in literature that, unlike other common voles, Brandt's vole is active on the soil surface exclusively during the day (Kucheruk and Dunaeva, 1948; Khrustselevskii and Kopylova, 1957). A detailed study on the conditions of activity of Brandt's vole was carried out by Khrustselevskii and Kopylova (1957). They found that this rodent significantly changes the periods and duration of its stay on the soil surface during different seasons of the year, which enables it to avoid overheating as well as overcooling. The reason why this species is habituated to primarily diurnal activity is not yet clear. But the digging activity of voles and lemmings is of great adaptive significance in avoiding the effect of unfavorable interactions of climatic factors on these rodents. However, it would be wrong to conclude that a fossorial life style enables common voles and lemmings to completely overcome the unfavorable effects of climatic factors. Therefore, these factors, together with feeding conditions, are decisive not only in the behavior of common voles and lemmings, but also in the morphophysiological conditions of their populations, dynamics of habitat distribution, and numbers.

Development and Phenology of Reproduction

As in other members of the subfamily Microtinae, neonates of common voles and lemmings are born blind, without pelage and teeth, and incapable of maintaining their body temperature at a constant level. Their eyes are covered with a pink skin, eyelids and eyelashes absent, pinnae not isolated, and the digits not separated. By the fifth day incisors appear, eyelids have formed, the pinnae distinguishable, and the body covered with short fur. They begin to crawl from the fifth day even though their digits separate fully only by the eighth day of life. Eyes normally begin to open about the tenth day.

Before eye-opening, neonates feed on milk and, after a few days, change over to independent feeding. The temperature required in nests for their normal development is about 25–30°C. This temperature is created by the parents who not only warm the nests with their body but also their progeny. Under optimum conditions, the progeny grows very rapidly. Newborns weigh, on the average, about 2.0 g. Their weight has doubled by the age of five days, and may reach 6.0–8.0 g by the time of eye-opening. After the eyes have opened, the growth rate slows down. If the female does not provide normal feeding to her offspring, their development is retarded. Eye-opening may be delayed by 5–7 days (Figure 62).

For rodents, the day of eye-opening is a break-point in many respects for their development and existence. By this time, the process of relatively rapid brain growth is completed (more rapid than body growth); morphological and biochemical formations create qualitatively new possibilities for rodent response to environment and the formation of conditioned reflexes (Orbeli, 1961; Himwich, 1962; Kuznetsova, 1969). By this time, the teeth and intestinal tract have developed so well (Golenishchev, 1954) that they enable a
365 changeover to independent feeding. A radical change in metabolic activity also takes place. The level of metabolism under constant



364 Figure 62. Effect of parental feeding conditions on gas exchange and period of eye-opening in neonates (from Kagantsova, 1952).

I—common vole; II—social vole: 1—optimum ration; 2—moisture deficit in parental food; peak of curve—day of eye-opening; abscissa—age in days; ordinate—O₂ (cm³)/min/g body weight.

optimum ambient temperature gradually increases up to eye-opening and thereafter decreases with age (Polyakov and Pegel'man, 1950, 1953; Kagantsova, 1952, 1953; Bashenina, 1962). According to Kuznetsova (1969), this phenomenon can be explained in the following: before eye-opening, voles are not able to maintain their body temperature and are without chemical thermoregulation, but with age the rapidity of their cooling gradually decreases and heat accumulation increases in the body. Therefore, under constant ambient conditions, a premise is created for a higher heat accumulation in the body, which also determines an increase in intensity of metabolism. When the ambient temperature was changed, such that the body temperature in all the experiments was the same (achieved by using a higher temperature for younger animals), the level of metabolism remained the same but was higher than after eye-opening.

After eye-opening, a steady decrease in metabolic intensity takes place with age. This is related not to an increase in body size but to the typical ontogenetic variability of organisms (Polyakov, 1950, 1964; Arshavskii, 1974).

Female sexual maturation under normal conditions begins at the age of 20–30 days. Their weight during this period varies from 12 to 20 g. However, many researchers have reported cases of very early maturation and pregnancy with a body weight of no more than 8.0 g. Bashenina (1962) reported a case of pregnancy in a common vole with a body weight of 7.2 g. Such early maturation and reproduction is particularly typical of narrow-skulled and common voles. Pregnant females weighing less than 12 g were not found among the social vole and the steppe lemming.

Normally, males become sexually mature at the age of 30–45 days when they weigh 18–25 g.

Conditions of heat exchange and feeding greatly influence the rate of sexual maturation of both females and males as well as their growth. If these conditions are not optimal during lactation, not only is the maturation period of the neonates protracted (see Figure 62), but their subsequent growth and development hindered. Such neonates are smaller in size and their maturation delayed even when provided an optimum environment subsequently. If a young animal experiences unfavorable environment after eye-opening, its maturation may be delayed by several months (Polyakov and Pegel'man, 1950, 1953; Kagantsova, 1952, 1953; Golenishchev, 1954). The level of metabolism of such animals is significantly lower than that of normal animals, leading to general nar-

rowing of the thresholds of optimum environmental conditions. As a result, individuals develop with poor viability or a lower level of viability (Polyakov, 1950, 1954, 1964).⁵

Data on the effect of feeding conditions and thermoregulation on the development of young voles living in steppe biotopes, and the period of sexual maturation and beginning of reproduction have also appeared in foreign literature in recent years (Conaway, 1971; Lynch and Folk, 1971; Myers and Krebs, 1971; Straka and Gerasimov, 1971; Krebs *et al.*, 1973; Lidicker, 1973, 1974; Spitz, 1974; and others). However, in some publications the most obvious facts are interpreted not in relation to dependence of phenology of reproduction on conditions of feeding and thermoregulation, but as an expression of the mechanisms of autoregulation initiated under the influence of population density. Thus, no attention is given to the physiological mechanism determining the dependence of sexual maturation and reproduction of voles on conditions of feeding and heat exchange, but rather great importance attached to stress responses observed in artificially crowded populations, up to a limit that is manifoldly higher than observed in nature (Adamchik and Val'kova, 1974). It appears more reasonable to determine the mechanisms that reflect the direct effect of food and conditions of heat exchange on the sex cycle of steppe voles.

The sexually mature virgin living under optimum conditions has a menstrual cycle consisting of four phases: prooestrus, oestrus, metaoestrus, and dioestrus. Each of these phases is characterized by a definite histological picture of vaginal smear corresponding to definite changes in the ovaries as well as in the reproductive tract (L'vova, 1940; Alikina, 1954, 1955, 1956; Golenishchev, 1954; Bashenina, 1962).

The sexual cycle has been most completely studied in the social, common and narrow-skulled voles, and the steppe lemming. Under normal conditions, it lasts for 2 to 7 days. The dormancy period lasts for 30 hours to 3 days, and the period of prooestrus and oestrus for 1 to 3 days. The total sex cycle, based on length of individual phase, is very similar to that of rats (Sakharov, 1933, 1937; Nemilov, 1938).

⁵The term "viability" has entered ecology but nevertheless requires elaboration. It is more correct to use this term to indicate the phenotypic properties of a population that are manifest in level of intensity of utilization of environmental resources for reproduction. In this respect, the term "viability" also differs from "vitality," as the concept of virulence differs from the concept of pathogenicity. The level of vitality and not vitality *per se* may be considered a synonym of viability.

Histological studies of the sexual cycle in the common and social voles and the steppe lemming at different phases of the sex cycle were used by Alikina (1954) to demonstrate the correlation between ovarian condition and vaginal smear. In the complete absence of signs of sexual activity in the female, the genital aperture is closed; the ovaries appear underdeveloped and are reduced in size. Most of the follicles are small and have one row of cells in the follicular epithelium (Figure 63). Rarely, spherical follicles with a cavity are found, measuring 97–100 μm and up 300–410 μm in diameter, and with a multilayered follicular epithelium.

The vaginal smear in the resting phase of a female with a normal sex cycle contains leucocytes and nucleated epithelial cells (Figure 64, A). The ovaries contain atrophied follicles with degenerate egg cells, follicles with a developing cavity (diameter 250–300 μm), and a multicellular follicular epithelium (120–161 μm). Yellow bodies are not found (Figure 64, B).

367 In the prooestrus phase, the vaginal smear contains several nucleated cells and individual callused scales (Figure 64, A), which appear as a result of desquamation of the vaginal epithelium. The number of scales and their appearance *per se* attest to an approaching oestrus phase. Mature follicles with a large cavity (450–660 μm in diameter) are found in this period in the ovaries (Figure 64, D). Follicles at the initial phase of cavity formation are 200–370 μm in diameter and those with a multicellular epithelium 260–300 μm in diameter.

In the oestrus phase, the vaginal smear contains only callused scales (Figure 64, E). Mature Graafian follicles are visible in the ovaries (Figure 64, F), with a diameter of 710–750 μm or even up to 900 μm .

In the metaoestrus phase (Figure 64, G), the vaginal smear contains three types of cells—leucocytes, callused scales, and epithelial cells. The ovaries (Figure 64, H) contain follicles with a developed cavity and multicellular epithelium and atrophied follicles. Yellow bodies are not present. Such bodies appear in voles and lemmings only if copulation has occurred during oestrus (Bodenheimer and Sulman, 1946; Alikina, 1954). Alikina demonstrated that in females isolated from males, mature follicles are not ruptured during oestrus, which leads to protraction of the oestrus period. This should be considered a specific adaptation in common voles and lemmings related to their very high reproductive potential (Polyakov, 1967). Thus, the possibility of females being fertilized in their very first mating with an active male increases. Stimuli

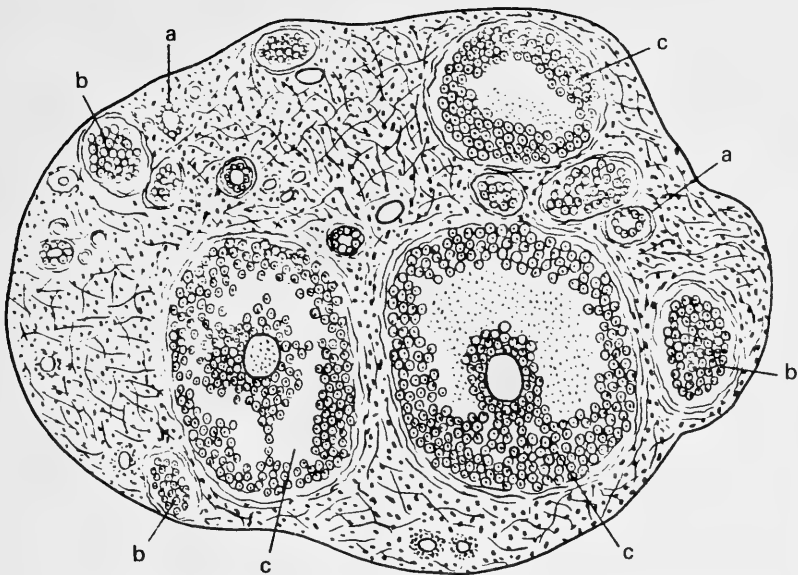
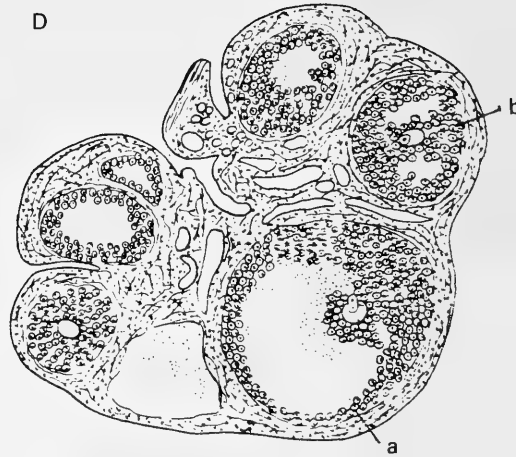
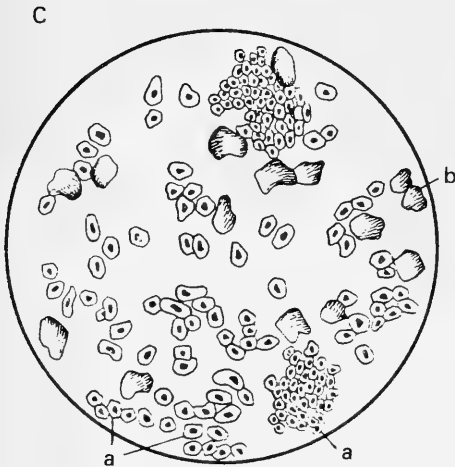
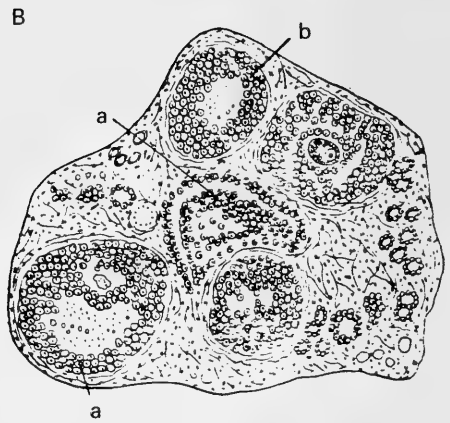
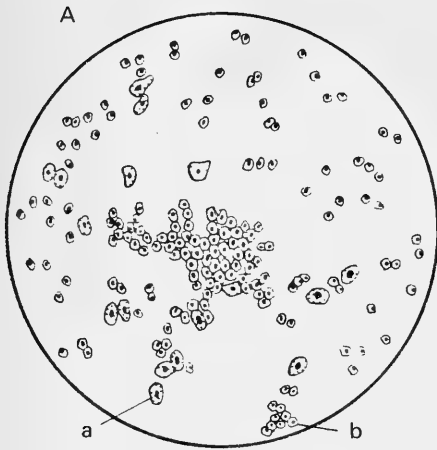


Figure 63. Structure of ovary of social vole corresponding to condition of female with a closed genital aperture ($\times 200$).

a—follicles with one row of cells in follicular epithelium; b—follicles with multilayered follicular epithelium, from $97\text{--}110\ \mu\text{m}$ to $190\text{--}250\ \mu\text{m}$ in diameter; c—follicles with developing lumen, from $300\ \mu\text{m}$ to $390\text{--}410\ \mu\text{m}$ in diameter (from Alikina, 1946).

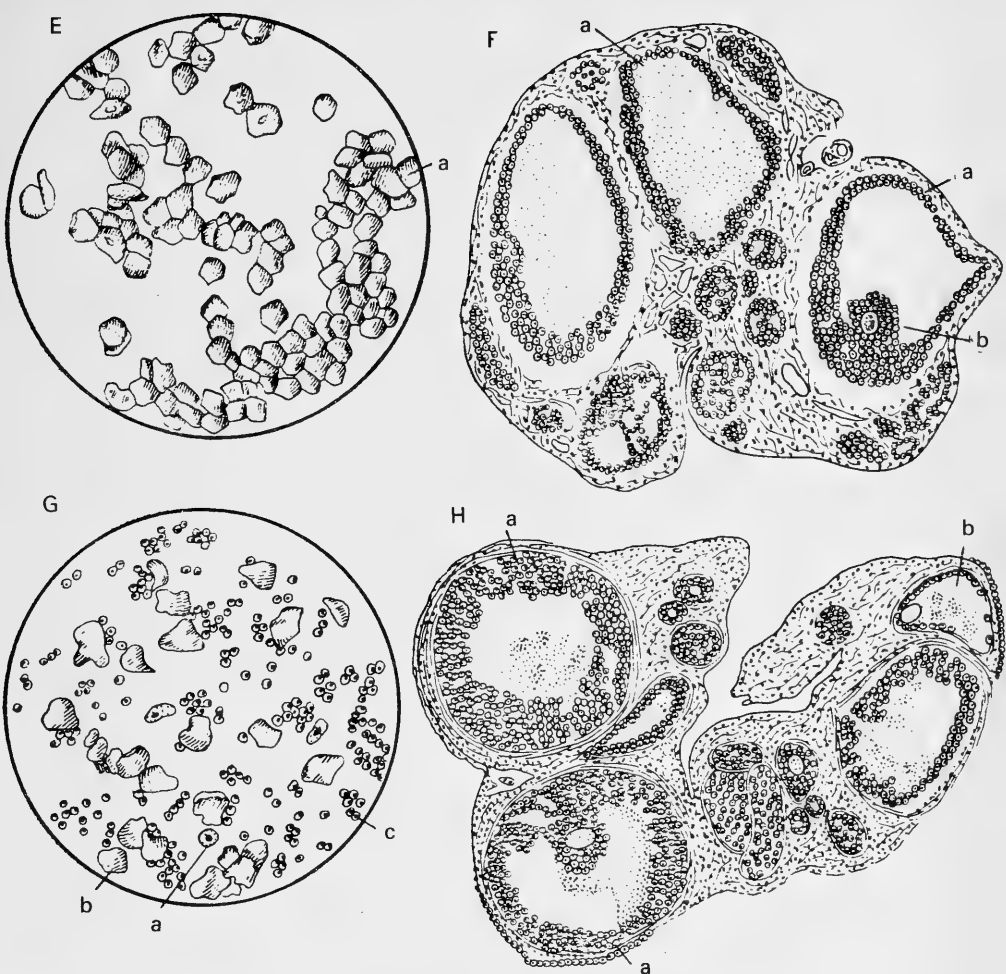
368 exert a marked influence on the course of the sexual cycle in this group of rodents—presence of burrows and nests, of males, and of courting. This can be judged from data published for other animals (Mashkovtsev, 1940; Polikarpova, 1941, 1947; and others). However, this does not exclude the great and decisive influence on the course of the sexual cycle in this group of animals exerted by conditions of feeding and thermoregulation. Numerous experimental findings obtained in the Laboratory of Weather Forecasts of the All-Union Plant Protection Research Institute and Field Experiments (Polyakov, Kagantsova, Golenishchev, Gladkina, Mokeeva, Askerov, and others), as well as reports in literature (Vereshchagin, 1946; Kovdyshev, 1950; Bashenina, 1962; and others) fully confirm this conclusion.

Experiments by Alikina (1954, 1956) and Golenishchev (1954) have shown that reduction in moisture content in the food of voles



by 30 to 50% in the presence of abundant grains and optimum environmental temperature, causes a fairly rapid termination of the sex cycle in both common and social voles and closure of the genital aperture. In females with an initial weight of 39.0–42.5 g (high viability), such a diet led to a weight reduction of 24–27 g, but the sex cycle, though exhibiting a protracted rest phase, was nevertheless prolonged.

In females who, as a result of feeding on a moisture-deficient diet lost no more than 50% body weight, and thereafter were given appropriate food, the sexual cycle was restored within 10 days. The social vole and the steppe lemming are slightly less sensitive to



368—369 Figure 64. Structure of ovaries and nature of vaginal smear of social vole at different stages of sex cycle (from Alikina, 1964).

A—vaginal smear in resting phase: a—nucleated epithelial cells, b—leucocytes; B—structure of ovary during resting phase: a—atrophied follicles, b—follicles with developing cavity ($\times 200$); C—vaginal smear corresponding to prooestrus phase: a—epithelial nucleated cells, b—callused scales; D—structure of ovary corresponding to prooestrus phase: a—almost mature follicles, b—follicles with maturing cavity ($\times 200$); E—vaginal smear during oestrus phase: a—callused scales; F—structure of ovary during oestrus phase: a—mature Graafian follicles with egg cells ready for discharge ($\times 200$); G—vaginal smear in metaoestrus phase: a—nucleated epithelial cells, b—callused scales, c—leucocytes; H—structure of ovary during metaoestrus phase: a—mature Graafian follicles, b—mature follicles ($\times 200$).

moisture reduction in food than the common and narrow-skulled voles. The combination of moisture-deficient food and high environmental temperature (25–28°C) caused a rapid and significant weight loss in all voles and the lemming, and immediate termination of the sex cycle. Restoration of the sex cycle after changeover to optimum conditions was not observed in all females and was achieved only after a long time in others. Under natural conditions, sexually mature females trapped under conditions of heat and drought in summer, as shown by numerous observations on different species of voles in many areas of their range, are not capable of commencing reproduction in autumn. More often they die before the onset of favorable weather. Females which had not attained sexual maturity before drought set in, sometimes participated in autumn reproduction. They underwent a shift in optimum level toward higher temperatures and therefore could tolerate such conditions better than mature animals (Polyakov, 1937–1969; Mokeeva, 1949; Polyakov and Pegel'man, 1950, 1953; Askerov, 1953; Gladkina and Meyer, 1963; and others).

Cooling or a general food deficit during the autumn–winter period also causes termination of the sex cycle in mature females and delay maturation of young females. Therefore, we agree with Bashenina (1962) in that the winter break in reproduction of voles and lemmings is due to conditions of food and heat exchange. When these conditions are favorable (in haystacks under a stable snow cover), reproduction does not cease even during winter. The summer recess in reproduction is similarly explained by conditions of food base and climatic factors. There are reports in literature about the influence of light on the reproduction of voles (Baker and Ranson, 1932). Kalabukhov (1935) proposed that winter termination of reproduction in these rodents is related to reduction in daylength. Experimental data (Golenishchev, 1958; Bashenina, 1962) and numerous field observations have not confirmed this conclusion. Duration of daylength exerts no influence on the sex cycle of females and reproductive intensity of voles and lemmings included in this biological group.

In sexually mature male voles and lemmings, spermatogenesis is completed with the formation of spermatozoa which fill the seminiferous tubules and epididymes. Under normal conditions, the seminiferous tubules and epididymes are 91–156 μm in diameter (Figure 65, A, B). The weight of testes reaches 1.5–2.2% body weight, and they shift from the body cavity into the scrotum.

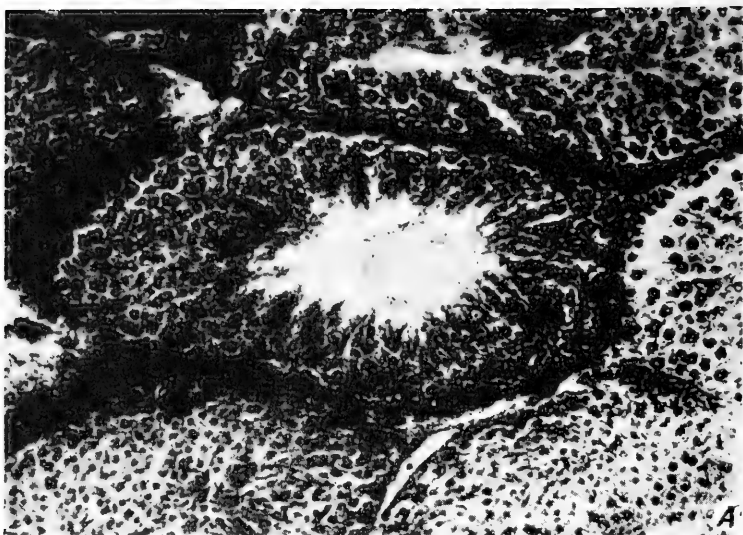
Isolation of males from females had no significant effect on intensity of spermatogenesis (Stieve, 1928; Suglitskii, 1939). But conditions of feeding and heat exchange exerted a very strong effect. The degree of suppression of spermatogenesis depends upon the extent and duration of unfavorable factors. A complete disruption of spermatogenesis leads to cessation of spermatozoan formation in the seminiferous tubules. Only Sertoli cells with a small number of spermatogonia develop in the tubule walls. Spermatogenic epithelium completely disappears and is found only in the lumen of some tubules in a mixed condition (Figure 65, C). The epididymes have empty ducts with complete disturbance of spermatogenesis or cells of spermatogenic epithelium are found in them (Figure 65, D). The total testicular and epididymal weight is much reduced, no more than 0.75–0.80% body weight. The testes are retained in the body cavity and cannot be felt in the scrotum. Usually, isolated spermatozoa with poor motility are found in a testicular smear of such males.

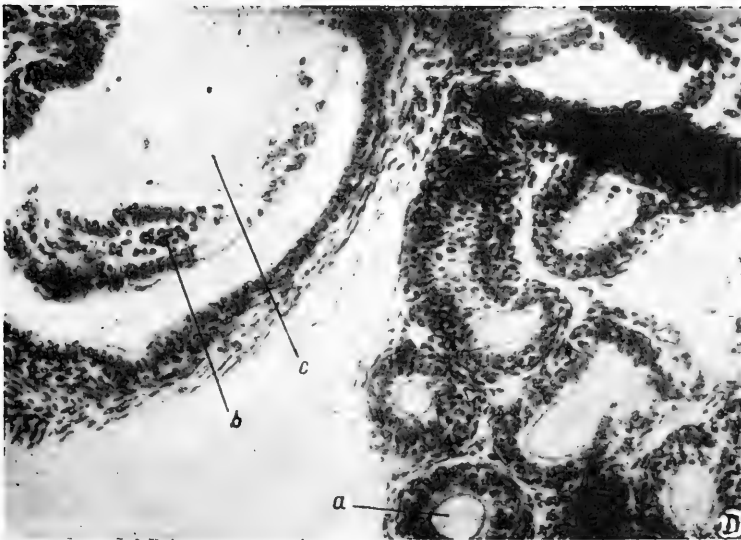
A weaker suppression of spermatogenesis is characterized by partial cessation of testicular functioning, the process ceasing with formation of spermatocytes. Spermatogenesis may continue in other parts of the testes. Other cells of the germinal epithelium are found in the epididymis together with spermatozoa. Motile sperms are found in smears of the epididymis. Probably, males with different intensity of spermatogenesis may differ significantly in sexual activity and ability to fertilize.

371 Under a combination of high temperature and moisture-deficient diet, suppression of spermatogenesis sets in quickly and intensely. This is observed even under optimum temperatures with a reduction in food moisture content by 20–50% of the required level.

Restoration of spermatogenesis after its strong or weak suppression was observed 10–12 days after the males were transferred to optimum conditions. Concomitant with restoration of relative weight of the testes, body weight was likewise restored. Unilateral castration of males demonstrated that the extent of suppression of spermatogenesis and rapidity of its restoration depend on how sharply conditions deviate from optimal. With a sharp deviation, suppression is greater and restoration less than under gradual change.

These results show that the phenology of reproduction of common voles and lemmings is determined by conditions of nutrition and heat exchange. If they are optimal, reproduction may





371 Figure 65. Condition of the testis and epididymis at different phases of activity in common voles (from Alikina, 1956).

A—section of testis during active spermatogenesis, seminiferous tubules with large number of spermatozoa; B—section of epididymis during active spermatogenesis, lumen filled with spermatozoa; C—section of testis under highly disturbed process of spermatogenesis; D—section of epididymis under highly disturbed spermatogenesis: a—empty lumen of seminiferous tubule, b—cell of germinal epithelium, c—chromosomes of disintegrated nuclei ($\times 240$).

take place throughout the year. Therefore, it would be erroneous to consider the seasonal nature of reproduction as a reflection of a genetically determined rhythm, consequent to selection of voles belonging to the genotype exhibiting a specific reaction to the environment (Shvarts, 1967; and others). Nonreproducing voles living in a field or fallow land during winter do not differ genetically from those living nearby in hayracks where reproduction is intense. Responses to environment and the limits of phenotypic variability of such responses under the influence of environment are not determined genetically.

Pregnancy, Fertility, and Intensity of Reproduction

Pregnancy continues for 20 days in common voles and lemmings. Cases of birth after 18–21 days are also found. The level of metabolism gradually increases during pregnancy, then decreases during the last days even though the embryo's weight is now one-third the mother's (Kargantsova, 1953). These facts led to the identification of two stages of pregnancy (Polyakov, 1950, 1954, 1964): during deteriorating survival conditions for the female, embryos are resorbed in the first stage but aborted in the second. Bashenina (1962) has identified three periods during pregnancy; her second and third periods correspond to mine, while her first period covers embryo implantation.

The next pregnancy may occur on the day of delivery or, in some cases, during lactation. However, under normal conditions, pregnancy occurs after lactation is completed and therefore even under intensive reproduction, the gap between two broods is about 30 days.

The maximum number of embryos recorded in common voles and lemmings is 10 to 13, and the minimum 1 to 2. There is one record of a vole with 15 embryos (Snigirevskaya, 1947), which could be considered a pathological case. Under natural conditions, I have found 20–23 neonates in a single nest, of slightly different ages (up to 3 days), which belonged to 3 females who were simultaneously feeding them. Under laboratory conditions, simultaneous feeding of neonates by several females is a fairly common phenomenon.

The number of embryos depends upon conditions of feeding and heat exchange, age of females, and frequency of conception. The conditions of feeding and heat exchange ultimately determine the energy resources the organism can release for reproduction. The number of maturing sex cells depends upon the latter, as well

as the sexual activity of females and males, the capacity to maintain the embryos formed during pregnancy, and the ability to feed the neonates.

372 In young females aged 20 to 30 days, not much energy is available for reproduction, and therefore they produce fewer offspring than older females. However, the birth and feeding of progeny is accompanied by such large energy losses that they *per se* become an inhibitory factor. Hence, with repeated births, the number of embryos declines. Under natural conditions, a female is able to have not more than four broods, more often 1 to 3. This is related to her total life expectancy, which is not more than 8 to 10 months, and to the limited duration of favorable seasons for reproduction. The conditions of existence for voles were uniform in the Laboratory of Forecasts of the All-Union Institute of Plant Protection, which created exceptional possibilities for their survival. Under these conditions, individual females lived for more than 3 years and cases of up to 30 broods were recorded (Pegel'man, 1951; Alikina, 1954). Up to 22 broods under laboratory conditions have been reported in literature (Frank, 1956).

The capacity of voles to reproduce is influenced not only by conditions of their existence, but also by conditions in which they lived and developed before attaining sexual maturity. Under natural conditions, it was often found that a large population existing in apparently favorable conditions for the species did not reproduce, or only stray breeding occurred. Such phenomena were always observed in populations that had survived prolonged drought (Polyakov, 1949a, 1954; Gladkina and Meyer, 1963; Lidicker, 1973, 1974). It often happens that in a population living in relatively poor conditions, the animals breed somewhat more intensely, with a larger number participating, than those existing in more favorable conditions.

Numerous field observations and precise laboratory experiments have made it possible to understand the ecological situation under which such phenomena become possible and are a regular feature. With the onset of drought and high temperatures, adult animals which have already reproduced, die. Juveniles, living and maturing in unfavorable conditions, even when favorable conditions return, exhibit low reproductive ability. Most such voles do not reproduce, and stray reproducing animals have fewer progeny of poor viability (Polyakov, 1950–1964; Askerov, 1953; Kagantsova, 1953; Golenishchev, 1954; Levi, 1955, 1958).

Intensity of reproduction is an integral index of a population. It involves several components—sex ratio, ratio of age groups, per-

centage of breeding females, and average number of embryos. Often the intensity of reproduction is judged only on the basis of percentage of pregnant females and number of embryos. This index should be considered inadequate since it does not allow assessment of the total possible brood, upon which greatly depends the directed changes in population strength. The number of embryos per hundred animals over a given period of time or season as a whole gives a more correct idea of reproductive intensity.

The intensity of reproduction in voles and lemmings is determined by the environmental conditions in which they live, as well as by the viability (survival ability) of the populations formed under the influence of conditions of their existence during the previous season. There can be several combinations of variable viability of populations and extent of favorable conditions of existence in which they may subsequently find themselves. I shall mention only the six most contrasting ones: (1) high viability and optimum conditions; (2) high viability and inhibitory conditions; (3) high viability and very unfavorable conditions; (4) low viability and optimum conditions; (5) low viability and inhibitory conditions; and (6) low viability and very unfavorable conditions. In the first and second cases, intensive reproduction and population increase may take place, while reproduction may be very weak and population density decrease in the fourth and fifth combinations. In the third combination, the population may be even more numerous, and can be renewed through reproduction with further improvement in conditions of existence. In the sixth combination the population dies out quickly and is not capable of initiating reproduction even with improvement in living conditions.

A few examples may be cited to illustrate the foregoing choices exercised in nature. In the foothill and steppe regions of Azerbaidzhan during the spring of 1941, autumn of 1947, autumn of 1951, and autumn of 1962, viable and intensively breeding populations of the social vole were observed, and consisting of animals of varying weight (up to 62 g). But this population did not reproduce in the same region during autumn in 1941, 1948, and 1952, and consisted of very small animals (Table 11) which were not viable. In autumn of 1963 (beginning of December), stray animals reproduced but could not compensate the population losses and the rodents numerically decreased. Yet autumn in Azerbaidzhan is usually a favorable period for reproduction of the social vole. Therefore, the difference in intensity of reproduction in a particular year cannot be explained solely on the basis of environmental conditions

to which the populations were exposed during this period. Similar data have been reported for *Microtus californicus* by Lidicker (1973, 1974).

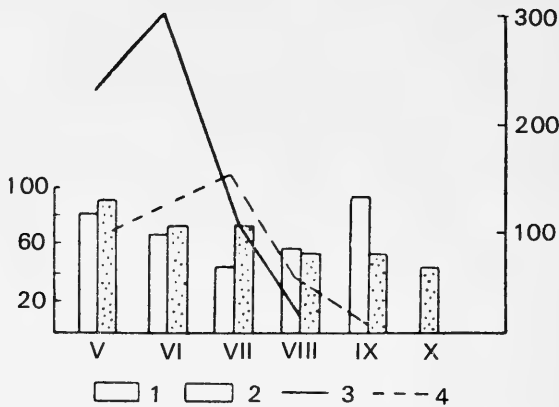
The general state of two populations of the common vole from montane meadows in Azerbaidzhan (Dashkesan region, 1951 and 1952) is shown in Tables 12 and 13; the intensity of their reproduction during this period and conditions of food base are shown in Figure 66 (3,863 animals examined; Askerov, 1953). Succulent plants were taken to characterize the food base. This index is very significant for the common vole. The quantity of food in the sub-alpine meadows was sufficient in both years, and if at all depletion occurred, it was in plant moisture content.

It is not difficult to see that the two populations differed significantly in 1951 and 1952 in reproductive intensity and general state. In May, 1951 voles weighing less than 35 g constituted 68.8% and in June 56.7% of the population. In spite of intensive reproduction commencing from the end of March and an increase in total rodent population (Figures 67 and 70), the average vole weight increased compared to May. This may serve as an index of rapid growth of juveniles, which is typical of a viable population. In the same habitat, in May, 1952, voles weighing less than 35 g constituted 96.6% of the population and in June, 84.5%.

374 Reproduction in both years began almost at the same time. In June, 1952 an increase in average vole weight as well as in

Table 11. Percentage of weight groups of social vole in major habitats of Martuni region of Azerbaidzhan, summer of 1941

Habitat	Weight groups (g)	Ratio of groups in different months (%)					No. of voles examined
		June	July	Aug.	Sept.	Oct.	
Virgin land	29.0-33.5	10.0	6.3	6.9	0.0	1.3	762
	19.5-22.6	73.6	63.2	85.5	70.8	80.3	
	10.7-16.3	16.4	30.5	7.6	29.2	18.4	
Green crops	29.4-34.1	19.4	6.7	12.8	8.2	2.6	688
	20.4-22.8	68.7	78.7	78.0	94.0		
	14.3-16.7	11.9	9.2	8.5	13.8	3.4	



375 Figure 66. Duration and intensity of reproduction of common vole and condition of moisture content of food in 1951 and 1952 in subalpine zone of Azerbaïdzhān.

1—moisture content of food in 1951; 2—1952; 3—number of embryos per hundred voles in 1951; 4—1952 (from Askerov, 1953). Abscissa—months; left ordinate—moisture percent of food; right ordinate—number of embryos per hundred voles.

population was noted. However, the voles were heavier, on average, during spring and at the beginning of summer of 1951 than in 1952. Conditions of feeding and heat exchange in May and June of 1951 and 1952 were almost poorer or even slightly more favorable in 1952 (Figure 66). Thus moisture content of food in May, 1951 was 81.35% and in June 72.42%; values in 1952 were 82.9% and 75.2% respectively. Intensity of reproduction in 1951 was much higher (Figure 66). On mountain slopes during May, 1951, 74.3% females reproduced and 72.8% in June; reproduction in ravines was 61.8% in May and 57.9% in June; in 1952, 37.5% females reproduced on slopes in May and 40% in June; in ravines 33.3% in May and 37.9% in June.

375 The number of embryos per hundred females was much higher in 1951 than in 1952 (Figures 69 and 70).

All the foregoing differences between populations in these two years cannot be explained solely by conditions of their existence during the period of study, since these were generally more favorable in 1952 when reproduction was less intensive. The viability of the

Table 12. Indices of weight of populations of common vole in habitats located in a ravine in subalpine meadows of Azerbaidzhan during 1951-1952 (from Askerov, 1953)

Year	Month	Frequency of different weight groups in population (%)									
		Up to 15 g	15.1-20 g	20.1-25 g	25.1-30 g	30.1-35 g	35.1-40 g	40.1-45 g	45.1-50 g	More than 50 g	
1951	May	5.9	16.3	13.4	17.0	16.2	14.0	4.4	8.4	4.4	
	June	22.3	10.3	5.2	8.6	10.3	16.0	10.8	5.7	10.8	
	July	22.7	21.7	6.4	3.4	12.3	9.8	14.3	5.5	3.9	
	August	26.9	40.4	1.1	2.3	9.3	6.9	4.6	4.9	3.6	
	September	36.3	68.4	2.9	4.1	12.8	1.1	1.2	0.0	0.0	
	October	30.3	47.6	0.0	5.3	0.0	0.0	0.0	0.0	0.0	
1952	May	20.7	0.0	0.0	55.2	20.7	3.4	0.0	0.0	0.0	
	June	24.1	12.1	0.0	15.5	32.8	12.1	3.4	0.0	0.0	
	July	31.6	9.1	9.2	2.6	19.7	18.4	10.5	2.6	0.0	
	August	38.1	27.2	1.8	10.9	10.0	5.5	6.3	0.0	0.0	
	September	36.9	43.4	3.7	9.8	2.1	1.0	2.1	1.0	0.0	
	October	37.1	52.6	8.9	1.4	0.0	0.0	0.0	0.0	0.0	

Table 13. Indices of weight of populations of common vole in habitats located on mountain slopes in subalpine meadows of Azerbaidzhan during 1951-1952 (from Askerov, 1953)

Year	Month	Frequency of different weight groups in population (%)									
		Up to 15 g	15.1-20 g	20.1-25 g	25.1-30 g	30.1-35 g	35.1-40 g	40.1-45 g	45.1-50 g	More than 50 g	
1951	May	6.78	20.89	12.16	12.16	13.51	14.86	11.49	5.40	2.75	
	June	15.17	11.18	5.69	8.98	11.24	13.48	9.53	11.80	12.30	
	July	22.66	13.30	5.90	7.88	15.66	15.76	9.36	7.39	1.99	
	August	19.50	38.59	2.07	3.70	13.35	7.90	9.50	3.30	2.10	
	September	42.10	40.50	0.80	7.40	9.10	0.0	0.0	0.0	0.0	
	October	23.50	64.70	5.90	5.90	0.0	0.0	0.0	0.0	0.0	
1952	May	23.50	2.0	5.80	37.30	19.60	5.80	3.90	0.0	1.90	
	June	33.0	11.60	0.90	12.70	17.70	19.50	2.90	0.90	0.90	
	July	27.00	12.00	9.00	4.50	15.00	14.20	6.00	9.70	2.60	
	August	38.30	23.20	4.60	7.10	6.60	13.20	6.00	1.00	0.0	
	September	45.60	44.40	2.90	1.80	3.50	1.20	0.60	0.0	0.0	
	October	51.90	41.50	3.80	2.50	0.0	0.0	0.0	0.0	0.0	

populations differed (Polyakov, 1950–1967) before they reached these conditions. The reduced viability in 1952 is explained by the fact that the food moisture content in July and August, 1951 was insufficient (48.14% in July and 58.82% in August), coupled with a comparatively high temperature. As a result, vole reproduction ceased in August, 1951, mortality occurred among heavy individuals (more than 35 g) who even in July constituted more than 25% of the total population, and development of juveniles was delayed, who commenced reproduction only in spring of 1952.

Kagantsova (1952, 1953) simulated the conditions rodents may face during drought. Young of common and social voles, 15–20 days old (sexually mature), were used in three experimental series each with its own control group. Broods were divided into equal numbers for experimental and control groups. In the first experiment, the rodents were maintained for four months on a moisture-deficient diet (oats with a moisture content of 23% and hay, with 25–40% of the required quantity of succulent food, i.e., root tubers) at 18–20°C. In the second experiment, the rodents were maintained for 50 days on the same ration as in the first experiment but at 28–31°C. In the third experiment, they were kept on a ration with sufficient moisture content but at a temperature of 28–31°C. A total of 83 broods of social vole (406 animals) and 112 broods of common voles (550 animals) were used in these experiments. Control animals in the third experiment received an excessive quantity of hay and oat grain soaked in water as well as tubers.

Another series of experiments, under less severe conditions of survival, were conducted for the common vole by Golenishchev (1954). Gladkina and colleagues (1962, 1963a, b) conducted a comparative study in the same program using different subspecies of the narrow-skulled vole and the steppe lemming.

The average weight of the social vole at the commencement of the first experiment was 19.6–19.8 g, and after one month 12.4 g (62% of initial weight); weight in the control had reached 28.6 g (140% of initial level). Experimental rodent weight after four months was 10.8 g (54% of initial weight) and in control 33.4 g (170% of initial weight). In the common vole, at the commencement of the experiment the average weight was 17.4 g, and after four months 9.7 g (55% of initial weight); control animals of the same age (4 months and 20 days) weighted 30.8 g (172% of initial weight). Further maintenance of experimental voles on diminished rations resulted in mortality.

The level of metabolism of the experimental voles was lower than in control, a critical metabolic point observed at a lower temperature, total intensity of chemical thermoregulation less (Figure 67), and stability of body temperature at lower environmental temperatures much less than in control. Keeping the animals in a chamber at 0°C for 1.5 hr caused a reduction in body temperature of the experimental social vole group to 17.7° , and 13 of 25 (52%) died due to excessive cooling. At 5°C , after 1.5 hr the body temperature dropped to 15.6°C and 33% of the animals died of chill. Control animals at 0°C after 1.5 hr showed a decrease in body temperature by 6.7°C but none died of chill.

In the common vole from the first experiment, at 0°C the body temperature after 1.5 hr decreased to 14.6°C and 39% animals died (7 of 18), while in control the body temperature under these conditions decreased only by 4°C without consequences.

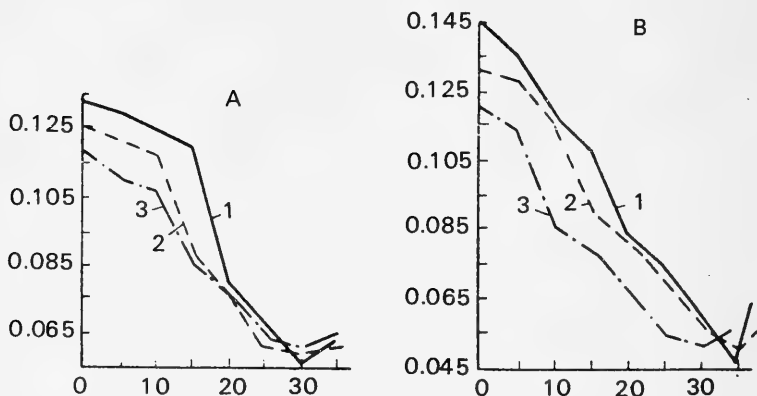


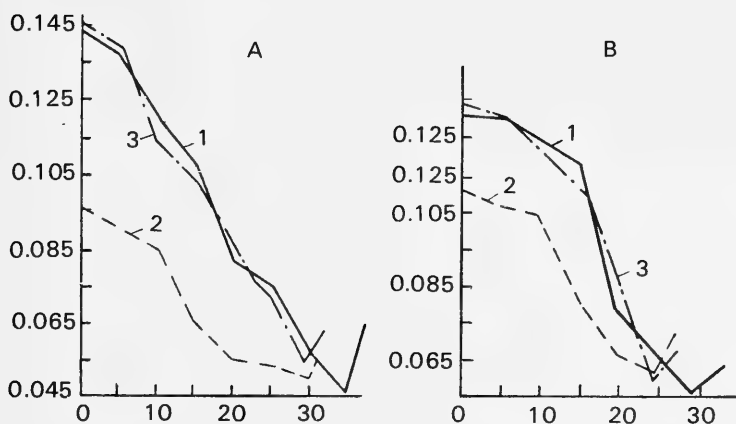
Figure 67. Effect of gas exchange on voles under conditions of the first experiment and subsequent maintenance of animals in optimum conditions.

A—common vole; B—social vole: 1—control (optimum conditions), 2—after development under experimental conditions, 3—after transfer from experimental conditions to optimum conditions and life under these conditions for four months (from Kagantsova, 1952). Abscissa—temperature of chamber, $^{\circ}\text{C}$; ordinate— O_2 (cc) requirement/min/g body weight.

A temperature of 36°C caused no overheating of the social vole in control, while experimental animals were overheated even at 30°C; at 32°C, 68% animals (12 of 19) died and at 35°C mortality was 100%. Overheating of the common vole from the first experiment began at just 27°C, while all the animals died at 30°C. In control no overheating was recorded even at 33°C.

All the experimental voles became sexually mature at the age of 4.0 months and 20 days. In control, the first litter appeared at the age of 2.0 months; and thereafter each family produced a litter, on the average, after an interval of 30 days.

In the second experiment, the animals were even more inhibited than in the first. Their initial weight of 20.3 g fell after 50 days to 10.6 g (52.2%). Control animals in the same period showed an increment of 147% over initial weight. In experimental voles, a significant decrease was recorded in metabolic activity, intensity of chemical thermoregulation (Figure 68), and range of tolerable temperature. In voles of the second experiment, the body temperature changed more rapidly under the influence of ambient temperature than in voles from the first experiment.



377 Figure 68. Effect of gas exchange on voles under conditions of the second experiment and subsequent maintenance of animals in optimum conditions.

Legend same as in Figure 67.

In the third experiment, young social voles maintained at 30–31°C initially grew rapidly and thereafter showed a decline. At the age of 90 days experimental animals weighed less than control. In common voles maintained at 28–29°C, no initial acceleration in growth was observed. Toward the end of the experiment, in both groups, a reduction in metabolic level together with a distinct shift of optimum to higher temperatures was recorded. Thus, when the experimental social voles were maintained for 1.5 hr at 36°C, their body temperature rose by 2.1° (up to 40.6°C) and they all lived. Of the control animals, five died due to overheating under these conditions. Maintenance of experimental rodents at 0°C for 1.5 hr caused a drop in body temperature of the social vole by 12.3°C and in the common vole by 10.0–10.2°C there were no mortalities. Under the same conditions, the body temperature of the controls fell by 6.7°C in the social vole and 4.0°C in the common vole.

Sexual maturity set in earlier in all the experimental rodents than in control. The earliest brood of experimental common voles was obtained at the age of 37 days and of social voles at 42 days. Over a period of three months, seven broods (32 young ones) were obtained from five experimental common vole females versus 12 broods (61 young ones) from five control females. Four experimental social voles produced five broods (22 neonates) in three months versus four control females who produced eight broods (40 neonates). Therefore, despite earlier maturation and adaptation of the organism to existence at high temperatures, the overall intensity of reproduction in experimental voles was half that in control. It should be noted that control voles obtained less than normal succulent food and hence reproduced 30% less intensively than usually observed under laboratory conditions.

Voles of the first and second experiments, after maintenance at the prescribed conditions, were subsequently transferred to an optimum regime. This period for voles of the first experiment coincided with the age of 4 months and 20 days and for the second experiment, 2 months and 10 days. They were kept for four months under an optimum regime. Over this period their body weight doubled but was still far less than in control (Table 14). The level of their metabolism was higher but the critical point still remained in the lower temperature range (see Figures 67 and 68). The range of temperature tolerated was narrower than in control (Table 15).

After their transfer to an optimum regime, common voles from the first experiment began reproducing after 2.5 months (at the age of 7 months and body weight of 20.5 g). Social voles from

this experiment began reproducing 3.0 months after their transfer to an optimum regime (at the age of 7.5 months and body weight of 22.6 g). During their five-month period of existence in an optimum regime, only 4 of the 7 experimental common vole females reproduced. They yielded 5 broods totaling 19 newborns. The largest brood size was 4 and the smallest 2. For the same period, 126 neonates were obtained from 4 control females. Of the 6 social vole females of this experiment, 5 did not reproduce even after a five-month stay in an optimum regime. Only one female produced a single brood (4 neonates) over the five-month period. For the same period, 6 control females produced 180 offspring.

Of the 5 social voles females in the second experiment, only 2 began reproducing after 3.5 months in an optimum regime. In an optimum regime of six months these two females produced three broods (5 neonates). For the same period, five control females produced 26 broods with a total of 127 offsprings. Of the four common vole females in this experiment, only two began reproducing three months in an optimum regime. During their six-month stay in an optimum regime, only two broods totaling 3 progeny were obtained. For the same period 22 broods totaling 109 progeny were obtained from four control females.

A comparison of brood size for 10 experimental and 10 control females for the entire period, including their stay in inhibiting and optimum conditions yielded the following results. In a 10-month-period 27 offsprings were produced by common vole females in the first experiment but six in the second, while common vole* females produced 6 in the first experiment and 10 in the second. In control, 423 and 368 progeny were obtained over this period from common vole females, and 365 and 370 from social vole females.

Viability of the progeny from experimental females was very low. Some newborns did not survive even to the eye-opening stage. Eye-opening was delayed by 5–6 days (Figure 62). Only after changeover to independent feeding did the progeny of the surviving experimental voles gradually level off with control progeny.

These data rather convincingly show that reproduction intensity of voles and lemmings is solely determined by environmental conditions in which the populations develop and live. Yet the numerical strength of a population and any change in numbers depend in particular on reproductive intensity. This situation is confirmed by the results presented in Figures 69 and 70. Reproduction of

*Misprint in the Russian original; should read "social vole"—Eds.

Table 14. Change in body weight of voles kept under an optimum regime after development in unfavorable conditions (from Kagantsova, 1952, 1953)

Treatment	Weight at time of transfer to optimum regime	Weight during maintenance at optimum regime toward end of			
		1st month	2nd month	3rd month	4th month
Common vole					
First experiment	9.7	18.7	20.1	20.3	20.5
Control	30.6	30.7	30.9	31.0	31.3
Second experiment	8.4	12.5	16.5	17.6	18.1
Control	29.4	29.8	30.1	30.2	30.7
Social vole					
First experiment	10.8	19.4	21.6	22.4	22.6
Control	32.4	32.6	32.8	33.0	33.4
Second experiment	10.6	13.8	17.4	18.8	19.9
Control	30.2	30.9	31.2	31.8	32.3

the common vole in the subalpine meadows of Azerbaidzhan was more intensive in 1951 than in 1952. Accordingly, the numerical strength of this species was also higher in 1951. However, reproduction of voles stopped earlier in 1951 than in 1952. Accordingly, their number was higher in autumn of 1952. It is important to note that viability of populations, upon which their intensity of reproduction depends, largely determines the possibility and intensity of interaction of mortality factors in a population.

From the foregoing results it is possible to judge the significant change in mortality and overall survival in populations with different levels of viability resulting from the influence of climatic factors. However, it is important to note that even the effect of biotic factors on mortality depends largely on the viability of a rodent population.

As shown by Pegel'man (1958), voles that had experienced even less suppression than those in the experiments described above during their period of development showed a lower resistance to rat and murine typhus. When infected, the virulence of the pathogen increased; contrarily, in animals of normal viability the virulence of the bacteria decreased (Pegel'man and Bobovich, 1958). Fenyuk

379 **Table 15. Change in body temperature of voles held 1.5 hr in a thermostat chamber, then maintained in an optimum regime for 4 months after first and second experiments (from Kagantsova, 1952, 1953)**

Conditions of maintenance before changeover to optimum regime	Temperature of chamber (°C)	Change in body temperature (\pm °C)	Experimental outcome
Social vole			
Maintenance for 4 months at 18–20°C with insufficient succulent food (first experiment)	0	–15.1	32% died
Maintenance for 50 days at 28–30°C with insufficient succulent food (second experiment)	0	–17.0	One died (5%)
Control	0	–6.7	All lived
First experiment	32	+3.5	38% died
Second experiment	32	+3.7	33% died
Control	0	+1.5	All lived
Common vole			
Maintenance for 4 months at 20°C with insufficient succulent food (first experiment)	0	–12.7	20% died
Maintenance for 50 days at 28–31°C with insufficient succulent food (second experiment)	0	–14.9	30% died
Control	0	–4.0	All lived
First experiment	27	+3.2	30% died
Second experiment	27	+3.5	32% died
Control	30	+1.0–1.5	All lived

and Sheikina (1960) found in their interesting study that the life span of voles is short; only 0.1% newborns live to the age of 10 months. Their data show that mortality increases during epizooties (in the phase of decreasing numbers).

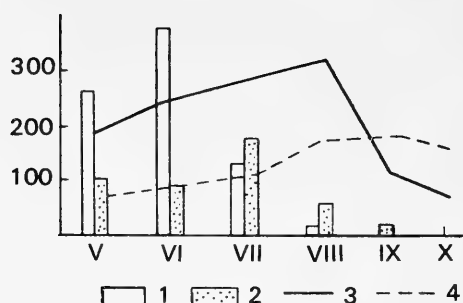


Figure 69. Dependence of numerical dynamics of common vole on intensity of reproduction in slope habitats, subalpine zone of Azerbaijan, Dashkesan region.

1—number of embryos per 100 voles in 1951; 2—same, 1952; 3—change in population (caught in 100 traps per day) in 1951; 4—same, 1952 (from Askerov, 1953). Abscissa—months; left ordinate—number of embryos per 100 voles; right ordinate*—percentage trapped.

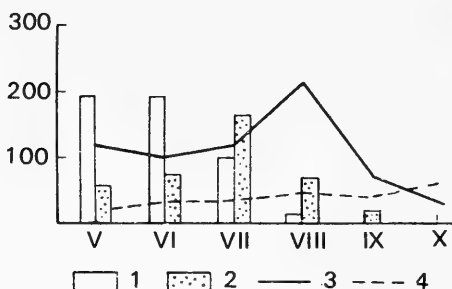


Figure 70. Dependence of numerical dynamics of common vole on intensity of reproduction in ravine habitats, subalpine zone of Azerbaijan, Dashkesan region.

Legend same as in Figure 69.

Interesting data have recently been obtained in western France (Martinet and Spitz, 1971) characterizing seasonal changes in growth, fertility, and mortality of common voles. A relationship has been traced between the photoperiod and state of vegetation on the

*Not given in original—Eds.

one hand, and fertility, growth rate, and mortality of voles on the other. It has been demonstrated both in extensive field material (11,400 voles) and under experimental conditions that males and females born in March, April, and May grew faster up to age four months, those born in September–October grew very slowly, while those born in June–August occupied an intermediate position. Voles born in September–October–November recovered growth and at age six–seven months had attained the size of March-born voles at age two–three months. This is the age group responsible
381 for spring reproduction. Mortality was maximum during winter months, particularly among the group that reproduced in late spring. Reproductive intensity was maximum in March and survival of March-born neonates maximum. Indices of growth, reproduction, and survival correlate well with food quality. However, it is not clear what the relationship of these indices is to photoperiod—direct, or indirect through state of food. The latter appears more probable.

Thus, one cannot refute that factors determining reproductive intensity in a population of voles and lemmings largely determine their mortality. Under intensive reproduction a rapid population growth is not only determined by high brood size, but also because several factors of mortality exert no influence on the changing trend in population number. Under poor reproduction, a sharp fall in overall population density is determined not only because the brood fails to replenish the “natural loss”, but primarily because mortality increases relatively, with new factors becoming involved, which were ineffective under intensive reproduction resulting in high population survival. These conditions are applicable not only to such factors of mortality as epizooties, but also to the influence of predators on the rodent population. Under intensive reproduction, mortality due to predators is relatively low and is never a factor suppressing the population growth of voles (Formozov, 1948; Kadochnikov, 1953; Thiollay, 1968; and others). This is explained by other reasons. First, an increase in number and activity of predators always lags behind periods of population growth of their prey. Secondly, in the first period of increase in vole numbers, the rodents are generally less prone to extermination. Only during the peak population number, when the wave of intensive reproduction has virtually subsided, does the role of predators as a factor of mortality increase.

These trends are quite significant for understanding the processes of formation and numerical dynamics of voles and lemmings.

Populations and Their Formation

All biologists agree that a population, and not an individual animal, should be considered the form of existence of a species. However, there is no single opinion as to which spatial group should be considered a population (Polyakov, 1940, 1967, 1969; Polyakov and Shumakov, 1954; Dubinin and Glembotskii, 1967; Shvarts, 1967, 1969; Naumov, 1967; Popov, 1968; Panteleev, 1968; Timofeev-Resovskii *et al.*, 1969; and others). Various interpretations of populations are related to the fact that in forms exhibiting different types of adaptation to the environment, populations occupy spaces differing in area and extent of ecological similarity. Furthermore, populations of individual biological forms may differ in stability of response to environmental changes. Therefore, phenotypic and genotypic variability affect population formation differently (Polyakov, 1967, 1969). This being so, it is difficult to find a formula that would be equally applicable to a common group of species and could be understood as precisely as the concept of organism.

I consider the following concept acceptable:

Population is a group of individuals belonging to a single species having approximately similar physiological properties (taking into account age-dependent properties) in view of their development and existence under approximately similar conditions typical of a particular habitat (biotope or region). Because of the nature of adaptations common for the species, the appearance of populations of an individual species is possible over a fairly restricted space; such species represent a greater population variability. Other species form a fairly uniform population over a large geographic region; they are characterized by a small number of populations (Polyakov and Shumakov, 1954, p. 280).

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Subsequent definitions have emphasized that populations do possess "a definite degree of similarity of gene pool" and "common morphophysiological-ecological properties" (Shvarts, 1967, 1969; Panteleev, 1968). However, such additions add nothing essentially new for identification of populations. Every biologist knows that populations having common physiological properties must be homogeneous to a certain extent in their morphology, responses to environment and particularly the environment in the territory occupied by them, and that they should have a common gene pool by and large.

There has been a tendency in recent years to exclude from the definition of population all that is associated with the direct effect of the environment on its formation, especially conditions of feeding and heat exchange. An attempt is being made to return to the genetic interpretation of the term "population". This is because the term was introduced by geneticists to differentiate pure lines from a mixture of genotypes. Later, "population" was introduced in ecology to designate settlements differing in morphophysiological characteristics due to environment (Kashkarov, 1945). However, after the development of population genetics, many ecologists began to define population from the viewpoint of genetics.

The characterization of a population given above is from an ecologist's point of view, and primarily deals with differences introduced in its condition by the environment. In this case, the nature of these differences is not identified—are they the consequence of phenotypic or genotypic changes of the organism forming a population? The definition of a population from a geneticist's viewpoint differs significantly. Here, primary importance is given to genotypic uniformity and extent of isolation, while the direct influence of environment on morphophysiological variability of individual groups is not taken into account (Dubinin and Glembotskii, 1967; Timofeev-Resovskii *et al.*, 1969). Thus, Timofeev-Resovskii and his colleagues (1969, p. 67) characterize a population as follows:

... an aggregate of individuals of a particular species during a sufficiently long period of time (a large number of generations) living on a specific territory in which some degree of panmixis occurs, there are no notable isolation barriers, and which is separated from neighboring similar populations by some degree (sometimes more, sometimes less) of isolation pressure.

In practice, when comparing two populations, attention is paid to differences in age composition, phenology and intensity or reproduction, habitation density, and some morphological characters, in particular, such a derived character as weight of compared age groups. Naturally, a comparison of populations can be perfected and elaborated by using various morphophysiological criteria (Shvarts *et al.*, 1967). In this case, it should be borne in mind that morphophysiological criteria help reveal differences in genetic or geographic populations only for forms with a low sensitivity to the energy resources of the environment and climatic factors. In forms more sensitive to such factors, these criteria are less applicable for determining

seasonal populations. Therefore, while investigating populational differences, it is necessary to consider which biological form the ecologist is dealing with. It is well-known that the vast majority of animal species inhabiting the earth belong to forms exhibiting a distinct response to climatic factors and energy resources (Zavadskii, 1968; Strel'nikov, 1970), and may comprise not only genetic, but also geographic habitat-related, and biotopic populations, and polyvoltine forms can even have seasonal forms (Polyakov, 1973). But in recent formulations of the concept of "population," insufficient attention is paid to the role of environment in its formation. It is obvious, however, in most animals species, populations are confined to specific habitats (biotopes)—a fact recognized long ago (Polyakov, 1940). In populational changes, a greater role of selection of certain genotypes by the environment is visualized (Shvarts, 1967, 1969) rather than the formation of their phenotypic properties by the environment. This one-sided tendency is readily rectified if we recognize that the more sensitive the response of a species to its environment and the greater the range of its phenotypic variability, the more varied will be its population structure. Common voles and lemmings belong to populations of all ranks—genetic, geographic, terraineal, biotopic, and seasonal—as is allowed by the biological form. This fact permits a better understanding of the life of populations of a species and parameters of their variability in time and space.

Considering the great theoretical and practical significance of a concrete concept of populations, I shall endeavor to show how and which factors influence the formation of populations of common voles. I use here the unpublished data included in my doctoral dissertation (Polyakov, 1950). Z.P. Nazarova, N.P. Kadoschnikova, and V.K. Shepeleva took part in its compilation (assessing the food base of the common vole in Vinnits district). Populations of the social vole were studied in steppe Crimea in 1936 and the mountains of Karabakh in 1941, while populations of the common vole were studied in Vinnits district in 1938 and 1939.

Habitats were compared in terms of microclimate, general nature of plant canopy, weight of vegetation and its moisture content. Populations were compared in terms of each age group, periods of sexual maturation, phenology, and reproductive intensity. Age groups were identified through systematic and continuous sampling from populations based on external morphological features and body weight. Naturally, errors cannot be excluded; however, general differences in populations of the

habitats compared are irrefutable and the factors causing these differences quite apparent.

In Crimea the habitats of the social vole and in the Vinnits district the habitats of the common vole differed little in microclimate and climate of the locality. They did not differ in such indices as temperature at a depth of 20 cm from indices recorded by the nearest meteorological station. This allows us to consider that the differences in the populations compared in a given geographic region were caused not by climatic factors, but by feeding conditions—which differed significantly (Table 16). However, variation in the conditions of the populations in each habitat in different seasons and their overall differences in each region were caused not only by conditions of the food base, but also by climatic factors. The territorial boundaries of habitats and periods of their conditions being more or less optimum for voles, were determined by the nature and periods of agricultural operations.

385 The following legend is used to designate age groups:

- P — Parental group. In Crimea and Vinnits district this was a homogeneous group of overwintered rodents
- F_1, F_2, F_3 — Progeny of the first, second, and third broods of the parental group, i.e., the first generation
- F_1^1, F_2^1, F_3^1 — Progeny of the first, second, and third broods from F_1
- F_1^2, F_2^2, F_3^2 — Progeny of the first, second, and third broods from F_2
- F_1^3, F_2^3, F_3^3 — Progeny of the first, second, and third broods from F_3

All the progeny of $F_1, F_2,$ and F_3 constitute the second generation.

- K_1^1, K_2^1, K_3^1 — Progeny of the first, second, and third broods from F_1^1
- K_1^2, K_2^2, K_3^2 — Progeny of the first, second, and third broods from F_2^1
- K_1^3, K_2^3, K_3^3 — Progeny of the first, second, and third broods from F_3^1
- L_1^1, L_2^1, L_3^1 — Progeny of the first, second, and third broods from F_1^2
- L_1^2, L_2^2, L_3^2 — Progeny of the first, second, and third broods from F_2^2
- L_1^3, L_2^3, L_3^3 — Progeny of the first, second, and third broods from F_3^2

- M_1^1, M_2^1, M_3^1 — Progeny of the first, second, and third broods from F_1^3
 M_1^2, M_2^2, M_3^2 — Progeny of the first, second, and third broods from F_2^3
 M_1^3, M_2^3, M_3^3 — Progeny of the first, second, and third broods from F_3^3

The entire group beginning with K_1^1 and ending with M_3^3 constitutes the third generation. The process of generation formation could not be followed further, and the rodents were grouped according to the period of their birth ("September," "October" groups).

It is quite possible that a large part of the third generation of voles and lemmings were able to participate in reproduction only under favorable conditions of the year.

The number of rodents belonging to different broods and generations which could be analyzed is shown in Tables 17 and 18. In spite of the fact that their total number is fairly large, individual groups were insufficient for complete characterization due to the fact that their total number in the population was small.

Periods of sexual maturation in all age groups were determined from the appearance of the first pregnant females. Commencement of pregnancy was determined from the condition of embryos (Polyakov, 1940). Survival of voles up to time of sexual maturity was estimated by comparing the number of embryos with number of voles caught in a population (number of embryos taken as 100%). Further decline in an age group from one brood to another was calculated by the formula

$$\frac{A_2 \times 100}{A_1},$$

where A_1 = initial number of rodents of a given age group per unit (10 ha);

A_2 = number of rodents recorded in next period of comparison.

Data characterizing the rate of maturation of the age groups of the common vole and their survival in different habitats in Vinnits district is presented in Tables 19 and 20. It should be noted that uniformity of conditions of existence of the rodents within the limits of each habitat produced uniformity in each population, particularly during periods of development. Deviations in the period of sexual maturation or in the appearance of the earliest and latest brood within the limits of the reproducing individuals of a definite age group of a population, did not exceed 15 days except in autumn (20

Table 17. Number of common voles examined in 1938 in individual habitats in each age group (Vinnits district)

Habitat	Age group	Before first brood	At time of different broods and their development				After reproduction	Total
			1st	2nd	3rd	4th		
Wheat— standing crop and stubble	P	—	3	4	16	14	4	41
	F ₁	—	4	61	38	—	—	103
	F ₂	—	90	24	32	—	4	150
	F ₁	16	66	17	9	—	7	115
	F ₃	90	34	41	—	—	—	165
	F ₄ , F ₂ ¹ , F ₁ ²	244	52	—	—	—	—	296
	August-born	264	—	—	—	—	—	264
	September-born	451	—	—	—	—	—	451
	October-born	74	—	—	—	—	—	74
	Clover	P	—	4	4	11	—	—
F ₁		—	4	42	4	—	2	52
F ₂ , F ₁ ¹		—	39	5	13	—	—	57
F ₃ , F ₂ ¹ , F ₁ ² , K ₁ ¹		86	—	174	—	—	10	117
F ₃ , F ₂ ² , K ₂ ¹		10	10	—	—	—	12	32
September- and October-born		123	—	—	—	—	—	123
Forest		P	—	—	4	19	—	—
	F ₁	4	35	16	—	—	—	55
	F ₂ , F ₁ ¹	—	34	10	6	—	—	50
	F ₃ , F ₁ ² , F ₂ ¹ , K ₁ ¹	—	28	21	25	—	4	78
	F ₁ ³ , F ₂ ² , K ₁ ¹	20	10	—	—	—	6	36
	September-born	66	—	—	—	—	—	66
	October-born	26	—	—	—	—	—	26

days). This led to the inclusion of voles in which reproduction was delayed—virgin females—which, in turn, reduced the percentage of breeding females in a given group in the brood under consideration. However, coincident periods of appearance of neonates often were not observed even with 100% gestating females.

389 Throughout the warm period of the year, common voles experienced almost no suppression in all habitats, although the degree of favorability differed in them. The adult part of the population

387 **Table 18. Number of social voles examined in 1936 in individual habitats in each age group (Crimea)**

Habitat	Age group	Before first brood	At time of different broods and their development				After reproduction	Total
			1st	2nd	3rd	4th		
Wheat field	P	12	52	36	17	8	—	125
	F ₁	25	50	12	—	—	—	87
	F ₂ , F ₁ ¹	—	50	—	—	—	—	50
	F ₃ , F ₂ ¹	12	—	—	—	—	—	12
Barley stubble	Migrant	—	12	22	50	—	—	84
	August-born	—	18	50	—	—	24	92
	September-born	22	106	—	—	—	32	160
Fallow	October-born	40	—	—	—	—	—	40
	P	4	2	10	5	—	—	21
	F ₁	5	15	—	—	—	—	20
	F ₂	—	20	20	15	—	—	55
	F ₃ , F ₁ ¹	9	23	15	—	—	—	47
	F ₁ ²	—	54	—	—	—	11	65
Virgin land (grazing land)	August-, September-, and October-born	43	—	—	—	—	—	43
	P	3	10	10	5	—	—	28
Virgin land (grazing land)	F ₁	6	6	—	—	—	—	12
	F ₂	7	18	26	17	—	4	72
	F ₃ , F ₁ ¹	42	105	—	—	—	—	147
	F ₁ ²	—	39	—	—	—	—	39
	September- and October-born	67	—	—	—	—	—	67

reproduced quite intensively and the juveniles attained sexual maturity comparatively rapidly and began to breed. However, neonate maturation varied from 20 to 68 days, excluding those that remained sexually immature during winter (did not begin to reproduce). During spring and summer, voles in the forest became sexually mature earlier than those in the wheat and clover fields. Voles in the forest had better feeding conditions up to August. Together with succulent vegetation, they consumed buds and ripening seeds. As a result, in the first half of the breeding season, 14 different age

Table 19. Average number of neonates in a brood (numerator) and percentage of females participating in reproduction (denominator) in different age groups of the common vole populations investigated

Habitat	Age group	Age up to first brood (days)	Number of neonates in brood and percentage of females participating in reproduction											
			March	April	May	June	July	Aug.	Sept.	Oct.	Nov.			
Wheat standing crop and stubble	P	Up to 200	—	$\frac{7}{100}$	$\frac{7}{100}$	$\frac{7}{83}$	$\frac{7}{83}$	$\frac{7}{83}$	$\frac{7}{83}$	$\frac{7}{83}$	$\frac{7}{83}$	$\frac{7}{83}$	—	—
	F ₁	56	—	—	$\frac{6}{100}$	$\frac{6}{100}$	$\frac{6}{100}$	$\frac{6}{83}$	$\frac{6}{83}$	$\frac{6}{83}$	$\frac{6}{83}$	$\frac{6}{83}$	$\frac{6}{83}$	—
	F ₂	60	—	—	—	$\frac{5.8}{46}$	$\frac{5.8}{46}$	$\frac{5.8}{46}$	$\frac{5.4}{100}$	$\frac{5.4}{100}$	$\frac{5.4}{100}$	$\frac{5.5}{90}$	$\frac{5.5}{90}$	$\frac{5.5}{90}$
	F ₁ ¹	42	—	—	—	—	—	$\frac{5.4}{47}$	$\frac{5.4}{47}$	$\frac{5.4}{47}$	$\frac{4.5}{57}$	$\frac{4.5}{57}$	$\frac{4.5}{57}$	$\frac{6.3}{87}$
	F ₃	30	—	—	—	—	—	—	$\frac{3.7}{27}$	$\frac{3.7}{27}$	$\frac{3.7}{27}$	$\frac{6.0}{50}$	$\frac{6.0}{50}$	$\frac{6.0}{50}$
July-born		40	—	—	—	—	—	—	—	—	—	$\frac{4.0}{5}$	$\frac{4.0}{5}$	$\frac{4.0}{5}$

Clover	P	Up to 200	—	—	$\frac{7.6}{100}$	$\frac{0.0}{0.0}$	$\frac{0.0}{0.0}$	—	—
	F ₁	51	—	$\frac{6.0}{100}$	$\frac{6.7}{100}$	$\frac{7.0}{100}$	—	—	—
	F ₂ , F ₁ ¹	44	—	—	—	$\frac{6.1}{73}$	$\frac{6.0}{100}$	$\frac{6.3}{77}$	—
	July-born	60	—	—	—	—	—	$\frac{4.5}{50}$	$\frac{5.3}{100}$
	August-born	68	—	—	—	—	—	—	$\frac{2.0}{20}$
	P	Up to	200	—	—	$\frac{7.25}{75}$	$\frac{0.0}{0.0}$	—	—
Forest	F ₁	40	—	$\frac{6.0}{50}$	$\frac{6.4}{90}$	$\frac{7.0}{71.4}$	$\frac{0.0}{0.0}$	—	—
	F ₂ , F ₁ ¹	38	—	—	—	$\frac{6.7}{87}$	$\frac{6.0}{100}$	$\frac{4.0}{100}$	$\frac{0.0}{0.0}$
	F ₃ , F ₂ ¹ , F ₁ ² , K ₁ ¹	20	—	—	—	$\frac{5.0}{75}$	$\frac{5.5}{87}$	$\frac{4.4}{92}$	$\frac{0.0}{0.0}$
	August-born	36	—	—	—	—	—	$\frac{5.0}{40}$	$\frac{0.0}{0.0}$

388 Table 20. Rate of maturation, survival, and fertility of common voles in different habitats

Habitat	Age group	Periods of maturation	Duration of maturation (days)	Percent-age of survival up to maturity	Average weight during maturation period (g)	Percent-age of females participating in first brood	Average no. neonates in first brood
Wheat crop, 1938	F ₁	April, May	56	—	28-32	100	6.0
	F ₂	May 20-July 20	60	—	26.0-27.4	46	5.8
	F ₁	June 6-July 18	42	—	20.2-20.6	47	4.5
	F ₃	June 23-July 23	30	50	15.0-17.0	27	3.7
	F ₄ , F ₂ ¹ , F ₁ ²	July 16-Aug. 25	40	40	23.0-25.0	5	4.0
Clover, 1938	F ₁	April 10-June 1	51	—	—	—	6.0
	F ₂ , F ₁ ¹	May 25-June 8	44	—	21.0-22.5	73	6.1
	F ₃ , F ₂ ¹ , F ₁ ² , K ₁ ¹	June 30-Aug. 29	60	50	26.7	50	4.5
	F ₃ , F ₂ ¹ , K ₂ ¹	August 1-Sept. 27	68	52	15.4-18.8	20	2.0
	F ₁	April 10-May 20	40	—	—	—	—
Forest, 1938	F ₂ , F ₁ ¹	May 23-July 1	38	—	23.2-25.0	87	6.7
	F ₃ , F ₁ ¹ , F ₂ ¹ , K ₁ ¹	June 30-July 20	20	23	14.0	75	5.0
	August-born	July 25-Sept. 1	36	22	18.0-20.5	40	5.0

Wheat crop,	F ₁	May 1-June 10	40	—	—	—	5.5
1939	F ₂	June 10-July 10	30	—	—	—	6.0
	F ₁ ¹	June 20-July 20	30	—	—	—	5.0
	F ₂ ¹ , F ₁ ²	July 15-Aug. 25	38	—	—	—	4.8
	K ₁ ¹	August 1-Sept. 10	40	—	—	—	4.6

groups attained sexual maturity in this habitat, 10 groups in clover, and only 7 groups in the wheat field.

In the second half of the breeding season, the extent of favorable conditions for the common vole in the habitats under comparison changed even more. In the clover field, August-born rodents reached sexual maturity quickly and began to breed in autumn. Sexual maturation of voles in the wheat stubble and forest ceased in August and none of the progeny began to breed until late autumn. Probably, the new clover growth after harvesting was a more favorable food for the voles than plants in the forest, which had ceased vegetative growth, and the wheat stubble. August- and September-born groups of voles were numerically largest. Although only 20% of the females reproduced, their total brood size was larger, which greatly affected the population number in clover in autumn and before the onset of winter.

The more rapid the onset of sexual maturity, the less the weight of voles during the period of the first brood. The least weight was seen in young pregnant females born in July in the glade (average 14 g and minimum 12.5 g). However, the average number of neonates in the first brood of this group was 5, and 75% of the females trapped had participated in breeding activity. The other age groups, which began reproducing at a higher body weight, had a smaller number of neonates per brood and a smaller percentage of reproducing females.

The most rapid rate of sexual maturation was observed in voles during periods when favorable conditions of feeding and heat exchange combined. In Vinnits district, this was observed during the hottest period—in June and July. During this period the temperature in the nests did not fall below 20–22°C (see Table 10). In autumn, when the temperature in the burrows dropped below 15°C, maturation of the voles slowed down. In October, minimal reproduction of young animals was recorded only in the clover crop.

Reproduction differed in intensity among the sexually mature percentage of the population in the habitats under comparison. Thus, one age group (F_1) bred in October in wheat stubble, two age groups (born in July and August) in clover, and none in the forest. Although these differences were associated with conditions of feeding in the habitats under comparison, they were not manifest in the body weight of voles that had stopped breeding (Table 21). It may be assumed that during this period, in addition to food moisture content and general nutritiousness, some vitamins were

present in large quantities (Kalabukhov, 1967; Bondarenko *et al.*, 1968; Saulich, 1972).

An important index of population condition may be participation of adult animals in breeding. It can be seen from Table 19 that the percentage of females participating in each brood was higher in the forest and clover than in the wheat stubble. The capacity of females for repeated gestation is associated with conditions of development for the neonates. Development of the progeny was more rapid in the clover field and the forest than in the standing wheat crop and stubble field. Delay in development of offspring
390 leads to prolongation of lactation in females and increases stress on their energy balance, which delays their next pregnancy. Such a sequence of events has been experimentally confirmed by many researchers (L'vova, 1940; Kagantsova, 1953; Golenishchev, 1954).

The number of neonates in one brood was highest in overwintered rodents and gradually decreased from generation to generation (see Table 19). It was higher in the clover field than in the forest, and higher in the forest than in the standing wheat crop. The number of progeny was lowest in broods preceding total termination of reproduction. This index of population state depends on conditions of existence as well as on intensity of reproduction *per se*, which also becomes a factor suppressing population growth.

Characterization of the social vole population in Crimea based on such indices as composition of age groups, their rate of development, reproductive intensity, and change in body weight is given in Tables 22, 23, and 24. The food status of the habitats under comparison has already been given in Table 16. Some idea of the microclimate of these habitats can be obtained from the data presented in Table 25. It may be seen from Table 9 that burrow temperature during the hottest period did not rise above 32.2°C and in the nests above 25°C.

Based on microclimate, the habitats under comparison were generally homogeneous if those differences associated with plant canopy (density of coverage and height) and soil compactness are excluded. In a plain terrain typical of the area under study, the microclimate of the habitat differs little from the climate of the entire area. The habitats showed significant differences in relation to food, however. To the characteristics presented in Table 16 it should be added that the wheat field in stubble contained a large quantity of weeds in early spring, accounting for 10% of the total plant canopy. This added an element of variability in the feeding of voles and promised a more nutritious food base in this habitat in

Table 21. Average weight (g) of adult common voles in different habitats during period of last broods and termination of reproduction in 1938 (Vinnits district)

Habitat	Age group	Body weight during period of reproduction				Body weight after termination of reproduction (October)	
		August, 2nd brood		September, 3rd brood		Females	Males
		Females	Males	Females	Males		
Wheat stubble	F ₂	31.0	33.0	36.5	35.6	38.0	39.5
	F ₁	29.4	28.0	32.3	28.9	34.0	33.5
	F ₃	27.8	28.2	—	—	31.0	30.0
Clover*	F ₂ , F ₁ ¹	31.0	31.0	34.4	37.0	30.5	31.0
	July-born	29.2	30.0	—	—	—	—
	F ₂ , F ₁ ¹	—	—	37.5	37.7	37.5	37.7
Forest	F ₃ , F ₁ ² , F ₂ ¹ , K ₁	30.0	31.0	—	—	34.5	33.0

*Values indicated for period of termination of reproduction pertain to end of October and November.

391 Table 22. Average number of neonates in brood (numerator) and percentage of females participating in reproduction (denominator) in different age groups of social vole populations (Crimea, Jankoi region)

Habitat	Age group	Age before 1st brood (days)	Number of neonates in brood and percentage of females participating in reproduction											
			March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.		
Wheat crop and barley stubble	P	About 110	$\frac{5.3}{100}$	$\frac{5.1}{94}$	$\frac{4.2}{77}$	$\frac{3.5}{50}$	—	—	—	—	—	—	—	
	F ₁	23	—	$\frac{5.2}{44}$	$\frac{4.0}{100}$	$\frac{3.5}{30}$	—	—	—	—	—	—	—	
	F ₂ , F ₁ ¹	40	—	—	—	$\frac{3.6}{44}$	Field plowed	—	—	—	—	—	—	
	Migratory	—	—	—	—	—	—	—	$\frac{3.0}{100}$	$\frac{3.2}{100}$	$\frac{3.2}{88.2}$	$\frac{3.2}{88.2}$	$\frac{0.0}{0.0}$	
Fallow	August-born	16-20	—	—	—	—	—	—	—	$\frac{4.5}{62.5}$	$\frac{3.0}{96}$	$\frac{0.0}{0.0}$	$\frac{0.0}{0.0}$	
	September-born	45-60	—	—	—	—	—	—	—	—	—	$\frac{3.2}{11.3}$	$\frac{0.0}{0.0}$	
	P	About 110	$\frac{5.0}{100}$	$\frac{7.5}{66.6}$	$\frac{3.0}{50}$	—	—	—	—	—	—	—	—	
F ₁	55-60	—	—	—	$\frac{4.0}{14.3}$	—	—	—	—	—	—	—		

(continued)

392 Table 23. Rate of maturation, survival, and fertility of social vole in different habitats (Crimea, Jankoi region)

Habitat	Age group	Maturation period	Duration of maturation (days)	Survival up to maturation (%)	Average weight (g)	% females participating in reproduction	Average no. neonates in brood
Virgin land (grazing land)	F ₁	March 20—April 23	40	8.0	13.2	66	4.5
	F ₂	April 24—Sept. 1	120	15.0	16.5	50	3.0
Fallow	F ₁ ¹ , F ₂	May 20—Oct. 4	150	69.0	15.1	43.5	3.0
	F ₁ ²	Sept. 20—Oct. 15	25	60.0	12.7	5.0	3.0
	F ₁	March 20—May 15	55	—	14.3	14.3	4.0
	F ₂	April 20—June 20	60	56.0	15.7	45.2	2.5
	F ₃ , F ₁ ¹	May 20—Sept. 5	108	75.0	17.0	78.4	3.5
	F ₁ ²	July 15—Oct. 7	94	78.0	15.7	36.5	2.4
Wheat crop on fallow	F ₁	March 25—April 18	23	24	14.9	50.0	4.0
Wheat crop on stubble	F ₂ , F ₁ ¹	May 1—May 16	16	15	12.6	40.0	4.0
Wheat crop—stubble	F ₁	March 25—April 15	20	19.7	13.2	44.0	5.2
Barley stubble After poor crop harvest	F ₂ , F ₁ ²	April 25—June 1	36	32.0	13.2	44.0	3.6
	August-born	Aug. 15—Sept. 1	16	77	12.9	62.5	4.5
	September-born	Sept. 20—Oct. 12	22	35	13.7	11.3	3.2

394 **Table 25. Daily fluctuations in temperature (°C) in burrows (at depths of 30–50 cm from entrance) and at soil surface in habitats of the social vole (steppe Crimea, 1936)**

Habitat	Date	Place temperature recorded	Time of recording			
			7:00 a.m.	1:00 p.m.	7:00 p.m.	1:00 a.m.
Fallow	June 8	Soil surface	25	50	10	11
		Vole burrow	18	21	21	20
Wheat field	June 11	Soil surface	28	60	22	18
		Vole burrow	17	19	20.5	20
	July 21	Soil surface	35	60	21	19
		Vole burrow	18	21	28	28
Fallow	July 31	Soil surface	30	49	31	28
		Vole burrow	27.5	27	31	31
Grazing land	Aug. 22	Soil surface	34	61	34	18
		Vole burrow	24	25	30	31
Barley stubble	Sept. 14	Soil surface	12	31	14	7
		Vole burrow	15	16	16	17
Grazing land	Sept. 17	Soil surface	7	25	10	9
		Vole burrow	14	15	18	18
Barley stubble	Oct. 27	Soil surface	4	20	2	2
		Vole burrow	5	6	8	6

March–April when some of the weeds flowered and subsequently produced seeds. The wheat grown on fallow was devoid of weeds, the soil contained more moisture, and therefore the wheat plants remained succulent and green for a longer time. This created a better food base in the wheat crop grown on fallow compared to wheat grown in the stubble field in May and June.

394 Vegetation developed in spring and autumn on the virgin grazing land. But even at this time the vegetation cover was no more than 40% of the soil surface, nor did it fruit due to intense cattle grazing. Fallow plant growth started later than on virgin land and in cultivated fields. In April, May, and June, a dense plant cover with large stems developed here. During barley harvesting, 3.0–4.0 gtl/ha grain was lost, which began sprouting at the end of August. The vole population here comprised rodents migrating after July plowing of wheat fields adjoining the barley field on three

sides. Plowing was done on 640 hectares and 320 hectares were inhabited.

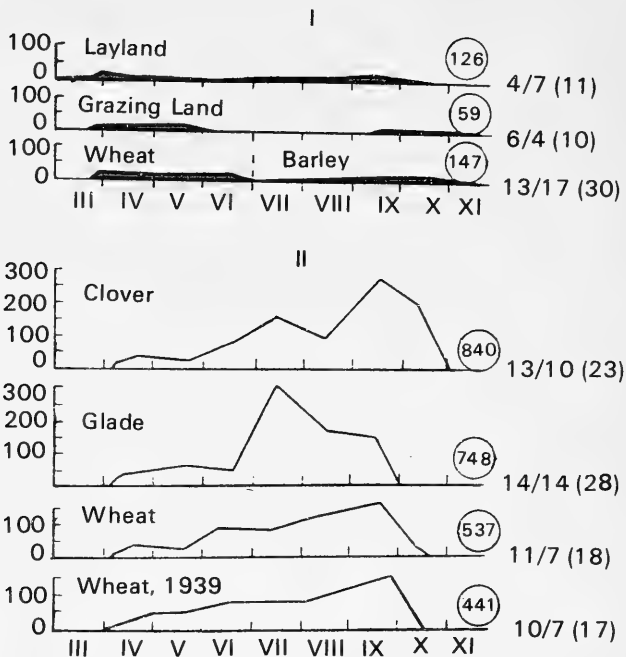
Sexual maturation of the adult group F_1 was comparatively more rapid in all habitats, but twice faster in the wheat field than in the fallow and virgin grazing land. Subsequently, maturation of the progeny was rapid only in the wheat field. Its dependence on conditions of food base is quite obvious. In October (September-born animals), voles took a longer time to mature in barley stubble than during the warm period. However, this group did not attain sexual maturity on fallow and virgin land and did not participate in breeding until the onset of winter.

In 1936, the reproductive intensity of voles in all habitats was lower and the rodents were small compared to the populations of social voles from Azerbaidzhan in the years of intensive reproduction. The number of neonates per brood, even when all females of the given age group participated in reproduction, was relatively small. Spring reproduction started almost simultaneously in all habitats. Reproduction on virgin land and fallow ceased in summer, since the overwintered rodents had disappeared by this time and the suppressed F_1 , F_2 and F_1^1 groups had not yet reached sexual maturity. In autumn, reproduction ceased in all habitats in November and on fallow in October.

As a result of variable speed of maturation in the groups (despite plowing of the wheat stubble), 17 age groups reproduced over the season in cultivated land, 7 on fallow, and only 4 on virgin land. In the cropped area, third and partly fourth generations participated in breeding, while only the second generation took part on virgin land and fallow.

To demonstrate in a comparative manner the intensity of reproduction in each habitat occupied by the common vole in Vinnits district and by the social vole in Crimea, estimations were made on five overwintered pairs (Figure 71). With an equal initial number, further calculations were done considering actual numbers: change in age groups, sex ratio, developmental rates, survival and fertility, and reduction in number from one brood to another. It is readily seen that the number of neonates born in a population is directly related to conditions in which each group developed and lived. These differences are very large, and the general level of number of individuals in a population is always associated with them.

In comparing living conditions of common voles in the Vinnits district with living conditions of social voles in the Crimean steppes, it is readily evident that in June conditions were less favorable for



396 Figure 71. Birth rate of 10 overwintered voles and their progeny in individual habitats: I—Crimea, Jankoi region, Sverdlov Collective Farm, 1936 (*Microtus socialis*); II—Ukrainian SSR, Vinnits district, Pogrebishche region, Nova Zhittaya Collective Farm, 1938 (*M. arvalis*).

Numerator—number of age groups not reaching sexual maturity; denominator—number of age groups reaching sexual maturity and participating in reproduction; figures in parentheses—total number of age groups formed in population; figures in circles—total number of animals born. Ordinate—number of animals born; abscissa—time (months).

the latter species. This is understandable if we consider that steppe Crimea forms the periphery of the social vole's range, while Vinnits district is the optimal zone for the common vole. Irrigation in the Crimean steppes and introduction of perennial grasses in crop rotation significantly improved the living conditions of the social vole in steppe Crimea and the adjacent regions of Kherson district. The improvement in food base contributed to the formation of a population with a higher viability, greater rate of maturation of neonates, as well as fertility and general intensity of reproduction.

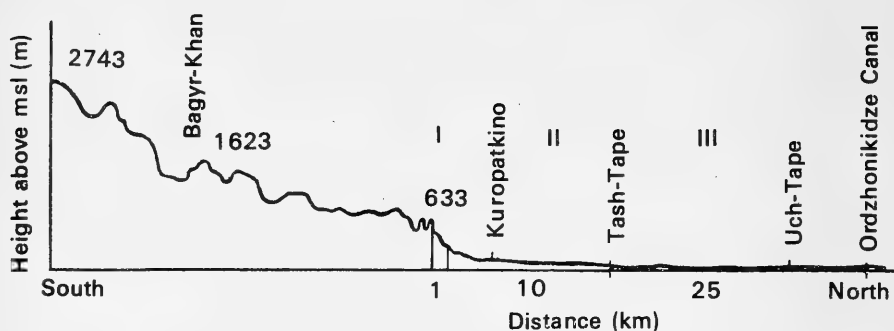
Food resources of the social vole in its main habitats in the

396 foothills of Karabakh are characterized in Table 16. During the period when rodent breeding terminates (beginning of summer) there is a sharp fall in the moisture content of food. Thus, the moisture content of barley plants decreases from 70–75% in May to 40% beginning of June and 30% by the end of this month. On virgin land it decreases from 60–65% in May to 40% in June (Mokeyeva, 1949).

The relief of the Karabakh foothills is schematically shown in Figure 72. The line passes through Kirs Mountain, Kuropatkino village, and up to the Ordzhonikidze Canal (plain steppe). The profile covers the hill tract, foothills, and adjoining Mil'skaya steppe. The zone of rainfed agriculture had extended to Tash-Tape by 1950 and is presently making further inroads into the steppe. Above Kuropatkino, crops extend into the mountains as a continuous block approximately up to Point 633 but alternate with belts of virgin and fallow along the ridges. Above Point 633 and up to 1,300 m, crops occupy no more than 20% of the territory, the remainder either covered with shrubs or under orchard. The entire belt of rainfed crops between the forest zone and virgin uncultivated steppe up to 1950 was only 30 km but has now reached 40 km. Work in this region was carried out in 1941 and again from 1946–1950. The area was revisited in 1952 and 1963, when reports of en masse reproduction of the social vole were received, and a detailed study undertaken in 1964 when rodent population declined (Gladkina, 1968a, b).

In 1941, studies were conducted during the period of en masse reproduction of the social vole. The rodents occupied the entire cropped area, virgin land, and fallow from the foothills up to Ordzhonikidze Canal. The direct reason for this population explosion, covering the territory of the present Fizuli, Martuni, Agdam, and Agdzhabedi regions, was a hailstorm in 1940. Crops were damaged at the stage of maturity. Consequently, a large area was not harvested and left to "windfall" (self-sowing). This was followed by a warm and humid winter and also a humid spring. Decade temperatures during January–April totaled 84.5°C versus the normal 66.0°C. The total precipitation in 1941 from January to May was 460.4 mm versus the average annual norm of 177 mm. All this created favorable conditions for vegetative growth and vole existence.

397 In areas left to windfall in May, 1941, up to 1,660 voles/ha were counted (50,000 burrows). Such areas constituted about 30% of the total cropped area. In the remaining cropped fields from 100 to 300



397 Figure 72. Schematic cross section (profile of locality) along the line: Kirs Mountain—Kuropatkino—Ordzhonikidze Canal.

Abscissa—distance (km); ordinate—height above msl (m).

voles (up to 10,000 burrows) per hectare were counted. In virgin land in May, there were 100 voles/ha (up to 12,000 burrows).

Over 3,000 voles were examined during April and May and the results subjected to preliminary processing (Table 26).^{*} Data on the population state during summer have already been presented in Table 11.

In spring of 1941, many voles in field crops weighed more than 40 g, with a maximum weight of 52 g. The standard weight of breeding adult voles was 30–40 g. The percentage of gestating females was high and each produced 8–10 embryos or neonates. Voles on virgin land were smaller; adults did not exceed 32–34 g in weight and reproduction was less intensive, as shown in Table 26. After termination of reproduction, the rodent number dropped sharply and rapidly (Figure 73); large individuals disappeared from the population. The decline in vole numbers continued during summer and autumn, and only smaller individuals were found (see Table 11).

Gladkina (1968b) observed a replication of these data in these same regions in 1964 when, after en masse reproduction, which began in 1963 and continued up to spring of 1964, a fall in numbers
398 was observed during summer and autumn of 1964 (Tables 27 and

^{*}These results were lost during World War I.

Table 26. Change in birth rate in populations of the social vole in grain crops and virgin land (spring 1941)

Habitat	Increase in population (%) of voles weighing more than 12 g over			
	April 15-20	May 1-15	May 16-31	June 1-30
Grain crops	139	40	18.0	0.0
Virgin land	38.5	43.5	0.0	0.0

28). True, the rate of fall in numbers and the rapidity with which the population was depleted to smaller individuals in 1964 were not so great as in 1941. This is explained by a sharp deterioration in the animals' living conditions.

Thus the data presented in this section, like that characterizing reproduction of the common vole in montane grazing lands of Azerbaidzhan (see Tables 12 and 13), show how populations of this group of rodents develop and live in different habitats (biotopes). The differences recorded in their conditions are phenotypic. It should be emphasized that not only populations of different habitats, but also populations of a single habitat differ in different seasons. The same may be said of the seasonal populations of the social vole (Polyakov, 1964, 1967).

Populations in a biotope should be considered the major life form of the common vole and the lemming. The biotopic variability of a population appears through the integration of a three-pronged environmental influence on the formation of their morphophysiological properties. First of all, the neonate developing in different biotopes is subject to different microclimates and conditions of nutrition, which have a great impact on the state of viability of the individual and through it, of the population, when the corresponding age groups become adult. For the adult part of the population, the significant environmental conditions are those that govern intensity of reproduction, survival, and state of their viability. Finally, because of the differences in response of different age groups to environment, the importance of the latter is also specific for them. Thus, a unique response to environment is exhibited by populations of different age structure. On the whole, all these characterize populations in a biotope—differences in age structure, habitat density, reproductive intensity, and numerical dynamics. The data

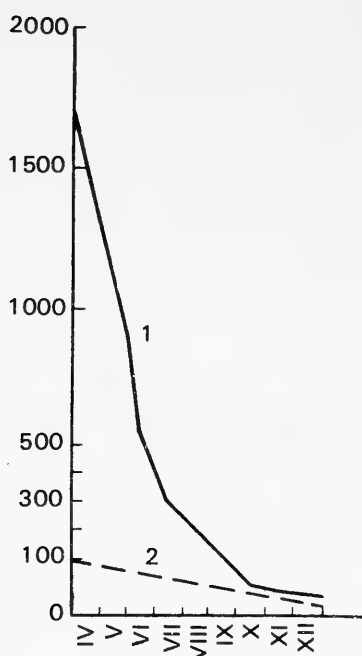


Figure 73. Change in number of social voles in the Karabakh foothills in 1941.

1—in crops; 2—on virgin land; abscissa—months; ordinate—number of individuals/ha.

presented above fully illustrate these aspects. At the same time, one should not ignore the effect of population structure on intensity of reproduction and population density itself, especially under conditions that make natural dispersal difficult or even totally exclude it. An interesting experiment along this line was carried out by Spitz (1968, 1974). He selected two similar fields of alfalfa occupied by the common vole (150 voles/ha), one of which was fenced and prevented rodent dispersal, while the other was not. The number of active males and females was higher in the fenced field; however, the average birth rate was lower. The author is inclined to explain this phenomenon by the presence of a mechanism of automatic control of fertility in the common vole population. I feel these facts may be explained in another way: (1) by females of all groups participating in reproduction in the fenced field (includ-

Table 27. Reproduction intensity of the social vole in 1964 in the steppe belt of the Karabakh foothills (from Gladkina, 1968b)

Dates of observation	Winter grazing grounds			Grain crops		
	Total no. of females	Pregnant females (%)	Embryos per female (%)	Total no. of females	Pregnant females (%)	Embryos per female (%)
March 23–April 18	56	80	6.9	50	56	7.8
May 5–15	19	16	5.2	42	64	7.2
June 5–13	69	4	—	25	4	4.0
July 5–18	41	0	—	25	24	3.1
August 4–18	—	—	—	18	33	2.1
October 22–28	25	8	3.0	39	15	4.2

Table 28. Composition of the social vole population by weight in 1964 on virgin land and in standing crops in the hill tract of Karabakh (from Gladkina, 1968b)

Month	No. of animals	Virgin land			No. of animals	Cropped				
		Weight group (%)				Weight group (%)				
		5-16 g	17-28 g	29-40 g		41-52 g	5-16 g	17-28 g	29-40 g	41-52 g
March-April	120	20	20	43	17	121	35	32	20	13
May	62	29	59	10	1	142	39	40	17	4
June	214	33	57	10	0	55	6	81	13	0
July-August	80	13	80	7	0	90	10	60	30	0
October	77	22	52	3	0	48	3	53	19	0

ing even the less fertile young ones), whereas young females could disperse more readily from the open field; (2) by deterioration of the food base in the fenced field (in this case, thinning of the alfalfa plants, thickening of their stems, and reduction in their foliage with almost unchanged total weight of plant stand); and (3) by a higher interference in the fenced area. Actually, populations in fenced and unprotected alfalfa fields differ and should be considered populations of different biotopes, although all the ecological indices except the possibility of dispersal are similar.

Dynamics of Habitat Distribution and Numbers

The groups of common voles and lemmings under consideration are characterized not only by high dynamics of population density in the biotopes occupied by them, but also by high variability in their habitat distribution. Only a combination of changes in population density and expanse of territory occupied by the animals offers a true picture of the numerical dynamics of a species in a given region or at a given point in the range. Yet many ecologists examining rodent numbers (Vinogradov, 1934; Sviridenko, 1934; Kalabukhov, 1935, 1937, 1947; Naumov, 1945, 1965, 1967; Formozov, 1947) and those of other animals (Lake, 1957; Makfedien, 1965; Viktorov, 1967, 1969) attach no importance to the dynamics of habitat distribution and identify changes in animal numbers with changes in population density. Such assumptions are justifiable when studying fluctuations in numbers in forms which have a stable response to environment, in which a comparatively small stable population is formed in the territory occupied. However, they are incorrect if the viable form has a labile response to the environment, as do most animal species. This leads to the nonapplicability of the principle of concreteness in theoretical generalization—the regularities inherent in some form being attributed to those in which they do not exist (Polyakov, 1968a, 1973).

In common voles and lemmings, given their exceptional lability of response to the environment, a change in numbers is related to intensity of reproduction. With high reproduction, their population density increases and the rodents spread to new biotopes and form new populations in them. Here the relationships within the population leading to accentuation of dispersal interference or even competition (Mil'n, 1964; Rafes, 1968) stimulate the process of dispersal (Polyakov, 1967, 1968a, b; Christian, 1970). Herein probably lies the adaptive significance of the unique relations within

the population in the biological forms examined. With low intensity of reproduction or its cessation, population numbers decrease, the number of biotopes and populations likewise decrease, and the "settled condition" of the voles increases—facts also reported by Fenyuk and Sheikina (1938). Therefore, all those factors that influence reproductive intensity become important in determining the tendency of population dynamics.

It was demonstrated earlier that conditions of feeding and heat exchange exert a maximum influence on reproductive intensity of common voles and lemmings. The food base depends greatly on climatic factors (precipitation, temperature, transeaporation, and so forth). These conditions also determine the regime of heat exchange and energy losses necessary for this purpose. Therefore, we must recognize that climatic factors, because of their indirect and direct influences on populations of a given biological group of rodents, acquire decisive importance in their population dynamics.

Intensity of reproduction, as shown above, is associated with a definite condition of viability of populations and their morphophysiological characters. These characters are formed under the influence of those environmental conditions in which the population developed. On them depends the nature of population's response to the environmental conditions in which it continues to live. The vitality of populations is determined not only by birth rates, but also by the possible effect of factors of mortality of animal numbers, especially epizooties and predators.

Considering these factors, the numerical dynamics of common voles and lemmings should be viewed as the result not only of quantitative, but also of qualitative changes in populations (Polyakov, 1950–1967).

A distinction is made between seasonal and multiannual population dynamics (Polyakov, 1964). Seasonal dynamics is the result of favorable and unfavorable seasons for rodents during the year. Reproduction of voles and lemmings takes place during the favorable season (or seasons), as a result of which their number increases. They do not reproduce during an unfavorable period and their number decreases.

401 It has already been shown that individual habitats differ in a favorable season in extent of optimum life conditions created in them for the population of a given species. This determines dissimilar phenology and reproductive intensity of individual populations and unique seasonal numerical dynamics in each habitat. Thus, in the breeding season in 1936, the social vole population in the

Jankoi region on virgin grazing land increased 180% and in standing crops (despite plowing of a large area and resultant mortality of part of the population) by 415% (see preceding section). The extent of favorable breeding seasons in one and the same habitats in different years is also dissimilar. This is reflected in the intensity of breeding and level of population strength in individual years (see Figure 70).

The extent of population suppression during an unfavorable period of the year also differs significantly in individual habitats and in different years in one and the same habitats. The ultimate effect of an unfavorable season on the state of a population depends on its viability. Highly viable populations survive well in such seasons, while populations of lower viability survive with great difficulty or are completely wiped out.

Furthermore, unfavorable seasons in individual years usually differ markedly from the multiannual standard in extent of their effect on populations. If the severity of such conditions weakens, then such seasons may become quite favorable for rodents. In such cases, breeding does not terminate and the moment a favorable season commences, the population becomes more numerous, with higher viability, and is capable of intensive reproduction. If the conditions during an unfavorable season become more severe and longer in duration, the populations die out or become less viable by the commencement of a favorable season.

In the steppe and foothill regions of Azerbaidzhan, summer is the suppressing season for the social vole. In individual years, drought begins in May and continues up to October–November. In these conditions, populations are greatly suppressed and the rodents die in all habitats, except places of conservation where the situation remains more favorable. Such an ecological situation developed in 1941, 1945, 1948, and 1953. However, it so happens that sometimes rains occur periodically throughout summer and intensive vegetative growth is restored in August. In these conditions, social vole populations maintain high viability in all habitats and begin to multiply already in August. Reproduction and increase in numbers continue in winter and by spring the animals are numerous. Such a situation was observed in 1940, 1944, 1947, 1952, and 1962.

In temperate latitudes, winter as well as early winter and early spring periods are critical seasons for voles and lemmings. However, with a good food base available and abundant stable snow cover, this period may even be favorable for rodents. This is particularly

true if they have bred at the end of summer and during autumn, leading to the formation of "winter populations". With a poor and unstable snow cover and insufficient food base, winter becomes fatal. Its significance increases if the rodents have stopped breeding earlier and "spring populations" begin overwintering. Such a phenomenon is observed during severe summer drought, which portends a poor food base for overwintering.

402 There is a significant similarity between seasonal and multiannual changes in numbers of common voles and lemmings. The similarity is that increase in numbers of a species is related to intensity of breeding and associated with dispersal to new habitats (biotopes). Concomitantly, there is a significant difference between seasonal and multiannual numerical dynamics. The difference lies in the smaller range of variability of viability of populations with seasonal changes in numbers. Even in such forms as the common vole and the lemming which have a labile response to the environment, the viability of populations in one year changes to a lesser extent than that observed throughout the entire cycle of fluctuations in their numbers—from depression to peak to decline in numbers. Therefore, the state of viability of a population during the seasons of a year characterizes some part of the multiannual cycle of its variability (Polyakov, 1964, 1968b).

The complete multiannual cycle of population dynamics of common voles and lemmings exhibits five phases, each of which reflects not only the level of numbers, but also the state of viability of each population (Figure 74).

The depression phase in numbers of a species is characterized by its occurrence only at places of conservation—habitats where even in periods of a universal unfavorable combination of ecological conditions, the species does have a chance for survival. Here populations may reproduce or may be somewhat suppressed, but they do not completely lose viability. The numerical level of a species during the period of depression in a given area of the range depends on what percentage of the area of the entire territory is occupied by conservation habitats. However, it will always be the lowest compared to other phases of its multiannual dynamics.

The dispersal phase (beginning of increase in numbers) of a species begins after a general improvement in living conditions for it in the conservation habitats and beyond their limits. This creates a prerequisite for increase in viability of populations at places of conservation, increase in habitat density, and increase in interference within the populations which stimulates their dispersal.

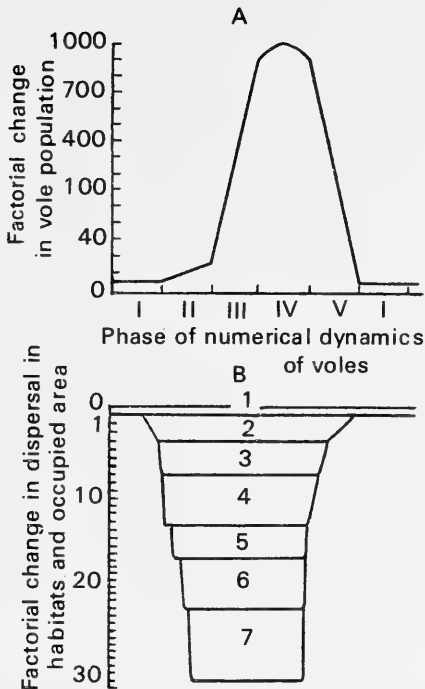


Figure 74. Probable relationship, level of numbers and habitat distribution of common voles and lemmings in different phases of the multiannual cycle of population dynamics.

A—change in number of rodents; B—change in habitat distribution; I—depression phase; II—dispersal phase; III—phase of en masse reproduction; IV—phase of peak numbers; V—phase of fall in numbers.

1—conservation habitats; 2 to 7—dispersal habitats.

At the same time, a favorable environment beyond the limits of conservation places ensures survival and intensive reproduction of animals that have dispersed and formed new populations. Often, such newly formed populations find themselves in more favorable conditions than prevailed at places of conservation. An essential feature of this phase is the formation of highly viable, reproducing populations in new habitats beyond the limits of places of conservation.

The phase of en masse breeding is characterized by vigorous increase in numerical strength of populations in all habitats due to

high fertility, rapid development of progeny, and the latter's better survival. The numerical strength of a species should be greatest beyond the limits of places of conservation. Its level in individual
403 habitats may differ but the area occupied in this phase is maximum. Populations are universally characterized by the highest viability, and the influence of factors of dispersal weakest. Ecological conditions during this phase are optimum for a species in every habitat. This phase is thus characterized by maximum intensity of reproduction in all habitats and larger-sized individuals constitute the population.

The possibility is not ruled out that inbreeding intensifies in each population because of an increase in habitat density. I encountered females simultaneously feeding progeny in a single nest only during years of en masse rodent breeding. During this period, females became pregnant at the earliest age and individuals of different generations were seen in a single excavation. All this serves as an indirect confirmation of inbreeding.

"Ecological inbreeding" is also not excluded during this period. This essentially means that rodents living in optimum uniform conditions develop rapidly. This may maximalize the biological properties of the mating partner to the same extent that actual inbreeding would. The basis for this conclusion is the method used by animal breeders in overcoming undesirable consequences of consanguineous mating, described even by Darwin (1951). For this purpose, breeders rear related partners under different conditions from a very early age. This has such an influence on them that the progeny formed is of the same quality as one obtained from unrelated parents. Therefore, one may expect that similar conditions of rearing of unrelated progenitors from very early ontogenesis can induce in their offspring a phenomenon similar to inbreeding.

Chentsova (1969) showed that in the narrow-skulled vole and the steppe lemming, inbreeding actually decreases intensity of reproduction and probably other indices of viability of a population of these rodents. At the same time, voles and lemmings possess several adaptations that weaken the consequences of inbreeding (Polyakov, 1950, 1954, 1956).

All this permits us to assume that intensive breeding even under conditions of optimum environment involves factors responsible for subverting the viability of a population. Besides possible inbreeding, emaciation of females may also become such a factor. It is known that individual broods cause emaciation of the mother, due to exceptionally high energy expenditure during pregnancy and

suckling of progeny. She begins to produce broods of fewer number, lactation is protracted, and the period between deliveries longer. These conditions also take their toll on the viability of the progeny. These purely endogenous reasons may lead to a decrease in intensity of breeding even under optimum environment. But such a situation arises only with a prolonged period favoring reproduction of common voles and lemmings. The suppression of reproduction and, consequently, the end of the phase more often sets in as a result of exogenous reasons—deterioration of the food base and conditions of heat exchange.

The phase of peak numbers is the culmination point of en masse breeding and signals the beginning of its termination. Living conditions deteriorate for most populations during this period. This deterioration may be the result of a natural or untimely onset of an unfavorable season. In cultivated areas, it may be caused by some intensive agronomic practice—harvesting or plowing of fields. As a result of these, and partly the endogenous conditions mentioned above, intensity of breeding decreases in all populations, and in some cases ceases completely, the viability of rodents decreases, and mortality increases. Ultimately, the general increase in numbers is halted. A concentration of rodents, and even their occupation of new habitats may be noted in individual areas, but such migrations are not accompanied by intensive reproduction. A sharp reduction in intensity of breeding right up to total cessation, reduction in rodent size, and slower development of neonates, serve as the major indications that the phase of peak numbers has begun. Epizootics may appear during this period—the same mortality factor seen during the dispersal phase and during en masse breeding. The influence of predators and parasites as a mortality factor among rodent populations also increases.

It should be noted that, depending on the extent of rodent dispersal, food availability in a habitat, duration of phase of dispersal, and ecological features of an area and season, the phase of peak numbers may proceed differently and may set in at different habitat densities. Thus, in the steppe region of Azerbaidzhan, the phase of peak numbers of the social vole occurred first in virgin wormwood—herbage habitats (winter pastures). Here a total of 100–200 rodents were counted per hectare. In rainfed cropped areas, this phase began later, at a rodent density of 1,500/ha. In subalpine meadows, the common vole peaked at a density of more than 1,000/ha. In low-lying flooded meadows in France (polders), the maximum number of common voles was 1,520 and in alfalfa

1,025 (Spitz, 1963). All these facts confirm that the maximum number of voles, like the onset of peak numbers, is not determined by population density, but by factors influencing its viability.

The phase of fall in numbers is characterized by a further sharp deterioration in population viability, a still greater decrease in rodent size, reduction in resistance to the effects of unfavorable environmental factors, and a higher susceptibility to infectious diseases. As a result, the number of rodents falls drastically and they may completely disappear in some habitats. The rapidity of fall in numbers differs significantly throughout the region, depending on intensity and duration of action of inhibitory factors. It may also differ in individual habitats. For example, in winter pastures of Azerbaidzhan, as mentioned above, the social vole after completing reproduction in May disappears not later than end of July, while in rainfed crops it may survive up to late autumn in spite of a higher habitat density. However, a characteristic feature of this phase is that populations which have irreversibly lost their viability do not reproduce beyond the limits of their places of conservation, even if they survive until the onset of a new favorable season. Populations are conserved only at places of conservation where environment has not caused such a strong and irreversible loss of viability as in dispersal habitats.

Multiyear numerical dynamics usually does not upset the established seasonal rhythm of reproduction. However, during phases of dispersal and en masse breeding, periods of intensive reproduction are protracted and only curtailed during the phase of peak and fall in numbers. The nature of the cycle may change under the influence of environmental conditions. Under early deterioration of conditions, the cycle may be disrupted in the dispersal phase. In this case, the dispersed population dies without reproducing. It may so happen that the conditions deteriorate for a short period in the peak phase. Then the population stops reproducing for a while only in individual habitats, where a reduction in density of habitation is seen. After a short interval, reproduction is resumed and a new peak in numbers formed. In such a case, the cycle is twin-peaked. This situation was observed in the steppe and foothill regions of Azerbaidzhan in 1963–1964. En masse breeding of the social vole began here in autumn of 1962, and started to decline end of summer of 1963, especially in the foothills. But by spring of 1964, populations in several habitats in the steppe began intensive breeding and their numbers rose. Only in summer of 1964 did the

decline phase finally set in. Gladkina (1968b) has also recorded the foregoing data.

The duration of cycles and their frequency in each species differ significantly in individual regions of the range, and depend on many factors. The relative size of refuges, ratio of duration and extent of optimum or extreme nature of favorable and unfavorable seasons, and size of areas of possible dispersal habitat spread and extent of their favorable nature for a given species, are of special importance. It may be considered a rule that the more elevated the refuge area of a species, the higher its minimum numbers during the period of depression. With a large area of optimum refuge, a brief improvement in living conditions suffices to initiate en masse breeding. With a very limited area of refuge, the minimum numbers of a species fall sharply at the time of depression and a much longer period of favorable ecological conditions is required for en masse breeding to take place. Usually, such a situation rarely develops and the cycle is disrupted in the dispersal phase, after which the phase of depression of numbers begins anew. However, if the ecological situation remains favorable for a long period, the difference between total rodent numbers during periods of depression and peak numbers is several-fold greater than in the case of wide rodent dispersal during the period of depression.

Researchers who attribute great significance to endogenous factors in population dynamics do not take into account the significance of variation in different years in food base and climatic effects, nor the conditions for reservation and dispersal of the species in individual regions of the range. The cyclic nature of population dynamics and its manifestation in individual regions of the range are considered a consequence of variability of population density itself (Christian, 1971a, b; Myrberget, 1973; Davis and Christian, 1974). Although supporters of this view recognize the specificity of the mechanism of dynamics in different biological forms, generally the impression created is that the consequence is the cause (Adamchevska-Andzheevska and Nabaglo, 1974). However, contradictions can be avoided by accepting that intrapopulation and interspecific relationships are formed under the influence of the food base and state of physical factors of the environment. These positions become particularly apparent when changes in the cyclic nature of dynamics of steppe vole are examined, which occur as a result of rearrangement of ecological conditions under the influence of intensive agriculture.

In the agricultural regions of Western and central Europe, en masse breeding of the common vole is presently observed every 3–4 or 3–6 years. This is facilitated by crops of alfalfa and clover, which occupy 15–20% of the total cultivated land. They serve as excellent habitats for conservation of voles, and grain, mustard, and other crops have become places for dispersal of rodents. Intensive control measures have been taken against the common vole to protect the crops from decimation, but cannot completely eliminate the increase in vole population (Elton, 1942; Klemm, 1957a, b, 1964, 1966; Hammer and Sutova, 1963; Spitz, 1963; Straka, 1966, 1967a).

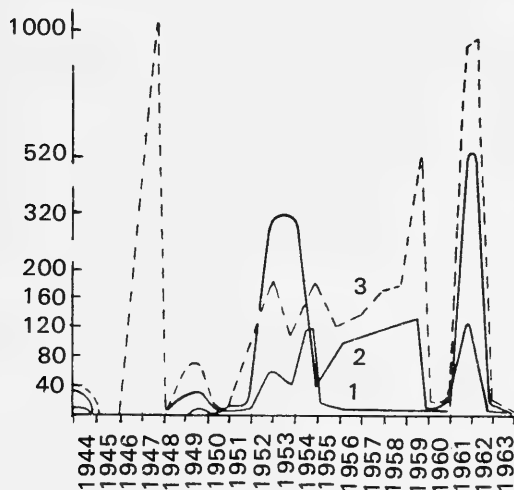
406 In the European part of the USSR, en masse breeding of voles was repeated at intervals of 2–4 to 8–11 years (Bashenina, 1962). It occurred more often in old agricultural regions than in relatively recently reclaimed lands (Dinesman, 1955). Unfortunately, to date no analysis has been done here of the frequency of en masse breeding taking into consideration the ratio of areas of places of conservation and spread. However, such a study was carried out by Prokof'eva (1968, 1969) in the Stavropol' territory. Over a period of 20 years, under her guidance plague eradication organizations collected material which was unique in terms of the diversity and completeness of territory covered, and characterized the habitat distribution and numbers of voles and other rodents in different seasons. While processing these results, Z.V. Prokof'eva traced the dynamics of numbers and habitat distribution of the common vole differentially in sheep's fescue-stipa steppes, herbage-grass steppe, and forest-steppe, and that of the social vole in sheep's fescue-stipa steppe and semidesert (Figure 75 and 76). She showed that the more extensive the refuge of these species, the better the conservation of the populations in them, the more frequent en masse breeding, the higher the number of animals in the peak phase, and the wider their dispersal over the territory.

The fescue-stipa steppe is less favorable for the common vole. Fields of perennial grasses, uncultivated area along forest belts, and forest belts with a sparse woodland serve here as refuges for this species. Such areas constitute about 27% of the total territory, but the reliability of conservation in them is not high since in summer the populations are subject to the lethal effect of droughts, and in winter to snowless frost. Therefore, the depression phase here is quite prolonged (about five years). Only with a combination of favorable overwintering and a very humid spring–summer period is it reduced to two years. In the phase of peak numbers, the maximum density is 150 voles/ha. They occupy 60 to 85% of the total

territory. The decline phase proceeds quickly, within 2–5 months, and in snowless winters in a few days.

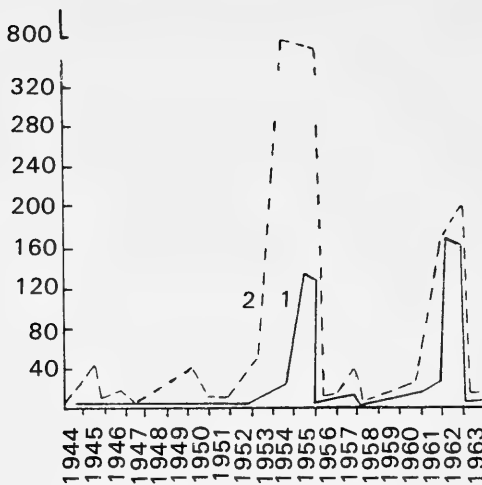
407 In the herbage-grass steppe, refuge habitats of the common vole constitute about 32% of the area, but better ensure rodent protection against the lethal effect of a snowless winter as well as from drought during summer. Therefore, a higher number of rodents is conserved during the period of depression. The depression phase continues for only 1.5–3.5 years and the phase of population increase (spread) passes quickly, within 5–10 months. Voles are able to occupy 40–45% of the total territory over this period of time. At the time of peak numbers, the maximum density may reach 300–520 voles/ha and they may cover 80–92% of the total territory. The decline in numbers is rapid during late autumn and winter.

In the forest-steppe, refuge habitats of the common vole constitute more than 39% of the total territory. Favorable conditions are more widespread here than in the zones described above. Therefore, the depression phase continues for only 6–12 months. The dispersal phase is also very brief and quickly passes into the phase



406 Figure 75. Phases of multiyear numerical dynamics of the common vole in fescue-stipa steppe (1), herbage-grass steppe (2) and forest-steppe (3) from 1944 to 1963 (from Prokof'eva, 1969).

Abscissa—years; ordinate—number of voles per hectare.



406 Figure 76. Phases of multiyear numerical dynamics of the social vole in semidesert (1) and fescue-stipa steppe (2) (from Prokof'eva, 1969).

Legend same as in Figure 75.

of en masse breeding. Practically speaking, the norms for this zone are the phases of en masse breeding and peak numbers. These phases were recorded 12 times over a period of 20 years. Up to 1,000 voles/ha were counted in the phases of en masse breeding and peak numbers, and they occupied cultivated fields completely. These phases continued for 1–2 years. Here we have a picture somewhat similar to that observed by Spitz (1963) for the low-lying meadows of France. Numbers declined rapidly during the autumn-winter period.

The semidesert in the Stavropol' territory is hardly a favorable zone for the social vole. From 23–42% of the territory is occupied by crops. The refuge habitats constitute an area equal to a fraction of a percent of the total territory. Therefore, the depression phase is protracted. So, too, is the dispersal phase (2.5–3.0 years) and often disrupted by conditions unfavorable for voles. Over a 20-year period, en masse breeding was noted here only twice (in 1954–1955 and 1962), when the maximum number density was 230 voles/ha and rodents were spread over 80–90% of the territory. The phase of decline passed quickly.

In sheep's fescue-stipa steppe, where agricultural development is intensive, more favorable conditions have been created for the

social vole. Here refuges occupy about 27% of the total territory (fields of perennial grasses, fringes of forest belts, haylands, and partly pastures). Therefore, only 1.0–1.5 years are required from the depression phase to peak numbers. Over a 20-year period, five en masse breedings were recorded (1953, 1954, 1955, 1961, 1962). During the phase of peak numbers up to 800 voles/ha were recorded, covering 90–95% of the total territory.

These examples show that where agricultural production increases the reserve areas of voles, it creates conditions for their frequent en masse reproduction or their appearance at places where they were not found earlier. This has been demonstrated by Dinesman (1955), Maksimov (1964), and Prokof'eva (1968). However, wherever agricultural production reduces the refuge area for voles and lemmings, en masse reproduction becomes impossible in regions where earlier the animals were common and much larger. An example confirming this conclusion was the termination of en masse breeding of the steppe lemming and narrow-skulled vole in northern Kazakhstan and western Siberia after virgin lands were reclaimed during 1953–1956 (Polyakov, 1968b; Gladkina, 1969).

408 In northern Kazakhstan and adjacent areas of western Siberia, en masse reproduction of the narrow-skulled vole and steppe lemming was observed about once in four years before the reclamation of virgin lands. These were recorded when a winter of abundant snow followed a humid summer. Then, in the vegetative season following such a winter, wide dispersal and high numbers of voles and lemming occurred.

409 Peat meadows, forest fringes, and forest fellings, and low-lying wet parts of steppes served as extensive conservation places for voles and lemmings. Their total area was quite large and conditions favorable for rodents prevailed during winter and summer. During plowing of virgin land, all the areas where voles and lemmings had earlier been conserved, were overturned. Thus the plant cover and microclimate changed and these places became inhospitable for rodent conservation during periods of numerical depression.

Figure 77 shows the weather conditions under which en masse breeding of the narrow-skulled vole and the steppe lemming occurred in northern Kazakhstan before reclamation of virgin lands. Similar weather conditions developed in 1956–1957, 1960–1961, 1965–1966, 1969–1970, but en masse breeding was not recorded. With the preservation of very limited areas of places of conservation for voles and lemmings, a single favorable year does not suffice for their en masse breeding, and more prolonged favorable periods

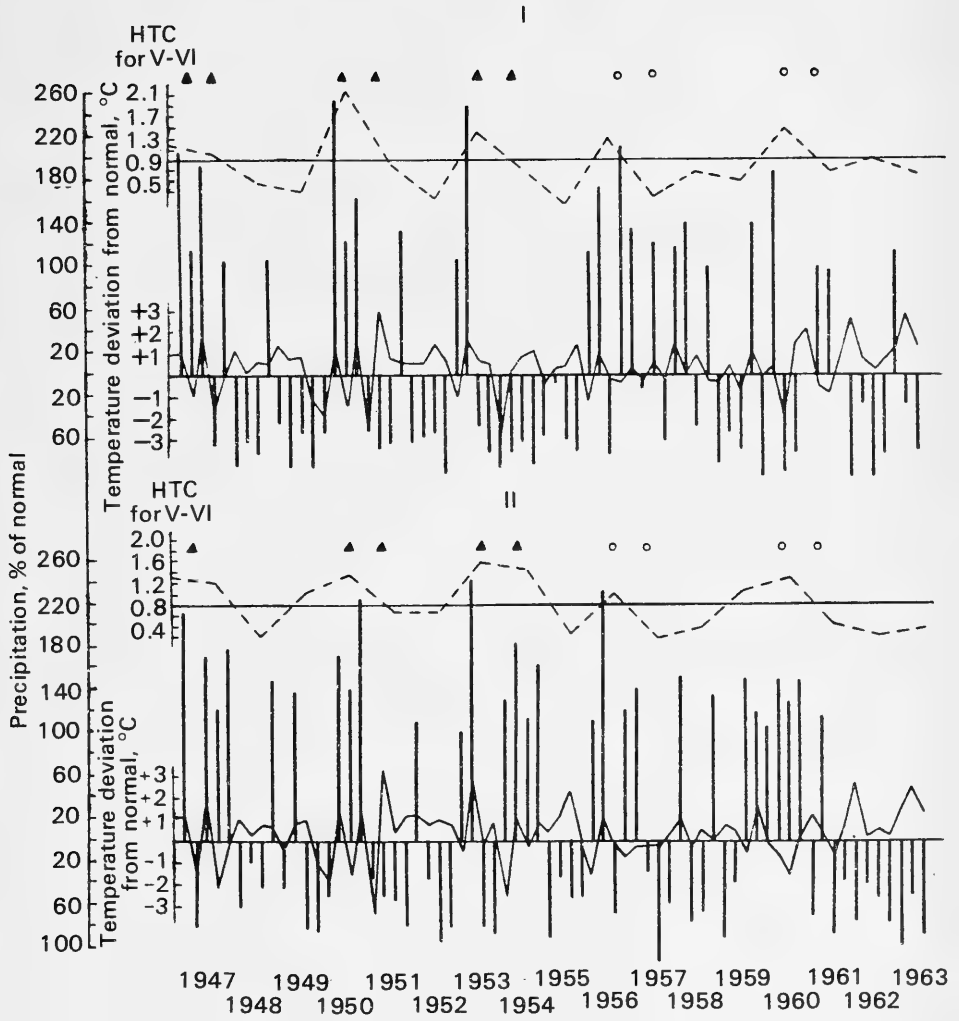
are not possible here. Therefore, a favorable year gives rise to only a narrow local increase in reproductive intensity of rodents, which leads neither to high numbers nor to widespread dispersal.

Coming now to an assessment of the role of conservation places in determining numbers and population structure of a species, we should keep in view the interspecific relations in the ecosystem as well. In this case, a system of territorial utilization by a species developing in this region and passing through all the phases of its dynamics cycle, can be considered an adaptation at the biocenotic level. In this context, the types of settlement of the Afghan vole in Turkmenia, described by Heptner (1956), evince great interest. Possibly, he was the first to state the idea that types of settlements (and the entire dynamics of habitat distribution) as an adaptation of the species, reflect the need for rational utilization of a territory and its energy resources. These properties are formed and selected under the dynamic influence of state of food resources in time and space. V.G. Heptner reported that conservation places of the Afghan vole are characterized not only by richness of food resources, but by isolation from the other settlements of rodents, which protects the voles from fatal epizootics. Thus, the types of vole settlements that develop in different regions specifically depend on relief, soil, plant association, and settlements of other animals.

The above-examined causes of the dynamics of habitat distribution and numbers of common voles and lemmings permit us to find reliable criteria for forecasting their numbers over long as well as relatively short periods in connection with prospective plans for agricultural development in different part of the country. More-

408 Figure 77. Dependence of en masse reproduction of the steppe lemming and the narrow-skulled vole on weather conditions in northern Kazakhstan before reclamation of virgin lands and loss of this relationship after their reclamation.

I—Kustanai district (Fedrovka); II—Kokchetav district (Ruzevka). Bars—deviation of total precipitation from mean over different seasons (%); solid line—deviation of mean monthly temperature from normal (°C); broken line—deviation of hydrothermal coefficient (HTC) from normal (from Selyaninov, 1928); triangles—years of en masse breeding of voles and lemmings; circles—years with weather conditions favorable for en masse breeding that did not take place after reclamation of virgin land. Abscissa—sequence of seasons (autumn, winter, spring, summer) and years.



over, a knowledge of these causes may be used in understanding the problems of intraspecific differentiation of rodents and, consequently, their microevolution.

Predicting Habitat Distribution and Numbers

The damage caused by voles and lemmings varies in different parts of the USSR. It depends on the species' capability for periodic population explosions. This, in turn, depends on conditions for conservation of its populations during unfavorable periods and dispersal during favorable periods. A general idea of the regions in which damage due to individual vole and lemming species is notable can be obtained from Figure 78. Forestalling damage inflicted by voles and lemmings is tantamount to precluding en masse breeding. Therefore, control of these rodents is effective only when planning is based on predictions of their habitat distribution and numbers.

411 Knowledge of the causes underlying the dynamics of habitat distribution and numbers of a given species enables us to forecast these phenomena over some period of time. The ultimate objective of such predictions is determination of the control measures needed in specific habitats—agricultural fields—in order to prevent rodent damage.

In this context, a question arises: What information about the state of populations and environment makes such forecasts possible? One perforce must deal with minimum information for large and not always ecologically homogeneous regions. Usually this information is reported by persons with a minimal background in ecology, yet its analysis must provide a clear answer to the validity of measures of great economic importance. Therefore, development of a method of forecasting habitat distribution and numbers of common voles and lemmings (as well as other animals) led not only to the identification of dependable criteria, whereby we can judge the tendency of these phenomena over a definite period, but also to the formation of a rational system of observations that enable us to obtain the information requisite for these criteria.

Studies on the ecology and physiology of common voles and lemmings has made it possible to establish that for each species at any point in its range throughout the year, favorable seasons combine with unfavorable ones. This determines the seasonal dynamics of numbers and habitat distribution of rodents. Organizational and management practices significantly influence the numbers and habitat distribution (Polyakov, 1950, 1968b). Variations in such

practices in individual areas of the rodent's range, combined with extent of favorable or severe seasons in a year, or over several years, lead to significantly different consequences. Ultimately, these are reflected in size of conservation and dispersal habitats, periods and extent of their suitability for occupation by the rodent, and formation of viable populations.

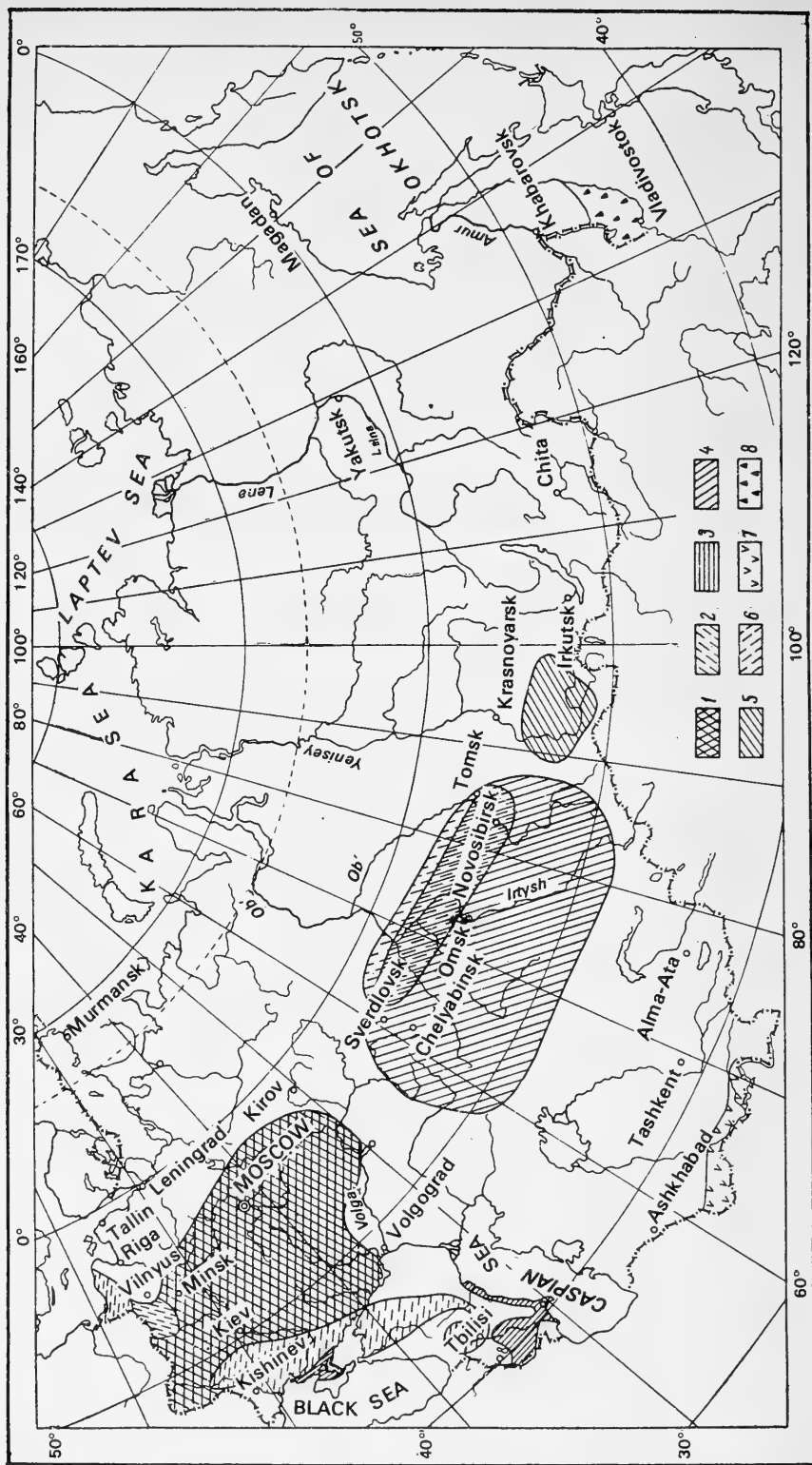
Given the foregoing, the first stage in the development of a method for predicting vole and lemming populations in the USSR was the identification of those territories (zones) in which comparatively similar alternation of optimum and extreme seasons occur and places of conservation and dispersal centered in homogeneous biotopes. This work was approximately finished by 1950 but cannot be completed even now, since agricultural development continues to significantly influence ecological condition (Polyakov, 1961a, b, 1968a, b; Gladkina, 1968a, b, 1969).

The second stage was to ascertain the places of conservation and dispersal within the limits of each zone and to establish approximate ratios. This is essential for differential forecasting of level and rate of change in vole and lemming numbers in each region of the zone. This work has just begun, and is most completed in Stavropol' (Prokof'eva, 1968, 1969). Similar regionalization of Azerbaidzhan was done earlier (Polyakov, 1949a, 1950). The absence of such regionalization precludes the possibility of predicting trends in change of rodent numbers.

Selection of prediction criteria was the third stage. Today, the following may be considered the most reliable: habitat distribution of voles and lemmings in specific seasons, age composition of the population at this time, and intensity of reproduction. Even habitat distribution alone, if followed systematically and its differences known compared to previous seasons, sufficiently characterizes trends in change in vole and lemming numbers, making it possible to determine their multiyear cycle of dynamics.

412 The fourth stage involved development of a system of observations on the state of populations and formation of phases, as well as development of methods of assessing the same.

At present, the entire USSR has been divided into 15 zones, each of which is more or less uniform in nature of change of optimum and extreme seasons for common voles and lemmings and in type of biotopes serving as places of conservation and dispersal (Figure 79). Some zones are subdivided into regions differing in relative size of conservation places for voles and, consequently, in numerical level and dynamics (*Metodicheskie...*, 1970).



The main criterion for determining a phase in the cycle of numerical dynamics of voles and lemmings is their habitat distribution after favorable and unfavorable seasons. Indirect indices of the state of a population (intensity of reproduction, age composition, morphophysiological state) are used only when there are no data on the state of the environment of rodents for the preceding seasons. They are necessary if a distinction is to be made between the phase of en masse reproduction and the phases of peak numbers and decline in numbers.

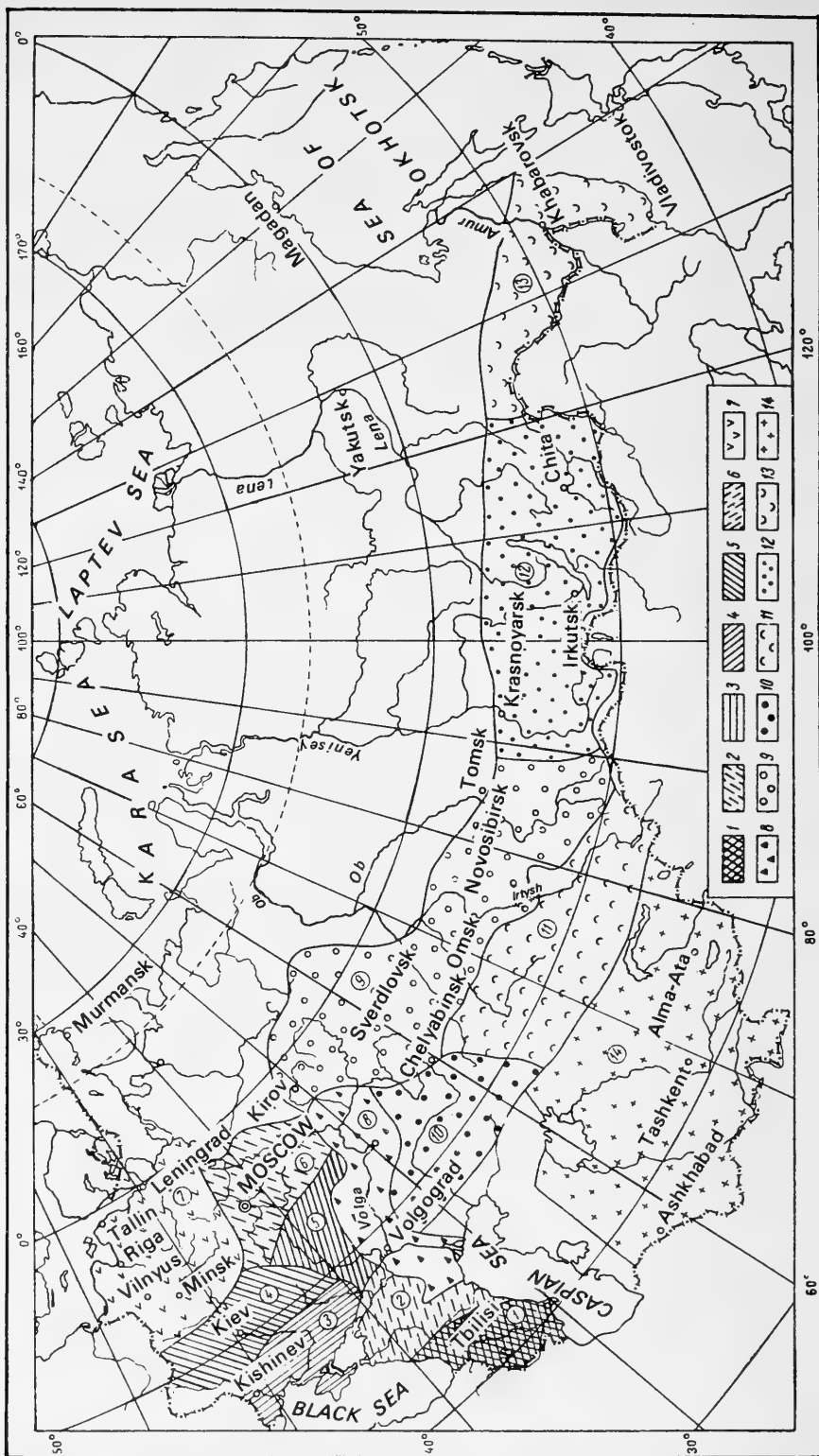
Systematic observations document the influence of habitat distribution, assessment of numbers from indirect indices, and reproductive intensity of voles and lemmings both after unfavorable and favorable seasons, in all two series of observations and estimates. Tables are compiled for each zone, presenting information on indices of environmental conditions in the previous season, and habitat distribution and numbers in a given season, so that trends of growth or decline in numbers as well as need for preventive measures can be determined. Indices of state of populations are not included in these tables, but one obtains an idea about them from an analysis of the environmental conditions in the preceding season and habitat distribution of rodents in a given season (Polyakov, 1950, 1958, 1961a, 1968b). Such indices are not redundant, especially when expedient preventive measures must be decided.

I would like to illustrate how prediction criteria and the system of observations in different zones are applied in solving the question of expediency of preventive measures against voles and lemmings.

I. *Trans-Caucasus*: The social vole is scattered here in the steppe and foothill regions. Usually, extreme conditions are created for this species in summer, and optimum conditions in autumn, winter, and spring. However, there also may be years when

Figure 78. Zone of damage inflicted by voles and lemmings.

1—chronic damage by the common vole; 2—en masse breeding of the common vole; 3—periodic en masse breeding of the narrow-skulled vole and the steppe lemming before reclamation of the virgin land; 4—[omitted in Russian original—Eds.]; 5—increase or same level of damage by the narrow-skulled vole and the steppe lemming after reclamation of virgin land; 6—en masse breeding of the water vole; 7—damage caused by the Afghan vole; 8—damage caused by the reed vole.



the summer is only slightly oppressive and the winter very cold and oppressive. Refuges of social voles in the steppe regions are gorges, river valleys, and areas adjoining irrigation canals. In the foothill regions, such areas are confined to the northern slopes of hillocks, overgrown shrubs, areas adjoining irrigation canals, orchards, vineyards, and lucerne fields. Places of dispersal in both regions are grain crops and grazing grounds.

In both groups of regions, an increase in numbers of social vole is observed with a combination of a relatively humid summer with a subsequent humid autumn, warm winter, and humid spring. In this case, even in August populations reproducing intensively are created at places of dispersal, which attain maximum numbers in May of the following year.

At present, the intensity of agronomic measures and quality of individual preventive measures have increased. Furthermore, preventive measures against voles are well-organized. These programs forestall en masse breeding of the social vole in conditions that up to 1952 encouraged it (Makarova and Polyakov, 1963). However, in years of favorable weather conditions, the dispersal phase of voles and the onset of large-scale breeding are always observed. The course of this cycle is interrupted by preventive programs which, in this case, are absolutely essential, as well as by planned agronomic measures. If the refuge period suitable for voles is protracted and preventive measures only partially effective, en masse breeding is the inevitable result. Such was the case in 1963–1964 (Gladkina, 1968b).

Peak numbers of social voles always coincide with the beginning of summer, and numerical decline occurs at the end of summer, in autumn, and in winter. At present, the refuge habitats for the social vole has increased in the steppe zone due to increased area under grain crops and extension of irrigation. This situation caused prolongation of the period of decline in rodent numbers in 1964, and probably also accelerated their numerical increase compared to the foothill regions (Gladkina, 1968b).

In the subalpine and alpine zone of Trans-Caucasus, the common vole is distributed primarily in summer grazing lands.

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- 413 Figure 79. Schematic map of zones within limits of which similar criteria for predicting numbers of steppe voles and lemmings are used. Administrative divisions within each zone are given in the text.

Here refuges for this species are abundant and hence high numbers and frequent en masse breeding are observed. Decline in common vole numbers occurs if the weather during July and August is relatively hot and dry (Askerov, 1953).

Systematic observations of social vole populations take into account primarily their habitat distribution in September and March. Concomitantly, the extent of favorable effect of preceding seasons throughout the year is taken into consideration from such indirect indices as weather conditions (compared to multiyear average), magnitude of harvest of grain crops, time of harvest and quality of produce, and time and quality of fallow cultivation. Direct assessment of reproductive intensity of voles in September enables the determination of probable rate of increase in numbers, if the populations are in the dispersal phase, or rate of their mortality if they are in the phase of numerical decline. Reproductive intensity in March enables assessment of probable population growth rate up to the beginning of summer depression.

Preventive measures in late autumn and winter are helpful in fields of winter grain crops, if they have an average of more than 50 living burrows (more than 10–15 inhabited colonies) per hectare. In early spring (end February—beginning March) in Trans-Caucasus, control measures against voles should be implemented if intensive reproduction was recorded and there are more than 100 living burrows per hectare (more than 20–30 inhabited colonies).

II. *Northern Caucasus*: This zone covers Rostov district, Krasnodar and Stavropol' territories, Kabardino-Balkaria, northern Osetia, Checheno-Ingushetia, and Dagestan. This territory is diverse, since it includes plains and hill areas; there are belts of forest-steppes, steppes, semideserts, broad-leaved and coniferous forests, and subalpine and alpine areas. The agricultural regions in this zone exhibit common features—vole habitats of conservation and dispersal are confined to similar biotopes. However, the ratio of areas of these places is not the same in individual regions, confined to definite terrains, which has a significant effect on the numerical dynamics of voles (Prokof'eva, 1969).

The damage inflicted by the common vole is most obvious in the relatively moist foothill and forest-steppe regions where the average annual precipitation exceeds 500 mm. Damage done by the social vole is primarily seen in dry steppe plains and semidesert regions.

415 Refuges for common voles are fields of perennial grasses, orchards, outcrops of grassy vegetation along rivulets and ravines, sparse turfy places, forest belts and their uncultivated trails, road-

sides and, in winter, also haystacks and stacks. Fields of grain and wide-rowed crops, pastures, and fallow serve as places of dispersal of this species.

The main refuges of the social vole are fields of perennial grasses, depressions in virgin land steppes where soil moisture is higher, trails along forest belts, and haystacks. Fields of grain crops and grazing lands serve as places of dispersal.

The two vole species reproduce year-round in this zone under a favorable combination of conditions, but usually a winter recess and a short summer suppression occur. With an unfavorable combination of conditions, summer suppression may cause a break of two to three months in reproduction and snowless winters may kill a large percentage of the viable population within a few days.

Penetration of the common vole into the arid zone of northern Caucasus is confined to extremely limited refuge areas for this species during summer (Prokof'eva, 1968). Penetration of the social vole into the zone of higher humidity is probably limited by its questionable survival here during the cold period of the year.

An increase in numbers of both vole species occurs if a moderately humid autumn, warm snowless or cold winter with abundant snow, early but humid spring, and summer with a good harvest of grain crops and grasses follow a humid summer. The favorable effect of such weather on voles can significantly increase if harvesting is protracted, unwrapped harvested material left in the fields, and autumn cultivation delayed.

Decline in numbers begins after a dry summer or as a result of a snowless winter.

Systematic observations of vole populations in this zone take into account their habitat distribution at the commencement of spring, mid-summer, and in autumn. If the dispersal phase is observed in autumn, additional observations are recorded during winter. Even if the winter is snowless and warm, vole reproduction does not terminate. Investigations are directed toward determining the usefulness of immediate preventive measures in cropped fields.

Preventive measures in winter grain crops during autumn and winter are required if the fields contain more than 100 living burrows, or more than 20–30 inhabited colonies per hectare. Spring control measures in winter crops are carried out at the same minimum density of occupation after a cold winter with abundant snowfall. If the winter was warm and snowless, control measures during spring should be conducted in winter grain crops when there are more than 200 living burrows (more than 40 inhabited colonies)

per hectare, and in crops of perennial grasses with more than 100 living burrows (more than 20–30 colonies) per hectare. Increase in minimum threshold of population density after a warm snowless winter is associated with the fact that intensity of rodent reproduction in spring will be less than after winters of abundant snow and that the food base for voles may be poor.

Preventive measures against voles in years of numerical depression in fields of perennial grasses during snowless and warm winters as well as early spring are useful if no more than 20–30 living burrows per hectare (5–10 occupied colonies) are observed.

416 III. *Steppe Zone of the Ukraine and Moldavia*: This zone includes Odessa, Nikolaev, Kherson, Crimea, Zaporozh'e, Dnepropetrovsk, Donetsk, and Voroshilovgrad districts, and southern regions of Moldavia. Within the limits of this zone, irrigation is being extended in Odessa, Nikolaev, and Kherson districts, steppe Crimea, and southern parts of Zaporozh'e and Dnepropetrovsk districts. Social and common voles are widespread here and the steppe lemming, though rare, has also been reported. For both vole species this zone may be considered the ecological periphery of their range. Therefore, large-scale breeding is observed relatively rarely here. Usually, reproduction abates during the dispersal phase. But extension in recent years of the area under irrigation has improved conditions for vole conservation and their numbers have increased. In short, an optimum situation has been created for voles, encouraging frequent en masse breeding.

Fringes of forest belts, forest belts *per se*, ravines, overgrown shrubs, banks of irrigation canals and their adjoining areas of shallow groundwater, serve as refuges for the common vole. Its places of dispersal include vineyards, orchards, pastures, haylands, fields of perennial grasses, and the marginal zone of winter grain crops. It occupies all types of crops during large-scale breeding.

The social vole during the period of numerical depression is observed in laylands and individual fields of perennial grasses. In the northern part of the zone, it is found only on relatively elevated areas, and in the southern part in plains and more humid areas. Here the areas adjoining irrigation canals and borders of irrigated fields also serve as refuges. In the dispersal phase, it occupies fields of perennial grasses and winter grain crops. During en masse breeding, it occupies all grain crop fields.

Years of humid vegetative growth, high yields, and short warm winters with less snow or completely snowless, are favorable for voles. Years of drought and cold, snowless, icy winters are fatal for

voles. Peak numbers are recorded in autumn and their decline in winter.

Systematic observations comprise two surveys, one in early spring and one in autumn. In spring (March) special attention should be paid to determine number of burrows in crops of perennial grasses and winter grain crops left in autumn. With the presence of more than 100 living burrows per hectare (20–30 inhabited colonies) in these fields, preventive measures are recommended. In autumn (October–November), fields of perennial grasses and early winter grain crops are surveyed. If more than 50 living burrows per hectare (15–20 inhabited colonies) are found, preventive measures are recommended.

IV. *Forest-Steppes of the Ukraine and Moldavia*: This zone includes the northern part of Moldavia, Trans-Carpathians, L'vov, Volynsk, Rovenno, Ternopol, Ivano-Frankovsk, Chernovits, Vinnits, Khemel'nity, Zhitomir, Kiev, Cherkassy, Kirovograd, Sumi, Poltava, and Kharkov districts. In this zone, three regions can be identified in the Ukraine—left bank of the Dnieper, right bank of the Dnieper, and western Ukraine proper. In terms of conditions favorable for life for the common vole and refuge areas, western Ukraine holds first place and the right bank of the Dnieper second. Steppe lemmings penetrate the left bank of the Dnieper, but pose no significant economic threat.

The main refuge areas of the common vole are laylands, fringes of forest belts, forests *per se*, fields of perennial grasses, and in winter, also steppe hayracks. The period of vegetative growth is favorable for voles. Cold autumns, winters of unstable snow cover, and cold, humid early springs are fatal for them. Agronomic measures have a great effect on the conservation and numbers of voles. Leaving the stubble of winter grain crops unplowed over winter is extremely favorable for them; deep plowing of stubble is fatal for them. Spring dispersal is generally universal in this zone, but en masse breeding not seen due to wet autumns and complete deep plowing of grain and wide-rowed crop fields.

Systematic observations comprise two surveys, one in spring (second half of March—beginning of April) and the other in autumn (October). If it is not possible to complete deep autumn plowing and the harvested field is plowed only in spring, the possibility of voles spreading to fields of winter grain crops in April increases. In such cases, besides examining refuge it is recommended that fields of winter grain crops also be investigated at the end of April. If, on the average, more than 100 living burrows per hectare are

found in these crops and in fields of perennial grasses, preventive measures must be taken immediately (while it is still cold). The autumn investigation is essential for assessing the expected situation in spring. Control of voles in autumn is usually not practiced in this zone. Possibly, it would be useful in individual years to implement control measures against rodents in haystacks left in fields of plowed stubble. A large concentration of voles and intensive reproduction are likely during winter in such haystacks.

V. Central Chernozem Zone: This zone includes Orlov, Kursk, Belgorod, Voronezh, Lipets, Tambov, and Penza districts and Moldavian ASSR. The common vole, widespread in this zone, reproduces en masse only under an exceptional lack of cultivation, as was observed during the war years. Usually, a decline in numbers of this species begins at the dispersal phase.

Haystacks and racks, fields of perennial grasses, open areas in forest belts, roadsides, forest fringes, gorges, and meadows serve as refuges for the common vole. The dispersal phase is characterized by the occurrence of voles in winter grain crops. During large-scale breeding, they occupy all crop fields. In spite of their low numbers, voles annually cause damage to fruit orchards by gnawing the bark of the trees in winter.

The period of vegetative growth, from April to October, is favorable for reproduction of voles; reproduction is often suppressed in summer, especially in drought years. Winter reproduction is noted only in haystacks and racks. Seasonal peak numbers are observed in autumn and decline with winter. An increase in vole numbers is facilitated in this zone by a warm spring without the return of cold spells, moderately warm summer with high humidity, warm and long autumn, and winter with abundant snowfall without warming and ice formation. In these conditions, if grain crops are poorly harvested and stubble left uncultivated during winter, en masse breeding of voles takes place the following vegetative period.

Summer drought, winter warming and icing, timely crop harvesting, and autumn cultivation are fatal for voles in this zone.

Systematic observations comprise two surveys per annum. The spring survey (April) should determine the usefulness of preventive measures in fields of perennial grasses and winter grain crops. Such measures are rarely required if, on the average, less than 100 living burrows per hectare (more than 20–30 occupied colonies) are recorded. The autumn investigation assesses the general distribution of voles and determines the usefulness of preventive measures

within and without orchards. Orchards and directly adjacent areas, as well as fields of perennial grasses and winter grain crops are examined in autumn. Vole control in and around orchards is advantageous if isolated colonies are noted. Rational control measures against rodents are essential in autumn and winter in haystacks and racks.

VI. *Central Non-Chernozem Zone*: This zone includes Kalinin, Moscow, Yaroslavl', Ivanovo, Vladimir, Ryazan, Kaluga, Tula, Bryansk, and Smolensk districts. The area under cultivation in this zone constitutes about 35–50% of the total land area, the remainder being under forest or marshland. The major refuges of common voles are haystacks and racks in meadows and fields of perennial grasses not flooded during spring and autumn. Fields of perennial grasses, grain crops, meadows, laylands, and forest fellings become places of dispersal.

The breeding season continues from April to October; the voles reproduce vigorously in haystacks during winter (Strel'nikov, 1940; Bashenina, 1962; Maksimov, 1964; and others). Increase in vole numbers is possible if an early warm spring changes into a moderately humid summer, long warm autumn, and snowy winter without warming. If many stubble fields remain unplowed in such weather conditions after a good grain crop poorly harvested, the phase of en masse breeding begins in spring. Numbers peak in autumn and decline in winter and early spring.

As yet, conditions for en masse breeding of voles have not occurred in this zone. Usually, only the dispersal phase begins, which is disrupted by agronomic and prophylactic measures. However, voles still cause significant damage to fruit plantations even at their present numerical level.

Systematic observations comprise two surveys: spring (April) and autumn (September end—beginning October). The usefulness of preventive measures in fields of perennial grasses and winter grain crops becomes clear in spring. If the preceding year was favorable, with an average of more than 100 living burrows per hectare (more than 30 inhabited colonies), the field requires protection. Major attention is paid in autumn to the occupation of orchards and adjoining lands by voles. Isolated living colonies detected in grounds surrounding orchards are immediately poison-baited. Rodent control should be carried out in a planned manner during autumn and winter in stacks and hayracks. These measures help protect hay from spoilage and sharply decrease the total number of rodents at the beginning of spring.

VII. *Northwestern Zone*: This zone can be subdivided into the Baltic region, which includes Kaliningrad district, Lithuania, Latvia, and Estonia; the eastern region includes Belorussia, and Leningrad, Pskov, and Novgorod districts.

About 40% of the land area in the Baltic region is under agriculture; drainage of moist cultivable lands and laylands is widely practiced. Winter in this zone is characterized by an unstable snow cover. The common vole survives the cold period in hayracks as well as in drained parts of fields and grazing lands, and along slopes of drainage canals. During the period of vegetative growth, the vole's wide dispersal is noted almost every year, and higher numbers seen in fields of perennial grasses and grain crops in autumn. Autumn cultivation and excessive humidity during late autumn, winter, and early spring are fatal for voles. By spring, they are primarily found only in refuges. Significant fluctuations in numbers of the common vole are observed every year in Kaliningrad district. Numerical fluctuations are less sharp in the Baltic republics due to deterioration of conditions for rodent conservation during the cold period of the year.

419 In the eastern region, field crops occupy about 25% of the territory. Late autumn and early spring are unfavorable for the common vole. Winter is characterized by a stable snow cover. Refuges of the common vole are hayracks and stacks, small elevated parts of meadows and fields of perennial grasses; winter reproduction is possible in open biomes under the snow. The general numerical level and dispersal of the common vole during the warm season are less in the eastern region than in the Baltic region.

The common vole causes serious damage to hayracks and stacks in the northwestern zone where control measures against it should be followed every year. Damage to fruit plantations is observed during winter and hotbeds and hothouses in spring. The expediency of preventive measures in crop fields in the Baltic regions remains unclear.

Systematic observations comprise two surveys, spring and autumn. The spring investigation strives to identify rodent conservation places to offset damage to hotbeds and hothouses and, in autumn, to orchards. Areas adjoining hotbeds or hothouses occupied by rodents are treated during spring and those adjoining orchards in autumn.

In the non-chernozem of the RSFSR, in accordance with the decision of the Central Committee of CPSU and the Council of Ministers of the USSR, intensification of agriculture is underway.

Specifically, land reclamation, creation of cultivated meadows and pastures, and fodder resources are being expanded. Such measures will greatly improve conditions for the conservation and dispersal of *Microtus arvalis* and *M. subarvalis*.

VIII. *Volga Zone*: This zone can be subdivided into two regions—the Volga-Kama and Lower Volga. The Volga-Kama region includes Gorky, Ul'yanovsk, and Kuibyshev districts, Tataria, Chuvashia, Mordovia and Mari ASSR; the Lower Volga region comprises Volgograd, Saratov, and Astrachan' districts, and Kalmytskaya ASSR. In the Volga-Kama region, the common vole primarily damages perennial grasses and orchards as well as hotbeds and hothouses, although it is fairly well-dispersed in open biotopes (Popov, 1960). Its nests in this region are laid at particularly shallow depths since the summers are moderately warm and winters abundant in snow. Therefore, deep plowing is highly fatal for the settlement of this species. Vole habitat distribution in cultivated fields is largely determined by the periods and quality of postharvest stubble plowing.

Hayracks and stacks, fields of perennial grasses, roadside areas, grazing lands, forest fellings, and field-protection belts, threshing floors, vegetable stores, and residential buildings serve as refuges for the common vole. When rodent numbers are large, they inhabit fields of winter grain crops from autumn. En masse breeding has not been observed in this region.

In the Volga-Kama region, systematic observations comprise two surveys, spring and autumn. If more than 100 living burrows per hectare (more than 30 occupied colonies) are observed in fields of grain crops and perennial grasses, extermination measures are warranted. The autumn survey determines the validity of protective measures in orchards and hayracks. All the colonies of common voles detected in autumn near, in, and around orchards are poison-baited. With the dispersal of rodents in fields, their control here in late autumn and in hayracks and stacks during winter, becomes essential.

420 In the Lower Volga region, common vole populations are suppressed in a hot and dry summer, especially in the Astrachan' district and Kalmytskaya ASSR; the social vole (a more drought-resistant form) is sympatric here. During the winter period, the two species are exposed to the fatal consequences of icing and sharp changes in temperature with a relatively unstable snow cover. Ultimately, the vole numbers are reduced and the damage caused by them here rarely significant. Their refuges are individual fields

of perennial grasses, fringes of forest belts, low-lying fallow areas, haystacks and racks, borders of irrigated fields, and embankments of irrigation canals. Perennial grasses, grain crops, laylands, and orchards serve as dispersal places.

An increase in vole population is facilitated by conditions that lead to a high yield of winter and spring grain crops: a prolonged warm and humid autumn, winter with high and stable snow cover, mild spring with good moisture available, and a moderately warm and humid summer. If under these conditions, there is loss of grain during harvests and stubble of grain crops remains unplowed during winter, the vole population may explode. Timely crop harvest and early postharvest cultivation can prevent the phase of en masse breeding.

Systematic observations comprise two surveys, spring (March—beginning April) and autumn (October). If more than 100 living burrows (more than 20–25 inhabited colonies) are found in spring in fields of winter grain crops, as well as in the fields of perennial grasses, and more than 200 living burrows (40–50 occupied colonies per hectare in spring grain crops, preventive measures are mandatory in these fields.

IX. Ural and Western Siberia Zone: This zone includes Bashkirian ASSR, Perm, Sverdlovsk, Kurgan, Chelyabinsk, Omsk, Tyumen, Novosibirsk, and Kemerovo districts, Altai territory, and Kirov district. Northern regions of western Siberia and the Urals are excluded from this zone. Comparatively little damage due to common and narrow-skulled voles is observed in this zone, and by the steppe lemming in the south. The two vole species are periodically suppressed during summer by drought and high temperature and in winter by strong frosts with a relatively thin layer of snow cover at the beginning and end of this period. With the termination of breeding in July, as a consequence of drought and heat, the cold resistance of the rodents during winter is low. On the contrary, if the summer is rainy and the rodents multiplied well into autumn, then cold-resistant populations develop, which are capable of multiplying under snow given the availability of a good food base. In this case, conditions may be created for a sharp increase in number of voles the following year after a winter with abundant snowfall.

Hayracks and stacks, borders of forest fellings, banks of water bodies that do not overflow, and forest belts with a good snow cover in winter, serve as refuges of the common vole. With an increase in numbers, fields of perennial grasses, grain crops, hotbeds, orchards, and areas adjoining the latter, are occupied by voles.

Refuges of the narrow-skulled vole are forest fringes and fellings, overgrown shrubs, embankments of irrigation canals in fields of perennial grasses, and parts of fallow and haylands with a good grass cover, which are not flooded and have a stable snow cover during winter. With an increase in rodent numbers, fields of perennial grasses and grain crops, fallow and haylands, and haystacks and racks are occupied.

421 The steppe lemming, found in southern Chelyabinsk district, eastern Kurgan district, in Kulunda, Aleisk, and partly the Barabinsk steppes, is conserved well on moist but unflooded wormwood-grass fallow and in fields of perennial grasses. With an increase in numbers, the rodent spreads to fields of grain crops.

Systematic observations for rodent control comprise surveys in spring and autumn. Voles and lemmings are widespread if the preceding vegetative period was humid, leading to good green crops, and the winter had an abundant snowfall; such conditions encourage the onset of en masse breeding among rodents. Protective measures should be taken soon after thawing if there are more than 100 living burrows per hectare in fields of perennial grasses and along boundaries of fields to be sown with spring grain crops. If voles and lemmings are found in spring only within the limits of their refuges, protective measures are not required.

The autumn survey is undertaken to determine the state of rodent populations before their wintering. If the summer was dry and hot and the yield of grain crops lower than average, the autumn survey is not necessary. In such years, rodents are depressed and may be found only within the limits of their conservation places. In years of high yields and good vegetative growth, a wide dispersal of voles and lemmings is possible during autumn, and investigation becomes mandatory. The probable level of rodent numbers in the coming year can be judged from the degree of their dispersal. However, even with wide dispersal, the further fate of vole and lemming populations will depend largely on winter and early spring conditions. If winter is cold and snowfall light, the rodents will be fewer in spring. Their number will be high after abundant snow and en masse breeding will commence in spring.

X. *Zone of Western Kazakhstan and Orenburg District*: This zone includes the Orenburg, Uralsk, Aktyubinsk, and Gur'ev districts. The common vole and steppe lemming occur in agricultural regions of this zone. En masse breeding of these species has been recorded in recent years. The rodents are usually found in places of conservation, and their dispersal phase observed under a favorable

combination of weather and agronomic conditions, followed by a depression phase. Fringes of forest fellings and belts, embankments of irrigation canals, and slopes of riverine turf along river valleys flooded with water, constitute refuge of the common vole. In the dispersal phase, the common vole is found in fields of perennial grasses and grain crops.

The steppe lemming is conserved in areas of wormwood-grass laylands under a good snow cover during winter. In the dispersal phase it is found in crop fields.

Systematic observations on voles and lemmings comprise spring and autumn surveys of fields to identify habitat distribution of these rodents. Control measures for crop protection are not undertaken.

XI. *Zone of Northern, Central, and Eastern Kazakhstan*: This zone includes Kustanai, Kokchetav, northern Kazakhstan, Tselinograd, Pavlodar, Karaganda, Semipalatinsk, and eastern Kazakhstan districts. The narrow-skulled and common vole as well as the steppe lemming are distributed here. Before large-scale reclamation of virgin lands during 1953–1955, reproduction of the narrow-skulled vole and the steppe lemming was recorded in this zone periodically (see pp. 589–590). After reclamation of virgin lands, the refuge for these rodent species decreased sharply, making en masse breeding at earlier levels impossible. At present, the dispersal phase is observed under favorable situations, followed by a decline in numbers. Conditions for conservation of the common vole improved with cultivation of virgin lands, leading to some increase in its numbers (Gladkina, 1968a, 1969). However, conditions for en masse breeding of this species do not exist. Increase in number of common voles is also disrupted at the dispersal phase.

The narrow-skulled vole is conserved at fringes of forest fellings and virgin land with tall grass near forest fellings, if these places are not flooded during spring, and also in forest belts, along banks of channels, and sometimes in old fields of perennial grasses.

The steppe lemming is conserved in fields of perennial grasses, along slopes of ravines, and in individual pockets of fallow where growing vegetation is preserved for a longer time. It is found during the dispersal phase in areas of perennial grasses and grain crops.

Common voles are conserved in the forest belt, borders of fellings, and in denuded parts near kitchen gardens and field crops. In the dispersal phase, this rodent appears in standing crops, hayracks, and kitchen gardens. If straw bundles are left in fields, this vole overwinters in them.

Absence of winter grain crops and limited places for conservation outside cultivated lands significantly reduce the possible increase in numbers and damage due to voles and lemmings in this zone. Therefore, extermination measures are not practiced. Systematic observations comprise spring and autumn surveys to identify rodent habitat distribution. If the crop is well-harvested and postharvest cultivation timely, some increase in rodent population is prevented. Spring grain crops inhabited by these rodents incur some damage which, under favorable conditions, is observed not earlier than June. However, present methods cannot ensure effective control of voles and lemmings.

Recently, windbreak plantations have been adopted in this zone to prevent soil erosion. There is reason to believe that this will lead to an increase in conservation area for voles and lemmings and thus an increment in their numbers.

XII. *Eastern Siberia Zone*: This zone includes the Krasnoyarsk territory, Tuva, Buryat and Yakutian ASSR, Irkutsk and Chita districts. Agricultural crops in this extremely diverse territory in terms of weather conditions, occupy no more than 5.0% of the total area, but in individual pockets cover more than 60%.

The narrow-skulled vole causes significant damage to agriculture; the damage caused by the steppe lemming is more local, while Brandt's vole is the most active in the extreme south.

The climatic conditions of this zone offer an extremely limited summer for rodent reproduction and practically exclude the possibility of winter breeding. Conservation of voles and lemmings during winter is possible only in areas of good snow cover. Forest fringes, birch fellings among crops, forest belts, individual pockets of virgin land with tall vegetation, laylands, and hayracks and stacks, serve as refuges of the narrow-skulled vole. If a high-yield year is followed by a winter of abundant snow, dispersal of the narrow-skulled vole in fields and pastures is possible.

423 In Krasnoyarsk (southern regions), the steppe lemming is widespread and conservation places are fields of perennial grasses and virgin land pockets with a stable grass cover. With an increase in numbers, the density of habitats increases in these areas and, to a lesser extent, in fields of grain crops.

Brandt's vole has a limited distribution in the dry steppe regions of Chita district. Areas of fallow and haylands with a stable grass cover serve as places for its conservation. With an increase in numbers, it damages fallow and haylands and spreads into standing crops.

Preventive measures in eastern Siberia are presently carried out sporadically and locally when there is a significant increase in rodent population. Possibly, preventive measures will become more extensive in view of the large-scale introduction of erosion-prevention measures. Systematic observations comprise spring and autumn surveys with a view to determining habitat distribution of voles and lemmings.

XIII. *Far East Zone*: This zone includes the Primorye and Khabarovsk territories and Amur district. The group of lemmings under examination is not economically important in the Far East zone.

XIV. *Soviet Central Asian Zone*: This zone includes the southern districts of Kazakhstan, Uzbekistan, Kirgizia, Tadzhikistan, and Turkmenia. Four species of the group of rodents under study have been recorded in this territory—the social, narrow-skulled, Trans-Caspian, and Afghan voles. The first three are distributed locally, living only in conservation places occupying small discontinuous areas, and therefore occur in small numbers. The Afghan vole rarely breeds en masse in Tadzhikistan and Turkmenia since control measures are taken against it. The last population explosion of this species was recorded in 1955.

The Afghan vole experiences strong suppression in the dry hot period. Its reproduction ceases at this time and is resumed in winter (Popov *et. al.*, 1968). Refuges for this rodent are steppe areas in foothills characterized by a relatively cold microclimate in summer and more succulent vegetation; the northern slopes are sometimes overgrown with shrubs and banks of rivulets and valleys are verdant (Heptner and Shukurov, 1950; Heptner, 1956). With an increase in numbers, this rodent extensively occupied fallow and rainfed grain crops. Reproduction is facilitated by such weather combinations as a relatively humid spring and summer followed by an early autumn and relatively warm winter.

Systematic observations consist primarily of a single survey in October–November. If the year was favorable for the Afghan vole and it is found in fields of grain crops in autumn (wheat, winter barley), these fields should be treated in winter. In such years the survey must be repeated in February. With the discovery in this month of more than 200 living burrows (40–50 inhabited colonies) per hectare, repeat treatment is immediately executed.

In years of a hot and dry summer, only a single survey need be done in autumn.

Thus, systematic observations for recording the state of a rodent population and criteria for forecasting its numbers, assume unique

combinations of habitat distribution and morphophysiological conditions of the population in individual years in each zone. At the same time, seasonal variability in reproductive intensity and mortality in limited regions of the range of a particular species may follow a strict annual pattern. This could be due to the relative constancy in climatic variations in different seasons or to the similar stable manifestation of change in environmental conditions over
424 different seasons because of agronomic practices. In the USSR, such relatively stable rhythms of change in environmental conditions for the common vole are created in the right bank forest-steppe zone of the Ukraine. A similar strict cyclic rhythm in the seasonal state of the common vole has been reported from several places in France (Spitz, 1963, 1970). Seasonal rhythms in reproductive intensity and mortality of voles, in Spitz's opinion, permit forecasts of their numbers for three to six months, then for one year, using estimates of fertility of populations. He assumes a direct correlation between intensity of fertility and survival. Such forecasting should be considered a variant of the methods used in the USSR. Our predictions, based on estimation of state of population, determined from habitat distribution, morphological conditions, numbers, and also the environmental conditions under which numbers increase, likewise lead to an assessment of probable fertility and eventual survival.

Intraspecific Structure and Microevolution

The mechanism determining the formation of biotopic populations of common voles and steppe lemmings as well as the nature of their numerical dynamics in individual regions of the range were examined above. These aspects permit some generalizations regarding the intraspecific structure and microevolution of this group of rodents.

The starting stage in intraspecific differentiation is the formation of biotopic populations. As was indicated above, morphophysiological differences in biotopic populations are primarily determined by age structure and conditions of heat exchange and feeding in which each age group comprising these populations develops. Morphophysiological differences in biotopic populations for a given group of rodents, like their seasonal variation, are primarily phenotypic. These properties change over the course of several generations. It has been demonstrated that all morphological and physiological properties of biotopic populations are formed during

the ontogenesis of each individual according to the conditions of feeding and heat exchange in which it developed and, consequently, of the entire age group to which it belongs. We have considered those physiological mechanisms which determine the relative expediency of phenotypic variability of age groups, in particular the formation of spring and winter (seasonal) populations. It can be assumed that during the formation of the phenotype, depending on the environmental conditions in which ontogenesis occurs, the particular response appears to be programmed according to the environment in which the organism finds itself in the future. This programming is reflected in the morphophysiological characteristics of the organism. This process leads to the selection of those genotypes that will ensure optimum phenotypic variability of populations for the established distribution of energy resources in a given locality for the species and their variation in time and space. If all the forms of variability of populations (seasonal) occupying a given biotope, such as seen in the voles under study, which respond variously to the environment, were associated only with the replacement of genotypes, this would have retarded rodent response to environmental conditions, precluded programming optimal responses during ontogenesis, and resulted in extinction of these species.

425 The next stage of intraspecific differentiation is related to the degree of diversity of the biotopic populations formed in individual regions of the range and to the dynamics of their habitat distribution and population. It was earlier demonstrated that the larger the area of conservation habitats of the species, the higher its numbers and the more frequent en masse breeding. When the area of conservation places is very limited, the cycle of multiyear dynamics is not completed; only phases of depression and dispersal are seen. Furthermore, the frequency, completeness, and rapidity of individual phases of a multiyear cycle of numerical dynamics depends on the extent of optimum conditions for populations in their conservation and dispersal habitats. These conditions together determine not only the aforesaid nature of numerical dynamics, but also the specificity of variation of the entire complex of biotopic populations in each region of the range.

If a complete multiyear cycle of dynamics of habitat distribution and numbers is observed, then it is easy to note the large range of variation in viability of populations and, consequently, their morphophysiological conditions. It suffices to compare populations in stages of dispersal and en masse breeding with their conditions

during the period of numerical decline to form some idea about the limits of such variability.

Thus, with reference to the biotopic population, the terrainal population should be considered a higher category. Such complexes of biotopes are typical of environments that ultimately determine the total spread of a given species in its territory, the dynamics of habitat distribution and numbers, as well as the morphophysiological state of biotopic populations. Selection occurs in each terrain of genotypes which can most efficiently utilize the environmental resources prevailing within the limits of a given terrain, which leads to corresponding phenotypes.

Terrainal complexes with their unique dynamics of formation of biotopic populations give rise to a geographic population. The properties of a geographic population are determined not only by the totality of the same in each terrain, but also by the unique changes in energy resources and climatic factors typical of a given geographic space. It is this situation which leads to the formation of subspecies from geographic populations.

The foci of severe damage by the social vole in Azerbaidzhan may serve to exemplify the relation between terrainal and geographic populations. The entire territory of the republic is occupied by a single geographic population of this species. However, its distribution is not uniform. Several foci of distribution have been identified in Azerbaidzhan (Polyakov, 1950), the largest of which are Maraza-Shemakha, Ismailly-Aksu, Khaladno-Vartashan, Fizuli-Martuni, Khanlar, and Mugan. Each of these foci is characterized by a unique combination of conservation places for the social vole and concomitant dispersal places. All these foci are more or less isolated territories and within their limits almost no places suitable for conservation of the social vole in the critical season exist. Therefore, en masse breeding of this species often takes place in individual foci at different times.

The population structure of species of steppe voles and lemmings, forms exhibiting the most labile response to variation in environmental energy resources and climatic factors, is depicted schematically in Figure 80. Liability of response has developed in these rodents due to the need for adaptation to winter cold and summer drought and high temperatures.

A precise line cannot be drawn between geographic and terrainal populations in every case. Yet, they may differ in area occupied. The boundaries of a geographic population are easily drawn. Sometimes such populations are separated by space not occupied

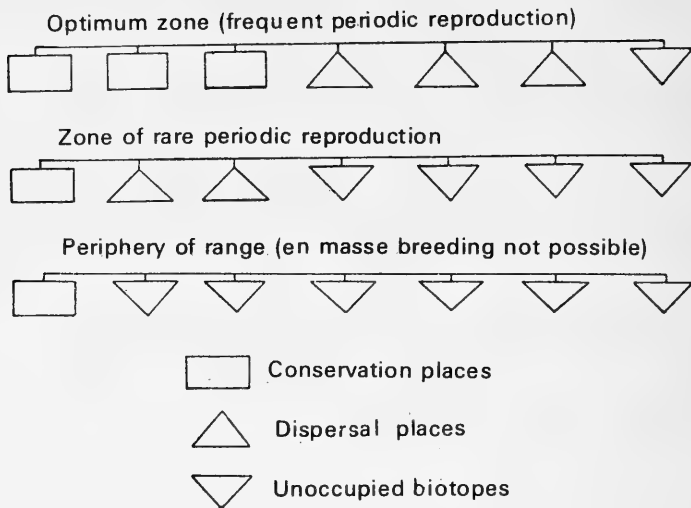


Figure 80. Schematic population structure of species of steppe voles and lemmings characterized by maximum liability of response to the environment in the subfamily Microtinae.

by this particular species, as in the example cited above. The number of biotopic, terrainal, and geographic populations, like the subspecies, may be much higher than shown in the scheme (Figure 80); only the principle of coordination of population structure is depicted. At the same time, one may assume that in optimum terrains there ought to be greater diversity of biotopic populations. In the case of steppe voles and lemmings, probably it would be more correct to speak not about the optimum and periphery of a range, but about optimal and nonoptimal terrains. The range boundary, like the presence of territories within it not occupied by a given species, is determined by the absence of biotopes suitable for conservation of its populations during critical periods of existence.

Let us now examine the variation in absolute values of some morphophysiological characters in the groups of voles and lemmings under study, as an index of liability of their response to the environment.

A comparison of the skull measurements of subspecies of the common vole found in the USSR (Ognev, 1950) with the terrainal population of *Microtus a. transcaucasicus* from the Dashkesan region of Azerbaidzhan, investigated by Levi in 1952 and 1954 (Levi,

1955), is presented in Table 29. In 1952, the Dashkesan population was characterized by low viability, comparatively smaller size, and suppressed breeding. In 1954, this population was characterized by greater viability, larger size, and greater breeding intensity. This condition was akin to the one noted in 1951 (see Tables 12 and 13).

It is interesting to compare the intraspecific variability of characters with their variability in the Dashkesan population in optimal and nonoptimal years. It should be noted here that S.I. Ognev, who had considerable material for each subspecies, actually used only a small fraction including that dissimilar in characters. Only "typical" indices for each subspecies were selected and the remainder of the collection not analyzed. Probably, only such a system of analysis permitted a comparatively specific characterization of morphological differences between various subspecies of the common vole. It should be emphasized, however, that the characters selected for comparison do not fall in the category of highly variable characters.

Thus, the condylobasal length in all subspecies of the common vole distributed in the USSR varies in the range of 23.1–28.3 mm, and in the investigated Dashkesan population in the range of 23.2–28.6 mm. The zygomatic width in the two populations is respectively: 12.1–16.0 and 12.8–16.5; length of nasals 6.1–9.0 and 6.25–8.3; and length of dental row 5.0–6.5 and 5.8–6.8 mm. The Dashkesan population revealed a narrow range of variability for length of nasals which, in voles, grow throughout life (Vinogradov, 1922; Levi, 1955, 1958). Hence, it can be concluded that the animals studied in the Dashkesan population were more homogeneous in age composition and included more younger animals than the collection examined by S.I. Ognev. The adult part of the Dashkesan population was somewhat older in 1954 than in 1952. For an objective analysis of the degree of variability in subspecies of the common vole and in the Dashkesan population of this species, only the condylobasal length was used and the comparison done in two stages. The main statistical indices of the condylobasal length of the skull of subspecies of the common vole and the Dashkesan population are given in Table 30. Table 31 presents the matrix of comparison of the same taxa with the Dashkesan population in 1952 and 1954 together with the combined population. Analysis of the data of Table 30 shows that the dispersion in condylobasal length of skull in the Dashkesan population (combined) is more than in the species as a whole, characterized on the basis of indices for the subspecies reported by Ognev (1950).

Table 29. Absolute measurements (mm) of skull of different subspecies of the common vole (*Microtus arvalis* Pall.) (mean values given in parentheses) (from Levi, 1955)

Subspecies	No. of animals	Condylobasal length	Zygomatic width	Length of nasals	Length of dental row
<i>M. a. duplicatus</i> Röhrig and Börner	386	23.1-26.2 (24.7)	12.1-14.8 (13.44)	6.1-7.8 (7.4)	5.2-6.2 (5.7)
<i>M. a. rossiae-meridionalis</i> Ognev	446	24.3-28.3 (25.7)	14.0-15.6 (14.51)	6.8-8.2 (7.45)	5.8-6.3 (5.92)
<i>M. a. macrocranicus</i> Ognev	162	25.8-27.3 (26.3)	14.5-16.0 (15.47)	7.0-9.0 (8.17)	5.8-6.5 (6.05)
<i>M. a. gudaureus</i> Ognev	45	23.8-24.3	13.1-15.2	6.1-8.0	5.3-6.2
<i>M. a. transcaucasicus</i> Ognev	133	24.0-26.9 (25.38)	13.3-15.7 (14.53)	7.0-8.3 (7.88)	5.2-6.0 (5.58)
Population of the same subspecies in 1952	32	23.2-26.4 (24.4)	12.8-15.8 (14.18)	6.25-7.6 (6.95)	5.8-6.5 (6.14)
Population of the same subspecies in 1954	28	25.6-28.6 (26.7)	14.4-16.5 (15.4)	6.8-8.3 (7.6)	5.8-6.8 (6.2)
<i>M. a. iphigeniae</i> Heptner	105	24.7-26.5 (24.47)	13.9-15.2 (14.48)	7.0-9.0 (7.71)	5.7-6.2 (5.93)
<i>M. a. ruthenus</i> Ognev	132	22.0-25.3 (23.58)	12.3-14.4 (13.23)	6.1-7.6 (6.82)	5.0-5.8 (5.49)
<i>M. a. transuralensis</i> Serebr.	182	23.2-25.9 (24.4)	13.9-14.9 (13.92)	6.1-8.0 (7.05)	5.2-6.0 (5.48)

<i>M. a. caspicus</i> Ognev	167	24.0-26.2 (25.2)	13.3-15.2 (14.2)	7.0-8.0 (7.52)	5.4-6.3 (5.95)
<i>M. a. obscurus</i> Eversmann	34	24.3-26.9 (25.2)	13.9-15.2 (14.35)	6.5-7.6 (7.22)	5.4-6.3 (5.8)
<i>M. a. kirgisosum</i> Ognev	19	24.6-26.1 (25.8)	14.2-15.0 (14.8)	7.1-7.6 (7.24)	6.0-6.1 (6.0)
<i>M. a. innae</i> Ognev	37	23.7-25.3 (24.58)	13.6-15.2 (14.36)	6.3-7.6 (6.93)	5.3-6.0 (5.7)

Character variability is given in Table 31. In each entry, the numerator shows how many times higher the variation (dispersion) of the character in the taxon of the row is, indicated by the corresponding number (see Table 30), than in the taxon of the column. Thus, for example, 1/2.49 indicates that in the taxon of the column the variability is 2.49 times higher. Statistically insignificant numbers are enclosed in parentheses. In the comparison of mean values, expressed in percentages, the plus sign (+) indicates that it is higher in the taxon in the horizontal line than in the taxon in the vertical line, while a minus sign (−) indicates that the mean index is higher in the taxon in the vertical line.

429 The analysis shows that variability of the Dashkesan population taken as a whole is not less, but probably higher than the variability of the species, arrived at by combining the data for typical members of all the subspecies.

Data characterizing indices of craniometric characters of social vole populations from the Ismailly region of Azerbaidzhan SSR investigated in different phases of the multiyear cycle of numerical dynamics, and all the subspecies of this species characterized from the type members of Ognev (1950), are summarized in Table 32. Statistical analysis of these results showed that variability of the indices of the characteristics compared in the Ismailly population is close to the value typical for the entire species.

In those regions of the range where the species by and large does not move outside the limits of its refuges and its population increase is disrupted at the initial phase of dispersal, conditions are created for a greater range of variability in biotopic populations. Under these conditions, the morphophysiological characteristics of biotopic populations are quite similar every year.

Naumov (1937–1967) repeatedly noted that fertility is higher at the periphery of the range of the species than in the optimum conditions of the range. He explains this as a compensatory adaptation associated with higher mortality of animals on the periphery as a result of increased stress of interspecific relations. I have already shown that such an explanation unilaterally considers the reproductive ecology of rodents at the periphery and under the optimum conditions of the range (Polyakov, 1949b). On the periphery of the range a species is primarily located in conservation habitats. Optimum conditions are found for rodents in such habitats, albeit for a short period in the year. Therefore, their progeny here is small and fewer generations mature and reproduce throughout the year; however, individual broods of reproducing animals are

Table 30. Comparison of indices of condylobasal length of skull of subspecies of the common vole and the Dashkesan population

Taxon No.	Taxon	X	S	D	n
I	All subspecies of <i>Microtus arvalis</i> according to Ognev (1950)	24.27	0.99	0.96	93
II	Combined material of Ognev (1950) and Dashkesan population	24.29	1.25	1.57	153
III	<i>M. a. duplicatus</i>	24.63	0.56	0.32	31
IV	<i>M. a. ruthenus</i>	23.68	0.92	0.84	17
V	<i>M. a. transuralensis</i>	23.40	0.67	0.46	27
VI	<i>M. a. transcausicus</i> (only from Ognev's material)	25.39	0.80	0.63	18
VII	<i>M. a. transcausicus</i> (material of Ognev and Dashkesan population)	25.45	1.12	1.25	78
VIII	<i>M. a. transcausicus</i> (Dashkesan population in 1952)	24.40	0.77	0.59	32
IX	<i>M. a. transcausicus</i> (Dashkesan population in 1954)	26.70	0.74	0.55	28
X	<i>M. a. transcausicus</i> (combined Dashkesan population in 1952 and 1954)	25.50	1.16	1.35	60

X—arithmetic mean of character; S—mean quadratic deviation of character; D—dispersion; n—number of animals actually used in assessment.

larger. Under optimum conditions of the range, the breeding season is longer. The rodents here occupy habitats that differ more in extent of favorable conditions than on the periphery of the range, and many age groups participate in breeding. All this leads to a greater variation in individual fertility. Therefore, if the average individual fertility (number of neonates in brood) is compared, it is higher on the periphery than in the optimum of the range. But the total number of animals born in a population throughout the year will be higher in the optimum part of the range than at the periphery.

The interdependence of biotopic and geographic variability of a population is revealed by the fact that the latter is manifested through the eurytopic nature and numerical dynamics of the species in different regions of the range. Under optimum conditions, periodic changes in habitat distribution and numbers provide far more

Table 31. Comparison matrix of subspecies of the common vole and Dashkesan population based on condylobasal length of skull (numerator—variability of taxon for row; denominator—variability along column)

I	(-1.8%)	-45.0%	+62.2%	+103.4%	-125.7%	-112.3%	(-14.8%)	-279.8%	-114.6%
1.64/1	II	-35.0%	(+27.3%)	+88.4%	-105.0%	-97.7%	(-10.6%)	-234.1%	-100.2%
1/3.0	1/4.91	III	+124.8%	+197.2%	-110.3%	-92.6%	(+34.2%)	-314.1%	-95.2%
(1/1.14)	(1/1.87)	2/62.1	IV	(+34.7%)	-199.6%	-183.3%	-85.3%	-326.5%	+174.1%
1/2.07	1/3.41	(1.44/1)	(1/1.83)	V	-269.5%	-222.0%	-138.1%	-464.8%	-221.0%
1/1.52	1/2.49	1.97/1	(1/1.33)	(1/1.37)	VI	(-6.1%)	+126.8%	-170.6%	(-11.0%)
(1.30/1)	(1/1.26)	(3.91/1)	(1.49)	2.72/1	(1.98/1)	VII	+109.5%	-131.9%	(4.5%)
1/1.63	1/2.66	1.84/1	(1/1.42)	(1.28/1)	(1/1.07)	(1/2.12)	VIII	-305.1%	-111.7%
1/1.75	1/2.85	(1.72/1)	(1/1.53)	(1.20/1)	(1/1.15)	1/2.27	1/1.07	IX	+123.2%
(1.41/1)	(1/1.16)	4.22/1	1.61/1	2.93/1	2.93/1	(1.08/1)	2.29/1	2.45/1	X

Note: Roman numerals denote taxa compared (for details see Table 30).

Table 32. Range in variation of skull size (mm) in different subspecies of the social vole (*Microtus socialis* Pallas) found in the USSR (Ognev, 1950) and in populations of *M. s. binominatus* Ellermann from Ismailly, Azerbaidzhan SSR, examined at different phases of the multiyear cycle of numerical dynamics (from Mamedov, 1952)

Groups compared	n	Condylo-basal length	Zygo-matic width	Inter-orbital width	Length of nasals	Length of bullae
All subspecies	306*	22.5–29.7	12.6–17.3	3.2–4.5	5.2–8.3	7.3–10.2
Ismailly population	104	23.0–27.5	13.0–16.5	3.5–5.0	5.0–10.0	6.0–9.7

*Includes 61 specimens of the subspecies *M. s. binominatus*.

ecological information on the maintenance and enrichment of the gene pool of a geographic population. Conditions deciding the stenotopic nature of the species at the periphery of the range with a small amplitude of variation in numbers reduce the possibility of enrichment of the gene pool of a population. Ultimately, the geographic populations acquire differences in many morphophysiological and ecological features. Lackey (1957) came to the same conclusion after studying the geographic population of *Peromyscus leucopus*.

As mentioned above, subspecies represent a further qualitative isolation of a geographic population. They differ in nature of response to the environment. The nature of change in the response, depending on environmental conditions, is completely maintained but the limits shifted from optimal to higher to lower values (Gladkina, Meyer and Mokeeva, 1962, 1963a, b, 1966; Polyakov, 1967, 1969; Gladkina and Mokeeva, 1970a, b). However, the difference in subspecies, even though associated with adaptation to some limited number of leading environmental factors, involves the function of almost every system ensuring homeostasis of the organism and its populations. Therefore, subspecies may differ in a series of characters but, as indicated by the statistical analysis of results (see Table 31), not equally sharply.

A study of subspecies of the narrow-skulled vole and the steppe lemming showed that their morphophysiological differences, while not always, and not for all the indices compared, are nonetheless

statistically significant and functionally stable. There is sufficient basis to state that *Lagurus lagurus abacanicus* differs persistently and statistically from all other subspecies of the steppe lemming. The subspecies *L. l. agressus* differs from *L. l. lagurus* mainly in mobility, response to food, and heat conductivity of pelage. Subspecies of the narrow-skulled vole differ primarily in response to food.

It is probable that differences in food base in different regions of the range are the first significant factors determining the variability of geographic populations of a group of rodents in the direction of their separation into subspecies (Vorontsov, 1967). However, differentiation may also take place under the influence of conditions of heat exchange.

The responses of subspecies to conditions of heat exchange develop uniquely in different species, depending upon the nature of their adaptation to changes in climatic factors. Thus, a comparison of *L. l. abacanicus* and *Microtus gregalis dukelskiae* (living in southern Krasnoyarsk) with *L. l. lagurus* and *M. g. gregalis* (from northern Kazakhstan) (Table 33) shows that the lemming subspecies differ significantly but the vole subspecies do not. For steppe lemmings occupying open biotopes, adaptations to the environment have developed so markedly that this subspecies is distinctly differentiated from others. For narrow-skulled voles living along fringes of forest fellings and other relatively humid biotopes shaded in summer and covered with snow during winter, significant differences in adaptation to climate have not developed.

Thus, four basic, qualitatively different categories of development within a species can be identified, viz., biotopic populations, terraineal populations, geographic populations, and subspecies. Adaptational variability covers these four categories but may also be noted at the level of the individual organism. Each category exhibits unique differences that play an important role in microevolution.

431 Variability has been noted for the following indices at the individual level within biotopic populations: seasonal change in activity; type of neural responses; sexual activity and fertility; variation in acclimation to high and low temperatures; locomotory activity; fattening and the several external and internal characters associated with it; differences in nature of response to the environment associated with the stage (phase) of ontogenesis and its rate; individual immunity to diseases; and individual differences in utilization of edaphic conditions. Selection may take place for

Table 33. Morphophysiological differences in subspecies of the steppe lemming (*Lagurus lagurus*) and the narrow-skulled vole (*Microtus gregalis*) (from Gladkina and Mokeeva, 1970a, b)

Indices for comparison	Subspecies of steppe lemming			Subspecies of narrow-skulled vole		
	<i>L. l. abacanicus</i>	<i>L. l. agressus</i>	<i>L. l. lagurus</i>	<i>M. g. dukelskiae</i>	<i>M. g. gregalis</i>	<i>M. g. raddei</i>
Average body weight of adult animal, g	32	22	20	21	21	26
Average body length, mm	102	88	85	93	94	103
Level of basic metabolism (O ₂ in cc/min/g):						
at 0°C	0.130	0.170	0.175	0.175	0.180	0.150
at 14°C	0.095	0.120	0.124	0.121	0.125	0.112
Critical metabolism, at °C	32.0	30.0	32.0	32.0	32.0	32.0
Level of metabolism at critical temperature (O ₂ in cc/min/g)	0.050	0.070	0.080	0.080	0.080	0.075
Heat conductivity of fur, mcal/cm ² /sec	2.6	2.7	2.8	3.0	2.93	3.06
Mobility—running in a drum, m/day	3374	4744	4440	—	—	—

(continued)

Indices for comparison	Subspecies of steppe lemming		Subspecies of narrow-skulled vole			
	<i>L. l. abacanicus</i>	<i>L. l. agressus</i>	<i>L. l. lagurus</i>	<i>M. g. duketskiae</i>	<i>M. g. gregalis</i>	<i>M. g. raddei</i>
Food requirement per day, mg/g						
body weight:						
Grain	95	103	105	95	120	150
Hay	150	180	175	150	200	190
Carrot	600	500	450	750	600	580

these characters within biotopic populations. In this context, it should be noted that biotopic populations will be more viable depending on diversity of age structure and individual variability within each age group (Polyakov, 1961a; Kalabukhov, 1962). At the same time, it should be borne in mind that optimal conditions ensure high individual variability and diversity of age groups in biotopic populations, while extreme conditions sharply reduce the age composition of populations.

Biotopic populations may differ in density of settlement, age structure, sex ratio, seasonal variability, phenology, breeding intensity, developmental rates of progeny and their survival, immunity against diseases, resistance to unfavorable effect of physical factors of the environment, behavioral characteristics, and mean and range of all forms of individual variability in the animals that make up the population. Together, these features of populations characterize a different utilization of favorable combinations of environment for reproduction and different survival rates under unfavorable conditions for existence. Selection of biotopic populations occurs along these lines in the process of seasonal and multiyear changes in conditions of existence.

432 Populations in landscapes are differentiated into a complex of populations by the capacity and degree of optimization for species in those biotopes to which each restricts itself during periods of extreme environmental conditions, and which are settled when conditions are optimal. Such "landscape" populations differ in numbers, numerical dynamics, habitat distribution of the species, range of variability and morphophysiological conditions of biotopic populations, and in position occupied by the species of biocenosis.

Geographic populations differ in degree of variability of topographic complexes and, consequently, greater or lesser possibility of conservation and enrichment of the species germplasm. Furthermore, individual regions of the range differ in composition and nature of alternation of optimal and extreme conditions of existence over different seasons and years. These conditions together determine the direction of variability in geographic populations. On the whole, they differ in position occupied in the biocenosis, conditions of conservation and survival coefficient, food availability and aspects of feeding, morphophysiological characters and amplitude of their variability, intensity of breeding, dynamics of habitat distribution and numbers, and in behavior. The extent of differences in the geographic population is determined not by the distance separating the regions under comparison and not even by their isolation (Ter-

ent'ev, 1966), but by the stability and absolute values of differences in the totality of living conditions. Selection in geographic populations occurs in the directions of increase in those adaptations which ensure survival under an extreme combination of conditions in the area occupied and rapid restoration of numbers with the onset of optimal environmental conditions.

Subspecies differ not only in totality of response to the environment, but also in indices of optimal environmental conditions and norms of response to it. Evolution of a subspecies into a species is associated with those changes in morphology and physiology that lead to its reproductive isolation or (initial) lower fertility of hybrid progeny. In this respect, the subspecies *L. l. abacanicus*, compared to other subspecies of this species, already stands at the threshold of independent species status (Gladkina, Meyer and Mokeeva, 1963a, b, 1966; Gladkina and Mokeeva, 1970a, b).

The entire population structure has an important adaptive significance for a given biological group of animals. It is determined by the nature of their response to the most important environmental factors, such as energy resources and climate factors. Intraspecific and interspecific relationships in each of the categories of species differentiation develop under the control of energy resources of the environment and climate factors. For a given biological group of animals, this means the most effective utilization of environmental resources and the most flexible system of responses to the latter's variability in time and space. Therefore, intraspecific differentiation should be considered an adaptation of definite life forms or biological groups within them. This adaptation is unique for different life forms. Therefore, if a species is an undisputed qualitative unit for all animals, then even a subspecies is considered by some researchers to be a conditional category. The fact that S.I. Ognev was forced to specially select "typical forms" in order to provide reliable morphological characteristics of the subspecies, ignoring the greater part of his collection, only confirms the opinion expressed by Mayr* (1971). At the same time, if the question of intraspecific differentiation is considered an adaptation of definite life forms and biological groups, their reality and regularity of formation become more apparent. This is a very important consideration when identifying the tendencies of microevolution of harmful organisms in connection with all the forms of influence exerted by modern civ-

*Not listed in the bibliography—Eds.

ilization on the biosphere, and in developing a general biological theory for the conservation of nature.

Damage and Control Measures

The damage caused by steppe voles is manifested only in areas under agriculture. In natural ecosystems, there is no reason to consider consumption of vegetation a damage. Moreover, there is sufficient reason to believe that voles as phytophages perform an essential function in natural ecosystems (Batzli and Pitelka, 1970; Babinska, 1972; Abaturov, 1974; Grant, 1974).

Common voles and lemmings cause great damage to crops and pastures by eating growing vegetation, and to fruit plantations by gnawing the bark of trees. Maximum losses due to these rodents are noted in the years of their maximum numbers. En masse breeding of rodents, called "rat invasions" in prerevolutionary Russia, simultaneously covering large areas, caused famines through crop loss and depletion of hay fields and pastures. In addition, epidemics erupted as the pathogens of disease were spread by the rodents. Today, systematic observations are conducted on the status of vole and lemming populations, which involve regional and national forecasts of their numbers, and control measures implemented. On the whole, in the USSR, preventive measures are implemented every year over an area of 3.5 to 9.5 million hectares (Polyakov, 1968b). A decisive role for preventing en masse breeding of voles and lemmings is played by management and agronomic practices, viz., timely and proper harvest, and postharvest cultivation. Other measures are auxiliary. Together, these measures presently prevent en masse breeding of common voles and lemmings in large agricultural regions. However, local increases in numbers are quite frequent. In 1963–1964 the social vole multiplied on a large scale in Azerbaidzhan, Georgia, and Armenia; in 1966–1967 and 1973–1975 an increase in numbers of the common vole was reported from southern Ukraine and northern Caucasus. The common vole has locally increased in numbers almost every year in the subalpine zone of the Caucasus and Trans-Caucasus.

It is difficult to carry out a comprehensive estimation of the financial losses caused by voles and lemmings and to date this has not been done. I have estimated that in 1952, en masse breeding of common voles in Azerbaidzhan led to the expenditure of about 6 million rubles on prevention of epizootics among domestic animals and of epidemics; the loss caused to agriculture was more than 10

million rubles. Probably, the losses incurred during the 1963–1964 population explosion of the social vole in Azerbaidzhan were no less.

Now we have identified the zones for each species of the group under study, where the damage caused is manifested through periodic en masse breeding or is chronic even with a relatively low number of rodents (see Figure 78). Voles cause chronic damage to fruit plantations and spoil coarse fodder in stacks and hayracks. It is difficult to estimate these losses, but judging from information supplied by the Forecasting Service of the USSR, it may be assumed that, on the average, in each collective and state farm losses up to 300–500 rubles are sustained through the chronic harmful activity of voles and lemmings. For the USSR as a whole, this totals 25–35 million rubles per annum. If to this we add losses incurred during local en masse breeding of rodents and the expenditure on control measures, the total loss for the USSR would be approximately 50–60 million rubles.

434 Expansion of irrigated areas and floodlands in the Ukraine, northern Caucasus, and the Volga region; increase in irrigated areas under perennial grasses in all regions of the European part of the USSR; and land reclamation in the non-chernozem zone of the RS-FSR, have created conditions for a sharp increase in numbers of steppe voles and thus the damage done by them. The total cropped area requiring protection from voles has rapidly increased since 1970. In 1974 more than 9 million hectares were treated. Even if we consider that about one-third of this area was treated with Bactorodencide, which did not produce the desired effect, the total area treated remains large. Moreover, it appears that such extensive treatment will become almost an annual necessity.

Voles are also considered serious pests in countries adjoining the USSR. Intensive control measures are periodically implemented against the social vole in Iran (Farahbakhsh, 1961). Systematic intensive control of the common vole, which severely damages clover and lucerne crops, is carried out in Bulgaria, Rumania, Czechoslovakia, the GDR, the FRG, and France (Klemm, 1957a, b; Straka, 1966; Gaisler *et. al.*, 1967; Giban, 1974b; and others).

Control measures against voles and lemmings change according to ecological conditions and number of rodents to be controlled.

In field conditions, poisoned grain baits are often used. Wheat serves as the bait and zinc phosphide mixed with vegetable oil as the poison and then smeared on the grain.

Voles and lemmings do not actively search for grain, as susliks (*Citellus*) or rats (Muridae) do, but eat it when they chance upon it. They feed on grain mainly during the cold part of the year and almost do not touch it in hot weather. Therefore, poisoned baits are used only during late autumn, in a snowless winter, and in early spring. Attempts are made to concentrate a lethal dose of poison for an adult vole on a single grain of wheat.

The composition of the bait is changed depending on the state of the rodent population. During the period of numerical increase of common voles and lemmings (in the phases of dispersal and en masse breeding), 10 parts zinc phosphide and 3 parts vegetable oil are used for 100 parts of grain. In this case, 3.0–3.5 mg zinc phosphide is smeared on one grain, which can cause death to a vole or lemming weighing 40–45 g. In the phase of numerical decline, when the population is weak and consists of small animals, zinc phosphide at 3.0% grain weight is used. In this case, 1.0 mg zinc phosphide suffices for effective poisoning of one vole on a single grain. In 1953 ground grain was used to control social voles in Azerbaidzhan when the populations were in the decline phase. This proved efficacious; less than 1.0 mg zinc phosphide was required for poisoning weak rodents (Polyakov, 1968b).

Bait consumption depends upon the method of distribution and density of rodent settlements. Often the bait is spread near vole colonies. For a colony occupying an area up to 20 m², 5–10 g bait are so spread that up to 1.0 g (30 grains) are distributed per m² along the periphery of the most frequented entrances. Placement of the bait in small heaps is not advisable as this poses a danger for domestic animals. With uniform distribution of the bait, its consumption is comparatively small and does not exceed 0.5–1.0 kg per hectare. True, if the boundaries of the colonies are fused and the entire soil appears riddled with burrow openings, then 3.5 kg bait
435 is required per hectare. In this case, the field staff spread 10–15 g bait after every five steps to the right and the next five steps to the left. Each operation covers an area of 10–15 m².

Quite often in poisoning large areas, bait-spreaders sit on seats specially mounted on tractor trailers used for harrowing. The interval between places of bait-spreading is 8–10 m. Using such trailers, four bait-spreaders can treat 300–400 hectares per day.

In using airplanes for bait-spreading, the ratio is 5.0 kg bait per hectare. However, aerial treatment is less effective than ground-spreading and much more costly (Polyakov, 1961a, b).

In Azerbaidzhan, spraying of the wheat crop with a 5.0% aqueous solution of sodium arsenite was done several times in winter. Spraying was done from airplanes at 50 liters solution per hectare.

Grain bait is used to control voles in and around orchards in the prewinter period. Baiting points of long duration are prepared during winter. For this, after determining the depth of snow cover by means of spades over an area of 0.5 m², the snow is dug to soil surface. Then 100–150 g of hay or straw are laid on the ground and 100–120 g poisoned bait placed on top; the snow, after dusting with zinc phosphide, is respread and the area leveled. Each point should be such that the snow around it is not trampled and remains loose. For this, bait points should be approached from one side, covering the bait with snow without trampling it, and returning by the same path after the operation. If the snow around the bait is packed, the voles cannot reach it. Such points are fixed at 10 to 20 places per hectare. Places of long-duration poisoned baits are tagged. In early spring, before the snow cover has completely thawed, the residual bait is collected and buried to at least 70 cm in soil so that it cannot be consumed by domestic animals.

Ratindan, a slow-acting blood anticoagulant, is used to control voles during winter in hayracks. It is applied in the form of a fine dust containing only 5.0% of the active principle to the base of the haystack. Coarse ground grain or groats are recommended as bait. The bait is dusted with the poison at the rate of 3.0% grain weight and placed in the hayracks in specially constructed bait boxes. The boxes consist of three triangular planks with openings on the sides and 60–80 cm long. Between 100–200 g bait are placed in each box, which is inserted in the hayracks (stacks) parallel to the soil surface, taking care not to spill the bait. One box is used for every 8–10 m³ hayrack or stack. The bait should be supplemented every 20–30 days if rodents continue to survive.

As shown by experiments in Novgorod district (Tumanov, 1968), November–April is the best time for vole control in hayracks. In this period, green matter rich in vitamin K, which blocks the action of the anticoagulant, is not available to voles. This method can destroy up to 93–95% of the voles inhabiting hayracks.

In Czechoslovakia (Gaisler *et al.*, 1967), grain poisoned with zinc phosphide was used as bait in hayracks to control the common vole. The bait was also kept in specially constructed boxes or tubes. It was considered expedient to initiate control measures soon after the erection of hayracks, to prevent breeding of the rodents and to reduce losses. Using baits with zinc phosphide in hayracks

and stacks is considered more dangerous than baits poisoned with Ratindan.

436 In recent years, at the initiative of Sokur (1970), ammonia water has been used to control rodents in hayracks in the Ukraine. Special equipment permits pumping the liquid into the hayracks directly from ammonia-carrying machines. About 10–12 liters ammonia solution per cubic meter is recommended.

Zinc phosphide is widely used in grain baits to control voles in foreign countries. Thus, in France in 1958, at the time of en masse breeding of the common vole, 4 million hectares were treated with grain bait of zinc phosphide (personal communication from J. Giban, Agricultural Attaché, Soviet Embassy in France, and Head of the Laboratory of Small Vertebrates of the National Agricultural Research Institute).

In several countries, Endrin, a product of diene synthesis, has been used to control voles in fields of lucerne and clover (Israel, Bulgaria, Czechoslovakia, Hungary, Rumania, etc.). In Bulgaria (Straka, 1963b), Endrin is used in water. For one hectare 750–1,000 ml of 20% Endrin is mixed in 1.0–2.0 ton of water. Tractor-operated sprayers were employed soon after the clover or lucerne was harvested. In the period of intensive breeding of voles, 1,000 ml Endrin was consumed, and 750 ml during winter (after the breeding season). Vole mortality reached 92.2–95.1%. This preparation has also been used in other countries (200 g/ha of 65% Endrin). In such concentrations, Endrin is harmless for domestic as well as fur-bearing animals after a quarantine of 40 days. The doses used were not harmful for the latter animals, and any danger to the former averted by quarantine. In the USSR, products containing diene synthesis are prohibited for plant protection, which include Endrin and Dieldrin (also successfully used in other countries for rodent control). However, grain poisoned with zinc phosphide is generally spread on the soil surface in the USSR, while in many other countries it may only be placed inside burrows to reduce the danger of poisoning beneficial grain-feeding animals, especially birds. At present, much attention is being paid in all countries to the selection of zoocides that would pose less danger than zinc phosphide to beneficial animals. Chemicals of the indandione group, which are blood anticoagulants, appear promising. In France, Chlorphacinon has been widely tested on the common vole (Giban, 1970; Grolleau, 1971). It has been demonstrated that a poison content of 2.0% in wheat grain and 20 kg bait per hectare placed inside rodent burrows led to 75–80% mortality of the initial

number of 200–500 voles per hectare. With uniform spreading of the same quantity of bait on the soil surface, efficacy decreased (about 60%); spreading in rows at intervals of 5.0 m, which ensured a more concentrated supply of bait, was satisfactorily efficacious (above 70%). For beneficial animals, especially birds, this method is completely harmless—a fact experimentally tested on partridges.

Giban (1970) considers Chlorphacinon a promising preparation for vole control under field conditions. However, a very high bait consumption limits its utilization. Furthermore, anticoagulant preparations are capable of inducing a rapid selection of hereditarily resistant rodent forms—a fact demonstrated in rats (Greaves and Ayres, 1969).

437 Problems of rodent control have repeatedly been discussed in international conferences (Fourth Vertebrate Pest Conference, 1970; Bionomics and Control of Rodents, 1971; and others). It is often remarked that in solving the problem of rodent control, the latest results of investigations are not fully explored (Cushing, 1970), which tends to keep the problem pending.

Attention has now focused on the selection of chemicals capable of disturbing reproduction of rodents of any genus. Such preparations are called chemical sterilants. To date, this problem is not sufficiently solved to allow practical application (Marsh and Howard, 1970). Researchers have determined which sterilants can produce the desired effect, but a large number of such chemicals is needed if they are to be used in accordance with the requirements of a species. Furthermore, it is essential to take into account the specific action of each chemical.

In the USSR, microbiological methods of rodents control are under intensive scrutiny (Kandybin, 1963; *Metodicheskie...*, 1970). The bacteria of salmonellosis are being used: Isachenko (*Salmonella decumanicidum*) and No. 5170 of Prokhorov (*S. tiphimurida rodentia*). The efficacy of these preparations depends on how they are used, quality of preparation and, most importantly, state of the rodent population. The microbiological method of rodent control is not practiced abroad; it is prohibited by law in the GDR. In the conferences mentioned above, this method was described as unpromising and dangerous for other species, i.e., other members of the biocenosis (Radwan, 1970).

HYDROPHILOUS FORMS OF VOLES

General Characteristics

This group includes vole species that have clearly adapted to wet and coastal biotopes of freshwater reservoirs. The extent of this affinity is variable. This adaptation is maximally expressed in *Ondatra* (*O. zibethica* L.) followed sequentially by the water vole (*Arvicola terrestris* L.), reed vole (*Microtus fortis* Büchn.), Ungur or Maximovich's vole (*M. unguensis* Kastschenko), Sakhalin vole (*M. sachalinensis*), and root vole (*M. oeconomus* Pall.). This biological property, which has left an imprint on all interactions with the environment, is determined by a higher requirement for succulent food. For example, during its breeding period the water vole requires food containing more than 67% water (Voronov, 1954b).⁷ *Ondatra* probably feed on even more succulent food.

Animal association with reservoirs has resulted in several adaptations, including swimming, diving, and food collection on water and sometimes under water. These adaptations have been perfected in muskrats, somewhat less so in the water vole, and lesser still in other species of this group. The muskrat has a small swimming membrane between the digits of the hind limbs and a fairly long tail flattened ventrally and covered with horny plates that serve as a special device for swimming, and especially for diving. Furthermore, some morphophysiological properties are variably developed in this group of voles, which ensure diving and life under water. Galantsev (1965a, b) reports the presence of venous sinuses located outside the chest cavity, in which blood collects during diving, enabling the animal to slow its heartbeat under water by one-fifth to one-tenth; this, in turn, facilitates a comparatively long dive and swim without a change of air in the lungs. As noted earlier, venous sinuses are also present in the common vole (Tumanov, 1968). In
438 this animal, these structures collect blood during entry into burrows and nests when heat discharge decreases sharply and it becomes necessary to reduce the intensity of blood circulation. It is probable that in hydrophilous voles the new function of these sinuses developed through enhancement of its earlier use of the same order, since these animals are also burrowers, and their aquatic mode of life probably developed as a subsequent specialization.

⁷Formozov (1947), based on a personal communication from A.G. Voronov, reported that during summer the water vole consumes food containing 80% water.

Swimming also caused the appearance of certain other adaptations directed toward reducing heat discharge. These include a denser and comparatively longer pelage, especially in the autumn–winter–spring period; increased fat secretion by the epidermis, which decreases wetting of the pelage; and a significant fat reserve in rodents in the autumn–winter period. The latter has been reported by many researchers (Formozov, 1947; Sludskii, 1948; Pantelev, 1968; and others).

All voles included in this group are phytophagous. Animals (fishes, amphibians, mollusks) occupy an insignificant place in their diet (Sludskii, 1948; Pantelev, 1968; Giban, 1974a). Plants with a high water content during summer, required by hydrophilous voles, can survive in our latitudes only in reservoirs, near them, or in marshes. This probably explains the attraction of these rodents to water.

This group is characterized by a unique specialization with regard to selection of biotopes and adaptation for life in them. This is expressed in several morphophysiological and behavioral characteristics. It has been noted that the more completely a species is adapted to life near water, the wider its range, and the more diverse its occupation of a zone. At present, muskrats have the widest range—from the Trans-Polar region to the subtropical zone in North America and Eurasia, and among the aborigines, this is true of the water vole. The relatively less hydrophilous forms have a more restricted range.

Body size is also associated with degree of hydrophily, an aspect studied by Pantelev (1968, 1974). The more hydrophilous species have a larger body and, within a species, the largest forms are found in populations more intimately associated with water reservoirs.

Because the water vole and muskrat are economically the most important species, their ecology has been better studied.

Feeding

All the species of this group feed on the most succulent plant parts. Actually, their diet changes with the season, which is decided by plant phenology and the animal's requirement for food of a different composition in accordance with conditions of heat and water exchange.

The muskrat expends a great quantity of water (in relation to its body weight) in vital activities. According to Shcheglova (1953), it expends 2.53 to 3.46 g water for every gram of oxygen consumed.

The suslik (*Citellus pygmaeus* Pall.), which may be considered a moderate hydrophile, requires food containing at least 40–50% water (Mokeeva and Skholl, 1958) and expends about 2.0 g water per 1.0 g oxygen consumed.

The muskrat is characterized by the most stable food requirements. It can feed year-round on reed (*Phragmites communis*), pondweed (*Potamogeton* sp.), reedmace (*Typha* sp.), and water lily (*Nymphaea* sp.), collecting food from the soil and water surface as well as under water (Sludskii, 1948). This diet includes a fairly large number of species of semiaquatic and aquatic plants, whose importance for rodents is determined by their freshness and succulence. Sludskii (1948) has listed 27 species of edible plants for eastern Siberia. Muskrats eat animal food only in the absence of, or scant reserves of plant food. This usually happens
439 in winter and early spring. Muskrats do not store food for winter.

Polyphagy is more pronounced in the water vole compared to the muskrat. Green plant parts are dominant in its diet during the period of intensive vegetative growth. True, populations living in floodplains of large rivers are compelled during floods to feed temporarily on branches and bark of shrubs and trees (Formozov, 1947). They consume large quantities of fruits at the end of the vegetative period. Rhizomes of different plant species are dominant in their diet during winter and autumn (Maksimov and Andrusovich, 1959; Popov, 1960). The water vole rarely resorts to food collection under water. It stores food for the winter—fleshy roots, rhizomes, and spikes of grain crops. However, reports are available that it only eats the grain after it has sprouted (Pantelev, 1968).

The feeding of the reed vole and the Ungur vole has much in common with that of the water vole. They, too, store food for winter and exhibit seasonal changes in preferred foods (Plyater-Plokhotskii, 1935; Nekipelov, 1936; Heptner and Shvetsov, 1960; Shvetsov, 1967). The root vole probably feeds on food with a relatively lower water content and also consumes unsprouted grains.⁸ In regions where the root vole occurs together with the water vole, their major habitats are separate and differ in extent of moisture content. If the water vole occupies hummock-marshes flooded with water, the root vole lives only in the narrow peripheral belt of these marshes (Pantelev, 1968).

Feeding on succulent food containing a relatively large quantity of cellulose but poor in calorific value, because of their com-

⁸I became convinced of this after visiting the vivarium of Professor K. Zimmermann in Humboldt University, Berlin (1957).

paratively larger body size hydrophilous voles are forced to consume a relatively large quantity. The muskrat, according to experimental data compiled by Pashkevich (1967), consumes 650–700 g food every day and, sometimes, more than 1.0 kg. This constitutes 60–80% of its body weight. Formozov (1947) believed that the water vole daily consumes food weighing about 85% of its body weight. Panteleev (1968) has reported that the water vole may consume in a single day “100–120 g of plant matter” but has not indicated the body weight of the rodents studied. The abundant cellulose intake in this group of voles is reflected in the morphology of the digestive tract, viz., a relatively longer intestine and better developed blind gut.

Habitats

All the forms in this group of voles are characterized by the relative permanency of the biotopes they occupy. However, stenobiotic behavior is variably expressed in different species, in accordance with their food specialization and affinity for water reservoirs. The muskrat is a stenobiont because it cannot live outside freshwater. Water reservoirs that do not freeze to the bottom during winter, with some vegetation along their banks, are essential for its survival. Furthermore, this species requires places that are suitable for construction of shelters—steep banks for digging burrows or floating mats in which large nests can be laid, over which shelters, or so-called “hut,” can be constructed. Other factors are not of grave significance (Sludskii, 1948). The muskrat lives along lake shores, river banks where the current is slow, and river deltas. Floods can temporarily dislodge it along river banks and excessive
440 drying of lakes may force it to follow the water line or even migrate to another water body. However, typically, such natural vagaries do not cause seasonal changes in the biotopes occupied by the muskrat, which is not so of other voles of this group.

The root vole is relatively stenobiotic since it lives only in areas adjoining reservoirs, rich in succulent vegetation, but does not spread to the reservoir *per se*. The areas of habitats optimal for this species increase when marshes dry out. Therefore, marked seasonal changes in biotopes are also not observed in this vole.

The water vole, probably the reed vole, and the Ungur vole live directly on the banks of reservoirs, in shallow water areas, and in marshes, at least during the breeding season when the rodents

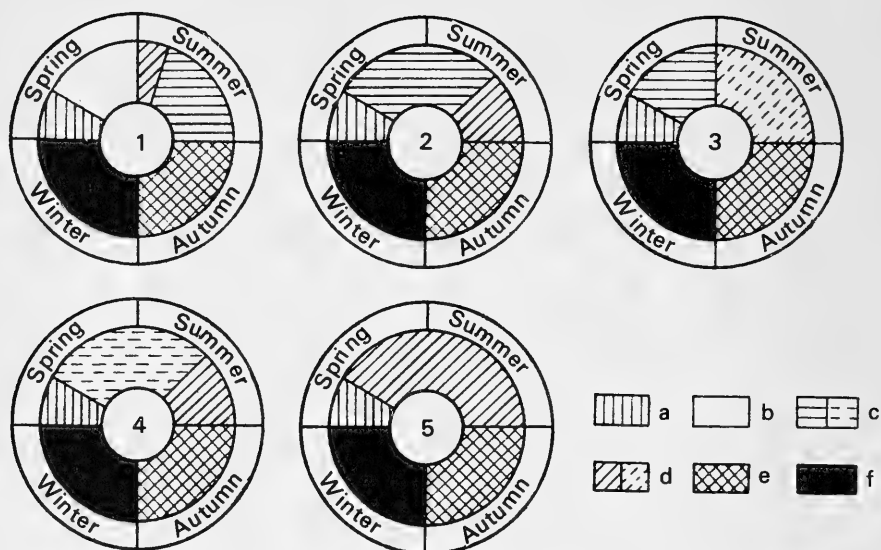
particularly need succulent food. However, even in this period the areas of such habitats change significantly due to floods, precipitation, or drought, and consequently their occupation by voles. After the breeding season, voles move to dry parts where they can find optimum food and a favorable microclimate during winter. Hence their habitat distribution changes regularly from one season to the next. Numerical dynamics of these species, as well as the mode of its assessment and understanding the factors influencing this aspect, are associated with habitat distribution.

The extent of occupation of coastal regions of reservoirs as a function of bank height and steepness has been studied in Czechoslovakia. Clay banks more than 1.0 m in height and covered with grassy-ruderal or littoral vegetation are optimal. The water vole lives in such places year-round and does not perform seasonal migrations (Zejda, 1974; Kminiak, 1974).

441 The seasonal change of habitats has been best studied for the water vole. Panteleev (1968) identified six seasonal periods in its annual life cycle, which develop in a unique manner in individual geographic populations: early spring survival in snowmelt; spring–summer period near water; living in floods; summer period of existence away from reservoirs; autumn period of intensive digging activity; winter period of fossorial life (Figure 81).

Burrows and Digging Activity

The construction of living quarters in this group of voles, like their total behavior, is associated with the extent of attachment to water. Three types of living quarters are found for muskrats—burrows, “huts,” and a combination of burrow-hut. The burrow of a muskrat has one to six entrances, which open under water at a depth of 10–80 cm from the water surface; the rodents dig tunnels into the burrow under water. Only with a drop in water level of the reservoir, is the burrow opening of a muskrat visible above water. Such burrows are usually abandoned and new burrows made or new openings dug from inside. There are no burrow openings on the soil surface. If such an opening forms accidentally due to roof collapse, the rodent immediately plugs it with soil from inside. Nests are laid above the water level in the reservoir and above the level of groundwater, and are 20 cm × 20 cm up to 30 cm × 50 cm. In addition to the nest, several other chambers are built in which the rodents rest or feed (Sludskii, 1948; Mitskus, 1974).



440 Figure 81. Seasonal periods of life of different geographic populations of the water vole (from Panteleev, 1968).

Types of geographic and terrainal populations: 1—floodplain; 2—marsh-meadow-field; 3—lake-floodplain; 4—foothill-rivulet; 5—sub-alpine meadow.

Seasonal periods: a—surviving thaw; b—surviving floods; C—near water (coastal); d—terrestrial (waterless) life; e—intensive digging activity; f—fossorial life.

Dotted hatches (c and d) indicate lack of distinct expression of given period. Duration of seasonal periods (wedges in circle) comparable only within limits of the same time of year.

“Huts” are often built in winter in areas rich in food, when such areas are at a distance from the burrow. They are made of plant material (reeds, etc.). The chamber diameter of the “hut” at the base may reach 4.0 m, and the height of this domed structure up to 1.5 m. Tunnels are laid under water from the “hut” and air holes cut in ice. The rodent does not make outlets from the “hut” (Sludskii, 1948). Construction of a “hut” at places rich in food facilitates economy of energy for food collection. In the case

of combined living quarters, a burrow may be connected with the "hut" or the "hut" may be built above the burrow (when the water level rises).

New adaptations have been observed in muskrat populations living in the severe conditions of eastern Siberia. The rodents make pathways along the bottom of the reservoirs below the frozen layers. Furthermore, families combine during winter, which offsets cooling with less energy loss, and together prepares homes for overwintering (Komarov, 1974).

The type of burrow built by the water vole changes significantly in different seasons in view of the biotopes it occupies. The brood burrow of the summer type is built above the banks of a reservoir and has several openings right next to the water surface or even under water, as well as an opening on dry land. The total length of the tunnels is not much (3.0–4.0 m), but they are often linked to runways made by moles, along which the water vole may move tens of meters on the soil. Tunnels and nests do not exceed more than 40 cm in depth and more often are 10–25 cm. Additional feeding burrows are dug simultaneously nearby; these are connected to the main burrow by surface paths. The rodents feed or even hide inside them when endangered. Nests are not prepared in these burrows. Animals living in marshes or shallow water areas build nests on hummocks or floating mats. Such nests are unique in shape and range in size from 20 cm × 24 cm to 26 cm × 32 cm or more (Formozov, 1947).

During floods, water voles are forced to hide in elevations, and use any shelter (hollows of trees, heaps of dry twigs, hayracks, etc.) or construct temporary burrows.

442 The migration of water voles from biotopes of summer dwelling is associated with a change in conditions of their food base; thus it occurs with different intensity in different periods in different regions and in different years in one and the same place. During this period, they migrate to meadows, overgrown shrubs in river valleys, kitchen gardens, and fields of different crops, i.e., places where the food base is sufficient, especially food for winter storage. The migrants live a settled life in individual burrows, the making of which is associated with very intensive digging activity. Tunnels are laid shallowly, often near the soil surface, and chambers and nests built at depths of 15–25 cm (up to the upper vault). The area occupied by the winter burrows of each animal, depending upon food availability of the habitat, varies from 18 to 68 m² (Pantelev, 1968). The boundaries of the chosen areas are actively guarded by

its host, but with high density of occupation the entire area is completely dug up and distinguishing between individual burrows becomes impossible. Moreover, in addition to settled voles, many continue to migrate under such conditions in search of new habitats.

The water vole leads primarily a fossorial life during winter, collecting food in the paths to its burrow (rhizomes and bark of shrubs near the root collar and deciduous trees). Often, these animals enter tree plantations (orchards, forest nurseries) through the tunnels dug by moles and cause severe damage. Like other voles, they, too, move freely under snow.

During winter, the water vole, like other forms of this group, often disperses into hayracks, vegetable stores, cellars, and even buildings. The type of settlement and burrows built by the reed and Ungur voles are generally similar to those described for the water vole (Shvetsov, 1967).

Reproduction

This group of voles is characterized by a fairly high reproductive potential, although it is slightly less than in the steppe vole and the lemming. The lowest reproductive potential has been recorded for the muskrat. Its pregnancy continues for about 25 days (Lavrov, 1957) or even 29–30 days (Sludskii, 1948), or 25–27 days (Reimov, 1968). The next pregnancy may not occur for 2 to 3 weeks after the first litter is born. Reimov (1968) has reported that only well-fed females mate 15–20 days after delivery. Neonates open their eyes on the 12th day of life. Lactation continues for 21–25 days. Females may participate in reproduction only at the age of 3–4 months. Therefore, young animals in the northern parts of the range do not produce broods in the year of their birth (Dobrovolskii, 1952; Lavrov, 1957; and others). Only in the southern regions of the range may some migrant females produce a brood (Sludskii, 1948; Reimov, 1968). Pregnancy in the remaining vole species of this group continues for about 20 days, eye-opening of neonates begins on the 10th–11th day of life, and newborns breed vigorously in the year of their birth (Formozov, 1947; Frank and Zimmermann, 1956; Panteleev, 1968).

The general impression about individual development of hydrophilous vole and their weight (on the example of root voles) under normal conditions is as follows: 1-day-old—concha developed, wool absent, eyelids not separated; 3-day-old—concha distinguished; 5-day-old—concha isolated; 10-day-old—eyes open; 13 day-

old—capable of coordinated movement, rises on its hind legs during feeding; 18-day-old—capable of independent life. Adult animals attain the typical oily sheen in their pelage at about 6 months of age (Frank and Zimmermann, 1956).

443 The breeding periods of muskrats almost coincide with the duration of vegetative growth in the area occupied by them. Thus, in the lower reaches of the Ili River, the first pregnant females are usually seen mid-March, and the second pregnancy recorded in mid-May. In the Kola Peninsula, the first pregnancy begins in the first 10 days of May, in Karelia at the end of April, and in the Arkhangel'sk district in mid-May; in Moscow district, it occurs in early April; in the USA (Louisiana, 29° N and Maryland, 37–30° N), winter breeding among muskrats has been reported (Sludskii, 1948; Dobrovolskii, 1952; Lavrov, 1957; and others). The total duration of the breeding period of muskrats in southern Kazakhstan is 180 days, Kara-Kalpak 180–195 days, eastern Siberia (52° N) 140 days; northeastern Siberia (63° N) 110 days, and in areas more southward (56° N) 120–125 days (Sludskii, 1948; Dobrovolskii 1952; Reimov, 1968).

The number of broods produced by muskrat females after winter in different regions of their range in the USSR varies from 2 to 4, more often from 2 to 3. Thus, in the southern regions of eastern Siberia, from 65.9 to 70.6% females birth two broods per annum, 23.5–26.8% birth three, and 5–10% only one. In the northern regions of eastern Siberia, 80–95% females produce two broods and about 20% only one. In the Amu-Darya delta, 41% females have three broods, 48% have two, and 11% have one (Dobrovolskii, 1952; Reimov, 1968). In Yakutia, 1–2 broods are recorded per annum (Stupina, 1961).

Among muskrats, only females from the first brood of overwintered rodents are able to participate in breeding in the year of their birth. Thus, in the Amu-Darya delta, 5.2% such females reproduced in 1960, 13.0% in 1961; 8.6% in 1962; 6.9% in 1963 and 7.6% in 1964 (Reimov, 1968). Normally, the muskrat reproduces only after overwintering, at the age of 8–10 months (Sludskii, 1948).

In the breeding season, 43–62% of the migrating animals perish, and about 25% survive up to the breeding season of the next year. The total life span of the muskrat is maximum among voles. Many progenitors breed for 2–3 years (Sludskii, 1948; Reimov, 1968).

The brood size of the muskrat is relatively large. According to Sludskii, it varies from 2 to 14, and the average for the lower reaches of the Ili River is 7.93. The average size over different years

(data analyzed for 7 years) is fairly standard, 7.32–8.09. In the northern parts of the range, the brood size is 8–9. There is a regular decrease in brood size with every successive litter within the same breeding season, which is typical of all voles producing several broods in the season.

The total number of neonates delivered by a single female over the breeding season varies from 15 to 24. There is no difference in the total fertility of the females from the northern and southern regions of the range (Sludskii, 1948). Yet, there is a significant relationship between fertility, body weight, and age in muskrats. Females with a body weight of 700–799 g have a total of 5.5–8.3 placental spots in the uterus; at a body weight of 1,000–1,099 g—17.5–18.1; and at a body weight of 1,300–1,399 g—22. The number of placental spots decreases to 17.2 in heavier and older animals (Reimov, 1968). These results show that in spite of comparatively uniform feeding, breeding intensity among muskrats may depend significantly on the extent of food supply.

Other voles of the group under examination are characterized by an almost similar duration of breeding season. This is related to the fact that their breeding, like that of the muskrat, significantly depends on periods of vegetative growth of aquatic and littoral plants. However, breeding intensity of the other hydrophilous voles is significantly higher than in the muskrat. Up to 4–5 broods have been recorded for the female water vole after winter. Females born during spring can produce 1–2 and sometimes up to 4 broods. In forms living in the subalpine zone, the breeding season is longer than in populations living near water and, possibly, a larger number of generations participate (Panteleev, 1968.) As a result, besides the overwintered parents, their first and second generations (3 generations) participate in reproduction every year.

In spite of this, the role of the current year's brood in the total rejuvenation of the population is less than that of overwintered rodents. Some researchers, who have made a significant contribution to the study of the ecology of this group of voles, consider it almost negligible (Folitarek *et al.*, 1951; Maksimov, 1959a, b). Others, on the contrary, believe that the level of numbers is determined by the breeding intensity of the current year's brood (Shvarts *et al.*, 1957). I see no contradiction here as everything depends on environmental conditions. If breeding starts late and terminates early, the population will be less numerous and the contribution of the current year's individuals in its rejuvenation will be insignificant. If breeding commences early and continues intensely

up to autumn, the current year's brood may play a decisive role in population rejuvenation. Panteleev (1968) has reported convincing data that the good survival and intensive breeding of voles from the first brood of the overwintered animals yield a twofold increase in population over the breeding of overwintered rodents. However, it should be understood that the first brood in particular of overwintered animals often dies in floods or for other reasons (Formozov, 1947; Panteleev, 1968); breeding of the second subsequent broods of overwintered rodents always exerts a limited influence on changing population numbers.

The life span of the small hydrophilous voles is much less than that of the muskrat. Overwintered root voles do not survive beyond September (Karsaeva, 1955a, b). Not more than 10% water voles can overwinter a second time and participate in breeding the following year. There is no reason to believe that their breeding intensity is reduced. Therefore, it may be concluded that the major viable part of the population in all voles of this group is replaced every year.

The brood size is 6–8 per female, which approximately corresponds to the fertility of the muskrat or is slightly less. If we take the size of its own broods and the broods of its reproducing offspring as an index of population growth for each overwintered female, some values can be obtained characterizing the total breeding ability of this group of voles. The total offspring of an overwintered female with 3 broods and 7 neonates in each brood will be 21. If the sex ratio is equal, the offspring of 3 broods of voles from the first generation will be $3.5 \times 21 = 73.5$. Therefore, the total for every overwintered vole will be $21 + 73.5 = 94.5$, which is about four times more than in the muskrat. Here it is clear that the higher the number of the current year's brood participating in reproduction, the higher will be the total increase in population.

Intrapopulation relationships are similar in this group of voles. Is the muskrat an exception? *Ondatra* are monogamous. Pairs are fixed in spring and their total progeny over the reproductive season (sometimes 2–3 broods) live as a single family up to the following spring. The whole family utilizes one nest and the parents look after the progeny (Korsakov and Shilo, 1967). This situation has an important adaptive significance since it increases the survival of the newborns and makes the survival of populations easy during winter, especially in the northern parts of the range. Dobrovol'skii (1952) showed that in Siberian conditions, the larger the family size, the higher and more stable the temperature in the

nest during winter (Table 34). Small families may not be viable in the northern parts of the range since the energy losses on heat production and preservation of tunnels in ice leading to food under water would be very high.

However, it should be kept in mind that for establishing a large viable family and ensuring its existence in a single nest, a rich food base—abundance of food over a comparatively small area—is essential. Therefore, survival of the muskrat in the northern regions of the range is possible only in places with an abundant food base for this rodent. This situation also explains the higher fertility of the muskrat in the northern regions of the range. In the south, where survival of small families is also possible, these rodents may be satisfied even with poor food, which generally decreases the mean indices of fertility but makes it possible for them to disperse more widely, even into places of low food supply.

Sexual activity is universally observed in the muskrat at the beginning of icemelt in rivers and lakes. Families break up in this period and pairs form which ultimately disperse. The relationship between males and the pairs formed becomes intimate, stimulating dispersal of the rodents. At this time the musk gland reaches maximum activity and its secretion is used to “mark” an occupied area. Thus, intrapopulational relationships in early spring stimulate dispersal of the muskrat and occupation of new areas, which also has a definite adaptive significance (Sludskii, 1948; Dobrovol'skii, 1952; Christian, 1970, 1971a, b).

Table 34. Dependence of nest temperature on family size of muskrat in winter (from Dobrovol'skii, 1952)

Date of observation	Temperature (°C)	Temperature (°C) in nests with family numbering				
		18 and more	16	9	5	2
Dec. 15	-25.8	18	13; 15; 11.7	10; 8	7.5; 5	0.2; 1
Jan. 15	-32.0	17; 18	16	9; 10	0.5; 8	1; 0
Feb. 15	-24.0	17; 18	12; 17	9; 10	0.3; 7	0

All the remaining voles are polygamous. With their typical breeding intensity, this has a great adaptive significance since inbreeding decreases. At the same time, due to early maturation, young females are covered by old males, which increases the tendency toward heterosis in the population (Shvarts, 1969), since progenitors of different age facilitate conservation of the germplasm of the population.

During their settle period of life, voles actively defend occupied areas, especially in floodplains. For most settled females individual (personal) areas do not change throughout the summer along the length of the shoreline, but may increase in depth with reservoir desiccation. Individual (personal) areas of males are more variable. An individual area of a family consists of 1–8 female areas and, on the average, 2 male areas. Each female is visited in April–May by an average number of 3 males, and during June–September by 1–2 males. In the Barabinsk lowlands, water voles do not have individual areas because they use an entire marsh or part of it (Panteleev, 1968) as a common territory. With high occupation density or enforced concentration of rodents at the time of snowmelt and floods, the defense reflex for personal territories decreases.

The age structure of the muskrat population is always complex, considering the duration of its life span. A population may comprise three age groups in spring that are older than one year (more than 1 year, more than 2 years, and more than 3 years old) and three age groups of less than one year of age (animals of the first, second, and third broods of the preceding year). Each of these two major age groups may be dominant depending on wintering conditions. With a favorable combination of conditions at the time of overwintering, there will be a preponderance of young animals. The autumn population comprises groups of old (surviving 1, 2, and 3 winters) and young animals born in the first, second, and third broods of the given year. Young animals are usually 5–6 times more numerous and those of the first brood dominant.

In the remaining voles, the age composition in spring is comparatively uniform and represented by animals that have yet to start breeding, which were born in the previous year. The population composition in autumn is more varied but neonates born at the end of the last breeding season predominate.

In general, the sensitivity of the population of this group of voles to environmental conditions is somewhat lower than in the steppe vole and the lemming but mobility is higher. Therefore, biotopic populations form in the territories of greater ecological

variation. These are more terrainal populations than biotopic ones. The boundaries of each encompass a complex of biotopes that ensure survival of the species, taking into account seasonal migrations.

Homogeneous populations of the muskrat form in large reservoirs or in systems with a uniform food base. Such populations are characterized by similar phenology and breeding intensity, survival of young animals and mortality of adults and, consequently, density of colonization and structure. If the food base or climatic conditions of the reservoirs (or their systems) differs, then this is reflected in all the indices which determine the structure and properties of the muskrat population. Such is the course of population formation in muskrats which, based on the complex of occupied biotopes, should be considered terrainal rather than biotopic populations.

The formation of populations is by and large the same in the remaining voles of this group. However, it is more difficult to determine the boundaries of each due to their seasonal change of biotopes. One may say that for species living in the coastal part of the reservoirs during the vegetative growth period and in marshes, breeding intensity and development and breeding of the young will depend entirely upon the optimal state of these habitats from the abundance of places suitable for vole existence at this time. Survival of a population during winter depends on the favorable conditions in places settled by voles after migration from their breeding habitats. Here, not only the extent of favorable conditions of these places is important, but also the relative area occupied by them in the land relief. All this determines the "volume of habitats" (Panteleev, 1968), which creates the specificity of populations and numerical level of the water vole, as well as other species of this group. These facts must be considered while examining the numerical dynamics of hydrophilous voles and the formation of their geographic populations.

Numerical Dynamics

As in reproductive potential, so in numerical dynamics the muskrat differs from other hydrophilous voles. Increase and decline in numbers occur in the muskrat but their range is not similar to that of other voles of this group. An increment in muskrat numbers is accompanied by a higher density of habitats and expansion of occupied area during spring. A decline in numbers is characterized by a reduction in occupied territory and lower density of settlements.

Reservoir conditions, that is, their food supply for this species during the vegetative growth period as well as in winter, availability of places suitable for building nests, absence of drying, and only partial freezing of the reservoir may be considered decisive factors in the fluctuation of muskrat numbers. With a good food supply, a muskrat family will occupy the coastal belt over a distance of 10 m and the water surface of the reservoir directed toward the center up to 50–80 m. Therefore, food reserves in large reservoirs, which are beyond the limits of 80 m from the water line are not utilized by the muskrat. Assessment of the potential suitability of a reservoir for the muskrat is based on this and, considering the food value, even the probably density of its habitation can be determined. Dobrovol'skii (1952) has reported the following: for eastern Siberia, lakes with a sharply expressed zone of water lily and pondweed, on the average, contain 10.4 muskrat families per hectare; lakes with a partly conserved zone of water lily and pondweed contain 7.87 muskrat families per hectare; and sedge-trefoil marshes contain 3.53 muskrat families per hectare.

The breeding intensity of the muskrat, as mentioned earlier, is fairly stable, and linked with the relative stability of food availability. Therefore, the numerical strength of families does not fluctuate significantly over the years (Table 35). Similar values have been reported for other rodents with regard to extent of stability of breeding intensity (Sludskii, 1948; Reimov, 1968).

The survival of muskrats is decided by many factors (extent of freezing or drying of reservoirs, predator activity, epizootics, and so forth). However, food conditions and availability of places for nest building are decisively influential. Therefore, the decline and significant increase in muskrat numbers are determined by these conditions (Sludskii, 1948; Dobrovol'skii, 1952; Lavrov, 1957; Zlobin, 1974; and others). Revenue categorization of these habitats is based on the degree of their suitability for muskrats and the rational size of catches from each region determined in order to ensure optimum population density (Lavrov, 1957; Klimov and Korsakov, 1969).

448 Some zonal features of the numerical dynamics of the muskrat should be emphasized. A change in nature of occupation of a reservoir and population density in the south is associated primarily with reservoir conditions during the summer (desiccation and salinity), and in the north during winter (depth of freezing).

The numerical dynamics of other hydrophilous voles has not been so well-studied. The water vole has received the most atten-

Table 35. Numerical strength of muskrat families in various years during autumn at the Tunkin muskrat farm, eastern Siberia (from Dobrovol'skii, 1952)

Year	Percentage of families numbering								Average composition of family (numbers)
	Up to 14	15	16	17	18	19	21	24	
1935	11.1	48.2	14.8	11.1	3.7	3.7	3.7	3.7	16.1
1936	15.1	31.1	35.4	17.2	1.0	1.0	2.0	4.1	16.5
1937	23.1	41.3	16.8	10.1	2.7	2.9	1.0	2.1	15.9
1938	11.2	49.1	14.9	11.1	3.7	3.9	3.5	3.7	16.1
1941	28.1	39.0	15.3	8.2	5.1	2.3	1.0	1.0	15.5
1946	23.1	40.3	17.8	9.1	3.7	2.9	1.0	2.1	16.0
1950	—	—	—	—	—	—	—	—	16.5

tion and it may be assumed that the trends revealed for this species are applicable to other voles of this group.

The water vole is characterized by a very high range of numerical fluctuations within a population and density of territory occupied. Besides seasonal changes in numbers, fluctuations are also distinctly manifested over the years. Formozov (1957) has reported typical results: in spring of 1942 in the Volga delta, voles were found on a large scale; "thousands of animals" were counted during the period of floods over a short distance covered by boat; but in July and August, 1943, during numerous surveys, they were sighted only twice and their traces discernible twice. During the 1943 surveys, wild boars were far more numerous than water voles. Yet such fluctuations in water vole numbers were not recorded everywhere. For a large part of its extensive range, relatively stable low numbers have been recorded. En masse breeding alternating with extinction has been noted in regions where favorable combinations of life conditions are replaced by extremely unfavorable ones. Such conditions and a corresponding fluctuation in numbers of water voles are seen in floodplains and deltas of large rivers, lake systems, and marshy areas with an intermittent water supply.

Extensive floods are fatal for the water vole in floodplains and deltas of large, medium, and even comparatively small rivers. Many animals die, being pushed out of their burrows and nests due to food shortage, predators, epizootics due to animal debility, and overcooling. However, high floods covering large areas create an exclusively

favorable food base for voles for one to three years as well as conditions for nesting. This leads to a population increase or even en masse breeding. Numbers may decline as a result of a new flood, excessive drying of the floodplains (with a long absence of floods), a scant food base, and reduction in areas suitable for rodent existence.

In lake systems with a fluctuating water supply, changes in numbers of water voles may occur either through an increase in inundated area or reduction of the same. Depending on the region and topography of the locality, flooding or desiccation of lakes may lead to one and the same result—an increase in area suitable for occupation by water voles.

In marshy regions (where hummock-marshes prevail), the number of water voles is determined not only by conditions favorable for rodent reproduction during the period of vegetative growth, but also for their survival in winter. Conditions favorable for vole breeding in marshy regions develop in wet years when areas suitable for habitation increase significantly. Conditions favorable for vole wintering in many regions (in particular, western Siberia) are created by man through planting of field crops and kitchen gardens in areas adjoining marshes. In wet years, the most favorable conditions for water voles are created not only in marshes, but also in agricultural fields. Possibly, agricultural areas adjacent
449 to marshes and the forest-steppe zone of western Siberia contribute to the frequent en masse breeding of the water vole and its high numbers. Man has increased the "habitat area" for this species over a large territory.

In some regions of eastern Siberia, especially in the Angara valley, an increase in the range of the water vole has been noted (Stupina, 1961), which may be related to the increase in area under agricultural crops, providing better conditions for overwintering of this species.

Considering the above, it became possible to determine the regions of en masse breeding of water voles and to identify criteria for predicting their numbers (Formozov, 1947; Maksimov, 1959b, 1969; Panteleev, 1968).

Many researchers have reached the conclusion that fluctuations in water vole numbers (possibly, other hydrophilous forms also) are linked with the cycle of solar activity (Maksimov, 1966; Panteleev, 1968; and others). In regions where the water regime in territories occupied by voles is not affected by man and depends solely on atmospheric phenomena, this conclusion is quite logical. True, recognizing the relationship between change in number of water

voles and periodicity of solar activity adds nothing new to our understanding of the causes of this phenomenon. For forecasting dynamics, such an association has an extremely tentative value. The numerical dynamics of voles does exhibit general regularities, but its magnitude, the duration of individual phases in each cycle, and the total duration of these cycles are not similar. That is why none of the en masse breedings of the water vole (and of other rodents also) is identical to the types of increase and decline noted in the same region, total duration and length of each phase, population density, and territory occupied. Not only are there differences in the extent of direct effect of solar activity on factors of numerical dynamics of voles in individual cycles of their en masse breeding, but also the periodicity of solar activity per se is not standard in intensity and duration of intervals between cycles (Eigenson *et al.*, 1948).

The above statement is illustrated by the data presented in Table 36. If we base our conclusions on the index of pelt harvest, it may be stated that there were four periods of en masse breeding of water voles over a 30-year period in the forest-steppe regions of Novosibirsk district: 1934–1940, 1947–1951, 1953–1954, and 1956–1962. These periods differed significantly in magnitude. Pantelev (1968), attempting to “fit” numerical dynamics into a
450 definite cycle, could identify only three en masse breedings for the same period. While determining the periods of each of these breedings, he entered into a discussion with Maksimov (1966). Maksimov believed that an en masse breeding occurred during 1936–1938 (peak in 1937), 1947–1950 (peak in 1948), and 1956–1962 (peak in 1958–1960). Pantelev identified the following years—1936–1938, 1948–1950, and 1958–1961—and thinks that 1939, 1947, and 1951 should not be included in the periods of large-scale breeding. I cannot concur in his conclusion since 1939 and 1951 were the years of termination of the decline phase of numbers, and 1934 and 1947 were the years increase was initiated. But such a discussion hardly clarifies the problems under analysis and only complicates the issue. Both Pantelev and Maksimov support the concept of cyclic periodicity of en masse breeding of the water vole. Therefore, they ignored the increase in numbers during 1953–1954, which did not end in en masse breeding. A similar rise in numbers was observed during 1966–1968. Such increases in particular should not be ignored if the severe damage caused by the water vole in the forest-steppe zone of western Siberia is to be curtailed, as this information permits timely preventive measures.

Table 36. Dynamics of pelt collection of water voles (thousands) in the forest-steppe regions of Novosibirsk district (Kishtov, Kargat, Severnyi Kuibyshev, Ubin, Vengeron, and Chulym) during 1934–1963 (from Panteleev, 1968)

Year	Pelts collected	Year	Pelts collected
1934	38.6	1949	332.1
1935	131.3	1950	554.3
1936	324.4	1951	86.7
1937	821.7	1952	3.7
1938	483.4	1953	49.5
1939	122.6	1954	50.5
1940	21.0	1955	6.0
1941	1.8	1956	303.9
1942	2.7	1957	256.8
1943	3.9	1958	760.8
1944	6.0	1959	1,792.6
1945	2.1	1960	1,204.1
1946	7.2	1961	693.9
1947	97.4	1962	98.0
1948	298.1	1963	1.7

At present, the most reliable criteria for forecasting numbers of hydrophilous voles are: nature of their dispersal, intensity of breeding, and environmental conditions in each season of the year in a given region.

In spite of several specific features of the ecology of hydrophilous voles, ultimately that scheme is suitable for forecasting their population and understanding the mechanism of formation of geographic populations, which I have proposed for the common vole and the steppe lemming. Each region has conservation habitats and dispersal habitats. Areas of conservation habitats are of major importance in the breeding season since habitats suitable for overwintering become limited only in the case of excessive numbers. The numerical level of a species and frequency of en masse breeding depend on the combination of conservation and dispersal habitats. This idea is encapsulated in Panteleev's (1968) "volume of habitats". The term "volume of habitats" indicates the area of biotopes suitable for the water vole (for breeding or overwintering) expressed in percentage of total territorial area in a given region or

part thereof.

In migrating to wintering places, water voles do not move more than 2.0–3.0 km from breeding places. Thus the probable suitability of a territory for conservation, breeding, and dispersal of the water vole can be determined for any region. Characteristics of the natural complexes of the northern part of the Barabinsk lowland are presented in Table 37. There are sufficient grounds to believe that marsh-birch forests and marsh biomes are less suitable for water voles. Wintering places (meadows and fields) are scarce here and marshes *per se* limited in suitability for breeding of this species during the vegetative period.* Marsh-forest-meadow, meadow-field, and marsh-hummock environments are suitable for the water vole. Habitats suitable for breeding and overwintering are represented here on a wider scale under optimum combinations. If the number of voles in the first group of biotopes is always low and increases rare (only with perennial drought are conditions suitable for breeding and wintering created here), in the second group, numbers will be higher and increases more frequent.

Over the greater part of its range, where it breeds near small rivers, rivulets, lakes, and ponds, the water vole population is relatively stable since the conditions necessary for its existence during the vegetative growth period remain almost unchanged. But numbers decrease with the construction of dams on large rivers to regulate discharge, thereby eliminating floods in the floodplains (Davidovich, 1961). For the muskrat, such measures lead to a reduction in area of optimum biotopes and, correspondingly, a fall in numbers (Lavrov, 1957).

Geographic Populations

Formation of geographic populations of the hydrophilous voles is closely related to the combination of conditions in individual regions of the range, which determine the structure of terrainal populations (Maksimov, 1956), dynamics of density of settlement and dispersal, phenology and intensity of breeding, and survival of individual age groups. In general, the same principle of identification of geographic populations is applicable here as was described for identification of geographic populations of the common vole and the steppe lemming.

*These are the so-called upland marshes. In years of drought, when hummock-marshes dry up, the water vole may be conserved here.

Table 37. Characteristics (%) of natural territorial complexes in southern part of Barabinsk lowland (from Pantelev, 1965)

Natural territorial complex	Forest-steppe	Meadows and fields	Marshes	Lakes
Marsh-birch forests	50	1-4	35-45	less than 0.2
Marsh-forest-meadow	25-50	20-40	15-20	0.2-1.0
Meadow-fields, marsh-hummocks	5-20	30-60	20-50	5.0
Marshes	0-10	0	80-100	5-20

Pantelev (1968) has identified six forms of geographic (in his terminology, "terrainsal") populations of the water vole: floodplain, marsh-meadow-field, lake-floodplain, foothill-rivulet, subalpine-forest, and maritime-meadow. Probably, populations in individual regions exhibiting diffuse dispersal should likewise be separated since the water vole is always found in large numbers in these cases (it is not really correct to call them interriverine populations; Pantelev, 1968).

All the identified populations differ not only in nature and characteristics of annual cycle (see Figure 81), levels and dynamics of numbers and age structure, but also in morphology (Pschorn-Walcher, 1953; Popov, 1960; Pantelev, 1968; and others). Morphologically, animals in a population of the hydrophilous vole, like the common vole (see pp. 621-627), may differ significantly even within limits of a single region in different years of differing favorable conditions for existence. This has been convincingly demonstrated by Shvarts (1969) on Kucheruk's material.

452 Terrainsal and geographic variability are manifested to a lesser degree in the muskrat than in other hydrophilous voles. However, even within the Novosibirsk district, definite biotope complexes can be identified, which are characterized by specific populations of the muskrat. Thus, Klimov and Korsakov (1969) have identified five zones in this region (taiga, forest-steppe, steppe, Ob', and floodplains of the Ob') where unique geographic populations of the muskrat develop.

Sludskii (1948) has identified five terrainsal populations in the floodplains of the Ili River, which together constitute a single geographic population. These are the freshwater lakes and inlets of

Balkhash region (7 families separated by a distance of 100–200 m); floodplain lakes (isolation 100–300 m); slightly saline lakes 0.01 to 3.0–5.0 ha in area among sand hummocks (each family occupies one lake); salt lakes where only temporary settlements are found; and, finally, small streams and narrow strips (families separated by a distance of 100–300 m).

Geographic populations may evolve into subspecies. This happens when adaptations are determined by the stable influence of specific conditions of vital factors typical for each region. Conditions of feeding and heat exchange often are the factors producing subspecies variability in rodents. Several concepts have been formulated regarding the mechanisms causing adaptive responses of geographic populations of rodents and their genetic fixations (Polyakov, 1954, 1956, 1964, 1967, 1969; Naumov, 1963; Shvarts, 1968, 1969; and others). One feature common to these concepts is that a population is a “unit of variability”; the progression of a variability series leads from a biotopic (or terrainal) population to a geographic population, and from a geographic population to a subspecies, and thence to a species. Differences of opinion arise from differences in understanding of the mechanisms of formation of all categories of populations.

I have demonstrated that the entire specificity of ontogenetic characters of rodents ensures the formation of a phenotype (individuals and age groups) in the direction of maximum compatibility with a given environmental situation (Polyakov, 1964, 1967, 1969; Polyakov and Kuznetsova, 1971). This enables the rodents to better utilize the available energy resources of a biotope or complex of biotopes. However, this adaptation involves morphophysiological differences in quality of the biotopic (terrainal) populations as well as individual age fractions within each. The latter fact determines a change in the age structure of populations over the seasons—age groups best adapted to conditions of each season survive.

Concomitantly, the mechanisms influencing and directing phenotypic adaptive variability of each age group and consequently of the biotopic populations, determine the genotypic fixation of the adaptations formed. The probable paths of transition from phenotypic variability to genotypic variability have been shown by Schmalhausen [Shmalgauzen] (1966).

The geographic populations of this group of voles primarily differ in variability of terrainal populations and their interaction. Therefore, they differ in conditions of enrichment of populational

germplasm with regard to the probable rate of adaptive variability and rate of development into subspecies.

Subspecies of small hydrophilous voles in the USSR have been identified. Yet, as rightly pointed out by Gromov and his colleagues (1963), the general trends in geographic variability of these rodents, especially the water vole, are still insufficiently studied. Separation of subspecies is difficult because subspecies variability often overlaps variability of geographic and terrainal populations, or their perennial variability. Furthermore, it should be noted that similar geographic populations exist within the limits of the range of different subspecies.

435 Subspecies of the muskrat, acclimated relatively recently in the USSR (in many regions not more than 25 years ago), are still in the process of evolution. However, there is sufficient basis for their separation (Gromov *et al.*, 1963).

Practical Significance

Hydrophilous voles are of practical importance for different reasons: they are objects of the fur industry, cause damage to agriculture, and act as vectors of infectious diseases.

In the USSR, the muskrat has become a valuable object of the fur industry. Its homeland is North America. The muskrat was introduced in Europe in 1905 and ten pairs were released near Prague. Almost the entire population now covering Europe and the Asian part of the USSR owes its origin to these ten pairs. The muskrat was introduced in the USSR from Finland in 1927 and was released on Solovets Island in the White Sea and Kargin'sk Island near Kamchatka. Intensive artificial dispersal throughout the country was subsequently implemented and by 1944, the number of muskrats was 45,284. Today, as a result of artificial and natural dispersal, the muskrat occupies almost every region suitable for its existence in the USSR (Sludskii, 1948, 1961, 1962; Lavrov, 1957; and others).

In 1935 in the USSR, 3,820 muskrat pelts were processed, in 1956 just over 6 million, and now their average annual production is more than 5 million (Larin, 1967; Korsakov, 1974). Because of improved organization of the fur industry, the number of pelts processed could be increased significantly. Muskrat catches in Kazakhstan could be increased to about 2.5 million pelts per annum; the total contribution of Kazakhstan to the national production to date is 37% (Sludskii, 1971; Strautman, 1961; Tavrovskii, 1961).

Possibly, about 8 million muskrat pelts could be collected per annum in the USSR. About 16 million are collected annually in the USA (Sludskii, 1948). As noted by many specialists, to increase pelt production of the muskrat, not only is it necessary to provide good living conditions for the rodents, but also to conduct hunting in a planned manner. Inadequate hunting is often followed by overcrowding of the muskrat population and depletion of its food base. The consequences of inadequate hunting can be more threatening than somewhat excessive hunting.

In the USSR, the muskrat has caused no damage to agricultural crops to date. Damage to hydroreclamation structures, mainly in the Baltic Republics (Mitskus, 1974), is still not so great as to warrant concern. In Western Europe, the muskrat causes significant damage to field crops, dams, etc. here and there. Hence control measures are implemented (intensive catching) to restrict its spread and numbers (Klemm, 1952, 1954; Putset, 1956; Giban, 1974a).

Among the other hydrophilous voles, only the water vole is an object of the fur industry. Its commercial exploitation in the USSR was initiated in 1926–1927. In some years, as many as 20 million pelts have been collected (Lavrov, 1932). But collections are far lower nowadays; even in years of en masse breeding, they total no more than 2–3 million.

The damage done by hydrophilous voles, except for the muskrat, is several-fold greater than the price of their fur. It is most acute in the autumn–winter period. The water vole living in meadows, kitchen gardens, and cropped fields destroys much of the yield and makes harvesting difficult because of digging activity. Such damage is particularly severe in years of en masse breeding in regions where the water vole is common (western 454 Siberia, Belorussia, subalpine zone of the Caucasus). In western Siberia alone, severe damage due to the water vole has been estimated as covering 13 million hectares. These comprise areas of hummock-marshes between which comparatively small islands of agricultural crops are planted (Maksimov, 1956, 1969; Folitarek *et al.*, 1959).

Other vole species of this group cause similar damage but it is more localized.

The water vole causes damage everywhere, even at very low numbers, to fruit plantations, forest nurseries, and in some places in western Siberia and Altai, even to forest plantations. During winter and early spring it gnaws the bark of trees and destroys their root system by feeding on it, which leads to tree mortality or signif-

icant stunting. This kind of damage is economically significant as it occurs systematically throughout the range. A single rodent can kill or damage several trees during winter (Formozov, 1947; Klemm, 1957b, 1958; Folitarek *et al.*, 1959). The total annual average damage due to the water vole in the USSR is estimated at 5–6 million roubles. In the GDR, the annual damage to horticulture has been estimated at 1.3–1.5 million marks, and in some years at 5 million marks (Wieland, 1973).

The role of hydrophilous voles in spreading tularemia is very significant, especially during seasonal changes of habitat (Kraft, 1961). Thus, Formozov (1947) justifiably concluded that the "water vole is the main source of tularemia epizooties in the USSR, and the associated epidemic spurts of tularemia among people" (p. 14). This statement has been confirmed by many researchers (Kon-drashkin, 1955; Klimov and Folitarek, 1959; Maksimov, 1959a). In several regions, hydrophilous voles cause tularemia among populations of the muskrat, which is not considered a carrier of this infection.

Tularemia develops in man through contact with the water vole during an epizooty or with infected aquatic sources. The epizooty usually develops among voles in early spring when conditions in nature are most unfavorable for them (poor food supply, flooding of burrows), which causes suppression of the population. Voles are hunted more intensively during this period because easier to catch and because their fur is of greater value in spring. Thus conditions for human infection with tularemia are created, if preventive measures (vaccination) are not taken.

Sick voles are easy prey to carnivores, who may carry dead bodies some distance and spread infection to water reservoirs, thus creating conditions for human infection through contaminated water resources.

Water voles often live in haystacks, especially when the grain has not been properly threshed and germinating seeds are available. Infection may occur in man during transport of these stacks and their utilization. Finally, cases of human infection have been traced to blood-sucking dipterans (woodlice, mosquitoes, puffballs, houseflies, and clegs). The transmission of tularemia has been noted one to two years after an epizooty has drastically reduced a population of water voles (Formozov, 1947).

The conditions described above make it mandatory to carry out systematic control of some species of hydrophilous voles, especially the water vole.

Control of Water Voles

In the USSR, control measures are implemented regularly and on a large scale only against the water vole. The methods used are quite suitable for control of other voles of this group should the need arise.

455 The organization of preventive measures against the water vole differs significantly in regions where it multiplies en masse from regions where large-scale breeding does not take place but damage is chronic. In the former regions, systematic observations are conducted on populations and extermination measures employed only with the threat of extensive damage. In the second group of regions, control measures are implemented at the first detection of voles.

In western Siberia and Belorussia, systematic observations of water vole populations entail three surveys: spring, summer, and autumn. A spring survey of crop fields is conducted only when the number of water voles is high and their dispersal in autumn significant. If none is found in the fields in autumn, the spring survey is not necessary. Instead, the work is limited to data on spring catches of voles and an estimate of their numbers by hunters. The summer study is done to determine the period and intensity of vole dispersal to crops. This survey is carefully done everywhere, especially in years favorable to rodent breeding. The autumn survey is likewise conducted every year, to assess the total population of voles throughout their range in a given region.

A systematic study and comparison of results from each farm in a given region make it possible to determine the tendency for change in number of voles and to make a general forecast of their distribution in the coming year and season. In case of a drop or suppression of numbers, the forecast for the coming year is usually reliable when based on sufficient information. When conditions are conducive to an increase in vole populations, predictions for the forthcoming year are less reliable. Lack of precision in such forecasts (usually made at the end of summer) may be due to several phenomena in the forthcoming year, e.g., extremely unfavorable, cold winter with less snowfall; a cold late spring; or a dry spring. Such conditions cause suppression of the population and prevent manifestation of those tendencies of its reproduction evidenced in the previous year and taken into account in the forecast.

Regardless, predictions of intensity of vole reproduction combined with systematic observations on their actual distribution, can serve as the basis for planning and timely organization of protective measures.

Arch traps are an important means for controlling hydrophilous voles. Catching is particularly intensive during spring and during the migration of rodents to crops at the end of summer and beginning of autumn. It is essential that catches be done in furrows bordering the crop adjoining the places of spring–summer conservation of voles (Folitarek *et al.*, 1959). The soil ridge is turned toward the crop. Experience over the years has shown that the use of plowed furrows sharply increases the intensity of vole catching and almost completely precludes casual catches of martens (*Mustelidae*). Cylinders are very effective traps; they are pushed into the furrow in an absolutely upright position with their upper periphery flush with the bottom of the furrow and carefully covered with soil. The cylinder is generally 30 cm high and 21–22 cm in diameter. The distance between arch traps and cylinders may vary from 10 to 50 m.

456 Bait poisoned with zinc phosphide is widely used in control of the water vole. Mashed potatoes, carrot cut into pieces of 0.5 cm³ and its foliage, reedmace, and other succulent plants may be used as bait for poisoning isolated colonies. Zinc phosphide is used at the rate of 6.0% product by weight. The treated bait is placed at the rate of 6.0–10.0 g near the living holes and in the burrows, on runways, and on “dining tables” (places of eating where freshly nibbled material is found). To avoid poisoning of beneficial animals, the bait should be placed under a cover made from wooden planks cut in the form of hoods, in pieces of earthen pipes, and other such objects. Voles will readily accept food in such places, while it remains inaccessible to birds and other animals.

Soaked peas and maize (corn) are used as a bait where the number of water voles is high and there is a need for protecting crops over large areas (Panteleev, 1968). Zinc phosphide is used at the rate of 7.0–10.0% dry weight of grain, which has priorly been coated with vegetable oil at 2.0% dry weight. Such bait is spread manually, depending on the tactics and objective of the control measures.

When voles are highly numerous,¹⁰ poison is spread along the border of fields before the rodents commence migration. One to two

¹⁰Considered so if 10 voles are caught per 100 traps in one night at places adjoining crops.

strips 10–20 m wide around the fields are seeded with bait at the rate of 3.0–4.0 kg/ha by means of seed drills or an airplane. If the field is intersected by a road, poisoned bait is also spread on both shoulders of the road.

If voles occupy a large cropped area, the bait is spread from airplanes and helicopters. Border belts and roads are treated first, as done in the protective border treatment. Thereafter, bait is spread in the field at intervals of 25 m marked with sign posts (this operation is never done without sign posts). The dose is 10–12 kg bait/ha and the bait spread in narrow strips with a gap of 18–20 m between. The average consumption of bait is about 3.0–4.0 kg/ha if, in a single night, 10 voles are caught per 100 traps laid in areas adjoining a cropped field.

In the early 1970s glycerol-fluoride (Gliflor) was tested for controlling water voles under their usual en masse breeding in western Siberia, according to the method recommended by V.A. Bykovskii (*Metodicheskie . . .*, Moscow, 1973, pp. 11–15, 29–30). The organizational participation of the Novosibirsk and Omsk Plant Protection Stations made extensive testing possible (over more than 100,000 hectares). Gliflor was used as a grain bait of specific composition: dry peas were soaked in an aqueous solution of the preparation at a concentration of 0.24–0.30% chemical solution to volume of water and 0.4–0.6% grain weight. Maximum pea absorption of the fluid in a ratio of 0.6:1 was ensured. The first concentration is recommended for ground control measures and the second for aerial treatment.

The best indices of technical efficiency of Gliflor were 93% (Novosibirsk district, 1973) and 95% (Omsk district, 1974), obtained from ground treatment at 9–12 kg bait/ha or 3.0–4.0 kg/ha cropped area. Highly satisfactory results were also obtained when the bait was spread by means of an NRU-0.5 unit attached to a “Belarus” tractor. Concentration of bait preparation, method of preparation, and rate of consumption did not change [V.A. Bykovskii, *Result of State Trials of Rodenticides and Repellents in 1973* (Izd. VIZR and State Chemical Commission of the USSR, Ministry of Agriculture, Moscow, 1974), p. 10].

457 Aerial spreading of pea seeds soaked with 0.6% Gliflor at the rate of 3.0–4.0 kg/ha gave less stable results. Results improved with small doses of RPS in combination with single-strip spreading. But aerial treatment still needs to be improved.

The efficacy of water vole control depends on time and quality of operation. Chemical treatments usually lead to no more than 60%

mortality in a population. But if control measures are undertaken in autumn, voles do not breed, and those slightly poisoned usually die later during winter. Therefore, this level of efficacy may be considered acceptable.

A preparation of aluminum phosphide, manufactured in the form of tablets weighing 3.0 g by the firm "Delicia," is used in the GDR for controlling the water vole. Placed on moist soil, these tablets release hydrogen phosphide gas, which is poisonous for animals. Vertical holes are dug into burrows and a tablet of aluminum phosphide dropped inside. This preparation is a fire hazard and can easily poison the surrounding air. Therefore, it is marketed in sealed iron tins containing metallic capped tubes with three tablets in each tube. The efficacy of this preparation is high according to GDR experts (Weiland, 1973).

FOREST VOLES

General Characteristics

This group of voles primarily includes the forest voles proper from the genus *Clethrionomys* (*C. glareolus* Schreb.—bank vole, *C. frater* Thom.—Tien Shan red-backed vole, *C. rutilus* Pall.—northern red-backed vole, *C. rufocanus* Sundev.—large-toothed red-backed vole), which long ago adapted to life in forest biogenocenoses. Some members of the genus *Microtus* are also included in this group (*M. agrestis* L.—field vole, *M. subterraneus* Selys-L.—European pine vole, *M. majori* Thom.—Turkish pine vole, *M. schelkovnikovi* Sat.—Shelkovnikov's pine vole), which have probably more recently and less completely adapted to life in forests. Association with forest biogenocenoses greatly reduced the effect of high summer temperature and drought on this group of voles but made them more dependent on this food base. Periodicity of food harvest is observed in forests but as such harvests involve different dominant plant species, the range of variation in the food base for rodents over the years and seasons is not as great as in the steppes (desert, tundra). This has led to a great leveling of relationships between components of forest biogenocenoses, increasing the importance of interspecific and intraspecific relationships in the population dynamics of all species, including rodents (Polyakov, 1972). Intraspecific differentiation is significantly associated with food specialization in this group of voles.

Forest voles proper (*Clethrionomys*) survive in such forests where the underbrush provides the necessary additional food in years of poor seed harvest from trees and shrubs. Their penetration south is mainly restricted to the forest-steppe zone. In the north, they spread to the tundra zone along intrazonal biotopes. In addition, within the limits of their main range, they often occupy various manmade structures. In mountain regions, forest voles rise to the talus zone.

458 Voles of the genus *Microtus* included in this group, are relatively more specialized since their penetration into the forest biogenocenoses was associated with adaptation to unique niches. Thus they occupy relatively small areas, mainly living in southern forests and penetrating north up to the forest-steppes. The field vole is an exception, ranging from the western regions of Europe up to Yakutia. However, it occupies montane biotopes of interzonal character everywhere (river valleys, hummock-marshes, and wet meadows; Klemm, 1957b). Green plant parts have a more important place in the feeding of *Microtus* species included in this group than in forest voles *per se* (Girenko, 1952; Sviridenko, 1952; Klemm, 1957b).

Feeding, Thermoregulation, Rhythm of Activity

Seeds of woody and partly grassy vegetation, mushrooms, berries, and lichens are the primary dietary elements of forest voles. The vegetative parts of herbaceous plants are consumed in small quantity; broad-leaved meadow grasses are preferred. Some species additionally eat significant quantities of roots, branches, and bark of trees and shrubs. Animal food is consumed rarely and in small amounts. The majority of researchers who have studied the feeding habits of this group of voles report a predominance of protein-rich food in their diet (Obraztsov, 1951; Sviridenko, 1951; Koshkina, 1953, 1957; Kulaeva, 1956, 1958a; Klemm, 1957b; Lapin, 1958; and others). Under experimental conditions, the voles of this group died when maintained on vegetative plant parts in the absence of seeds. Others voraciously consumed a large quantity of seeds from different trees which the steppe vole refused (Sviridenko, 1951).

Food specialization in forest voles proper is manifested in species numerically predominant in northern regions characterized by continental climate and lower availability of seeds of woody plants and shrubs, in higher consumption of the vegetative parts

of herbaceous plants. Thus, the large-toothed red-backed vole is a more voracious consumer of green vegetation than the bank vole and northern red-backed vole (Koshkina, 1953, 1957; Pearson, 1962; Voronstov, 1967).

Intraspecific food specialization reflects the nature of the foods and general food availability for populations in the region occupied by them. A tendency to shift toward feeding on seeds of grassy plants has been noted in the bank vole in northern regions of the range (Koshkina, 1967). In the western parts of the range (England), this species eats vegetative parts of grasses in comparatively large quantities (Watts, 1968).

Voles of the genus *Microtus* included in this group, feed mainly on vegetative plant parts; however, seeds also occupy an important place in their diet. The diet of field voles is highly variable (Klemm, 1957b). Seeds are found in all seasons in the stomach contents of the European pine vole in the Ukraine and in autumn are as frequent as green vegetative parts (Girenko, 1952). Grass predominates in the diet of this species in the Caucasus; roots, rhizomes, seeds, berries, and insects are eaten only as supplements (Sviridenko, 1952). Voles of the genus *Microtus* are not capable of eating seeds of stone fruits and nuts of which have a hard shell, but relish small seeds with a thin shell (Girenko, 1952; Sviridenko, 1952). Food specialization of these voles is reflected in the morphology of their intestinal tracts. In forms consuming predominantly seeds, there is an elongation of the small intestine (its length relatively greater than body length), while the size of the thick, straight blind gut has reduced. Measurements of rodent intestines are accompanied by some error since they may stretch somewhat and differences in diameter due to age and sex are quite probable. Nevertheless, in spite of some known discrepancies in obtained results, the findings of Naumov (1948), Girenko (1952), Kulaeva (1956, 1958a), and Bashenina (1969), presented in Table 38, in general support the conclusions drawn above. Kulaeva (1958a), based on a study of the stomach morphology, considers the bank vole and the Tien Shan vole preferential grain eaters.

In thermoregulation, this group of voles is characterized by adaptation to relatively high temperatures, almost a similar range of preferred (optimum) temperatures, and some difference in chemical thermoregulation in low temperatures (Table 39; also see Pearson, 1962).

At low temperatures the large-toothed Tien Shan vole expends minimal energy on thermoregulation. This indicates its better adap-

tation to cold. However, energy losses are higher in the optimum temperature range than in other voles, which suggests a poor adaptation to high ambient temperatures. Compared to steppe voles, forest voles are characterized by greater resistance to low temperatures and less resistance to high temperatures, as well as a higher
460 metabolism. The total heat production in forest voles is higher, and therefore the cardiac index (relative weight of heart to body weight) is higher (Table 40). The food-storage instinct is poorly developed in forest voles. However, all researchers have reported stored food in the burrows of these rodents, consisting of cones and seeds of woody trees, roots, etc. The largest food storage has been recorded for the genus *Microtus*.

The activity of rodents of this group is primarily nocturnal, but may be multiphasial in some seasons (Pearson, 1962).

Habitat selection is related to nature of feeding. Studies conducted in France (Birkan, 1968; Thiollay, 1968) have shown that bank voles are more numerous in forests containing varied underbrush. They prefer young forests (age 6–13 years). In northern regions of its range, the bank vole is much more numerous in more mature forests, rich in underbrush, second only to the biotopes of the northern red-backed and the large-toothed red-backed vole (Koshkina, 1953; Kulaeva, 1956).

Burrows and Digging Activity

Forest voles are poor diggers. They usually use different natural shelters and covers for building nests and dig burrows only in their absence. According to the findings of T.M. Kulaeva, 87% of the nests of the bank vole in Raifsk forest (Tatar SSR) were located in stumps and trunks of fallen trees and 22% in the soil. With an increase in vole numbers, digging activity increases. Tunnels leading to nests built in fallen trunks and stumps are no more than 1.5 m long while those to nest chambers located underground reach 14.18 m. Nest-building at the base of tree trunks and shrubs as well as in heaps of dead wood has also been noted. All nests of the northern red-backed vole are located under individual stones, between stones and under-tree roots; to date, no underground burrows have been found. In winter, the Tien Shan vole builds nests under snow (Fedosenko, 1965), which is typical of the steppe vole.

Nests are made from dry plant materials; summer nests are built from grass stems split lengthwise. Building new nests in different seasons as new broods appear has also been noted.

Table 38. Relative size of intestine and some of its sections in the adult vole

Vole species	Length of intestine as percent of body length	Ratio of dimensions of intestine (%)			Author
		Small intestine	Large intestine	Blind gut	
Common Vole	661	44.3	38.7	17.0	N.V. Bashaenina
	590	51.7	43.3	5.0	T.M. Kulaeva
Bank vole	821	58.2	29.2	12.6	N.V. Bashaenina
	650	68.3	26.7	5.0	T.M. Kulaeva
Northern red-backed vole	950	58.8	28.8	12.4	N.P. Naumov
	796	59.3	31.5	9.2	N.V. Bashaenina
	710	62.0	33.2	4.8	T.M. Kulaeva
Tien Shan vole	548	50.3	37.4	12.3	N.V. Bashaenina
	590	56.0	36.7	7.3	T.M. Kulaeva
Field vole	685	42.3	40.4	17.3	N.V. Bashaenina
European pine vole	700	41.2	35.6	23.2	T.M. Kulaeva

Table 39. Some characteristic responses to ambient temperature in forest voles compared to the common vole (from Bashenina, 1968)

Species	Preferred ambient temperature (°C)	Lethal ambient temperature (°C)	Heat production (kcal/g/hr)	
			Optimum	Cold
Common vole	20.67-0.59	35-36	0.011	0.036
Field vole	20.85-0.56	35-37	0.012	0.039
Bank vole	20.2	35	0.014	0.042
Northern red-backed vole	21.50-2.06	35	0.012	0.043
Large-toothed red-backed vole	21.0	35	0.014	0.034
Tien Shan vole	19.01-0.42	35-37	0.014	0.034

Table 40. Cardiac index and index of heat production in different vole species (Bashenina, 1969)

Species	Relative weight of heart (%)	Heat production (kcal/kg/h)	
		Basic metabolism at optimum temperature	Basic metabolism in cold
Common vole	5.55	11	36
Field vole	7.14	11	35
Bank vole	6.5	14	42
Northern red-backed vole	8.0	12	42
Large-toothed red-backed vole	6.8	14	34
Tien Shan vole	5.93	14	34

461 Voles of the genus *Microtus* included in this group, have retained their capacity for more intensive digging activity. Tunnels of the European pine vole reach a depth of 20 cm in summer burrows and their total area is not large. Burrows prepared for overwintering have a greater tunnel length, up to 38 cm, occupying a larger area; chambers are also present (Girenko, 1952).

The voles of this group are relatively settled. Females and males occupy permanent places, their area slightly decreasing with an increase in rodent numbers (Koshkina, 1953, 1957; Kulaeva, 1946). A seasonal change in habitats is maximally evident in the field vole (Pilyavskii, 1969, 1970). The possibility is not excluded that this is mainly typical of populations living on mountain slopes.

Reproduction

Like the steppe vole, all members of the forest vole group have a high reproductive potential. The eyes of neonates open on average on the 10th day of life. Females may become sexually mature at the age of one month (or even earlier); duration of pregnancy is about 20 days, and the number of neonates in a brood reaches 10–11; subsequent broods are possible every month. In nature, only a small number of voles live more than a year. The population is rejuvenated every year at least to the extent of 90%, and the current year's broods constitute about 90% of the total population

by autumn (Semenov-Tyan-Shanskii, 1970). Voles older than one year do not make a significant contribution to reproduction.

Some differences in indices of potential fertility of this group of voles obtained by various authors, reflect species differences in biology or arise from the fact that differences occur in the actual course of reproduction under specific conditions (Kulicke, 1956, 1960; Klemm, 1957b; Sviridenko, 1959, 1967). At the same time, the actual reproductive intensity of voles possessing the necessary energy resources and high energy expenditure on thermoregulation with a fall in ambient temperature, is below the very narrow optimum range. These conditions also determine the unique actual phenology and reproductive intensity in each species of this group of voles in different regions of the range in different years, similar to that in different species in the same geographic region. In the latter case, the specificity of environmental requirements and responses to such conditions are manifested (Koshkina, 1953; Kulaeva, 1956). Sviridenko (1957) carefully analyzed the literature available on the reproductive phenology of the bank vole in different regions of its range. He showed that the total duration of the breeding period throughout the year in the northern part of the range (Karelia, Lapland National Reserve) is 3.5–4.5 months, and in the south (Kiev, Trans-Carpathian districts, Moldavia) 7.0–8.0 months. The average number of newborns in a group is lower in the north (3.2–5.7) than under optimum conditions (5.8–6.1) and in the southern part of the range (4.5–6.0). As rightly pointed out by P.A. Sviridenko, these data are not entirely compatible. However, it is clear that the longer the period of breeding, the greater the probability of not only subsequent broods in overwintered rodents, but also in those born in spring and summer. To this should be added the fact that reproductive phenology serves as the most objective index of response of rodent population to extent of favorable weather conditions. Rudyshin (1959) indicates that the bank vole reproduces from March to October in western regions of the forest-steppes of the Ukraine under normal conditions, and also during winter in favorable years. Similar phenomena have been reported by Zejda (1962) for Moravia, and Kulicke (1960) and Birkan (1968) for Western Europe.

Reproductive intensity, that is, frequency of successive broods in sexually mature animals, number of neonates in a brood, and rapidity of maturation of newborns, are associated with phenology. Many researchers have noted in passing an increase
462 in reproductive intensity in forest voles given a good food base

and favorable weather conditions (Popov, 1960; Zejda, 1962, 1966; Sviridenko, 1967; Andzhevskii, 1974; Buyal'ska, 1974; Sokolov and Balagura, 1974). The specific results presented by many authors on number of broods in overwintered and young rodents, number of neonates in a brood, and variability of these indices over different seasons and years, indisputably confirm the general statements made above. The Tien Shan vole (overwintered individuals) in alpine regions of the Trans-Iliian Alatau, breeding from April–May to August–September produces two to three broods. Breeding commences ten days later in the northern slopes than in the southern, and continues more uniformly. Neonates of the first generation of overwintered individuals usually produce one brood per season, but immediately after years of high seed yield of spruce and berries of mountain ash, second broods have been recorded (Fedosenko, 1965). Spring populations of this species consist of individuals aged 9–11 months. Active young individuals (weight 8.0–9.0 g) appear at the end of June–beginning of July. In September, semiadult individuals constitute 64–84% of the population.

Koshkina (1953) has shown that the number of neonates in a brood increases toward autumn in the bank vole of the Lapland National Reserve. This is related to the appearance of seeds, berries, and mushrooms in summer. The average brood size in overwintered females in June–beginning of July, 1952 was 4.8, increasing to 6.2 in August–early September. In the large-toothed red-backed vole, which mainly consumes vegetative green plant parts, the brood size did not change in different seasons (5.5 in 1949 and 5.25 in 1950). In years of good food availability, both voles bred equally well. Old females produced two to three broods each. The young from the June and July broods developed and matured very quickly, and began to reproduce at the age of 25–30 days in the large-toothed red-backed vole and 35–40 days in the bank vole. Those born in June were able to have two broods in the year of their birth. But with a poor harvest of seeds, berries, and mushrooms (1950), the large-toothed red-backed vole, which feeds primarily on vegetative plant parts, multiplied intensively, while the bank vole (also southern red-backed vole) was emaciated and bred very poorly. Old females produced one brood over the season, the number of neonates per brood was less, the young developed slowly and did not participate in breeding, and reproduction ceased earlier than usual.

In Moravia, according to the findings of Zejda (1966), the fecundity of bank voles was higher in depressions even at minimum altitudes (average number of embryos 4.902 ± 0.065) than in voles living 1,000 m above msl (4.090 ± 0.104 embryos). The largest number of neonates per brood was reported in May, and the smallest in autumn and winter. Broods of females of larger size and weight were largest while those of old females were smallest.

In years of intensive breeding, when a large number of young animals with a body weight of even less than 15 g participate, the average number of embryos per gestating female is lower in a year of population suppression, when only larger overwintered individuals reproduce (those that remained in relatively optimal conservation habitats), producing one or two broods each. This fact is confirmed by the data presented in Table 41.

Andzhevskii (1974) shows that an isolated population of bank vole obtained by supplementary feeding with oats under natural conditions, led to a radical increase in reproductive intensity, which began in January and not in April. Hence, already in April 50% of the population consisted of animals born in winter. The population strength increased manifold toward autumn, compared to control, which received no supplementary food. The author has emphasized that additional feeding of the population increased the breeding season, led to involvement of new adult groups in reproduction, and produced a manifold population increase and density compared to control. In this context, it is difficult to understand the conclusions drawn by that school of thought (Buyal'ska, 1974) which contends that early changes in population density of this species, even

Table 41. Number of embryos in a brood depending on weight of female bank vole (from Sviridenko, 1957)

Female weight (g)	Number of embryos		Number of placental spots	
	Range	Mean	Range	Mean
15-20	2-8	4.2	2-9	4.4
20.1-25	2-9	5.1	2-9	5.1
25.1-30	3-9	5.5	2-9	5.9
30.1-35	2-8	5.6	2-7	5.8

under the same experimental conditions with supplementary feeding, leads only to mortality and not to a change in reproductive intensity.

Koshkina (1953) pointed out another very important situation: in favorable years and availability of good quality food, a larger than usual percentage of a population survives the winter (60–75%). Similar data were recorded by Zejda (1962), but in relation to favorable weather conditions during winter, permitting reproduction of the vole.

Thus the major reproduction indices of the forest vole, its biology, and general dependence of reproductive intensity on conditions of energy resources in the environment and climatic factors, are quite similar to those described for the steppe vole. Probably, only the lability of responses of populations to the environment *per se* is slightly less. It is important to emphasize that even survival of bank vole populations is higher under conditions favorable to their reproduction. This should be considered an important prerequisite for understanding trends in their population dynamics.

Population Dynamics

Based on the reproduction ecology of forest voles, it can be concluded that reproductive intensity and phenology determine trends in population density and dispersal. Numerous researchers who have studied the ecology of these voles, have reached this conclusion (Koshkina, 1953; Popov, 1960; Sviridenko, 1967; and others). Therefore, it may be assumed that factors determining the phenology and intensity of reproduction in each species of this group (energy resources and climatic factors) also decide population dynamics. Sviridenko (1964), who studied the dynamics of habitat distribution and numbers of bank vole for eight years in the national reserve "Aleksandriya" (Kiev district), also came to this conclusion. He wrote:

The main factor determining the reproductive intensity and increase in number of voles is feeding conditions. Close on the heels of a seed harvest of woody plants follows an increase in population of bank voles. The main reasons for mortality among bank voles during winter are shortage of food, unfavorable weather conditions (sharp warming with settling of the snow cover and formation of an ice crust in years of poor snow, which prevents the rodents from

searching for food on the ground and in snow), and also predators (p. 22).

464 The habitat distribution of forest voles probably changes in a smaller range than that of the steppe vole. However, conservation habitats can be found everywhere, in which the species is conserved even in years of population suppression, as well as dispersal habitats in which it appears in years of en masse breeding. For example, conservation habitats of the bank vole in the national reserve "Aleksandriya" were the oak forest and old mixed plantations with dense underbrush. Old oak plantations devoid of underbrush served as dispersal habitats as well as oak plantations, glades, and also areas under agricultural crops. The dynamics of habitat distribution of voles is primarily related to the dynamics of seed harvest of woody trees (Sviridenko, 1967).

In most regions occupied by forest voles, the area of conservation habitats is fairly large. The difference with respect to area of conservation places and dispersal places is less for these rodents than in most regions occupied by the steppe vole. Therefore, frequent rises in population of forest voles are observed. Sviridenko (1967) observed three peaks over an 8-year period in the southern part of the range of the bank vole; Semenov-Tyan-Shanskii (1970) observed seven peaks for all three species of forest voles over a 30-year period in the northern part of their range. The range of population fluctuations is narrower in these voles than that in the steppe vole. But there is a similarity in the population dynamics of forest and steppe voles, in the causes responsible for it, and also in the mechanism directing this process. Yet some researchers, even those who earlier held this view, disagree with this concept and attribute the decisive role in the dynamics of forest voles to intrapopulation relationships (Koshkina, 1967, 1969; Semenov-Tyan-Shanskii, 1970; Ivanter, 1974). Let us now examine the theoretical and factual material forming the basis for this conclusion.

T.V. Koshkina's theoretical basis (1967, 1969, 1974) is described in the introduction to her articles (1967, 1969, 1974). It primarily posits the presence of populational homeostasis revealed by ecologists from other countries (without specifically citing authors) and the specific mechanisms controlling it. She states in her second article that "the environmental conditions at different levels of rodent population and different conditions of their populations interact markedly on the animals. Under optimum conditions, the rodent population fluctuates to a great extent independent of external factors" (p. 5).

In the last 10–15 years interesting data have been collected on the hierarchical relationships in populations of different animal groups and the mechanisms which may influence reproductive intensity and even survival of individuals of different age groups and hierarchies (see reviews by Christian, 1970; Maers, 1970). However, in assessing the biological significance of these factors, there is unilateral tendency against which I have already spoken (Polyakov, 1967, 1969). Researchers mostly visualize mechanisms of automatic regulation of numbers in hierarchical relationships acting on the principle of feedback, without taking into account the conditions of external environment. Their primary objective is to ensure dispersal and formation of new populations when favorable conditions are created. But they pay no attention to the fact that under extreme conditions, in rodents in particular, the intrapopulation stress caused by the hierarchy decreases. With great pleasure, I have come to know that Christian (1970), who has made a great contribution to the study of hierarchical relationships in rodents, but who earlier interpreted such merely as a mechanism of automatic control of population dynamics, now considers them in the same perspective that I do. Moreover, he believes that hierarchical relationships facilitate the dispersal of certain genotypes of a population, which contribute to the enrichment of germplasm and microevolution.

The assertion of T.V. Koshkina that in different states a population responds differently to similar conditions is quite correct. I have also noted this fact several times (Polyakov, 1949a, b, 1950). It is well-known that at different phases of population dynamics, not only factors determining reproduction but also mortality exert a unique effect. I have indicated the mechanisms responsible for this (Polyakov, 1950, 1964, 1967, 1969). The state of a vole population and its response to the environment in a given season are determined by the conditions of feeding and heat exchange in which the animals developed in the preceding years. T.V. Koshkina has not listed the mechanisms producing the difference in response of a population of differing quality to the environment, but uses this assertion to emphasize that abundance of food and climatic factors do not always influence the population dynamics of voles. This concept leads to the conclusion that vole numbers change under optimum conditions irrespective of external factors. Probably, it is assumed that the external environment may be optimum under natural conditions for the species for several seasons or years, or over an indefinite period of time. By

then, perhaps, it will have also lost its importance as a regulating factor. Some researchers think so: The species survives, ergo the environment is optimal for it. Actually, the optimal environment for rodents (and other animals) endures for a relatively short period even in extensive territorial tracts and is more or less unfavorable for them for the greater part of time and over most of their territory. The whole system of adaptations of a species is directed toward survival under similar natural situations. This system of adaptations also includes hierarchical relationships within the population and all the forms of dependence upon the state of energy resources of the environment and the formation of responses to its condition programed during ontogenesis. The principle of feedback means that the environment *per se* (primarily energy resources and climate factors) forms the entire system of responses of a population to its condition in the future (Polyakov, 1969). Unfortunately, insufficient knowledge of the physiology of rodents (and of other animals) and the formation of characters during ontogenesis, leads many ecologists to the erroneous conclusion that the effect of energy resources and climatic factors on the population cannot operate on the feedback principle. This has tempted some researchers to attach no importance to the energy resources of the environment in population dynamics (Viktorov, 1967). Actually, the energy resources of the environment and climatic factors program the entire system of populational responses to the ecological situation, including intraspecific and interspecific relationships. The study by Wynne-Edwards (1970) is of great interest; he demonstrated that the food base is a factor acting on animal populations through the feedback principle. In experimental studies on the role of population density as a factor influencing fecundity of animals and survival of their progeny, researchers have always considered food abundance. When the space remained the same but the food supply changed, the dependence of population density was decided particularly by the latter factor. Populations receiving three times more food than control reached a stabilization level of population density 1.8 and 2.5 times higher than in control. Under field conditions, I have repeatedly observed that the density of a population reached at peak population strength is always decided by abundance of food during en masse breeding.

Thus the theoretical propositions of T.V. Koshkina cannot be considered indisputable and fully valid. The voluminous material collected by her characterizing the population dynamics of the northern red-backed vole could also be interpreted in the same

manner as done by Sviridenko (1967) in his analysis of population dynamics of the bank vole. However, some corrections are necessary for its systematization. First of all, the cycle of population dynamics of the voles should be divided into five and not three phases as done by T.V. Koshkina, who combined the phases of depression and dispersal and the phases of peak and fall in numbers. Were this done, the importance of food as a factor determining reproductive intensity and rise and fall in the population, would become apparent.

The criteria for forecasting the number of northern red-backed voles proposed by T.V. Koshkina (1969) are fully acceptable. She recommends that the probable tendency towards change in rodent numbers in the coming year be based on data pertaining to their numbers, composition of population, phenology, and reproductive intensity in the preceding year (in other words, indices characterizing populations). Forecasting is easily done from such data. However, it is very difficult to obtain such initial information for large territories. Therefore, one has to base conclusions regarding the population in the previous year on indirect indices, mainly food supply as the major factor forming their structure and morphophysiological properties of all age groups. Hence a practical system of predicting numbers of forest voles in the future should be based on the actual availability of initial information. Characteristics of food yield and climatic factors may readily be considered available components. Utilization of these factors in forecasting poses greater scientific difficulty than direct results on state of the rodent population. However, it should not be concluded that the importance of "external factors" in population dynamics should thus be ignored. The purpose is to identify the mechanisms that influence internal environment, morphophysiological properties of populations, as well as inter- and intraspecific relations. To date, these mechanisms have not been identified for the forest vole.

O.I. Semenov-Tyan-Shanskii (1970), based on traditional estimation in the Lapland National Reserve, has demonstrated the effect of the cyclic nature of population dynamics of forest voles and shown that each phase is characterized by its own unique intensity of reproduction. In the years of population increase (1958, 1962, 1967, 1968), not a single young male reached sexual maturity and only 2.0% of the young females produced broods. The author sought a correlation between condition of population strength and climatic factors during these years but found none. This is understandable considering the results available on the mechanism of the effect of

climatic factors on the condition of rodent populations (Polyakov, 1950, 1969). He also mentions that the indices of reproduction and mortality change in different phases of population dynamics. The difference in rate of sexual maturation of young animals at different phases of the cycle plays the major role in change of index of reproductive intensity. Reproductive intensity has a reverse correlation with population density (the reasons for this have already been examined). Hence it may be assumed that population density is of decisive importance in determining intensity of reproduction of voles. I have already shown that such an assumption is erroneous.

467 The system of analysis of results employed by O.I Semenov-Tyan-Shanskii does not correspond to our present understanding of the mechanism of influence of feeding and climatic factors on the state and reproduction of rodent populations. Formally speaking, he is right that in the phase of peak numbers, under maximum density of settlements, reproductive intensity will be minimum, and at the end of depression and during dispersal when the population density is minimum, reproductive intensity will be maximum. Given the foregoing discussion it is hardly necessary to explain that such a formalistic approach is now archaic. The consequence is taken as the cause.

It is important to discuss the data compiled by Chitty and colleagues (1968) on the field vole, proving that winter mortality in this species after peak reproduction is not determined by the condition of the food base. Individual voles were released into special open-air cages (1.0 m²) situated in a meadow on the outskirts of Oxford. Because the natural vegetation was sufficient to feed the overwintering voles, it was concluded that not food availability, but rather population density *per se* led to mortality among field voles in 1961 after peak numbers in autumn of 1960. I personally know D. Chitty to be an intelligent experimentalist. Nevertheless, I have to assume that in interpreting his results, he did not take into account rodent response after peak numbers to the environment. It was earlier shown that a large part of the population located beyond the limits of conservation places loses viability and dies even when returned to optimal conditions (Polyakov, 1950–1969). In 1948, at the time of peak numbers of the social vole in Azerbaïdzhan, I caught a sizable batch of rodents and housed them in the laboratory in Leningrad. However, not a single female from this batch reproduced and all the rodents died, even though favorable conditions were created for them. I think that such a situation could well arise after peak numbers in the field vole.

Thus, efforts to negate or undermine the role of energy resources and climatic factors in the numerical dynamics of the forest vole as well as utilization of indices of their condition for predicting reproduction, cannot be considered well-founded. Yet the importance of intrapopulational relations should not be totally ignored; they undoubtedly play a greater role in the numerical dynamics of forest voles than in steppe voles.

Populations of the forest vole, because of the biotopes they occupy and their reproductive phenology, cannot be subjected to such seasonal variation as is typical for the steppe vole; they do not form "spring populations" (Polyakov, 1968b). Therefore, the numerical dynamics of the forest vole depends less on climatic factors than in the steppe vole. Dependence on food resources is fully maintained. However, this dependence simultaneously augments stress of interspecific relationships among forest voles, which is related to the greater balance of relationships between components of the forest biocenosis compared to the steppe vole (Volkov, 1971; Polyakov, 1973). For the same reason, the dynamics of habitat distribution of the forest vole is lower than in the steppe vole. Therefore, the stress of relationships in the course of population dynamics may be greater and exert a stronger effect on reproductive intensity than in the steppe vole. However, considering these situations as applicable to specific geographic regions, it is important not to treat them as absolute and not to contrast the importance of one group of factors over another.

Population Variability

Judging from the variability of population intensity and survival of the forest vole according to the state of energy resources and climatic factors, one may propose that this group of rodents is characterized by all the forms of populational variability noted for the steppe vole, including seasonal variability. However, the latter does not have the same adaptive significance for this group of voles as for the steppe vole, especially for those living in regions with a distinct continental climate.

To date, no studies have been conducted to reveal the mechanisms forming different levels of populational variability in different voles, nor to reveal the population structure of their habitats in individual regions of the range. The available publications mainly present an analysis of dependence of criteria used for spreading subspecies.

In presenting an analysis of the ecological morphology of the forest vole, Kulaeva (1958a) concluded that the evolution of species of this group proceeded "on a close biotopic base of the northern forests". This is responsible for the similarity in major morphological characteristics among species. Incidentally, differences in structure of the extremities, reflecting different adaptability of the species to digging activity as well as climbing trees, were established in this process. Some special problems arise, however, when studying intraspecific variability.

In terms of methodology, the work of Gerasimov (1969) is interesting. He has attempted to analyze the ontogenetic variability of those characters of the bank vole used in separating subspecies. A similar study was done by Serafinski (1968), who analyzed seasonal and terrainal variability of populations of the bank vole in terms of characters used in taxonomy. In particular, he demonstrated that coloration of the bank vole changes so much in different seasons that this character cannot be used for separating subspecies. Similarly, Rossolimo (1962a, b) undertook studies of geographic variability for separating the bank vole and northern red-backed vole. She concluded that there are no dependable characters for the separation of subspecies of the northern red-backed vole, since all the characters analyzed by her exhibit marked variability depending on conditions in which the population lives. The zygomatic width, interorbital width, and width of brain case are comparatively more reliable for diagnosis.

Bol'shakov (1968) analyzed the relationships of clinal and subspecies variability in forest voles. He demonstrated that characters such as body length, relative size of skull and its parts, length of tail and hind foot, and coloration exhibit a well-expressed clinal variability. Internal characters, he concluded, reflect features of adaptation to environmental conditions in the area occupied (Bol'shakov, 1962, 1965; and others). Nevertheless, based on the totality of even phenotypically changing characters, a new subspecies of the northern red-backed vole was separated (Bol'shakov and Shvarts, 1965).

Bashenina (1969), after analyzing extensive data characterizing the variability of internal characters, concluded that "population variability under inadequately differing conditions of existence (in particular the microclimate of the ground layer of air and soil, in which small rodents actually live) is greater than geographic variability" (p. 110). In other words, biotopic variability is greater than geographic variability. A similar opinion has been voiced by

469 Mayr (1971, Russian translation). Contradictions in discussions of the populational variability of the group of forest voles arise from the fact that in the studies conducted and analyses of their results, no attempt was made to determine the gradations of population structure of the species. Probably, forest voles have a genetic population (subspecies) as well as geographic, terrainal, and biotopic populations. Therefore, in collecting data, one should clearly understand which population is being sampled. Criteria for judging differences in each level of populational variability should be selected while taking into account their variation in ontogenesis during the process of formation of the phenotype. In this respect, I feel it is important to use for rodents the methods of analysis of population variability developed and used by Vasil'ev and Efimov (1970) for gerbils.

Practical Significance

Forest voles living in natural biogenocenoses can hardly be considered harmful animals, although they significantly retard the rejuvenation of forests by destroying seeds and partly eating roots, branches, and seedlings of trees and shrubs, which cannot be considered entirely harmless. As shown by Volkov (1971) from studies in the Central Forest Reserve, the forest vole, together with the ground squirrel, birds, and insects, participates in the destruction of spruce seeds. These seeds are totally destroyed in years of low and moderate yield. Only in years of high seed yield is a small fraction preserved, leading to the rejuvenation of spruce. However, the spruce population does not stand to lose through the influence of herbivores, since its rejuvenation depends on physiologically viable seeds. One must also remember that forest voles are an important dietary component for valuable fur-bearing animals. Therefore, there is hardly any justification for controlling the forest vole in natural forests.

The activity of the forest vole must be considered in a different light in reforestation projects, nurseries, parks, and even in natural forest biotopes exposed to strong anthropogenic influence. Here, all researchers have rightly noted the damage caused by the group of forest voles (Obraztsov, 1951; Sviridenko, 1951; Girenko, 1952; Klemm, 1957). Control measures to protect tree plantations must be taken under these conditions.

The field vole causes much damage to coniferous plantations in Finland and Norway. Planned control measures are taken against

it (Millimyaki, 1974; Millimyaki and Paasikallio, 1974).

The forest vole plays a significant role in epizootics and epidemics. The latter may become serious due to the frequent migration of these voles into human working and living premises. Many species of bugs and mites have been detected on these rodents, which may be vectors of disease (Mohr, 1950; Kulaeva, 1958a; Lapin, 1958; Nazarova, 1968; and others). I.V. Nazarova has shown that of the 21 species of bugs found on the bank vole in the Volga-Kama territory, 3 are important in the epidemiology of spring-summer encephalitis, 4 in tularemia, 2 in hemorrhagic fever, 1 in erysipelas, and 1 in plague. Of the total number of bug species parasitizing the bank vole, 58% are dangerous from an epidemiological point of view. Therefore, in individual cases, preventive destruction of the forest vole must be done to forestall the spread of these dangerous diseases.

Control Measures

Large-scale control of the forest vole is not to be done but sometimes it is necessary to check them in very small foci of conspicuous damage. Grain baits containing zinc phosphide are used in destroying them and the prescription the same as that for the steppe vole. However, spreading the bait on the soil surface is not recommended because it endangers grain-eating birds in forest plantations. Up to 0.5 g bait should be placed in each burrow. If the burrows are difficult to detect, then 25–30 cm deep holes can be dug with a stick or drill and 10–15 g poisoned bait placed inside. Such holes serve as places for long-duration poisoning of rodents (Sviridenko, 1951). Sometimes, protective wire netting is used in nurseries to protect the seeds of particularly valuable trees (Sviridenko, 1951).

The microbiological method based on utilization of rodent typhoid bacteria of the genus *Salmonella* has been tested with positive results in control of the bank vole. The bactorodenticide preparation is applied in a manner similar to grain bait using zinc phosphide (Kandybin, 1963; *Methodological Notes for Field Trials of Bactorodenticides*, Leningrad, 1970). As mentioned earlier, the bacterial method of rodent control is not favored in other countries (Marsh and Howard, 1970).

TUNDRA VOLES

General Characteristics

Tundra voles include true lemmings (*Lemmus lemmus* L.—Norway lemming, *L. obensis* Brants—Siberia lemming, *L. amurensis* Vinogradov—Amur lemming), the wood lemming (*Myopus schisticolor* Lill.) and the Arctic lemming (*Dicrostonyx torquatus* Pall.). Also included in this group are *Microtus hyperboreus* Vinogradov (North Siberian vole) and *M. middendorffii* Poljakov (Middendorff's vole).

All these rodents exhibit a distinct adaptation for life in conditions of tundra and the northern subzone of taiga, which are characterized by unique impoverished phytocenoses; slow rejuvenation of plant cover; long cold winter; extremely unfavorable (critical) transitions between winter and spring, and between autumn and winter; an almost complete absence of summer (season with a mean daily temperature above 15°C); and frozen, often oversaturated soil over most of the year.

The major adaptive characteristics of tundra voles are directed toward overcoming the systematic action of low temperatures and high humidity, and rational utilization of the energy resources created by the phytocenoses of tundra in the northern taiga. Yet adaptation to high temperatures and drought, also faced by these rodents in the zone of their distribution, is not reflected in their morphological traits.

471 Tundra voles are relatively large in size; their body weight reaches 120 g, which is almost twice greater than the maximum weight of the steppe vole. Furthermore, they have a dense pelage which lengthens significantly during the winter period. Their feet are densely covered with hair. Lemmings accumulate significant fat reserves for winter. Such adaptations facilitate thermoregulation during prolonged existence under conditions of high humidity and low temperatures (Tyulin, 1940). Nests and communicating tunnels are laid in dense snow cover where an optimal microclimate is created during the coldest part of the year. The claws of lemmings lengthen in winter, making it easier to dig tunnels even in very compact snow (Dunaeva, 1948).

Lemmings can breed and attain sexual maturity year-round, even under snow in extremely severe winters. Signs of adaptations to life in the north are also manifested in their reproduction biology (Shvarts, 1961). Pregnancy, for example, is as short as that in the steppe vole, i.e., 18–20 days. The energy losses of pregnant females

are large but far less than during lactation. Probably, the need to reduce the stress of energy losses in female lemmings during lactation explains why neonates develop slowly in this period and open their eyes on the 14th–15th day (Dunaeva, 1948) versus the 8th–10th day in steppe voles. On switching to independent feeding, young lemmings grow rapidly. The lactation period of lemmings is much more prolonged than in the steppe vole.

Seasonal change of habitats is a regular feature in tundra voles, for the purpose of selecting optimum habitats during critical seasons of the year, and large-scale migrations in years of high numbers are typical for some species. These movements usually occur along moist soil and in melting snow to overcome water barriers. Such would not be possible if tundra voles did not have a nonwetttable pelage (Tyulin, 1940). Thus, these voles constitute a unique biological group, a fact noted by all those who have studied their biology (Dunaeva, 1948; Nasimovich *et al.*, 1951; Koshkina and Khalanskii, 1962; Kalela, 1963; Koshkina, 1970; Vinokurov and Orlov, 1974).

Feeding and Habitats

Lemmings feed on growing parts of plants of low calorific value. The quantity of food consumed in a day is more than twice their weight (Dunaeva, 1948). This ratio is probably even higher in lactating females.

Tundra voles are polyphagous. They eat as many as 50 plant species in a single region (Nasimovich *et al.*, 1951). However, their optimum diet includes only a few plant species. For the Ob' lemming, the major food is sedges and cottongrass. The Arctic lemming additionally eats the leaves of willows, dwarf Arctic birch, bog whortleberry, cowberry, and bark of shrubs (Dunaeva, 1948). Green moss, cottongrass, sedges, and some grasses constitute the major dietary components for other lemming species as well (Koshkina, 1970).

Lemmings do not store food for winter. Favorable places for wintering are limited to areas of considerable snow accumulation, which serves as a safeguard against chilling. At such places the food resources are almost completely destroyed during the long polar winter. This situation stimulates a change of habitat during spring. These rodents breed intensively and lead a settled life during the warm season. They also feed intensively and dispersal of the young to new habitats occurs systematically at this time. According to Tikhomirov (1959), the Ob' lemming, even at average numbers, consumes 93% of the cottongrass available per year in typical habi-

tats, or about 3.0 tons (airdry) per hectare. Koshkina (1970), citing data from Shultz, states that in June, 1960 there were 175 brown lemmings per hectare in Cape Barrow, which should have eaten 20 kg plants (airdry) every day. Due to lack of abundance of food, the lemmings were compelled to disperse.

In years of en masse breeding, lemmings, predominantly phytophages in the north, definitely affect the state of the plant cover here, which is reflected not only in the well-being of their populations, but that of other animals living in this zone.

The quantity and quality of the food base of lemmings depend on weather conditions in the summer period. If the summer is less cloudy, then favorable conditions are created for vegetative plant growth; the latter is poor during cold and cloudy weather and the nutritional quality of the plants deteriorates. Thus the effect of climate factors on the state and dynamics of lemming populations is significantly evidenced through the food base (besides the direct effect in the critical seasons of spring and autumn).

All researchers have noted that lemmings concentrate during winter at places where suitable snow cover forms early and sufficient food base exists. Traces of migration to such places have been detected on snow even at the beginning of winter (Dunaeva, 1948; Nasimovich *et al.*, 1951). Winter conservation places of the Ob' lemming are areas of moss and dwarf Arctic birch, hummock-tundra, and depressions between hillocks and lake basins. A large quantity of snow accumulates here, covering the short shrubs of willows and dwarf Arctic birch (Dunaeva, 1948). Winter conservation places of the Norwegian lemming occur mainly in sedge-cottongrass, marshes, and overgrown shrubs along depressions of montane tundra (Pushkina, 1970). Most of the winter conservation places of the Arctic lemming are concentrated on slopes of high tundra, running to lake shores, in basins, and also in low-lying moss and turf-hummocks. The snow cover in these places is very thick and not windswept.

When the snow melts in spring (end of May—beginning of June), the wintering habitats of lemmings become unsuitable. But it is difficult for the rodents to find another place during this period. Elevated parts of tundra or marshes with elevated turf-ridges are apparently the most optimal (Dunaeva, 1948).

Lemmings spread in spring to areas sufficiently moist and rich in food, in particular sedges, dwarf Arctic birch, etc. (Dunaeva, 1948). The autumn period is usually unfavorable due to oversaturation of the soil and a scant food base at places of summer breeding.

This stimulates migration of the rodents to places where they subsequently winter.

The intensity of seasonal migration, judging from the data of many investigators, depends on the topography of the area, combination of biotopes, territory suitable for hibernation and survival during the critical periods of spring and autumn, and the population strength of the rodents. The more variable the combination of such biotopes, the more favorable the territory for survival of lemmings, and the less intensive their migrations as long as their numbers do not increase greatly.

Burrows and Digging Activity

Lemmings usually have simple burrows during the summer period, with two to three shallow tunnels leading to a large spherical nest with a thick lower wall. Only in turfed or sandy areas are the burrows deeper, with a larger number of entrances. The architectonics of a burrow are determined by the depth of soil layer and proximity of permafrost layer, which lies at a depth of 20–30 cm (Dunaeva, 1948; Nasimovich *et al.*, 1951).

The Ob' lemming throws out the soil when digging summer burrows, the dry weight of which is 200–800 g. The total number of burrow entrances in the summer varies from 400–10,000/ha; most of these are old entrances and only 10% are dug afresh. Lemmings dig out 6–250 kg soil from burrows per hectare. Drained areas free of vegetation are created on the soil thrown out by lemmings. Ultimately, these determine the mosaic nature of the plant canopy (Tikhomirov, 1955).

Nests are situated not far from the entrances, which ensures a favorable temperature in them. The temperature in burrow tunnels at a depth of 10–12 cm reaches 7–8°C in summer and falls to 3–4°C and below with increasing depth. It has been concluded that low temperatures in burrows help lemmings avoid ectoparasites (Dunaeva, 1948).

In wet areas, nests are laid in hummocks or under shrub cover. Communicating paths are laid in the form of tunnels; their tracks run through dense vegetation (Nasimovich *et al.*, 1951; Kalela, 1963). Winter nests are built in snow, slightly above the soil surface. They are probably surrounded by a dense and wide network of runways made in the snow at different depths and on the soil surface. Air holes are not discernible above burrows. In the case of intensive winter breeding, dispersal of the young also occurs primarily along

the runways under the snow, although traces of movement are also detectable on the snow. The snow at wintering places of lemmings is literally crisscrossed with their tunnels, which should make catching by predators extremely difficult (Dunaeva, 1948; Nasimovich *et al.*, 1951).

Nests built in snow make it much easier for lemmings to withstand winter cold with a minimum loss of energy to thermoregulation. Measurements of temperature on the snow surface and on the soil surface under snow in January revealed a difference even during the day of up to 22.5°C; with a fall in temperature on the snow surface to -26.5°C, the temperature on the soil surface did not drop below -4.4°C (Nasimovich *et al.*, 1951).

Reproduction

Pregnancy continues in lemmings for 18–20 days. From 1 to 11 neonates may be born, more often 4 to 8. The number is less (4.5) in young females than in adult (5.8) and older animals (first brood 8.2, second brood 6.7). Lactation continues up to 22 days but the next pregnancy often occurs soon after delivery. Usually, if good food is available, females on completing lactation bear another brood. Toward the end of the summer breeding season, about 2.5–3.0 months, many overwintered females (about 25–30%) produce 2 broods each and the others 3 broods each (Dunaeva, 1948).

The number of neonates in a brood greatly depends on the female's weight, which is controlled by age and feeding. The latter, of course, depends on food base. Female Norwegian lemmings weighing up to 40 g produced, on the average, 4.17 offspring; with a body weight of 40–50 g—4.96; 50–60 g—5.33; 60–70 g—5.91; and more than 70 g—6.76 (Koshkina and Khalanskii, 1962).

Newborns of the Ob' and Norwegian lemmings weigh 3.4–4.0 g. Those of the Arctic lemming weigh slightly more, up to 4.7 g; one female birthed a single young animal weighing 6.2 g. Eye-opening commences in neonates on the 14th–15th day of life and changeover to independent feeding at the age of about 20 days. At this time lemmings weigh more than 10 g but their weight depends on the conditions of feeding of the female and number of neonates in the brood. The fewer the neonates, the larger the offspring at time of changeover to independent feeding (Dunaeva, 1948; Nasimovich *et al.*, 1951). Klemm's report (1957b) that eye-opening occurs in lemmings on the 10th day of life is apparently wrong.

Young female Norwegian lemmings begin to reproduce at about 2 months of age, having attained a weight of about 30 g (Nasimovich *et al.*, 1951). About 70% of the young females participate in breeding in the summer season, of which some produce 2 broods each (Dunaeva, 1948). According to Koshkina and Khalanskii (1962), females weighing 20–30 g participate in breeding to the extent of 26.7%; those weighing 30–40 g—73.3%; and 40–50 g and more than 50 g—100%.

A second breeding cycle, given a good food base, occurs in winter. Old females may participate after overwintering, but generally the participants are animals born in summer and young who attain sexual maturity during winter. The life span of lemmings does not exceed 12–15 months. Therefore, a female may not produce more than 3–4 broods during her life.

Reproduction intensity is determined in lemmings by the food base. Spring and autumn breaks in reproduction are caused by unfavorable climatic factors and associated seasonal migrations.

It has been estimated that in the absence of infant mortality, the progeny of a single female in a year could number 1,500 to 2,000 animals (Koshkina, 1970). The largest brood size occurs during the summer breeding season. However, winter breeding plays a decisive role in numerical dynamics of lemmings. All researchers agree that the large-scale appearance of lemmings is always preceded by intensive reproduction in winter. Only then do they occupy all their biotopes in the summer season and commence large-scale migrations in autumn. Large-scale spring migrations are also possible after intensive winter reproduction (Kalela, 1963). Lemming numbers can increase 100-fold during winter (Koshkina, 1970).

Numerical Dynamics

The numerical dynamics of lemmings has long attracted the attention of biologists because it reflects economic conditions in the large northern territories. The range of fluctuations in numbers is vast—from isolated animals difficult to detect in large areas to massive hordes appearing everywhere and migrating even through water barriers, oblivious to danger from man and predators.

Three theories have been proposed to explain the numerical dynamics of lemmings: (1) effect of factors of external environment on populations (food and weather); (2) effect of predators and epizooties; and (3) occurrence of intrapopulation regulatory mechanisms. All three theories have been deemed unsatisfactory (Cough,

1965). Reports in literature show that these theoretical propositions, like those derived from analysis of population dynamics of other groups of rodents, should not be contrasted but, more appropriately, synthesized. The role of each group of factors, to which a decisive importance is attributed in the population dynamics of lemmings, is manifested uniquely in individual phases of the cycle (Polyakov, 1964, 1967, 1969). Therefore, I have considered all the phases of the cycle and tried to characterize the influence of the above-mentioned factors on them.

In the phase of depression of numbers, a population is preserved only in conservation places. It is represented by isolated individuals who are probably permanent dwellers of these habitats and actively defend them against attack by other animals. Maybe, some animals are settled migrants. Food resources are extremely poor during the period of migration because severely depleted by the lemmings during large-scale reproduction. If peak numbers coincide with the end of summer, restoration of the plant canopy cannot occur by winter. Therefore, the population may enjoy a food supply only in those restricted places where food resources were not available to lemmings during the warm season (low-lying areas filled with water, and so forth). Such areas are optimum for wintering with the establishment of snow cover, but their volume is probably quite restricted. Reproduction is not observed in winter in these conditions. Furthermore, even the aggressive nature of interactions within the population is suppressed, attested to by the occurrence of several adult individuals in a single nest to make thermoregulation easier (Dunaeva, 1948). The maximum population decline probably occurs when reproduction ceases at the beginning of autumn.

If the lemming number is already high after a favorable winter and growth of plants slow, the rodents quickly destroy all the food available when the progeny of the first brood of overwintered animals change over to independent feeding. Reproduction ceases early in the population and, soon after, a decline in numbers occurs. A large number of rodents may be conserved under these conditions in the depression phase, and conditions for survival of the population may have improved by the time of wintering.

The state of a population during the phase of depression and its subsequent emergence from it, greatly depend on when the depression sets in. The most important factor in this case may be the condition of the food base. When numbers peak in late autumn, the depression may be severe and protracted; depression in mid-summer may be less severe and of shorter duration.

The onset of the dispersal phase depends on food harvest and population state. Food harvest is determined by climatic factors. Furthermore, cycles of productivity are also possible, which have yet to be studied (Tikhomirov, 1959, 1963). Even if the subsequent year is high-yielding, after a severe depression in numbers this cannot have a sharp and stimulating effect on the population. However, given a less severe depression under the same conditions, the onset of the dispersal phase is possible. These reasons explain why the state of a lemming population appears sometimes to accord with the state of the food base (Semenov-Tyan-Shanskii, 1970).

Under normal conditions, the dispersal phase may begin in the second or third year after total depression. It is characterized by enhanced interference, which stimulates dispersal and increases reproductive intensity. The commencement of this phase is probable associate with summer reproduction. However, food yield should be so high during this phase that it cannot be depleted by lemmings in summer habitats up to the end of the reproduction season. What is more important, food should be sufficient everywhere in winter habitats where intensive breeding will occur under snow. In this case, peak numbers may be noted toward the end or middle of the
476 next breeding season. The phase of peak numbers depends on the food yield in the year following winter reproduction. If the food yield proves satisfactory, the peak will occur later, but with a poor yield, earlier.

During the phase of dispersal of lemming populations and large-scale multiplication, climatic factors may have a direct effect on the speed with which each phase is completed. If critical periods are protracted, a large part of the population may die, initiating the speedy onset of the subsequent phase. Contrarily, a favorable spring and long warm dry autumn can significantly hasten the phases of dispersal and en masse reproduction (Nasimovich *et al.*, 1951). Accordingly, we may expect that a combination of unfavorable climatic factors intensifies lemming extermination by predators, while a combination of favorable weather conditions in critical seasons diminishes the effect of predators. Intrapopulational relationships may also be affected by conditions of weather and food base during critical seasons. Under a favorable combination of these factors and low numbers, intrapopulational relationships merely stimulate lemming dispersal. Under unfavorable conditions and the same population density, interference becomes acute since the area of regions optimum for lemming existence becomes restricted.

Peak numbers always coincide with deterioration of the food base or the onset of critical seasons. The fact that lemmings are capable of "demolishing" their food base cannot be doubted. All researchers have noted that summer reproduction of lemmings cease earlier in years of peak numbers than usual. This fact is sometimes used to illustrate the occurrence of "automatic control of reproduction" in lemming populations. Koshkina (1970) has shown that phenology and reproductive intensity may be associated with the state of the food base.

Decline in numbers is precipitated by several factors. Food base and climatic factors are of major importance, but the significance of predators and epizooties should not be overlooked. In this phase, predators and epizooties exerts a marked influence on the dynamics of lemming populations, accelerating their numerical decline.

The decline in lemming numbers is accompanied by large-scale migrations of rodents destined to die. The scale of this phenomenon is so extraordinary and the the adaptive significance so unclear that some scientists have doubted the actual facts (Clough, 1965). There is no basis for doubting the facts, even though their magnitude may differ significantly in different species and in different cycles of en masse reproduction. To me it appears that the migration of lemmings can be understood from the same principle as governs large-scale flights of various species of locusts (Acridoidea). In the case of en masse reproduction, larval hordes band together and proceed to move (migratory locusts). They cannot remain stationary because they rapidly decimate all vegetation in their path. Their concentration in swarms creates the best heat conditions for development. The adult winged locust can fly long distances (sometimes thousands of kilometers). Rapid depletion of food at places where swarms settle also stimulates migration. However, most locusts in swarms die. Some may reach such areas where it is possible to create a new center for the species or to enrich the germplasm of the population already exiting there (Polyakov, 1964). Probably, the adaptive significance of large-scale migrations of lemmings can be 477 similarly explained, although this adaptation should have lost its past significance under present geological conditions.

A few words about the automatic nature of the numerical dynamics of lemmings. Many researchers believe that these animals are endowed with a rhythm of population fluctuation as a property of a definite life form irrespective of environment. Environmental factors do not determine this rhythm but may disturb it to some extent (Sdobnikov, 1959; Semenov-Tyan-Shanskii, 1970). The

rhythm observed in lemmings actually becomes a consequence of the entire complex of adaptive features of a given group of animals on the one hand, and of the state of the environment in which they live on the other. Generally speaking, one may assume that the rhythm of numerical dynamics is typical for all living animals but manifested only in some. This is determined not by the internal properties of the species, but by the environment in which its population live. It is further demonstrated by the fact that within the limits of the range, the rhythm of population dynamics of any species is not observed everywhere. Therefore, it must be concluded that the rhythm in population dynamics in individual species and in different geographic regions of the range of a particular species, are created by the environment or, more precisely, the relationships between the population and the environment in which it lives.

Variability of Population

Lemmings, as a form quite sensitive to environmental conditions and distinguished by a relatively high mobility, should, perhaps, have terrainal populations similar to geographic ones. However, this aspect of the tundra vole has not been studied.

Krivosheev and Rossolimo (1966) have, practically speaking, combined the Siberian (*L. sibiricus* Kerr.), Norwegian, Ob', and Amur lemmings into a single species. They have shown that genetically they constitute a single species with geographic populations separable due to "ecophenotypic variability." The authors have differentiated Arctic, pine, and southern tundra and taiga populations. Probably, such populations could be termed terrainal since they are formed as a result of phenotypic conditions in the environment.

Identification of terrainal or geographic populations in lemmings (irrespective of correctness of the argument regarding their species affinity) formed by the environment as a phenotypic structure, permits us to conclude with considerable confidence that even the dynamics of these populations is formed by the environment as a phenotypic phenomenon. Therefore, the rhythm of population dynamics of lemmings should be considered a property formed by the environment, primarily by energy resources.

Practical Significance

Lemmings are of great economic importance in the northern regions. Their numerical dynamics is reflected in the plant cover

and population strength of carnivores, birds, and herbivorous mammals (Sdobinkov, 1959; Battsli, 1974). Dependence on the lemming population is particularly evident in such valuable carnivores as the Arctic fox (*Alopex lagopus* L.). In the cycle of matter and energy in the Arctic region, lemmings are of value from the standpoint of human interests.

Some botanists (Tikhomirov, 1955) believe that lemming activity depletes the plant cover in the tundra and is an important factor in the change and dynamics of the plant canopy.

HIGH-MONTANE VOLES

General Characteristics

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This group includes the Asian high-montane voles of the genus *Alticola* (*A. macrotis* Radde—lemming vole or Siberian high-montane vole, *A. argentatus* Severtz.—North Siberian vole, *A. strelzovi* Kastsch.—Strel'tsov's vole or flat-skulled vole) and the European high-montane or snow voles of the genus *Chionomys* (*C. gud* Satun.—Gudaur snow vole, *C. nivalis* Mart.—European snow vole, *C. roberti* Thom.—Robert's vole). Differences in the biology of the Asian and European high-montane voles are considerable, but nevertheless important features of similarity are evident in adaptation to, and life in alpine regions.

The type of thermoregulation of voles, as mentioned above, is such that they are compelled to be burrow dwellers. The soil layer in high mountain regions is not thick, excluding valleys, and may freeze to some depth. Mainly these conditions have directed the adaptation of forms of voles penetrating high into mountains. Species which continued to be burrow dwellers have occupied the valleys and been forced to specialize primarily in a fossorial mode of life (*Prometheomys*). These narrowly specialized forms are less numerous and sparsely distributed (see p. 695). Another mode of adaptation led them to live in empty places between rocks and taluses, permitting a wider coverage of mountain regions. Steppe forms usually occupy the zone of alpine and sub-alpine meadows where the general ecological situation is close to that in the plains. Occupation of empty places among rocks and taluses produced several morphological adaptations and evolved some new features of complex behavior. In some cases "flattening" of the skull has occurred, which makes it easier to penetrate cracks; in other cases the speed of locomotion has increased and the capability for climbing

among rocks has developed. These led to elongation of the digits and tail. Specific features of behavior are associated with structure of dwelling places and collection and storage of food. Species and populational differentiation of high-montane voles is associated with the climatic peculiarities of the area occupied by them and the vertical zonality of their habitats.

Feeding and Habitats

High-montane voles feed on plants growing in the vicinity of their settlement. Their diet includes cereal grasses, lichens, leaves of shrubs, berries, and seeds. Some authors (Shubin, 1959) have noted a significant selectivity of food plants among high-montane voles. This condition and poor plant cover in the biotopes occupied by them decide the constantly low population density of high-montane voles. The feeding area per female of Strel'tsov's vole is about 1,000 m².

In spite of the monotony of the terrain inhabited by high-montane voles, they exhibit specific differences and even different geographic populations within a species. Thus, the lemming vole, or Siberian high-montane vole becomes a dweller of large taluses along mountain slopes in between areas of hummock-herb-lichen tundra and cereal-grass meadows. The density of settlement in such places reaches 100–200 animals/ha. This species is more
479 common in alpine and subalpine belts but is sometimes found at the border of montane forests. Along the Okhotsk coast, where areas of montane tundra with taluses and a sparse carpeting of bushes continue up to sea level, this species (in Magadan) is found at a height of 30–70 m above msl (Kapitonov, 1959; Kishchinskii, 1966). Strel'tsov's vole lives in rocks and rock dumps. Hard rocks with horizontal cracks are preferred, near which sufficiently abundant vegetation grows. With an increase in numbers of this species, every place is inhabited in which nest-building is possible; with a decrease in population, these rodents occupy only those places located not more than 15–20 m away from the nearest feeding area. Rodents very rarely live in rocks where the nearest food available lies at a distance greater than 200–300 m from their shelters (Shubin, 1959). This trend permits us to conclude that the greater the distance of the feeding area from the place of shelter, the greater the energy expended by voles on food collection, which negates a favorable energy balance. Probably, the numerical dynamics of the forest vole is related to this condition.

European high-montane voles occupy openings in rocks, rock dumps, and sometimes brushwood clumps formed by windfallen wood, at a height of 1,000–2,900 m above msl (Tatarinov, 1954; Stepanov, 1957; Martirosyan, 1970).

Shelter Construction and Food Storage

The dwelling places of high-montane voles are confined to places having a long cold winter, usually with a poor snow cover that is often windblown. Rocks are better heat conductors than soil and hence chill more in winter. Cold summer nights do not permit rocks to accumulate heat and, probably, very optimum conditions of microclimate are thereby created at this time for voles. The shelters occupied by high-montane voles are adapted to their existence through the construction of special barriers, namely nests, in which heat insulation is insured by covering the bed with a thick layer of excreta.

Digging activity is seen in the lemming vole only in those settlements where stones are covered with soil and vegetation grows well on them. Burrows have been detected at such places, as well as soil dumps and runways connecting individual entrances. In most cases, entrances to shelters are located in hollows and cracks among stones and rocks; traces of digging activity have not been noticed here (Kapitonov, 1959; Kishchinskii, 1966). The nest probably plays the major role in thermal insulation in winter. The possibility is not excluded that with a deep and stable snow cover, these voles construct nests under the snow.

Strel'tsov's vole on occupying a shelter, rearranges it appropriately, making walls of small stones and other materials cemented with its excreta (constituting 70% of the total construction). Such walls often reach 8.0–10.0 m in length and 1.0 m in height, but sometimes their height is 20–40 cm and length 2.0–3.0 m. They are very durable and can stand for several years; probably several generations participate in their construction. Their width at the base varies from 20–30 to 100 cm, and at the top, 5–20 cm. Stones used in construction reach 35 g in weight (Shubin, 1959). The purpose of these structures is to protect the animals against wind, rain, snow, and predators. Possibly, Strel'tsov's vole does not construct such defensive walls for all shelters throughout its range (Bannikov, 1948). The floor of the shelter is covered with a layer of excreta, which provides thermal insulation, and a nest 9–12 cm in diameter (summer nest) is laid at one end. During winters with a

stable snow cover that is at least 30–40 cm deep, Strel'tsov's vole builds nests under the snow. These are located in direct proximity to the entrance to summer shelters (70–80 cm away). Several communication tunnels, 10–15 m and longer, are laid from the nests under snow (Shubin, 1959).

European high-montane voles construct summer nests in shelters and, if conditions permit, "manage" during winter under the snow.

The search for food is typical to some extent of all high-montane voles. The quantity of hay stored in small stacks by Strel'tsov's vole reaches 3.0–8.0 kg per family. These food reserves are collected throughout the warm season with the whole family participating; the search for food covers a radius of 100–200 m. The stacks are compacted and stabilized with stones and sprayed with urine. On drying, the urine forms a coating that prevents the hay from soaking and rotting. Stocking of hay reserves after winter has often been noted and additional stores secured during the new vegetative season (Shubin, 1959). Food reserves of the European high-montane voles consist of herbaceous vegetation; spruce cones and berries are rarely included. Individual stacks may weigh from several grams to 6.0 kg, more often, 1.0–1.5 kg (Stepanov, 1957).

Reproduction and Numerical Dynamics

Pregnancy continues in Strel'tsov's vole for about 20 days; neonates open their eyes on the 12th day of life; and lactation continues for 16–18 days (Shubin, 1961). The duration of pregnancy, lactation, and period of eye-opening is probably similar for other species of high-montane voles (Frank, 1954). Females may mate on the day of delivery, but a second pregnancy occurs in only a few animals, depending on favorability of life conditions. The number of neonates in a brood may reach 11–12. The phenology and reproductive intensity of individual species and geographic populations of the same species differ, which is greatly reflected in the age structure of colonies and intrapopulation relationships.

Reproduction of the lemming vole in the Kolyma plateau begins at the end of May, when much of its territory is still under snow. Over-wintered females produce two broods in the season. Years of early spring are more favorable for breeding (Kishchinskii, 1966).

Winter reproduction is assumed in Strel'tsov's vole for at least some females. Two broods are observed in overwintered animals during the warm period, but only a small number of females pro-

duce a second brood. Spring-born females bear a single brood while those born in summer do not reproduce. Intensity of reproduction is influenced by food availability and duration of vegetative period (Shubin, 1959, 1961).

Overwintered females of the European high-montane voles can produce 3 broods over the vegetative season; only a small number of females bear a third brood however. Young females from the first litter produce 2 broods each. Of the current year's females, 31% have 1 brood, 20% bear 2, and 49% do not participate in reproduction. Overall reproductive intensity is determined by the state of the food base (Martirosyan, 1964). Stepanov's assumption (1957) that the Gudaur vole is capable of producing 5 broods in the season is apparently erroneous.

The reproductive potential of high-montane voles is slightly less than the steppe voles. However, their actual fecundity is comparatively low anyway, and directly influenced by climatic factors (short
481 vegetative period) and food deficiency. Therefore, it is difficult to agree with Pokrovskii and Bol'shakov (1968) that the low reproductive intensity of high-montane voles stems from favorable* conditions and is caused by intrapopulational regulatory mechanisms. It is better explained by stress in energy balance and difficulty in replenishment of energy losses.

High-montane voles live in families. During the period of intensive reproduction, young animals on reaching sexual maturity, disperse to form independent families. All researchers have noted that rodents which have not attained sexual maturity by autumn overwinter with their parents. This probably makes thermoregulation easier for the female during winter since huddling decreases body heat loss. Relationships within the family become intimate in spring, since it consists of several sexually mature males and females, which leads to the dispersal of some. This permits us to emphasize that intrafamilial and intrapopulational relationships develop under the influence of definite external conditions and are subject to the need for the most effective survival under unfavorable effects (in the sense of depletion of energy resources). Concomitantly, they help demarcate the territory occupied by a population when favorable conditions develop. En masse reproduction among high-montane voles, as observed in steppe, tundra, and forest forms, does not take place. However, their numbers vary in different years. Factors influencing reproductive intensity are

*[sic], probably unfavorable is meant—Eds.

climatic conditions and food availability. These factors also decisively affect the mortality of high-montane voles and their population dynamics. Attention was drawn above to the fact that in the phase of low numbers, high-montane voles are conserved only in such shelters as are close to a food supply. With an increase in rodent numbers, new shelters are established at some distance from the places of food availability. This makes a favorable energy balance difficult for that part of the population living in new dwellings, and they seem doomed to death. Additionally, shelters widely separated from the food base increase chances of rodent mortality due to predators. Ultimately, the population is again conserved only in shelters close to feeding areas.

Utilization of the same shelter by many generations of voles exacerbates the role of infection in their survival as well as the role of ectoparasites in the spread of infectious diseases. Thus, mortality due to liver damage and cestodes has been noted among Strel'tsov's vole. A total of 14 species of bugs, 3 species of ixodid mites, 1 species of gamaid mites, and 2 species of helminths, as well as coccids and blood parasites have been reported for this species (Shubin, 1961).

Practical Significance

High-montane voles have a restricted importance, mainly epizootiological. Control measures are not taken against them.

FOSSORIAL VOLES

This group includes the long-clawed mole vole (*Prometheomys schaposchnikovi* Satun.). It should be noted that in several families of the order Rodentia, there are forms adapted primarily to a fossorial life style. Specialization of these forms in this direction did not continue equally, although similar properties appear in them convergently.

An underground mode of life is associated with large energy losses in digging activity. However, it offers an advantage to the rodent in maintaining body temperature at an optimum level with
482 minimum loss of energy resources, and probably also increases their survival rate through protection against extreme climatic factors and decrease in mortality due to predators.

The reasons why the long-clawed mole vole changed over to a fossorial life style have not been elucidated. However, opinions have

been voiced regarding the reasons for their digging activity. Nau-mov (1948) believes that digging intensified as a result of sparse plant cover. Gambaryan (1952) thinks it is related to the need to hide from predators when vegetation is sparse. I assume that the need to escape extreme climatic factors developing at the soil surface was highly significant in the evolution of a fossorial mode of life. It enabled many groups of rodents to penetrate deserts and regions with a sharp continental climate, with no change in the physiology of their thermoregulation.

The long-clawed mole vole occupies valleys in the belt of alpine and subalpine meadows (Gambaryan, 1952; Yatsenko, 1958a). Researchers differ in opinions regarding the feeding of this rodent. Some believe that it feeds primarily on fruits and bulbs (rhizomes) of plants, while other authors think green plant parts are primary (Gambaryan *et al.*, 1957; Yatsenko, 1957, 1960). In summer, aerial plant parts probably play a decisive role in the diet of the long-clawed mole vole. In other seasons, however, roots and bulbs can hardly be replaced by such (Yatsenko, 1957; personal communication from Yu.A. Lyaister).

The long-clawed mole vole is almost equally active throughout the day and night, judging from intensity of digging activity (Gambaryan *et al.*, 1957). Its burrows are fairly complex underground structures. The nest is laid at a depth of 40–50 cm (sometimes 30 and 60 cm) and occupies a chamber about 20–30 cm × 15–20 cm. A second chamber, slightly smaller in size, is hollowed near the nest. Small branches, 3.0–4.0 cm in diameter, commence from the second chamber to the surface where feeding runways are laid at a depth of 10–20 cm (under a layer of turf). After extending the feeding runway to the soil surface, the vole eats the surrounding vegetation to a radius of 20 cm, then plugs this entrance with soil, forms another exit, and so on (Gambaryan *et al.*, 1957). On the average, 1,910 soil heaps have been counted in one hectare during summer in areas inhabited by the long-clawed mole vole, which destroys 9.3% of the plant canopy. The average volume of these heaps was 1,967 cm³ and 3.8 m³ soil/ha thrown out (Yatsenko, 1958a, b). During summer, one vole can push out 5.0–7.0 kg soil per day (Gambaryan *et al.*, 1957).

Burrows of the long-clawed mole vole result from the concerted efforts of many generations and, probably, serve as paths for rodent dispersal and communication between members of the family (Ognev, 1948; personal communication from Yu.A. Lyaister).

During winter the long-clawed mole vole builds large nests under snow, right on the soil surface. These have a highly branched network of communication tunnels under the snow, which may reach 3.0–4.0 m in length in 1.0 m² of area (Lyaister, 1973).

The biology of reproduction of the long-clawed mole vole has not been sufficiently studied. It is believed that pregnancy continues for not more than a month (Gambaryan *et al.*, 1957). Judging from the growth rate of neonates, it may be concluded that pregnancy does not extend beyond 22–24 days. Young animals, according to Yatsenko (1958b), start to disperse at the age of 22 days and are equal in size to adult rodents at the age of 2.0 months. Dispersal of the new generation continues up to the age of 40 days.

A brood contains 2–5 neonates, more often 3. Overwintered females produce 2 broods each season (Gambaryan *et al.*, 1957). It may be assumed that young animals from the first brood of overwintered parents are capable of bearing one brood.

483 In spite of the meager information available on the biology of the fossorial vole, it is very clear that it constitutes a unique biological group, whose study would prove quite interesting. The digging activity of the long-clawed mole vole and destruction of vegetation during feeding definitely have an adverse effect on the grass cover. However, because the actual distribution of this species is limited, damage is fairly localized.

CONCLUSIONS

Voles as a life form are subject to vast energy losses in thermoregulation. This is due to their exceptional dependence on energy resources in the environment and to climatic factors that simultaneously affect the state of such energy resources and the energy expenditure of rodents. The wide variability of these factors in different seasons and years led to a compensatory adaptation in the form of high reproductive potential (Polyakov, 1964). However, its realization necessitated even greater energy losses during pregnancy, especially during lactation and, consequently, an even higher dependence of the state of the population on environmental energy resources. This led to a major adaptation in voles, involving a labile response to the state of the food base and climatic factors. The evolution of their morphology, physiology, and ethology continued under the direct control of these very factors, and their variability over different seasons and years in those zones and regions occupied by these rodents.

In the steppe and semidesert zones, voles were compelled to adapt concomitantly to summer heat and drought and winter cold and periods of excessive moisture. Therefore, the maximum lability of environmental response is seen in the steppe vole. A consequence of this is the variability of population structure of the species. Steppe voles comprise genetic populations (subspecies), geographic, terrain, biotopic, and seasonal populations (Polyakov, 1959). The intrapopulation relationships in this biological group are governed by the most rational utilization of energy resources in the zone they occupy.

Voles do not survive in the desert *per se* since they lack the ability to adapt to life in the climatic and dietary conditions found there. However, they penetrate deserts along interzonal areas. Steppe voles also penetrate forests along steppe regions, but do not survive in forest biocenoses. Yet higher lability of response, physical factors, and food resources caused intensification of microevolution in steppe voles. At least in Russian fauna, they are represented by the largest number of species as well as subspecies, compared to voles living in other zones.

484 Compared to steppe voles, biological differences in other groups of voles reflect the adaptation of each to climatic and edaphic factors as well as to energy resources in the zones occupied by them. These in particular have led to differences in external and internal morphology, physiology, ethology, and finally reproductive potential. There is hardly a need to explain the adaptive significance of differences in morphology of the limbs, condition of pelage and its changes in different seasons, difference in structure of alimentary tract, nature of digging activity, behavior associated with shelter-building, seasonal change of habitats, food storage, and so on. Nor is there a need to explain why the instinct for food storage has developed in high-montane and hydrophilous voles, while this property has not developed in lemmings and most steppe voles, or is highly elementary. All these properties very clearly reflect adaptive significance, are fairly self-explanatory, and require no discussion. Hence I have dealt only with the characteristic properties leading to reduction in reproductive potential in voles of tundra and alpine regions, since their interpretation could be disputed.

Reduction in reproductive potential of the lemming and the high-montane vole is directly related to prolongation of the period of eye-opening of neonates, the entire lactation period and, consequently delay in onset of another pregnancy. Furthermore, the developmental period of neonates and commencement of their own

reproduction are also protracted. The number of broods ultimately decreases in overwintered animals and in young ones, and the total progeny of a population in a year decreases sharply. Naturally, in individual years these indices differ but, on the whole, they are much lower in steppe lemmings, in which three to four generations can reproduce in one season and not two, as in lemmings, high-montane voles, and most species of hydrophilous voles.

Reduction in reproductive potential of the foregoing groups of voles is primarily associated with nonavailability of sufficient energy resources during the maternal feeding of neonates, when energy expenditure is particularly high. Under these conditions, forms with a slower growth rate of young progeny and a longer lactation period could have been selected, which made it possible to decrease the intensity of energy expenditure by lactating mothers. It should be remembered that these voles are comparatively large in size. The relatively larger body size of voles changing over to an independent life is also an adaptation which makes their thermoregulation easier. All the same, the energy losses of a young animal to maintenance of body temperature and growth rate are so high that sexual maturation is delayed. For this very reason, young rodents live longer in the parental nest and periods of dispersal are protracted. Joint living permits parents and offspring to economize energy losses to thermoregulation. Thus vole populations also ensure the most economical expenditure of food resources which, however, should be considered not a cause but a consequence of adaptation to these conditions.

This explanation is arguable because one may consider the developed system leading to relatively more economic utilization of energy resources in biogenocenoses as the main stimulus of adaptation by populations. However, this is refuted by the fact that even with such properties of the population, food resources in biogenocenoses are periodically totally destroyed by lemmings and high-montane voles, who therefore begin to expend more energy on food collection than they are capable of restoring. Hence the "sparing" attitude of rodent populations toward energy resources in biogenocenoses should be considered a consequence of the need to ensure a favorable energy balance.

The population dynamics of voles and the factors determining it are associated with the above question. I tried to demonstrate earlier that climatic factors and energy resources of the environment have a decisive effect on all biological groups of voles. However, their direct influence is not always apparent and is mani-

fested uniquely in different biological groups. Some mechanisms of the influence of these factors on the formation of properties of the population, nature of its response to the environment, and dependence on its condition, have been elaborated for the steppe vole. These mechanisms have been more poorly studied for voles of other groups. In addition, their intrapopulational relationships are more complex than in the steppe vole. This compels us to attribute to intrapopulational relationships in particular the role of a factor regulating populations. In this context, using relatively scant
485 information, an attempt was made to demonstrate that intrapopulational relationships are determined by the state of energy resources of the environment and climatic factors. I feel that this theory should not be applied selectively to the facts, using the method of their comparison, but rather an attempt should be made to synthesize them and find a logical and sequential explanation for the totality of data. I have tried to use this as a guideline but only the future will show to what extent I have been successful.

Finally, it should be noted that the population structure of a species should also consider the labile nature of its responses to energy resources in the environment. This question required special discussion. However, in describing the most important biological groups of voles, I have attempted to show the differences in populational structure of the species constituting these groups.

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